

Bark and Wood Boring Insects in Living Trees in Europe,
a Synthesis

Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis

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Ips sexdentatus (six-spined engraver beetle), a bark beetle attacking pines (photo taken by Janin – INRA).

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Preface

This book is the final product of a European joint research project that allowed around 100 scientists from 24 European countries to work together actively from November 1998 to December 2002. It presents a commented synthesis on the research work done in Europe on bark beetles, bark weevils, longhorn beetles, buprestid beetles, and other xylophagous insects that attack living trees. The project was granted by the European Community, in the framework of the COST Actions, under the title “Bark And Wood Boring Insects in Living Trees (BAWBILT)”. The idea of such a synthesis was born in 1995 from a core interest in bark beetles, matured while enlarging the scope to other groups in 1996 and the project was approved by the Committee of Senior Officials of COST at the beginning of 1998. COST (Cooperation in the field of Scientific and Technical research) is a permanently open call by the European Commission for proposals that favour actions such as networks, which aim at developing communications and exchanges between European researchers and federating research groups at the European level. It has several divisions including the section “Forest and Forestry Products”, to which the BAWBILT Action belongs.

The objective of this book is to present a synthesis of BAWBILT organisms, while providing a European focus. The ambition is thus more than a presentation of the biology of the European BAWBILT species. The book reviews and comments on all the European literature on these insects, while considering the biological aspects (trees, insects, associated organisms, and their relationships), but it also compares the available information and interpretations to those concerning similar species in other continents. Indeed, for several BAWBILT organisms, especially bark beetles, research is a global process, and studies, in parallel to the European ones, have often been carried out mainly in North America. As a consequence, although this synthesis is centred on the European species, numerous references from North American studies are cited. This allows important generalizations in the conclusions and the theoretical models. It also highlights specific differences in the European species, as well as the strengths and shortcomings of the European research. This comparative approach is more or less developed in each of the different chapters, depending on the topic concerned. Some chapters, although largely referring to the European species, present a synthesis of both European and North American species. Others, while presenting such a synthesis, make a comparison by directing attention to which results come from studies on the European or the North American species. Others, due to the European focus of the subject, deal with European results.

After a section presenting the structure and the information sources of the BAWBILT group, and the characteristics of damage and control of the European BAWBILT organisms in general, the book is structured in four parts: bark beetles; weevils; buprestids and longhorns; non-coleopteran BAWBILT organisms. In each of these parts, a commented review of all European literature is done, under approximately the same organisational canvas: taxonomy and phylogeny; general biology, life cycles and relations with abiotic factors; chemical ecology and host

finding; host resistance; associated fungi; natural enemies. In each part, all factors of population dynamics, each corresponding to a particular chapter, are thus considered with their role, making unnecessary a special chapter on this subject. The general characteristics of the population dynamics are however presented in the chapter on general biology. The book ends with a concluding chapter presenting research needs and priorities for Europe. An index of scientific names is given.

All chapters presented in this book have been peer reviewed by at least two independent reviewers prior to acceptance. The book is the result of a collective work gathering together all existing European competence, but it is not simply a collection of different chapters written independently by specialists. It is rather the fruit of a real collective synthesis in which all European specialists on BAWBILT organisms have participated.

A CD accompanies the book. It contains a relational database gathering together all BAWBILT research papers (including some “grey literature”) published in Europe during the last 30 years as well as the most important ones that have been published previously. The references from other continents used for the synthesis are not contained in the CD but are included in the lists of references at the end of the different chapters. The CD also contains a series of colour pictures illustrating the different chapters.

The editors

Acknowledgments

The project was carried out with financial support from the Commission of the European Communities, COST specific program, E16 COST Action “Bark and wood boring insects in living trees”. This support greatly facilitated communications between all European BAWBILT scientists, and the joint work, thus allowing building the foundations of the present synthesis. However, the ideas expressed in this book do not necessarily reflect the views of the Commission and in no way anticipate the Commission’s future policy in the corresponding areas.

The numerous reviewers of the chapters are thanked for their constructive remarks, as well as the English speaking authors of the book for revising the English in most of the chapters written by their non English speaking colleagues. Thanks also to D. Sauvard (INRA, France) who prepared the index of scientific names and the CD containing the database and the colour pictures. The BAWBILT colleagues who provided colour pictures are also acknowledged. P. Romary (INRA, France) helped in preparing pictures and M. Pitsch (INRA, Nancy) provided the background picture of the cover. Non-EU and EU scientists not involved in the Action, and who presented lectures during a plenary meeting must also be thanked (list 1).

It must be especially emphasized that this synthesis would not have been possible without the efficient participation in the Action of all the European BAWBILT colleagues who, even if they were not authors of a chapter or if their country is not a member of COST, worked very hard in the different working groups and the plenary workshops, and in their respective countries, to gather all the necessary information and build the databases of the synthesis, and in this way contributed to the achievement of the project aims. All these colleagues are gratefully acknowledged. The list of all European BAWBILT colleagues who were involved actively in the Action is presented below in alphabetical order for each participating country (list 2).

List 1. Experts invited to give a lecture during the final plenary meeting in Vienna (Austria).

- Ayres, Matthews P., Department of Biological Sciences, Hanover, USA. “Tree susceptibility to bark beetle attacks in relation to climatic changes”.
- Govender, Prem, Forestry and Agricultural Biotechnology Institute, University of Pretoria, Republic of South Africa. “Pest problems in relation to invasive forest insect species and introduced tree species in South Africa”
- Haack, Robert A., USDA Forest Service, East Lansing, USA. “Invasive forest insect species in North America”.
- Jactel, Hervé, Institut National de la Recherche Agronomique, Pierrotin, France. “Tree species biodiversity and pest dynamics”
- Raffa, Kenneth F., Department of Entomology, University of Wisconsin, Madison, USA. “Role of insect-fungus relationships on population dynamics and host selection behavior in forest insects”
- Wagner, Michael R. School of Forestry, North Arizona University, Flagstaff, USA. “Drought and bark beetle outbreaks”.

List 2. BAWBILT experts who participated actively in the Action.

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The BAWBILT bases in Europe

Chapter 1

THE BAWBILT CONTEXT IN EUROPE

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WHAT ARE EUROPEAN BAWBILT?

Typically, BAWBILT organisms, the Bark And Wood Boring Insects in Living Trees, correspond to the guilds of insects that develop, at least part of their life cycle, inside living xylem or phloem tissues of trees. Strictly following that definition, weevils such as *Hylobius* species, whose adults feed on trees externally and the larvae develop inside dying stumps, should not belong to the BAWBILT organisms. However, to circumscribe all xylophagous and phloeophagous insects of living trees, the concept has been enlarged to include weevils. BAWBILT is thus more than a guild but rather an assemblage of several guilds that have been studied in parallel with some similarities in their relations with living host trees. As a consequence of this distinction, all insects that attack only dead trees are excluded. Galling insects are also excluded because they do not operate as true xylophagous or phloeophagous species. The project focused on the European BAWBILT species. However, not only the indigenous species have been considered, but also the European introductions (e.g. the eucalyptus borer *Phoracantha semipunctata* introduced several decades ago, the longhorn borers *Anoplophora* species discovered only few years ago in central and southern Europe). The list of the species that have been considered as European BAWBILT is presented in table 1. Two North American bark beetle species *Dendroctonus ponderosae* and *Dendroctonus rufipennis* are cited in this list, although not introduced to Europe, because they have been intercepted in English ports and are the subjects of several European studies. They will however not be considered as European species in the synthetic chapters. Europe has been interpreted inclusively in its broadest geographical manifestation, latitudinally from the Mediterranean Sea to Northern Norway, and longitudinally from Iceland to the western part of Russia.

Table 1. Recorded European BAWBILT species. Main synonyms are in brackets

Isoptera	
Kalotermitidae	
	<i>Kalotermes flavicollis</i>
Heteroptera	
Aradidae	
	<i>Aradus cinnamomeus</i>
Coleoptera	
Buprestidae	
	<i>Agrilus angustulus</i>
	<i>Agrilus biguttatus</i> (<i>A. pannonicus</i>)
	<i>Agrilus populneus</i> (<i>A. suvorovi</i>)
	<i>Agrilus viridis</i>
	<i>Coroebus florentinus</i> (<i>C. bifasciatus</i> , <i>C. fasciatus</i> , <i>Coraebus florentinus</i>)
	<i>Coroebus undatus</i> (<i>Coraebus undatus</i>)
	<i>Melanophila picta</i> (<i>Trachypteris picta</i>)
	<i>Phaenops cyanea</i> (<i>Melanophila cyanea</i> , <i>M. tarda</i>)
Cerambycidae	
	<i>Anoplophora chinensis</i>
	<i>Anoplophora glabripennis</i>
	<i>Arhopalus rusticus</i> (<i>Criocephalus rusticus</i>)
	<i>Cerambyx velutinus</i>
	<i>Lamia textor</i>
	<i>Monochamus galloprovincialis</i>
	<i>Monochamus sartor</i>
	<i>Monochamus sutor</i>
	<i>Phoracantha semipunctata</i>
	<i>Saperda carcharias</i> (<i>Anaereaa carcharias</i>)
	<i>Saperda populnea</i> (<i>Compsidia populnea</i>)
	<i>Tetropium castaneum</i> (<i>Isarthron castaneum</i>)
	<i>Tetropium fuscum</i>
	<i>Tetropium gabrieli</i> (<i>Isarthron gabrieli</i>)
Curculionidae	
	<i>Cryptorhynchus lapathi</i> (<i>Cryptorrhynchus lapathi</i>)
	<i>Hylobius abietis</i> (<i>Hylobitelus abietis</i>)
	<i>Hylobius pinastri</i> (<i>Hylobitelus pinastri</i>)
	<i>Otiorrhynchus arcticus</i>
	<i>Otiorrhynchus nodosus</i> (<i>O. dubius</i>)
	<i>Otiorrhynchus singularis</i> (<i>O. picepes</i> , <i>Brachyrinus singularis</i>)
	<i>Otiorrhynchus sulcatus</i> (<i>Brachyrinus sulcatus</i>)
	<i>Pissodes castaneus</i> (<i>P. notatus</i>)
	<i>Pissodes harcyniae</i> (<i>P. hercyniae</i>)
	<i>Pissodes piceae</i>

Pissodes pini

Pissodes piniphilus

Scolytidae

Cryphalus piceae (*C. numidicus*)

Dendroctonus micans

Dendroctonus ponderosae (*D. monticolae*)

Dendroctonus rufipennis (*D. borealis*, *D. engelmanni*, *D. obesus*)

Gnathotrichus materiarius

Hylastes angustatus

Hylastes ater

Hylastes attenuatus

Hylastes brunneus

Hylastes cunicularius (*Hylesinus cunicularius*)

Hylastes opacus

Hylesinus crenatus

Hylurgus ligniperda

Ips acuminatus

Ips amitinus

Ips cembrae

Ips duplicatus

Ips sexdentatus

Ips typographus

Leperisinus varius (*L. fraxini*, *Hylesinus fraxini*, *H. varius*)

Orthotomicus erosus

Phloeosinus armatus

Phloeosinus bicolor (*P. aubei*)

Phloeosinus thujae (*P. prostratus*, *P. serrifer*)

Phloeotribus scarabaeoides (*P. oleae*)

Pityogenes chalcographus

Pityogenes conjunctus (*P. alpinus*, *P. baicalicus*)

Pityogenes trepanatus

Pityokteines curvidens

Pityokteines spinidens

Pityokteines vorontzovi (*P. vorontzoia*)

Pityophthorus pityographus

Polygraphus poligraphus (*P. pubescens*)

Scolytus intricatus (*Eccoptogaster intricatus*)

Scolytus laevis (*Eccoptogaster laevis*)

Scolytus multistriatus (*S. orientalis*, *S. ulmi*, *Eccoptogaster multistriatus*)

Scolytus ratzeburgi (*Eccoptogaster destructor*, *E. ratzeburgi*)

Scolytus scolytus (*S. geoffroyi*, *Eccoptogaster scolytus*)

Scolytus sulcifrons

Scolytus triarmatus

Tomicus destruens (*Blastophagus destruens*, *Myelophilus destruens*)

Tomicus minor (*Blastophagus minor*, *Myelophilus minor*)

Tomicus piniperda (*Blastophagus piniperda*, *Myelophilus piniperda*)

- Trypodendron domesticum* (*Xyloterus domesticus*)
Trypodendron lineatum (*Xyloterus bivittatum*, *X. lineatus*)
Trypodendron signatum (*Apate signatus*, *Xyloterus signatus*)
Xyleborus dispar (*X. pyri*, *Anisandrus dispar*, *A. pyri*, *Apate dispar*)
Xylosandrus germanus (*Xyleborus germanus*)
- Platypodidae
Platypus cylindrus (*P. cylindriformis*)
- Lepidoptera
Tortricidae
Rhyacionia buoliana (*Evetria buoliana*, *Retinia buoliana*)
- Cossidae
Cossus cossus (*C. ligniperda*, *Phalaena cossus*)
Zeuzera pyrina (*Z. aesculi*, *Cossus aesculi*)
- Sesiidae
Paranthrene tabaniformis (*Aegeria tabaniformis*, *Sesia tabaniformis*)
Sesia apiformis (*Aegeria apiformis*, *Trochilium apiforme*)
Synanthedon myopaeformis (*Aegeria myopaeformis*, *Sesia myopaeformis*)
- Pyralidae
Dioryctria splendidella (*D. sylvestrella*)
- Diptera
Agromyzidae
Phytobia betulae (*Agromyza betulae*, *Dendromyza betulae*)
- Hymenoptera
Siricidae
Sirex cyaneus (*S. abbottii*)
Sirex juvencus (*Paururus juvencus*)
Urocerus augur
Urocerus gigas
-

OBJECTIVES AND RESULTS OF THE BAWBILT ACTION

As in many other research fields, research on BAWBILT in Europe during the last 50 years has suffered from the fragmentation of the research community in about 35 countries and an almost equal number of languages. Until recently, this situation was a handicap for the community of European scientists, with the consequence of little exchange of information, duplication of research in some specialities, gaps in others, and very limited possibilities for syntheses. International collaborations, when they existed, were generally limited to a few bilateral exchanges. This problem has progressively decreased during the last 15 years, partly due to the development of modern and rapid communication systems, but mainly to financial support from the EU for large cross-border projects involving several European partners. Under these circumstances, national funding has often had secondary importance for many research teams. This fragmented situation of European research in the BAWBILT field was the first reason for building this Action. Moreover, from a practical point of view regarding damage and control of forest

pests, almost each country has its own strategy. Survey and damage are often evaluated using different techniques and units of measurement, depending on the country, while decisions on control methods are not reached using the same theoretical and practical frameworks. Evidently, a common strategy for survey, damage evaluation and control methods throughout Europe, based on the existence of ecological boundaries rather than political borders, would be more appropriate to the biology of the pests and would thus be more efficient, especially in the case of widespread pests, expansion of localized pests or accidental introductions. The need to define European standards for such a common approach was another reason for building the BAWBILT network.

A general aim was to consolidate the knowledge base for BAWBILT that would support improvement in forest conservation and protection in future. The practical objectives of the BAWBILT COST Action were thus: 1- to increase communication between European scientists; 2- to build a balance-sheet on damage caused by BAWBILT organisms in Europe; 3- to make proposals for more concerted and efficient control strategies at the international level; 4- to build a catalogue and a synthesis of research papers and research activities on BAWBILT in Europe; 5- to make proposals for a European research policy in that field; 6- to publish the results of the network activities.

A priority result of this Action is thus the strengthening of collaborations between European scientists. New collaborations and wide exchange of information have been established, and exchanges of young scientists realized. No team is any longer isolated and all BAWBILT teams are now known throughout Europe. Another positive result is the assembly of a database that includes all recent European references to BAWBILT and some of the older ones. The third important result of the Action is the present synthetic book which would have not been possible until recently. For the first time, and thanks to an open communication forum between scientists from most European countries working together in the framework of the same European Project, a synthesis at the scale of the European continent has been built taking into account all research fields related to all BAWBILT organisms.

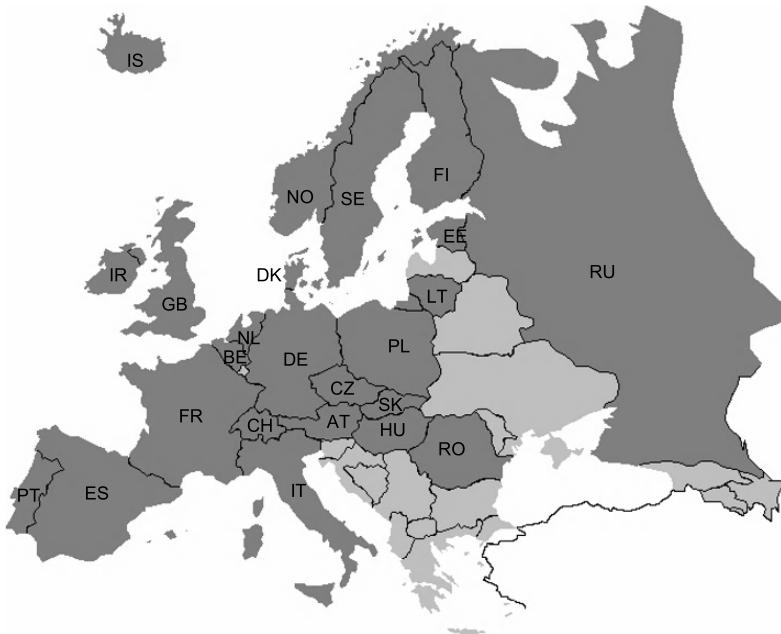
PARTICIPANTS AND ORGANIZATION OF THE RESEARCH WORK

A total of 101 experts belonging to 59 Institutions and 24 countries participated actively in the Action. All natural areas of Europe were represented (Fig. 1). However, gaps existed in the geographic coverage of Europe since countries from Eastern Mediterranean sea and the Balkans and from Central Eastern Europe were not able to participate. The list of the participating countries with their representatives is given in the acknowledgment chapter (list 2).

The research work was structured into six tasks corresponding to the practical objectives presented above.

Task 1 was devoted to facilitating communication between scientists. A directory of European experts in the field of BAWBILT was built (task 1a, Battisti and Faccoli, chapter 2). All European experts with experience of BAWBILT

organisms were approached through a questionnaire, including those not directly involved in the network. Their research fields, objectives, methods and particular experience were included in the directory, with indexes by key-words and country.



*Figure 1. European countries having participated in the BAWBILT network (in dark grey).
Pale grey: other European countries. Austria (AT), Belgium (BE), Czech Republic (CZ),
Denmark (DK), Estonia (EE), Finland (FI), France (FR), Germany (DE), Hungary (HU),
Iceland (IL), Ireland (IR), Italy (IT), Lithuania (LT), Norway (NO), Poland (PL), Portugal
(PT), Romania (RO), Russia (RU), Slovakia (SK), Spain (ES), Sweden (SE), Switzerland
(CH), The Netherland (NL), United Kingdom (UK)*

This directory facilitated exchange of information and can continue to be used as a basis for building cooperative links. It can also been used to define fields or specialities where the BAWBILT research group could be particularly effective. A second aspect (task 1b) was the building of a BAWBILT WEB site where the project is presented, together with the fields of interest of the participants. The WEB site is accessible at <http://www.bio.ic.ac.uk/staff/srl/bawbilt/bawbilt.htm>. Periodic working plenary meetings accompanied by poster sessions and working group meetings also facilitated contact between participants (see below).

Task 2 dealt with damage. The aim was to collect data which would form a basis for later definition of research priorities. A geographic and quantitative balance-sheet of damage has been established (Grégoire and Evans, chapter 4; Långström and Day, chapter 19; Evans *et al.* chapter 20; Långström *et al.* chapter 22). Quantitative assessments of damage have been made by taking into consideration

the periods, the areas, the volumes, the number of trees, and the financial losses, depending on the available data. Types of damage and the most frequently cited species have been identified. The results have also been analyzed by country.

Task 3 was the review of control strategies (Grégoire and Evans, chapter 4; Långström and Day, chapter 19; Evans *et al.* chapter 20; Långström *et al.* chapter 22). Current strategies in all BAWBILT species were assessed. The aim was to suggest improvements and standardisations for more concerted and efficient actions at the European level. Strategies have been classified in different control practices and monitoring options.

Task 4 was the assembly of a catalogue and the synthesis of research papers and activities. A period covering the last 30 years has been chosen because it corresponds to a considerable diversification of the topics and increase in the numbers of researchers active in the BAWBILT field. A full bibliography was first compiled and organized in a catalogue. Classification was based on different topics defined by key-words included in a thesaurus and a database was built, which also includes data on damage and control (Gilbert and Sauvard, chapter 3). Indexes by author, pest, tree species and country complete the catalogue. The syntheses by research fields, which form the different chapters of this book, were then built by using the database, in parallel with data from non European regions to allow comparisons. As with task 1, these syntheses have helped in recognizing areas where the BAWBILT group could be particularly effective. As with tasks 2 and 3, they have been used to define research priorities. In addition, together with the results from tasks 2 and 3, the achievement of task 4 provides a state of the art reference book useful for future research.

Task 5 focused on defining research priorities for Europe in the BAWBILT field. It was carried out after completion of tasks 2, 3 and 4, and in agreement with the objectives of the EU research program (Lieutier *et al.*, chapter 23).

Task 6 has been completed through the publication of the present book with the joint CD.

MANAGEMENT OF THE BAWBILT ACTION

The organization of the BAWBILT network was based on the existence of a National Responsible Scientist (NRS) in each participating country, having a role of promoter and coordinator for all other scientists in his/her country. The NRS was in charge of organizing tasks 1a, 2, 3 and 4 in his/her country in concert with other scientists and with a National Task Scientist (NTS) for each task. Thus, in each country, there were 1 NRS and 4 NTS, except for countries with less than 4 participants where the same person was in charge of several tasks. Each NTS contributed to the European syntheses with the NTS from other countries, for the task for which he/she had responsibilities. The European syntheses were carried out in working groups under the supervision of Task Coordinators (TC). There was one working group for each of the tasks 1a, 2, 3 and 4, plus one special working group charged with making coherent and gathering together the databases from each other group. Each group (except the database group) was composed of at least one

representative (the corresponding NTS) of each participating country and chaired by the corresponding TC. These groups met periodically, especially on the occasion of plenary meetings gathering all participants in the Action. Most often, groups 2 and 3 met together. The list of the BAWBILT species (Table 1) was prepared in each country and then discussed and definitely adopted in plenary session. The modalities of the general synthesis and its publication (tasks 5 and 6) were discussed between all participants during plenary meetings. Task 5 and the coordination of task 6 were assumed by the Chairman of the Action assisted by the Vice-chairman and the scientists in charge of coordinating the different parts of the book, in collaboration with the TCs.

The network was managed by a management committee composed of two representatives of each COST country, and chaired by the chairman of the Action. Participants in the Action, who were not members of this committee but participating in the working groups, were invited to each management committee meeting, thus giving opportunities to hold plenary sessions. Seven management committee meetings and plenary sessions were held: Brussels (Belgium, 28-29 January 1999), Florence (Italy, 1-2 July 1999), Cracow (Poland, 13-14 April 2000), Granada (Spain, 26-28 October 2000), Helsinki (Finland, 20-22 July 2001), Orléans (France, 24-25 May 2002), Vienna (Austria, 6-7 December 2002). In addition to managing the network and having working plenary and group meetings, these sessions were the opportunity for the BAWBILT members to present the scientific results of their work as posters. A special day was arranged during the final plenary meeting, when five non-EU and one EU experts were invited to give presentations on topics enlarging the strict field of BAWBILT. The list of these experts with the presented topics is given in the acknowledgment chapter (list 1).

Chapter 2

THE DIRECTORY OF EUROPEAN EXPERTS

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1. INTRODUCTION

The aim of sub-task 1a was to build a directory of European scientists working with BAWBILT organisms. Experts were approached via a national responsible who collected information concerning personal details, research activities, host plant and insect group/species. Results were indexed by keywords and by countries. The directory is accessible at the web site <http://lubies.ulb.ac.be/bawbilt/> and is regularly updated by each expert. Any change or new entry is formally checked by task 1a responsible before it becomes accessible to the public.

2. RESULTS AND DISCUSSION

A total of 201 experts from 23 countries (no expert from Russia has registered) were included in the directory. The number of experts in each country is presented in Fig. 1.

The number of experts was not closely related to the area covered by forest in each country. This could be due to several factors, such as the local importance of BAWBILT organisms, or the presence of specialised research teams working with BAWBILT organisms or with specialised forest plantations, e.g. *Eucalyptus* in Portugal. Experts belonged mainly to public research institutes (49.1 %) and universities (46.4 %), whereas a small number was employed in private enterprises (4.5 %).

The fields of interest within BAWBILT organisms cited by experts are presented in Tab. 1. Control and monitoring methods were the topics sharing the highest interest, followed by basic biology and ecology, with special attention to chemical communication and insect-tree relationships. Natural enemies and systematics were also covered by a considerable number of experts, and so were the relatively new fields such as insect genetics and conservation biology.

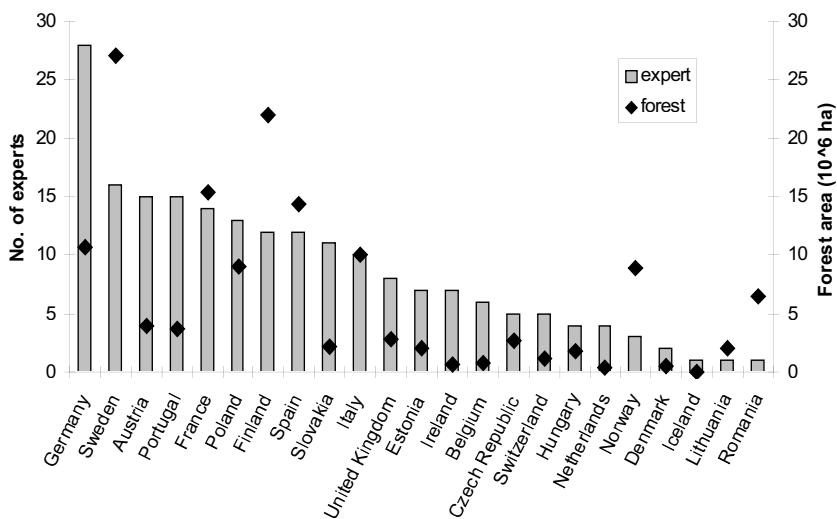


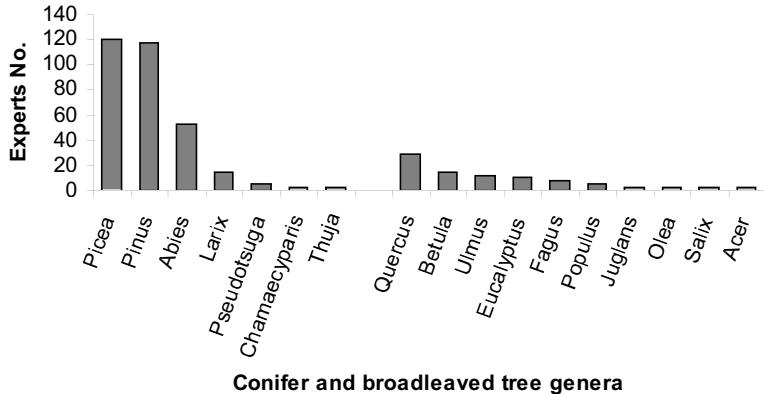
Figure 1. Distribution of experts involved in BAWBILT among 23 countries which showed an interest in the project. Forest land is taken from FAO 'Forest Resources Assessment 2001'.

All experts expressed their interest in one or several BAWBILT organisms host-plants (415 records), mostly recorded as tree genus or species (Fig. 2). Conifers were largely preferred over broadleaved trees, even if the area occupied by the two groups of trees is similar (FAO, 2001). This is probably related to the more extensive use of conifer trees in plantations. The ongoing restoration of these secondary stands with broadleaved trees in many countries will likely move the future attention to broadleaved trees (Battisti, 2000). Most experts expressed their interest in northern conifer trees, whereas southern species of trees, and especially broadleaves, appeared to be largely under-represented.

A total of 159 experts expressed their interest in one or several BAWBILT organisms (246 records; Fig. 3). Beetles, and dominantly conifer bark beetles and *Hyllobius spp.*, were by far the favourite group of most experts. This pattern reflects the distribution of the preferences expressed for the host trees. The presence of species new to Europe (e.g. the longhorn beetles *Anoplophora spp.*) or potential vectors of the recently introduced pine wood nematode (*Monochamus spp.*) is indicative of the readiness to undertake new research on these organisms, which represent serious threats to the European forests.

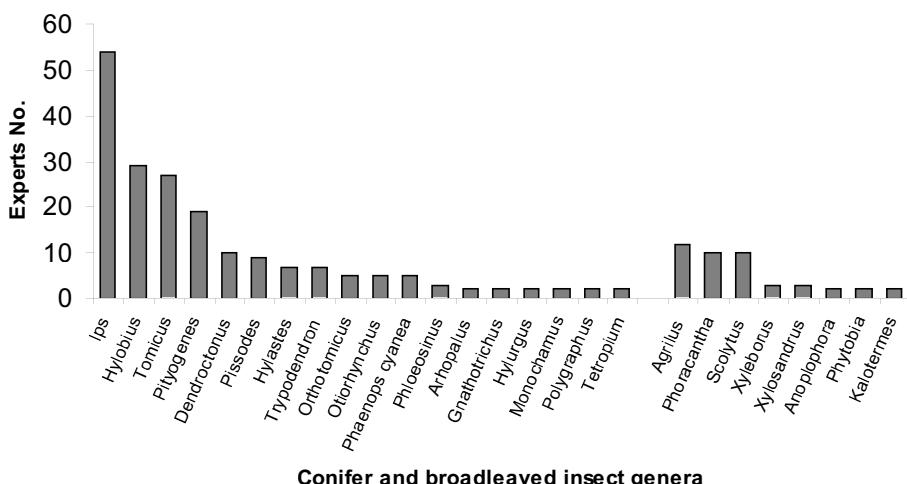
The directory can provide a good starting point to strengthen the collaboration among European experts, with the development of common projects and the exchange of information. It may also show gaps in the research on BAWBILT in Europe, which need to be filled by future work. More attention should be paid to alien species, especially in relation to their potential as vectors of plant pathogens, and to the role of BAWBILT organisms in deciduous stands. Biodiversity and

conservation issues deserve more attention too, as they may play an important role in the future management of European forests.



Conifer and broadleaved tree genera

Fig. 2. Preferences expressed by experts for a tree genus. There was no upper limit to the number of preferences for each expert. Preferences are listed in order of decreasing abundance within conifer and broadleaved trees, respectively. Tree genera with only one record (No. 11) were excluded.



Conifer and broadleaved insect genera

Fig. 3. Preferences expressed by experts for insect genera. There was no upper limit to the number of preferences for each expert. Preferences are listed in order of decreasing abundance within conifer and broadleaved trees, respectively. Insect genera with only one record (No. 21) were excluded.

Table 1. List of fields of interest in BAWBILT organisms expressed by 198 experts. There was no upper limit to the number of preferences of each expert.

Field of interest	Experts No.
Forest management – Control methods	89
Forest management – Monitoring	59
Insect – Basic biology	53
Insect – Population study	40
Insect – Chemical communication	32
Insect – Natural enemies	32
Insect-Tree relationship – Tree susceptibility	26
Insect – Systematic	25
Insect-Tree relationship – Host defences	23
Forest management – Management	17
Forest management – Damage	16
Insect – Geographic distribution	15
Insect – Genetics	13
Forest management – Risk assessment	13
Insect – Conservation biology	11
Insect – Dispersal	8
Insect-Tree relationship – Attack strategies	8
Insect – Insect performance	4
Insect-Tree relationship – Entomological techniques	2
Forest management – Legislation	2
Other – Urban and amenity trees	2
Insect – Anatomy and physiology	1
Other – Fire ecology	1
Other – Data management	1
Total of preferences expressed by 201 experts	492

3. REFERENCES

- Battisti A., 2000. The role of phytophagous insects in the restoration process of secondary coniferous stands. In. *Forest Ecosystem Restoration*. H. Hasenauer (ed.), Proceedings International Conference Vienna 10-12 April 2000. Institut Forest Growth, BOKU, Vienna.
- FAO, 2001. Forest Resources Assessment. <http://www.fao.org/forestry/fo/country/index>.

Chapter 3

THE BAWBILT DATABASE

Gathering and sharing information related to BAWBILT organisms

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1. INTRODUCTION

Several tasks of the BAWBILT Cost Action (Task 1a: Directory of European scientists; Task 2: Synthesis of damage; Task 3: Control method; Task 4: Catalogue and synthesis of research papers and research activities) required the collection, treatment and display of data from participating countries. Although it was not identified as a separate task in the initial action outline, it became quickly obvious that the development of a common on-line database would greatly facilitate data exchange from and to participating countries. A separate working group was thus set-up in Florence meeting (July 1999) that worked in parallel as the other working groups throughout the duration of the BAWBILT action.

No specific resource had been planned for the development of the database. The main challenge was thus to find a good balance between simplicity such as to allow the developments to be carried out by our own limited resource, flexibility to do not restrict further potential uses of the database, and functions required by the separate tasks.

2. OBJECTIVES AND DESIGN

The general aims of the BAWBILT database were i) to allow country representatives or experts to enter and modify information regarding their countries, ii) to facilitate the synthesis of these data by task coordinators, and iii) to allow data

retrieval by the BAWBILT community and by the public. Three modules corresponding to separate tasks were developed (Table 1). Task 2 & 3 were grouped in a single module because damage and control are closely related and shared many common fields.

Table 1. *Characteristics of the three database modules. Tasks : 1a: Directory of experts, 2 & 3: Damage and control methods, 4: Literature. CR: Country representative. TC: Task Coordinator. Access to 2 & 3 module was internal up to the end of these tasks.*

<i>Task</i>	<i>Data entry</i>	<i>Data validation</i>	<i>Access</i>
1a	Anyone	CR / TC	Public
2 & 3	CR	—	Internal then public
4	Registered scientists	CR / TC	Registered scientists

The database was designed in MS Access 2000. On-line data entry, validation and retrieval procedure were written in MS Active Server Page (ASP) using the MS Internet Information Server 4 (IIS4) as web server. Several tables were shared by all modules: the list of species (See chapter 1) established in Krakow's meeting (April 2000), the list of host-plant species (appendix A), the list of participating countries (See chapter 1), and a subject thesaurus (appendix B).

2.1. Input data

The procedure for entering and modifying data is common to all modules. The user search firstly for records already present in the database. The user has then the possibility to add a new record to the list, or to update an existing record. The directory of experts (task 1a) records data per individual expert such as personal details (title, affiliation, address, phone, fax, e-mail, URL), area of interest (according to the subject thesaurus), BAWBILT species and host-plant species. The table on damage and control methods (tasks 2 & 3) records information grouped by country and by BAWBILT species: species relationship to the host; type of impact; type and extent of damage; damage estimates; type and extent of control strategies; and type of monitoring, risk rating or decision-support systems. The literature database records data per individual reference including classical bibliographic fields (authors, year, title source, etc.) in addition to several indexing fields (text language, summary language, geographic region, ecological region, BAWBILT species, host-tree, subject), additional description fields (BAWBILT abstract¹, BAWBILT abstract author, availability within the BAWBILT community, commentaries) and administrative fields (reference country and validation status).

2.2. Outputs

The procedure for retrieving data is also common to all modules. The user searches through the database according to criteria entered in search forms, receives a list of output records with limited amount of displayed details and has the possibility to

access the complete records by selecting any of the records displayed in the list. Queries on experts can be done by last name, country, BAWBILT species, host-tree, subject or by any combination of these fields. Queries on damage and control methods can be done by country, pest species, host-tree or by any combination of these fields. Queries of the literature database can be done at two levels: basic search with a limited number of search fields such as classical bibliographic fields, or advanced search offering the possibility to search though all fields used in the literature database.

3. DISCUSSION AND POTENTIAL IMPROVEMENTS

The database has efficiently played its role in facilitating information gathering regarding experts, damage & control methods, and literature for the present synthesis. However, at the present stage of development, it is not as such a satisfying information source in a longer term perspective. Several steps should be achieved in order to make it a valuable knowledge resource regarding BAWBILT organisms.

Firstly, a solution should be found to ensure that the database remains up to date. This would require a network of researcher willing to regularly check the data, contact country representatives to request updated information, and add, edit or delete relevant records.

Secondly, we received a lot of feedback from users who used the database during the BAWBILT action. Several forms and procedures for data entry and searches need to be modified according to these feedback.

Finally, the current type of outputs do not take yet fully advantage of the database structure and data. For example, searches are currently made separately within each module and cross-searches that would allow to display in a single page all experts, damage and control method records, and references related to a given species would be a valuable output. Another valuable output of the database would be to allow on-the-fly comparison of damage and control methods regarding one species between countries across Europe.

It is believed that the database will probably not survive the BAWBILT COST action if none of these steps is achieved. Conversely, given the critical mass of data brought together to date, and if a limited amount of resource is put together to achieve these steps, the BAWBILT database could become a highly valuable knowledge base regarding BAWBILT organisms and contribute in a long term perspective to better address threats caused by these pests to European forests.

The database can be accessed at: <http://lubies.ulb.ac.be/bawbilt>

4. NOTES

- 1 This field is designed to allow country representative to enter abstracts of reference from gray literature having no text nor abstract written in English.

5. ACKNOWLEDGEMENTS

The authors wish to thanks all those who attended the database working group meetings, peoples providing feedback on the use of the database and those who participated actively to its development, in particular: Andrea Battisti, John Byers, Jacopo de Silva, Hugh Evans, Helmut Feichter, Valeria Francardi, Jean-Claude Grégoire and Anne Franklin.

APPENDIX A: HOST-PLANT SPECIES

Abies sp., Abies alba, Abies cephalonica, Abies grandis, Abies lasiocarpa, Abies nobilis, Abies nordmanniana, Abies procera, Abies sibirica, Acer sp., Acer campestre, Acer platanoides, Acer pseudoplatanus, Acer tataricum, Aesculus hippocastanum, Alnus sp., Alnus cordata, Alnus glutinosa, Alnus incana, Betula sp., Betula pendula, Betula pubescens, Carpinus betulus, Carya ovata, Castanea sativa, Celtis australis, Celtis tournefortii, Ceratonia siliqua, Cercis siliquastrum, Chamaecyparis lawsoniana, Chamaerops humilis, Corylus sp., Corylus avellana, Corylus colurna, Cupressus sempervirens, Cydonia oblonga, Erica azorica, Eucalyptus sp., Fagus sp., Fagus orientalis, Fagus sylvatica, Frangula sp., Fraxinus sp., Fraxinus angustifolia, Fraxinus excelsior, Fraxinus ornus, Ilex perado, Juglans sp., Juglans cinerea, Juglans nigra, Juglans regia, Juniperus sp., Juniperus brevifolia, Juniperus excelsa, Juniperus oxycedrus, Larix sp., Larix decidua, Larix gmelinii, Larix kaempferi, Larix leptolepis, Larix × eurolepis, Laurus azorica, Myrica faia, Olea sp., Ostrya sp., Picea sp., Picea abies, Picea omorika, Picea sitchensis, Pinus sp., Pinus halepensis, Pinus cembra, Pinus contorta, Pinus nigra var austriaca, Pinus nigra var corsicana, Pinus pinaster, Pinus pinea, Pinus strobus, Pinus sylvestris, Platanus × acerifolia, Populus sp., Populus alba, Populus alba × canescens, Populus deltoides, Populus euramericana, Populus nigra, Populus tremula, Populus trichocarpa, Prunus sp., Prunus avium, Prunus serotina, Pseudotsuga menziesii, Quercus sp., Quercus frainetto, Quercus ilex, Quercus petraea, Quercus pubescens, Quercus robur, Quercus rubra, Quercus suber, Robinia pseudoacacia, Salix sp., Salix alba, Salix caprea, Salix fragilis, Sequoia sempervirens, Sorbus sp., Sorbus aria, Sorbus aucuparia, Sorbus austriaca, Sorbus domestica, Sorbus hybrida, Sorbus intermedia, Sorbus latifolia, Sorbus torminalis, Tamarix africana, Thuja plicata, Tilia sp., Tilia cordata, Tilia platyphyllos, Tilia tomentosa, Tsuga heterophylla, Ulmus sp., Ulmus campestris, Ulmus glabra, Ulmus montana, Ulmus procera, Vaccinium cylindraceum.

APPENDIX B: SUBJECT THESAURUS

Insect related keywords: Systematic, Basic biology, Geographic distribution, Anatomy and physiology, Communications, Dispersal, Pathology, Population study, Insect performance, Entomological technique. Insect-tree relationship related keywords: Tree finding, Tree susceptibility. Forest management related keywords: Forest management, Insect damage, Risk assessment, Pest management, Legislation. Other keywords: Abiotic factor, Insect - fungus relationship, Natural enemy, Non target organism.

Chapter 4

DAMAGE AND CONTROL OF BAWBILT ORGANISMS AN OVERVIEW

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1. INTRODUCTION

The BAWBILT database on damage and control (Gilbert and Sauvard, chapter 3) was queried in January 2003. It then contained 478 entries, on 95 species of the BAWBILT list, with entries from 19 countries. In each entry, a series of fields concerned the total areas potentially affected, the types of damage (death of trees, caused by the insects themselves or by pathogenic fungi, timber degrade, impact on growth, on erosion, on avalanches,...), quantitative assessments of damage (periods, areas, volumes of timber, numbers of trees, financial losses), and scoring (+ to +++) for aggressivity and for territorial coverage. A series of fields regarding control practices (e.g. do nothing, sanitary thinning, clearfelling, traptrees, pheromone trapping, insecticide treatments) and monitoring options (e.g. visual assessments, pheromone trapping, questionnaires) was also available.

To avoid unnecessary duplication, damage and control are covered together in this section.

In this short overview, we shall first identify the most frequently cited species and then provide statistics per country. Finally, we shall analyse more closely the data available on the "top ten" species, i.e. those species that were scored +++ for aggressivity at least three times. This more detailed analysis will consider the types of damage, quantitative information when available (numbers of trees/volume killed, acreages, etc) and control methods.

2. THE MOST DAMAGING PESTS

Table 1 lists important pest species which were scored +++, and Table 2 lists those which were either scored +++ or ++. Ten species, among which were seven Scolytids, received a +++ score at least three times: *Hylobius abietis* (Coleoptera: Curculionidae), *Ips typographus*; *Ips acuminatus*; *Pityogenes chalcographus*; *Scolytus multistriatus*; *Scolytus scolytus*; *Scolytus laevis*; *Tomicus piniperda* (Coleoptera: Scolytidae), *Phaenops cyanea* (Coleoptera: Cerambycidae) and *Rhyacionia buoliana* (Lepidoptera: Tortricidae). Two species received the most attention for both damage and, not surprisingly, control: *Ips typographus* (15 citations) and *Hylobius abietis* (12 citations).

Table 1. BAWBILT organisms scored +++ in the BAWBILT database

Species	Number of occurrences
<i>Ips typographus</i>	15
<i>Hylobius abietis</i>	12
<i>Pityogenes chalcographus</i> ; <i>Scolytus multistriatus</i> ; <i>Scolytus scolytus</i>	6
<i>Ips acuminatus</i>	5
<i>Tomicus piniperda</i>	4
<i>Phaenops cyanea</i> ; <i>Rhyacionia buoliana</i> ; <i>Scolytus laevis</i>	3
<i>Cryptorhynchus lapathi</i> ; <i>Dendroctonus micans</i> ; <i>Ips duplicatus</i> ; <i>Ips sexdentatus</i> ; <i>Paranthrene tabaniformis</i> ; <i>Pissodes castaneus</i> ; <i>Tomicus minor</i> ; <i>Trypodendron lineatum</i> ;	
<i>Zeuzera pyrina</i>	2
<i>Agrilus biguttatus</i> ; <i>Gnathotrichus materiarius</i> ; <i>Hylastes ater</i> ; <i>Hylastes cunicularius</i> ; <i>Hylobius pinastri</i> ; <i>Ips amitinus</i> ; <i>Ips cembrae</i> ; <i>Leperesinus varius</i> ; <i>Monochamus sartor</i> ; <i>Pissodes piniphilus</i> ; <i>Pityokteines curvidens</i> ; <i>Polygraphus poligraphus</i> ; <i>Saperda</i> <i>carcharias</i> ; <i>Saperda populnea</i> ; <i>Scolytus intricatus</i> ; <i>Scolytus triarmatus</i> ; <i>Sirex juvencus</i> ; <i>Tetropium gabrieli</i> ; <i>Trypodendron domesticum</i> ; <i>Urocerus gigas</i>	1

3. SPECIES PER COUNTRY

The numbers of species considered to be significant pests varied greatly between countries (21 +++ pests in Romania, 16 in Germany, 1 in Belgium, France or The Netherlands): Fig. 1 and Table 3. It is unclear how much these differences can be explained by local variations in forest coverage, forest uses, tree species, silvicultural practices, climate, topography, etc. Part of these differences may also stem from divergences in damage assessment methods and criteria. For example, numbers of trees killed, cubic metres of timber lost, financial value of timber degrade or areas "hit" by a pest give quite different damage assessments. An important outcome of the BAWBILT programme could be to discuss more carefully the status of the species identified as aggressive and to determine the key factors leading to their highly damaging status.

Table 2. BAWBILT organisms scored either +++ or ++ in the BAWBILT database

Species	Number of countries
<i>Ips typographus</i>	16
<i>Hylobius abietis</i>	15
<i>Scolytus scolytus; Tomicus piniperda</i>	9
<i>Ips acuminatus; Pityogenes chalcographus; Scolytus multistriatus; Tomicus minor</i>	8
<i>Ips amitinus</i>	7
<i>Hylastes cunicularius; Ips sexdentatus</i>	6
<i>Ips cembrae; Phaenops cyanea; Pityokteines curvidens; Polygraphus poligraphus; Rhyacionia buoliana; Scolytus intricatus</i>	5
<i>Agrius biguttatus; Cryptorhynchus lapathi; Dendroctonus micanus; Hylastes ater; Ips duplicatus; Pissodes castaneus; Pissodes piniphilus; Saperda carcharias; Tetropium gabrieli</i>	4
<i>Cryphalus piceae; Paranthrene tabaniformis; Pityokteines vorontzovi; Saperda populnea; Scolytus laevis; Trypodendron domesticum; Trypodendron lineatum; Zeuzera pyrina</i>	3
<i>Cossus cossus; Leperesinus varius; Pissodes piceae; Pityokteines spinidens; Pityophthorus pityographus; Sesia apiformis; Tetropium castaneum; Urocerus gigas; Xyleborus dispar</i>	2
<i>Agrius populneus; Aradus cinnamomeus; Gnathotrichus materiarious; Hylesinus crenatus; Hylobius pinastri; Hylurgus ligniperda; Monochamus sartor; Orthotomicus erosus; Phloeotribus scarabaeoides; Phoracantha semipunctata; Pissodes pini; Pityogenes conjunctus; Scolytus ratzeburgi; Scolytus triarmatus; Sirex juvencus; Trypodendron signatum</i>	1

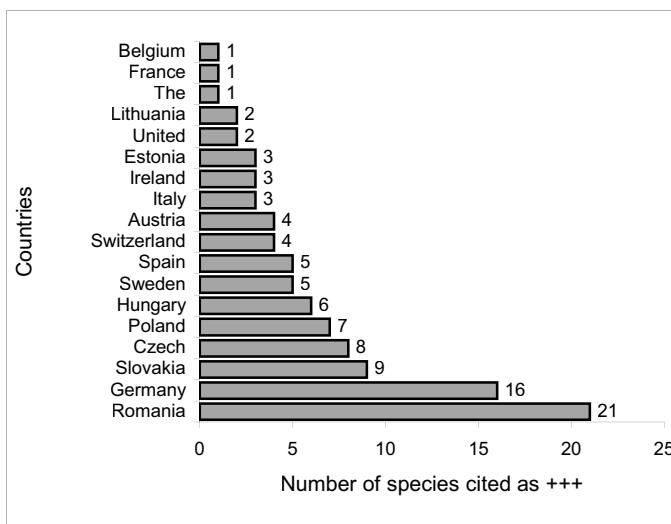


Figure 1. Numbers of +++ species in the different BAWBILT countries

Table 3. Pests scored +++ in the different BAWBILT countries

Species	Countries
<i>Ips typographus</i>	Austria; Belgium; Czech Republic; Estonia; France; Germany; Hungary; Ireland; Lithuania; Poland; Romania; Slovakia; Sweden; Switzerland; United Kingdom
<i>Hylobius abietis</i>	Austria; Czech Republic; Estonia; Germany; Hungary; Ireland; Lithuania; Poland; Romania; Slovakia; Sweden; United Kingdom
<i>Pityogenes chalcographus</i>	Austria; Czech Republic; Germany; Hungary; Romania; Slovakia
<i>Scolytus multistriatus</i>	Czech Republic; Germany; Slovakia; Spain; Sweden; Switzerland
<i>Scolytus scolytus</i>	Czech Republic; Germany; Slovakia; Spain; Switzerland; The Netherlands
<i>Ips acuminatus</i>	Germany; Romania; Slovakia; Spain; Switzerland
<i>Tomicus piniperda</i>	Czech Republic; Poland; Slovakia; Spain
<i>Phaenops cyanea</i>	Czech Republic; Germany; Poland
<i>Rhyacionia buoliana</i>	Hungary; Ireland; Romania
<i>Scolytus laevis</i>	Germany; Slovakia; Sweden
<i>Cossus cossus</i>	Italy; Romania
<i>Cryptorhynchus lapathi</i>	Hungary; Romania
<i>Dendroctonus micans</i>	Germany; Romania
<i>Ips duplicatus</i>	Poland; Slovakia
<i>Ips sexdentatus</i>	Germany; Spain
<i>Paranthrene tabaniformis</i>	Italy; Romania
<i>Pissodes castaneus</i>	Hungary; Poland
<i>Tomicus minor</i>	Czech Republic; Romania
<i>Trypodendron lineatum</i>	Germany; Romania
<i>Zeuzera pyrina</i>	Italy; Romania
<i>Agrius biguttatus</i>	Germany
<i>Aradus cinnamomeus</i>	Finland
<i>Gnathotrichus materiarius</i>	Germany
<i>Hylastes ater</i>	Romania
<i>Hylastes cunicularius</i>	Romania
<i>Hylobius pinastri</i>	Estonia
<i>Ips amitinus</i>	Romania
<i>Ips cembrae</i>	Germany
<i>Leperesinus varius</i>	Italy
<i>Monochamus sartor</i>	Romania
<i>Pissodes piniphilus</i>	Austria
<i>Pityokteines curvidens</i>	Romania
<i>Polygraphus poligraphus</i>	Romania
<i>Saperda carcharias</i>	Romania
<i>Saperda populnea</i>	Romania
<i>Scolytus intricatus</i>	Poland
<i>Scolytus triarmatus</i>	Sweden
<i>Sirex juvencus</i>	Romania
<i>Tetropium gabrieli</i>	Germany
<i>Trypodendron domesticum</i>	Germany
<i>Urocerus gigas</i>	Romania

4. DAMAGE OF THE "TOP TEN" SPECIES

4.1. *Ips typographus*

Table 4 provides scoring and quantitative data for *Ips typographus*. Although incomplete, available information from ten countries indicates that over a potentially threatened area of 7,640,000 ha, at least 2,819,000 ha were attacked between 1990 and 2001, resulting in the death of 31,643,000 m³ of spruce. Most of the data are connected to the 1990 storms. Austria (11,000,000 m³), Poland (6,270,000 m³), Germany (5,900,000 m³) and Slovakia (4,490,000 m³) reported the highest losses.

Table 4. Damage caused by *Ips typographus*

Country	Host age	Threatened Area (ha)	Tree death ¹	Timber ¹ degrade	Avalanche ¹	Erosion ¹	Cosmetic ¹	Physical danger for people ¹	Period	Volume (m ³)	Area (ha)
Austria	Pole	2,000,000	2	2	2	2			1992-2000	11,000,000	no data
Belgium	Older	no data	2	2			2		1992	250,000	no data
France	Older	no data	3						1990-01	1,500,000	no data
Germany	Older	3,233,001	2						1990-98	5,901,254	192,760
Hungary	Pole	24,000	2	2					1990-97	420,000	no data
Lithuania	Older	221,155	3	1					1998-2001	no data	27,462
Poland	Older	230,000	3			3	3		1990-99	6,270,000	no data
Romania	Older	600,000	3	3	3	3	3		1991-2000	811,195	2,598,833
Slovakia	Pole	600,000	3		2	2	3		1990-99	4,490,086	no data
Switzerland	Older	492,000	2	2	2	2			1993-95	1,000,000	no data
Total (of available figures)		7,640,156	35	12	9	12	8	3	1990-2001	31,642,535	2,819,055

¹ Scoring from 1 to 3

4.2. *Hylobius abietis*

Death of coniferous transplants is, expectedly, the major impact of this species. A total of 3,418,000 ha is regarded as threatened, of which 88,000 ha were seriously damaged between 1980 and 2000 in Germany, Hungary, Lithuania, Romania, and Slovakia (Table 5).

4.3. *Pityogenes chalcographus*

Available information from eight countries indicates that over a potentially threatened area of 8,784,000 ha, at least 595,400 ha were attacked between 1990 and 2000, resulting in the death of 7,828,000 m³ of conifers (Table 6). Although Poland reported the highest losses (6,270,000 m³), this volume concerns the damage caused by the complex of species occurring on Norway spruce, in which *I. typographus* is dominating.

Table 5. Damage caused by *Hylobius abietis*

Country	Threatened Area (ha)	Tree death ¹	Period	Area (ha)
Austria	3,000,000	2		
Germany	6,466,455	2	1990-98	14,643
Hungary	246,000	2	1980-98	2,400
Ireland	8,000	3		
Lithuania	7,264	2	1997-2001	9,142
Poland	27,000	2		
Portugal	1 080 800	2		
Romania	180,000	3	1991-2000	60,719
Slovakia	15,000	3	1990-99	1,354
Spain	100,000	2		
United Kingdom	15,000	3		
Total	3,418,264	39	1980-2000	88,258

¹ Scoring from 1 to 3

Table 6. Damage caused by *Pityophthorus chalcographus*

Country	Threatened Area (ha)	Period	Number of trees	Volume (m ³)	Area (ha)
Austria	2,500,000	1992-01		600,000	
Germany	3,233,001				
Hungary	246,000				
Poland	513,000	1999		6,270,000	
Portugal	1 080 800				
Romania	1,200,000	1999-2000	730,049	730,049	595,400
Slovakia	600,000	1900-99		227,457	
Switzerland	492,000				
Total	8,784,001	1900-2000	730,049	7,827,506	595,400

4.4. *Scolytus multistriatus* and *S. scolytus*

Damage by these two species was usually reported together, as the vectors for Dutch Elm Disease have not always been identified with complete accuracy. Much greater damage obviously occurred throughout Europe from the late 1970s, but was not reported in the BAWBILT database. The reason for this is probably the generally doubtful status of *Ulmus* species as forest trees (Table 7).

Table 7. Damage caused by *Scolytus multistriatus* and *S. scolytus*

Country	Threatened Area (ha)	Period	Number of trees	Volume (m ³)	Area (ha)
Spain		1984-99	3,000,000		
Slovakia	1,500	1990-99		10,711	
Romania	1,000	1991-2000			524
Portugal	221,600				
Total	224,100	1991-2000	3,000,000	10,711	524

4.5. *Ips acuminatus*

Although nine countries provided quantitative data on this species, only Poland reported high losses on pines (a total of 12,838,000 m³ killed by BAWBILT organisms between 1990 and 1999: Table 8). The same 12,838,000 m³ are also cited in connection with *Tomicus piniperda* and *Phaenops cyanea* in Poland (Tables 9 and 10). The specific status of these three species found on the same dead pines in Poland is unclear in the database; it results from the method used for data collection in this country, namely the evidence of the volume of killed trees regardless the insect species causing the mortality (the volume of tree killed by *I. acuminatus* is much lower).

4.6. *Tomicus piniperda*

Eight countries provided quantitative data for this species. Its status in Poland is unclear (see above), however this species is one of the most aggressive and important pine pests in this country. Significant losses were reported in Slovakia (93,000 m³) and large acreages were reported in Spain (200,000 ha: Table 9).

Table 8. Damage caused by *Ips acuminatus*

Country	Threatened Area (ha)	Period	Number of trees	Volume (m ³)	Area (ha)
Austria	200,000	1993-2002 (?)		3,000	
Germany	2,800,433				
Poland	6,780,000	1990-99		12,838,000	
Romania	90,000	1991-2000	8,109	2,028	2,235
Slovakia	120,000	1990-99		7,400	
Spain	1,100,000	1990-99	10,000		
Switzerland	45,000	1992-2000			30
Total	11,135,433	1990-2000	18,109	12,850,428	2,265

Table 9. Damage caused by *Tomicus piniperda*

Country	Threatened Area (ha)	Period	Number of trees	Volume (m ³)	Area (ha)
Switzerland	45,000				
Spain	4,500,000	1990-99		200,000	
Slovakia	120,000	1990-99		93,177	
Romania	45,000	1991-2000	8109	2,028	2,235
Portugal	1 080 800				
Poland	6,780,000	1990-99		12,838,000	
Hungary	217,000				
Germany	2,800,433				
Total	14,507,433	1990-2000	8,109	12,933,205	202,235

4.7. *Phaenops cyanea*

Five countries provided quantitative data for this species (Table 9). The larger figures concern Poland; the status of *P. cyanea* in this country is similar as for *T. piniperda*, which is not resulting clearly from the data in BAWBILT database (see comments in previous section).

Table 10. Damage caused by *Phaenops cyanea*

Country	Threatened Area (ha)	Period	Volume (m ³)
Slovakia	110,000	1990-99	1,159
Romania	50,000		
Poland	4,400,000	1990-99	12,838,000
Hungary	217,000		
Germany	3,233,001		
Total	8,010,001	1990-99	12,839,159

4.8. *Rhyacionia buoliana*

Four countries provided quantitative information on this species. Significant damage was reported on young pines in Hungary (17,300 ha) and in Romania (2,500 ha: Table 11).

Table 11. Damage caused by *Rhyacionia buoliana*

Country	Threatened Area (ha)	Period	Area (ha)
Slovakia	100000	1990-99	343
Romania	10,000	1991-2000	2,495
Ireland	100,000		
Hungary	217,000	1980-98	17,300
Total	327,000	1980-2000	20,138

4.9. *Scolytus laevis*

A total of 1,500 ha was reported to be potentially threatened by this species in Slovakia, but no quantitative information on damage is available.

4.10. Synthesis of quantitative data on damage

Table 12 provides a synthetic account of the information above.

Table 12. A synthesis of quantitative data on damage caused by the "top ten" species

Species	Number of countries where data available	Threatened Area (ha)	Period	Number of trees	Volume	Area (ha)
<i>Ips typographus</i>	10	7,640,156	1990-2001		31,642,535	2,819,055
<i>Hylobius abietis</i>	11	3,418,264	1980-2000			88,258
<i>Pityogenes chalcographus</i>	8	8,784,001	1900-2000	730,049	7,827,506	595,400
<i>Scolytus multistriatus</i> and <i>Scolytus scolytus</i>	4	224,100	1991-2000	3,000,000	10,711	524
<i>Ips acuminatus</i>	7	11,135,433	1990-2000	18,109	12,850,428	2,265
<i>Tomicus piniperda</i>	8	14,507,433	1990-2000	8,109	12,933,205	202,235
<i>Phaenops cyanea</i>	5	8,010,001	1990-99		12,839,159	
<i>Rhyacionia buoliana</i>	4	327,000	1980-2000			20,138

5. CONTROL

During the early stages of BAWBILT there was considerable discussion on the types of control measures that should be included in the database. General agreement was reached on a number of categories of control which are shown in Appendix 1. On-line data entry was carried out by 19 countries and most of the control options were accessed, although not for all organisms in the list. However, it was interesting to note that the number of control measures adopted was related to the degree of aggressivity indicated in the Damage part of the database. Consequently, we have analysed the control data using the list of organisms, in the same order of aggressivity summarised in Table 3. This is presented as a series of Tables for each of the principal control categories in Appendix 1, namely Quarantine, Silvicultural Management, Chemical Insecticide Application, Trapping Out, Biological Control, Other Control Strategies, Monitoring, Risk Rating and Decision Support Systems. The degree of employment of each strategy varied with the type of pest and, particularly with the damage rating of that pest.

5.1. Quarantine

This category is concerned principally with prevention of movement of pests between countries and, in some cases, within countries. The results are shown in Table 13. In many respects, it is surprising that there were so many entries in this category. It can only be assumed that the measures are related to the international movement of wood and wood products from the countries concerned to other countries with restrictions on importation of the named pests.

5.2. Silvicultural Management

This category contains the most commonly employed management options for BAWBILT organisms. This reflects the possibility of enhancing tree health and, thereby, increasing the ability of living trees to defend themselves against attack by a range of pests, especially those entering through the bark. The results are shown in Table 14.

Removal of breeding material through forest sanitation or, as an extreme measure, clearfelling is practised for most of the pests in Table 14. These are traditional measures and, although expensive to implement if they have to be carried out early in the economic life of a crop, can provide some financial return from sales of extracted timber.

5.3. Chemical Insecticide Application

Results for this analysis are shown in Table 15. Not all the organisms in the table have been managed using insecticides and relatively few were treated as standing trees; in this category the target is universally the adult stage. The most common usage was for treatment of felled trees either to prevent attack or to prevent emergence of the organisms that were breeding in the felled material.

5.4. Trapping Out

This is an alternative approach to silvicultural management and involves the deliberate use of material to attract the adult stages of the BAWBILT pests and then to remove the material before a full breeding cycle and subsequent emergence can take place or, in the case of pheromone traps, to prevent adult pests from reaching susceptible host trees. The results are shown in Table 16. The measures have been most commonly employed against Scolytidae, aided by the known attraction of the adult stages to freshly cut or damaged trees. There are also commercially available pheromone lures for the majority of the most damaging Scolytidae.

Table 13. Quarantine control measures employed against the most aggressive BAWBILT organisms as listed in Table 3. The figures represent the numbers of countries which implemented different types of quarantine measures against each species

Species	Movement restrictions	Storage restrictions	Physical Treatment					
			Debarking	Covering	Processing	Composting	HT/KD	Wet storage
<i>Ips typographus</i>	3	3	9	4	3	1	2	5
<i>Hylobius abietis</i>	1	1	1					1
<i>Pityogenes chalcographus</i>			4	3	2	1	1	4
<i>Scolytus multistriatus</i>	1	1	3		1			4
<i>Scolytus scolytus</i>	2	1	3		1			3
<i>Ips acuminatus</i>			1	2	3			3
<i>Tomicus piniperda</i>		1	5	1	1		2	3
<i>Phaenops cyanea</i>			2	1	1			2
<i>Rhyacionia buoliana</i>								1
<i>Scolytus laevis</i>	1	1	1					1
<i>Cossus cossus</i>								1
<i>Cryptorhynchus lapathi</i>					1			2
<i>Dendroctonus micans</i>	4		6	3	1	1	2	2
<i>Ips duplicatus</i>	2		4	1	1	1	2	1
<i>Ips sexdentatus</i>	1	1	4	2	1		1	
<i>Paranthrene tabaniformis</i>								1
<i>Pissodes castaneus</i>				2				2
<i>Tomicus minor</i>			1	4	1	2		2
<i>Trypodendron lineatum</i>	1	3	2	1	1	1	3	1
<i>Zeuzera pyrina</i>					1			2
<i>Agrius biguttatus</i>								
<i>Gnathotrichus materiarius</i>	1	1	1	1				1
<i>Hylastes ater</i>				1				
<i>Hylastes cunicularius</i>				1				1
<i>Hylobius pinastri</i>								
<i>Ips amitinus</i>	1		8	3	3	1	2	4
<i>Ips cembrae</i>	1		4	3	1		1	
<i>Leperesinus varius</i>			2		1			2
<i>Monochamus sartor</i>			1					
<i>Pissodes piniphilus</i>			2	1				
<i>Pityokteines curvidens</i>			4	2	1			3
<i>Polygraphus poligraphus</i>			2	1	1			1
<i>Saperda carcharias</i>		1						1
<i>Saperda populnea</i>								1
<i>Scolytus intricatus</i>			2					1
<i>Scolytus triarmatus</i>								
<i>Sirex juvencus</i>			1		1			1
<i>Tetropium gabrieli</i>			2	2	1			1
<i>Trypodendron domesticum</i>	1	1		1			1	
<i>Urocerus gigas</i>			1		1			1

Table 14. Silvicultural management measures employed against the most aggressive BAWBILT organisms as listed in Table 3. The figures represent the numbers of countries which implemented silvicultural management methods of each category for each species

Species	Sanitary felling					Silvicultural choice	Forest sanitation
	Clear felling	Selective thinning	Site preparation	Pruning	Physical protection		
<i>Ips typographus</i>	9	9				3	12
<i>Hylobius abietis</i>			10		7	8	4
<i>Pityogenes chalcographus</i>	3	5		1		2	5
<i>Scolytus multistriatus</i>	2	10		2		4	6
<i>Scolytus scolytus</i>	3	8		2		2	5
<i>Ips acuminatus</i>	3	8		1		1	7
<i>Tomicus piniperda</i>	4	8		1			12
<i>Phaenops cyanea</i>	1	3		1		2	2
<i>Rhyacionia buoliana</i>		1		1		1	1
<i>Scolytus laevis</i>		5				2	2
<i>Cossus cossus</i>	1	4		4	2	1	3
<i>Cryptorhynchus lapathi</i>	2	3	1	1	1		3
<i>Dendroctonus micans</i>	2	7			1	2	5
<i>Ips duplicatus</i>	1	3				1	4
<i>Ips sexdentatus</i>	3	7					5
<i>Paranthrene tabaniformis</i>	1	3		3	1	1	3
<i>Pissodes castaneus</i>	1	4				2	9
<i>Tomicus minor</i>	2	4		1		2	8
<i>Trypodendron lineatum</i>					1		1
<i>Zeuzera pyrina</i>		3	1	5		1	2
<i>Agrylus biguttatus</i>	2	4		1		1	2
<i>Gnathotrichus materiarius</i>		1					1
<i>Hylastes ater</i>		1	2		1	1	4
<i>Hylastes cunicularius</i>			1		1	2	3
<i>Hylobius pinastri</i>			1			1	
<i>Ips amitinus</i>	3	5				1	5
<i>Ips cembrae</i>	1	6				1	4
<i>Leperesinus varius</i>		2			1	1	2
<i>Monochamus sartor</i>							1
<i>Pissodes piniphilus</i>	2	3					1
<i>Pityokteines curvidens</i>	2	4		1		2	2
<i>Polygraphus poligraphus</i>	1	3					1
<i>Saperda carcharias</i>	1	4	1				3
<i>Saperda populnea</i>		4	1	1			2
<i>Scolytus intricatus</i>		4				1	4
<i>Scolytus triarmatus</i>		1				1	
<i>Sirex juvencus</i>		1					5
<i>Tetropium gabrieli</i>	1	2					
<i>Trypodendron domesticum</i>	1	1			1	1	2
<i>Urocerus gigas</i>		1					6

Table 15. Chemical insecticide measures employed against the most aggressive BAWBILT organisms as listed in Table 3. The figures represent the numbers of countries which use chemical insecticide treatments on each category of trees for each pest species.

	Standing trees	Transplants	Felled trees	Systemic	
				Transplants	Mature trees
<i>Ips typographus</i>			10		
<i>Hylobius abietis</i>	2	14		6	
<i>Pityogenes chalcographus</i>			5		
<i>Scolytus multistriatus</i>	3		2		2
<i>Scolytus scolytus</i>	2		2		1
<i>Ips acuminatus</i>			6		
<i>Tomicus piniperda</i>	1		6		
<i>Phaenops cyanea</i>			2		
<i>Rhyacionia buoliana</i>	2	1			
<i>Scolytus laevis</i>			1		
<i>Cossus cossus</i>	4				
<i>Cryptorhynchus lapathi</i>	2	2		1	1
<i>Dendroctonus micans</i>			3		1
<i>Ips duplicatus</i>			1		
<i>Ips sexdentatus</i>			4		
<i>Paranthrene tabaniformis</i>	4	2		2	
<i>Pissodes castaneus</i>	1	1	1	1	
<i>Tomicus minor</i>			5		
<i>Trypodendron lineatum</i>			4		
<i>Zeuzera pyrina</i>	5				
<i>Agrilus biguttatus</i>			1		
<i>Gnathotrichus materiarius</i>			1		
<i>Hylastes ater</i>		5		3	
<i>Hylastes cunicularius</i>		6		3	
<i>Hylobius pinastri</i>		1			
<i>Ips amitinus</i>			4	1	
<i>Ips cembrae</i>			3		
<i>Leperesinus varius</i>			1		
<i>Monochamus sartor</i>			1		
<i>Pissodes piniphilus</i>			2		
<i>Pityokteines curvidens</i>			4		
<i>Polygraphus poligraphus</i>			3		
<i>Saperda carcharias</i>	3				
<i>Saperda populnea</i>	1	2		1	
<i>Scolytus intricatus</i>			2		
<i>Scolytus triarmatus</i>					
<i>Sirex juvencus</i>			1		
<i>Tetropium gabrieli</i>			1		
<i>Trypodendron domesticum</i>	1		3		
<i>Urocerus gigas</i>			2		

Table 16. Trapping out measures employed against the most aggressive BAWBILT organisms as listed in Table 3. The figures represent the numbers of countries which use different types of trapping out measures against each species.

	Trap trees	Trap logs	Pheromone traps	Baited trees	Baited slash
<i>Ips typographus</i>	7	9	12	7	1
<i>Hylobius abietis</i>		4	2		1
<i>Pityogenes chalcographus</i>	3	3	7	2	1
<i>Scolytus multistriatus</i>	3	2	4	1	
<i>Scolytus scolytus</i>	3	2	4	1	
<i>Ips acuminatus</i>	5	4	1	1	
<i>Tomicus piniperda</i>	7	8	1		
<i>Phaenops cyanea</i>	3	1			
<i>Rhyacionia buoliana</i>				2	
<i>Scolytus laevis</i>	1	1	1		
<i>Cossus cossus</i>	1	1	1		
<i>Cryptorhynchus lapathi</i>					
<i>Dendroctonus micans</i>	1				
<i>Ips duplicatus</i>	2		2		
<i>Ips sexdentatus</i>	4	5	2	1	
<i>Paranthrene tabaniformis</i>	1		1		
<i>Pissodes castaneus</i>			5		
<i>Tomicus minor</i>	6	7	1		
<i>Trypodendron lineatum</i>	1	1	2	1	
<i>Zeuzera pyrina</i>	1	1			
<i>Agrilus biguttatus</i>	1	1			
<i>Gnathotrichus materiarius</i>					
<i>Hylastes ater</i>	1	2			
<i>Hylastes cunicularius</i>	1	1			
<i>Hylobius pinastri</i>					
<i>Ips amitinus</i>	6	3			
<i>Ips cembrae</i>	1	1	2		1
<i>Leperesinus varius</i>	1	1			
<i>Monochamus sartor</i>	1	1			
<i>Pissodes piniphilus</i>	1	1			
<i>Pityokteines curvidens</i>	3		1	1	
<i>Polygraphus poligraphus</i>	2				
<i>Saperda carcharias</i>					
<i>Saperda populnea</i>					
<i>Scolytus intricatus</i>	2	1			
<i>Scolytus triarmatus</i>					
<i>Sirex juvencus</i>	1	1			
<i>Tetropium gabrieli</i>					
<i>Trypodendron domesticum</i>	2		1	1	
<i>Urocerus gigas</i>	1	1			

5.5. Biological Control

Although this category was included in the list of control measures, there were very few records of use of biological control agents and, therefore, a full analysis has not been carried out. However, this is covered in more detail elsewhere in this book (Kenis *et al.*, chapters 11 and 18; Kenis and Hilszczanski, chapter 21).

5.6. Monitoring

Part of effective management of pests is knowledge of their distribution and abundance, especially in relation to availability of breeding material. Monitoring is, therefore, an important element in making decisions about whether to apply active control measures. Most countries implemented some form of monitoring system and these are listed for the major pests in Table 17. The most commonly employed measures use a combination of visual surveys, supplemented by use of various trap systems using pheromones/attractants or trap trees/logs. Remote sensing has rarely been employed and may offer opportunities for further development in the future.

5.7. Risk Rating and Decision Support Systems

This category received relatively few responses, but would appear to offer promise for future integrated management of the most serious pests. Results of the analysis are shown in Table 18. As with other control measures, the development of risk models and decision support systems has made most progress with the most serious pests, especially for *I. typographus*. It is likely that this approach will expand in the future, especially with the increasing use and sophistication of GIS systems that are now available.

6. CONCLUSIONS

Overall the information in the BAWBILT database has provided useful summaries of the range of control measures employed by the member countries. The range of measures has, predictably, been linked to the degree of severity of the damage caused by the listed pests. It was not, however, possible to carry out cost-benefit analyses of the various control measures carried out or even to assess the relative efficacy of those measures. This indicates that improved quantification of the cost and effectiveness of pest management for BAWBILT organisms could be a priority for the future. In addition, work should aim to integrate experiences from the countries involved in this COST action to develop procedures of wide applicability for management of BAWBILT pests.

Table 17. Monitoring systems employed against the most aggressive BAWBILT organisms as listed in Table 3. The figures represent the numbers of countries which use different types of monitoring systems against each species

Species	Pheromones/ attractants	Trap trees/logs	Visual survey/ sampling	Remote sensing	Questionnaire
<i>Ips typographus</i>	14	9	13	3	4
<i>Hylobius abietis</i>	3	5	11	0	3
<i>Pityogenes chalcographus</i>	7	4	9	0	3
<i>Scolytus multistriatus</i>	1	3	6	0	1
<i>Scolytus scolytus</i>	2	3	6	0	2
<i>Ips acuminatus</i>	1	4	6	0	1
<i>Tomicus piniperda</i>	1	5	8	0	2
<i>Phaenops cyanea</i>	0	2	4	0	2
<i>Rhyacionia buoliana</i>	2	1	5	1	2
<i>Scolytus laevis</i>	0	2	2	0	1
<i>Cossus cossus</i>	1	0	5	1	2
<i>Cryptorhynchus lapathi</i>	0	0	5	0	2
<i>Dendroctonus micans</i>	0	3	9	2	1
<i>Ips duplicatus</i>	4	4	3	0	2
<i>Ips sexdentatus</i>	3	3	7	0	1
<i>Paranthrene tabaniformis</i>	1	0	2	0	2
<i>Pissodes castaneus</i>	1	3	5	0	0
<i>Tomicus minor</i>	1	5	7	0	1
<i>Trypodendron lineatum</i>	3	1	3	0	1
<i>Zeuzera pyrina</i>	3	0	6	1	0
<i>Agrilus biguttatus</i>	0	2	3	0	2
<i>Gnathotrichus materiarius</i>	0	0	2	0	0
<i>Hylastes ater</i>	0	0	3	0	1
<i>Hylastes cunicularius</i>	0	0	5	0	1
<i>Hylobius pinastri</i>	0	0	1	0	0
<i>Ips amitinus</i>	3	7	7	0	2
<i>Ips cembrae</i>	3	3	4	0	2
<i>Leperesinus varius</i>	0	0	4	0	1
<i>Monochamus sartor</i>	0	0	0	0	0
<i>Pissodes piniphilus</i>	0	0	4	0	0
<i>Pityokteines curvidens</i>	0	1	4	0	2
<i>Polygraphus poligraphus</i>	1	1	4	0	1
<i>Saperda carcharias</i>	0	0	5	0	1
<i>Saperda populnea</i>	0	0	3	0	1
<i>Scolytus intricatus</i>	0	1	3	0	3
<i>Scolytus triarmatus</i>	0	0	1	0	0
<i>Sirex juvencus</i>	0	0	1	0	0
<i>Tetropium gabrieli</i>	0	0	1	0	1
<i>Trypodendron domesticum</i>	1	0	3	0	2
<i>Urocerus gigas</i>	0	0	1	0	0

Table 18. Risk rating and decision support systems employed against the most aggressive BAWBILT organisms as listed in Table 3. The figures represent the numbers of countries which use different risk rating and decision support systems for each species.

Species	Risk models			GIS	Decision support systems
	Local scale	Regional scale	National scale		
<i>Ips typographus</i>	3	7	1	2	1
<i>Hylobius abietis</i>	1	2			1
<i>Pityogenes chalcographus</i>	3	2			1
<i>Scolytus multistriatus</i>		1			
<i>Scolytus scolytus</i>	1	1			
<i>Ips acuminatus</i>	3	2			
<i>Tomicus piniperda</i>	2	2		1	
<i>Phaenops cyanea</i>					1
<i>Rhyacionia buoliana</i>	2				
<i>Scolytus laevis</i>		1			
<i>Cossus cossus</i>	1				
<i>Cryptorhynchus lapathi</i>	1				
<i>Dendroctonus micans</i>	1			1	
<i>Ips duplicatus</i>		1			
<i>Ips sexdentatus</i>	1	1			1
<i>Paranthrene tabaniformis</i>	1	1			
<i>Pissodes castaneus</i>					
<i>Tomicus minor</i>	2				
<i>Trypodendron lineatum</i>	1				1
<i>Zeuzera pyrina</i>	1				
<i>Agrilus biguttatus</i>					1
<i>Gnathotrichus materiarius</i>					
<i>Hylastes ater</i>	1				
<i>Hylastes cunicularius</i>	1				
<i>Hylobius pinastri</i>					
<i>Ips amitinus</i>	3			1	
<i>Ips cembrae</i>	1				1
<i>Lesperesinus varius</i>					
<i>Monochamus sartor</i>	1				
<i>Pissodes piniphilus</i>	1	1			
<i>Pityokteines curvidens</i>	1				1
<i>Polygraphus poligraphus</i>	1				
<i>Saperda carcharias</i>	1				
<i>Saperda populnea</i>	1				
<i>Scolytus intricatus</i>		1			
<i>Scolytus triarmatus</i>					
<i>Sirex juvencus</i>		1			
<i>Tetropium gabrieli</i>					
<i>Trypodendron domesticum</i>					1
<i>Urocerus gigas</i>					

Appendix 1: Categories of control measures in the BAWBILT Database

Quarantine	Movement restrictions Storage restrictions Physical treatment	Debarking Covering Processing Composting Heat treatment/KD Wet storage Burning
Silvicultural management	Sanitary felling Site preparation Pruning Physical protection Silvicultural choice Forest sanitation Other	Clear felling Selective thinning
Chemical insecticide application	Standing trees Transplants Felled trees Systemic	Transplants Mature trees
Trapping out	Trap trees Trap logs Pheromone traps Baited trees Baited slash Other	
Biological control	Predators Parasitoids Microbial control	Bacteria Fungi Nematodes Protozoa Viruses Other
Other control strategies	Interruption of attack: thinning Prevention of attack Fallow period Ectomycorrhizae	
Monitoring	Pheromone traps Trap trees/logs Visual surveys Remote sensing Other	
Risk rating and Decision Support Systems	Risk models	Local scale Regional scale National scale
	GIS Decision support systems	

Part 1

Bark Beetles

Chapter 5

TAXONOMY AND SYSTEMATICS OF BARK AND AMBROSIA BEETLES

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1. INTRODUCTION

Bark beetles in a wide sense include the true bark beetles (many Scolytidae), which breed in and feed on the phloem (phloeophagous species), and the ambrosia beetles (many Scolytidae, and all Platypodidae), which bore into the wood and feed primarily on symbiotic ambrosia fungi living in the tunnels (xylomycetophagous species). Some Scolytidae also develop in hard seeds and fruits (spermophagous species), in the central pith of twigs and other small stems, or in the petioles of fallen leaves (myelophagous species). We use the term 'bark beetles' to cover all these categories, unless otherwise specified. Bark beetles usually live in scattered habitat units, which are suitable for breeding for only a single generation of beetles. This means that the new generation of adults must disperse to find new breeding sites. These two features mean that bark and ambrosia beetle populations are very variable both in space and time, depending on the spatial and temporal availability of suitable breeding material. The study of their temporal and spatial dynamics is very important both because of their economic importance in forests, and the ease with which these small beetles can be transported to, and become established in, new areas. The majority of species breed in dead or dying tissues, and are not normally of economic importance. However, such species can become economically important if their galleries create holes in timber used for furniture or veneer, or if they transport pathogenic fungi to living trees during a period of feeding by young adults to mature the gonads. The relatively small number of species that attack living trees, saplings or seedlings, or the seeds of commercial crops (e.g. coffee, palms) are sometimes of major economic importance, causing damage estimated in millions of

dollars. Such losses occur in both temperate and tropical zones, especially where there are monocultures and plantations, which can provide suitable conditions for rapid population increase, for example following extensive windfalls. As a result, the beetles have been of particular interest to foresters for hundreds of years, and much of the work on them has been done by forest entomologists.

2. HISTORICAL STATUS OF THE FAMILY SCOLYTIDAE AND PLATYPODIDAE

2.1. Historical overview

The first five species of Scolytidae to be described were named by Linnaeus (1758), and placed in his genus *Dermestes*. All are European species, but now placed, of course, in other genera. Geoffroy (1762) described the genus *Scolytus* for the species *S. scolytus*, and transferred Linnaeus' species to the genus *Bosstrichus*. Fabricius (1801) included 52 species of scolytid in his monograph, and added the genus *Hylesinus*. He also described the first platypodid species, *Platypus cylindrus*, although in the genus *Bosstrichus*. Latreille (1807) was the first to consider the scolytids at the family level, and Shuckard (1840) the platypodids. Later, in the 19th century, several authors increased the number of species and genera in both families. Here we should mention especially the monographs of Chapuis (1865) on Platypodidae and Chapuis (1869) on Scolytidae, and the monograph of Eichhoff (1879) on Scolytidae, which laid the foundation for later studies. The first catalogue of Scolytidae (including Platypodidae) was included in the systematic catalogue of Gemminger and Harold (1872), who listed 534 valid species in 60 genera.

In the first half of the 20th century, there were great advances in bark beetle systematics. Blandford monographed the species of Central America in the series of contributions between 1895–1905. In the set Coleopterorum Catalogus, Hagedorn (1910a) catalogued the genera and species of Scolytidae (1234 species in 115 genera), and Strohmeyer (1912) those of Platypodidae (323 species in 13 genera). These authors also contributed fascicles on their respective families to the series Genera Insectorum (Hagedorn 1910b; Strohmeyer 1914a,b). Reitter (1913) provided a workable key to the species of Europe and neighbouring countries. In North America, the studies of A.D. Hopkins and M.W. Blackman greatly advanced the work of J.L. LeConte in the previous century. Much more work was also done on tropical species, particularly by the German Hans Eggers, the Austrian Karl Schedl, and the Pole Marian Nunberg. In the second half of the 20th century, major contributions have been made in the palearctic region by A. Balachowsky (France), A. Pfeffer (Czech Republic), V.N. Stark (the former Soviet Union), J. Murayama and A. Nobuchi (Japan). In the Americas, we have the important works of S.L. Wood and D.E. Bright, and in the old world tropics, those of F.G. Browne, and H. Roberts (United Kingdom). In particular, our knowledge of bark beetle classification has benefited from the generic level studies of Wood (1986) on Scolytidae and Wood (1993) on Platypodidae. Many others have also contributed, and accompanying this systematic knowledge, there has been considerable advance in

our knowledge of the biology and ecology of the beetles. Recently some new specialists have begun publishing to continue taxonomic studies. In addition, molecular studies have begun both to add to our knowledge, and to cast doubt on currently accepted classifications.

After the catalogues of Hagedorn and Strohmeyer, no further attempt was made to catalogue the families worldwide until the work of Wood and Bright (1992). These authors provided a detailed catalogue giving not only a list of all genera and species with synonyms, but information on types, host plants and distribution, and a list of references to each species. The catalogue deals with 5 812 species in 225 genera in 25 tribes, illustrating the enormous increase in knowledge of bark and ambrosia beetles since the early years of the century. Two supplements to this catalogue have appeared (Bright and Skidmore 1997, 2002) bringing the work up to the year 1999. Together, these works form what must be one of the finest references available to workers on any family of beetles.

2.2. *Bibliographies*

Because of the importance of bark beetles in forest protection and forest industry, many works and notices about their biology, faunistics and forest protection methods have been published in forestry-oriented papers. This caused problems in collating information, and the need for bibliographical work developed. The first bibliography was published by Trédl and Kleine (1911) in the journal *Entomologische Blätter*, including 1 800 citations. In 1939, a new Kleine bibliography was published in the *Stettiner Entomologische Zeitung* including nearly 4 000 citations. In 1946 – 1949, Schedl published a continuation of these bibliographies in *Zentralblatt für das Gesamtgebiet der Entomologie*, and later he collected all these works together in *Bibliografia Mundial Sobre Scolytidae e Platypodidae* (Schedl 1974), which lists nearly 5 000 citations of particular articles or monographs as well as giving a list of sources for the bibliography (journals etc.). As indicated above, numerous, more or less locally oriented faunas, check-lists, catalogues and smaller monographs, as well as the descriptions of the new species, were published by numerous authors within the 20th century. The most recent comprehensive bibliography of Scolytidae and Platypodidae was published by Wood and Bright in 1987 (including 21 488 references). Supplements to this are by Wood and Bright (1987) (2 664 references), Bright and Skidmore (1997) (1 420 references) and Bright and Skidmore (2002) (1 341 references). This is an outstanding series of publications giving us a total overview of both families, Scolytidae and Platypodidae, from a bibliographical as well as a systematic view. We may mention here the difficulty of continuing such a huge work. The number of citations is increasing rapidly and it is doubtful if one or even a small group of specialists will be able to gather and collate all this information and prepare further Supplements or a more comprehensive work. The development of a computerized version would help.

2.3. *Recent status of the families Scolytidae and Platypodidae*

Traditionally both taxonomic groups, Scolytidae and Platypodidae, have been considered as separate families within the superfamily Curculionoidea, although K.E. Schedl, in particular considered them to form a separate superfamily Scolytoidea. Crowson (1967) included both these families in the Curculionidae, primarily on the basis of the absence of convenient larval characters that could separate them from that family. However, the family status for all these groups was still generally accepted, although rather strong comments were made on this topic (Wood 1973, pers. comm.). The leading authority on the families, Stephen Wood (1973, 1986) has continued to maintain them as distinct families. His arguments are based primarily on the presence of a distinct 'pregular' sclerite (=submentum) and 'pregular' sutures (but see Lyal 1995), and on the presence of denticles on the tibiae or stout socketed setae (occasionally secondarily lost). Wood (1986) notes that, although platypodid larvae are distinguishable from those of other curculionoids, those of some scolytids are not. However, he suggests that this may be related to simplification and reduction resulting from small size. More recently, and particularly since the publication of Lawrence and Newton (1995), there has been a tendency to reconsider the two families, or at least the Scolytidae, as subfamilies of Curculionidae. This opinion is based partly on morphological (Thompson 1992; Kuschel 1995) and partly on molecular data (Marvaldi *et al.* 2002). It is also possible that the platypodids should be included as a tribe within the subfamily Scolytinae (Kuschel *et al.* 2000; Farrell *et al.* 2001), although Marvaldi *et al.* (2002) argue that the evidence for this is weak. Arguments are likely to continue for some time before a consensus is reached. Forest entomologists, unconcerned with the niceties of systematic position, will no doubt continue to consider the Scolytidae and Platypodidae as distinct families for some time to come – as we have done here. In the meantime, the change has brought some inconvenience to those working on the two groups, for the Zoological Record has lumped them within the Curculionidae, so that workers have to search through the whole of this large section to try to locate new information.

The situation in systematics of the whole superfamily of Curculionoidea was nicely characterized by Alonso-Zarazaga and Lyal (1999), from which we would like to cite a few sentences:

"The superfamily Curculionoidea ('weevils') contains a significant proportion of all known species of Coleoptera and includes, as presently understood, the largest family of animals, the Curculionidae. Although the group is large, conspicuous and important (and perhaps for all these reasons), the systematics at almost all levels is chaotic, and access to current nomenclature very difficult."

In modern treatments of the Curculionoidea (notably Thompson 1992; Kuschel 1995; Zimmerman 1994 and the beetle catalogue of Lawrence & Newton 1995) widely differing family concepts are used. The range of accepted families in recent works is between 22 and 6, and the number of subfamilies between 100 and 10! (Kuschel 1994). This would not be very important if the various concepts were consistent and differences were simply in rank. Unfortunately this is not so, and many subfamilies, tribes and genera 'float' between higher taxa without any clear idea being given in the papers making the changes of what characters indicated these

placements and how these characters were interpreted. Thus present classifications (of Curculionoidea) are a mixture of monophyletic, paraphyletic and polyphyletic taxa."

3. TAXONOMY

3.1. Identification

For any economically important insect group, a sound taxonomic and biological knowledge is an essential basis for any attempt at management or control. The accurate determination of the species involved is the basis for decision-making. Without this knowledge, actions taken could well be ineffective or erroneous. This is true for the bark beetles, which, as indicated earlier, have a variety of habits. Management and control strategies must be related to the habits of the particular species involved.

In Europe, the bark beetle fauna is well known, and there are both regional and more local keys available which will allow an accurate identification of nearly all species if used with care. In the authors' opinion, the most useful and up-to-date key to the bark beetles of the European region and neighbouring areas, extending from North Africa to Central Asia, is the publication by Pfeffer (1995). Other keys for more local areas include Balachowsky (1949) (France); Hansen (1956) (Denmark); Pfeffer (1955, 1989) (Czech Republic and Slovakia); Nunberg (1954) (Poland); Karaman (1971) (Macedonia); Stark (1952) (Russia). The older publications should be used with some care, because there have been considerable taxonomic changes at generic and specific levels, new and changed synonymy, and most importantly, newly introduced species, which do not appear in some of the keys. Fortunately, Wood's generic revisions of Scolytidae (Wood 1986) and Platypodidae (Wood 1993) provide a means to determine at least the genus of introduced species. In addition, two publications, which include distribution maps, should be mentioned – Lekander *et al.* (1977) covering the Nordic countries, and Bovey (1987) covering Switzerland. Again, it needs to be remembered that the distribution of a number of species of bark beetle is changing, in response to changes in host distribution, climate, etc. (see below).

3.2. Basis of Classification

3.2.1. External Morphology

The most recent classification of Scolytidae and Platypodidae at the tribal and generic levels is that of Wood (1986, 1993). This has been fairly generally accepted, although there are problems with the delimitation of some tribes and genera, and the inclusion of certain genera within the Platypodidae. Some changes may be expected in the future. Wood (1986) divides the Scolytidae into two subfamilies and 25 tribes. Both subfamilies and the following fifteen tribes are represented in the European area: Hylesininae: Hylastini, Hylesinini, Tomicini, Phloeotribini, Phloeosinini, Hypoborini, Polygraphini; Scolytinae: Scolytini, Ipini, Dryocoetini, Crypturgini,

Xyloterini, Xyleborini, Cryphalini, Corthylini. The Platypodidae is a largely tropical family, and only two species are present in Europe, both in the tribe Platypodini.

The classification of Wood is based almost entirely on external morphology. Wood (1978, 1993) has discussed in detail the characters which are of value in classifying the families at tribal and generic levels, and only a brief resume will be given here, omitting the Platypodidae, for which reference can be made to Wood (1993). In the Scolytidae, many characters of the head are used in classification. The frons presents characters (shape, sculpture and ornamentation) useful at almost all levels from tribe to sexual differences. The eyes are usually elongate-oval, but may be entire, emarginate, or divided into two parts, as in *Trypodendron* and most species of *Polygraphus*. The antenna is of considerable importance in classification. The primitive number of funicular segments (7) is often reduced. The number is characteristic of certain tribes (e.g. Hylastini (7), Xyloterini (4)), and can be useful in separating genera. The club is extremely variable, and can be conical, compressed or obliquely truncate, symmetrical or asymmetrical, with sutures visible on both sides or only one, with three or one segments, and occasionally with five or more pseudosutures. In the genus *Phloeotribus*, the segments of the antennal club are lamellate and independently movable.

In the thorax, the shape of the pronotum is important. In the Hylesininae, it is not strongly declivous anteriorly, and the head is visible from above; in the Scolytinae, changes in the axis of the anterior foramen from vertical to oblique, have led to the restructuring of the segment, so that the sternal area is shortened, and the dorsal part of the pronotum has become declivous, and the head is largely or entirely concealed beneath it. The detailed form of the pronotum is often characteristic of genera. The shape and visibility of the scutellum is a very useful character, primarily at generic level, but also at subfamily level. In the Hylesininae, the scutellum, if visible, is usually small, convex, and slightly depressed below the level of the elytra in a sutural notch. In the Scolytinae, it is usually large and flat, and lies flush with the elytral surface. However, there are many exceptions to this in the Xyleborini.

The elytra are extremely variable in structure and sculpture. In the Hylesininae, the basal margins of the elytra are procurved and slightly raised and bear a row of crenulations; in the Scolytinae, the basal margin is unarmed and usually forms a straight, transverse line across the body. Again there are exceptions to this in the Xyleborini, related to the presence of mycangia in or near the elytral bases. The variation in elytral form and sculpture is particularly important at the specific level, but particular elytral forms can be characteristic of certain genera. The metepisternum is usually visible throughout its length in scolytids, but in the tribes Cryphalini and Corthylini, it is largely covered by the elytra and only the anterior part is visible. Further metathoracic characters are discussed by Wood (1978). Whilst of clear classificatory importance, they have the disadvantage of being hidden from view unless one elytron is removed, or the elytra are spread, and are difficult to use in keys. The legs are also important in classification, especially the tibiae. The tibiae bear spines on the outer margin that may be unsocketed or socketed, the latter presumed to have a setal origin. In the Scolytini (and some other extra-limital groups) they have been secondarily lost, and the tibiae bear simply an

apical curved spine. The shape of the tibia is also important in separating certain tribes and genera. The presence or absence of a groove for reception of the tarsus is also used in classification (e.g. Cryphalini). The size of separation of the coxae is used to separate some genera (e.g. *Xyleborus* and *Xylosandrus*).

The abdomen has not been much used in scolytid classification, although its sculpture is important in separating species of *Scolytus*. In the Scolytini and Xyloctonini, the elytra are flat, and the abdomen ascends to meet them. In the majority of scolytids the elytra are declivous, and the abdomen correspondingly more or less flat.

The majority of the ambrosia beetles have mycangia. These are cuticular tubes, pouches or pits of various sizes, associated with glandular cells and opening to the surface of the body. They are used to carry the spores of the symbiotic ambrosia fungi. They may be found in many parts of the body (head, thorax, and elytra), but are usually constant in position in particular genera (Beaver 1989). As yet, they have not been used in classification.

3.2.2. Sexual dimorphism

Nearly all Scolytidae and Platypodidae are sexually dimorphic to some degree. Structures involved include the frons (e.g. *Hylesinus*, *Trypodendron*), the elytral declivity (some *Crypturgus* species), or both (*Ips*, *Pityokteines*, *Phloeosinus*), the abdominal ventrites (*Scolytus*), and the presence of mycangia (*Scolytoplatypus*). Various combinations of these and other characters may also be involved. Many scolytids and platypodids can stridulate producing sounds which are used in inter-individual interactions. Three types of stridulatory systems of the file-pectrum type are found in the Scolytidae, and one in the Platypodidae, nearly always less well developed (or absent) in the female than in the male (Lyal and King 1996). The differences between the sexes are greatest in the inbreeding groups (e.g. Xyleborini, some Dryocoetini and Cryphalini) in which the male is dwarfed, wingless, and with reduced eyes, and usually with reduced sclerotisation. It may have a similar form to the female, or the pronotum may be modified in various ways. The extreme case is the genus *Ozopemon* (Dryocoetini), in which the male is neotenous and larviform, but has a well-developed aedeagus. In the Platypodidae, the sculpture of the elytra is always better developed in the male. There may also be differences between the sexes in the structure and ornamentation of the frons, and in the presence, number and size of the mycangia, and in other characters.

3.2.3. Internal Morphology

Internal morphology has not been generally used in the classification of bark beetles. Hagedorn (1910c) attempted to use the mouthparts as the basis of his classification of Scolytidae, but his scheme is unworkable. Mouthparts have some value in separating the major divisions of the Platypodidae (Wood 1993). Characters of the mouthparts have occasionally been used to distinguish species (Erichson 1836), as have the internal sclerotized processes in the proventriculus (e.g. Nobuchi 1969). Other characters of the alimentary canal could also be of some taxonomic value (Thomas 1967; May 1995). Sometimes entomologists have tried to use the

characters of the copulatory organs, mainly in males (e.g. Israelson 1972), but also females (e.g. Fuchs 1911). The characters of the male aedeagus do have value taxonomically, but most workers on the bark beetles have based their classifications primarily on more easily visible external characters.

3.2.4. Immature Stages

Knowledge of the immature stages of Scolytidae and Platypodidae remains limited, and there have been rather few papers published. Thomas (1957) provided a useful discussion of the use of larval anatomy in bark beetle studies, and Lekander (1968) published the most comprehensive survey of scolytid larvae so far. Browne (1972) reviewed the characters of many platypodid genera. These papers, together with the work of May (1993), suggest that a classification based on larval morphology would be reasonably concordant with one based on adult characters. However, most papers have dealt with the description of the larvae (rarely pupae) of particular species, and have not attempted to integrate their work into a more general scheme. This is an area of research in which much more work needs to be done.

Another feature which has been used in the preliminary identification of the true bark beetles is the form of the gallery system below the bark. This often has a form, which is characteristic of a species (see for example the figures in Balachowsky (1949) or Pfeffer (1995)). The form of the gallery system is less informative in the non-phloeophagous bark beetles.

4. GEOGRAPHICAL DISTRIBUTION

4.1. General distribution

More than 6000 species of Scolytids and approximately 1500 species of platypodids have now been described worldwide. More than 600 scolytid species occur in North America and nearly 900 species occur in the Palaearctic region. We can easily conclude from these numbers, that the main centre of geographical distribution and species diversity of bark and ambrosia beetles is in the subtropical and tropical regions. It is also in this region that much speciation seems to have occurred, particularly in the tribes Dryocoetini, Xyleborini, and Cryphalini. This diversification seems to have been related to the evolution of an inbreeding strategy, characterised by sib-mating before the new generation of females emerges from the gallery system, haplodiploidy (in Dryocoetini and Xyleborini), or its genetical equivalent, pseudoarrhenotoky (in Cryphalini), and sex ratios strongly biased towards females. This strategy seems to have evolved once in the evolutionary line including the Dryocoetini and Xyleborini (Jordal *et al.* 2000), and separately in the Cryphalini. The advantages of the strategy are that it increases the biotic potential of the species because nearly all individuals are female, and can reproduce; secondly that the colonization of isolated habitats is made easier if both male and female do not need to find the habitat at the same time (Beaver 1977). By these facts the particular species can easily distribute into the new territories. The reasons for the relative lack of species adopting the strategy in the temperate zone remain unclear.

The total number of species of bark beetle in Europe depends on where the geographical boundaries are set, particularly in the East (whether the Caucasian countries are included or not), and whether African island groups, such as the Canary Islands, are included. Quite large areas are sometimes omitted from databases and recent publications, giving totals that vary from about 250 – 300 species. (By contrast, the island of Borneo in the Southeast Asian tropics, with an area less than 10% of Europe has a fauna of about 600 described species, with many more undescribed.) The regional distribution of bark beetles depends on many factors, but is determined mainly by climate and the distribution of the host plants. In considering the host plants, it is important to consider historical changes in host plant distribution, the frequency of occurrence of species in the region, and forest management practices. In recent decades, commercial trade has also had a large and important influence on bark beetle distribution (see below).

The local distribution of bark beetles is related primarily to the presence of suitable habitat for breeding and for use as a food source. Sudden increases in the abundance of suitable habitat, e.g. following a windfall, may result in the course of 2–3 years in a population reaching outbreak proportions. This can be important if the presence of very large numbers of beetles allows them to overcome host resistance, and successfully attack and kill living trees. However, most species remain at low population densities on a regional scale, although they may be abundant locally.

4.2. Introduction of exotic species and changes in distribution

One of the consequences of increased international trade has been the introduction of 'exotic' species into countries outside their normal distributional range. According to some estimates, approximately 20% of the species of bark beetle found in Europe have actual or potential importance as forest pests, having economically important consequences for the forest and timber industries. For this reason, we have to care about both the introduction of new species and possible pests into Europe, and also the export of pest species to other countries. Some of the more important bark beetle pests in North America have been imported from Europe (e.g. *Scolytus multistriatus* (Marsham), *Tomicus piniperda* (L.)). It is not only the introduction of these exotics that is important, but the fact that they may carry with them pathogenic microorganisms and fungi (Wegensteiner *et al.* 1996). Probably all bark beetles, not just the ambrosia beetles, are associated in some way with fungi. The primary role of the mycangia of ambrosia beetles is to carry symbiotic fungi, but they, and the body surface, may sometimes transport spores of fungi, which are pathogenic to the host trees, as with the well-known example of the Dutch elm disease fungus (Webber 2000).

The most important sources of potential pest species for Europe are areas which are similar climatically, e.g. temperate and subtropical areas of Asia and North America. The most frequent introductions into Europe have been from the Far East (Siberia), Japan and the U.S.A. (e.g. *Gnathotrichus materiarius* (Fitch), and *Xylosandrus germanus* (Blandford), both of which are ambrosia beetles). Other species have increased their natural distribution as a result of changes in their

environment. An example is the important forest pest, *Ips typographus* (L.), which was originally restricted in its distribution to the native territory of its host plant, spruce (*Picea*). Because of the development of extensive plantations of spruce, mostly in monoculture, throughout much of Europe, its range has increased very rapidly, and it can now be found everywhere that spruce is planted. In other cases, species have moved into warmer climates from northern areas, or from higher to lower elevations on mountains. If, as a result, they become multivoltine in the warmer climate, they may more likely become pests. Some species which have increased their distribution in Europe in the last hundred years are *Ips amitinus* (Eichhoff), *I. duplicatus* (Sahlberg), *Orthotomicus robustus* (Knotek), *Pityophthorus micrographus* (L.) and several species in the tribe Xyleborini (Pfeffer and Knížek 1989). Internal trade can also result in changes in distribution within Europe (e.g. *Dendroctonus micans* (Kugelann)).

The primary points of entry of exotic species are likely to be the ports of coastal states, which import goods from all over the world. Direct trade in lumber or wood products can introduce bark beetles, but they are often present in the pallets and dunnage of other commodities, and can easily escape the attention of inspectors. As restrictions on the import of untreated or unbarked timber have been introduced, such packing has become a frequent source of introductions. It is very important to be prepared for such introductions, and to be able to correctly determine the species involved. Once this has been done, knowledge of the bionomics of the species in its native habitat is essential in order to determine the possible consequences of its establishment. The majority of imported species do not establish themselves, but the economic consequences of even one doing so can be very great.

We can divide introduced species into three categories:

1. Individuals of the exotic species are introduced into a new territory, but do not find conditions suitable for their breeding and development, and die. Such species are unimportant from an economic point of view.
2. Introduced individuals find suitable conditions and survive initially because they can establish a new brood in a suitable host plant. However, because of the unsuitable climate, the whole population dies, usually within one year.
3. Introduced individuals find the suitable conditions for their development, establish and become new permanent members of the local fauna. Here we can recognize three grades:
 - a. Established species persist but do not cause any economic or other damage, and are not aggressive against the native fauna.
 - b. Established species, which fully occupy a free or previously, by other species, occupied niche. They may eliminate native species, but do not cause any economic or other damage.
 - c. Established species, which fully occupy a free or previously, by other species, occupied niche, and may eliminate some native species, but the new conditions facilitate their multiplication to outbreak status, resulting in economic and other damage.

In all these cases, not only climatic conditions and the presence of suitable breeding material can influence the result, but also the presence or absence of

natural enemies. However, natural enemies react only after a time delay to the presence of a new host or prey population, and their influence may be too small or too late. It is also important to note that species, which mate before dispersal, such as the Xyleborini, have a greater chance of establishing new populations, because only the female, and not both sexes, need to be introduced into the new country at the same time.

The European and Mediterranean Plant Protection Organization lists the following non-European species on its quarantine list (<http://www.eppo.org/>): *Dendroctonus adjunctus* Blandford, *Dendroctonus brevicomis* LeConte, *Dendroctonus frontalis* Zimmermann, *Dendroctonus ponderosae* Hopkins, *Dendroctonus pseudotsugae* Hopkins, *Dendroctonus rufipennis* Kirby, *Dryocoetes confusus* Swaine, *Gnathotrichus sulcatus* (LeConte), *Ips calligraphus* (Germar), *Ips confusus* (LeConte), *Ips grandicollis* (Eichhoff), *Ips lecontei* Swaine, *Ips paraconfusus* Lanier, *Ips pini* (Say), *Ips plastographus* (LeConte).

All of these species are native to North America, where some of them are very important pests, partly because they are able, through mass attacks, to overcome the resistance of living trees, and cause extensive tree mortality. It may be noted that species from the eastern half of the Palaearctic region and tropical regions are not included in the list, except *Scolytus morawitzi* Semenov is mentioned in additional list. As the candidates for including are *Ips hauseri* Reitter and *I. subelongatus* (Motschulsky). EU ranges between quarantine pests two species namely, *Pseudodityophthorus pruinosus* (Eichhoff) and *P. minutissimus* (Zimmermann), and other bark beetles species as Scolytidae spp. – all non-European species related to plants of conifers over 3 m in height, other than fruit and seeds, wood of conifers (Coniferales) with bark, and isolated bark of conifers (Coniferales), originating in non-European countries.

5. REFERENCES

- Alonso-Zarazaga, M.A., & Lyal, C.H.C. 1999. *A world catalogue of families and genera of Curculionoidea (Insecta: Coleoptera) (Excepting Scolytidae and Platypodidae)*. Barcelona: Entomopraxis, S.C.P.
- Balachowsky, A.S. 1949. *Coleoptères Scolytides*. Faune de France 50. Paris: Paul Lechevalier.
- Beaver, R.A. 1977. Bark and ambrosia beetles in tropical forests. In. *Proceedings, Symposium on forest pests and diseases in Southeast Asia*, April 1976. BIOTROP Special Publication No. 2. Bogor, Indonesia.
- Beaver, R.A. 1989. Insect-fungus relationship in the bark and ambrosia beetles. In. *Insect-fungus interactions*, N. Wilding, N.M. Collins, P.M. Hammond, and J.F. Weber (Eds). London: Academic Press.
- Bovey, P. 1987. *Coleoptera, Scolytidae, Platypodidae*. Insecta Helvetica, Catalogus. Zürich: Société entomologique suisse.
- Bright, D.E., & Skidmore, R.E. 1997. A Catalog of Scolytidae and Platypodidae (Coleoptera), Supplement 1 (1990–1994). Ottawa: NRC Research Press.
- Bright, D.E., & Skidmore, R.E. 2002. A Catalog of Scolytidae and Platypodidae (Coleoptera), Supplement 2 (1995–1999). Ottawa: NRC Research Press.
- Browne, F.G. 1972. Larvae of the principal old world genera of the Platypodinae (Coleoptera: Platypodidae). Royal Entomological Society of London, Transactions, 124, 167–90.
- Crowson, R.A. 1967. The natural classification of the families of Coleoptera: Addenda and corrigenda. Entomologist's Monthly Magazine, 103, 209–14.

- Eichhoff, W.J. 1878. Ratio, descriptio, emendatio eorum Tomicinorum qui sunt in Dr. Medin. Chapuisi et autoris ipsius collectionibus et quos praetereare cognovit. Societe Entomologique de Liege, Memoires, (2)8, 1+iv+531p., 5pls.
- Erichson, W.F. 1836. Systematische Auseinandersetzung der Familie der Borkenkäfer (Bostrichidae). Archiv für Naturgeschichte 2, 45-65.
- Fabricius, J.C. 1801. Systema eleutherorum, secundum ordines, genera, species, adjectis synonymis, locis, observationibus, descriptionibus. Vol. 1. Kiliae: Bibliopol. acad.
- Farrell, B.D., Sequeira, A.S., O'Meara, B.C., Normark, B.B., Chung, J.H., & Jordal, B.H. 2001. The evolution of agriculture in beetles (Curculionidae: Scolytidae and Platypodinae). Evolution, 55, 2011-27.
- Fuchs, A.G. 1911. *Morphologische Studien über Borkenkäfer. I. Die Gattungen Ips DeGeer und Pityogenes Bedel.* Hab. techn. Hochschule Karlsruhe. München: C. Wold und S.
- Gemminger, M., von Harold, B. 1872. *Catalogus Coleopterorum, hucusque descriptorum synonymicus et systematicus. Scolytidae, Brentidae, Anthribidae, Cerambycidae.* München: Monachii.
- Geoffroy, E.L. 1762. *Histoire abrégée des insectes qui se trouvent aux environs de Paris; dans laquelle ces animaux sont rangés suivant un ordre méthodique.* Tome premier. Paris: Durand.
- Hagedorn, J.M. 1910a. Coleoptera Fam. Ipidae. In: *Genera Insectorum*, Wytsman (Ed.). Brussels: Wytsman.
- Hagedorn, J.M. 1910b. Ipidae. In: *Coleopterorum Catalogus*, Schenckling (Ed.). Berlin: W. Junk.
- Hagedorn, J.M. 1910c. Diagnosen bisher unbeschriebener Borkenkäfer (Col.). Deutsche Entomologische Zeitschrift, Ser. 2, 1-13.
- Hansen, V. 1956. Biller. XVIII Barkbiller, Danmarks Fauna, Bd. 62. Copenhagen: G.E.C. Gads.
- Chapuis, F. 1865. *Monographie des Platypides.* Liege: H. Dessain.
- Chapuis, F. 1869. *Synopsis des Scolytides.* J. Desoer, Liege.
- Israelson, G. 1972. Male copulatory organs of Macroneesian species of *Aphanarthrum* Wollaston. With designations of lectotypes and descriptions of new taxa (Col. Scolytidae). Entomologica Scandinavica 3, 249-57.
- Jordal, B.H., Normark, B.B., & Farrell B.D. 2000. Evolutionary radiation of an inbreeding haplodiploid beetle lineage (Curculionidae, Scolytinae). Biological Journal of the Linnean Society, 71, 483-99.
- Karaman, Z. 1971. *Coleopteres, Scolytidae (Coleoptera-Insects).* Fauna de Macedonia. Skopje: Musée d'Histoire Naturelle de Skopje.
- Kleine, R. 1939. Die Gesamtliteratur der Borkenkäfer (Ipidae und Platypodidae) bis einschliesslich 1938. Stettiner Entomologische Zeitung 100, 1-184.
- Kuschel, G. 1995. A phylogenetic classification of Curculionoidea to families and subfamilies. Memoir of the Entomological Society of Washington 14, 5-33.
- Kuschel, G., Leschen, R.A.B., & Zimmerman, E.C. 2000. Platypodidae under scrutiny. Invertebrate Taxonomy 14, 771-805.
- Latreille, P.A. 1807. *Genera crustaceorum et insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata.* Vol. 2. Paris: Amand Koenig.
- Lawrence, J.F., & Newton, A.F. 1995. Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In: *Biology, Phylogeny, and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson. Volume two*, Pakaluk, J., Slipinski, S.A. (Eds). Warszawa: Muzeum i Instytut PAN.
- Lekander, B. 1968. Scandinavian bark beetle larvae, descriptions and classification. Skogshögskolan: Institutionen för Skogszoologi.
- Lekander, B., Petersen, B.B., Kangas, E., & Bakke, A. 1977. The distribution of bark beetles in the Nordic countries. Acta Entomologica Fennica, 32, 1-37, 78 maps.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis.* Tomus I. Editio decima, reformata. Holmiae: Laurentii Salvii.
- Lyal, C.H.C. 1995. The ventral structures of the weevil head (Coleoptera: Curculionidae). Memoirs of the Entomological Society of Washington, 14, 35-51.
- Lyal, C.H.C., & King, T. 1996. Elytro-tergal stridulation in weevils (Insecta: Coleoptera: Curculionoidea). Journal of Natural History, 30, 703-73.

- Marvaldi, A.E., Sequeira, A.S., O'Brien, & C.W. Farrell, B.D. 2002. Molecular and morphological phylogenetics of weevils (Coleoptera, Curculionoidea); do niche shifts accompany diversification? *Systematic Biology*, 51, 761-85.
- May, B.M. 1993. Larvae of Curculionoidea (Insecta: Coleoptera): a systematic overview. *Fauna of New Zealand*, Number 28. Lincoln: Manaaki Whenua Press.
- May, B.M. 1994. An introduction to the immature stages of Australian Curculionoidea. In Zimmerman, E.C. *Australian Weevils* (Coleoptera: Curculionoidea). Melbourne: CSIRO Publishing.
- Nobuchi, A. 1969. A comparative morphological study of the proventriculus in the adult of the superfamily Scolytoidea (Coleoptera). Japan, Government Forest Experiment Station, Bulletin, 224, 39-110.
- Nunberg, M. 1954. Klucze do oznaczania owadów Polski, Czesc XIX Chrzaszcze – Coleoptera, Zeszyt 99-100, Korniki – Scolytidae, Wyrynniki – Platypodidae. Warszawa: Państwowe Wydawnictwo Naukowe.
- Pfeffer, A. 1955. Kůrovci – Scolytoidea. *Fauna ČSR*, svazek 6. Praha: ČSAV.
- Pfeffer, A. 1989. Kůrovcovití Scolytidae a jádrohlodovití Platypodidae. *Zoologické klíče*. Praha: Academia.
- Pfeffer, A. 1995. *Zentral- und westpaläarktische Borken- und Kernkäfer (Coleoptera: Scolytidae, Platypodidae)*. Basel: Pro Entomologia.
- Pfeffer, A., & Knížek, M. 1989. Problematika kůrovčů introdukovaných do Evropy. *Lesnická Práce*, 68, 311-12.
- Reitter, E. 1913. Bestimmungs-tabelle der Borkenkäfer (Scolytidae) aus Europa und den angrenzenden Ländern. *Wiener Entomologische Zeitung*, 32, 1-116.
- Schedl, K.E. 1946. Nachtrag zur Gesamtliteratur der Borkenkäfer (Ipidae und Platypodidae) von R. Kleine 1939. *Zentralblatt für das Gesamtgebiet der Entomologie* 1, 32, 63-64, 96, 123-28, 185-90.
- Schedl, K.E. 1947. Nachtrag zur Gesamtliteratur der Borkenkäfer (Ipidae und Platypodidae) von R. Kleine 1939. *Zentralblatt für das Gesamtgebiet der Entomologie* 2, 63-64.
- Schedl, K.E. 1948. Nachtrag zur Gesamtliteratur der Borkenkäfer (Ipidae und Platypodidae) von R. Kleine 1939. *Zentralblatt für das Gesamtgebiet der Entomologie* 3, 1-57.
- Schedl, K.E. 1974. *Bibliografia mundial sobre Scolytidae e Platypodidae*. Vol 1 and 2. Lisboa: Junta de Investigaciones do Ultramar.
- Shuckard, W.E. 1840. *The British Coleoptera Delineated, consisting of Figures of all the Genera of British Beetles, drawn in Outline* by W. Spry, M.E.S. London: W. Crofts.
- Stark, V.N. 1952. *Zhestkokrylye, Koroedy*. Fauna SSSR. Moskva, Leningrad: Akademia Nauk SSSR.
- Strohmeyer, H. 1912. Familie Platypodidae. In. *Coleopterorum Catalogus*, W. Junk and S. Schencking (Eds.). Berlin: W. Junk.
- Strohmeyer, H. 1914a. Coleoptera: Fam. Chapuisiidae. In. *Genera Insectorum. Fasc. 162*, P. Wytsman (Ed.). Bruxelles: Wytsman.
- Strohmeyer, H. 1914b. Coleoptera: Fam. Platypodidae. In. *Genera Insectorum. Fasc. 163*, P. Wytsman (Ed.). Bruxelles: Wytsman.
- Thomas, J.B. 1957. The use of larval anatomy in the study of bark beetles (Coleoptera: Scolytidae). *Canadian Entomologist* 89 (Supplement 5).
- Thomas, J.B. 1967. A comparative study of gastric caeca in adult and larval stages of bark beetles (Coleoptera: Scolytidae). *Entomological Society of Ontario, Proceedings*, 97, 71-90.
- Thompson, R.T. 1992. Observations on the morphology and classification of weevils (Coleoptera, Curculionoidea) with a key to major groups. *Journal of Natural History* 26, 835-91.
- Trédl, R., & Kleine, R. 1911. Übersicht über die Gesamtliteratur der Borkenkäfer vom Jahre 1758-1910. *Entomologische Blätter* 7, 1-180.
- Webber, J.F. 2000. Insect vector behaviour and the evolution of Dutch elm disease. In: *The Elms: Breeding, Conservation, and Disease Management*. Dunn (Ed.). Kluwer, Boston.
- Wegensteiner, R., Weiser, J., & Führer, E., 1996. Observations on the occurrence of pathogens in the bark beetle *Ips typographus* L. (Col.:Scolytidae). *J. Appl. Entomol.* 120, 190-204.
- Wood S.L. 1973. On taxonomic status of Platypodidae and Scolytidae (Coleoptera). *Great Basin Naturalist* 33, 77-90.
- Wood, S.L. 1978. A reclassification of the subfamilies and tribes of Scolytidae (Coleoptera). *Annales de la Societe Entomologique de France*, 14, 95-122.
- Wood, S.L. 1986. A reclassification of the genera of Scolytidae (Coleoptera). *Great Basin Naturalist Memoirs* (10). Provo, Utah: Brigham Young University.

- Wood, S.L. 1993. Revision of the genera of Platypodidae (Coleoptera). Great Basin Naturalist 53, 259-81.
- Wood, S.L., & Bright, D.E. 1987. A Catalog of Scolytidae and Platypodidae (Coleoptera), Part 1: Bibliography. Great Basin Naturalist Memoirs (11). Provo, Utah: Brigham Young University.
- Wood, S.L., & Bright, D.E. 1992. A Catalog of Scolytidae and Platypodidae (Coleoptera), Part 2: Taxonomic Index. Great Basin Naturalist Memoirs (13). Provo, Utah: Brigham Young University.
- Zimmerman, E.C. 1994. *Australian Weevils (Coleoptera: Curculionoidea)*. Melbourne: CSIRO Publishing.

Chapter 6

GENETIC TOOLS IN SCOLYTID RESEARCH

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1. INTRODUCTION

At the beginning of the 1960's, allozyme electrophoresis revolutionised many research fields, including those of systematic and population genetics. In the mid 1990's, the polymerase chain reaction (PCR) improved DNA sequencing and lead to the flourish of molecular markers for systematic and population genetic studies. Many of these techniques have been applied to scolytid research and have helped answering phylogenetic and phylogeographic questions. This review deals with species within the databank of the EU funded *Bark and Wood Boring Insects in Living Trees* (BAWBILT). Papers that deal with topics like the bark beetle sexual evolution or host-beetle co evolution are not described in this review (e.g. Normark *et al.* 1999, Farrell *et al.* 2001, Jordal 2002).

2. PHYLOGENETICS

American scolytid specialists Steven Wood and Donald Bright called to attention the lack of students of scolytid systematics (Wood & Bright 1998 - personal communication at the European Entomological Congress). It will be important to define scolytid species by sequencing specific regions of the DNA and these diagnostic markers need to be associated with morphological characters that define the species as it is also proposed by Tautz *et al.* (2003). The data entries in the Genbank, allow scientists worldwide to use the existing ones for their analysis.

2.1. Genus *Ips*

In Central Europe *Ips* species are characterized by differences in morphology, structure of galleries, host specificity and aggressiveness. An analysis with a partial region of the mitochondrial DNA revealed high inter-specific and low intra-specific

sequence divergence. A phylogenetic analysis both with maximum parsimony and distance method clustered *I. typographus*, *Ips cembrae*, *I. amitinus*, *I. duplicatus* and *I. acuminatus*, and put *I. mannsfeldi* and *I. sexdentatus* like the two outgroup species. *I. mannsfeldi* and the outgroup *O. erosus* emerged as sister pairs. These findings agree with Cognato & Sperling (2000), except that *Ips acuminatus* does not have the close relationships to the eight spined bark beetles. *I. mannsfeldi* was further removed from *Ips* to *Orthotomicus* (Cognato & Vogler 2001) as already proposed by Wood (1982) and Escherich (1923). It is further likely that the genus *Orthotomicus* comprises two genera (Cognato personal communication).

The eight spined larch bark beetles that infest various *Larix* species in Europe and Asia were analysed (Stauffer *et al.* 2001). *Ips subelongatus*, *Ips fallax*, *Ips shinanonensis* and *Ips cembrae* var. *engadinensis* were often treated as synonyms of *I. cembrae*. These four taxa are distinguished by host tree and geographic distribution, as morphological diagnostic characters are deficient. The European populations differed by 4.3% from the Asian populations. The phylogenetic analysis placed the European and Asian haplotypes in significantly distinct clusters. The results suggest that the *I. cembrae* complex contains at least two taxa: *I. cembrae* in Europe and *I. subelongatus* in Asia.

In 1913, Fuchs described *Ips amitinus* var. *montana* as a race of *Ips amitinus*. The differences were based on the different host trees and on body size. The main host of *I. amitinus* is *Picea abies* and of *I. amitinus* var. *montana* are *Pinus cembra* and *Pinus montana*. Four populations of *I. amitinus* and two populations of *I. amitinus* var. *montana* were studied in order to evaluate evolutionary and ecological implications of this race differentiation. Behavioural, ecological and DNA analysis revealed no evidence to suggest distinct races (Stauffer & Zuber 1998).

Ips japonicus was first described by Niijima (1909) on Yezo spruce, *Picea jezoensis* and Sachalin spruce, *Picea glehnii* in Japan. In literature *Ips japonicus* is often mentioned as a form of *I. typographus*. Pfeffer (1994) and Wood (1982) described *Ips japonicus* as synonym of *I. typographus*. Phylogenetic relationship of *I. typographus* f. *japonicus* and *I. typographus* populations helped to define their taxonomy. The European haplotypes and the Asian haplotypes formed monophyletic clusters, indicating that these two forms are geographically isolated (Stauffer *et al.*, unpubl. data).

2.2. Genus *Tomicus*

The genus *Tomicus* contains six species within Europe and Asia which infest pine species. *T. piniperda* and *T. minor* are Eurasian species, *T. destruens* occurs in the Mediterranean area, and *T. brevipilosus*, *T. puellus* and *T. pilifer* are found in Asia. The pine shoot beetle *T. piniperda* and its sibling species *T. destruens* were often synonymised in the past (e.g. Schedl 1932). Recent phylogenetic analyses based on the mitochondrial and nuclear genes, revealed two distinct species supported by many characters (Gallego & Galián 2001, Kerdelhué *et al.* 2002, Kohlmayr *et al.* 2002). These results confirm the classification of Pfeffer (1994) and Wood & Bright (1992). On the other hand, both mitochondrial and nuclear markers showed that a

new species of *Tomicus*, morphologically undistinguishable from *T. piniperda*, occurs in Yunnan Province, China, causing heavy tree damages on *Pinus yunnanensis* (Duan *et al.* unpublished data)

3 ECOLOGICAL GENETICS OF SCOLYTIDS

Adaptations and differentiation of wild populations in relation to their environment as explained by the genetics is the subject of *Ecological Genetics*. This research field often includes experimental ecology of natural populations through a combination of field and laboratory work. Behavioural and eco-physiological characteristics such as aggression, dormancy reaction, pheromone response, vary geographically and are often associated with the genetic structure of a population or individual. The understanding of such characters is important for long-term biological pest control programs.

3.1. *Pityogenes chalcographus*

Intra-specific investigations show that *P. chalcographus* form races within Europe. Antennal size and spine morphology of the elytral declivity revealed significant differences between Northeast and Central European populations (Führer 1978). Allopatric females were partly rejected by males, in mating experiments which simultaneously presented sympatric and allopatric females (Sturis & Führer 1979). Post-zygotic incompatibilities were observed for the few instants of fertilisation (Führer 1976, 1977). Mating among Scandinavian, Polish and Alpine races resulted in different degrees of inter-population heterosis (Führer & Klipstein 1980). Analysing the sperm polyploidy inter-popular hybrids showed increased polyploid sperm (Führer 1980). Isozyme electrophoreses revealed significant differences among populations reared at the institute (Ritzengruber 1990), however, no significant conclusion could be given regarding the race formation.

3.2. *Ips typographus*

The European spruce bark beetle (*Ips typographus*) populations are reported to show variation in their reaction towards synthetic pheromone traps and vary in their epidemiological behaviour. In order to quantify the degree of population differentiation and to estimate the levels of gene flow, European populations were analysed by sequence analysis (Stauffer *et al.* 1999). The data of a partial sequence of the mitochondrial DNA and an enzyme analysis suggested that the population structure of the European *I. typographus* has been influenced by events which took place during and after the last ice age. Populations were forced into refugial areas in the south and in the area north of Moscow along with the host tree. After amelioration of temperature, beetles spread perpendicular to the distribution of *P. abies*. *I. typographus* migrated from the south to the north and not from the east (Moscow) to the west as did the host tree. Whilst there is evidence for high gene flow among populations, founder effects can still be detected in the North. The

distribution of the genotypes in the European populations might explain the behavioural and epidemiological differences.

Allozymes were used to study the genetic variation of local populations of *Ips typographus* during the last two decades (Stauffer *et al.* 1992, Pavlicek *et al.* 1997, Gruppe 1997, Viktorinová 1999). These studies showed that *I. typographus* populations had a lack of heterozygotes. Several groups addressed the association of genetic variation with obligate and facultative diapausing beetles (Perny 1992, Gasser 2001), pioneer beetles (Stauffer 1994) and pheromone reacting beetles (Leitinger & Schreiber 1990, Hösle 1999). However, significant results could not be demonstrated either.

3.3. *Ips acuminatus*

Ips acuminatus was described to have bisexual and clonal (parthenogenetic) females (Kirkendaal 1983). Although both forms are morphologically indistinguishable, they were separated by differences in the mitochondrial DNA. A restriction enzyme facilitates the distinction (Kirkendaal personal communication).

3.4. *Tomcus piniperda*

Besides *P. sylvestris*, 16 other pine species and *Picea* spp. (Wood & Bright 1992, Pfeffer 1994) are recorded as host trees of *T. piniperda*. Host association can be an important factor in speciation. There was little indication that host choice affects the genetic structure of *T. piniperda* (Kerdelhué *et al.* 2002). The phylogeographic analysis of European, Chinese and American populations revealed 25 haplotypes that are being analysed using a nested clade analysis (Ritzerow *et al.*, 2003). The Central & Northern European, American populations had most of the haplotypes in common whereas the Iberian populations had haplotypes not found in Central Europe. The postglacial history of *Pinus sylvestris* suggests that the Pyrenees were likely a major barrier for gene flow and thus also for the insect. The Northern Chinese populations had also haplotypes which were not found in Europe - the sequence divergence was quite low with 1,5%. A high mitochondrial sequence divergence (4,2%) between European and Asian *T. minor* was detected, but interestingly they apparently revealed almost no divergence on nuclear sequences (Duan *et al.* unpublished data).

4. PERSPECTIVES

In phylogeographic questions it will be important to develop faster evolving markers in order to be able to analyse questions from the most recent past and regarding quarantine control. A method that has been applied in many plant and animal species during the last decade is the use of microsatellites. Much effort has been dedicated to isolate microsatellite primers for coleopteran species, however, only few polymorphic loci have been characterised, yet, compared to other insect orders. Microsatellite loci have been reported from chrysomelids (Batley *et al.* 1998),

carabids (Keller & Largadièr 2001), and also recently for scolytids (Kerdelhué *et al.* 2003, Berg *et al.* 2003, Sallé *et al.* 2003). In latter isolations, the five loci from *T. piniperda* showed cross-species amplification to three other *Tomicus* species (Kerdelhué *et al.* 2003), five loci were isolated from *Ips typographus* (Sallé *et al.* 2003) and 14 loci from *Coccotrypes carpophagus* (Berg *et al.* 2003) were scored. In *Ips typographus* further reports on four microsatellite loci from Pavlová (2000) and three loci isolated by Stauffer (1998) were described.

It will be important to isolate also other nuclear markers like in the non-coding regions that so far seem to have more variable sites. Viktorinová (2001) partially isolated the α -amylase gene. The intron-exon structure was used for exon-primed intron-crossing (EPIC) PCR. This method was subsequently used for population structure analysis.

5. REFERENCES

- Batley, J., Edwards, K.J., Wiltshire, C.W., Glen, D., Karp, A. 1998. The isolation and characterization of microsatellite loci in the willow beetles, *Phyllodecta vulgarissima* (L.) and *P. vitellinae* (L.). *Molecular Ecology*, 7, 1436-37.
- Berg, P.R., Dawson, D.A., Pandhal, J.P., Kirkendaal, L.R. & Burke, T. 2003. Isolation and characterization of microsatellite loci from two inbreeding bark beetle species (*Coccotrypes*). *Molecular Ecology Notes*, in press.
- Cognato, A.I. & Sperling, F.A.H. 2000. Phylogeny of *Ips* DeGeer species (Coleoptera: Scolytidae) inferred from mitochondrial cytochrome oxidase I DNA sequence. *Molecular Phylogenetics and Evolution*, 14, 445-60.
- Cognato, A.I. & Vogler, A.P. 2001. Exploring data interaction and nucleotide alignment in a multiple gene analysis of *Ips* (Coleoptera: Scolytidae). *Systematic Biology*, 50, 758-80.
- Escherich, K. 1923. *Die Forstinsekten Mitteleuropas*. Vol. 2. Berlin: Parey Verlag.
- Fuchs, G. 1913. Forstzoologische Ergebnisse einer Sommerreise ins Engadin. *Naturwissenschaftliche Zeitschrift für Land- und Forstwirtschaft*, 11, 65-86.
- Führer, E. 1976. Fortpflanzungsphysiologische Unverträglichkeit beim Kupferstecher (*Pityogenes chalcographus* L.) - Ein neuer Ansatz zur Borkenkäferbekämpfung? *Forstarchiv*, 114-17.
- Führer, E. 1977. Studien über intraspezifische Inkompatibilität bei *Pityogenes chalcographus* L. (Col., Scolytidae). *Journal of Applied Entomology*, 83, 286-97.
- Führer, E. 1978. Rassendifferenzierung bei *Pityogenes chalcographus* (Col., Scolytidae). I. Morphologische Merkmale. *Journal of Applied Entomology*, 86, 392-402.
- Führer, E. 1980. Spermapolyploidie durch interpopuläre Bastardierung bei *Pityogenes chalcographus*. *Naturwissenschaften*, 67, 410.
- Führer, E. & Klipstein, E.L. 1980. Rassendifferenzierung bei *Pityogenes chalcographus* L. (Col., Scolytidae). III. Fertilität intraspezifischer F_1 -Bastarde. *Forstwissenschaftliches Centralblatt*, 99, 85-90.
- Gallego, D. & Galián, J. 2001. The internal transcribed spacers (ITS1 and ITS2) of the rDNA differentiates the bark beetle forest pests *Tomicus destruens* and *T. piniperda*. *Insect Molecular Biology*, 10, 415-20.
- Gasser, G. 2001. *Das Gradationsrisiko von Borkenkäfern in sekundären Fichtenbeständen im Lichte des genetisch-physiologisch bedingten Auftretens von Voltinismus-Typen beim Buchdrucker, Ips typographus*. Diploma-thesis, University of Natural Sciences & Applied Life Sciences.
- Gruppe, A. 1997. Isoenzymatische Variation beim Buchdrucker *Ips typographus*. *Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie*, 11, 659-62.
- Hösle, P. 2000. *Molekulare und ethologische Analyse der intraspezifischen Variation einer Population des Buchdruckers, Ips typographus*. Diploma-thesis, University of Natural Sciences & Applied Life Sciences.

- Jordal, B.H. 2002. Elongation factor 1 α resolves the monophyly of the haplodiploid ambrosia beetles Xyleborini (Coleoptera: Curculionidae). *Insect Molecular Biology*, 11, 453-66.
- Keller, I. & Largadièr, C.R. 2001. Identification of one X-linked and five autosomal microsatellite loci in *Carabus violaceus* (Coleoptera, Carabidae) and their applicability to related taxa. *Molecular Ecology*, 2, 290-92.
- Kerdelhué, C., Mondor-Genson, G., Rasplus, J.Y., Robert, A. & Lieutier, F. 2003. Characterization of five microsatellite loci in the pine shoot beetle *Tomicus piniperda* L. (Coleoptera, Scolytidae). *Molecular Ecology Notes*, 3, 100-01.
- Kerdelhué, C., Roux-Morabito, G., Forichon, J., Chambon, J.M., Robert, A. & Lieutier, F. 2002. Population genetic structure of *Tomicus piniperda* L. (Curculionidae, Scolytinae) of different pine species and validation of *Tomicus destruens* (Woll.). *Molecular Ecology*, 11, 483-94.
- Kirkendall, L.R. 1983. The evolution of mating systems in bark and ambrosia beetles (Coleoptera, Scolytidae and Platypodidae). *Zoological Journal of the Linnean Society*, 77, 293-352.
- Kohlmayr, B., Riegler, M., Wegensteiner, R. & Stauffer, C. 2002. Morphological and genetic identification of the three pine pests of the genus *Tomicus* (Coleoptera, Scolytidae) in Europe. *Agricultural and Forest Entomology*, 4, 151-57.
- Leitinger, R. & Schreiber, J.D. 1992. Populationsgenetische Untersuchungen an *Ips typographus* L. (Coleoptera, Scolytidae) unter biogeographischen Aspekten. *Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie*, 8, 348-52.
- Niijima, Y. 1909. The scolytids of Hokkaido. *Tohoku Imperial University of Sapporo. Journal of Coll. Agric.*, 3/2, 109-79.
- Nobuchi, A. 1969. A comparative morphological study of the proventriculus in the adult of the superfamily Scolytoidea (Coleoptera). *Japan, Government Forest Experiment Station, Bulletin*, 224, 39-110.
- Normark, B.B., Jordal, B.H. & Farrell, B.D. 1999. Origin of a haplodiploid beetle lineage. *Proceedings of the Royal Society London, Series B*, 266, 2253-59.
- Pavlíček, T., Žurovcová, M. & Starý, P. 1997. Geographic population-genetic divergence of the Norway spruce bark beetle, *Ips typographus* in the Czech Republic. *Biologia, Bratislava*, 52, 273-79.
- Pavlová, E. 2000. *Isolation and characterization of the G6PDH gene and nine microsatelite sequences of the bark spruce beetle, Ips typographus L.* Master thesis, University of South Bohemia, České Budějovice.
- Perny, B. 1991. *Populationgenetisch Untersuchungen bei diapausierenden und nicht diapausierenden Käfern von Ips typographus aus zwei verschiedenen Höhenlagen*. Diploma-thesis, University of Natural Resources & Life Sciences.
- Pfeffer, A. 1994. *Zentral- und westpaläarktische Borken- und Kernkäfer (Coleoptera: Scolytidae, Platypodidae)*. Pro Entomologia, c/o Naturhistorisches Museum Basel.
- Ritzengruber, O. 1990. Isoenzymanalyse verschiedener *Pityogenes chalcographus* L (Col., Scolytidae) II Populationsstruktur, Populationsdifferenzierung. *Journal of Applied Entomology*, 55, 55-63.
- Ritzerow, S., Konrad, H. & Stauffer, C. 2003. Phylogeographic analysis of European *Tomicus piniperda* (Coleoptera: Scolytinae) populations. *Molecular Ecology*, submitted.
- Sallé, A., Kerdelhué, C., Breton, M. & Lieutier, F. 2003. Characterization of microsatellite loci in the spruce bark beetle *Ips typographus* (Coleoptera: Scolytinae). *Molecular Ecology Notes*, in press.
- Schedl, K.E. 1932. Scolytidae, Platypodidae. In. *Catalogus Coleopterorum Regionis Palaearctica*, A. Winkler (Ed.) Wien: Eigenverlag.
- Stauffer, C. 1994. *Ecological aspects of genetic and physiological variation of Ips typographus L. (Col., Scolytidae)*. Doctoral thesis, University of Natural Resources & Life Sciences.
- Stauffer, C. 1998. *Ecological genetics in scolytid species*. Habilitation thesis, University of Natural Resources & Life Sciences.
- Stauffer, C., Kirisits, T., Nussbaumer, C., Pavlin, R. & Wingfield, M.J. 2001. Phylogenetic relationships between the European and Asian eight spined larch bark beetle populations (Coleoptera, Scolytidae) inferred from DNA sequence and fungal associates. *European Journal of Entomology*, 98, 99-105.
- Stauffer, C., Lakatos, F. & Hewitt, G. 1997. Phylogenetic relationships of the bark beetle species of the genus *Ips* DeGeer. *Insect Molecular Biology*, 6, 233-40.
- Stauffer, C., Lakatos, F. & Hewitt, G.M. 1999. Phylogeography and postglacial colonization routes of *Ips typographus* (Col., Scolytidae). *Molecular Ecology*, 8, 763-74.
- Stauffer, C., Leitinger, R., Simsek, Z., Schreiber, J. & Führer, E. 1992. Allozyme polymorphism of nine Austrian *Ips typographus* populations. *Journal of Applied Entomology* 114, 17-25.

- Stauffer, C. & Zuber, M. 1998. *Ips amitinus* var. *montana* (Col., Scolytidae) is synonymous to *Ips amitinus*: a morphological, behavioural and genetic re-examination. Biochemical Systematics and Ecology, 2, 171-83.
- Stürjes, H.J. & Führer, E. 1979. Rassendifferenzierung bei *Pityogenes chalcographus* L. (Col., Scolytidae) II. Partnerdiskriminierung bei der Paarung. Allgemeine Forst- und Jagdzeitung, 150, 99-101.
- Tautz, D., Arctander, P., Minelli, A., Thomas, R.H. & Vogler, A.P. 2003. A plea for DNA taxonomy. Trends in Ecology and Evolution, 18, 70-74.
- Viktorinová, I. 1999. *Allozyme analysis of European populations of the bark spruce beetle, Ips typographus L.*. Bachelor thesis, University of South Bohemia, České Budějovice.
- Viktorinová, I. 2001. *The α-amylase gene as a potential molecular marker for Ips typographus, L. populations*. Master thesis, University of South Bohemia, České Budějovice.
- Wood S.L. & Bright D.E. 1992. *A Catalog of Scolytidae and Platypodidae (Coleoptera), Part 2: Taxonomic Index*. Great Basin Naturalist Memoirs (13). Utah: Brigham Young University.
- Wood, S.L. 1982. *The Bark and Ambrosia Beetles of North America (Coleoptera: Scolytidae): A Taxonomic Monograph*. Great Basin Naturalist Memoirs, No 6, Brigham Young University.

Chapter 7

GENERAL BIOLOGY OF BARK BEETLES

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1. INTRODUCTION

Bark and ambrosia beetles are a small group of insects from the huge Coleoptera family Curculionidae (they were formerly separated in the families Scolytidae and Platypodidae). They are small endophytic beetles, living inside plant tissues during their whole life except short periods of their imaginal stage. The bark beetles generally live inside and consume phloem, a thin but nutritious tissue between outer bark and wood, while ambrosia beetles live inside wood and feed on symbiotic fungi. This group includes some of the most injurious insects for trees, especially the tree-killing bark beetles, so-called because the death of their host tree is normally necessary to the success of their reproduction (Grégoire and Evans, chapter 4). Bark and ambrosia beetles are particularly damaging for conifers. It is the most important group of the European BAWBILT, including alone half of the recorded species. Most of them are bark beetles, so this term will be used in the following to refer to all bark and ambrosia beetles.

Considering their economic importance, bark beetles have been the subject of many studies since the beginning of forest entomology (Ratzeburg 1839; Escherich 1923; Schwenke 1974), and a large part of them is concerned with their general biology. These studies mainly deal with species considered as the most injurious. Forty-seven BAWBILT bark beetle species are recorded in Europe, but one fifth of the related studies deals with *Ips typographus*, half of them deals with only six species (*I. typographus*, *Dendroctonus micans*, the species complex *Tomicus piniperda* / *T. destruens*, *Pityogenes chalcographus* and *Trypodendron lineatum*) and three quarters deals with only twelve species (the previous ones plus *Scolytus scolytus*, *Ips sexdentatus*, *S. multistriatus*, *I. amitinus*, *Tomicus minor* and *I. acuminatus*). On the other hand, very few studies deal with the biology of half of the European BAWBILT bark beetles. Consequently, knowledge about bark beetle biology varies greatly according to species. The main traits are generally known for

all of them, but details only for a few. So it is often necessary to extrapolate from the well-known European species or from closely related species living in other part of the world, mainly in North America where similar species exist.

The majority of European bark beetle species does not belong to BAWBILT. They generally live on dead trees or branches. Their biology, often poorly known, appears similar to BAWBILT species, but their particular features will not be taken into account in this paper. Research about bark beetles is a world process, and similar studies have often been performed in different parts of the world. However, this review is centred on European studies, so non-European results will be cited only if they differ from European ones or if there is no European equivalent.

2. LIFE CYCLE

2.1. Standard bark beetle life cycle and particularities

Life cycle description has been the main subject of a large part of the publications about bark beetles since the beginning of forest entomology. Their main features are well known and consistent, at least for the most important species (Chararas 1962), allowing a synthetic description of the life cycles.

A bark beetle life cycle is organised at each generation around a basic cycle with three phases: reproduction, development, maturation and dispersal (Fig. 1). Each of these phases could present different characteristics, leading to a rather large variability of life cycles among these species. Furthermore, the basic cycle could be repeated one or several times a year and interrupted by overwintering.

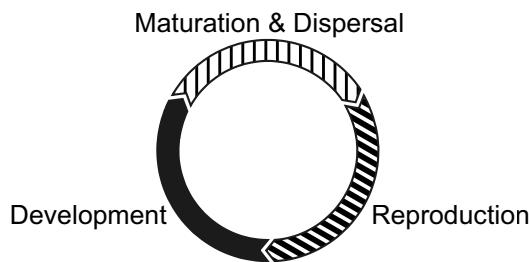


Figure 1. Basic bark beetle life cycle. Hatching density indicates the proportion of each phase which is endophytic.

2.1.1. Reproduction phase

The reproduction phase begins when mature insects arrive on their host tree. The choice of this tree is discussed elsewhere in this book (Byers, chapter 8; Lieutier, chapter 9). Most species are aggregative, a large number of adults arriving on the host tree in few hours or days. This behaviour helps meetings between males and females. It is generally controlled by pheromones and more rarely by primary attractants. In some species, such as *Dendroctonus micans*, each insect attacks the host tree alone. The tree choice mechanism is poorly known in this case.

Mating generally occurs on the host tree. In polygamous species (*Ips*, *Pityogenes*), the male arrives first and bores an entrance hole and a mating chamber in the phloem where it waits for females. The sex ratio during reproduction varies from 1 to 4 or more females per male depending on species and local conditions (Kirkendall 1983). On the other hand in monogamous species (*Scolytus*, *Trypodendron*, *Tomicus*) the female arrives first and bores the entrance hole and the beginning of a gallery where the male joins it. *Platypus*, whose males initiate galleries, is a notable exception (Kirkendall 1983). The sex ratio during reproduction is equilibrated in these species.

The mating behaviour have been described in several species (Chararas 1962; Paynter *et al.* 1990). Males and females recognise themselves using a combination of semiochemical and sonic stimuli, but this sequence have been mainly described in north American species (Rudinsky and Ryker 1977). Mating takes place on the bark or in the mating chamber, if it exists.

In some species like *Xyleborus dispar* or *Dendroctonus micans* males are not found during the reproduction phase. Mating takes place during maturation and dispersal phase (see below) and females alone bore the gallery.

After mating, if it occurs, the female (each of them in polygamous species) bores a breeding gallery. The male could help to clear away frass, but it does not take part in gallery boring. The pattern of this gallery is species specific. In phleophagous species it could be longitudinal (*Tomicus piniperda*, *Scolytus scolytus*), transverse (*Tomicus minor*, *Leperesinus varius*), radiating from the mating chamber (*Ips typographus*, *Pityophthorus pityographus*), circular (*Cryphalus piceae*), or irregular (*Dendroctonus micans*) (Fig. 2). Eggs are generally laid in the sides of the gallery, each in a small hole, but *D. micans* just lays an egg heap in the gallery. In xylomycetophagous species (*Trypodendron*, *Xyleborus*) the gallery drives straight in the wood where it is more or less branched. Egg heaps are laid in the branches.

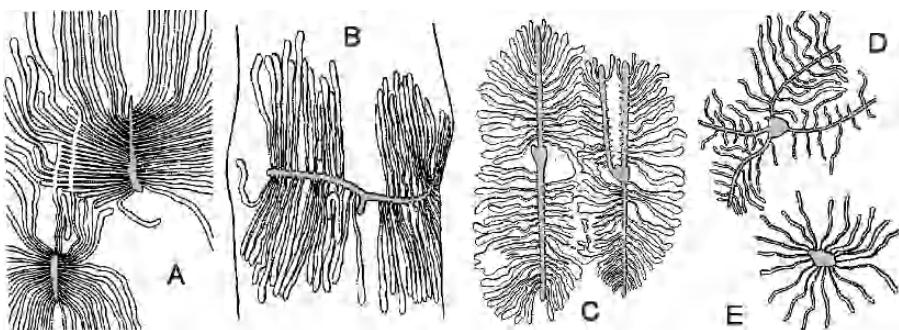


Figure 2. Examples of bark beetle gallery systems. Maternal galleries are in grey. A: *Scolytus scolytus*. B: *Leperesinus varius*. C: *Ips typographus*. D: *Pityophthorus pityographus*. E: *Cryphalus piceae*. From Balachowsky 1949, modified.

2.1.2. Development phase

The development phase is entirely endophytic. Larvae and pupae are unable to survive outside of the host tree. Post-embryonic development is similar in all species, with 3 to 5 larval stages and pupa, but larval behaviour varies, mainly between phloeophagous and xylomycetophagous species.

Larvae of phloeophagous species feed on phloem, generally boring individual galleries more or less perpendicular to the maternal gallery, together constituting a gallery system. The pattern of larval galleries is species specific but less variable than maternal ones (Fig. 2). The larvae moult in their gallery. Pupation takes place in little individual chambers bored by the old larvae in the phloem (*I. sexdentatus*) or in outer bark (*T. piniperda*). Some species have particular characteristics, such as *T. minor* whose old larvae feed on fungi which have invaded phloem (Långström 1983b). *D. micans* larvae have a very specific behaviour. They are gregarious, boring collectively from the egg chamber bored by the female. The cohesion of the group of larvae is assured by a specific pheromone (Grégoire *et al.* 1982; Storer *et al.* 1997).

Larvae of xylomycetophagous species remain inside the maternal gallery and generally do not bore wood. They feed on symbiotic fungi called Ambrosia. The fungus is inoculated by the female during gallery boring. It invades wood from where it extracts its nutrients. Larvae eat the mycelium and the fructifications which develop in the gallery. Pupation takes place in the gallery and young adults are contaminated by fungus when they move within it.

2.1.3. Maturation and dispersal phase

After the imaginal moult, bark beetles need a period of maturation before being able to reproduce. It allows the achievement of sclerotisation, the constitution of fully functional wing muscles and genitals, and the storage of energy reserves. The imagoes need to undertake a maturation feeding to achieve this maturation (Gries 1986).

In most species like *I. typographus* maturation takes place where development has taken place. Maturing beetles eat remaining phloem around the galleries (phloeophagous species) or symbiotic fungus (xylomycetophagous species). When mature, adults emerge from the brood material using the maternal entrance hole, any other hole in the bark, or if necessary by perforating it. They immediately search a suitable host for reproduction. In these species maturation and dispersal are clearly separated, and only one flight, named the swarming flight, occurs during the basic life cycle.

In some species however, maturation does not take place in the brood material but in the crown of healthy trees. *Tomicus* species bore axial maturation galleries in the pine shoots (Långström 1983a; Fig. 3), while *S. multistriatus* and *S. scolytus* feed on elm crown and particularly buds. Furthermore, beetles can change shoot or tree several times during maturation, especially when the attacked shoot dries out. In these species maturation and dispersal are then mixed. Their basic cycle presents two main flights, an emergence flight after emergence and a swarming flight before reproduction, and some minor flights could occur between them. Maturation feeding in the crown of healthy trees could weaken them due to shoot destruction or

pathogen inoculation, and could thus predispose these trees to subsequent reproductive attacks as observed with the Dutch elm disease (Kirisits, chapter 10).



Figure 3. Shoot damage on Scots pine due to maturation feeding of *Tomicus piniperda* (Photo F. Lieutier).

Mating could occur during the maturation and dispersal phase. In species normally mating during their reproduction phase, it has sometimes been observed that a fraction of adults have mated before the beginning of this phase (Janin and Lieutier 1988, for *T. piniperda*). But in some species mating normally occurs during the maturation phase. *D. micans* and *X. dispar* siblings mate in their breeding material before their emergence. The females then emerge and search for a host tree for reproduction. The males' future is poorly known. They seem to die rapidly but they might also search for other females at least in other broods on the same tree.

2.1.4. Succession of generation and overwintering

Most species go through several successive basic life cycles while climatic conditions are favourable. They generally have one generation a year in northern Europe and two in central Europe, sometimes more in southern Europe or during the warmest years. The *Tomicus* species differ from the others because they are strictly monovoltine. *T. destruens* is also the only species to reproduce during autumn instead of spring and summer. *D. micans* is another exception. It presents about one generation each 18 months, and individuals are poorly synchronised, so all stages could be encountered in all seasons, depending on the year (Vouland and Schwester 1994).

The succession of basic life cycles is complicated by the existence of one or several sister broods. During the reproduction phase females which have bored a maternal gallery could re-emerge and establish a new maternal gallery where they lay new eggs. This new gallery could be bored in the same tree, or in a new one. Males are not necessary (Sauvard 1993). Females feed in the gallery before re-emergence to regenerate wing muscles. Females from species maturing in the crown could also undertake new maturation feeding in this place (Salonen 1973). The sister broods have often been confused with real generations established by female offspring, leading to mistakes in determining the number of generations a year.

Bark beetles overwinter as imagoes during the maturation and dispersal phase. Larvae seem generally not able to survive during the cold season, except for *D. micans* which could overwinter at all stages. Most species overwinter in their breeding material, waiting for spring to emerge. A part of the beetle population could also overwinter in specific irregular feeding galleries bored during autumn. On the other hand, some species have particular overwintering places. *I. typographus* (Biermann 1977; Botterweg 1982; Austara *et al.* 1993) and *T. minor* (Bakke 1968) thus partly overwinter in the forest litter around the tree where they have developed. *T. piniperda* beetles have the most complex behaviour. In northern and central Europe they mainly overwinter in small galleries bored in the bark of a healthy tree collar (Salonen 1973). In southern Europe they mainly overwinter, as do *T. destruens*, in the pine shoots where they mature, these shoots being on trees or fallen on the litter (Salonen 1973). *T. minor* seems to have similar geographic variation (Fernandez Fernandez and Pajares Alonso 1999).

The longevity of bark beetle imagoes is some months, nearly one year for the overwintering generations. When they have bred, parent bark beetles usually seem not able to survive to winter (Austara and Midgaard 1986), but some authors have observed this possibility in experimental conditions (Schroeder and Risberg 1989).

2.2. Life cycle variability and regulation

Bark beetle life cycles could vary according external conditions. Most studies are related to temperature effects. As poikilotherms, bark beetles are sensitive to temperature. Its effect on reproduction and development has been extensively studied (Bakke 1968; Annila 1969; Saaremaa 1985). The development is generally stopped under 5 to 10°C and its rate increases rapidly up to 25 to 30°C, and then decreases until lethal temperatures at around 35 to 40°C (Fig. 4). These temperatures vary according to species, often in accordance with their latitudinal distribution. Gallery construction and oviposition rate on one hand and pre-emergence maturation rate on the other hand vary similarly with temperature.

Flight period is also sensitive to temperature. Each species has a temperature threshold under which flight initiation is inhibited, for example 12°C for *T. piniperda* and 18°C for *I. typographus*, and above it flight activity increases with temperature. Contrary to endophytic process, flight is also clearly dependent on other external conditions. Bark beetles fly only during the day (Salonen 1973;

Lanne *et al.* 1987; Byers and Löfqvist 1989). Their flight activity is favoured by high luminosity (Franklin and Grégoire 1999) and inhibited by rain and strong wind. Combined with the temperature effect, this explains why bark beetles primarily fly during sunny days without wind, and in early afternoon (Bakke 1968; Annila 1969; Salonen 1973).

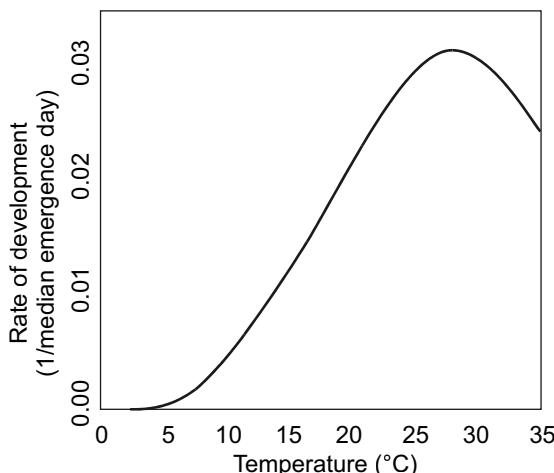


Figure 4. Influence of temperature on the development rate of *Tomicus piniperda*. From Saarenmaa 1985, modified.

Species precocity is mainly determined by the flight temperature threshold, low values of which allow beetles to fly earlier in the spring. However, maturity of the overwintering beetles also influences precocity. In some species such as *T. piniperda* the overwintering adults have finished their maturation, so they can swarm as soon as temperature increases beyond the flight temperature threshold. This reinforces the effect of the low flight temperature threshold for *T. piniperda*, so that this species is the most precocious European bark beetle. On the other hand, most species have not finished their maturation at the end of the winter. They must achieve it before swarming, so this does generally not occur the first time the flight temperature threshold is reached.

In autumn, bark beetles cease reproduction activity in order to overwinter. Factors inducing this behaviour have not been frequently studied. When overwintering occurs in a particular location, the movement from brood material to this location seems to be induced by the first occurrence of low temperature (Annila 1969 for *I. typographus*; Salonen 1973, Långström 1983a for *T. piniperda*). In other species, inhibition of emergence could similarly be due to low temperature, but photoperiod seems also to be involved, as for *P. chalcographus*. In this species short photoperiods inhibit emergence, but high temperatures suppress this effect (Führer and Chen 1979).

Temperature effects largely control bark beetle life cycles, especially the number of generations a year. High temperature allows fast oviposition, development and

maturity, thus a short generation time, as well as earlier swarming in the spring. A larger number of generations could thus be completed during a favourable season. This explains why most bark beetle species complete one generation a year in the northern part of their distribution area and two or more in its southern part. This could also partly determine the geographic distribution of some bark beetles. The low frequency of *I. sexdentatus* and *I. acuminatus* in southern Scandinavia could be explained by temperature conditions that allow the beginning of a second generation which cannot be achieved before the winter, leading to dramatic mortality (Bakke 1968).

The *Tomicus* species are exceptions. *T. piniperda* and *T. minor* are always monovoltine, while, if they can achieve one generation a year near to the polar circle, temperature conditions in southern Europe are certainly sufficient for at least a second generation. There is then certainly a factor inhibiting reproduction of young imagoes in the summer. Photoperiod or the necessity of low temperature to achieve maturation could be involved in this regulation but this aspect has not been studied. Similarly, the factor inducing *T. destruens* reproduction in the autumn remains unknown.

Synchronisation of bark beetle individuals is important for their reproduction, especially for aggregative species for which only simultaneous attack of a large number of insects could be successful. The temperature effect on reproduction and development could not allow this synchronisation because temperature greatly varies between beetle location (exposure, shade, position on the tree). Cold winter temperatures are certainly an important factor. They destroy the developing broods, thus eliminating the most divergent individuals. This effect is, however, less effective in southern Europe or on species such as *D. micans* which could overwinter as larvae. Moreover, its cost for species is high, so most species have probably developed other regulation systems to avoid the possibility that some hot days in autumn will lead to dramatic mortality. Cold winter temperatures are probably also the main synchronising factor in northern and central Europe for species such as *T. piniperda* for which all individuals are mature during overwintering and wait in quiescence for the first fair days to swarm. However, they could hardly explain synchronisation of individuals in southern Europe or in species which achieve maturation during spring. These different factors could thus partly explain individual synchronisation, each factor being more or less important depending on species, but they cannot explain all observations. There is probably another mechanism to synchronise swarming, but this aspect has not really been studied.

2.3. Concluding remark

Many studies have been done on European bark beetle life cycles, but the choice of their focus is unbalanced. A lot of them are descriptions of the cycle in a particular region, especially swarming dates. If these results are useful for pest management, as in further research, they give few insights into cycle regulation and are hardly transferable to other regions. Progress in the comprehension of life cycles of the

most common species needs detailed studies on the effects of the different factors, including temperature but also other factors such as photoperiod, and their interactions. This could lead to models applicable in large areas of Europe.

3. DISTRIBUTION AND HOST RANGE

3.1. Distribution

The distribution of bark beetles could be described at three levels: within a tree, within a forest or forest region, and within a continent. The biogeography of bark beetles is discussed elsewhere in this book (Knížek and Beaver, chapter 5; Stauffer, chapter 6). Within-tree and within-forest distributions present completely different patterns.

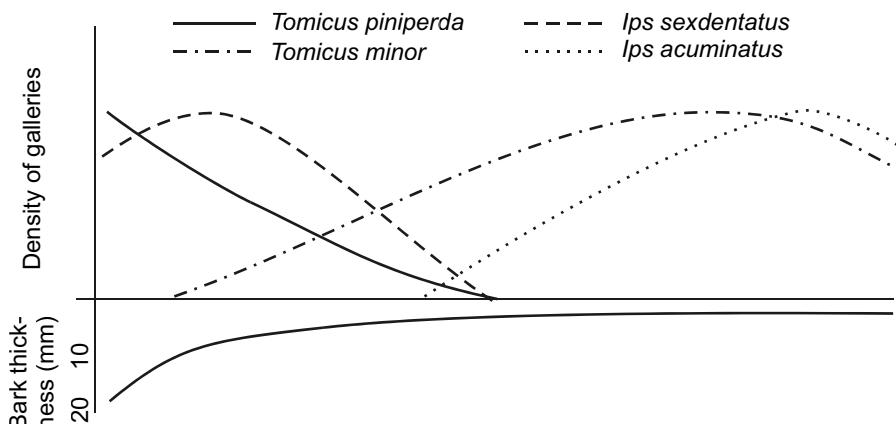


Figure 5. Schematic illustration of within-tree distribution of bark beetle galleries on pine stems, in relation to bark thickness. From Bakke 1968, modified.

The main features of within-tree distribution have been known for a long time, but in contrast to the north American situation, this has only been extensively studied in a few species, especially *T. piniperda*. Most species attack the bole or main branches. Attack distribution is organised around the gradient from the base to the top of the bole (Fig. 5). Attack density is maximal near the bole base, regularly decreasing towards its top, and becoming negligible above a certain height (Bakke 1968; Nilssen 1978; Saarenmaa 1983; Bouhot *et al.* 1988). This distribution is correlated with the bark thickness (Saarenmaa 1983), but other possible factors have been poorly studied. When boles are laid on the ground, beetle distribution also varies between the upper and lower side, probably according to beetle thermal preference (Bouhot *et al.* 1988). Inside a tree section, attack distribution is regular (Nilssen 1978; Schlyter and Löfqvist 1990), which is interpreted as resulting from beetle optimal spacing behaviour (De Jong and Sabelis 1988). This distribution could however vary among trees. It could particularly be disturbed by bole crossing,

inter-specific competition or irregular sunlight (Bouhot *et al.* 1988; Jakus 1998). It also become irregular, with attacked patches, when attack density is low. Attack distribution could be constant (*T. piniperda*) or change (*I. sexdentatus*) during the attack sequence (Bouhot *et al.* 1988). The latter seems to be related to the existence of aggregation and anti-aggregation pheromones. Aggregation pheromone first concentrates attacks on one part of the tree and then, when critical density is reached, anti-aggregation pheromone shifts them to other parts of the tree.

Some species such as *I. acuminatus* or *P. chalcographus* attack the upper part of the bole and the branches (Fig. 5). Some data is available on their distribution in the bole (Bakke 1968), but their distribution in the branches seems have not to have been studied, perhaps because this part of the tree is more irregular than bole.

Within-tree distribution has also been studied during the maturation phase, when it occurs in the tree crown. The beetles use the whole crown but generally prefer its upper part (Riedl 1973, for *S. multistriatus*; Långström 1980, 1983a for *T. piniperda*).

In contrast to within-tree distribution, within-forest distribution of bark beetles is highly aggregative. All beetles are concentrated in a small number of trees, isolated or in small patches, or in another scattered sites such as logs or logging residues, all of them changing at each beetle generation. Such a distribution is difficult and expensive to describe, and has rarely been studied. Some data however exist on the distribution of *I. typographus* during outbreaks in central Europe (Jakus *et al.* 2003). Gilbert (2001) also demonstrated that trees attacked by the solitary species *D. micans* are randomly distributed in a forest plot, and beetles frequently attack the same trees during several years.

The distribution of beetles which mature in the crown is a very special case. It is rather continuous and thus much easier to study. It has been demonstrated that *T. piniperda* is distributed with decreasing density in a circle about 1 kilometre around its main reproduction sites (Sauvard *et al.* 1987; Långström and Hellqvist 1990).

To get round the difficulty of within-forest bark beetle distribution, some studies have analysed this distribution at a larger scale. These recent studies, based on spatial analyses, allowed the determination of different site characteristics, such as tree age and density, altitude and slope, and forest structure, which are correlated to bark beetle density (Gilbert 2001; Jakus *et al.* 2003; Netherer 2003).

3.2. Host range

European bark beetle host range has been known for a long time (Balachowsky 1949; Chararas 1962). Most phloeophagous species are normally specific to one tree genus (*I. typographus*, *D. micans* and *P. chalcographus* on *Picea*, *I. acuminatus* and *Tomicus* species on *Pinus*, *S. multistriatus* and *S. scolytus* on *Ulmus*...). Only some species attack trees from closely related genus, such as *Phloeosinus bicolor* on different Cupressaceae (*Cupressus*, *Juniperus*). Besides their usual hosts, they have adaptation capabilities. Most of them have been accidentally observed and can develop experimentally (Chararas 1973; Wainhouse and Beech-Garwood 1994) on a rather wide variety of hosts. Their specificity is thus probably more related to beetle

choice behaviour, determined by the semiochemical content of the host (Byers, chapter 8), than to developmental constraints. Adaptation capabilities of these bark beetles allow them to attack different exotic trees, especially congeners of their usual host (Sitka spruce, exotic pines, exotic Cupressaceae such as *Thuja* for *P. bicolor*). They could allow southern species to attack new hosts in the north of their current geographic distribution following global climatic change.

Phloeomycetophagous species are more polyphagous, generally attacking different broadleaves (*Trypodendron domesticum*) or different conifers (*T. lineatum*). *Xyleborus dispar* is extremely polyphagous, attacking a wide range of broadleaves, including forest trees and fruit trees. This polyphagy could be due to their mycetophagy which reduces direct interactions between the insects and their hosts.

Bark beetle preference between different hosts has been poorly studied in Europe (Walker and Ross, 1975; Chararas *et al.* 1982; Lieutier *et al.* 1997). A possible reason is the low species richness of this continent where, in many regions, each of the main bark beetle species has only one natural usual host (such as Norway spruce for *I. typographus* and Scots pine for *I. sexdentatus* and *T. piniperda* in central and northern Europe). Knowledge about this preference would be useful in forest management, especially in multispecies pine forests in southern Europe. This need will probably increase with increasing area of non indigenous tree species in many European regions, and future change of insect and tree distribution following global climatic changes. Very few data is available on intraspecific variations of bark beetle preference.

4. DISPERSAL

Dispersal is an essential element of bark beetle biology. Except during outbreaks, bark beetles are generally unable to reproduce on healthy trees (Lieutier, chapter 9), and their reproduction usually entirely destroys the host tree, which is thus not available for their offspring. At each generation, they must then find rare suitable trees existing in the forest. As these trees are likely to be randomly distributed and their distribution widely changes from year to year, their location is generally unpredictable for the insects. Bark beetles have thus developed elaborate mechanisms to find their hosts, mainly based on use of semiochemicals and in most species on aggregation behaviour (D.L. Wood 1982). These mechanisms are discussed elsewhere in this book (Byers, chapter 8). The importance of bark beetle dispersal in their biology and in outbreak development has lead to several studies to estimate dispersal capacity in the laboratory and effective dispersal in the field.

Flight capacities have been studied in the laboratory for some species, using flight mills (Forsse 1989 and included review; Jactel 1993). The beetles are tethered on an arm which can freely turn round an axis. This method is well adapted to bark beetles (Forsse 1989). It places them in very artificial conditions, but allows the determination of maximum flight capabilities and their distribution in beetle populations.

These studies show that bark beetles have high flight capabilities with wide individual variations. Some individuals, 10 to 30%, seem unable to fly. This result could however partly be an artefact because beetles are generally tested only once, and beetles tested several times could fly on one day but not on another (Forsse and Solbreck 1985). On the other hand, numerous beetles are able to fly for one or several hours: a quarter of *I. sexdentatus* or *I. typographus* individuals fly for more than an hour, and up to four to six hours (Forsse and Solbreck 1985; Jactel 1993), and repeat this flight over several successive days (Forsse 1989). Excluding short flight (less than one minute), the distribution of flight capabilities among individuals is log-normal (Fig. 6). Flight speed is between 1 and 2 ms⁻¹, so a notable proportion of bark beetles populations can actively fly tens of kilometres.

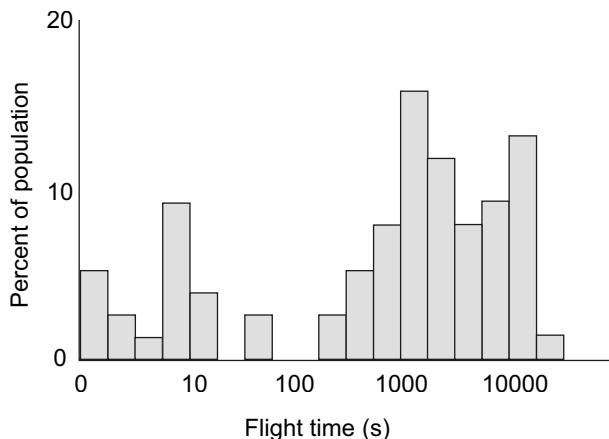


Figure 6. Distribution of flight duration of *Ips typographus* individuals ($N=76$). From Forsse and Solbreck 1985, modified.

Bark beetle effective dispersal in the forest is difficult to determine. It is impossible to follow them during their flight due to their small size and high speed, so this aspect has been studied using indirect methods. Most data are provided by mark-recapture experiments and capture of beetles outside their normal location. These methods give information on effective dispersal distance of the captured beetles, but no information about their flight behaviour. Mark-recapture experiments also give information about the distribution of effective dispersal inside the released population, but this must be carefully interpreted because only a small fraction of beetles is recaptured.

Mark recapture studies show that bark beetles can fly from a few meters to at least 1 to 4 kilometres (Botterweg 1982; Jactel 1991; Zumr 1992; Zolubas and Byers 1995; Duelli *et al.* 1997). The duration of flight is generally short: more than 80% of released *I. sexdentatus* are recaptured the same day (Jactel 1991). Longer dispersal is indicated by captures of bark beetles outside their normal location. Nilssen (1984) thus observed *I. typographus* more than 40 kilometres from the nearest forest, and some smaller bark beetles up to 150 kilometres from it. In that

case the beetles have probably been partly carried by wind. Other data on effective dispersal is given by the invasion of Finland by *I. amitinus* (Koponen 1980). The expansion of this species has been estimated to cover about 20 km a year, indicating that a large part of its population disperses to a distance of the same order.

In species with two flights such as *T. piniperda*, the emergence flight also contributes to dispersal. In this species, beetles seem to disperse about 1 kilometre around their brood trees during this flight (Sauvard *et al.* 1987).

Effective dispersal depends on availability of suitable host trees, but also on receptivity of the beetles to external stimuli. Most beetles are not receptive to tree or congener attractiveness at the beginning of their flight, and this receptivity increases during the flight. Such an increase is also observed with starvation, indicating it is probably due to decreasing energy reserves (Sanders 1983; Gries 1985; Jactel 1991). Interactions between flight and semiochemicals are discussed elsewhere in this book (Byers, chapter 8). High receptivity of re-emergent beetles to host stimuli seems to explain their low-range field dispersal (Anderbrandt 1985; Zolubas and Byers 1995)

Both laboratory and field experiments agree with high dispersal capabilities of all bark beetle species, over at least several kilometres. Flight duration is similar among populations from different locations and with different outbreak status (Forsse 1991), and the variability is mainly observed inside populations. Factors determining individual flight capabilities are unclear. Sex and size are not correlated with them (Botterweg 1982; Forsse and Solbreck 1985; Jactel 1993). The relation between fat content and flight duration is doubtful. Long flyers have higher fat content (Jactel 1993) and fat content decreases during dispersal (Botterweg 1982, Gries 1985), indicating that lipids are consumed as a result. However, the relation between individual fat content and flight duration is not significant (Botterweg 1982; Forsse and Solbreck 1985; Jactel 1993). Nematode parasitism also seems to have little influence on flight duration (Forsse 1987). It is possible that flight capabilities are mainly genetically determined.

Bark beetle behaviour during dispersal is poorly known. Some experiments indicate that they generally fly at low altitude, between 2 and 10 metres (Forsse and Solbreck 1985; Duelli *et al.* 1986). However, 5 to 15% of beetles fly above 20m, i.e. above the canopy, and could then be carried at long distance by wind. In the absence of host stimuli, flight direction seems mainly influenced by wind, most beetles flying with the wind (Helland *et al.* 1984; Jactel 1991). In contrast, they fly against the wind to locate a pheromone source. Flight direction is also influenced by light, the beetles preferring areas with high luminosity (Lobinger and Skatulla 1996).

5. REPRODUCTION

5.1. Reproduction mode

Bark beetle reproduction is usually classical sexual reproduction. Birth sex ratio is generally equilibrated in most phloeoecious species, even in polygamous ones such as *I. typographus* (Annala 1971). Sex ratio of these polygamous species shifts

in favour of females after emergence, perhaps due to higher male mortality but this point remains unclear. On the other hand, birth sex ratio is highly biased in some species such as *D. micans* and most of the xylomycetophagous species (*Xyleborus*, *Xylosandrus*, but not *Trypodendron*), with 1 male for 5 females or more. This unbalanced sex ratio is often associated with high sexual dimorphism with small and generally flightless males. Female excess is balanced by high rates of polygyny. The sex ratio control mechanism is unknown.

Parthenogenesis has been observed in some species, especially *I. acuminatus* (Kirkendall 1990). Its populations contain a highly variable proportion of pseudogamous females (from about 0 to more than 90%), resulting in a biased sex-ratio. These females are triploid. Their reproduction is clonal but needs mating.

Reproductive incompatibility between allopatric populations has been observed in *P. chalcographus* (Führer 1977). This phenomenon seems related to the existence of sperm polyploidy (Klipstein 1986).

5.2. Reproductive success

Due to its importance in population dynamics, bark beetle reproductive success has been studied intensively. It can be described by two parameters, beetle productivity and offspring quality. Beetle productivity is the number of emerging beetles per parent female. It results from female fecundity and brood survival. Bark beetle fecundity is generally high, about several tens of eggs per female gallery. Brood survival depends on natural enemies and host resistance (These aspects are discussed by Kenis *et al.*, chapter 11, Wegensteiner, chapter 12, and Lieutier, chapter 9), but generally it is mainly dependent on intraspecific competition, except in solitary species. Offspring quality is a synthetic parameter indicating the ability of the new generation of beetles to survive and reproduce (Wellington 1977; Sahota and Thomson 1979). It also depends on intraspecific competition.

The importance of intraspecific competition in bark beetle reproductive success results from their biology. Most of them are aggregative, a large number of attacks being necessary to their success on a living tree (Lieutier, chapter 9). The negative consequence of this strategy is the increase of intraspecific competition. In polygamous species, it also increases due to within-harem competition (Kirkendall 1989). Bark beetles have developed different adaptations to limit this competition. In most species an anti-aggregation process stops aggregation as soon as a sufficient attack density is reached (Byers, chapter 8). The effect of density is also reduced by the optimisation of spacing between gallery systems (see 3.1). Finally, increasing attack density induces an earlier re-emergence of the females and thus reduces their fecundity (Thalenhorst 1958; Ogibin 1973; Anderbrandt *et al.* 1985; Sauvard 1989) (Fig. 7). These adaptations are, however, unable to avoid an increase of larval density when attack density increases (Anderbrandt *et al.* 1985; Jactel and Lieutier 1987; Sauvard 1989), resulting in increasing larval mortality by starvation and perhaps cannibalism, even if larvae seem able to avoid each other (De Jong and Saarenmaa 1985; De Jong and Grijpma 1986). Globally, when attack density increases, the beetle productivity continuously decreases. The offspring number per

bark unit area first rapidly increases with egg number, then stabilises at an optimum and finally decreases due to dramatic larval mortality (Saarenmaa 1983; Sauvard 1989). Observed attack densities in the field often correspond to the optimum. At high density the population multiplication rate could decrease below the threshold of population replacement (Thalenhorst 1958; Anderbrandt *et al.* 1985).

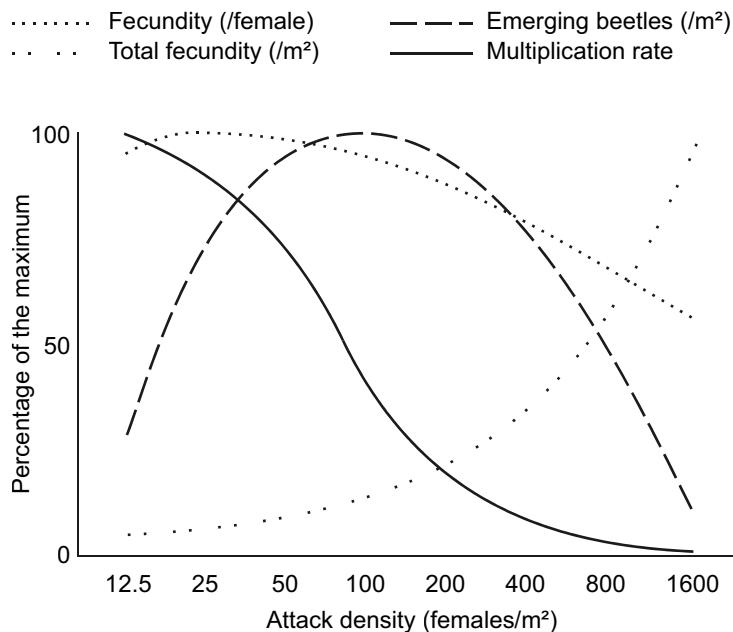


Figure 7. Influence of intraspecific competition on reproductive success of *Tomicus piniperda*. From data from Sauvard 1989.

Intraspecific competition also has a negative effect on offspring quality (Anderbrandt and Schlyter 1989). Increasing attack density results in decreasing beetle size, weight and fat content (Thalenhorst 1958; Botterweg 1983; Saarenmaa 1983; Anderbrandt *et al.* 1985). Moreover, small size and low fat content are correlated with low pheromone production (Birgersson *et al.* 1988) and low survival (Anderbrandt 1988), while, as indicated above, their effect on dispersal potential remains unclear. Finally, high attack density reduces the offspring reproductive success of *I. typographus* (Anderbrandt *et al.* 1985), but species with maturation outside of breeding sites, such as *T. piniperda*, could escape this effect (Sauvard 1989).

Determination of bark beetle reproductive success must take into account the existence of sister broods, but this aspect has been rarely studied. Sister brood fecundity and reproductive success are similar to those of first broods, and are not related to first brood conditions (Anderbrandt and Löfqvist 1988; Sauvard 1993). As high attack density induces early re-emergence, it allows females to devote less time to their first brood when this takes place under high competition, and thus to

optimise distribution of their eggs among different sites (Anderbrandt 1988b). Early re-emergence could also allow females to produce more successive broods. From this point of view, sister broods could also be considered as a mechanism for reducing negative effects of intraspecific competition.

Many abiotic factors have been recorded as influencing bark beetle reproductive success, especially larval mortality: drought (Salonen 1973; Lieutier 1975), development temperature and high temperature reached under sunny bark (Annila 1969), rain and phloem decay (Sauvard 1989). However, their effects are poorly documented.

6. OVERWINTERING

Overwintering is a critical phase for insects in a temperate climate such as in Europe. Winter cold temperatures decrease or eliminate bark beetle feeding and dispersal capabilities, but the main risk is freezing. Bark beetles are not tolerant to freezing which kills them. They have thus developed behavioural and physiological adaptations to survive during winter.

Behavioural adaptations aim at avoiding the coldest temperatures. Most species overwinter in their breeding site where bark allows limited protection. Species with specific overwintering sites are much more protected. They overwinter in the litter or in the tree collar where temperature is much higher than in the air above, especially when snow, a good insulator, covers the ground (Bakke 1968). Snow could also protect beetles in logs or felled trees (Wermelinger 2000). Migration to the overwintering sites seems to be induced by the first occurrence of low temperature in the autumn (see 2.2). This allows these species to adapt their overwintering site to local temperature: breeding or maturation sites in southern Europe, litter and tree collar in northern Europe.

As a physiological adaptation, bark beetles have developed supercooling capabilities, being able to tolerate negative temperature up to -15 to -30°C without freezing (Bakke 1968; Annila 1969). The cold-hardiness varies according to stage and season. It is generally low for larvae, medium for newly emerged imagoes and maximal in hibernating imagoes. It results from a physiological process during autumn. The beetles stop feeding, eliminate gut content, reduce their water content and accumulate in their haemolymph various supercooling substances such as trehalose, glycerol, ethylene glycol or antifreeze proteins (Barson 1974; Gehrken 1984, 1989, 1992, 1995; Hansen and Sømme 1994; Netherer 2003). Supercooling is dramatically reduced in the presence of water (Gehrken 1992), so optimal cold-hardiness needs a proper overwintering site.

Overwintering survival of bark beetles results of the combination of both behavioural and physiological adaptations, which vary according to species. In northern countries, some species such as *T. piniperda* survive with a rather high supercooling point (-18°C) owing to well-insulated overwintering sites (tree collar), while other species such as *I. acuminatus* overwinter in branches directly exposed to low temperature but have a low supercooling point (-33°C) (Bakke 1968).

7. ANATOMY AND PHYSIOLOGY

Bark beetle anatomy has been described for a long time (Balachowsky 1949; Chararas 1962), and rarely studied recently. It is similar to other coleopteran insects. Bark beetle physiology has also rarely been studied. Their small size, the difficulty of rearing them outside logs where they are poorly accessible, and the poor expected utility for forest management prevent such study. Among the more important physiological functions, only nutrition and reproduction seem to have been studied.

Bark beetles are able to digest a large variety of carbohydrates, including soluble ones, starch and some hemicelluloses, but not cellulose (Chararas 1983). Their digestion is helped by some micro-organisms such as yeasts which complement the insect enzymatic set and provide it with vitamins (Pignal *et al.* 1988). Precise nutrition requirements are unknown.

Reproductive physiology is characterised by maturation cycles, especially in females (Zumr and Soldán 1981; Långström 1983). Gonadal maturation begins during the maturation and dispersal phase but it is not completed before arrival in the breeding site. There, flight muscles and fat body regress while ovarioles develop (Lieutier 1982). The opposite process occurs at the end of oviposition, before female re-emergence. This cycle corresponds to nutrient transfer between flight muscles, fat body and ovarioles (Lieutier 1983). It is repeated for each sister brood.

Besides maturation cycles, bark beetles present seasonal variations of the concentration of different compounds, mainly energetic compounds such as fat or glycogen which are stored during autumn as supercooling compounds and used during winter (Botterweg 1982; Zumr *et al.* 1985; Krauße-Opatz *et al.* 1995). Some bark beetles also exhibit low oxygen consumption during autumn and the beginning of winter indicating a diapause (Gehrken 1985, with *I. acuminatus*; Netherer 2003, with *I. typographus*). The physiological control of these cycles is poorly known.

Sensorial organs and physiology, especially olfaction, and pheromone biosynthesis have been well studied in relation to host localisation process. Results are discussed elsewhere in this book (Byers, chapter 8).

8. POPULATION DYNAMICS AND OUTBREAK DETERMINATION

Population dynamics aims to describe and explain changes in population levels of a species. To succeed, it has to synthesise all traits of the species biology and to determine what are the key factors which explain these changes.

Most bark beetle species share many characters of their biology and population dynamics. They are aggregative beetles which irregularly present important outbreaks, classified as pulse eruptive (Thalenhorst 1958; Berryman 1987). Outbreaks generally extend from 5 to 7 years during which time many trees are killed (Bombosh 1954; Schroeder and Lindelöw 2002; Jakubš *et al.* 2003; Fig. 8). When beetles are installed on a tree, their reproductive success is mainly regulated by intraspecific competition, so offspring population level is determined by tree bark surface, and at a population level by the abundance of trees which are susceptible to be successfully attacked. This abundance is itself determined by the equilibrium

between population level and tree resistance, which is the key factor in bark beetle population dynamics. Each tree is able to contain beetle attacks up to an attack density threshold above which the tree dies, allowing beetle reproduction (Lieutier, chapter 9). This threshold depends on genetic and physiological factors.

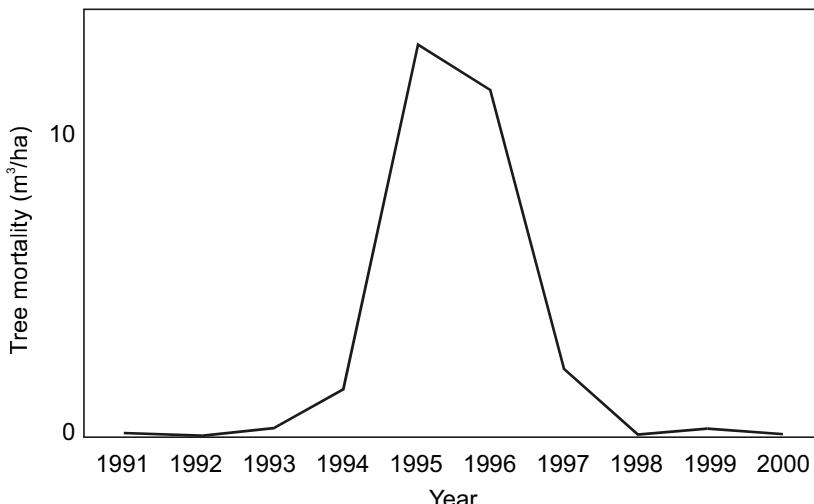


Figure 8. Intensity of *Ips typographus* outbreaks in the Slovak Tatra Mountains in 1991-2000.
From Jakuš *et al.* 2003, modified.

In endemic conditions, bark beetles are not numerous enough to kill healthy trees, so they reproduce on felled or dying ones and logging residues. These sites are too rare to allow population increase. An outbreak happens when a perturbation raises beetle population level and/or lowers tree resistance (Berryman 1982). This allows beetles to attack living trees and thus provides them a large amount of susceptible trees, inducing a positive feedback where population increase allows increase of available hosts, and then new population increase. This feedback induces a rapid increase of population level and a spread of the outbreak to neighbouring areas.

The event inducing an outbreak is generally a climatic accident, mostly storm but also fire, snow-break or severe drought, which provide breeding material to initiate beetle population increase. However, an outbreak generally develops only if there are helping factors reducing tree resistance, such as presence of old trees, storm-induced root damage, drought, defoliation or any other stress. An outbreak is also favoured by climatic conditions favourable to insect development such as high temperature.

Outbreak spreading has been mainly studied in central Europe, on *I. typographus* (Jakuš *et al.* 2003). During the progradation phase the outbreak mainly spreads by initiation of new attacked tree spots. These spots generally appear within some hundreds meters of an old one. On the contrary, during the culmination and retrogradation phases, the outbreak mainly spreads by further expansion from the

old spots. This behavioural change may be related to the gradual exhaustion of susceptible trees, which decreases the interest to search for them.

Outbreak decline generally happens when there are no more weakened trees due to their death or strengthening. Beetles must attack the remaining trees with a higher population density, which reduces their multiplication rate up to a point when they are unable to maintain the population level. This induces a negative feedback leading to its fast decrease. Bark beetle natural enemies or unfavourable climatic conditions could also be involved in outbreak decline, with varying degrees of importance (Kenis *et al.*, chapter 11; Wegensteiner, chapter 12).

Some species, especially the solitary species *D. micans*, do not correspond to this model of population dynamics (Grégoire 1988). Contrary to other species, *D. micans* is able to successfully attack trees without aggregation. Its population dynamics seem mainly to depend on its interactions with the specific predator *Rhizophagus grandis* (Kenis *et al.*, chapter 11). When the predator is present, it is able to maintain bark beetle population at a low level. Outbreaks occur when the bark beetle invades forests where the predator is missing, and they decline some years after when the prey is rejoined by its predator. So, as *D. micans* has gradually invaded Europe over the course of a century, outbreaks have been regularly observed on their invasive front. Population dynamics of xylomycetophagous species is poorly studied. It seems mainly to depend on the availability of suitable wood, but factors allowing attacks on living trees are unclear.

Bark beetle population dynamics are mainly viewed as interactions between beetle and its host, but these insects are also interacting with other organisms. Relationships with fungi and natural enemies are discussed elsewhere in this book (Kiritsits, chapter 10; Kenis *et al.*, chapter 11; Wegensteiner, chapter 12), but bark beetles also interact with other xylophagous insects. Interactions between bark beetles have been rarely studied in Europe. There are few species and they are generally rather well ecologically separated by host, within-tree distribution (bole vs. crown) or flight precocity (early-flyer species such as *T. piniperda* vs. late-flyer such as *I. sexdentatus*) (Grünwald 1986; Amezaga and Rodriguez 1998). Thus, if interspecific competition could occasionally occur and disturb their distribution (Bakke 1968; Schlyter and Anderbrandt 1993), it seems to be of low importance in their dynamics. Similarly, as bark beetles are generally the first xylophagous insects attacking a tree and they develop rapidly, they are rarely disturbed by other xylophagous insects. By comparison, their activity is an essential element of the constitution of the biotope of the xylophagous species which succeed them.

The theoretical model of aggregative bark beetle population dynamics has been mainly inferred from data obtained at a tree level, but it has not been really tested in the field, and it is difficult to use in forest management due to several difficulties. The first one is the lack of a good estimator of bark beetle populations. Due to their aggregative distribution, they are difficult and expensive to sample, and trapping is only moderately reliable due to its sensitivity to local conditions (Bakke and Strand 1981). The poorly defined but large area occupied by a bark beetle population, which is related to high dispersal capabilities of the beetles, increases this difficulty. Extensive sampling studies have been conducted in North America at tree, forest and regional level (Coulson, 1979), but they are adapted to epidemic populations

which are not encountered in the intensively-managed European forests. Most authors thus use damage level as population estimator, but it is not very precise due to the variability of attack density. The second difficulty is the complexity of the model itself, which depends on characteristics and reactions of three organisms, beetle, tree and generally associated fungi, some of which such as tree resistance are difficult to estimate. Finally, several parameters of population dynamics are poorly known, especially mortality during dispersal phases and the importance of sister broods in the field. The incidence of insect quality in population dynamics is also poorly understood.

The field test of this theoretical model and its application to forest management need to have verifiable predictions. Such predictions might be obtained by building a mathematical model of bark beetle population based on this theoretical model. As outbreaks are often induced by climatic accident, the model will not predict them. However it could be useful for hazard rating and for outbreak management by predicting future population level changes and consequences of different pest control options. Such a model will be complex, so it could only be built at a European level. It also must be modular to progressively integrate the different factors. Some characteristics of bark beetle populations have already been modelled (Saarenmaa 1983, 1985; Anderbrandt 1986), but they remain isolated. Modelling capabilities of bark beetle life cycles and dynamics are thus much lower in Europe than in North America (Coulson 1979; Fettig *et al.* 2001).

Another approach to bark beetle population dynamics has been recently developed, particularly resulting from the availability of new tools to manage space-time data (Geographic Information Systems, spatial analysis). These tools allow analysis of bark beetle epidemiology and are often associated with remote sensing (aerial and space imagery) as tool for mapping (Gilbert 2001; Otto and Schreiber 2001; Wichmann and Ravn 2001; Jakubš *et al.* 2003). They are also used to define outbreak hazard rating of different sites according to the characteristics of the station, the trees or the beetle population (Gilbert 2001; Netherer 2003). They could finally identify the most suitable sites for different bark beetle species (Jakubš 1995). Besides their direct interest for hazard rating, such results could reveal important factors in bark beetle population dynamics which have to be precisely studied. Such an approach would thus be complementary to bark beetle population modelling.

9. CONCLUSION

European bark beetles have been intensively studied for about two centuries. Even if their results are partially biased by their focus on a small number of highly damaging species, these studies have allowed a good comprehension of the life cycle and to lesser extent an understanding of the population dynamics of these insects. For a forest manager, their main features are 1) their cryptic behaviour, so their damage is often only visible after they have left trees, 2) their high dispersal capabilities, allowing extensive redistribution of their population at each generation, 3) their high reproduction capabilities, and consequently 4) their ability to develop sudden outbreaks, mainly in relation to climatic hazard. However, that does not

minimise their ecological role as a first step in forest regeneration, and the forest health problems that their attacks often highlight.

European research on bark beetles has suffered from the division of the research community on the basis of countries or languages, even though this problem is declining, notably as a result of European Union projects. This division has favoured duplication in different countries and redundant studies which are often difficult to synthesise. It could be an obstacle to future research. As the main features of the life cycles and dynamics of bark beetles are rather well known, future investigations would probably be progressively focussed on the interactions between different factors. Such complex research needs effective cooperation of several researchers with different specialities. Modelling might be a useful enabling approach for such studies.

10. REFERENCES

- Amezaga, I., & Rodriguez, M.A. 1998. Resource partitioning of four sympatric bark beetles depending on swarming dates and tree species. *Forest Ecology and Management*, 109, 127—35.
- Anderbrandt, O. 1985. Dispersal of reemerged spruce bark beetles, *Ips typographus* (Coleoptera, Scolytidae): a mark-recapture experiment. *Zeitschrift für Angewandte Entomologie*, 99, 21—25.
- Anderbrandt, O. 1986. A model for the temperature and density dependent reemergence of the bark beetle *Ips typographus*. *Entomologia Experimentalis et Applicata*, 40, 81—88.
- Anderbrandt, O. 1988a. Survival of parent and brood adult bark beetles, *Ips typographus*, in relation to size, lipid content and re-emergence or emergence day. *Physiological Entomology*, 13, 121—29.
- Anderbrandt, O. 1988b. Reproduction and competition in the spruce bark beetle *Ips typographus*. Thesis Lund University.
- Anderbrandt, O., & Löfqvist, J. 1988. Relation between first and second brood production in the bark beetle *Ips typographus* (Scolytidae). *Oikos*, 53, 357—65.
- Anderbrandt, O., & Schlyter, F. 1989. Causes and effects of individual quality in bark beetles. *Holarctic Ecology*, 12, 488—493.
- Anderbrandt, O., Schlyter, F., & Bergersson, G. 1985. Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus*. *Oikos*, 45, 89—98.
- Annila, E. 1969. Influence of temperature upon the development and voltinism of *Ips typographus* L. (Coleoptera, Scolytidae). *Annales Zoologici Fennici*, 6, 161—207.
- Annila, E. 1971. Sex ratio in *Ips typographus* L. (Col., Scolytidae). *Annales Entomologici Fennici*, 37, 7—14.
- Austarå, Ø., & Midtgård, F. 1986. On the longevity of *Ips typographus* L. adults. *Journal of Applied Entomology*, 102, 106—11.
- Austarå, Ø., Midtgård, F., & Sæther, T. 1993. Densities of hibernating *Ips typographus* in the forest litter around attacked and killed spruce trees, with records of spring emergence and flight patterns. *Meddelelser fra Skogforsk*, 46, 1—12.
- Bakke, A. 1968. Ecological studies on bark beetles (Coleoptera: Scolytidae) associated with Scots pine (*Pinus sylvestris* L.) in Norway with particular reference to the influence of temperature. *Meddelelser fra det Norske Skogforsøksvesen*, 83, 441—602.
- Bakke, A., & Strand, L. 1981. [In Norwegian] Pheromones and traps as part of an integrated control of the spruce bark beetles. Some results from a control program in Norway in 1979 and 1980. *Rapport fra det Norsk Institutt for Skogforskning*, 5, 1—39.
- Balachowsky, A. 1949. *Faune de France. 50. Coléoptères Scolytides*. Paris: Librairie de la Faculté des Sciences.
- Barson, G. 1974. Some effects of freezing temperatures on overwintering larvae of the large elm bark beetle (*Scolytus scolytus*). *Annals of Applied Biology*, 78, 219—24.
- Berryman, A.A. 1982. Population Dynamics of Bark Beetles. In: *Bark beetles of North American Conifers. A System for the Study of Evolutionary Ecology*, J.B. Mitton, K.B. Sturgeon (Eds.). Austin: University of Texas Press, 264—314.

- Berryman, A.A. 1987. The Theory and Classification of Outbreaks. In: *Insect Outbreaks*, P. Barbosa, J.C. Schultz (Eds.). San Diego: Academic Press, 3—30.
- Biermann, G.M. 1977. Zur Überwinterung des Buchdruckers, *Ips typographus* (L.), in der Bodenstreu (Col., Scolytidae). Zeitschrift für Angewandte Entomologie, 84, 59—74.
- Birgersson, G., Schlyter, F., Bergström, G., & Löfqvist, J. 1988. Individual variation in aggregation pheromone content of bark beetle *Ips typographus*. Journal of Chemical Ecology 14, 1737—61.
- Bombosch, S. 1954. Zur Epidemiologie des Buchdruckers (*Ips typographus* L.). In: *Die Große Borkenkäferkalamität in Südwestdeutschland 1944-51*, G. Wellenstein (Ed.). Ulm: Forstschutzstelle Südwest, Ringingen, Ebner, 239—83.
- Botterweg, P.F. 1982. Dispersal and flight behaviour of the spruce bark beetle *Ips typographus* in relation to sex, size, and fat content. Zeitschrift für Angewandte Entomologie, 94, 466—89.
- Botterweg, P.F. 1983. The effect of attack density on size, fat content and emergence of the spruce bark beetle *Ips typographus* L. Zeitschrift für Angewandte Entomologie, 96, 47—55.
- Bouhot, L., Lieutier, F., & Debouzie, D. 1988. Spatial and temporal distribution of attacks by *Tomicus piniperda* L. and *Ips sexdentatus* Boern. (Col., Scolytidae) on *Pinus sylvestris*. Journal of Applied Entomology, 106, 356—71.
- Byers, J.A., & Löfqvist, J. 1989. Flight initiation and survival in the bark beetle *Ips typographus* (Coleoptera: Scolytidae) during the spring dispersal. Holarctic Ecology, 12, 432—40.
- Chararas, C. 1962. *Scolytides des Conifères*. Paris: Paul Lechevalier.
- Chararas, C. 1973. Faculté d'adaptation d'*Orthotomicus erosus* Woll. à des conifères autres que ses essences hôtes habituelles. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, D, 276, 555—58.
- Chararas, C. 1983. Régime alimentaire et activités osidasiques des insectes xylophages. Bulletin de la Société Zoologique de France, 108, 389—97.
- Chararas, C., Revolon, C., Feinberg, M., & Ducauze, C. 1982. Preference of certain Scolytidae for different conifers. Journal of chemical Ecology, 8, 1093—1109.
- Coulson, R.N. 1979. Population dynamics of bark beetles. Annual Review of Entomology, 24, 417—47.
- De Jong, M.C.M., & Grijpma, P. 1986. Competition between larvae of *Ips typographus*. Entomologia Experimentalis et Applicata, 41, 121—33.
- De Jong, M.C.M., & Saarenmaa, H. 1983. A mechanistic simulation model for the movement and competition of bark beetle larvae (Coleoptera, Scolytidae). Ecological Modelling, 27, 109—38.
- De Jong, M.C.M., & Sabelis, M.W. 1988. How bark beetles avoid interference with squatters: an ESS for colonization by *Ips typographus*. Oikos, 51, 88—96.
- Duelli, P., Studer, M., & Näf, W. 1986. Der Borkenkäferflug außerhalb des Waldes. Zeitschrift für Angewandte Entomologie, 102, 139—48.
- Duelli, P., Zahradník, P., Knižek, M., & Kalinová, B. 1997. Migration in spruce bark beetles (*Ips typographus* L.) and the efficiency of pheromone traps. Journal of Applied Entomology, 121, 297—303.
- Escherich, K. 1923. *Die Forstinsekten Mitteleuropas. 2. Käfer*. Berlin: Paul Parey.
- Fernandez Fernandez, M.M., & Pajares Alonso, J.A. 1999. Shoot feeding and overwintering in the lesser pine shoot beetle *Tomicus minor* (Col., Scolytidae) in north-west Spain. Journal of Applied Entomology, 123, 321—27.
- Fettig, C.J., Fidgen, J., McClellan, Q.C., & Salom, S.M. 2001. *Sampling Methods for Forest and Shade Tree Insects of North America*. USDA Forest Service FHTET-2001-01.
- Forsse, E. 1987. Flight duration in *Ips typographus* L.: insensitivity to nematode infection. Journal of Applied Entomology, 104, 326—28.
- Forsse, E. 1989. Migration in bark beetles with special reference to the spruce bark beetle *Ips typographus*. Thesis Sveriges Lantbruksuniversitet, Uppsala.
- Forsse, E. 1991. Flight propensity and diapause incidence in five populations of the bark beetle *Ips typographus* in Scandinavia. Entomologia Experimentalis et Applicata, 61, 53—57.
- Forsse, E., & Solbreck C. 1985. Migration in the bark beetle *Ips typographus* L.: duration, timing and height of flight. Zeitschrift für Angewandte Entomologie, 100, 47—57.
- Franklin, A.J., & Grégoire, J.C. 1999. Flight behaviour of *Ips typographus* L. (Col., Scolytidae) in an environment without pheromones. Annals of Forest Science, 56, 591—98.
- Führer, E. 1977. Studien über intraspezifische Inkompatibilität bei *Pityogenes chalcographus* L. (Col., Scolytidae). Zeitschrift für Angewandte Entomologie, 83, 286—97.

- Führer, E., & Chen, Z.Y. 1979. Zum Einfluß von Photoperiode und Temperatur auf die Entwicklung des Kupferstechers, *Pityogenes chalcographus* L. (Col., Scolytidae). Forstwissenschaftliches Centralblatt, 98, 87—91.
- Gehrken, U. 1984. Winter survival of an adult bark beetle *Ips acuminatus* Gyll. Journal of Insect Physiology, 30, 421—29.
- Gehrken, U. 1985. Physiology of diapause in the adult bark beetle, *Ips acuminatus* Gyll., studied in relation to cold hardness. Journal of Insect Physiology, 31, 909—16.
- Gehrken, U. 1989. Supercooling and thermal hysteresis in the adult bark beetle, *Ips acuminatus* Gyll. Journal of Insect Physiology, 35, 347—52.
- Gehrken, U. 1992. Inoculative freezing and thermal hysteresis in the adult beetles *Ips acuminatus* and *Rhagium inquisitor*. Journal of Insect Physiology, 38, 519—24.
- Gehrken, U. 1995. Correlative influence of gut appearance, water content and thermal hysteresis on whole body supercooling point of adult bark beetles, *Ips acuminatus*. Comparative Biochemistry and Physiology. A: Physiology, 112, 207—14.
- Gilbert, M. 2001. Spatial Ecology of *Dendroctonus micans* (Kug.) (Coleoptera: Scolytidae). Thesis Université Libre de Bruxelles.
- Grégoire, J.C. 1988. The Greater European Spruce Beetle. In: *Dynamics of Forest Insect Populations*, A.A. Berryman (Ed.). New York: Plenum Press, 455—78.
- Grégoire, J.C., Braekman, J.C., & Tondeur, A. 1982. Chemical Communication between the Larvae of *Dendroctonus micans* Kug. (Coleoptera, Scolytidae). In: *Les médiateurs chimiques agissant sur le comportement des insectes. Symposium international. Versailles, 16-20 novembre 1981*. Paris: Institut National de la Recherche Agronomique, 253—57.
- Gries, G. 1985. Zur Frage des Dispersion des Buchdruckers (*Ips typographus* L.). Zeitschrift für Angewandte Entomologie, 99, 12—20.
- Gries, G. 1986. Zur Bedeutung des Reifungsfrasses für die Dispersion des Kupferstechers, *Pityogenes chalcographus* L., (Coleoptera: Scolytidae). Zeitschrift für Angewandte Zoologie, 73, 267—79.
- Grünwald, M. 1986. Ecological segregation of bark beetles (Coleoptera, Scolytidae) of spruce. Journal of Applied Entomology, 101, 176—87.
- Hansen, L.O., & Sømme, L. 1994. Cold hardness of the elm bark beetle *Scolytus laevis* Chapuis, 1873 (Col., Scolytidae) and its potential as Dutch elm disease vector in the northernmost elm forests of Europe. Journal of Applied Entomology, 117, 444—50.
- Holland, I.S., Hoff, J.M., & Anderbrandt, O. 1984. Attraction of bark beetles (Scolytidae) to a pheromone trap. Journal of Chemical Ecology, 10, 723—52.
- Jactel, H. 1991. Dispersal and flight behaviour of *Ips sexdentatus* (Coleoptera: Scolytidae) in pine forest. Annales des Sciences Forestières, 48, 417—28.
- Jactel, H. 1993. Individual variability of the flight potential of *Ips sexdentatus* Boern. (Coleoptera: Scolytidae) in relation to day of emergence, sex, size, and lipid content. The Canadian Entomologist, 125, 919—30.
- Jactel, H., & Lieutier, F. 1987. Effects of attack density on fecundity of the scots pine beetle *Ips sexdentatus* Boern (Col.; Scolytidae). Zeitschrift für Angewandte Entomologie, 104, 190—204.
- Jakuš, R. 1995. Bark beetle (Col., Scolytidae) communities and host and site factors on tree level in Norway spruce primeval natural forest. Journal of Applied Entomology, 119, 643—51.
- Jakuš, R. 1998. Patch level variation on bark beetle attack (Col., Scolytidae) on snapped and uprooted trees in Norway spruce primeval natural forest in endemic condition: effects of host and insolation. Journal of Applied Entomology, 122, 409—21.
- Jakuš, R., Grodzki, W., Jezík, M., & Jachym, M. 2003. Definition of Spatial Patterns of Bark Beetle *Ips typographus* (L.) Outbreak Spreading in Tatra Mountains (Central Europe), Using GIS. In: *Proceedings: Ecology, Survey and Management of Forest Insects, 2002 September 1-5, Kraków, Poland*, M.L. McManus, A.M. Liebhold (Eds). USDA Forest Service General Technical Report NE-311, 25—32.
- Janin, J.L., & Lieutier, F. 1988. Existence de fécondations précoce dans le cycle biologique de *Tomicus piniperda* L. (Coleoptera: Scolytidae) en forêt d'Orléans. Agronomie, 8, 169—72.
- Kirkendall, L.R. 1983. The evolution of mating systems in bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae). Zoological Journal of the Linnean Society, 77, 293—352.
- Kirkendall, L.R. 1989. Within-harem competition among *Ips* females, an overlooked component of density-dependent larval mortality. Holarctic Ecology, 12, 477—87.

- Kirkendall, L.R. 1990. Sperm is a limiting resource in pseudogamous bark beetle *Ips acuminatus* (Scolytidae). *Oikos*, 57, 80—87.
- Klipstein, E.L. 1986. Cytologie und Spermapolyplloidie bei *Pityogenes chalcographus* L. (Col., Scolytidae). *Journal of Applied Entomology*, 102, 285—95.
- Koponen, M. 1980. Distribution of *Ips amitinus* Eichhoff (Coleoptera, Scolytidae) in Finland in 1974–1979. *Notulae Entomologicae*, 60, 223—25.
- Krause-Opatz, B., Köhler, U., & Schopf, R. 1995. Zum energetischen Status von *Ips typographus* L. (Col., Scolytidae) während Jungkäferentwicklung, Überwinterung, Dispersion und Eiablage. *Journal of Applied Entomology*, 119, 185—94.
- Långström, B. 1980. Distribution of pine shoot beetle attacks within the crown of Scots pine. *Studia Forestalia Suecica*, 154, 1—25.
- Långström, B. 1983a. Life cycles and shoot feeding of the pine shoot beetles. *Studia Forestalia Suecica*, 163, 1—29.
- Långström, B. 1983b. Within-tree development of *Tomicus minor* (Hart.) (Col., Scolytidae) in wind-thrown Scots pine. *Acta Entomologica Fennica*, 42, 42—46.
- Långström, B., & Hellqvist, C. 1990. Spatial distribution of crown damage and growth losses caused by recurrent attacks of pine shoot beetles in pine stands surrounding a pulp mill in southern Sweden. *Journal of Applied Entomology*, 110, 261—69.
- Lanne, B.S., Schlyter, F., Byers, J.A., Löfqvist, J., Leufvén, A., Bergström, G., Van Der Pers, J.N.C., Unelius, R., Baeckström, P., & Norin, T. 1987. Differences in attraction to semiochemicals present in sympatric pine shoot beetles, *Tomicus minor* and *T. piniperda*. *Journal of Chemical Ecology*, 13, 1045—67.
- Lieutier, F. 1975. Humidité et dessèchement en milieu sous-cortical : conséquences pour la faune associée. *Annales de Zoologie Écologie Animale*, 7, 171—83.
- Lieutier, F. 1982. Les variations pondérales du tissu adipeux et des ovaires, et les variations de longueur des ovocytes, chez *Ips sexdentatus* Boern. (Coleoptera: Scolytidae); relations avec le parasitisme par les nématodes. *Annales de Parasitologie Humaine et Comparée*, 57, 407—18.
- Lieutier, F. 1983. Variations du volume et de la concentration en protéines et en acides aminés de l'hémolymphé chez les adultes d'*Ips sexdentatus* Boern. (Coleoptera, Scolytidae). *Zeitschrift für Angewandte Entomologie*, 95, 447—57.
- Lieutier, F., Vouland, G., & Pettinetti, M. 1997. Test de choix de pins méditerranéens par les Scolytides et autres insectes xylophages en conditions naturelles. *Revue Forestière Française*, 49, 215—24.
- Lobinger, G. von, & Skatulla, U. 1996. Untersuchungen zum Einfluss von Sonnenlicht auf das Schwarmverhalten von Borkenkäfern. *Anzeiger für Schadlingskunde Pflanzenschutz Umweltschutz*, 69, 183—85.
- Netherer, S. 2003. Modelling of bark beetle development and of site- and stand-related predisposition to *Ips typographus* (L.) (Coleoptera: Scolytidae). A contribution to risk assessment. Thesis Universität für Bodenkultur Wien.
- Nilssen, A.C. 1978. Spatial attack pattern of the bark beetle *Tomicus piniperda* L. (Col., Scolytidae). *Norwegian Journal of Entomology*, 25, 171—75.
- Nilssen, A.C. 1984. Long-range aerial dispersal of bark beetles and bark weevils (Coleoptera, Scolytidae and Curculionidae) in northern Finland. *Annales Entomologici Fennici*, 50, 37—42.
- Ogibin, B. N. 1973. [In Russian] Effect of settlement density on *Ips typographus* fecundity. *Ecologiya*, 5, 66—72.
- Otto, L.F., & Schreiber, J. 2001. Spatial patterns of the distribution of trees infected by *Ips typographus* (L.) (Coleoptera, Scolytidae) in the National Park "Sächsische Schweiz" from 1996 to 2000. *Journal of Forest Science*, 47, 139—42.
- Paynter, Q.E., Anderbrandt, O., & Schlyter, F. 1990. Behavior of male and female spruce bark beetles, *Ips typographus*, on the bark of host trees during mass attack. *Journal of Insect Behavior*, 3, 529—43.
- Pignal, M.C., Chararas, C., & Bourgeay-Causse M. 1988. Yeasts from *Ips sexdentatus* (Scolytidae): enzymatic activity and vitamin excretion. *Mycopathologia*, 103, 43—48.
- Ratzburg, J.T.C. 1839. *Die Forst-Insekten. I. Die Käfer*. Berlin: Nicolai.
- Riedl, H.W. 1973. Aspects of the feeding behavior of *Scolytus multistriatus*, the primary vector of Dutch Elm disease, and a critical evaluation of present chemical control measures. *Dissertation Abstracts International*, B, 34, 2678.

- Rudinsky, J.A., & Ryker, L.C. 1977. Olfactory and auditory signals mediating behavioral patterns of bark beetles. In: *Colloques Internationaux du C.N.R.S.* 265. *Comportement des insectes et milieu trophique*, 195—209.
- Saarenmaa, H. 1983. Modeling the spatial pattern and intraspecific competition in *Tomicus piniperda* (Coleoptera, Scolytidae). *Communicationes Instituti Forestalis Fenniae*, 118, 1—40.
- Saarenmaa, H. 1985. Within-tree population dynamics models for integrated management of *Tomicus piniperda* (Coleoptera, Scolytidae). *Communicationes Instituti Forestalis Fenniae*, 128, 1—56.
- Sahota, T.S., & Thomson, A.J. 1979. Temperature induced variation in the rates of reproductive processes in *Dendroctonus rufipennis* (Coleoptera: Scolytidae): a new approach to detecting changes in population quality. *The Canadian Entomologist*, 111, 1069—78.
- Salonen, K. 1973. On the life cycle, especially on the reproduction biology of *Blastophagus piniperda* L. (Col., Scolytidae). *Acta Forestalia Fennica*, 127, 5—72.
- Sanders, W. 1983. Untersuchungen über das Verhalten des Kupferstechers *Pityogenes chalcographus* L. während der Flugphase. *Zeitschrift für Angewandte Entomologie*, 96, 125—31.
- Sauvard, D. 1989. Capacités de multiplication de *Tomicus piniperda* L. (Col., Scolytidae). 1. Effets de la densité d'attaque. *Journal of Applied Entomology*, 108, 164—81.
- Sauvard, D. 1993. Reproductive capacity of *Tomicus piniperda* L. (Col., Scolytidae). 2. Analysis of the various sister broods. *Journal of Applied Entomology*, 116, 25—38.
- Sauvard, D., Lieutier, F., & Lévieux, J. 1987. Répartition spatiale et dispersion de *Tomicus piniperda* L. (Coleoptera Scolytidae) en forêt d'Orléans. *Annales des Sciences Forestières*, 44, 417—34.
- Schltyter, F., & Anderbrandt, O. 1993. Competition and niche separation between two bark beetles: existence and mechanisms. *Oikos*, 68, 437—47.
- Schltyter, F., & Löfqvist, J. 1990. Colonization pattern in the pine shoot beetle, *Tomicus piniperda*: effects of host declination, structure and presence of conspecifics. *Entomologia Experimentalis et Applicata*, 54, 163—72.
- Schroeder, L.M., & Lindelöw, Å. 2002. Attacks on living spruce trees by the bark beetle *Ips typographus* (Col. Scolytidae) following a storm-felling: a comparison between stands with and without removal of wind-felled trees. *Agricultural and Forest Entomology*, 4, 47—56.
- Schroeder, L.M., & Risberg, B. 1989. Establishment of a new brood in *Tomicus piniperda* (L.) (Col., Scolytidae) after a second hibernation. *Journal of Applied Entomology*, 108, 27—34.
- Schwenke, W. 1974. *Die Forstsäädlinge Europas. 2. Käfer*. Hamburg: Paul Parey.
- Storer, A.J., Wainhouse, D., & Speight, M.R. 1997. The effect of larval aggregation behaviour on larval growth of the spruce bark beetle *Dendroctonus micans*. *Ecological Entomology*, 22, 109—15.
- Thalenhorst, W. 1958. Grundzüge der Populationsdynamik des großen Fichtenborkenkäfers *Ips typographus* L. Schriftenreihe der Forstlichen Fakultät der Universität Göttingen, 21, 1—126.
- Vouland, G., & Schwester, D. 1994. Bionomie et développement de *Dendroctonus micans* Kug. (Col., Scolytidae) dans le Massif central. *Annales des Sciences Forestières*, 51, 505—19.
- Wainhouse, D., & Beech-Garwood, P. 1994. Growth and survival of *Dendroctonus micans* on six species of conifer. *Journal of Applied Entomology*, 117, 393—99.
- Walker, C., & Ross, R. 1975. A comparison of maturation feeding of the elm bark beetles *Scolytus scolytus* (F.) and *S. multistriatus* (Marsh.) on English elm (*Ulmus procera* Salisb.) and six other elm taxa. *Plant Pathology*, 24, 187—91.
- Wellington, W.G. 1977. Returning the insect to insect ecology: some consequences for pest management. *Environmental Entomology*, 6, 1—8.
- Wermelinger, B. 2000. Wie viele Borkenkäfer überleben den Winter? *Bündnerwald*, 53, 67—68.
- Wichmann, L., & Ravn, H.P. 2001. The spread of *Ips typographus* (L.) (Coleoptera, Scolytidae) attacks following heavy windthrow in Denmark, analysed using GIS. *Forest Ecology and Management*, 148, 31—39.
- Wood, D.L. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. *Annual Review of Entomology*, 27, 411—46.
- Wood, S.L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Naturalist Memoirs 6.
- Zolubas, P., & Byers, J.A. 1995. Recapture of dispersing bark beetles, *Ips typographus* L. (Col., Scolytidae) in pheromone-baited traps: regression models. *Journal of Applied Entomology*, 119, 285—89.

- Zumr, V. 1985. [In Czech] Communities of beetles (Coleoptera) in the feeding sites of bark-beetles (Scolytidae) on Norway spruce (*Picea excelsa* Link.) in southern Bohemia. Sbornik Jihoceskeho Muzea V Ceskych Budějovicích Přírodní Vědy, 25, 45—48.
- Zumr, V. 1992. Dispersal of the spruce bark beetle *Ips typographus* (L.) (Col., Scolytidae) in spruce woods. Journal of Applied Entomology, 114, 348—52.
- Zumr, V., & Soldán, T. 1981. Reproductive cycle of *Ips typographus*, *I. amitimus* and *Pityogenes chalcographus* (Coleoptera, Scolytidae). Acta Entomologica Bohemoslovaca, 78, 280—89.
- Zumr, V., Nemec, V., & Stary, P. 1985. Seasonal changes in the nutrient content in the bodies of *Ips typographus* L. (Col., Scolytidae). Zeitschrift für Angewandte Entomologie, 100, 464—68.

Chapter 8

CHEMICAL ECOLOGY OF BARK BEETLES IN A COMPLEX OLFACTORY LANDSCAPE

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1. INTRODUCTION

The Scolytidae (bark and ambrosia beetles) comprise a taxonomic group of at least 6000 species that, although appearing similar, may differ widely in their ecology and biochemical adaptations to host trees. Bark beetle species that feed on phloem (a relatively thin layer just under the corky bark) are usually restricted to one or a few host species, whereas ambrosia beetle species that are xylomycetophagous (wood-feeding) and introduce symbiotic fungi for "cultivation" in their galleries generally colonize a larger range of hosts (S.L. Wood 1982). Most biological knowledge on bark and ambrosia beetles derives from studies on relatively few pest species in the genera *Dendroctonus*, *Ips*, *Scolytus*, *Xyleborus*, *Trypodendron*, *Tomicus*=*Blastophagus* (Fig. 1), *Pityogenes*, *Hypothenemus*, *Pityophthorus*, *Hylastes*, and *Gnathotrichus*.

Many of these species are obligate and facultative tree-killing bark beetles that comprise only about 10% of scolytid species in the United States and Canada (Raffa *et al.* 1993). However, these pests that kill trees are the most likely to significantly influence the evolution of the host tree and its chemistry.

The diversity of bark beetle biology, in which each species is adapted to only one or a few host tree species, probably has resulted due to natural selection from the great variety of plant biochemicals. It is also theorized that each species of tree has coevolved various chemicals to defend against the herbivorous selection pressures of the tree-killing bark beetles (Erlich and Raven 1965; Feeny 1975; Cates 1981; Berryman *et al.* 1985; Byers 1995). Semiochemicals (behavior modifying chemicals) from both the tree and the beetle have many functions during the life cycle of a bark beetle (for reviews see D.L. Wood 1982; Borden 1982, 1997; Lanier 1983; Birch 1984; Borden *et al.* 1986; Byers 1989a, b, 1995; Raffa *et al.* 1993; Schlyter and

Birgersson 1999). Host and non-host plant chemicals can be attractive, repellent, toxic, or nutritious to bark beetles. These chemicals may have affects on: (1) finding and accepting the host tree (host selection and suitability), (2) feeding stimulation and deterrence, (3) plant resistance, (4) pheromone/allomone biosynthesis and communication, and (5) attraction of predators, parasites and competitors of bark beetles.



Figure 1. Electron micrograph of male (top) and female *Tomicus piniperda* from Sweden.

Knowledge of bark beetle chemical ecology and insect-tree relationships is important to devising better ways of managing bark beetle populations and their damage to trees. The strategies that bark beetles use to avoid competition within and between species, to avoid unsuitable host and nonhost trees, to find their host trees and mates, and to maximize their reproductive success can be investigated with the purpose of eventually manipulating these processes to the detriment of the beetles. Most of the following presentation involves species in the genera *Dendroctonus*, *Tomicus*, *Ips*, and *Pityogenes*. Before presenting theories on possible strategies bark beetles use for locating suitable hosts and avoiding competition, it is useful to consider an overview of the life cycle and behavior of bark beetles in relation to semiochemicals.

2. BEHAVIORAL ECOLOGY AND PHYSIOLOGY IN THE LIFE CYCLE OF BARK BEETLES

In general, adults of bark beetles in the above genera overwinter in either forest litter (e.g., *Ips*, *Pityogenes*) or the brood tree (e.g., *Dendroctonus*, *Ips*, *Pityogenes*). In species that have several generations during the summer, emergence is from the brood



Figure 2. Storm-damaged Scots pine, *Pinus sylvestris*, releases monoterpenes attractive to both sexes of *Tomicus piniperda* in the early spring.

tree. *Tomicus piniperda* has a more complex life cycle in which adults overwinter in living, nonbrood trees (Salonen 1973; Långström 1983). After emergence, the adults of all species attempt to locate a host tree (termed the dispersal flight), either by orienting to pheromone or plant volatiles. Host suitability may be determined in flight or after landing on the tree. In the monogamous genera *Tomicus* and *Dendroctonus* (subfamily: Hylesininae), the females select the host tree and an entrance hole (attack) to begin construction of oviposition galleries in the phloem. In contrast, males of the polygynous genera *Ips* and *Pityogenes* (subfamily: Scolytinae) begin the entrance hole and later accept several females. In most cases, individuals of only one sex begin the attack, releasing a species-specific blend of chemicals comprising an aggregation pheromone (Byers 1989a). However, in *D. brevicomis*, the female and the joining male each produce a unique synergistic pheromone component that when combined elicit maximal attraction response (Silverstein *et al.* 1968; Kinzer *et al.* 1969). In *T. piniperda*, there is no evidence of an aggregation pheromone (Byers *et al.* 1985; Löyttyniemi *et al.* 1988); instead, host-tree chemicals induce aggregation (Fig. 2).

Species of bark beetles feed only on one or a few host tree species, which are perceived and located by means of the beetle's various sensory receptors that are located on their antennae and mouthparts. Except for morphological studies on *D. ponderosae* and *I. typographus*, little is known about the sensilla on the maxillary and labial palpi mouthparts of bark beetles (Whitehead 1981; Hallberg 1982). In these species there is clearly a large number of chemosensilla (Fig. 3), which appear to be important for host selection and food discrimination.

In other insects, the tarsi and ovipositor have chemosensilla that are involved in host acceptance (Städler 1984), but these structures have not been studied in bark

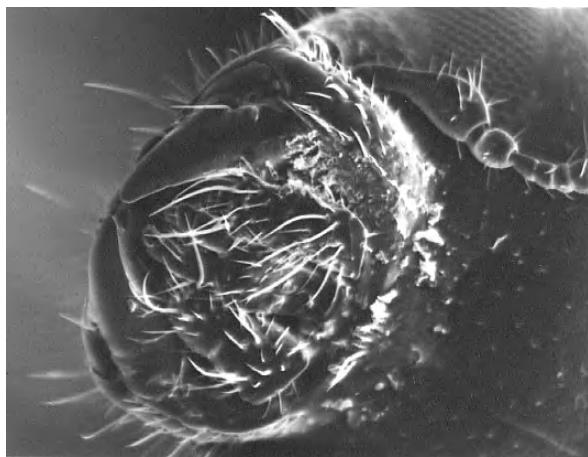


Figure 3. Electron micrograph of mouthparts of *Tomicus piniperda*.



Figure 4. Electron micrograph of antenna and eye of *Tomicus piniperda*.

beetles. Most work with bark beetles has focused on the antennae (Fig. 4), which are known to have sensilla responsive to volatile pheromone and host components, as well as other air-borne chemostimulants (Borden and Wood 1966; Payne *et al.* 1973; Payne 1979; Mustaparta 1984; Faucheux 1989).

The electrophysiological response of an insect to semiochemicals can be studied with an electroantennogram (EAG) of the whole antenna or by the single-cell technique that measures responses of specific receptor cells (Payne 1979). Each antennal receptor cell contains multiple acceptor sites that interact with the chemicals.

Bark beetle olfactory cells on the antennae have been shown to be of several functional types, which probably are found in all species. These types include: (1) a highly specific cell such as the ipsdienol-sensitive ones in *I. paraconfusus* and *I. pini* that are responsive only to one of two possible enantiomers (identical atomic structures but not superimposable, e.g., α -pinene in Fig. 5), (2) a pheromone-sensitive one that is also responsive to other synergists or inhibitors such as the frontalin cells of *D. frontalis*, which have at least two acceptor types each specific for one enantiomer of frontalin, and (3) a "generalist" type that responds to host monoterpenes as well as pheromones (Mustaparta *et al.* 1980; Payne *et al.* 1982; Dickens *et al.* 1985; Dickens 1986).

Vision plays a vital role during orientation flights of bark beetles, and in conjunction with antennae enable bark beetles to locate semiochemical sources. The eyes of many bark beetles (e.g., *Ips*, *Scolytus*, and *Pityogenes*) consistently have only about 100-240 ommatidia (Fig. 4), which is less than many insects (Chapman 1972; Byers *et al.* 1989a). Based on electrophysiological recordings, two color receptor types have been identified in the eyes with a maximum absorbance at 450 nm (blue) and 520 nm (green) (Groberman and Borden 1982).

Observations of *I. paraconfusus*, *I. typographus*, *D. brevicomis*, *P. chalcographus*, and *T. piniperda* in flight chambers under dim red light or in complete darkness using an electronic vibration detector indicate they will not fly after dark (Lanne *et al.* 1987; Byers and Löfqvist 1989; Byers unpublished). Bark beetles are attracted in greater numbers to traps baited with host odor or pheromone that are placed next to "tree trunk silhouettes" than to traps without such visual stimuli, indicating that beetles orient to the tree trunk during landing (Moser and Browne 1978; Borden *et al.* 1982; Tilden *et al.* 1983; Lindgren *et al.* 1983; Bombosch *et al.* 1985; Ramisch 1986; Chénier and Philogène 1989). Beetles of some species prefer to land on horizontal silhouettes rather than on vertical ones of the same size (Pitman and Vité 1969). Another indication that bark beetles have relatively poor visual acuity is that *T. piniperda* males must walk within 1 cm of a female beginning her entrance hole before they appear to detect her and initiate guarding behavior (Byers 1991). Both *T. piniperda* and *D. brevicomis* individuals can be induced to drop off a tree by movements of the human body about 2 m away (about the same angle of resolution and relative size, my observations).

Primary attraction to host tree volatiles can be considered to occur over a "long-" or "short-range." The concept of range differs between authors and depends on the insect considered. Here I consider long-range attraction for bark beetles to be flight orientation over a meter or more to a semiochemical source. In reality the division is arbitrary, since bark beetles may orient over practically any distance depending on the release rate of the semiochemical. At very high release rates the insect may not closely approach the source due to adaptation (Baker *et al.* 1988). However, the concept of range is valid at natural release rates. Attraction to pheromone is certainly long-range. For example, three parallel lines spaced 4.6 m apart and hung with sticky screens spaced every 1.5 m intercepted *I. paraconfusus* in a "V"-shaped pattern narrowing to a pheromone source of 50 males boring in a pine log (Byers 1983a). In this experiment, beetles appeared to orient over a distance of at least 17 m. *S. quadrispinosus* beetles

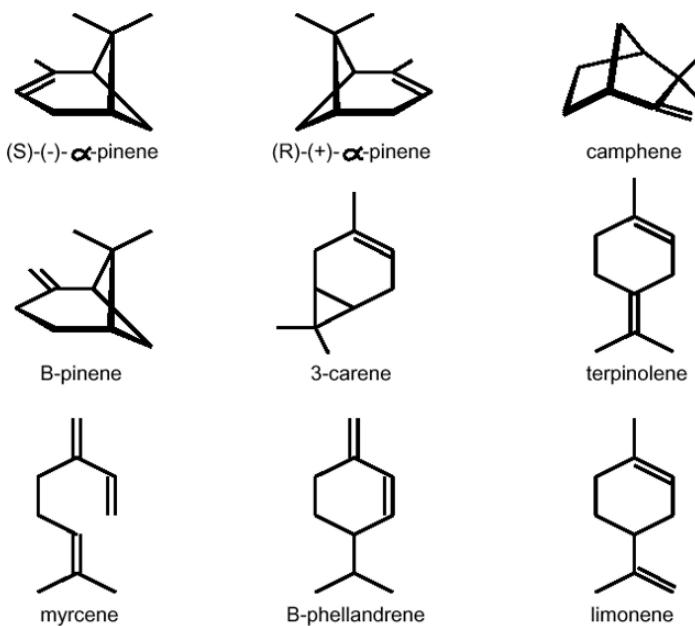


Figure 5. Major monoterpenes of conifers. Note that the enantiomers of α -pinene are identical except that they are non-superimposable (mirror images). Camphene, β -pinene, 3-carene, β -phellandrene, and limonene also have two enantiomers, although only (-)- β -pinene and (+)-3-carene are found in trees (Mirov 1961). Myrcene and terpinolene are achiral.

were intercepted by passive traps 12 m from a girdled hickory tree that was attracting these beetles (Goeden and Norris 1964). The distance over which beetles respond anemotactically depends primarily on the release rate of the volatile (under mild wind conditions). In Denmark, I once observed *I. typographus* flying slowly upwind (0 to 0.5 m/s ground speed) in 3 m/s gusty winds to a large fallen spruce tree under massive attack. During their orientation to this pheromone source, beetles were flying at 3-6 m in height from at least as far away as 50 m downwind. Jactel (1991) estimated that the maximum attraction distance of *I. sexdentatus* to pheromone-baited traps was 80 m.

An index of attraction strength for a particular semiochemical release rate is known as the "effective attraction radius" (*EAR*), which is proportional, but considerably smaller, than the maximum attraction distance (Byers *et al.* 1989a). The *EAR* is the radius that a trap would need to be enlarged, as a spherical "passive" trap, in order to intercept as many dispersing insects as were actually caught on the trap when baited. For example, the *EAR* of *T. piniperda* to a blend of three host monoterpenes, released at rates equivalent to a cut log of Scots pine from each of 10 traps along a 12-m high pole, was largest at the lowest trap (*EAR* = 1.3 m). The same design found an *EAR* of 3.2 m for *I. typographus* response to a blend of its pheromone components (Fig. 5). These comparisons indicate that the *EAR* can be larger for a pheromone than for host

volatiles. However, both these values would be greater at higher chemical release rates. Schlyter (1992) discusses several additional concepts of attraction distance, including the attraction range (the maximum distance over which insects can be shown to be attracted) and the sampling range (the distance over which insects reach a source in a given time period).

The optomotor anemotaxis mechanism for orientating to pheromone sources proposed for insects, especially moths (David *et al.* 1982; Baker 1989), also appears to function in bark beetles (Choudhury and Kennedy 1980). In this theory, a bark beetle attempts to fly directly upwind when in contact with a packet of pheromone-laden air of the plume, but casts (flies from side to side with respect to the source) when contact is lost. The beetle senses the wind direction while flying by observing the ground below: in no wind, or head-on wind, the ground moves directly underneath during flight. However, if the visual ground field also moves from right to left somewhat, for example, then wind is coming from the left, and the beetle turns to the left to minimize the transverse ground shift and keep the ground moving directly underneath, in this manner the insect heads upwind and toward the pheromone source.

Short-range attraction could be considered to occur within one meter of the source such as when flying along the trunk as I have observed for *T. piniperda*; however, after landing the beetle must use a mechanism other than optomotor anemotaxis. While walking, the ground does not move under the beetle due to wind, but the beetle probably can still sense wind direction by mechanoreceptors, and use "casting" or circling movements to locate the odor source. Beetles walking in an arena with laminar airflow respond to a point source of synthetic pheromone (or air from an attacked log) by walking directly upwind within the odor plume. If they walk outside the plume, they would experience a concentration gradient decline as they walked. By turning slightly with respect to the upwind angle (as detected by tactile hairs) they would either soon re-contact the odor or the concentration would further decline. In the later case they could reverse the angle or continue turning in a circle that would bring them into contact with the odor, whereupon they could walk directly upwind again. This mechanism is consistent with tracings of tracks of *I. paraconfusus* (Borden and Wood 1966) responding to pheromone in the laboratory olfactometer (see Birch 1984) as well as observations of other species in the genera *Ips*, *Dendroctonus*, *Tomicus*, and *Pityogenes* responding to pheromone or host odors in similar olfactometers (Byers *et al.* 1979; Byers and Wood 1981a; Lanne *et al.* 1987; Byers 1983a; Byers *et al.* 1990a, b).

After the beetle orients and lands on a host tree and begin to release an aggregation pheromone, the likelihood of successful colonization depends on (1) the population level of beetles available for recruitment to the attack and (2) the resistance and health of the tree and its ability to produce defensive resin (Fig. 6). Resistance of conifers, especially pines, to bark beetle attacks has long been attributed to the amount of resin exuded and pitch tubes formed (Webb 1906; Hodges *et al.* 1985). Dead beetles can often be seen in crystallized resin of pitch tubes. However, species of *Dendroctonus* and other aggressive bark beetles have a great ability to survive the "toxic" monoterpenes and suffocating mucilage and may struggle for hours in copious resin flows (*D. frontalis*, Hodges *et al.* 1979; *D. brevicomis*, Byers 1995). Drought and poor

water balance lower the resistance of conifers (Hodges and Lorio 1975; Hodges *et al.* 1979) probably by lowering the turgidity of resin duct cells, which lowers the oleoresin exudation pressure (OEP). A correlation between higher OEP and greater resistance of ponderosa pine to attack by *D. brevicomis* and *I. paraconfusus* has been reported (Vité 1961; Wood and Vité 1961; Wood 1962; Brown *et al.* 1987). Oleoresin and the monoterpenes indicate host resistance and therein are repellent to bark beetles in concentrated amounts (Struble 1957; Pitman *et al.* 1966; Berryman and Ashraf 1970; Bordasch and Berryman 1977; Byers *et al.* 2000; El-Sayed and Byers, 2000).

Beetles of many species have specialized areas of the integument or pouches called mycangia where symbiotic fungi are carried, and in some species nourished, until they are introduced inside the entrance tunnel where they grow into the tree (Happ *et al.* 1976; Whitney 1982; Bridges *et al.* 1985; Paine and Stephen 1987; Levieux *et al.* 1991). Some of the fungal species (genera *Ceratocystis*=*Ophiostoma*, *Trichosporium*) may attack the living tissues of the tree and paralyze the tree's ability to produce and exude resin for defense against the beetle (Mathre 1964; Horntvedt *et al.* 1983; Paine 1984; Raffa and Berryman 1987; Paine and Stephen 1987; Paine *et al.* 1988). Other fungal species of the beetle's mycangium grow in the galleries after the tree has been killed and appear important to the nutrition and growth of the larvae (Bridges and Perry 1985; Paine *et al.* 1988; Goldhammer *et al.* 1991). In ambrosia beetles, that generally attack unhealthy or dead trees, the adults and larvae feed on fungi lining the galleries instead of on the tree's tissues (Funk 1970; Furniss *et al.* 1987; Kajimura and Hijii 1992).

Successful colonization and reproduction by a bark beetle in a living tree requires release of enough aggregation pheromone to ensure the attraction of sufficient conspecifics to overwhelm the host tree defenses (Fig. 6); however, after killing the tree and securing mates, pheromone should stop in order to avoid further competition for bark areas (Byers *et al.* 1984; Berryman *et al.* 1985). Semiochemicals play a role in "cooperation" among beetles when killing the tree and in their avoidance of competition (discussed later). "Pioneer" beetles that attack the tree first may suffer most from the tree's defensive resin, but these beetles may have no choice but to attack due to low fat reserves. The later that a beetle arrives in the colonization sequence of the host, the poorer is the quality of the bark substrate due to (1) space utilization by established conspecifics (intraspecific competition) and (2) degradation by microorganisms (discussed subsequently).

Under the bark, females lay eggs that hatch to larvae and feed on the phloem for several weeks. Chemicals from both the plant and microorganisms could affect beetle survival at this time, but little is known about these interactions. However, once the tree is dead, there can be no natural selection on the insects to evolve different tree genotypes that produce chemicals harmful to beetles. The larvae pupate in the bark and become yellow, callow adults where they feed and mature until emerging. The beetles may begin a dispersal flight during the same season, or after overwintering in either the tree (*Dendroctonus*, *Pityogenes* and many *Ips*) or in the forest litter (*I. typographus* in colder climates). *Tomicus minor* and *T. piniperda* emerge from the bark and fly relatively short distances to the tops of pine trees where they bore into a shoot during the summer (Salonen 1973; Långström and Hellqvist 1991). In the autumn, beetles of

T. piniperda crawl down the trunk and bore into its base to overwinter, whereas *T. minor* overwinters in the litter (Salonen 1973; Långström 1983). The next sections will present the details of some olfactory strategies employed during dispersal to find mates and suitable host trees in which to reproduce.



Figure 6. *Dendroctonus brevicomis* in resin of ponderosa pine.

3. DISPERSAL FROM THE BROOD TREE OR OVERWINTERING SITE

Insects disperse when their habitat becomes unsuitable. This can be from a lack of food resources, mating possibilities, territories and suitable domiciles, or from the need to escape the local buildup of parasites and predators (c.f. Ricklefs 1990). Apparently for the same reasons, bark beetles emerge from the dead brood tree, or litter near the brood tree, and begin a dispersal flight seeking suitable host trees from among many non-host and unsuitable host trees (Fig. 7).

During dispersal, bark beetles and associated predators and parasites feeding or living in brood trees must locate a new host tree from among the relatively few widely scattered suitable hosts in the forest. The host tree is restricted usually to one or a few species and in most cases the bark beetles seek weakened, less resistant trees, or trees that are in the initial stages of death and decay. Also, beetles try to avoid feeding and reproduction in areas heavily colonized by conspecifics and competing species (Byers 1984, 1995; Fig. 8). Thus, it is expected that species have evolved behavioral responses to volatile host-plant chemicals that indicate the presence of a suitable host in which reproduction can occur.

The dispersal flight of a bark beetle may vary from only a few meters (as observed during epidemics) to possibly several kilometers. Several factors interact to cause the dispersal flight distance to vary between individuals. The most obvious

is that a beetle encounters a susceptible tree early in the dispersal flight. However, whether this tree is attacked may depend on the level of fat reserves that can be mobilized for flight (Atkins 1966, 1969; Byers 1999). A beetle should have higher reproductive fitness if it flies far from the brood tree since it can both avoid inbreeding



Figure 7. Many species of bark beetles disperse through a stand of Norway spruce in the spring (Torsby, Sweden).

with siblings and, probably more importantly, escape predators and parasites that are locally denser near the brood tree. Thus, the dispersal distance has been optimized over evolutionary time to balance the probably logarithmically increasing benefits of flying farther against the probably exponentially increasing likelihood of exhaustion and failing to find a host. The fat level required for lengthy dispersal will depend on the conditions in the brood tree during larval development; for example, disease, insect, and climatic factors will affect the nutritional quality of the host (Fig. 9). Severe competition among the larvae will reduce the size of adults as well as their fat content (Atkins 1975; Anderbrant *et al.* 1985). Parasites would reduce the size and fat content of some adults while predators would lessen competition for those remaining locally, thereby increasing the variability of dispersal range in the population. The population density of bark beetles should be stabilized by a frequency-dependant competition for the susceptible trees. This would produce increasingly stronger, longer-flying individuals with decreasing attack and larval density while producing weaker, shorter-flying individuals with increasing competition.

Knowledge of how far and where bark beetle populations disperse comes mainly from (1) mark-release-recapture studies using pheromone traps and from (2) the geographical occurrence of new infestations relative to previous ones. Both lines of

investigation are inconclusive since (1) only a few pheromone traps were used, usually some tens to hundreds of meters from the release site, so that a large proportion of



Figure 8. Spacing of attacks of *Ips typographus* (larger circles) and *Pityogenes chalcographus* (smaller circles) to avoid competition in the bark of Norway spruce (bark surface scraped smooth on left to reveal attacks that were circled with ink pen).

released beetles escaped, or (2) the origins of attacking beetles were uncertain. Several studies have placed various sized rings of pheromone traps around a source of marked beetles. For example, the spruce bark beetle of Europe, *I. typographus*, was recaptured at various outer distances from 120 to 1000 m (Botterweg 1982; Zumr 1992; Zolubas and Byers 1995; Duelli *et al.* 1997). In California, *I. paraconfusus* was recaptured in outer traps at 2 km (Gara 1963). The ambrosia beetle, *Trypodendron lineatum*, was recaptured at 500 m (Salom and McLean 1989). As expected, the widely spaced outer traps captured a small proportion of the released beetles, and the large gaps between traps probably allowed many to slip through as they drifted with the wind (e.g., gaps of 785, 1257, and 393 m in Zumr 1992; Gara 1963; and Salom and McLean 1989; respectively). An adverse effect of marking, although discounted, might also influence the dispersal.

The view that bark beetles can fly some tens of km is based less on mark-recapture studies and more on collections of beetles far from forests. Nilssen (1978) found two *I. typographus* in the stomach of a salmon 35 km from any spruce forest. Miller and Keen (1960) report results of studies by the US Forest Service in California where the western pine beetle, *D. brevicomis*, infested 'islands' of ponderosa pine, initially free of beetles, that were separated from the main forest by open sagebrush areas. They concluded that significant numbers of bark beetles must have flown a minimum of 3.2 km in one study, and 9.6 or 20 km in another study, to reach the infested trees.

Increasing competition among larvae due to increasing densities of parents laying broods was shown to reduce size and fat content of bark beetles (Atkins 1975; Anderbrant *et al.* 1985) and thus should decrease dispersal ranges. However, this seems in conflict with the statement of Forsse (1991) that flying time of *I. typographus* on flight mills was "similar among populations and appeared unaffected by outbreak



Figure 9. *Ips typographus* preparing to begin the dispersal flight after emerging from the duff in late May in Sweden.

conditions". Earlier, Forsse and Solbreck (1985) could not find any affect of sex or body size on the duration of flight on mills. Botterweg (1982) also concluded that there was little, if any, affect of beetle size or fat content on dispersal distance as monitored in field traps. However, he did find that fat content of beetles declined over the flight period. This was probably due to consumption of fat during host-seeking rather than later emergence of lower-fat beetles since beetle's sizes (elytral weights) did not decrease over the spring season. Birgersson *et al.* (1988) reported that newly emerged *I. typographus* averaged about 10% fat, while after 24 hours of flight exercise in a plastic box, they declined to only 5% since fat is used for energy. In trees, males with nuptial chambers had about 8% fat (possibly replenishing some after feeding), but after several more days of feeding after females had joined them, the males had 10% fat again.

Bark beetles appear capable of flying quite far in the forest since newly emerged *D. pseudotsugae* flew an average of 2 h on flight mills before resting (3 h total), while some individuals flew up to 8 h uninterrupted (Atkins 1961). Jactel and Gaillard (1991) flew *I. sexdentatus* on rotary flight mills and found that 50% of the beetles could fly more than 20 km, and 10% more than 45 km, based on about 50 interrupted flights. About 25% of *I. typographus* taken from litter in an outbreak area flew for over 1 h, and 10% for more than 2.5 h on flight mills, with a maximum flight of 6 h and 20 min recorded (Forsse and Solbreck 1985). At free-flying speeds of 1.9 to 2 m/s (Gries *et al.* 1989; Byers 1996a), a maximum range would be 41 to 45.6 km without wind transport. However, wing beat frequency declines with flight duration, which may affect flight range. In the only case studied, the wing beat frequency of *D. pseudotsugae* of about 95 Hz declines 18 % with flight time over 4 h to about 75 Hz (Atkins 1960). Speed on flight mills also declined from 1.11 m/s to 0.99 m/s (Atkins 1961).

4. DECIDING WHETHER TO ACCEPT A HOST OR CONTINUE TO DISPERSE

Tradeoffs regarding host plant acceptance by insects have been reviewed by Miller and Strickler (1984). They present a model (their Fig. 6.1) by Dethier (1982) where the decision by the insect whether to accept the plant is dependent on external (olfaction, vision, mechanoreception, and gustation) stimulatory and inhibitory inputs balanced against internal excitatory and inhibitory inputs. A graphical, and simplified, model of host acceptance is shown in Fig. 10 that is directly applicable to pioneer bark beetles. In this model, as the bark beetle flies around searching for suitable host trees (usually trees already under attack by conspecifics) they use up energy reserves of lipids (Atkins 1969; Thompson and Bennett 1971) and probably become increasingly willing to accept substandard hosts.

The beetle may, by chance, encounter several hosts during the dispersal flight that are more or less suitable for reproduction. The beetle will accept a host if the combination of the host suitability and fatigue level of the beetle is above the curve (Fig. 10); otherwise the beetle will continue searching for more suitable hosts. The curve is asymptotic to the Y-axis for those beetles that require flight before responding to semiochemicals, whereas the curve would intersect the Y-axis for species that are immediately responsive after emergence. The suitability of the host is determined by the nutritional quality, as well as by the density of established attacks by the same or other species of bark beetle that indicate the potential for damaging competition.

At the beginning of a dispersal flight, bark beetles are considered rather unresponsive to pheromone or host volatiles. The theory is that fat reserves are higher in freshly emerged beetles so that they have the ability for extended flight and can gain adaptive benefits from dispersal before responding to hosts (Borden *et al.* 1986; Anderbrant *et al.* 1985; Gries *et al.* 1990). Graham (1959) showed that continued flight exercise by *T. lineatum* caused an increase in responsiveness to visual and olfactory stimuli of the host. Freshly emerged *T. lineatum* and *D. pseudotsugae* required 30 or 90 min of flight, respectively, before responding to pheromone from female frass (Bennett and Borden 1971). Atkins (1966) found that female *D. pseudotsugae* with more than 20 %

fat (dry weight) were usually not responsive to the host, while those under 20 % fat were responsive and still could fly. Beetles with less than 10% fat had trouble flying since fat was required as an energy source (Atkins 1969). The fat metabolized by *D. pseudotsugae* consists mainly of C16 and C18 fatty acids (Thompson and Bennett 1971). Other studies have found that scolytid beetles in the genera *Trypodendron*, *Dendroctonus*, *Scolytus*, and *Ips* increased their responsiveness or upwind orientation to host and pheromone after continued flight exercise (Choudhury and Kennedy 1980; and cf. Borden *et al.* 1986).

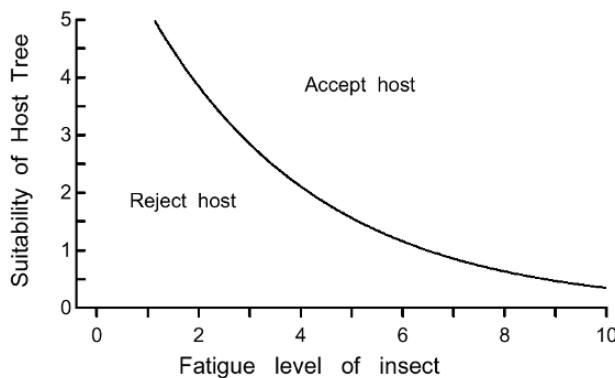


Figure 10. Theoretical curve for the acceptance of host trees by bark beetles depending on prerequisite flight exercise (asymptotic y-axis) and level of fatigue (amount of flight) and suitability of the host for reproduction (which depends on nutritional quality and density of colonization by competing bark beetles).

However, some bark beetles appear responsive to pheromone upon emergence. Lindelöw and Weslien (1986) found that overwintered *I. typographus*, collected and marked as they emerged from tents over forest litter, were caught in synthetic pheromone traps within minutes of release. Schlyter and Löfqvist (1986) suggested that preliminary experiments indicated *I. typographus* became more responsive to pheromone with flight exercise, but further details were not reported. The majority of *I. paracallosus* in California responded to aggregation pheromone soon after emergence (Wood and Bushing 1963; Gara 1963; Hagen and Atkins 1975). Botterweg (1982) also found that *I. typographus* can immediately respond to pheromone when beginning dispersal, and this is in accordance with his finding that beetles lost 40-50% of their fat over the winter. Possibly, second generation beetles in southern Europe would have higher fat content and consequently disperse further.

5. THEORIES OF HOW BARK BEETLES FIND SUITABLE HOST TREES

There are two general theories on how bark beetles find suitable host trees that have not been previously colonized by conspecifics releasing pheromone (McMullen and Atkins 1962). The first is that beetles locate such trees by orienting over several meters to volatile chemicals usually released by damaged or diseased trees (called "primary

attraction"). It seems that *Tomicus piniperda* finds hosts by primary attraction as the species is attracted to monoterpenes in the resin (Fig. 11).

The second theory is that beetles fly about and encounter suitable host trees at random, whereupon they land and test them by short-range olfaction or by taste. The two theories are not mutually exclusive, and one or the other may primarily operate in a particular species. In California, host finding by the important pests *D. brevicomis* and *I. paraconfusus* is thought to be a random process. Ponderosa pines that were killed by freezing with dry ice and then screened to prohibit bark beetle attack, did not have higher landing rates for the prevalent *D. brevicomis* and *I. paraconfusus* bark beetles (among other species) than did living trees. Landing rates on diseased and healthy trees also were similar. It was estimated that about one *D. brevicomis* beetle visited each tree in the forest each day (Moeck *et al.* 1981; D.L. Wood 1982). Logs of freshly cut ponderosa pine placed in sticky screen traps did not catch beetles of these species, while at the same time high numbers were attracted to synthetic pheromone or infested logs (Moeck *et al.* 1981).

In addition to *I. paraconfusus* and *D. brevicomis*, many species probably visit trees at random, whereupon the tree's resistance is tested during an attack. For example, *Scolytus quadrispinosus* was caught equally on traps placed in host shagbark hickory, *Carya ovata*, and nonhost white oak, *Quercus alba* (Goeden and Norris 1965). Berryman and Ashraf (1970) found attacks by *Scolytus ventralis* in the basal section of 74% of grand fir examined, while only 3.5% of these trees were colonized. Most unsuccessful attacks were abandoned before beginning the gallery. The attacks on grand fir appeared random during the early part of the flight period before aggregations resulted. Hynum and Berryman (1980) caught *D. ponderosae* in traps on 96% of the lodgepole pines (*P. contorta*) sampled, but only 66% of these pines were killed. Also, they found no differences in landing rates between killed and surviving lodgepole pines or between host and nonhost trees. A direct relationship between the numbers of *D. ponderosae* caught on unattacked trees and the numbers of trees upon which beetles landed was found in a study of lodgepole pines (Raffa and Berryman 1979). *I. grandicollis* landed equally on sticky traps on trees judged resistant or susceptible based on crown area (Witanachchi and Morgan 1981). However, Schroeder (1987) found an average of 35 *T. piniperda* landing on lower vigor Scots pine, *P. sylvestris* (as judged by less crown area), than on higher vigor trees (mean of 22 landing per tree). These differences could be due to secondary release of monoterpenes by beetles boring in the low vigor trees that were less able to resist attack.

There is some evidence that *I. typographus* is weakly attracted to host volatiles (Austås *et al.* 1986; Lindelöw *et al.* 1992) or monoterpenes such as α -pinene (Rudinsky *et al.* 1971), but other studies have not observed any attraction to host volatiles or synergism of pheromone and host volatiles (Schlyter *et al.* 1987a). A computer model by Gries *et al.* (1989), in which "beetles" must take a series of flights between trees in a grid (each flight to one of eight neighboring trees) and test each tree for suitability, showed that few beetles would find the widely scattered hosts designated as susceptible. Thus, they concluded that a mechanism of long-range

primary attraction would be required for maintenance of the population. However, a more recent computer model, in which beetles "fly" more naturally among randomly



Figure 11. Attraction of *Tomicus piniperda* to monoterpenes released from oleoresin exuding from cut end of a Scots pine log.

dispersed susceptible trees indicated that a significant proportion of the population could find the susceptible trees by chance interception of the trunk diameter (Byers 1993a, 1996a). If beetles then test the defenses of the potential host (although this rarely has been observed) then weaker, more susceptible, trees will not exude adequate resin and allow the beetle to produce aggregation pheromone. According to the later model, this will in effect greatly increase the effective "radius" of the tree (or EAR) so that many more in the population can quickly find and colonize these trees (Byers 1993a, 1996a).

In addition to the "random landing" and "primary attraction" to host volatile theories, some bark beetles may find weakened and susceptible host trees by orienting to volatiles produced by competing species during colonization. The volatiles can be host compounds that virtually any bark beetle would release upon attack (e.g., monoterpenes) or pheromone components of these other species. For example, *D. brevicomis* responds to pheromone components of *I. paracnifusus* in the laboratory (Byers and Wood 1981a); *I. typographus* responds to exo-brevicomin (from *D. micans* and *Dryocoetes* spp., Borden *et al.* 1987) when combined with its pheromone components (Tommerås *et al.* 1984); and several sympatric species of *Ips* in the southeastern United States are cross-attracted to infested pine logs in the field (Birch *et al.* 1980b).

Finally, bark beetles may be aided in locating suitable host trees by avoiding volatiles from (1) hosts fully colonized by conspecifics or competing species and (2) nonhost trees and plants. Avoidance of these types of substrates will be covered in

more detail in later sections on discriminating suitability of hosts, avoidance of competition and decaying colonized hosts, and avoidance of nonhosts.

6. STRATEGIES OF "PIONEER" BARK BEETLES

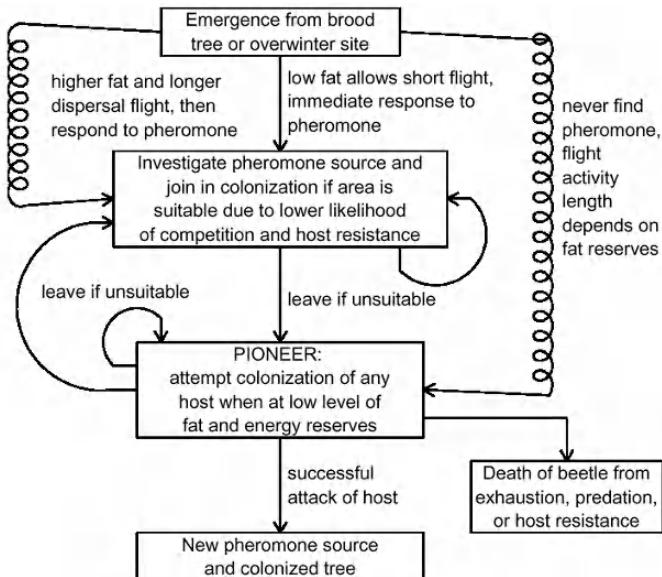


Figure 12. Conceptual model of dispersal and host-seeking ecology of "aggressive" bark beetles that use aggregation pheromones. Factors such as the beetle's fat reserves, chances of encountering pheromone, and level of competition and host suitability determine whether a beetle joins resident beetles in colonizing a tree or is the first "pioneer" to attack.

A beetle that lands on a tree and attempts to find a place on the bark to bore is termed a "pioneer" if there are few others present. Pioneers are presumed to encounter significant host resistance and resin when attacking compared to later arrivals ("joiners") when the tree is weakened or has succumbed (Berryman 1974; Raffa and Berryman 1979; Wood 1982; Byers 1995). Only males, in the case of *Ips* and *Pityogenes*, or females, in the case of *Dendroctonus*, initiate the entrance tunnel and can be pioneers, but the joining sex in the early stages of colonization must incur some increased risks of resinosis as well. One hypothesis is that since a few pioneers must attack the tree and survive to produce pheromone before numerous others of the population can exploit the resource, pioneers must be the largest and most vigorous beetles of the population. In Fig. 12, an alternative theory is presented for the dispersal and host-seeking flight under various conditions and circumstances. An individual should prefer to orient to pheromone and a tree under colonization, but if fat reserves become relatively low during dispersal, then a pioneer strategy becomes advantageous

compared to exhaustion in flight (as in Fig. 10). As fat reserves become dangerously low, the beetle might attempt to bore into any host tree in the expectation of encountering one of low resistance (Fig. 2). Thus, smaller beetles, such as those that suffered severe larval competition and have low fat (Anderbrant *et al.* 1985; Anderbrant and Schlyter 1989), or those that have used up their fat reserves during a host-seeking flight, regardless of size, are hypothesized to be the pioneers (Byers 1999).

If the pioneer beetle lands on a tree of low resistance that cannot produce sufficient resin to repel the beetle, then it has time to feed and excrete pheromone components with the fecal pellets. This then functions as a beacon to individuals of the population in the surrounding area that a weakened host can be exploited as a food and mate resource (Byers 1996a). Aggregation pheromone is an evolutionarily adaptive signal since only trees too weak to vigorously repel beetles with resin will allow beetles to produce pheromone and joining beetles will likely suffer less mortality than as a pioneer. Some species, usually termed less aggressive ones, such as the European pine shoot beetle, *Tomicus piniperda*, are attracted to monoterpenes volatiles produced after injury to the host tree by biotic or abiotic factors that indicate susceptibility (Byers *et al.* 1985; Byers 1995, 1996a).

7. HOST SEMIOCHEMICALS ATTRACTIVE TO BARK BEETLES

Species of bark beetle that regularly attack and kill living trees (termed "aggressive") have been shown nearly always to possess an aggregation pheromone, usually of two or more components, but are weakly, if at all, attracted by host volatiles alone (Vité and Pitman 1969; Byers 1989a, 1995). However, so-called "secondary" bark beetle species (those that arrive later after the tree has already been killed by the aggressive bark beetles or that feed as saprophytes in decaying trees) may not use an aggregation pheromone, but generally are strongly attracted to either host monoterpenes, ethanol or a combination (Kohnle 1985; Klimetzek *et al.* 1986; Schroeder 1988; Schroeder and Lindelöw 1989). Host volatiles are attractive to a number of forest scolytids including species in the genera *Scolytus*, *Dendroctonus*, *Hylurgops*, *Trypodendron* and *Tomicus* (Goeden and Norris 1964; Rudinsky 1966; Meyer and Norris 1967a; Moeck 1970; Byers *et al.* 1985; Lanne *et al.* 1987; Volz 1988; Lindelöw *et al.* 1992; Hobson *et al.* 1993; Macias-Samano *et al.* 1998).

Ethanol, probably released by microorganisms in decaying woody tissue (Graham 1968; Moeck 1970; Cade *et al.* 1970) and by alcoholic fermentation processes in stressed plants (Kimmerer and Kozlowski 1982; Kelsey 1994, 1996; Kelsey and Joseph 1997, 1999), is attractive to a wide variety of species of bark beetles (Moeck 1970, 1981; Magema *et al.* 1982; Montgomery and Wargo 1983; Kohnle 1985; Klimetzek *et al.* 1986; Schroeder 1987, 1988; Schroeder and Eidmann 1987; Phillips *et al.* 1988; Volz 1988; Chénier and Philogène 1989; Schroeder and Lindelöw 1989; Byers 1992a). Primary alcohols other than ethanol have not been reported as being attractive to scolytids. However, only a few studies have tested methanol (Moeck 1970; Montgomery and Wargo 1983; Byers 1992a); longer chain alcohols up to hexanol did not attract Scolytids in Sweden when they were known to be flying (Byers

1992a). Electroantennogram (EAG) responses of *T. piniperda* to a series of straight-chain alcohols indicated that the antennae respond increasingly to longer chain length up to a maximum between pentanol, and heptanol, and then decrease in responsiveness (Lanne *et al.* 1987). The response spectrum could be due in part to differences in volatility. Thus, although ethanol plays a role in host selection (discussed subsequently), the EAG response for ethanol is lower than for longer-chain alcohols, which are not attractive but rather repellent. 1-Hexanol (from deciduous trees) inhibits response of *T. piniperda* to attractive monoterpenes (Schlyter *et al.* 2000). Ethanol and CO₂ are the usual end products of sugar fermentation by microorganisms whereas methanol is not, which probably explains the evolution of the use of ethanol by forest insects. Moeck (1970) found methanol to be a minor constituent and ethanol a major constituent of extracts from Douglas-fir sapwood attractive to *T. lineatum*.

Various tree monoterpenes (e.g. α -pinene, myrcene, terpinolene, β -pinene, Fig. 5) and turpentine are also attractive to a large number of bark beetle species (Byers *et al.* 1985, 1992a; Phillips *et al.* 1988; Schroeder 1988; Chénier and Philogène 1989; Schroeder and Lindelöw 1989; Miller and Borden 1990; Phillips 1990; Hobson *et al.* 1993). Synergism between ethanol and various monoterpenes (or turpentine) is also of widespread occurrence (Nijholt and Schönherr 1976; Kohnl 1985; Vité *et al.* 1986; Phillips *et al.* 1988; Volz 1988; Schroeder 1988; Chénier and Philogène 1989; Schroeder and Lindelöw 1989; Phillips 1990). These compounds are not only important for primary attraction to plants, but also may play a role in enhancing the bark beetles' response to aggregation pheromone (Bedard *et al.* 1969, 1970; Pitman *et al.* 1975; McLean and Borden 1977; Borden *et al.* 1980, 1981; Paiva and Kiesel 1985; Byers *et al.* 1988; Miller and Borden 1990). Host-tree compounds, ethanol and monoterpenes, elicited increased entering rates of bark beetles *T. lineatum* and *P. chalcographus*, respectively, into pipe traps baited with aggregation pheromone (Vité and Bakke 1979; Bakke 1983; Byers *et al.* 1988). β -Phellandrene (Fig. 5) is slightly attractive alone to *I. pini* and enhances response to pheromone (Miller and Borden 1990), and so the monoterpene might induce entering of holes.

In most of the previously discussed studies, the discovery of host compounds attractive to bark beetles has been by the comparative approach (similar species are known to be attracted) or by surmising that identified chemicals in the host would be attractive. Thus, most studies are incomplete because of the possibility that there are still undiscovered chemicals important for attraction to the host. Byers *et al.* (1985) used the subtractive-combination bioassay and fractionation method (Byers 1992b) to rigorously identify the host volatiles responsible for aggregation of *T. piniperda*. A combination of (-)-(S)- α -pinene, (+)-(R)- α -pinene, (+)-3-carene, and terpinolene, or each alone, was effective in attracting both sexes (Fig. 5 and 11). During the isolation study, designed for detection of synergistic pheromone components, no evidence was found for beetle-produced compounds being attractive, in contrast to most bark beetles that aggregate en masse on hosts (Byers 1989a). Byers *et al.* (1985) quantified the release rates of α -pinene, terpinolene, and 3-carene from a freshly cut log of Scots pine (28 cm x 13 cm diam.) and found them each to be about 15 mg/day. Release of comparable amounts in the field competed favorably with a host log in attracting *T. piniperda*. They theorized that the beetle's attraction to monoterpenes functioned in

the selection of host species because other common tree species have less monoterpenes. In addition, this attraction to monoterpenes served in the beetle's recognition of its host's susceptibility since storm-damaged or felled trees have resinous wounds releasing monoterpenes and are less able to resist attack due to the injuries.

In the isolation of host volatiles attractive to *T. piniperda*, a gas-chromatographic adsorbent (Porapak Q), widely used for trapping insect pheromones, was used to collect headspace air from the infested pine logs. Unfortunately, Porapak Q will not retain ethanol molecules due to their small size. Thus ethanol could be a constituent of the attractive host odor. Vité *et al.* (1986) presented evidence that ethanol enhanced the attraction of *T. piniperda* to α -pinene and terpinolene (identified above) by about eight-fold, but these results are difficult to confirm since the chemical release rates were not given. They proposed that ethanol would be released from diseased trees and thus indicate their suitability to *T. piniperda*. Ethanol is attractive when released on healthy trees since *T. piniperda* were caught in ethanol-baited traps on trees; and these beetles also attacked trees baited with ethanol (Schroeder and Eidmann 1987; Byers 1992a). However, the attraction to ethanol in traps away from trees is weak or negligible, while monoterpenes in these traps are attractive (Schroeder 1988; Schroeder and Lindelöw 1989; Byers 1992a).

Ethylene is another chemical that may be released by diseased or dying trees that could be attractive to bark beetles. Campos *et al.* (1994) found that the olive bark beetle, *Phloeotribus scarabaeoides*, was attracted to logs of olive that released higher amounts of ethylene. Also, a chemical reaction of 2-chloroethylphosphonic acid caused ethylene to be released, which attracted the beetles in the laboratory (Campos and Pena 1995). Trees treated with the chemical released more ethylene and caught more beetles on traps than traps on control trees (Gonzalez and Campos 1995). Treated wood also released more ethylene that resulted in higher densities of attacks by olive bark beetles (Gonzales and Campos 1996). Inoculation of bark beetle-vectored fungi, *Ophiostoma minus* and *O. nigrocarpa*, into slash and loblolly pines induced ethylene release (Popp *et al.* 1995). Ethylene was also released from needles of Monterey pine inoculated with the pitch canker fungal pathogen, *Fusarium circinatum*. However, the twig-infesting *Pityophthorus* spp. was not attracted to ethylene, cut branches, or to branches plus ethylene (Bonello *et al.* 2001), although fungal infected branches were not tested. The authors concluded that host discrimination occurs after landing. More research is needed to determine if ethylene plays a role in primary attraction of other bark beetles to weakened hosts.

8. DISCRIMINATING THE SUITABILITY OF HOSTS

Plant suitability in insects was reviewed by Scriber (1984). A plant's suitability to bark beetles varies with its nutritional quality and composition of deterrents and toxins. Nonhost trees are probably less nutritional to a particular beetle than its hosts. The beetle in most cases would not be expected to be able to detoxify some of the toxins in nonhosts (which are avoided or not usually encountered) that may have evolved for use against herbivorous insects. A beetle would save much time and energy if it could

discriminate between the host and the nonhost and determine the suitability of the host by olfactory means from a distance without the need to land. Sometimes host and nonhost trees are adjacent and the beetle could land by mistake on the nonhost; however, short-range olfactory cues might indicate the inappropriateness of the nonhost bark substrate (Byers *et al.* 1998, 2000). If the beetle still could not decide, boring a short distance into the nonhost might reveal the lack of feeding stimulants or the presence of deterrents causing the beetle to leave (Elkinton and Wood 1980; Byers *et al.* 2000).

9. AVOIDANCE OF COMPETITION AND UNSUITABLE AREAS OF HOSTS

Verbenone is found in relatively large amounts (μg) in male hindguts of several bark beetles of North America, *D. frontalis*, *D. brevicomis*, *D. ponderosae*, and *D. pseudotsugae* (Renwick and Vité 1968; Rudinsky *et al.* 1974; Byers *et al.* 1984; Pierce *et al.* 1987) but in low amounts (ng) in *T. piniperda* (Lanne *et al.* 1987), or essentially absent in *I. paraconfusus*, *I. typographus*, and *P. chalcographus* (Byers 1983b; Birgersson *et al.* 1984, 1990). Verbenone (Fig. 13) inhibits the attraction of these beetles to their respective aggregation pheromones (Renwick and Vité 1969, 1970; Byers and Wood 1980; Bakke 1981; Byers *et al.* 1989c; Byers 1993b).

Exposure of male and female *D. brevicomis* to (+)- and (-)-enantiomers of α -pinene for several hours caused them to produce large amounts of (+)- and (-)-*trans*-verbenol in their hindguts (Fig. 13, Byers 1983c). However, the biosynthesis of verbenone in these beetles was not affected by exposure to α -pinene enantiomers, even though verbenone is structurally similar to α -pinene (Fig. 5) and is found in males landing on trees (Renwick and Vité 1968, 1970; Byers *et al.* 1984). The (-)-enantiomer of *trans*-verbenol (Fig. 13) inhibits female *D. brevicomis* from entering holes and may serve as a signal to arriving females that they should avoid areas colonized by conspecifics (Byers 1983c).

Both verbenone and *trans*-verbenol are produced by *D. brevicomis* beetles in the greatest amounts early in colonization so it was suggested that they play a role in reducing intraspecific competition (Byers *et al.* 1984), as well as interspecific competition with *I. paraconfusus* (Byers and Wood 1980). However, verbenone (and possibly *trans*-verbenol) are also produced increasingly in ageing logs infested by bark beetles (Birgersson and Bergström 1989; Byers *et al.* 1989c). A common bacterium, *Bacillus cereus*, also isolated from *I. paraconfusus*, can make *cis*- and *trans*-verbenol from α -pinene (Brand *et al.* 1975). Several yeasts from *I. typographus* can interconvert the verbenols, and when grown in a phloem medium they produced the oxygenated monoterpenes α -terpineol, borneol, myrtenol, terpenene-4-ol and *trans*-pinocarveol, compounds also shown to be released increasingly from bark beetle holes with age of attack (Leufvén *et al.* 1984, 1988; Birgersson and Bergström 1989). A mycangial fungus grown in culture media converted alcohol products of α -pinene to verbenone, the end product (Brand *et al.* 1976). These microorganisms are introduced by bark beetles during colonization and after buildup may release verbenone, thus signaling to flying beetles that remaining in these bark substrates would entail competition with established bark beetle colonies. Recently, verbenone was found in twigs of eastern

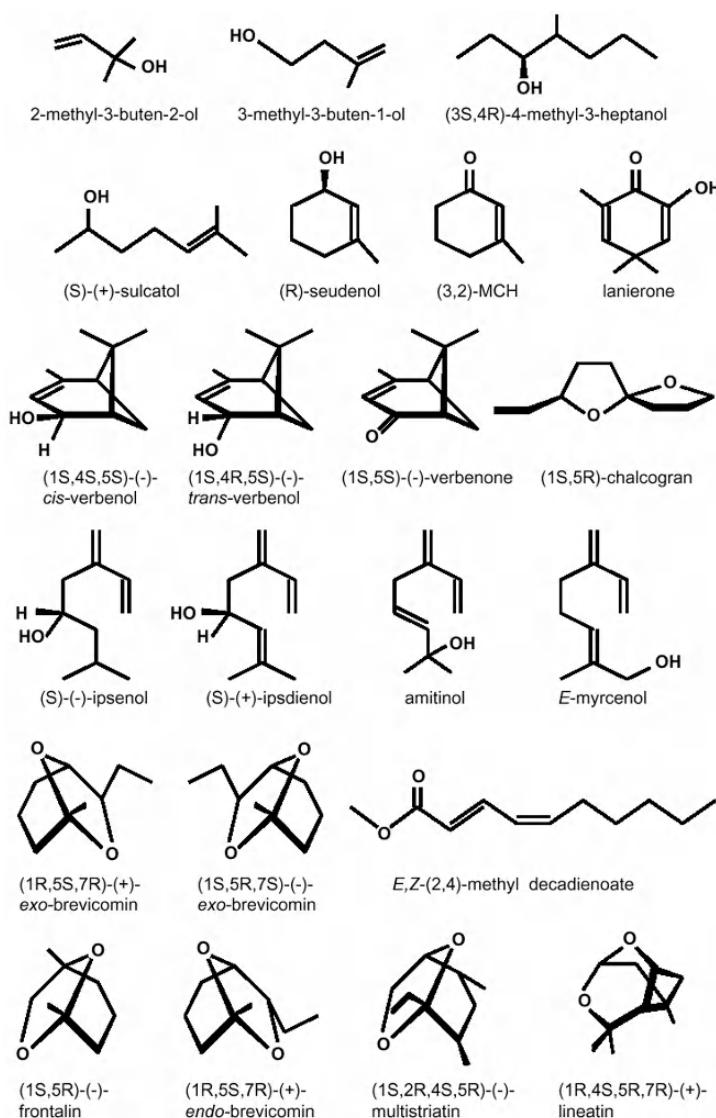


Figure 13. Pheromone components of bark beetles. Key: aggregation component (a), inhibitor of aggregation (i). Row 1: 2-methyl-3-buten-2-ol (a, *I. typographus*); 3-methyl-3-buten-1-ol (a, *I. cembrae*), 4-methyl-3-heptanol (a, *S. multistriatus*). Row 2: sulcatol (a, *G. sulcatus*, *G. retusus*); seudenol (D. pseudotsugae, D. rufipennis, D. simplex); MCH (i, D. pseudotsugae); lanierone (a, *A. pini*). Row 3: cis-verbenol (a, *I. paraconfusus*, *I. typographus*, *I. calligraphus*); trans-verbenol (a, *D. ponderosae*, *T. minor*; i, *D. brevicomis*); verbenone (i, *Dendroctonus*); chalcogran (a, *Pityogenes*). Row 4: ipsenol (a, *Pityokteines curvidens*, and many *Ips*: e.g. *I. paraconfusus*, *I. grandicollis*), ipsdienol (a, many *Ips*, e.g. *I. paraconfusus*, *I. duplicatus*, *I. pini*, *I. calligraphus*, *I.*

avulsus); amitinol (*a*, *I. amitinus*); *E*-myrcenol (*a*, *I. duplicatus*). Row 5: (+)-exo-brevicomin (*a*, *D. brevicomis*, *Dryocoetes*); (-)-exo-brevicomin (*a*, *Dryocoetes*); methyl decadienoate (*P. chalcographus*). Row 6: frontalin (*a*, many *Dendroctonus*); endo-brevicomin (*i*, *D. frontalis*); multistriatin (*a*, *S. multistriatus*); lineatin (*a*, *T. lineatum*). References to above pheromones are in reviews by Borden (1982) and Byers (1989a), and the following (Bakke 1975; Baker et al. 1977; Lanne et al. 1987; Borden et al. 1987; Byers et al. 1989b, 1990a, b; Teale et al. 1991; Camacho et al. 1993).

cottonwood, *Populus deltoids* (personal comm. from Carlos Flechtmann, in Huber et al. 1999).

Myrcene and α -pinene from host trees can be used as precursors of pheromones and allomones in some species of conifer-feeding bark beetles. However, recent research has shown that the majority of ipsdienol and ipsenol in *Ips* bark beetles results from *de novo* biosynthesis from simple acetate and mevalonate precursors (Seybold and Tittiger 2003). The later steps in the isoprenoid pathway lead to geranyl diphosphate and myrcene before being stereoslectively, and species-specifically, converted to various enantiomers of myrcene-like alcohols (e.g., ipsdienol, ipsenol, *E*-myrcenol, amitinol) that are pheromone components (Seybold et al. 2000; Seybold and Tittiger 2003). *D. brevicomis*, *I. paraconfusus* and *I. pini* occur sympatrically in California and Oregon and compete for ponderosa pine bark. Myrcene vapors can be converted only by male *D. brevicomis* to (+)-ipsdienol (Fig. 13), also a pheromone component of its competitor *I. paraconfusus* (Hughes 1973; Byers 1982). (+)-Ipsdienol inhibits response of both *D. brevicomis* and *I. pini* to their synthetic aggregation pheromones (Birch et al. 1980a; Lanier et al. 1980; Byers 1982). In Europe, ipsdienol, a pheromone component of *I. duplicatus* could act as an allomone to inhibit response of *I. typographus* (Byers et al. 1990b; Schlyter et al. 1992). Mated males of *I. typographus* produce small amounts of ipsdienol and ipsenol during colonization that might function in avoiding competition (Birgersson et al. 1984; Birgersson and Leufvén 1988; Birgersson et al. 1988). Although, ipsdienol was previously thought to be an aggregation pheromone component of *I. typographus* (Bakke et al. 1977), other studies have shown the compound to be either inactive or inhibit attraction of these beetles to *cis*-verbenol and methyl butenol, the most potent components (Schlyter et al. 1987b, c). Also, ipsdienol was not found in single males in a nuptial chamber, while it was detected in small amounts in later phases of attack when males had been joined by one or more females (Birgersson et al. 1988).

P. chalcographus of Europe (Fig. 14) produces a two- component aggregation pheromone consisting of chalcogran and methyl decadienoate (Francke et al. 1977; Byers et al. 1988, 1990a). Both chalcogran and methyl decadienoate (Fig. 13) cause *I. typographus* to avoid landing on traps releasing their aggregation pheromone components (*cis*-verbenol and methyl butenol) (Byers 1993b). However, *P. chalcographus* attraction to its pheromone was not inhibited by pheromone components of *I. typographus* even though the latter, and larger, beetle wins in competitive situations when both species attack simultaneously (Byers, unpublished).



Figure 14. *P. chalcographus* searching for a boring site on the bark of Norway spruce

However, if *P. chalcographus* precedes *I. typographus* on the host by just a few days then the former species will win in competitive situations (Byers, unpublished). Verbenone is increasingly released as colonized areas of *I. typographus* age (Birgersson and Bergström 1989) and the compound is inhibitory to *P. chalcographus* (Byers 1993b), as well as to *I. typographus* (Bakke 1981; Schlyter *et al.* 1989).

10. AVOIDANCE OF DECAYING OR FULLY COLONIZED HOSTS

As mentioned above, some microorganisms isolated from bark beetles or their gallery walls, may convert α -pinene to *cis*- and *trans*-verbenol, or *trans*-verbenol to verbenone. It was proposed that this process may account for termination of attack (Brand *et al.* 1976). Verbenone is increasingly released from ageing logs of spruce and pine colonized by bark beetles (*I. typographus*, Birgersson and Bergström 1989; *T. piniperda*, Byers *et al.* 1989c), possibly due to the activity of microorganisms. Byers (1989a, b) speculated that if verbenone is a consistent signal of microbial activity in decaying hosts, then bark beetle species may have evolved an avoidance to this compound (a kairomone) in order to avoid unsuitable hosts. The bark beetle then could have evolved to produce verbenone as a pheromone that reduced intraspecific competition, since the avoidance response was already existent. Other bark beetle species might then evolve to avoid species that produced verbenone (as an allomone), and so avoid interspecific competition. Sympatric species on the same host might coevolve responses to, and/or production of, verbenone since the chemical could serve as a signal for several types of beneficial information (kairomone, pheromone, and allomone).

Verbenone was reported to inhibit pheromone responses of over 10 species of bark beetle (Borden 1997). However, verbenone does not always inhibit bark beetles. For example, *H. palliatus* feeds in unhealthy or dying Scots pines that release verbenone

(Byers *et al.* 1989c), and the beetle's attraction to ethanol was not inhibited by verbenone (Byers 1992a). Angiosperm trees in a state of decay may not release verbenone since they probably do not have α -pinene, thus *T. domesticum* could evolve to avoid degrading nonhost pines by avoiding verbenone (Byers 1992a). Another bark beetle, *P. bidentatus*, attacks diseased limbs of Scots pine and is not affected by release rates of verbenone, which inhibit more aggressive bark beetles. This is probably because verbenone is expected to be present from the diseased host limbs (Byers *et al.* 2000). In the case of conifer bark beetles, Verbenone is increasingly implicated as a general sign of host unsuitability in conifer-killing bark beetles (due to microbial decay or competition with bark beetles). Therefore, it is paradoxical that conifers have not evolved the capacity to convert α -pinene, which they have in abundance, to verbenone in order to repel aggressive bark beetles.

Ethanol, also, sometimes reduces response to attractive baits. Klimetzek *et al.* (1986) tested different release rates of ethanol (24 to 125 mg/day) with an unreported release rate of α -pinene and terpinolene and found that the higher releases of ethanol inhibited attraction of *T. piniperda*. However, a control with either ethanol alone or terpenes alone was not reported. Schroeder (1988) increased the release of ethanol in five dosages over an even wider range from 0 to 50 g/day in combination with a 240-mg/day α -pinene release. In this case, the attraction of *T. piniperda* declined linearly with the logarithm of ethanol release, which is in conflict with the theory of Vité *et al.* (1986) that ethanol was synergistic with monoterpenes.

Schroeder and Lindelöw (1989) provided the first evidence that could integrate the disparate results. They found that high release rates of α -pinene were most attractive to beetles and that ethanol releases alone from 0 to 3 g/day were barely attractive. At a low release rate of α -pinene (2.4 or 22 mg/day), and thus low attraction, lower release rates of ethanol from 0 to 3 g/day had a synergistic effect when combined with α -pinene in attracting beetles (Schroeder and Lindelöw 1989). Their results are supported by Byers (1992a); i.e., a weak enhancement of attraction by ethanol at low release rates when blended with three host monoterpenes, but no observable effect of ethanol on the greater attraction to higher release rates of monoterpenes.

Ethanol released at even higher rates, 120 mg/day (Klimetzek *et al.* 1986) or 50 g/day (Schroeder 1988), inhibited the response of *T. piniperda* to monoterpenes. Therefore, the beetle could find diseased, but physically uninjured, trees by a weak response to a synergism between low monoterpene release rates and moderate ethanol rates - the hypothesis of Vité *et al.* (1986). Beetles would occasionally penetrate these trees, and if low in resistance would permit continued feeding. Resinosis and monoterpene release from the entrance holes would elicit increased numbers of beetles joining in a mass attack. Injured trees with wound oleoresin, and trees under attack with "pitch tubes", would have a higher monoterpene release and attract the greatest numbers of beetles, according to Byers *et al.* (1985). Trees with high ethanol release rates would indicate a tree in advanced decay and unsuitable for reproduction, and thus to be avoided, as theorized by Klimetzek *et al.* (1986). High monoterpene releases from trees (freshly wounded and not dead) would not naturally coincide with high ethanol release rates (presumably during decay after death). In addition, other compounds such as verbenone from decaying hosts would inhibit response to

monoterpenes from unsuitable hosts (discussed in the next part). These studies emphasize the need for releasing semiochemicals at known rates during tests in the field. In addition, measurements of the natural release rates of ethanol and monoterpenes from various host and nonhost substrates are necessary for further understanding of bark beetle chemical ecology.

11. AVOIDANCE OF NONHOSTS

According to studies discussed previously, bark beetles find their host tree by attraction to host volatiles (or after random landing and probing), as well as by avoiding chemicals from colonized hosts or decaying hosts. However, it is becoming increasingly apparent that many beetles avoid nonhost trees due to specific odors. It is inherently more difficult to isolate repellents and inhibitors used in avoidance behavior than to isolate attractants since tests of avoidance require one to first isolate the attractive host odors and then present these with and without the possibly inhibitory nonhost odors. Several studies indicate that at least some species of bark beetle avoid nonhost volatiles during their search for host trees. The attraction of both *T. piniperda* and *H. palliatus* to ethanol (1-6 g/day) was reduced by odors from cut logs of nonhost trees, birch, *Betula pendula*, and aspen, *Populus tremula* (Schroeder 1992). In future experiments, host logs (or monoterpenes and ethanol) should be tested instead of ethanol alone to simulate the host tree. Dickens *et al.* (1992) reduced the attraction response of *D. frontalis*, *I. grandicollis* and *I. avulsus* to aggregation pheromone by releasing the green-leaf volatiles, 1-hexanol and hexanal. *T. domesticum* colonizes wood of deciduous trees (e.g. *Fagus sylvatica*, *Quercus* spp. *Betula* spp.) and is known to be attracted to ethanol (Magema *et al.* 1982; Paiva and Kiesel 1985). Monoterpenes of Scots pine and verbenone (from decaying conifers) reduced response of this species to ethanol (Byers 1992a) and would provide a mechanism for avoiding nonhosts and unsuitable colonization areas. This also is valid for the hardwood-breeding species *Anisandrus dispar* (Schroeder and Lindelöw 1989).

Recently, the spruce bark beetles *Ips typographus* and *Pityogenes chalcographus* were shown to avoid volatiles of nonhost birch trees (both from bark and leaves, Fig. 15), which suggests the possibility that beetles may not enter areas of primarily birch (Byers *et al.* 1998). However, it is more certain that the beetle would leave a birch tree after landing due to a relatively high concentration of repellent nonhost volatiles at the surface of the bark.

There is increasing evidence that aggregation responses to semiochemicals by conifer-infesting bark beetles in several genera are reduced by volatiles from nonhost angiosperm trees (e.g. *Betula*, *Populus*, *Acer*) (Dickens *et al.* 1992; Schroeder 1992; Schlyter *et al.* 1995; Wilson *et al.* 1996; Guerrero *et al.* 1997; Borden *et al.* 1997, 1998; Deglow and Borden 1998; Byers *et al.* 1998, 2000; Poland *et al.* 1998; Zhang *et al.* 1999a, b, 2000, 2001; Huber *et al.* 1999, 2000, 2001; Huber and Borden 2001a, b; Poland and Haack 2000; Schlyter *et al.* 2000; Zhang 2003; Zhang and Schlyter 2003). These studies have found that some of the most important nonhost angiosperm compounds are (*Z*)-3-hexen-1-ol, (*E*)-2-hexen-1-ol, and 1-hexanol mostly from leaves, as well as *trans*-conophthorin from bark.



Figure 15. *Pityogenes chalcographus* were induced to land on birch trees by baits of aggregation pheromone but the individuals did not stay more than about 2 minutes due to odors from the bark (probably 1-hexanol, trans-conophorin, and other unidentified compounds, Byers et al. 1998).

Volatiles from leaves or bark of nonhosts birch (*Betula pendula*) and Norway spruce (*Picea abies*) also dramatically reduced the attraction of the bark beetle, *Pityogenes bidentatus*, to their aggregation pheromone components (*cis*-verbenol and grandisol) in the field. Surprisingly, odors from either the needles or bark of the host Scots pine, *Pinus sylvestris*, similarly inhibited attraction. Monoterpene of pine and spruce (α -pinene, β -pinene, terpinolene, and 3-carene), as well as ethanol, chalcogran and some nonhost green leaf alcohols [(*Z*)-3-hexen-1-ol, (*E*)-2-hexen-1-ol, and 1-hexanol], also reduced catches. Collections of volatiles from the field-tested plant tissues indicated they released monoterpene in amounts similar to the synthetics that inhibited responses. The varied plant and insect sources of these inhibitory compounds indicate that *P. bidentatus* bark beetles have evolved several strategies to increase their fitness by avoiding nonhost and unsuitable host trees in a complex olfactory landscape.

12. FEEDING STIMULANTS AND DETERRENTS

Presumably, a beetle must not only determine that the bark underneath is the proper host and is suitable for reproduction, but it must also judge potential competition by whether nearby areas have bark beetles beginning their attacks. Many species of bark beetle bore their entrance holes in a spaced or uniform pattern, indicating the beetles try to avoid competition (Byers 1984, 1992c, 1996c). In some cases, the beetle will bore through the outer bark, regardless of the host, until it encounters the phloem. For example, *I. paraconfusus* will bore through the outer bark of the nonhost white fir, *Abies concolor*, as readily as through bark of the host ponderosa pine. However, the

beetle only bores about 1 mm in white fir phloem and then leaves (Elkinton and Wood 1980). In the initial boring phase, gustatory (and possibly olfactory) stimulants, deterrents, and physiological factors are considered in a decision whether to continue feeding and excavating the gallery. The beetle probably can determine whether the host tissue is of good quality in terms of nutritional and moisture factors (Webb and Franklin 1978). The phloem of ponderosa pine, sugar pine (*P. lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), red fir (*Abies magnifica*), and several other conifers contain about equal amounts of glucose, fructose and sucrose (Smith and Zavarin 1960). Bark beetles have been induced to feed or lay eggs on several diets, but the most successful diets contained some percentage of host (usually phloem) tissue (Jones and Brindley 1970; Richeson *et al.* 1970; Whitney and Spanier 1982; Conn *et al.* 1984; Byers and Wood 1981b), indicating the presence of feeding or ovipositional stimulants. In experiments to introduce antibiotics, sucrose was found to increase feeding by *I. paraconfusus* in powdered cellulose diets (Byers and Wood 1981b).

Few studies have attempted to isolate feeding stimulants in conifer-feeding bark beetles, and none have isolated specific compounds. Elkinton *et al.* (1981) extracted ponderosa pine phloem successively with diethyl ether (partitioned with water), water and then methanol, and added these extracts to powdered cellulose diets. *I. paraconfusus* beetles were then given a choice between a control diet and a diet with extract. The diet with the ether extract did not cause beetles to remain longer and there was no preferential boring, but the extract did cause more feeding compared to the control. The water partition of the ether extract only caused beetles to remain longer. The water extract elicited more boring and feeding, while the methanol extract was inactive since feeding stimulants had already been extracted by the ether and water treatments. These results indicate that several compounds function in gustatory preferences. Solvent (methanol-water-benzene) extracts of lodgepole pine (*Pinus contorta*) bark were absorbed by tissue paper and shown to induce feeding by *D. ponderosae* (Raffa and Berryman 1982). The benzene fraction induced biting but not feeding while the polar fraction (water-methanol) caused continued feeding. Differences in feeding preferences for bark extracts varied widely between trees, but these differences could not be attributed to amounts of 13 monoterpenes as determined by gas chromatography (GC). Also, extracts of trees judged resistant, because beetles that had been forced to attack in cages either refused or discontinued attack, were as stimulatory to feeding beetles as those from susceptible trees. In contrast, Hynum and Berryman (1980) found greater feeding preferences for bark extracts of susceptible lodgepole pines than for comparable extracts of resistant lodgepole pine. However, the susceptible trees had been killed by the beetles before solvent extraction, which might have allowed microorganisms to produce additional feeding stimulants. White (1981) also found differences in gustatory deterrent and stimulatory properties of bark extracts from different trees of loblolly pine, *P. taeda*.

Most work on feeding stimulants and deterrents in beetles of deciduous trees involves the elm bark beetle, *Scolytus multistriatus*. Vanillin and syringaldehyde are short-range attractants inducing feeding in *S. multistriatus* (Meyer and Norris 1967b). Feeding stimulants were isolated from the bark of American elm, *Ulmus americana*, of which one was partially identified as a pentacyclic triterpene (Baker and Norris 1967).

Later some lignin intermediates and phenolics were suggested (Meyer and Norris 1974). Doskotch *et al.* (1973) succeeded in identifying another feeding stimulant in elm bark as a catechin xyloside. A tritiated catechol-feeding stimulant was shown to penetrate the gustatory receptor of *S. multistriatus* (Borg and Norris 1971). *Scolytus rugulosus* is stimulated to feed in fruit trees by several phenolic compounds (Chararas *et al.* 1982).

Scolytus multistriatus was induced to feed on sucrose pith disks when volatiles from benzene extracts of bark of nonhost trees (Eastern cottonwood, *Populus deltoides*, and yellow buckeye, *Aesculus octandra*) were placed 7 mm away (Baker and Norris 1968). However, these nonhost trees were not fed upon since they contained nonvolatile feeding deterrents, as shown by lowered feeding on a mixture of host and nonhost extracts compared to host extracts. *S. multistriatus* beetles do not attack the nonhost hickory, *C. ovata*, due to the presence of juglone (5-hydroxy-1,4-naphthoquinone), a feeding deterrent (Gilbert *et al.* 1967). Elm tree tissue infected by the fungus *Phomopsis oblonga* is avoided by *S. multistriatus* due to several complex feeding deterrents. These include oblongolide (isomer of dimethylnaphthofuranone), a norsesquiterpene lactone, two tiglic esters of 5,6-dihydro-5-hydroxy-2-pyrone, nectriapyrone, 4-hydroxyphenylethanol, 5-methylmellein as well as acids of 2-furoic, orsellinic, 3-nitropropanoic, and mellein-5-carboxylic (Begley and Grove 1985; Claydon *et al.* 1985).

Diterpene acids (e.g., abietic, levopimamic, neoabietic and palustric acids) have been isolated from ponderosa pine oleoresin (Anderson *et al.* 1969; Himejima *et al.* 1992) and these are known to be antifeedants against aphids and sawflies (Wagner *et al.* 1983; Schuh and Benjamin 1984; Rose *et al.* 1981). However, these compounds have not been tested on bark beetles. Tannins, phenolics and terpenoids that can inhibit feeding or digestion in other insects (Berenbaum and Isman 1989) could also affect bark beetles. Ponderosa pine bark extracted first with ether yields behenic and lignoceric acids, fatty alcohols, resin acids, and flavonols (quercetin and myricetin, pinoquercetin, pinomyricetin and dihydroquercetin). A subsequent acetone extract contains tannins and phlobaphenes, while a third hot-water extract has tannin (6-11 % dry weight of bark) and carbohydrates (Anderson 1962; Anderson *et al.* 1969). Many of these compounds are found only in the outer bark and although they may be important in deterring nonhost bark beetles, at least the host-adapted *I. paraconfusus* does not eat the outer bark (Elkinton and Wood 1980). However, host compounds of lower volatility at close range may be important in deterring attacks after landing. For example, Byers *et al.* (1998, 2000) found that *P. chalcographus* and *P. bidentatus* would not attack non-host birch or spruce, respectively, after briefly landing in response to pheromone baits (Fig. 13).

13. MANAGEMENT OF BARK BEETLES USING SEMIOCHEMICALS

Pheromones have been used in the field to disrupt mate finding in moths (Hodges *et al.* 1984; Zvirgzdins *et al.* 1984; Flint and Merkle 1984; Campion *et al.* 1989), beetles (Villavaso and McGovern 1981; Villavaso 1982), and flies (Jones *et al.* 1982). In most cases, relatively large quantities of pheromone (consisting of several pheromone

components) are more or less evenly distributed throughout the field to adapt (overload) sensory receptors or habituate behavioral response ('confusion') or to exhaust the individuals in orientation attempts (i.e. "wild-goose chases"). The best successes so far have involved straight-chain olefinic acetates, alcohols, and aldehydes of moths (Baker 1989; Byers 2002).

Bark beetles that colonize forest trees may present problems for disruption techniques for several reasons, one is that their pheromone components, usually oxygenated monoterpenes, are more volatile than moth straight-chain hydrocarbons (Byers 1989a). More important perhaps is that compared to moths even larger quantities are expected to be required for disruption of bark beetles since the latter individuals generally release higher rates (ng to $\mu\text{g}/\text{h}$) of pheromone components than moths (pg to ng/h) (Browne *et al.* 1979; Schlyter *et al.* 1987a; Bergersson and Bergström 1989; Byers *et al.* 1990a, b; Ramaswamy and Cardé 1984; Du *et al.* 1987). Furthermore, even higher quantities of synthetic pheromone are required to compete with pest bark beetles that typically release semiochemicals in large aggregations on their host tree as compared to individual female moths. Possibly because of these reasons, as well as the fact that both sexes are attracted by pheromone, several attempts to control bark beetles have used the mass-trapping method. This method employs traps, either sticky-screen (Browne 1978) or cylinder with holes/barrier type (Bakke 1989), baited with synthetic pheromone components. Traps releasing pheromone components have been used in control programs to lure other pest insects such as moths to their death (Haniotakis *et al.* 1991; Sternlicht *et al.* 1990).

Previous theoretical attempts at determining the effectiveness of pheromone mass trapping have used population dynamic models (Knipling and McGuire 1966; Roelofs *et al.* 1970; Beroza and Knipling 1972; Nakasuji and Fujita 1980; Nakamura 1982; Barclay 1984; Fisher *et al.* 1985; Barclay 1988; Barclay and Li 1991). These models are mathematically complex and make several assumptions about beetle survival and mating rates, as well as attraction rates to pheromone traps, which limits their application. There have been no models where 'insects' are moved in 'real' time and space in relation to traps of specific dimensions and positions, although two-dimensional models of 'correlated random walks' are probably close to reality (Byers 1993a, 1996a, b, 1999, 2000, 2001).

The first major attempt to control bark beetle populations using pheromone-baited traps was done in 1970 in California (Bedard *et al.* 1979; Wood 1980; DeMars *et al.* 1980). Large (1 x 2 m) sticky screens baited with *exo*-brevicomin and frontalbin, pheromone components of the western pine beetle, *Dendroctonus brevicomis* (Silverstein *et al.* 1968; Kinzer *et al.* 1969), plus the host monoterpene, myrcene (Bedard *et al.* 1969), were placed in ponderosa pine forests at Bass Lake, California. In four plots of 1.3 km² each, 66 pheromone traps were deployed in a grid of about 161 m spacing. Over a million beetles were caught and the test appeared to be successful since the number of trees killed by the beetle declined to 10% the pre-treatment level for several years (Bedard *et al.* 1979; Wood 1980; DeMars *et al.* 1980).

Norway and Sweden have extensive conifer forests, and in the 1970's a major outbreak of the European spruce engraver, *I. typographus*, devastated many areas (Austarå *et al.* 1984). Since the pheromone of this beetle had recently been identified

as a mixture of 2-methyl-3-buten-2-ol and (1S,4S,5S)-*cis*-verbenol (Bakke *et al.* 1977), an extensive mass-trapping control program was initiated in 1979 and may have led to the decline of outbreaks after 1980 (Bakke 1985, 1989; Vité 1989). Several other European studies have reported successful control of bark beetles with the intensive use of pheromone-baited traps (Vrkoc 1989; Richter 1991; Jakus 1998).

These pioneering studies of mass trapping using pheromones did have some deficiencies. Many of these studies lacked appropriate controls or check plots so it is not possible to determine the success of the control programs. Also, a combination of experience and intuition led to subjective estimates as to the level of trapping and the pheromone release rate ultimately employed for control of the population. Certainly, these questions are complex and it is not surprising that they were not solved entirely. Models that employ various parameters can help to understand mass trapping. The parameters include types of pheromone traps and spacings, bait strengths, and treatment durations in conjunction with different population densities and host stand conditions. This is a task with nearly unlimited possibilities. However, the models will not be a substitute for experimentation with some of the parameters in the field.

Weber (1987) was critical of pheromone trapping of bark beetles for control since he calculated that enough beetles would remain untrapped to then colonize susceptible hosts and replenish the population density due to an absence of competition. This assessment is conjectural since trapping experiments with different traps and pheromone dosages were not done. Also, the complementary effects of other forest management practices, such as removal of slash and infested trees to reduce populations, were not considered. The consequences of population reduction to densities below the threshold required to overcome tree resistance by means of a mass attack were also not considered (Berryman and Stenseth 1989; Berryman *et al.* 1989). In contrast, some models (Byers 1993a, 1996a) indicate that insect populations can potentially be drastically reduced with a small number of traps with an effective radius that seems smaller than what one might intuitively expect for pheromone baits. However, whether this population reduction is sufficient to affect natural matings and population levels over several generations is still an open question.

In many past control programs that used pheromone trapping, there has been the problem of finding control areas to determine whether the treatment has been effective. However, several monitor traps placed inside the control area (or even the control traps themselves) will indicate the population density and the progress of the control program. If no more insects are being caught, then obviously the control is a success, unless the flight period is over. This can be determined by monitoring traps placed in untreated areas, some distance away, but still within the same general biotope and climatic regime. Usually only one beetle or pair of bark beetles begin attack of a tree and at this time pheromone release is relatively low compared to a few days later when thousands of beetles participate in the mass attack. Thus, it seems advantageous to initiate mass trapping before beetles swarm in the spring and have time to build aggregations that can compete with traps for attraction of dispersing beetles. The population levels need only be reduced below the thresholds required to kill trees. In moths, reproduction can occur despite high trapping efficiency suggested

by the model because male moths may mate with females before being trapped (Roelofs *et al.* 1970).

There are several variables that can influence the trapping of the population so it does not follow the predictions based on simulation models or iterative equations. For example, the 'flight' speed used in models (2 m/s, Byers *et al.* 1989a) may be more than the speed observed for flying or wind-blown insects since they often stop to rest or feed (Byers 1996a). Also, in the case of bark beetles, there can be host volatiles that attract the beetles during their swarming flight, or trees under colonization where aggregation pheromones are released (Byers 1989a). Several studies have indicated that as the density of calling female moths increase, the catches on pheromone-baited traps increase relatively less or may decline, probably due to competition between the natural and synthetic sources (Raulston *et al.* 1979; Nakamura 1982; Witz *et al.* 1992). Traps can also be overloaded with caught insects, and synthetic pheromone release rates can diminish over time, which will cause catches in nature to differ from model predictions. Pheromone release rates can decrease (and the effective pheromone trap radius) due to compound degradation and in other cases due to exponential decline from substrates (e.g. rubber septa). Methyl decadienoate, a pheromone component of the bark beetle *Pityogenes chalcographus*, is especially sensitive to sunlight, and attraction rates can be halved in a few hours unless the compound is shaded. In models, the shape of pheromone plumes emanating from traps has been transformed to the *EAR*, which also reduces the correspondence between reality (some type of Gaussian time-averaged plume depending on the wind) and the models (a circle). Much research in the practical area is needed, unfortunately this is expensive and time and labor consuming.

14. ECOLOGICAL ASPECTS AND CONCLUDING REMARKS

Bark beetles are a keystone species, meaning that they are evolutionarily and historically a dominant component of the natural forest ecosystem. Without bark beetles, many thousands of microbial, nematode, mite, and insect species would become extinct since they rely on bark beetles to create a habitat for them (Dahlsten and Stephen 1974). The aggressive interactions between bark beetles and trees also must affect population genetics and evolution. Trees and parts of trees (shoots, cones, limbs) are killed when eaten by bark beetles or by fungi introduced during feeding so there is certainly a severe selection pressure on trees to evolve resistance mechanisms, which they have, but bark beetles have also evolved counter-resistance mechanisms (Byers 1995). This so-called evolutionary arms race continues, especially with man's activities introducing new species of tree and bark beetle. In spite of a general resistance having evolved in conifers, older, weak and unhealthy trees are removed by bark beetles, and microbial diseases, which greatly influences the age and species structure of the forest.

The main reason bark beetles have been studied so extensively is that they are perceived as pests that damage forests. Certainly at outbreak levels, bark beetles kill vast areas of conifer forests, which drastically affect the ecology and species composition for a considerable time. In forest plantations used only for the production

of fiber, bark beetles are indeed pests. In forests with residential tracts, bark beetles are a threat to the desired stability of old-growth stands. In wilderness areas and recreational forests, bark beetles may be tolerated as part of the natural ecosystem. In fact, bark beetles are a keystone species that naturally fluctuates in abundance as the forest ages and succession processes occur. Many forests are designated as multi-use, meaning that they are for recreation and for timber production. Obviously some uses preclude other uses, or are at least in conflict. There often must be a compromise between producing the most fiber per unit area (short term interest) and the maintenance of natural forest biodiversity (long term interest). Over the long term (longer than a human's lifetime), most forest ecosystems require disturbances that remove old trees and open the land to a succession of plant and animal species guilds. Either bark beetles or fire, or both, are well known to carry out this natural long-term cycling function. Man, however, usually does not appreciate these perturbative cycles that progress over many decades. The discussion about the role of bark beetles, fire, and overuse of forests by mankind will continue for many years to come, but research in all these areas will help to understand how to better utilize and enjoy nature.

15. REFERENCES

- Anderbrant, O., Schlyter, F. 1989. Causes and effects of individual quality in bark beetles. *Holarctic Ecology*, 12, 488-93.
- Anderbrant, O., Schlyter, F., & Birgersson, G. 1985. Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus*. *Oikos*, 45, 89-98.
- Anderson, A.B. 1962. The influence of extractives on tree properties II. Ponderosa pine (*Pinus ponderosa* Dougl.). *Journal of the Institute of Wood Science*, 10, 29-47.
- Anderson, A.B., Riffer, R., & Wong, A. 1969. Monoterpene, fatty and resin acids of *Pinus ponderosa* and *Pinus jeffreyi*. *Phytochemistry*, 8, 873-5.
- Atkins, M.D. 1960. A study of the flight of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae) II. Flight Movements. *Canadian Entomologist*, 92, 941-54.
- Atkins, M.D. 1961a. A study of the flight of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae) III. Flight capacity. *Canadian Entomologist*, 93, 467-74.
- Atkins, M.D. 1966. Laboratory studies on the behavior of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins. *Canadian Entomologist*, 98, 953-91.
- Atkins, M.D. 1969. Lipid loss with flight in the Douglas-fir beetle. *Canadian Entomologist*, 101, 164-65.
- Atkins, M.D. 1975. On factors affecting the size, fat content and behavior of a scolytid. *Zeitschrift für angewandte Entomologie*, 78, 209-18.
- Austarå, O., Annila, E., Bejer, B., & Ehnström, B. 1984. Insect pests in forests of the nordic countries 1977-1981. *Fauna Norvegica*, Series B, 31, 8-15.
- Austarå, O., Bakke, A., & Midtgård, F. 1986. Response in *Ips typographus* to logging waste odors and synthetic pheromones. *Journal of Applied Entomology*, 101, 194-98.
- Baker, B.H., Hostetler, B.B., & Furniss, M.M. 1977. Response of eastern larch beetle (Coleoptera: Scolytidae) in Alaska to its natural attractant and to Douglas-fir beetle pheromones. *Canadian Entomologist*, 109, 289-94.
- Baker, J.E., & Norris, D.M. 1967. A feeding stimulant for *Scolytus multistriatus* (Coleoptera: Scolytidae) isolated from the bark of *Ulmus americana*. *Annals of the Entomological Society of America*, 60, 1213-15.
- Baker, J.E., & Norris, D.M. 1968. Further biological and chemical aspects of host selection by *Scolytus multistriatus*. *Annals of the Entomological Society of America*, 61, 1248-55.
- Baker, T.C. 1989. Sex pheromone communication in the Lepidoptera: new research progress. *Experientia*, 45, 248-62.

- Baker, T.C., Hansson, B.S., Löfstedt, C., & Löfqvist, J. 1988. Adaptation of antennal neurones in moths is associated with cessation of pheromone-mediated upwind flight. *Proceedings of the National Academy of Sciences, U.S.A.*, 85, 9826-30.
- Bakke, A. 1975. Aggregation pheromone in the bark beetle *Ips duplicatus* (Sahlberg). *Norwegian Journal of Entomology*, 22, 67-69.
- Bakke, A. 1981. Inhibition of the response in *Ips typographus* to the aggregation pheromone; field evaluation of verbenone and ipsenol. *Zeitschrift für angewandte Entomologie*, 92, 172-77.
- Bakke, A. 1983. Dosage response of the ambrosia beetle *Trypodendron lineatum* (Oliver) (Coleoptera, Scolytidae) to semiochemicals. *Zeitschrift für angewandte Entomologie*, 95, 158-61.
- Bakke, A. 1985. Deploying pheromone-baited traps for monitoring *Ips typographus* populations. *Zeitschrift für angewandte Entomologie*, 99, 33-9.
- Bakke, A. 1989. The recent *Ips typographus* outbreak in Norway: Experiences from a control program. *Holarctic Ecology*, 12, 515-19.
- Bakke, A., Frøyen, P., & Skattebøl, L. 1977. Field response to a new pheromonal compound isolated from *Ips typographus*. *Naturwissenschaften*, 64, 98.
- Barclay, H.J. 1984. Pheromone trapping models for pest control: Effects of mating patterns and immigration. *Researches on Population Ecology*, 26, 303-11.
- Barclay, H.J. 1988.. Models for combining methods of pest control: food-baited and pheromone-baited traps containing either insecticide or chemosterilant. *Bulletin of Entomological Research*, 78, 573-90.
- Barclay, H.J., & Li, C. 1991. Combining methods of pest control: Minimizing cost during the control program. *Theoretical Population Biology*, 40, 105-23.
- Bedard, W.D., Tilden, P.E., Wood, D.L., Silverstein, R.M., Brownlee, R.G., & Rodin, J.O. 1969. Western pine beetle: field response to its sex pheromone and a synergistic host terpene, myrcene. *Science*, 164, 1284-85.
- Bedard, W.D., Silverstein, R.M., & Wood, D.L. 1970. Bark beetle pheromones. *Science*, 167, 1638-39.
- Bedard, W.D., Wood, D.L., & Tilden, P.E. 1979. Using behavior modifying chemicals to reduce western pine beetle-caused tree mortality and protect trees. In. *Current Topics in Forest Entomology*, W.E. Waters (ed.). U.S. Forest Service General Technical Report, WO-8.
- Begley, M.J., & Grove, J.F. 1985. Metabolic products of *Phomopsis oblonga* I. 3a,5a,6,7,8,9,9a,9b-octahydro-7,9b-dimethylnaphtho-1,2-c-furan-1-3h-one oblongolide. *Journal of the Chemical Society, Perkin Transactions 1*, 0, 861-4.
- Bennett, R.B., & Borden, J.H. 1971. Flight arrestment of tethered *Dendroctonus pseudotsugae* and *Trypodendron lineatum* (Coleoptera: Scolytidae) in response to olfactory stimuli. *Annals of the Entomological Society of America*, 64, 1273-86.
- Berenbaum, M.R., & Isman, M.B. 1989. Herbivory in holometabolous and hemimetabolous insects: contrasts between Orthoptera and Lepidoptera. *Experientia*, 45, 229-36.
- Beroza, M., & Knipling, E.F. 1972. Gypsy moth control with the sex attractant pheromone. *Science*, 177, 19-27.
- Berryman, A.A. 1974. Dynamics of bark beetle populations towards a general productivity model. *Environmental Entomology*, 3, 579-85.
- Berryman, A.A., & Ashraf, M. 1970. Effects of *Abies grandis* resin on the attack behavior and brood survival of *Scolytus ventralis* (Coleoptera: Scolytidae). *Canadian Entomologist*, 102, 1229-36.
- Berryman, A.A., & Stenseth, N.C. 1989. A theoretical basis for understanding and managing biological populations with particular reference to the spruce bark beetle. *Holarctic Ecology*, 12, 387-94.
- Berryman, A.A., Dennis, B., Raffa, K.F., & Stenseth, N.C. 1985. Evolution of optimal group attack with particular reference to bark beetles (Coleoptera: Scolytidae). *Ecology*, 66, 898-903.
- Berryman, A.A., Raffa, K.F., Millstein, J.A., & Stenseth, N.C. 1989. Interaction dynamics of bark beetle aggregation and conifer defense rates. *Oikos*, 56, 256-63.
- Birch, M.C. 1984. Aggregation in bark beetles. In. *Chemical Ecology of Insects*, W.J. Bell, R.T. Cardé (Eds.). Chapman and Hall, London.
- Birch, M.C., Light, D.M., Wood, D.L., Browne, L.E., Silverstein, R.M., Bergot, B.J., Ohloff, G., West, J.F., & Young, J.C. 1980a. Pheromonal attraction and allomonal interruption of *Ips pini* in California by the two enantiomers of ipsdienol. *Journal of Chemical Ecology*, 6, 703-17.
- Birch, M.C., Svhra, P., Paine, T.D., & Miller, J.C. 1980b. Influence of chemically mediated behavior on host tree colonization by four cohabiting species of bark beetles. *Journal of Chemical Ecology*, 6, 395-414.

- Birgersson, G., & Bergström, G. 1989. Volatiles released from individual spruce bark beetle entrance holes: quantitative variations during the first week of attack. *Journal of Chemical Ecology*, 15, 2465-84.
- Birgersson, G., & Leufvén, A. 1988. The influence of host tree response to *Ips typographus* and fungal attack on production of semiochemicals. *Insect Biochemistry*, 18, 761-70.
- Birgersson, G., Schlyter, F., Bergström, G., & Löfqvist, J. 1988. Individual variation in aggregation pheromone content of the bark beetle, *Ips typographus*. *Journal of Chemical Ecology*, 14, 1737-1762.
- Birgersson, G., Byers, J. A., Bergström, G., & Löfqvist, J. 1990. Production of pheromone components, chalcogran and methyl (E,Z)-2,4-decadienoate, in the spruce engraver *Pityogenes chalcographus*. *Journal of Insect Physiology*, 36, 391-5.
- Birgersson, G., Schlyter, F., Löfqvist, J., & Bergström, G. 1984. Quantitative variation of pheromone components in the spruce bark beetle *Ips typographus* from different attack phases. *Journal of Chemical Ecology*, 10, 1029-55.
- Bombosch, S., Engler, I., Gossenauer, H., & Herrmann, B. 1985. On the role of pheroprax influencing the settlement of *Ips typographus* on spruce. *Zeitschrift für angewandte Entomologie*, 100, 458-63.
- Bonello, P., Mcnee, W.R., Storer, A.J., Wood, D.L., & Gordon, T.R. 2001. The role of olfactory stimuli in the location of weakened hosts by twig-infesting *Pityophthorus* spp. *Ecological Entomology*, 26, 8-15.
- Bordasch, R.P., & Berryman, A.A. 1977. Host resistance to the fir engraver beetle, *Scolytus ventralis* (Coleoptera: Scolytidae) 2. repellency of *Abies grandis* resins and some monoterpenes. *Canadian Entomologist*, 109, 95-100.
- Borden, J.H. 1982. Aggregation pheromones. In: *Bark beetles in North American Conifers: a System for the Study of Evolutionary Biology*, J.B. Mitton, K.M. Sturgeon (Eds.). University of Texas. Austin, USA.
- Borden, J.H. 1997. Disruption of semiochemical-mediated aggregation in bark beetles. In: *Pheromone Research: New Directions*, R.T. Cardé, A.K. Minks (Eds.). Chapman and Hall, New York.
- Borden, J.H., & Wood, D.L. 1966. The antennal receptors and olfactory response of *Ips confusus* (Coleoptera: Scolytidae) to male sex attractant in the laboratory. *Annals of the Entomological Society of America*, 59, 253-61.
- Borden, J.H., Handley, J.R., McLean, J.A., Silverstein, R.M., Chong, L., Slessor, K.N., Johnston, B.D., & Schuler, H.R. 1980. Enantiomer-based specificity in pheromone communication by two sympatric *Gnathotrichus* species (Coleoptera: Scolytidae). *Journal of Chemical Ecology*, 6, 445-56.
- Borden, J.H., Chong, L., Slessor, K.N., Oehlschlager, A.C., Pierce, Jr., H.D., & Lindgren, B.S. 1981. Allelochemical activity of aggregation pheromones between three sympatric species of ambrosia beetles (Coleoptera: Scolytidae). *Canadian Entomologist*, 113, 557-63.
- Borden, J.H., King, C.J., Lindgren, S., Chong, L., Gray, D.R., Oehlschlager, A.C., Slessor, K.N., & Pierce, Jr., H.D. 1982. Variation in response of *Trypodendron lineatum* from two continents to semiochemicals and trap form. *Environmental Entomology*, 11, 403-8.
- Borden, J.H., Hunt, D.W.A., Miller, D.R., & Slessor, K.N. 1986. Orientation in forest Coleoptera: an uncertain outcome of responses by individual beetles to variable stimuli. In: *Mechanisms in Insect Olfaction*, T.L. Payne, M.C. Birch, C.E.J. Kennedy (Eds.). Clarendon Press, Oxford.
- Borden, J.H., Pierce, A.M., Pierce, Jr., H.D., Chong, L.J., Stock, A.J., & Oehlschlager, A.C. 1987. Semiochemicals produced by western balsam bark beetle *Dryocoetes confusus* Swaine (Coleoptera: Scolytidae). *Journal of Chemical Ecology*, 13, 823-36.
- Borden, J.H., Chong, L.J., Savoie, A., & Wilson, I.M. 1997. Responses to green leaf volatiles in two biogeoclimatic zones by striped ambrosia beetle, *Trypodendron lineatum*. *Journal of Chemical Ecology*, 23, 2479-91.
- Borden, J.H., Wilson, I.M., Gries, R., Chong, I.J., & Pierce, H.D. Jr. 1998. Volatiles from the bark of trembling aspen, *Populus tremuloides* Michx. (Salicaceae) disrupt secondary attraction by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *Chemoecology*, 8, 69-75.
- Borg, T.K., & Norris, D.M. 1971. Penetration of tritiated catechol: a feeding stimulant into chemo receptor sensilla of *Scolytus multistriatus* (Coleoptera: Scolytidae). *Annals of the Entomological Society of America*, 64, 544-7.
- Botterweg, P.F. 1982. Dispersal and flight behavior of the spruce bark beetle *Ips typographus* in relation to sex, size and fat content. *Zeitschrift für angewandte Entomologie*, 94, 466-89.
- Brand, J.M., Bracke, J.W., Markovetz, A.J., Wood, D.L., & Browne, L.E. 1975. Production of verbenol pheromone by a bacterium isolated from bark beetles. *Nature*, 254, 136-7.

- Brand, J.M., Bracke, J.W., Britton, L.N., Markovetz, A.J., & Barras, S.J. 1976. Bark beetle pheromones: production of verbenone by a mycangial fungus of *Dendroctonus frontalis*. *Journal of Chemical Ecology*, 2, 195-9.
- Bridges, J.R., Nettleton, W.A., & Connor, M.D. 1985. Southern pine beetle *Dendroctonus frontalis* (Coleoptera: Scolytidae) infestations without the bluestain fungus *Ceratocystis minor*. *Journal of Economic Entomology*, 78, 325-7.
- Bridges, J.R., & Perry, T.J. 1985. Effects of mycangial fungi on gallery construction and distribution of bluestain in southern pine beetle *Dendroctonus frontalis* infested pine bolts. *Journal of Entomological Science*, 20, 271-5.
- Brown, M.W., Nebeker, T.E., & Honea, C.R. 1987. Thinning increases loblolly pine vigor and resistance to bark beetles. *Southern Journal of Applied Forestry*, 11, 28-31.
- Browne, L.E. 1978. A trapping system for the western pine beetle using attractive pheromones. *Journal of Chemical Ecology*, 4, 261-75.
- Browne, L.E., Wood, D.L., Bedard, W.D., Silverstein, R.M., & West, J.R. 1979. Quantitative estimates of the Western pine beetle attractive pheromone components, *exo*-brevicomin, frontalin, and myrcene in nature. *Journal of Chemical Ecology*, 5, 397-414.
- Byers, J.A. 1982. Male-specific conversion of the host plant compound, myrcene, to the pheromone, (+)-ipsdienol, in the bark beetle, *Dendroctonus brevicomis*. *Journal of Chemical Ecology*, 8, 363-72.
- Byers, J.A. 1983a. Sex-specific responses to aggregation pheromone: regulation of colonization density by the bark beetle *Ips paraconfusus*. *Journal of Chemical Ecology*, 9, 129-42.
- Byers, J.A. 1983b. Influence of sex, maturity and host substances on pheromones in the guts of the bark beetles, *Dendroctonus brevicomis* and *Ips paraconfusus*. *Journal of Insect Physiology*, 29, 5-13.
- Byers, J.A. 1983c. Bark beetle conversion of a plant compound to a sex-specific inhibitor of pheromone attraction. *Science*, 220, 624-26.
- Byers, J.A. 1984. Nearest neighbor analysis and simulation of distribution patterns indicates an attack spacing mechanism in the bark beetle, *Ips typographus* (Coleoptera: Scolytidae). *Environmental Entomology*, 13, 1191-2000.
- Byers, J.A. 1989a. Chemical ecology of bark beetles. *Experientia*, 45, 271-83.
- Byers, J.A. 1989b. Behavioral mechanisms involved in reducing competition in bark beetles. *Holarctic Ecology*, 12, 466-76.
- Byers, J.A. 1991. Simulation of mate finding behaviour in pine shoot beetles, *Tomicus piniperda*. *Animal Behaviour*, 41, 649-60.
- Byers, J.A. 1992a. Attraction of bark beetles, *Tomicus piniperda*, *Hylurgops palliatus*, and *Trypodendron domesticum* and other insects to short-chain alcohols and monoterpenes. *Journal of Chemical Ecology*, 18, 2385-2402.
- Byers, J.A. 1992b. Optimal fractionation and bioassay plans for isolation of synergistic chemicals: the subtractive-combination method. *Journal of Chemical Ecology*, 18, 1603-21.
- Byers, J.A. 1992c. Dirichlet tessellation of bark beetle spatial attack points. *Journal of Animal Ecology*, 61, 759-68.
- Byers, J.A. 1993a. Simulation and equation models of insect population control by pheromone-baited traps. *Journal of Chemical Ecology*, 19, 1939-56.
- Byers, J.A. 1993b. Avoidance of competition by spruce bark beetles, *Ips typographus* and *Pityophthorus chalcographus*. *Experientia*, 49, 272-5.
- Byers, J.A. 1995. Host tree chemistry affecting colonization in bark beetles, In. *Chemical Ecology of Insects* 2. R.T. Cardé, W.J. Bell (Eds.). Chapman and Hall, New York.
- Byers, J.A. 1996a. An encounter rate model for bark beetle populations searching at random for susceptible host trees. *Ecological Modelling*, 91, 57-66.
- Byers, J.A. 1996b. Temporal clumping of bark beetle arrival at pheromone traps: Modeling anemotaxis in chaotic plumes. *Journal of Chemical Ecology*, 22, 2133-55.
- Byers, J.A. 1996c. Correct calculation of Dirichlet polygon areas. *Journal of Animal Ecology*, 65, 528-9.
- Byers, J.A. 1999. Effects of attraction radius and flight paths on catch of scolytid beetles dispersing outward through rings of pheromone traps. *Journal of Chemical Ecology*, 25, 985-1005.
- Byers, J.A. 2000. Wind-aided dispersal of simulated bark beetles flying through forests. *Ecological Modelling*, 125, 231-43.
- Byers, J.A. 2001. Correlated random walk equations of animal dispersal resolved by simulation. *Ecology*, 82, 1680-90.

- Byers, J.A. 2002. Internet programs for drawing moth pheromone analogs and searching literature database. *Journal of Chemical Ecology*, 28, 807-17.
- Byers, J.A., & Löfqvist, J. 1989. Flight initiation and survival in the bark beetle *Ips typographus* (Coleoptera: Scolytidae) during the spring dispersal. *Holarctic Ecology*, 12, 432-40.
- Byers, J.A., & Wood, D.L. 1980. Interspecific inhibition of the response of the bark beetles, *Dendroctonus brevicomis* and *Ips paraconfusus*, to their pheromones in the field. *Journal of Chemical Ecology*, 6, 149-64.
- Byers, J.A., & Wood, D.L. 1981a. Interspecific effects of pheromones on the attraction of the bark beetles, *Dendroctonus brevicomis* and *Ips paraconfusus* in the laboratory. *Journal of Chemical Ecology*, 7, 9-18.
- Byers, J.A., & Wood, D.L. 1981b. Antibiotic-induced inhibition of pheromone synthesis in a bark beetle. *Science*, 213, 763-4.
- Byers, J.A., Wood, D.L., Browne, L.E., Fish, R.H., Piatek, B., & Hendry, L.B. 1979. Relationship between a host plant compound, myrcene and pheromone production in the bark beetle, *Ips paraconfusus*. *Journal of Insect Physiology*, 25, 477-82.
- Byers, J.A., Wood, D.L., Craig, J., & Hendry, L.B. 1984. Attractive and inhibitory pheromones produced in the bark beetle, *Dendroctonus brevicomis*, during host colonization: regulation of inter- and intraspecific competition. *Journal of Chemical Ecology*, 10, 861-77.
- Byers, J.A., Lanne, B.S., Schlyter, F., Löfqvist, J., & Bergström, G. 1985. Olfactory recognition of host-tree susceptibility by pine shoot beetles. *Naturwissenschaften*, 72, 324-6.
- Byers, J.A., Birgersson, G., Löfqvist, J., & Bergström, G. 1988. Synergistic pheromones and monoterpenes enable aggregation and host recognition by a bark beetle. *Naturwissenschaften*, 75, 1 53-5.
- Byers, J.A., Anderbrant, O., & Löfqvist, J. 1989a. Effective attraction radius: a method for comparing species attractants and determining densities of flying insects. *Journal of Chemical Ecology*, 15, 749-65.
- Byers, J.A., Höglberg, H.E., Unelius, R., Birgersson, G., & Löfqvist, J. 1989b. Structure-activity studies on aggregation pheromone components of *Pityogenes chalcographus* (Coleoptera: Scolytidae): all stereoisomers of chalcogran and methyl 2,4-decadienoate. *Journal of Chemical Ecology*, 15, 685-95.
- Byers, J.A., Lanne, B.S., & Löfqvist, J. 1989c. Host-tree unsuitability recognized by pine shoot beetles in flight. *Experientia*, 45, 489-92.
- Byers, J.A., Birgersson, G., Löfqvist, J., Appelgren, M., & Bergström, G. 1990a. Isolation of pheromone synergists of bark beetle, *Pityogenes chalcographus*, from complex insect-plant odors by fractionation and subtractive-combination bioassay. *Journal of Chemical Ecology*, 16, 861-76.
- Byers, J.A., Schlyter, F., Birgersson, G., & Francke, W. 1990b. E-myrcenol in *Ips duplicatus*: an aggregation pheromone component new for bark beetles. *Experientia*, 46, 1209-11.
- Byers, J.A., Zhang, Q.H., Schlyter, F., & Birgersson, G. 1998. Volatiles from nonhost birch trees inhibit pheromone response in spruce bark beetles. *Naturwissenschaften*, 85, 557-61.
- Byers, J.A., Zhang, Q.H., & Birgersson, G. 2000. Strategies of a bark beetle, *Pityogenes bidentatus*, in an olfactory landscape. *Naturwissenschaften*, 87, 503-7.
- Cade, S.C., Hrufford, B.F., & Gara, R.I. 1970. Identification of a primary attractant for *Gnathotrichus sulcatus* isolated from western hemlock logs. *Journal of Economic Entomology*, 63, 1014-15.
- Camacho, A.D., Pierce, Jr., H.D., & Borden, J.A. 1993. Aggregation pheromones in *Dryocoetes affaber* (Mann.) (Coleoptera: Scolytidae): stereoisomerism and species specificity. *Journal of Chemical Ecology*, 20, 111-24.
- Campion, D.G., Critchley, B.R., & McVeigh, L.J. 1989. Mating disruption. In. *Insect Pheromones in Plant Protection*, A.R. Jutsum, R.F.S. Gordon (Eds.). Wiley and Sons, New York.
- Campos, M., Pena, A., & Sanchez-Raya, A.J. 1994. Release of ethylene from pruned olive logs: Influence on attack by bark beetles (Coleoptera, Scolytidae). *Journal of Chemical Ecology*, 20, 2513-21.
- Campos, M., & Pena, A. 1995. Response of *Phloeotribus scarabaeoides* (Coleoptera, Scolytidae) to ethylene in an olfactometer. *Experientia*, 51, 77-9.
- Cates, R.G. 1981. Host plant predictability and the feeding patterns of monophagous, oligophagous, and polyphagous insect herbivores. *Oecologia*, 48, 319-26.
- Chapman, J.A. 1972. Ommatidia numbers and eyes in scolytid beetles. *Annals of the Entomological Society of America*, 65, 550-3.
- Chararas, C., Katoulas, M., & Kouroumpas, A. 1982. Feeding preference of *Ruguloscolytus rugulosus* bark beetle parasite of fruit trees. *Comptes Rendus de l Academie des Sciences Serie III, Sciences de la Vie*, 294, 763-6.
- Chénier, J.V.R., & Philogène, B.J.R. 1989. Field responses of certain forest Coleoptera to conifer monoterpenes and ethanol. *Journal of Chemical Ecology*, 15, 1729-46.

- Choudhury, J.H., & Kennedy, J.S. 1980. Light versus pheromone-bearing wind in the control of flight direction by bark beetles, *Scolytus multistriatus*. *Physiological Entomology*, 5, 207-14.
- Claydon, N., Grove, J.F., & Pople, M. 1985. Elm bark beetle boring and feeding deterrents from *Phomopsis oblonga*. *Phytochemistry*, 24, 937-44.
- Conn, J.E., Borden, J.H., Hunt, D.W.A., Holman, J., Whitney, H.S., Spanier, O.J., Pierce, H.D.Jr., & Oehlschlager, A.C. 1984. Pheromone production by axenically reared *Dendroctonus ponderosae* and *Ips paraconfusus* (Coleoptera: Scolytidae). *Journal of Chemical Ecology*, 10, 281-90.
- Dahlsten, D.L., & Stephen, F.M. 1974. Natural enemies and insect associates of the mountain pine beetle *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in sugar pine. *Canadian Entomologist*, 106, 1211-17.
- David, C.T., Kennedy, J.S., Ludlow, A.R., Perry, J.N., & Wall, C. 1982. A reappraisal of insect flight towards a distant point source of wind-borne odor. *Journal of Chemical Ecology*, 8, 1207-15.
- Deglow, E.K., & Borden, J.H. 1998. Green leaf volatiles disrupt and enhance response to aggregation pheromones by the ambrosia beetle, *Gnathotrichus sulcatus* (LeConte) (Coleoptera: Scolytidae). *Canadian Journal of Forest Research*, 28, 1697-1705.
- DeMars, C.J., Slaughter, G.W., Bedard, W.D., Norick, N.X., & Roettgering, B. 1980. Estimating western pine beetle-caused tree mortality for evaluating an attractive pheromone treatment. *Journal of Chemical Ecology*, 6, 853-66.
- Dethier, V.G. 1982. Mechanisms of host-plant recognition. *Entomologia Experimentalis et Applicata*, 31, 49-56.
- Dickens, J.C. 1986. Specificity in perception of pheromones and host odours in Coleoptera. In: *Mechanisms in insect olfaction*, T.L. Payne, M.C. Birch, C.E.J. Kennedy (Eds.). Clarendon Press, Oxford.
- Dickens, J.C., Payne, T.L., Ryker, L.C., & Rudinsky, J.A. 1985. Multiple acceptors for pheromonal enantiomers on single olfactory cells in the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae). *Journal of Chemical Ecology*, 11, 1359-70.
- Dickens, J.C., Billings, R.F., & Payne, T.L. 1992. Green leaf volatiles interrupt aggregation pheromone response in bark beetles infesting southern pines. *Experientia*, 48, 523-4.
- Doskotch, R.W., Mikhail, A.A., & Chatterji, S.K. 1973. Structure of the water soluble feeding stimulant for *Scolytus multistriatus*: a revision. *Phytochemistry*, 12, 1153-55.
- Du, J.W., Löfstedt, C., & Löfqvist, J. 1987. Repeatability of pheromone emissions from individual female ermine moths *Yponomeuta padellus* and *Yponomeuta rorellus*. *Journal of Chemical Ecology*, 13, 1431-42.
- Duelli, P., Zahradník, P., Knizek, M., & Kalinova, B. 1997. Migration in spruce bark beetles (*Ips typographus* L.) and the efficiency of pheromone traps. *Journal of Applied Entomology*, 121, 297-303.
- El-Sayed, A.M., & Byers, J.A. 2000. Inhibitory effect of monoterpenes on response of *Pityogenes bidentatus* to aggregation pheromone released by piezoelectric sprayer for precision release of semiochemicals. *Journal of Chemical Ecology*, 26, 1795-1809.
- Elkinton, J.S., & Wood, D.L. 1980. Feeding and boring behavior of the bark beetle *Ips paraconfusus* (Coleoptera: Scolytidae) on the bark of a host and non-host tree species. *Canadian Entomologist*, 112, 797-809.
- Elkinton, J.S., Wood, D.L., & Browne, L.E. 1981. Feeding and boring behavior of the bark beetle, *Ips paraconfusus*, in extracts of ponderosa pine phloem. *Journal of Chemical Ecology*, 7, 209-20.
- Ehrlich, P.R., & Raven, P.H. 1965. Butterflies and plants: a study in coevolution. *Evolution*, 8, 586-608.
- Fauchoux, M.J. 1989. Morphology of the antennal club in the male and female bark beetles *Ips sexdentatus* (Boern.) and *Ips typographus* L. (Coleoptera: Scolytidae). *Annales des Sciences Naturelles Zoologie et Biologie Animale*, 10, 231-43.
- Feeny, P. 1975. Biochemical coevolution between plants and their insect herbivores. In: *Coevolution of Animals and Plants*, L.E. Gilbert, P.H. Raven (Eds.). Austin: University of Texas Press.
- Fisher, M.E., Van Den Driessche, P., & Barclay, H.J. 1985. A density dependent model of pheromone trapping. *Theoretical Population Biology*, 27, 91-104.
- Flint, H.M., & Merkle, J.R. 1984. Studies on disruption of sexual communication in the pink bollworm, *Pectinophora gossypiella*, (Lepidoptera: Gelechiidae) with micro encapsulated gossypure or its component Z,Z isomer. *Bulletin of Entomological Research*, 74, 25-32.
- Forsse, E. 1991. Flight propensity and diapause incidence in five populations of the bark beetle *Ips typographus* in Scandinavia. *Entomologia Experimentalis et Applicata*, 61, 53-57.

- Forsse, E., & Solbreck, C. 1985. Migration in the bark beetle *Ips typographus* L.: duration, timing and height of flight. Zeitschrift für angewandte Entomologie, 100, 47-57.
- Francke, W., Heemann, V., Gerken, B., Renwick, J.A., & Vité, J.P. 1977. 2-Ethyl-1,6-dioxaspiro[4.4]nonane, principal aggregation pheromone of *Pityogenes chalcographus* (L.). Naturwissenschaften, 64, 590-1.
- Funk, A. 1970. Fungal symbionts of the ambrosia beetle *Gnathotrichus sulcatus*. Canadian Journal of Botany, 48, 1445-8.
- Furniss, M.M., Woo, J.Y., Deyrup, M.A., & Atkinson, T.H. 1987. Prothoracic mycangium on pine-infesting *Pityophorus* spp. (Coleoptera: Scolytidae). Annals of the Entomological Society of America, 80, 692-6.
- Gara, R.I. 1963. Studies on the flight behavior of *Ips confusus* (LeC.) (Coleoptera: Scolytidae) in response to attractive material. Contributions of the Boyce Thompson Institute, 22, 51-66.
- Gilbert, B.L., Baker, J.E., & Norris, D.M. 1967. Juglone (5-hydroxy- 1,4-naphthoquinone) from *Carya ovata*, a deterrent to feeding by *Scolytus multistriatus*. Journal of Insect Physiology, 13, 1453-9.
- Goeden, R.D., & Norris, D.M. 1964. Attraction of *Scolytus quadrispinosus* (Coleoptera: Scolytidae) to *Carya* spp. for oviposition. Annals of the Entomological Society of America, 57, 141-6.
- Goeden, R.D., & Norris, D.M. 1965. The behavior of *Scolytus quadrispinosus* (Coleoptera: Scolytidae) during the dispersal flight as related to its host specificities. Annals of the Entomological Society of America, 58, 249-52.
- Goldammer, D.S., Stephen, F.M., & Paine, T.D. 1991. The effect of the fungi *Ceratocystis minor* Hedgecock-Hunt, *Ceratocystis minor* var. *barrasii* Taylor, and SJB 122 on reproduction of the southern pine beetle *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). Canadian Entomologist, 122, 407-18.
- Gonzalez, R., & Campos, M. 1995. A preliminary study of the use of trap-trees baited with ethylene for the integrated management of the olive beetle, *Phloeotribus scarabaeoides* (Bern.) (Col., Scolytidae). Journal of Applied Entomology, 119, 601-5.
- Gonzalez, R., & Campos, M. 1996. The influence of ethylene on primary attraction of the olive beetle, *Phloeotribus scarabaeoides* (Bern.) (Col., Scolytidae). Experientia, 52, 723-6.
- Graham, K. 1959. Release by flight exercise of a chemotropic response from photopositive domination in a scolytid beetle. Nature, 184, 283-4.
- Graham, K. 1968. Anaerobic induction of primary chemical attractancy for ambrosia beetles. Canadian Journal of Zoology, 46, 905-8.
- Gries, G., Nolte, R., & Sanders, W. 1989. Computer simulated host selection in *Ips typographus*. Entomologia Experimentalis et Applicata, 53, 211-17.
- Gries, G., Bowers, W.W., Gries, R., Noble, M., & Borden, J.H. 1990. Pheromone production by the pine engraver *Ips pini* following flight and starvation. Journal of Insect Physiology, 36, 819-24.
- Groberman, L.J., & Borden, H.J. 1982. Electrophysiological response of *Dendroctonus pseudotsugae* and *Ips paraconfusus* (Coleoptera: Scolytidae) to selected wave length regions of the visible spectrum. Canadian Journal of Zoology, 60, 2180-9.
- Guerrero, A., Feixas, J., Pajares, J., Wadhams, L.J., Pickett, J.A., & Woodcock, C.M. 1997. Semiochemically induced inhibition of behaviour of *Tomicus destruens* (Woll.) (Coleoptera: Scolytidae). Naturwissenschaften, 84, 155-7.
- Hagen, B.W., & Atkins, M.D. 1975. Between generation variability in the fat content and behaviour of *Ips paraconfusus* Lanier. Zeitschrift für angewandte Entomologie, 79, 169-72.
- Hallberg, E. 1982. Sensory organs in *Ips typographus* (Insecta: Coleoptera) - fine structure of the sensilla of the maxillary and labial palps. Acta Zoologica, 63, 191-8.
- Haniotakis, G., Kozyrakis, M., Fitsakis, T., & Antonidaki, A. 1991. An effective mass trapping method for the control of *Dacus oleae* (Diptera: Tephritidae). Journal of Economic Entomology, 84, 564-9.
- Happ, G.M., Happ, C.M., & French, J.R.J. 1976. Ultrastructure of the mesonotal mycangium of an ambrosia beetle *Xyleborus dispar* (Coleoptera: Scolytidae). International Journal of Insect Morphology and Embryology, 5, 381-92.
- Himejima, M., Hobson, K.R., Otsuka, T., Wood, D.L., & Kubo, I. 1992. Antimicrobial terpenes from oleoresin of ponderosa pine tree *Pinus ponderosa*: a defense mechanism against microbial invasion. Journal of Chemical Ecology, 18, 1809-18.
- Hobson, K.R., Wood, D.L., Cool, L.G., White, P.R., Ohtsuka, T., Kubo, I., & Zavarin, E. 1993. Chiral specificity in responses by the bark beetle *Dendroctonus valens* to host kairomones. Journal of Chemical Ecology, 19, 1837-46.
- Hodges, J.D., & Lorio, Jr., P.L. 1975. Moisture stress and composition of xylem oleoresin in loblolly pine. Forest Science, 21, 283-90.

- Hodges, J.D., Elam, W.W., Watson, W.R., & Nebeker, T.E. 1979. Oleoresin characteristics and susceptibility of four southern pines to southern pine beetle (Coleoptera: Scolytidae) attacks. Canadian Entomologist, 111, 889-96.
- Hodges, J.D., Nebeker, T.E., DeAngelis, J.D., Karr, B.L., & Blanche, C.A. 1985. Host resistance and mortality: a hypothesis based on the southern pine beetle-microorganism-host interactions. Bulletin of the Entomological Society of America, 31, 31-5.
- Hodges, R.J., Benton, F.P., Hall, D.R., & Dos, S.S.R. 1984. Control of *Ephestia cautella* (Lepidoptera: Phycitidae) by synthetic sex pheromones in the laboratory and store. Journal of Stored Product Research, 20, 191-8.
- Horntvedt, R.E., Christiansen, H., Solheim, H., & Wang, S. 1983. Artificial inoculation with *Ips typographus*-associated bluestain fungi can kill healthy Norway spruce trees. Meddelelser fra Norsk Institutt for Skogforskning, 38, 1-20.
- Huber, D.P.W., & Borden, J.H. 2001a. Angiosperm bark volatiles disrupt response of Douglas-fir beetle, *Dendroctonus pseudotsugae*, to attractant-baited traps. Journal of Chemical Ecology, 27, 217-33.
- Huber, D.P.W., & Borden, J.H. 2001b. Protection of lodgepole pines from mass attack by mountain pine beetle, *Dendroctonus ponderosae*, with nonhost angiosperm volatiles and verbenone. Entomologia Experimentalis et Applicata, 99, 131-41.
- Huber, D.P.W., Gries, R., Borden, J.H., & Pierce, H.D. Jr. 1999. Two pheromones of coniferophagous bark beetles found in the bark of non-host angiosperms. Journal of Chemical Ecology, 25, 805-16.
- Huber, D.P.W., Borden, J.H., Jeans-Williams, N.L., & Gries, R. 2000. Differential bioactivity of conophthorin on four species of North American bark beetles (Coleoptera: Scolytidae). Canadian Entomologist, 132, 649-53.
- Huber, D.P.W., Borden, J.H., & Stastny, M. 2001. Response of the pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae), to conophthorin and other angiosperm bark volatiles in the avoidance of non-hosts. Agricultural and Forest Entomology, 3, 225-32.
- Hughes, P.R. 1973. *Dendroctonus*: production of pheromones and related compounds in response to host monoterpenes. Zeitschrift für angewandte Entomologie, 73, 294-312.
- Hynum, B.G., & Berryman, A.A. 1980. *Dendroctonus ponderosae* (Coleoptera: Scolytidae) pre-aggregation landing and gallery initiation on lodgepole pine. Canadian Entomologist, 112, 185-92.
- Jakus, R. 1998. A method for the protection of spruce stands against *Ips typographus* by the use of barriers of pheromone traps in north-eastern Slovakia. Anzeiger für Schadlingskunde Pflanzenschutz Umweltschutz, 71, 152-8.
- Jactel, H. 1991. Dispersal and flight behavior of *Ips sexdentatus* (Coleoptera: Scolytidae) in pine forest. Annales des Sciences Forestières, 48, 417-28.
- Jactel, H., & Gaillard, J. 1991. A preliminary study of the dispersal potential of *Ips sexdentatus* Boern (Coleoptera: Scolytidae) with an automatically recording flight mill. Journal of Applied Entomology, 112, 138-45.
- Jones, R.G., & Brindley, W.A. 1970. Tests of eight rearing media for the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), from lodgepole pine. Annals of the Entomological Society of America, 63, 313-16.
- Jones, O.T., Lisk, J.C., Howse, P.E., Baker, R., Bueno, A.M., & Ramos, P. 1982. Mating disruption of the olive fruit fly *Dacus oleae* with the major component of its sex pheromone, In. *Fruit Flies of Economic Importance*. R. Cavalloro (ed.). Proceedings of the CEC/IIBC International Symposium, Athens, Greece.
- Kajimura, H., & Hijii, N. 1992. Dynamics of the fungal symbionts in the gallery system and the mycangia of the ambrosia beetle *Xylosandrus mutilatus* Blandford (Coleoptera: Scolytidae) in relation to its life history. Ecological Research, 7, 107-17.
- Kelsey, R.G. 1994. Ethanol synthesis in Douglas-fir logs felled in November, January, and March, and its relationship to ambrosia beetle attack. Canadian Journal of Forest Research, 24, 2096-2104.
- Kelsey, R.G. 1996. Anaerobic induced ethanol synthesis in the stems of greenhouse-grown conifer seedlings. Trees, 10, 183-8.
- Kelsey, R.G., & Joseph, G. 1997. Ambrosia beetle host selection among logs of Douglas fir, western hemlock, and western red cedar with different ethanol and α -pinene concentrations. Journal of Chemical Ecology, 23, 1035-51.
- Kelsey, R.G., & Joseph, G. 1999. Ethanol and water in *Pseudotsuga menziesii* and *Pinus ponderosa* stumps. Journal of Chemical Ecology, 25, 2779-92.

- Kimmerer, T.W., & Kozlowski, T.T. 1982. Ethylene, ethane, acetaldehyde and ethanol production by plants under stress. *Plant Physiology*, 69, 840-7.
- Kinzer, G.W., Fentiman, Jr., A.F., Page, T.F., Foltz, R.L., Vité, J.P., & Pitman, G.B. 1969. Bark beetle attractants: identification, synthesis and field bioassay of a new compound isolated from *Dendroctonus*. *Nature*, 211, 475-6.
- Klimetzek, D., Köhler, J., Vité, J.P., & Kohnle, U. 1986. Dosage response to ethanol mediates host selection by 'secondary' bark beetles. *Naturwissenschaften*, 73, 270-2.
- Knipling, E.F., & McGuire, J.U., Jr. 1966. Population models to test theoretical effects of sex attractants used for insect control. *USDA Information Bulletin*, 308, 2-4.
- Kohnle, U. 1985. Investigations of chemical communication systems in secondary bark beetles. *Zeitschrift für angewandte Entomologie*, 100, 197-218.
- Långström, B. 1983. Within tree development of *Tomicus minor* (Coleoptera: Scolytidae) in wind thrown scotch pine. *Acta Entomologica Fennica*, 42, 42-6.
- Långström, B., & Hellqvist, C. 1991. Shoot damage and growth losses following three years of *Tomicus* attacks in scots pine stands close to a timber storage site. *Silva Fennica*, 25, 133-45.
- Lanier, G.N. 1983. Integration of visual stimuli, host odorants, and pheromones by bark beetles and weevils in locating and colonizing host trees. In: *Herbivorous Insects: Host-Seeking Behavior and Mechanisms*, S. Ahmad (Ed.). Academic Press, New York.
- Lanier, G.N., Classon, A., Stewart, T., Piston, J.J., & Silverstein, R.M. 1980. *Ips pini*: the basis for interpopulational differences in pheromone biology. *Journal of Chemical Ecology*, 6, 677-87.
- Lanne, B.S., Schlyter, F., Byers, J.A., Löfqvist, J., Leufvén, A., Bergström, G., Van Der Pers, J.N.C., Unelius, R., Baeckström, P., & Norin, T. 1987. Differences in attraction to semiochemicals present in sympatric pine shoot beetles, *Tomicus minor* and *T. piniperda*. *Journal of Chemical Ecology*, 13, 1045-67.
- Leufvén, A., Bergström, G., & Falsen, E. 1984. Interconversion of verbenols and verbenone by identified yeasts isolated from the spruce bark beetle *Ips typographus*. *Journal of Chemical Ecology*, 10, 1349-61.
- Leufvén, A., Bergström, G., & Falsen, E. 1988. Oxygenated monoterpenes produced by yeasts isolated from *Ips typographus* (Coleoptera: Scolytidae) and grown in phloem medium. *Journal of Chemical Ecology*, 14, 353-62.
- Levieux, J., Cassier, P., Guillaumin, D., & Roques, A. 1991. Structures implicated in the transportation of pathogenic fungi by the European bark beetle *Ips sexdentatus* Boerner: ultrastructure of a mycangium. *Canadian Entomologist*, 123, 245-54.
- Lindelöw, A., & Weslien, J. 1986. Sex-specific emergence of *Ips typographus* L. (Coleoptera: Scolytidae) and flight behavior in response to pheromone sources following hibernation. *Canadian Entomologist*, 118, 59-67.
- Lindelöw, A., Risberg, B., & Sjodin, K. 1992. Attraction during flight of scolytids and other bark and wood-dwelling beetles to volatiles from fresh and stored spruce wood. *Canadian Journal of Forest Research*, 22, 224-8.
- Lindgren, B.S., Borden, J.H., Chong, L., Friskie, L.M., & Orr, D.B. 1983. Factors influencing the efficiency of pheromone baited traps for three species of ambrosia beetles (Coleoptera: Scolytidae). *Canadian Entomologist*, 115, 303-14.
- Löyttyniemi, K., Heliovaara, K., & Repo, S. 1988. No evidence of a population pheromone in *Tomicus piniperda* (Coleoptera: Scolytidae): a field experiment. *Annales Entomologici Fennici*, 54, 93-5.
- Macias-Samano, J.E., Borden, J.H., Gries, R., Pierce, H.D.Jr., Gries, G., & King, G.G.S. 1998. Primary attraction of the fir engraver, *Scolytus ventralis*. *Journal of Chemical Ecology*, 24, 1049-75.
- Magema, N., Gaspar, C., & Séverin, M. 1982. Efficacité de l'éthanol dans le piégeage du scolyte *Trypodendron lineatum* (Olivier, 1795)(Coleoptera: Scolytidae) et rôle des constituants terpeniques de l'épicéa. *Annales de la Société Royale Zoologique de Belgique*, 112, 49-60.
- Mathre, D.E. 1964. Pathogenicity of *Ceratocystis ips* and *Ceratocystis minor* to *Pinus ponderosa*. Contributions of the Boyce Thompson Institute, 22, 363-88.
- McLean, J.A., & Borden, J.H. 1977. Attack by *Gnathotrichus sulcatus* (Coleoptera: Scolytidae) on stumps and felled trees baited with sulcatol and ethanol. *Canadian Entomologist*, 109, 675-86.
- Mcmullen, L.H., & Atkins, M.D. 1962. On the flight and host selection of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae). *Canadian Entomologist*, 94, 1309-25.
- Meyer, H.J., & Norris, D.M. 1967a. Behavioral responses by *Scolytus multistriatus* (Coleoptera: Scolytidae) to host- (*Ulmus*) and beetle-associated chemotactic stimuli. *Annals of the Entomological Society of America*, 60, 642-6.

- Meyer, H.J., & Norris, D.M. 1967b. Vanillin and syringaldehyde as attractants for *Scolytus multistriatus* (Coleoptera: Scolytidae). Annals of the Entomological Society of America, 60, 858-9.
- Meyer, H.J., & Norris, D.M. 1974. Lignin intermediates and simple phenolics as feeding stimulants for *Scolytus multistriatus*. Journal of Insect Physiology, 20, 2015-21.
- Miller, D.R., & Borden, J.H. 1990. β -Phellandrene: kairomone for pine engraver *Ips pini* (Say) (Coleoptera: Scolytidae). Journal of Chemical Ecology, 16, 2519-31.
- Miller, J.M., & Keen, F.P. 1960. *Biology and Control of the Western Pine Beetle*. USDA miscellaneous publication # 800.
- Miller, J.R., & Strickler, K.L. 1984. Finding and accepting host plants. In: *Chemical Ecology, of Insects*, W.J. Bell, R.T. Cardé (Eds.). London: Chapman and Hall.
- Mirov, N.T. 1961. Composition of gum turpentines of pines. USDA Forest Service Technical Bulletin, No. 1239.
- Moeck, H.A. 1970. Ethanol as the primary attractant for the ambrosia beetle *Trypodendron lineatum* (Coleoptera: Scolytidae). Canadian Entomologist, 102, 985-94.
- Moeck, H.A. 1981. Ethanol induces attack on trees by spruce beetles *Dendroctonus rufipennis* (Coleoptera: Scolytidae). Canadian Entomologist, 113, 939-42.
- Moeck, H.A., Wood, D.L., & Lindahl, Jr., K.Q. 1981. Host selection behavior of bark beetles (Coleoptera: Scolytidae) attacking *Pinus ponderosa*, with special emphasis on the western pine beetle, *Dendroctonus brevicomis*. Journal of Chemical Ecology, 7, 49-83.
- Montgomery, M.E., & Wargo, P.M. 1983. Ethanol and other host derived volatiles as attractants to beetles that bore into hardwoods. Journal of Chemical Ecology, 9, 181-90.
- Moser, J.C., & Browne, L.E. 1978. A nondestructive trap for *Dendroctonus frontalis* Zimmerman (Coleoptera: Scolytidae). Journal of Chemical Ecology, 4, 1-7.
- Mustaparta, H. 1984. Olfaction. In. *Chemical Ecology, of Insects*, W.J. Bell, R.T. Cardé (Eds.). London: Chapman and Hall.
- Mustaparta, H., Angst, M.E., & Lanier, G.N. 1980. Receptor discrimination of enantiomers of the aggregation pheromone ipsdienol, in two species of *Ips*. Journal of Chemical Ecology, 6, 689-701.
- Nakamura, K. 1982. Competition between females and pheromone traps: Time lag between female mating activity and male trap captures. Applied Entomology and Zoology, 17, 292-300.
- Nakasui, F., & Fujita, K. 1980. A population model to assess the effect of sex pheromones on population suppression. Applied Entomology and Zoology, 15, 27-35.
- Nijholt, W.W., & Schönherz, J. 1976. Chemical response behavior of scolytids in West Germany and western Canada. Canadian Forest Service Bi-monthly Research Notes, 32, 31-2.
- Nilssen, A.C. 1978. Development of a bark fauna in plantations of spruce (*Picea abies* [L.] Karst.) in north Norway. Astarta, 11, 151-69.
- Paine, T.D. 1984. Influence of the mycangial fungi of the western pine beetle *Dendroctonus brevicomis* on water conduction through ponderosa pine seedlings. Canadian Journal of Botany, 62, 556-8.
- Paine, T.D., & Stephen, F.M. 1987. Fungi associated with the southern pine beetle: avoidance of induced defense response in loblolly pine. Oecologia, 74, 377-9.
- Paine, T.D., Stephen, F.M., & Cates, R.G. 1988. Moisture stress, tree suitability, and southern pine beetle population dynamics. In. *Integrated Control of Scolytid Bark Beetles*, T.L. Payne, H. Saarenmaa (Eds.). Blacksburg (USA): Virginia Polytechnical Institute and State University.
- Paiva, M.R., & Kiesel, K. 1985. Field responses of *Trypodendron* spp. (Col., Scolytidae) to different concentrations of lineatin and α -pinene. Zeitschrift für angewandte Entomologie, 99, 442-8.
- Payne, T.L. 1979. Pheromone and host odor perception in bark beetles. In. *Neurotoxicology of Insecticides and Pheromones*, T. Narahashi (ed.). New York: Plenum Publishing Company.
- Payne, T.L., Moeck, H.A., Willson, C.D., Coulson, R.N., & Humphreys, W.J. 1973. Bark beetle olfaction - II. antennal morphology of sixteen species of Scolytidae (Coleoptera). International Journal of Insect Morphology and Embryology, 2, 177-92.
- Payne, T.L., Richerson, J.V., Dickens, J.C., West, J.R., Mori, K., Berisford, C.W., Hedden, R.L., Vité, J.P., & Blum, M.S. 1982. Southern pine beetle: olfactory receptor and behavior discrimination of enantiomers of the attractant pheromone frontalalin. Journal of Chemical Ecology, 8, 873-81.
- Phillips, T.W. 1990. Responses of *Hylastes salebrosus* to turpentine, ethanol and pheromones of *Dendroctonus* (Coleoptera: Scolytidae). Florida Entomologist, 73, 286-92.
- Phillips, T.W., Wilkening, A.J., Atkinson, T.H., Nation, J.L., Wilkinson, R.C., & Foltz, J.L. 1988. Synergism of turpentine and ethanol as attractants for certain pine-infesting beetles (Coleoptera). Environmental Entomology, 17, 456-62.

- Pierce, Jr., H.D., Conn, J.E., Oehlschlager, A.C., & Borden, J.H. 1987. Monoterpene metabolism in female mountain pine beetles, *Dendroctonus ponderosae* Hopkins attacking ponderosa pine. Journal of Chemical Ecology, 13, 1455-80.
- Pitman, G.B., Renwick, J.A.A., & Vité, J.P. 1966. Studies on the pheromone of *Ips confusus* (LeConte). IV. Isolation of the attractive substance by gas-liquid chromatography. Contributions of the Boyce Thompson Institute, 23, 243-50.
- Pitman, G.B., & Vité, J.P. 1969. Aggregation behavior of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in response to chemical messengers. Canadian Entomologist, 101, 143-9.
- Pitman, G.B., Hedden, R.L., & Gara, R.I. 1975. Synergistic effects of ethyl alcohol on the aggregation of *Dendroctonus pseudotsugae* (Col., Scolytidae) in response to pheromones. Zeitschrift für angewandte Entomologie, 78, 203-8.
- Poland, T.M., Borden, J.H., Stock, A.J., & Chong, L.J. 1998. Green leaf volatiles disrupt responses by the spruce beetle, *Dendroctonus rufipennis*, and the western pine beetle, *Dendroctonus brevicomis* (Coleoptera: Scolytidae) to attractant-baited traps. Journal of the Entomological Society of British Columbia, 95, 17-24.
- Poland T.M., & Haack R.A. 2000. Pine shoot beetle, *Tomicus piniperda* (Coleoptera: Scolytidae), responses to common green leaf volatiles. Journal of Applied Entomology, 124, 63-70
- Popp, M.P., Johnson, J.D., & Lesney, M.S. 1995. Changes in ethylene production and monoterpene concentration in slash pine and loblolly pine following inoculations with bark beetle vectored fungi. Tree Physiology, 15, 807-12.
- Raffa, K.F., & Berryman, A.A. 1979. Flight responses and host selection by bark beetles. In. *Dispersal of Forest Insects: Evaluation, Theory and Management Implications*, A.A. Berryman, L. Safranyik (Eds.). Proc. second IUFRO conf., Canadian and USDA Forest Service.
- Raffa, K.F., & Berryman, A.A. 1982. Gustatory cues in the orientation of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) to host trees. Canadian Entomologist, 114, 97-104.
- Raffa, K.F., & Berryman, A.A. 1987. Interacting selective pressures in conifer-bark beetle systems: a basis for reciprocal adaptations? American Naturalist, 129, 234-62.
- Raffa, K.F., Phillips, T.W., & Salom, S.M. 1993. Strategies and mechanisms of host colonization by bark beetles. In. *Beetle-Pathogen Interactions in Conifer Forests* T.D. Schowalter, G.M. Filip (Eds.). London: Academic Press.
- Ramaswamy, S.B., & Cardé, R.T. 1984. Rate of release of spruce budworm *Choristoneura fumiferana* pheromone from virgin females and synthetic lures. Journal of Chemical Ecology, 10, 1-8.
- Ramisch, H. 1986. Host location by *Trypodendron domesticum* and *Trypodendron lineatum* (Coleoptera: Scolytidae). Zeitschrift für angewandte Zoologie, 73, 159-98.
- Raulston, J.R., Lingren, P.D., Sparks, A.N., & Martin, D.F. 1979. Mating interaction between native tobacco budworms and released backcross adults. Environmental Entomology, 8, 349-53.
- Renwick, J.A.A., & Vité, J.P. 1968. Isolation of the population aggregating pheromone of the southern pine beetle. Contributions of the Boyce Thompson Institute, 24, 65-8.
- Renwick, J.A.A., & Vité, J.P. 1969. Bark beetle attractants: mechanisms of colonization by *Dendroctonus frontalis*. Nature, 224, 1222-3.
- Renwick, J.A.A., & Vité, J.P. 1970. Systems of chemical communication in *Dendroctonus*. Contributions of the Boyce Thompson Institute, 24, 283-92.
- Richeson, J.S., Wilkinson, R.C., & Nation, J.L. 1970. Development of *Ips calligraphus* on foliage based diets. Journal of Economic Entomology, 63, 1797-9.
- Richter, D. 1991. Control of bark beetles in the five new states of the Federal Republic of Germany, In. A. Wulf and R. Kehr (Eds.). *Bark Beetle Hazards Following Storm Damage: Possibilities and Limits of Integrated Control*. Colloquium, Braunschweig, Germany. Communications from the Federal Biological Institute for Agriculture and Forestry, Berlin-Dahlem, No. 267.
- Ricklefs, R.E. 1990. Evolution, social behavior, and population regulation. In. *Ecology*. New York: W.H. Freeman and Company.
- Roelofs, W.L., Glass, E.H., Tette, J., & Comeau, A. 1970. Sex pheromone trapping for red-banded leaf roller control: Theoretical and actual. Journal of Economic Entomology, 63, 1162-7.
- Rose, W.F., Billings, R.F., & Vité, J.P. 1981. Southern pine bark beetles *Ips calligraphus*: evaluation of nonsticky pheromone trap designs for survey and research. Southwest Entomologist, 6, 1-9.
- Rudinsky, J.A. 1966. Host selection and invasion by the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, in coastal Douglas-fir forests. Canadian Entomologist, 98, 98-111.

- Rudinsky, J.A., Novak, V., & Svihra, P. 1971. Attraction of the bark beetle *Ips typographus* L. to terpenes and a male-produced pheromone. Zeitschrift für angewandte Entomologie, 67, 179-88.
- Rudinsky, J.A., Morgan, M.E., Libbey, L.M., & Putnam, T.B. 1974. Antiaggregative-rivalry pheromone of the mountain pine beetle, and a new arrestant of the southern pine beetle. Environmental Entomology, 3, 90-8.
- Salom, S.M., & Mclean, J.A. 1989. Influence of wind on the spring flight of *Trypodendron lineatum* Olivier (Coleoptera: Scolytidae) in a second-growth coniferous forest. Canadian Entomologist, 121, 109-20.
- Salonen, K. 1973. On the life cycle, especially on the reproduction biology of *Blastophagus piniperda* L. (Col., Scolytidae). Acta Forestalia Fennica, 127, 1-72.
- Schlyter, F. 1992. Sampling range, attraction range, and effective attraction radius: Estimates of trap efficiency and communication distance in coleopteran pheromone and host attractant systems. Journal of Applied Entomology, 114, 439-54.
- Schlyter, F., & Birgersson, G. 1999. Forest Beetles. In. J. Hardie, J., A.K. Minks (Eds.). *Pheromone in Non-Lepidopteran Insects Associated with Agricultural Plants*, Oxford: CAB International.
- Schlyter, F., Birgersson, G., Byers, J.A., Löfqvist, J., & Bergström, G. 1987a. Field response of spruce bark beetle, *Ips typographus*, to aggregation pheromone candidates. Journal of Chemical Ecology, 13, 701-16.
- Schlyter, F., Byers, J.A., & Löfqvist, J.. 1987b. Attraction to pheromone sources of different quantity, quality, and spacing: density-regulation mechanisms in bark beetle *Ips typographus*. Journal of Chemical Ecology, 13, 1503-23.
- Schlyter, F., Löfqvist, J., & Byers, J.A. 1987c. Behavioural sequence in the attraction of the bark beetle *Ips typographus* to pheromone sources. Physiological Entomology, 12, 185-96.
- Schlyter, F., Byers, J.A., Löfqvist, J., Leufvén, A., & Birgersson, G. 1988. Reduction of attack density of the bark beetles *Ips typographus* and *Tomicus piniperda* on host bark by verbenone inhibition of attraction to pheromone and host kairomone. In. *Integrated Control of Scolytid Bark Beetles*, T.L. Payne, H. Saarenmaa (Eds.). Blacksburg (USA): Virginia Tech. Press.
- Schlyter, F., Birgersson, G., & Leufven, A. 1989. Inhibition of attraction to aggregation pheromone by verbenone and ipsenol: density regulation mechanisms in bark beetle *Ips typographus*. Journal of Chemical Ecology, 15, 2263-77.
- Schlyter, F., Birgersson, G., Byers, J.A., & Bakke, A. 1992. The aggregation pheromone of *Ips duplicatus* and its role in competitive interactions with *I. typographus* (Coleoptera: Scolytidae). Chemoecology, 3, 103-12.
- Schlyter, F., Löfqvist, J., & Jakus, R. 1995. Green leaf volatiles and verbenone modify attraction of European *Tomicus*, *Hylurgops*, and *Ips* bark beetles. In. *Behavior, Population Dynamics, and Control of Forest Insects*, F.P. Hain, S.M. Salom, W.F. Ravlin, T.L. Payne, K.F. Raffa, KF (Eds.). Proceedings IUFRO Working Party Conference. Ohio State Univ.
- Schlyter, F., Zhang, Q.H., Anderson, P.A., Byers, J.A., Wadham, L.J., Löfqvist, J., & Birgersson, G. 2000. Electrophysiological and behavioural responses of *Tomicus piniperda* and *T. minor* (Coleoptera: Scolytidae), to non-host leaf and bark volatiles. Canadian Entomologist, 132, 965-81.
- Schroeder, L.M. 1987. Attraction of the bark beetle *Tomicus piniperda* to Scots pine trees in relation to tree vigor and attack density. Entomologia Experimentalis et Applicata, 44, 53-8.
- Schroeder, L.M. 1988. Attraction of the bark beetle *Tomicus piniperda* and some other bark- and wood-living beetles to the host volatiles α -pinene and ethanol. Entomologia Experimentalis et Applicata, 46, 203-10.
- Schroeder, L.M. 1992. Olfactory recognition of nonhosts aspen and birch by conifer bark beetles *Tomicus piniperda* and *Hylurgops palliatus*. Journal of Chemical Ecology, 18, 1583-93.
- Schroeder, L.M., & Eidmann, H.H. 1987. Gallery initiation by *Tomicus piniperda* (Coleoptera: Scolytidae) on Scots pine trees baited with host volatiles. Journal of Chemical Ecology, 13, 1591-9.
- Schroeder, L.M., & Lindelöw, A. 1989. Attraction of scolytids and associated beetles by different absolute amounts and proportions of α -pinene and ethanol. Journal of Chemical Ecology, 15, 807-18.
- Schuh, B.A., & Benjamin, D.M. 1984. The chemical feeding ecology of *Neodiprion dubiosus* Schedl, *N. rugifrons* Midd., and *N. lecontei* (Fitch) on Jack pine (*Pinus banksiana* Lamb.). Journal of Chemical Ecology, 10, 1071-9.
- Scriber, J.M. 1984. Host-plant suitability. In. *Chemical Ecology, of Insects*, W.J. Bell, R.T. Cardé (Eds.). London: Chapman and Hall.
- Seybold, S.J., & Tittiger, C. 2003. Biochemistry and molecular biology of *de novo* isoprenoid pheromone production in the Scolytidae. Annual Review of Entomology, 48, 425-53.

- Seybold, S.J., Bohlmann, J., & Raffa, K.F. 2000. The biosynthesis of coniferophagous bark beetle pheromones and conifer isoprenoids: evolutionary perspective and synthesis. Canadian Entomologist, 132, 697-753.
- Silverstein, R.M., Brownlee, R.G., Bellas, T.E., Wood, D.L., & Browne, L.E. 1968. Brevicomin: principal sex attractant in the frass of the female western pine beetle. Science, 159, 889-91.
- Smith, L.V., & Zavarin, E. 1960. Free mono- and oligosaccharides of some California conifers. TAPPI Journal, 43, 218-21.
- Städler, E. 1984. Contact chemoreception. In. *Chemical Ecology, of Insects*, W.J. Bell, R.T. Cardé (Eds.). Londong: Chapman and Hall.
- Sternlicht, M., Barzakay, I., & Tamim, M. 1990. Management of *Prays citri* in lemon orchards by mass trapping of males. *Entomologia Experimentalis et Applicata*, 55, 59-68.
- Struble, G.R. 1957. The fir engraver, a serious enemy of western true firs. US Agricultural Product Research Report II.
- Teale, S.A., Webster, F.X., Zhang, A., & Lanier, G.N. 1991. Lanierone: a new pheromone component from *Ips pini* (Coleoptera: Scolytidae) in New York. *Journal of Chemical Ecology*, 17, 1159-76.
- Thompson, S.N., & Bennett, R.B. 1971. Oxidation of fat during flight of male Douglas-fir beetles, *Dendroctonus pseudotsugae*. *Insect Physiology*, 17, 1555-63.
- Tilden, P.E., Bedard, W.D., Lindahl, Jr., K.Q., & Wood, D.L. 1983. Trapping *Dendroctonus brevicomis*: changes in attractant release rate, dispersion of attractant, and silhouette. *Journal of Chemical Ecology*, 9, 311-21.
- Tommerås, B.A., Mustaparta, H., & Gregoire, J.C. 1984. Receptor cells in *Ips typographus* and *Dendroctonus micans* specific to pheromones of the reciprocal genus. *Journal of Chemical Ecology*, 10, 759-69.
- Villavaso, E.J. 1982. Boll weevil, *Anthonomus grandis*, isolated field plot studies of disruption of pheromone communication. *Journal of the Georgia Entomological Society*, 17, 347-50.
- Villavaso, E.J., & McGovern, W.L. 1981. Boll weevil, *Anthonomus grandis grandis*, disruption of pheromonal communication in the laboratory and small field plots. *Journal of Georgia Entomological Society*, 16, 306-10.
- Vité, J.P. 1961. The influence of water supply on oleoresin exudation pressure and resistance to bark beetle attack in *Pinus ponderosa*. *Contributions of the Boyce Thompson Institute*, 21, 37-66.
- Vité, J.P. 1989. The European struggle to control *Ips typographus*: Past present and future. *Holarctic Ecology*, 12, 520-5.
- Vité, J.P., & Pitman, G.B. 1969. Insect and host odors in the aggregation of the western pine beetle. *Canadian Entomologist*, 101, 113-17.
- Vité, J.P., & Bakke, A. 1979. Synergism between chemical and physical stimuli in host selection by an ambrosia beetle. *Naturwissenschaften*, 66, 528-9.
- Vité, J.P., Volz, H.A., Paiva, M.R., & Bakke, A. 1986. Semiochemicals in host selection and colonization of pine trees by the pine shoot beetle *Tomicus piniperda*. *Naturwissenschaften*, 73, 39-40.
- Volz, H.A. 1988. Monoterpene governing host selection in the bark beetles *Hylurgops palliatus* and *Tomicus piniperda*. *Entomologia Experimentalis et Applicata*, 47, 31-6.
- Vrkoc, J. 1989. Use of insect pheromone in integrated pest management examples from Czechoslovakia. *Chem Scripta*, 29, 407-10.
- Wagner, M.R., Benjamin, D.M., Clancy, K.L., & Schuh, B.A. 1983. Influence of diterpene resin acids on feeding and growth of larch sawfly, *Pristiphora erichsonii* (Hartig). *Journal of Chemical Ecology*, 9, 119-27.
- Webb, J.L. 1906. The western pine destroying bark beetle. USDA Bureau of Entomology Bulletin, 58, Pt. II.
- Webb, J.W., & Franklin, R.T. 1978. Influence of phloem moisture on brood development of the southern pine beetle (Coleoptera: Scolytidae). *Environmental Entomology*, 7, 405-10.
- Weber, T. 1987. Can bark beetles be controlled efficiently by application of pheromone traps. *Allgemeine Forstzeitschrift*, 42, 87-9.
- White, J.D. 1981. A bioassay for tunneling responses of southern pine beetles to host extractives. *Journal of the Georgia Entomological Society*, 16, 484-92.
- Whitehead, A.T. 1981. Ultrastructure of sensilla of the female mountain pine beetle *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *International Journal of Insect Morphology and Embryology*, 10, 19-28.

- Whitney, H.S. 1982. Relationships between bark beetles and symbiotic organisms. In. *Bark Beetles in North American Conifers: a System for the Study of Evolutionary Biology*, J.B. Mitton, J.B., K.B. Sturgeon (Eds.). Austin: University of Texas Press.
- Whitney, H.S., & Spanier, O.J. 1982. An improved method for rearing axenic mountain pine beetles *Dendroctonus ponderosae* (Coleoptera: Scolytidae). Canadian Entomologist, 114, 1095-1100.
- Wilson, I.M., Borden, J.H., Gries, R., & Gries, G. 1996. Green leaf volatiles as antiaggregants for the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Journal of Chemical Ecology, 22, 1861-75.
- Witanachchi, J.P., & Morgan, F.D. 1981. Behavior of the bark beetle, *Ips grandicollis*, during host selection. Physiological Entomology, 6, 219-23.
- Witz, J.A., Lopez, J.D., Jr., & Latheef, M.A. 1992. Field density estimates of *Heliothis virescens* (Lepidoptera: Noctuidae) from catches in sex pheromone-baited traps. Bulletin of Entomological Research, 82, 281-6.
- Wood, D.L. 1962. Experiments on the interrelationship between oleoresin exudation pressure in *Pinus ponderosa* and attack by *Ips confusus* (LeC.) (Coleoptera: Scolytidae). Canadian Entomologist, 94, 473-7.
- Wood, D.L. 1980. Approach to research and forest management for western pine beetle control. In. *New Technology of Pest Control*. C.B. Huffaker (ed.), New York: John Wiley and Sons.
- Wood, D.L. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Annual Review of Entomology, 27, 411-46.
- Wood, D.L., & Bushing, R.W. 1963. The olfactory response of *Ips confuses* (LeConte) (Coleoptera: Scolytidae) to the secondary attraction in the laboratory. Canadian Entomologist, 95, 1066-78.
- Wood, D.L., & Vité, J.P. 1961. Studies on the host selection behavior of *Ips confusus* (LeConte) (Coleoptera: Scolytidae) attacking *Pinus ponderosa*. Contributions of the Boyce Thompson Institute, 21, 79-96.
- Wood, S.L. 1982. *The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph*. Great basin naturalist memoirs, Brigham Young Univ., Provo, Utah.
- Zhang, Q.H. 2003. Interruption of aggregation pheromone in *Ips typographus* (L.) (Col.: Scolytidae) by non-host bark volatiles. Agricultural and Forest Entomology, 5, 145-53.
- Zhang, Q.H., & Schlyter, F. 2003. Olfactory recognition and behavioural avoidance of angiosperm non-host volatiles by conifer-inhabiting bark beetles. Agricultural and Forest Entomology, *In press*
- Zhang, Q.H., Birgersson, G., Zhu, J., Löfstedt, C., Löfqvist, J., & Schlyter, F. 1999a. Leaf volatiles from nonhost deciduous trees: Variation by tree species, season, and temperature, and electrophysiological activity in *Ips typographus*. Journal of Chemical Ecology, 25, 1923-43.
- Zhang, Q.H., Schlyter, F., & Anderson, P. 1999b. Green leaf volatiles interrupt pheromone response of spruce bark beetle, *Ips typographus*. Journal of Chemical Ecology, 25, 2847-61.
- Zhang, Q.H., Schlyter, F., & Birgersson, G. 2000. Bark volatiles from nonhost angiosperm trees of spruce bark beetle, *Ips typographus* (L.) (Coleoptera: Scolytidae): Chemical and electrophysiological analysis. Chemoscience, 10, 69-80.
- Zhang, Q.H., Liu, G.T., Schlyter, F., Birgersson, G., Anderson, P., & Valeur, P. 2001. Olfactory response of *Ips duplicatus* to nonhost leaf and bark volatiles in inner Mongolia, China. Journal of Chemical Ecology, 27, 955-1009.
- Zolubas, P., & Byers, J.A. 1995. Recapture of dispersing bark beetles, *Ips typographus* L. (Col., Scolytidae) in pheromone-baited traps: regression models. Journal of Applied Entomology, 19, 285-89.
- Zumr, V. 1992. Dispersal of the spruce bark beetle *Ips typographus* (L.) (Col., Scolytidae) in spruce woods. Journal of Applied Entomology, 114, 348-52.
- Zvirgzdins, A., Lingren, P.D., Henneberry, T.J., Nowell, C.E., & Gillespie, J.M. 1984. Mating Disruption of a wild population of tobacco budworm, *Heliothis virescens*, (Lepidoptera: Noctuidae) with virelure. Journal of Economic Entomology, 77, 1464-69.

Chapter 9

HOST RESISTANCE TO BARK BEETLES AND ITS VARIATIONS

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1. INTRODUCTION AND DEFINITIONS

As with all other living organisms, trees are able to defend themselves against attacks and, during their colonization process, bark beetles face and must overcome a diversity of resistance mechanisms. Freshly felled trees, which pose very little resistance to bark beetles, represent an easily accessible source of food, while the very high resistance level of healthy trees makes them relatively inaccessible. By conditioning the quantity of available food, tree resistance is thus the real key-factor in the population dynamics of bark beetles that attack living trees. Consequently, two aspects will be first considered in this chapter: the tree side encompassing resistance mechanisms and their effects on bark beetles; the beetle side including the strategies used by the insect to overcome tree resistance and to succeed in establishing and breeding successfully.

The concepts of defence and resistance must be defined first. Following Karban and Baldwin (1997), one can consider that they correspond to two complementary “points of view” of the same phenomenon. Defence is considered from a tree’s perspective and refers to the necessity to stop beetle attacks to ensure survival. It also often supposes active mechanisms induced in response to attacks. Resistance refers to mechanisms hampering beetle establishment in its host and can involve both active induced and passive non-induced phenomena.

In a broad sense, resistance to bark beetles involves both mechanisms that act at a distance through chemical communication, before the aggressor reaches the tree, and mechanisms that act after physical contact between the host and its aggressor has been established. Since chemical communication between trees and bark beetles is largely developed elsewhere in this volume (Byers, chapter 8), this chapter concentrates on a strict definition of tree resistance and is limited to what happens after beetles have reached their host trees. In addition, because most bark beetle damage on living trees largely concerns conifers, very few data are available

regarding resistance of hardwood trees to these insects. Thus this chapter is organized by referring to European conifers, mainly Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*, but will make comparisons with studies carried out on species living outside Europe. First the different levels of tree resistance and the general mechanisms of induced defences are presented, followed by a discussion on the role and efficiency of these systems. Next, the beetle side will be considered by presenting beetle behavior when encountering tree resistance. A discussion on the effect of host resistance on bark beetle population dynamics will follow. Then, the variations in tree resistance depending on genetic and environmental factors will be considered in some detail. The possibilities of using tree resistance for bark beetle management will be only mentioned because it is largely developed previously, and the conclusion will focus on strengths and gaps in our knowledge of the relationships between tree resistance and the European bark beetle species.

2. NATURE AND CHARACTERISTICS OF THE TREE RESISTANCE SYSTEMS

Tree resistance systems have been presented in detail recently (Lieutier, 2002) and only a summary is provided here, focusing on the European specificities and results.

2.1. Levels / systems of tree resistance

Classically, the systems of tree resistance to attacks are separated into two groups according to the period of investment of the energy resources in defence. In preformed resistance, resources are invested in defence before beetle attacks, whereas they are mobilized only in response to aggression in the case of the induced resistance. In this latter situation, there is gene activation by the aggressors, followed by an increase in the syntheses of secondary metabolites involved in defence, often accompanied by neosyntheses and building of new structures. Secondary metabolites and histological structures also often occur in preformed resistance but they are produced before beetle attack.

2.1.1. Systems of preformed resistance

These systems represent the first line of resistance met by the aggressors (beetle or their associated fungi). Depending on the need for activation, two kinds of preformed defences can be distinguished (Karban and Balwin, 1997). The "constitutive defences" are active in the same state as they were before aggression. As an example, bark thickness can often be responsible for the failure of attacks by beetle species that localize attacks preferably in the upper part of the tree. Stone cell masses are lignin patches that can be found in large quantities in the phloem of Norway and Sitka spruce *Picea sitchensis*, and have been demonstrated to play a role in arresting attacks by *Dendroctonus micans* (Wainhouse *et al.*, 1990, 1997, 1998a). Low phloem moisture content can counteract oviposition and development of this species in Norway spruce (Storer and Speight, 1996). Calcium oxalate crystals, in combination with fiber rows, have also been suggested to contribute in

limiting bark beetle attacks in the phloem of Pinaceae (Hudgins *et al.*, 2003b). The “preformed induced defences” are represented by two main anatomical systems containing secondary metabolites. Blisters and resin canals store terpene compounds (Johnson and Croteau, 1987), while specialized phloem parenchyma cells store phenolic compounds (Franceschi *et al.*, 1998). Wounding these systems is necessary for their content to be released and to affect the attacking beetles.

Resin canal systems are largely developed in the genera without blisters, such as in Europe, *Pinus* and, to a lesser extent, *Larix* and *Picea*, while blisters are found mainly in *Abies* and *Cedrus*, which do not have resin canals. Typically, the resin duct system is a network of interconnected vertical (in the sapwood) and radial (in both the sapwood and the phloem) canals around which the cells responsible for resin synthesis are located. In case of wounding, resin is immediately released from this system and can cause failure of attacks when its flow is abundant. This flow, however, dries up very rapidly (1 to 3 days). Because vertical canals are much more numerous than radial ones, the resin flow released by a wound is generally correlated with the density of vertical canals. For the same reason, the direction of gallery boring is important for this defence system to play a significant role in tree resistance to bark beetles (Berryman, 1972; Lieutier, 1992). It has been demonstrated that resin flow can contribute significantly to the failure of *D. micans* attacks on Norway spruce, and this has been attributed to the horizontal direction of the maternal gallery that cuts both radial ducts and a high number of vertical ducts during the whole tunneling activity of the beetle (Lieutier *et al.*, 1992). It is much less efficient against species that bore vertical galleries because vertical ducts are cut, in that case, only at the very beginning of attack. Its role in such situations has been demonstrated to be very limited, as in Europe for *Ips typographus* on Norway spruce (Christiansen and Horntvedt, 1983), and *Ips sexdentatus* and *Tomicus piniperda* in Scots pine where resin flow can play a role in arresting the attacking beetles only at the time of initiating egg galleries (Lieutier *et al.*, 1988b, 1995; Schroeder, 1990). Similar conclusions have been drawn for North American species (Raffa and Berryman, 1983a; Nebeker *et al.*, 1988). Blisters are resin pockets located inside the outer bark. Their role in resistance has not been studied in Europe, but studies carried out in North America have demonstrated that, although important resin quantities can be released by wounding, beetles seem able to avoid them (Ferrell, 1983).

The polyphenolic parenchyma cell (PP cell) system has been described in detail in Norway spruce (Franceschi *et al.*, 1998; Krekling *et al.*, 2000). PP cells are organized in parallel concentric rows inside the phloem, inevitably resulting in their destruction and certainly in the release of large quantities of phenolic compounds when a beetle or its associated fungus invades the phloem. However, although the abundance of PP cells and the phloem content of certain soluble phenols before attacks are correlated with tree resistance (Storer and Speight, 1996; Franceschi *et al.*, 1998; Brignolas *et al.*, 1998), no direct demonstration of their role in preformed resistance has been provided yet.

2.1.2. Systems of induced resistance

Three main steps representing different degrees of complexity can be recognized

The “induced resin flow” is the simplest mechanism. It has been described as a stimulation of resin synthesis by the cells surrounding the resin canals and which are responsible for the synthesis of the preformed resin (Ruel *et al.*, 1998). However, because the chemical content of the new resin has not been investigated, it is not known if this stimulation is accompanied by modifications to the metabolism of the secretory cells. It is typically a wound reaction which appears after repeated wounding to the tree, and which produces larger quantities of resin than in the case of preformed resistance. Certainly, this reaction can extend the effect of the preformed resin flow in time. It has been described only in *Pinus taeda* in Southern USA but it certainly also exists in European pines, especially in regions, such as the Mediterranean basin, where trees are submitted to attacks all the year round.

The “hypersensitive reaction” of conifers to attacks by bark beetles and their associated fungi has been studied in various regions of the world, after Reid *et al* (1967) described it for the first time in a conifer (*Pinus contorta*) and suggested it could play an essential role in resistance to bark beetles. In Europe, it has been studied mainly in Norway spruce and Scots pine (Christiansen and Horntvedt, 1983; Christiansen, 1985a; Christiansen *et al.*, 1987; Lieutier *et al.*, 1989b, 1995; Delorme and Lieutier, 1990; Solheim and Langström, 1991; Langström *et al.*, 1992; Lieutier, 1993; Brignolas *et al.*, 1995a; Bois and Lieutier, 1997; among others) and has been demonstrated to play a fundamental role in resistance in most situations. The reaction is visible as a resin impregnated zone associated with extended cell necrosis, which develops usually longitudinally around each point of attack, in both the phloem and the sapwood, at a distance ahead of the area infested by the beetles and their associated fungi. This zone is considerably impoverished in sugars and enriched with terpenes and phenolic compounds, resulting from both stimulation of syntheses and neosyntheses, the products of which invade intercellular spaces, sieve cells and tracheids, leading to the death of the affected tissues (Christiansen and Ericsson, 1986; Lieutier and Berryman, 1988; Delorme and Lieutier, 1990; Langström *et al.*, 1992; Brignolas *et al.*, 1995a). Considerable changes occur in cell metabolism and activities. The cells involved in induced syntheses of terpenes are specialized phloem parenchyma cells, without relation to those involved in the synthesis of the preformed resin (Chencllet *et al.*, 1988; Lieutier and Berryman, 1988). The PP cells already involved in phenolic preformed resistance seem also to be responsible for the neosyntheses of the phenolics involved in the hypersensitive reaction (Franceschi *et al.*, 1988), but heavy changes occur in their metabolism (Brignolas *et al.*, 1995b; Chiron *et al.*, 2000). However, in spite of the delocalization of certain syntheses and considerable changes in cell metabolism, no cell division and cell differentiation seems to occur. The reaction ends with the formation of a wound periderm which develops after the aggressors have been stopped or at least considerably slowed down (Müllck, 1977; Lieutier *et al.*, 1990; Lieutier, 1993), and isolates the reaction zone and the included aggressors from the rest of the tree.

The extent of the resin impregnated zone (reaction zone) in the phloem has often been used to compare the defensive abilities of trees. However, its development results from both the host response and fungal growth, which has led to

contradicting interpretations after isolated inoculations (Raffa, 1991; Wallin and Raffa, 2001). Krokene and Solheim (1999) showed that low density inoculations do not always give a reliable estimate of tree resistance or of fungal virulence (see also Långström *et al.* 2001). Nevertheless, Wallin and Raffa (2001) consider that the delay in time after which this zone is measured is certainly of importance, if we admit that trees producing the most rapid and intensive response exhibit longer reaction zones with short delay, while the most susceptible trees need time to stop the fungus, thus allowing the reaction to grow over longer period leading to a longer reaction zone overall. They suggested that tree resistance levels should be compared by using a fungal confinement rate corresponding to the ratio of reaction zone length at day 6 to that at day 9. On the other hand, reaction zone length after punctual inoculations has been demonstrated to be an indicator of virulence useful for comparison of different fungi in the same tree (Lieutier *et al.*, 1989b, 1990; Långström *et al.*, 1993b) and different isolates within the same fungus species (Lieutier *et al.*, 2004).

The “delayed resistance” corresponds to the most complex changes occurring in response to bark beetle attack. The formation of the wound periderm mentioned above refers to that kind of tree reaction but it interferes mainly in wound healing processes and it is not discussed here. The phenomenon of “induced protection”, on the contrary, directly interferes in tree resistance. It has been described recently in Europe, in both Norway spruce and Scots pine (Christiansen *et al.*, 1999a; Krokene *et al.*, 1999, 2000, 2001), although it certainly also exists in other conifers. It corresponds to the induction of resistance to lethal densities of mass inoculations, in trees pretreated at levels below the lethal density, with a phytopathogenic fungus. A delay of at least one week after pretreatment is needed for the induction of resistance, and trees are protected for at least one year after pretreatment (Krokene *et al.*, 2003). The detailed mechanisms of the induced protection are still largely unknown but it has been hypothesized that traumatic resin ducts which usually form after wounding in the sapwood, after the same delay as induced protection, are involved (Krokene *et al.*, 1999, 2003; Christiansen *et al.*, 1999b; Nagy *et al.*, 2000). However, the induced protection stays local, whereas traumatic resin ducts can be observed up to a distance of several meters from the inoculation site after one year (Christiansen *et al.*, 1999b). If this hypothesis is true and because these resin canals are built *de novo* from cambial cells, induced protection would correspond to very complex changes involving cell division and differentiation. Modifications in the PP cells have been reported to be associated with this kind of resistance (Krokene *et al.*, 2003) supposedly in relation to methyl jasmonate release (Franceschi *et al.*, 2002; Martin *et al.*, 2002; Fäldt *et al.*, 2003; Hudgins *et al.*, 2003a). In the same tree species, a spatio-temporal study of host selection by *D. micans* in central France concluded there was induced susceptibility following successful attacks by previous beetle generations (Gilbert *et al.*, 2001). This does not exclude, however, the possibility that failed attacks increase tree resistance, in accordance with the delayed resistance phenomenon.

2.2. General mechanisms of induced defences

2.2.1. Complementarity and interdependence

The three main levels of complexity of induced defences, ranking from simple stimulation of cells already specialized in the same function to complex changes accompanied by building of new cells, are equivalent to a ranking from short term to long term responses. The induced resin flow appears only two to three days after the beginning of wounding (Ruel *et al.*, 1998). The hypersensitive reaction begins to be clearly visible in the phloem as soon as three days after attack, but is fully developed both histologically and chemically in 10 to 15 days, in Scots pine and Norway spruce as well (Lieutier *et al.*, 1990; Brignolas *et al.*, 1995a,b; Franceschi *et al.*, 1998). The formation of traumatic resin ducts, involving more complex changes, is slower. They need more than two weeks to be built locally, and one year at a distance of some meters (Christiansen *et al.*, 1999b; Nagy *et al.*, 2000). In terms of tree resistance to attacks, the induced defence systems thus seem to complement each others very well in time, after the rapid and brief action of the preformed resistance (Lieutier, 2002). Their relative role to that of the preformed resistance can also be modulated by various factors such as beetle behavior (gallery direction), tree species, or climatic factors (Lombardero *et al.*, 2000). In addition, interactions exist between different systems. In Norway and Sitka spruce, a negative correlation was found between the size of the phloem reaction zone and the concentration of stone cell masses in this tissue (Wainhouse *et al.*, 1997). At least for phenols, the same PP cells seem to be involved in constitutive, hypersensitive and delayed resistance (Franceschi *et al.*, 2000).

2.2.2. Induction, specificity and involved cells

Apart from their linkage in time, there are several essential characteristics that appear to be shared by the different degrees of induced response (Lieutier, 2002). They are all wound reactions, eventually stimulated when fungi are present, they are not specific in relation to the species of aggressor, and they generally involve phloem parenchyma cells.

In experiments using natural and artificial attacks on Scots pine by *T. piniperda* and *I. sexdentatus*, it has been shown that the hypersensitive reaction is a wound reaction, induced by the mechanical stress caused by the tunneling activity of the beetle, and that it can be considerably accelerated and amplified when a phytopathogenic fungus is present in the gallery (Lieutier *et al.*, 1988b, 1995). This was also demonstrated in Norway spruce submitted to artificial infestation by *Ceratocystis polonica*, a fungus associated with *I. typographus* (Brignolas *et al.*, 1995a, Franceschi *et al.*, 1998). Lieutier (1993) suggested that this mechanism of induction occurs in all hypersensitive reactions of conifers to attacks by bark beetles and their associated fungi. Induced protection has also been demonstrated to occur after pre-treatment with malt agar without fungus, although to a lesser extent than after pretreatment with fungus (Krokene *et al.*, 1999). This again suggests that fungus stimulates a wound reaction. Traumatic resin duct formation is typically a wound response which has been demonstrated to be stimulated by fungi (Christiansen *et al.*, 1999b; Nagy *et al.*, 2000). Exogenous applications of methyl jasmonate on the stems of Norway spruce and other Pinaceae, without wounding,

can trigger induced responses similar to those induced by wounding, fungal infection or bark beetle attacks (Franceschi *et al.*, 2002; Martin *et al.*, 2002; Hudgins *et al.*, 2003a). However, during a natural beetle attack, there is always a wound. It is thus conceivable that wounding causes the release of this phytohormone inside the tree tissues. The induced resin flow, by definition, is a wound reaction. Fungi may enhance it but no information is available to test this possibility.

The non specificity of defence is a consequence of the wound response. It has been demonstrated directly for the hypersensitive reaction. Whatever the aggressors (different beetles, different fungi, wounding), the development pattern of the hypersensitive reaction, as well as the associated chemical, anatomical and histological changes are identical in a tree (Delorme and Lieutier, 1990; Lieutier *et al.*, 1991a; Brignolas *et al.*, 1995a; Bois and Lieutier, 1997; Franceschi *et al.*, 1998). Changes in the type of aggressor elicit only variations in rapidity and extension of the reaction. Reported here for Scots pine and Norway spruce, the same results have been obtained in North American situations (Wong and Berryman, 1977; Müllck, 1977; Raffa and Smalley, 1995). Induced protection and formation of traumatic resin canals in Scots pine and Norway spruce are also non specific phenomena (Krokene *et al.*, 1999, 2001; Nagy *et al.*, 2000; Franceschi *et al.*, 2000; Hudgins *et al.*, 2003a). It has been hypothesized that induction by wounding, eventually followed by stimulation by fungi, and non specificity of the response are traits common to all induced defence mechanisms of conifers against bark beetle attacks (Lieutier, 2002).

Studied mainly in Norway spruce, PP cells interfere in many aspects of the hypersensitive reaction (see above). Krekling *et al.* (2000) presented their structure and development in detail, and Franceschi *et al.* (1998, 2000, 2002) generalized their role to all cases of induced responses in conifers (except induced resin flow). PP cells appear to play a major role in synthesis, storage, and modification of phenolic compounds in response to wounding, for both constitutive and inducible defences (Franceschi *et al.*, 1998, 2000).

2.2.3. Biochemical characteristics of the tree induced response

The chemical nature of the response to attacks by bark beetles and their associated fungi has been investigated for the hypersensitive reaction only and almost exclusively at the phloem level. In the pines *P. sylvestris* and *P. pinaster*, terpene concentration increases more than 100 times (Lieutier *et al.*, 1989a, 1991a). The relative composition in monoterpenes and resin acids varies slightly, but the main alteration in this chemical family is an absolute increase in the concentration of all compounds already present before attack (Delorme and Lieutier, 1990; Lieutier *et al.*, 1991a; Langström *et al.*, 1992). Similar results have been obtained in North American pines (Shrimpton, 1973a; Raffa and Berryman, 1982a; Raffa and Smalley, 1995). Only stimulation of syntheses seems to occur. On the contrary, investigations of phenolics in both Scots pine and Norway spruce revealed considerable changes in their relative composition (Lieutier *et al.*, 1991b, 1996c; Brignolas *et al.*, 1995a). The concentration of some compounds decreases while that of other increases, some being new for the concerned tissue. These new

compounds result from neosyntheses and not from degradation of pre-existing products or translocation, since alteration of related enzymatic activities as well as gene activation have been observed (Brignolas *et al.*, 1995b; Chiron *et al.*, 2000). The phenolic aspects of the phloem hypersensitive response to bark beetles and their associated fungi have not been deeply investigated in other conifers than Scots pine and Norway spruce, but they certainly occur in most conifer species.

The energy demand to the tree is considerable during the process of hypersensitive reaction and the source of energy used has been a matter of debate. Sugar and starch concentrations decrease in the close vicinity of the reaction zone (Christiansen and Ericsson, 1986; Långström *et al.* 1992). This could indicate that they may be used by the tree as a source of energy for responding to attacks, but also that they may be consumed by the fungus for its growth. Most European research conducted in Norway spruce and North American studies in pines have concluded that there is mobilization of products from current photosynthesis (Christiansen and Ericsson, 1986; Miller and Berryman, 1986; Christiansen *et al.*, 1987; Christiansen, 1992; Dunn and Lorio, 1992; Christiansen and Fjorne, 1993). However, recent experiments based on the use of labeled carbon in Scots pine pointed to an essential role of the tree reserves (Guérard, 2001).

3. MODE OF ACTION UPON THE AGGRESSORS

The effect of preformed resin flow on the aggressors has been largely studied in North America and few data are available from European situations. However, since beetle – fungus - tree relationships in North America have parallel counterparts in Europe, a transposition of the conclusions seems reasonable. The role of resin flow would mainly be wound cleansing by flushing the wounded tissues, followed by sealing the wound through resin crystallization (Berryman, 1972) and effect on beetles seems mainly relevant to antixenosis, leading them to modify their behaviour and leave quickly. Preformed resin would act against the aggressors physically, through flushing, viscosity and crystallization rate (Vité, 1961; Cates and Alexander, 1982), or chemically through toxicity of terpenes (Reid and Gates, 1970; Raffa *et al.*, 1985; Paine and Hanlon, 1994; Raffa and Smalley, 1995). It can also interfere with pheromone emission, resulting in stopping beetle aggregation (Raffa and Berryman, 1983a). However, although fungal spores can be flushed away, fungi can often tolerate the resin flow (Shrimpton and Whitney, 1968), whereas some beetle species are highly resistant to it, such as *D. micans* in Europe (Everaerts *et al.*, 1988; Grégoire, 1988). Moreover, in addition to its rapid drying up, resin flow exhibits high variability within a tree, as shown in Europe in Scots pine (Schroeder, 1990). Consequently and because the attacking beetles are often not killed and can escape, they can circumvent this system by finding a place on the same tree suitable for initiating a gallery (Lieutier *et al.*, 1995). The effect of the induced resin flow has not been studied specifically, but it is certainly comparable to that of the preformed one, provided that its chemical composition is the same.

The hypersensitive reaction is often said to act upon the aggressors through a combination of both physical and chemical factors, as well as through reduced

access to nutrients. This later effect would result from both nutrient depletion in the reaction zone and containment of the aggressors inside this zone, thus impeding their access to nutritive tissues located outside. The physical effect would consist in hardening of the resin impregnated tissues and resin flooding from the saturated tissues into the galleries. Hardened tissues would become unsuitable for the boring female and for the larvae that could hatch from already led eggs. Resin flooding would have consequences comparable to that of the preformed and induced resin flows, certainly complemented by an increased toxicity due to its higher terpene content. Nevertheless, only the chemical effect has been investigated through experimental approaches. In general, it relates to both antixenosis and antibiosis, and results from complementary actions of compounds from several families, mainly terpenes and phenols.

As with the preformed resin flow, research on the effect of terpenes involved in the hypersensitive reaction to bark beetles and their associated fungi has been mainly developed in North America. Assays with purified compounds demonstrated that a minimum concentration is necessary for terpene toxicity and that, at concentrations present in the reacting tissues, monoterpenes are toxic or repellent for beetles and inhibitory for beetle associated fungi, either by contact or vapor (Smith, 1963; Cobb *et al.*, 1968a; Shrimpton and Whitney, 1968; Bordash and Berryman, 1977; Raffa and Berryman, 1983b; Raffa *et al.*, 1985; Bridges, 1987; Raffa and Smalley, 1995; among others). Similar results have been obtained in Europe with *I. sexdentatus*, *T. piniperda* and their associated fungi, regarding Scots pine monoterpenes (Delorme and Lieutier, 1990). Although some monoterpenes, such as limonene, may be more toxic than others (Raffa *et al.*, 1985), all exhibit a high toxicity for beetles and a high inhibitory effect for fungi (Delorme and Lieutier, 1990). Results combine to suggest that the effect of monoterpenes on both beetles and their associated fungi are more due to the total quantity of these compounds rather than to some particular ones [Berryman and Ashraf (1970), Raffa and Berryman (1982a), Lieutier *et al.* (1991a), Raffa and Smalley (1995) for North American pines and firs; Delorme and Lieutier (1990) for Scots pine]. The same conclusion holds for resin acids as well (Långström *et al.* 1992).

The effects of phenolics in the context of conifer resistance to bark beetles have been investigated mainly in Europe, in both Scots pine and Norway spruce, but no assay has been performed on the insects themselves. They have a significant *in vitro* inhibitory effect on bark beetle associated fungi by contact but, unlike terpenes, it is remarkable that this effect is mainly due to some particular compounds, especially those that are neosynthesized during the hypersensitive reaction, with some of them acting synergistically (Brignolas, 1995; Bois and Lieutier, 1997; Bois *et al.*, 1999; Evensen *et al.*, 2000). Similar inhibitory effects of phenolics of North American pines have also been reported on *Ophiostoma* species (Hart and Shrimpton, 1979; Hart, 1981). However, phenols have not been demonstrated to have the same effect in nature (Hart and Shrimpton, 1979) and their role in conifer resistance to bark beetles and their associated fungi remains unclear, although correlations between phenol composition and resistance exist for both Norway spruce and Scots pine (see below VI.1).

4. BEETLE BEHAVIOR IN RELATION TO TREE RESISTANCE

Facing such a diversity of defence systems which together present efficient resistance to their attacks, bark beetles have evolved various behaviors to establish in their hosts. Raffa (1991) proposed that these behavioural traits could be used to separate beetle attack strategies, on the basis of exhausting tree defences, avoiding resistant trees or tolerating tree defences. Derived from a preliminary suggestion (Lieutier, 1992), Lieutier (2002) also proposed the use of beetle behavior but in another way which leads to a different grouping of beetle species that attack living trees into two main types of strategies: exhausting tree defences and killing the tree vs avoiding / tolerating tree defences and keeping the tree alive.

4.1. *The strategy of exhausting host defences (cooperative strategy)*

4.1.1. *The general model and the critical threshold of attack density*

An ancient and common observation forming the basis of the model used to describe the strategy of exhausting tree defences is that, in most bark beetles species attacking living trees, a minimum number of attacks is necessary to kill a tree and for successful establishment of the beetle populations, including successful oviposition and brood development. This fact has been well known by all European foresters for a long time and the corresponding scientific concept was first formulated by Thalenhorst (1958) before being largely developed by North American researchers (Safranyik *et al.*, 1975; Berryman, 1976, Raffa and Berryman, 1983a). It implies the existence of both a threshold of attack density that must be exceeded to allow the success of beetle attacks, and tree resistance mechanisms that are efficient below that level. The threshold levels thus quantify tree resistance to a given beetle species, as well as beetle aggressiveness for a given tree species (Berryman, 1976; Raffa and Berryman, 1983a; Christiansen *et al.*, 1987). The idea has then been used in North America and Europe to built models of bark beetle population dynamics (Berryman, 1976; Christiansen *et al.*, 1987, among others). The existence of such critical thresholds has been experimentally demonstrated in the field under various conditions for several beetle and conifer species, as for *I. typographus* in Norway spruce and *T. piniperda* and *I. acuminatus* in Scots pine in Europe (Mulock and Christiansen, 1986; Långström *et al.*, 1992; Långström and Hellqvist, 1993a,b; Guérard *et al.*, 2000a). In Europe, their level in healthy trees ranges from 300 to 850 attacks / m² depending on species and local conditions and is strongly influenced by tree health and genetic factors (see § 6). In North America on *Pinus ponderosa*, *Dendroctonus ponderosae* has been reported to have a critical threshold of attack density as low as 60 attacks / m² (Raffa and Berryman, 1983a). In Southwestern China, the critical threshold of a *Tomicus* species for *Pinus yunnanensis* is around 80 attacks / m² but is strongly influenced by the intensity of previous attacks in the shoots (Lieutier *et al.*, 2003c).

Since induced defence systems must be built rapidly at each point of attack in order to stop the aggressors, the existence of the critical threshold is supposed to result from the fact that the ability of the tree to rapidly mobilize its sources of

energy is limited, and the level of tree resistance is thus determined by this capacity (Christiansen *et al.*, 1987). The model of the strategy of exhausting tree defences is based on these energetic considerations. The strategy of the beetle population is to rapidly deplete the energy resources by increasing the energy demand to the tree until a level (critical threshold of attack density) above which the tree becomes unable to accelerate the energy mobilization. At this moment, the tree induced defences become inefficient, brood establishment begins and attacks can succeed.

4.1.2. Conditions for attack success

According to the model, everything that stimulates and increases the energy expenditure by the tree at the moment of beetle attack lowers the critical threshold of attack density and is thus useful to that strategy. It is possible to recognize typically four main characteristics in beetle biology that are important in this context (Lieutier, 2002).

- Mass aggregation on the host tree at the time of attacks is an essential and powerful tool for the beetle population, justifying the name of cooperative strategy that has also been given to that strategy. Most of the time, aggregation results from pheromones, but it can also be due to monoterpenes attractants emitted by the tree through the wounds caused by the first arrived beetles, as in the case of *T. piniperda* (Byers, chapter 8). In any case, it allows a rapid increase of the number of attacks on the host, of course necessary to reach a certain threshold of attack density, but also forcing the tree to respond at many places simultaneously, as each local induced reaction is stimulated by the beetle tunneling activity.

- Another biological characteristic in favor of the exhaustion strategy is related to gallery orientation. Because the reaction develops mainly in the longitudinal direction, longitudinal galleries should better stimulate it than transverse galleries.

- Occurrence of beetle attacks during the season of tree activity, when the tree is able to respond, is also a biological trait adapted to that strategy. Inside that period and referring to the growth – differentiation balance concept (Loomis, 1932; Lorio, 1986), spring attacks should even be even more efficient than summer or autumn attacks, because they occur during a period when tree growth is maximal and thus when less energy is available for defence, consequently favoring rapid tree exhaustion.

- An association with a phytopathogenic fungus is often also an efficient way to lower the threshold of attack density, since induced defences can be stimulated by phytopathogenic fungi introduced by the beetles in their galleries (see above). Similarly to the thresholds of attack density, by artificially mass inoculating trees with fungi, it is possible to define critical thresholds of inoculation density, above which tree resistance is overcome and trees are killed, while they resist and survive below [Hornvedt *et al.* (1983) and Christiansen (1985a) for *Ceratocystis polonica* in Norway spruce; Långström *et al.* (1993), Solheim *et al.* (1993) and Croisé *et al.* (1998b) for *Leptographium wingfieldii* on Scots pine; Guérard *et al.* (2000a) for *Ophiostoma brunneo-ciliatum* on Scots pine]. Values range from 400 to more than 1 000 inoculations per m². Similar results have been obtained for the North American species (Raffa and Berryman, 1983b). Such thresholds can be used to

quantify fungus pathogenicity and to compare tree resistance levels. However, to conclude that a bark beetle associated fungus contributes significantly to lowering the critical threshold of attack density of its vector, one must be able demonstrate that the stimulation of the induced defences by the fungus occurs effectively when the fungus is introduced by the beetle itself and not only after artificial inoculations. It has been pointed out that: 1- the frequency of association between beetles and fungi is very variable and often far from 100 % (Kirisits, chapter 10); 2- the tree response to one artificial inoculation depends quantitatively on the number of spores present in the inoculum, and a minimum number must be introduced into the wound for the fungus to be able to stimulate significantly the tree induced reaction (Lieutier *et al.*, 1988b; 1989). The usual method of artificial inoculation utilizes 5 mm diameter discs of 3-week-old agar cultures (Kirisits, chapter 10). One such inoculum introduced in a single hole contains a very high number of spores, far above the number introduced by a beetle in its gallery (Lieutier *et al.*, 1989a; 1995). Because fungus pathogenicity is measured with artificial inoculations, it follows from the two above remarks that there is no relation between beetle aggressiveness and pathogenicity of its associated fungus (Harrington, 1993; Paine *et al.*, 1997; Lieutier, 2002). A vigorous induced reaction to artificial inoculation and a low threshold of inoculation density, which reflect high fungus pathogenicity, are thus not sufficient information to conclude that the fungus plays a role in lowering the threshold of attack density (Lieutier, 1995; 2002). A typical example in Europe is given by *T. piniperda* and its associated fungus *L. wingfieldii* (see below).

4.1.3. Tissues colonization and tree death

In a strategy of exceeding a defined threshold for attack, tree death occurs as an unavoidable consequence of defence exhaustion. Since tree defences must be exhausted before brood establishment begins, tree death develops simultaneously to successful colonization of phloem by beetles, and both phloem and sapwood by fungi. The mechanisms of tree death have been a matter of debate, especially in Northern America, and it has often been concluded that fungi play a crucial role (ref. in Paine *et al.*, 1997). In fact, three complementary factors seem to be involved: sapwood invasion, occlusion and cavitation by the fungi, leading to the stopping of water transfer; phloem invasion by the beetles, leading to phloem destruction; and resin soaking that had occurred during the development of tree defences, sometimes resulting in the sacrifice of a considerable quantity of phloem and sapwood tissues. A detailed discussion has been presented in Lieutier (2002).

4.1.4. The species concerned

The strategy of exhausting host defences is employed by most bark beetle species that attack living trees. Table 1 summarises economically important European species matching that strategy, together with some counterparts from other continents, mainly North America, with a presentation of their biological

Table 1: Characteristics of the beetle behaviour and role of the associated fungi during attacks, and consequences of successful attacks for the tree, for different beetle species relatively to their attack strategies, in Europe and North America.

<i>Beetle strategy / tree defence</i>	<i>Region</i>	<i>Host tree species</i>	<i>Beetle species</i>	<i>Fungus role</i>	<i>Aggregation</i>	<i>Egg gallery orientation</i>	<i>Attack / tree activity</i>	<i>Tolerance to resin</i>	<i>Successful attacks kill tree</i>
<i>(= Cooperative Exhaustrum)</i>	Europe	Spruces	<i>Ips typographus</i>	Yes	Yes	Longit.	During	Yes	
		Pines	<i>Pityogenes chalcographus</i>	?	Yes	Oblique	During	Yes	
			<i>Ips acuminatus</i>	Yes	Yes	Longit.	During	Yes	
			<i>Orthotomicus erosus</i>	Yes	Yes	Longit.	During	Yes	
			<i>Ips sexdentatus</i>	Yes	Yes	Longit.	During	Yes	
			<i>Tomicus piniperda</i>	No*	No	Longit.	Before	Yes	
		Firs	<i>Pityokteines curvidens</i>	?	Yes	Transv.	During	Yes	
		Pines	<i>Dendroctonus ponderosae</i>	Yes	Yes	Longit.	During	Yes	
			<i>Dendroctonus frontalis</i>	No ?	Yes	Wind.	During	Yes	
		America	<i>Fir</i>	<i>Scolytus ventralis</i>	Yes	Yes	Transv.	During	Yes
<i>Avoid</i>	Europe	Dg. fir	<i>Dendroct. pseudotsugae</i>	Yes	Yes	Longit.	During	Yes	
		Spruces	<i>Dendroctonus micans</i>	No	No	Transv.	A. time	High	No
	North America		<i>Dendroctonus punctatus</i>	No	No	Transv.	A. time	High	No
		Pines	<i>Dendroctonus valens</i>	?	No	Tr + Lg	A. time ?	High	No
			<i>Dendroctonus terebrans</i>	?	No	Longit.	A. time ?	?	No

Dg. fir = Douglas fir; Longit. = longitudinal; Transv. = transversal; Wind. = winding; Tr + Lg = transversal and longitudinal; * = fungus present but no role; A.time = any time

characteristics concerned with the conditions for attack success. Typical cases are those of *I. typographus* in spruces and *I. sexdentatus*, *I. acuminatus* and *Orthotomicus erosus* in pines, of which all biological characteristics are in perfect accordance with the general model. All of them have aggregation pheromones and develop mass aggregation, have longitudinal galleries, attack during the season of tree activity (Sauvard, chapter 7), and are associated with fungi that stimulate the development of the tree hypersensitive reactions (Kirisits, chapter 10). Typical North American representatives are *D. ponderosae* and *Dendroctonus pseudotsugae*. The other European species possess only some of the typical biological characteristics but still fit the exhaustion strategy.

Pityogenes chalcographus bores oblique galleries in spruces. This particular behavior results in stimulation of the hypersensitive reaction and in an abundant resin flow (by cutting numerous resin ducts), both contributing to exhaustion of tree defences. Its associated fungi have not been studied. Nevertheless, this beetle seems to fit well with the exhaustion strategy. *Pityokteines curvidens* bores transverse egg galleries in *Abies alba*, but this orientation is not a handicap since resin ducts do not exist in firs. It aggregates on the attacked trees, but it is not known if associated fungi are able to stimulate tree defences. If this was the case, *Scolytus ventralis* would be its North American counterpart in *Abies grandis*. *T. piniperda* also refers to the exhaustion strategy. However, its associated fungus *L. wingfieldii*, although strongly pathogenic for Scots pine with a threshold of inoculation density around 400 inoculations / m² (Solheim *et al.*, 1993; Croisé *et al.*, 1998b), does not play any role in stimulating the tree hypersensitive reaction (Lieutier *et al.*, 1995), because of its very low frequency of association and also because of certainly too low a number of spores introduced by the beetle in its gallery (Lieutier *et al.*, 1989a; Lieutier, 1995). Tree defences can be exhausted only by repeated mechanical stimulation resulting from the longitudinal tunneling activity of the beetle. Moreover, attacks take place during winter (Sauvard, chapter 7), early before the rapid increase of tree activity in spring. All these biological characteristics result in a very high critical threshold of attack density on healthy or moderately weakened trees, and certainly explains why *T. piniperda* attacks succeed usually on very weak and dominated trees (Lieutier, 1995). In Southwestern China, another *Tomicus* species corresponds exactly to the situation of *T. piniperda* in Europe and develops the same strategy, except that, during their maturation feeding in the shoots, the maturing adults concentrate their attacks on the same trees (Ye and Lieutier, 1997). This results in a considerable lowering of the critical threshold of attack density on the stem, which makes this species able to kill trees by using the exhaustion strategy during subsequent stem attacks (Lieutier *et al.*, 2003c). In North America, *D. frontalis* could correspond to a situation intermediate between *P. chalcographus* (winding galleries and aggregation pheromones) and *T. piniperda* (role of the associated fungus questionable).

4.2. The strategy of avoiding host defences

4.2.1. The general model and the solitary behavior

This strategy has been typically described in Europe (Lieutier, 1992, 2002) and *D. micans* in Norway spruce is the best example. There is no stimulation or exploitation of tree's defences to overcome its resistance. On the contrary, everything is done to avoid the defence mechanisms, especially to minimize the development of the hypersensitive reaction. Firstly, there is typically no association with fungi, as demonstrated for *D. micans* (Lieutier *et al.*, 1992). Secondly, since tree exhaustion is not necessary, there is no beetle cooperation; beetles behave individually and do not have aggregation pheromones at the adult stage ("solitary strategy") (Grégoire, 1988). Thirdly and typically also, maternal galleries are transverse perpendicular to the direction of the usual development of the hypersensitive reactions. This behavior both minimizes the development of those reactions and also avoids contact between the boring female and toxic neo-synthesized compounds. Nevertheless, it obliges the female to cut through a large number of resin ducts, and thus supposes that they have a high resistance to the preformed resin. In Norway spruce however, the preformed resin flow is very weak, and adults of *D. micans* adults are highly resistant to constitutive resin (Grégoire, 1988). The consequence of egg gallery orientation is that larval galleries are longitudinal, which supposes a high resistance of the larvae to the neo-synthesized compounds and/or the development of special larval strategies to resist the hypersensitive reaction. *D. micans* has solved this problem through both a high tolerance of eggs and larvae to resin (Everaerts *et al.*, 1988) and the existence of aggregation pheromones at the larval stage (Grégoire *et al.*, 1982), allowing larvae of a same system to cooperate in boring a familial gallery faster than the tree develops its reaction. A fourth typical trait in this strategy, allowed by the absence of effects of the hypersensitive reaction on the attacking females, is that attacks can occur at any season.

The local particularities of the tree (preformed defences), at the places where the beetle attacks occur, play the most important role in determining the success or failure of oviposition. This is the case for moisture and stilbene content of the phloem (Storer and Speight, 1996), stone cell masses (Wainhouse *et al.*, 1990, 1998a), preformed resin flow (Lieutier *et al.*, 1992). Consequently and contrarily to the cooperative strategy where a threshold exists above which all attacks succeed, in the solitary strategy, attacks can succeed at one place while others can fail at another place of the same tree (Vouland, 1991). Moreover, in that solitary strategy, as a consequence of the non exhaustion of tree defences, the host is not killed by the successful attacks and the whole beetle life cycle takes place in a living tree, making that strategy a real parasitic one. With *D. micans*, tree death always occurs after several years and several generations in a same tree (Vouland, 1991).

4.2.2. Other related situations

Only a few bark beetle species represent the solitary attack strategy and there is no other known example than *D. micans* in Europe (Table 1). In North America, *D. punctatus* is typically equivalent to *D. micans* and fits in exactly with the same strategy. *D. valens* also probably refers to the strategy of avoiding host defences. It does not have aggregation pheromones and can reproduce without killing its host

(Raffa, 1991). It carries a highly pathogenic fungus but it is not clear if this fungus stimulates the tree induced reaction when introduced into the tree by the beetle itself. *D. terebrans* resembles *D. valens* but has longitudinal galleries.

5. EFFECT OF HOST RESISTANCE ON BARK BEETLE POPULATION DYNAMICS

5.1. *The case of the cooperative strategy*

Papers presenting a general model on the role of host resistance in bark beetle population dynamics in the case of the cooperative strategy have concerned almost exclusively North American species (Berryman, 1976, 1982; Coulson, 1979; Raffa and Berryman, 1983a; Raffa, 1991). In Europe, the American model has been applied and developed for *I. typographus* (Christiansen *et al.*, 1987). These models are based on comparisons between trees' resistance level (in terms of critical threshold of attack density) and real beetle attack density on trees (as a result from current population level).

During endemic periods, the densities of attacks on trees are low and only very weakened trees or felled trees can be successfully colonized because their resistance level is very low or nil. The beetle population varies with the availability of this material but, because such trees are depleted at each beetle generation, they are in insufficient number to sustain population increase. The population level is thus rarely sufficient to reach the critical threshold of attack density for healthy trees and to allow establishment on them. The reproductive gain is thus offset by losses during the search for available hosts (Raffa, 1991). However, if large quantities of trees become weakened or fallen, beetle populations can rapidly increase, and eventually exceed the critical threshold of attack density of healthy trees. A considerable quantity of material is then available for beetle reproduction, generating a positive feed-back cycle, and the populations can continue to expand, even if the weakened trees are depleted (Raffa, 1991). The epidemic period ends when all suitable trees are killed or when beetle levels are too low to overwhelm additional trees.

In Europe, many field observations corroborate these mechanisms. Following the two hurricanes "Lothar" and "Martin" that devastated forests and felled billions of trees throughout Western Europe in December 1999, populations of *I. typographus* and *I. sexdentatus* have exploded in 2000, leading to extensive killing of healthy trees in numerous places during 2001 and 2002 (Nageleisen, 2002, 2003). Trees weakened allowing beetle establishment and population increase have also resulted from pollution or fire (Christiansen, 1989; Langström *et al.*, 1999). Outbreaks often correspond to coincidences between a prolonged period of drought, supposed to lower the resistance of living trees, and sudden abundant reproductive material without defence (felled trees or broken branches) that favors population increase, as for *I. acuminatus* in South Eastern France in 1987 (Lieutier *et al.* 1988a).

5.2. The case of the solitary strategy

*D. mican*s can attack any tree and even seems to prefer healthy trees. Moreover, successful attacks do not kill the host and, therefore, a tree successfully colonized is still available for future generations. Thus a sufficient quantity of food is always present. Its accessibility depends mainly on local preformed resistance (resin, stone cell masses, phloem moisture and stilbenes). On the other hand, the efficacy of tree resistance in attack failure does not depend on the population level (contrary to the other strategy), since beetle strategy is individual and resistance based on local tree characteristics. This density independence thus poses questions about the role of tree resistance as a key-factor of beetle population dynamics. Rather, in the case of *D. mican*s at least, several field observations suggest that predators are the most important factor (Grégoire, 1988). Tree resistance is certainly the most important parameter that determines the success of female colonization of the tree and oviposition, and can thus contribute to lower the population levels during the search for an available host, but this effect very likely concerns a constant fraction of the beetle population. Larvae are well adapted to bore into resin impregnated phloem, and very little mortality due to the hypersensitive reaction occurs at this stage (Everaerts et al., 1988). Predation on eggs and larvae on the contrary seems to have the highest impact on brood development and on variations of population levels. There is no information on whether these comments can be applied to other beetles using the solitary strategy.

6. VARIATIONS IN TREE RESISTANCE TO BARK BEETLES

6.1. Role of genetic factors

The genetic dependence of certain factors involved in preformed defences of conifers has been known for a long time in both North America and Europe. This is the case for monoterpenes and resin acids (Hanover, 1966, 1975; Bernard-Dagan et al., 1971; Tobolski and Hanover, 1971; Baradat et al., 1975, 1978; Katoh and Croteau, 1998; among others), total resin yield (Mergen et al., 1955; Rudinsky, 1966), resin viscosity and rate of crystallization (Mergen et al., 1955; Buijtenen and Van Santamour, 1972; Nebeker et al., 1992), and resin flow (Nebeker et al., 1992). Bark structure (Nihoul et al., 1989) and sap pressure (Lévieux et al., 1988) have also been reported to be partially genetically dependent. All these parameters have often been suggested to contribute to genetic differences in tree resistance to bark beetles and their associated fungi, but no parallel has been established directly in these studies between variations in the parameters and variations in tree resistance.

Between-tree genetic differences in the length of the phloem reaction zone that develops in response to artificial aggressions have been reported in pines in both North America and Europe (Paine et al., 1993; Lieutier et al., 1996b), but no link to differences in tree resistance level was established. Moreover, absolute reaction zone length does not seem a good indicator of tree resistance (see 2.1.2). Genetic variations in the ability of the tree to synthesize terpenes after aggression have also

been mentioned in grand fir and interpreted in terms of tree resistance to bark beetles (Katoh and Croteau, 1998), but without data on parallel variations in resistance.

Within the same conifer species, the existence of varieties or provenances more resistant than others to bark beetle attacks was recorded several years ago, as in *Pinus elliotti* vs. *I. calligraphus* (Wilkinson, 1979) and *Abies concolor* vs. *S. ventralis* (Ferrell and Otrosina, 1996). Some evidence of intra-specific genetic differences in tree susceptibility to beetle attacks, parallel to differences in their capacity to respond to aggressions, have also been provided in North America, especially regarding resin exudation in *Pinus radiata* (Witanachchi and Morgan, 1981) and terpene synthesis in *P. contorta* (Raffa and Berryman, 1982a). However, the relationships between the genetic control of tree resistance to bark beetles or their associated fungi (defined in terms of critical thresholds of attack / inoculation density) and the parameters involved in resistance, have been intensively investigated only recently, mainly in Europe, in Scots pine and Norway spruce. Through a between clone comparison, the level of resistance of Norway spruce to mass inoculations with *C. polonica* and that of Scots pine to mass inoculations with *L. wingfieldii* have been demonstrated to be genetically controlled, and to vary in parallel to the phloem phenol composition both before attacks and in response to these attacks (Brignolas *et al.*, 1995b, 1998; Bois and Lieutier, 1997; Evensen *et al.*, 2000). In Norway spruce, these results were then extended to the whole species through comparisons mixing clones and provenances (Lieutier *et al.*, 2003a). In this tree species, the diversity of constitutive phloem phenols and the ability to induce phenol synthesis [especially (+)-catechin] in response to wounding have been proposed as predictors of tree resistance to fungus mass inoculation, and supposedly to bark beetles (Lieutier *et al.*, 1996a, 2003a; Brignolas *et al.*, 1998), whereas the ability of the tree to synthesize pinosylvin in response to aggression was proposed as predictor of Scots pine resistance (Bois and Lieutier, 1997). For Norway spruce, at the end of an outbreak, the proposed parameters were validated in the field as predictors of resistance to natural bark beetle attacks, but their validity during an outbreak peak seemed questionable (Lieutier *et al.*, 2003b). The PP cells, already reported to be involved in the resistance mechanisms of Norway spruce to mass inoculation with *C. polonica* (see above, II.2.2), have also been observed to differ greatly between resistant and susceptible clones (Franceschi *et al.*, 1998). While they are filled with dense bodies and occur in single rows in the phloem of susceptible clones, the rows are two cells thick and the cells are 40 % more numerous and show lighter deposits in the resistant clones. In response to fungus inoculation, the PP cells of the resistant clones enlarge and their phenolic bodies are considerably reduced, whereas these changes are much less marked in the susceptible clones (Franceschi *et al.*, 1998). In response to attack, the traumatic resin ducts are built earlier in the resistant than in the susceptible clones (Nagy *et al.*, 2000). The genetic determinism of conifer resistance to bark beetles has however never been investigated.

6.2. Variations with season and tree age

The only experiment taking into account the seasonal variations of the tree resistance level itself (level of the critical threshold of inoculation density) was carried out in Norway spruce (Horntvedt, 1988). It demonstrated that resistance to mass inoculations with *C. polonica* is lower in summer than in spring and autumn. Most studies related to the effect of season on the parameters of tree resistance have been carried out on North American pines (*P. taeda*, *P. echinata*, *P. ponderosa*, *P. contorta*) and were related to the length of the phloem reaction zone induced by isolated fungus inoculations. They generally referred to longer reaction zones in summer than in spring or autumn (Stephen and Paine, 1985; Cook *et al.*, 1986; Reid and Shrimpton, 1971). In Europe, Lieutier *et al.* (1993) reported smaller reaction zones in spring than in summer and autumn in Scots pine. In most cases, these results have been interpreted as consistent with a lower level of tree resistance in summer. In *P. ponderosa* however, Paine (1984) observed smaller reaction zones in summer than in autumn. Tisdale and Nebeker (1992) observed an increase of the resin flow in *P. taeda* between May and August.

It has often been reported that old trees are more susceptible than young ones to bark beetle attacks but no measurement of tree resistance has been performed in this direction. In Europe, reaction zones induced by single inoculations of Scots pine with *Ophiostoma brunneo-ciliatum* have been reported to be longer and to contain more resin in the oldest trees (Lieutier *et al.*, 1993). In North America, Shrimpton (1973b) in *P. contorta* and Raffa and Berryman (1982b) in *A. grandis* observed that the resin response was maximum for middle aged trees. DeAngelis *et al.* (1986) observed that radial resin duct density in *P. taeda* was negatively correlated to tree age.

6.3. Silvicultural aspects

6.3.1. Effect of tree vigor and dominance

Vigor of conifers, such as lodgepole pine in North America and Norway spruce in Europe, is positively correlated to the critical thresholds of inoculation or attack densities, whether this vigor is expressed by dominance (Sandness and Solheim, 2002) or productivity indexes (Waring and Pitman, 1983; Mulock and Christiansen, 1986). Ponderosa pine, white spruce (*Picea glauca*) and white fir (*Abies concolor*) with low productivity indexes or low growth efficiency are also more susceptible to attacks by beetles than highly vigorous trees (Larsson *et al.*, 1983; Hard, 1985; Ferrell *et al.*, 1994), and dominated Scots pines are more susceptible than intermediate or dominant trees (Cedervind *et al.*, 2003). However, Christiansen (1981 in Bakke, 1983) did not observe any relation between vigor of Norway spruce and its resistance to beetle mass attacks during a mass outbreak.

Several experiments, such as fertilization, have been performed to modify tree vigor in order to examine the consequences on tree resistance and its mechanisms. They are presented below in 6.5.2. Very little investigations have been done in natural conditions to measure the effect of tree vigor on the mechanisms of resistance, without any artificial treatment. In loblolly pine, the density of resin ducts was positively correlated with growth rates (DeAngelis *et al.*, 1986),

suggesting a positive effect on the preformed defence mechanisms. However in Scots pine, Kytö *et al.* (1999) did not observe any correlation between resin duct density and preformed resin flow and, after modifying tree vigor by fertilization, they even observed a weak negative correlation between vigor index and resin flow or phloem constitutive phenol concentration (Kytö *et al.*, 1998, 1999). In Norway spruce, Baier *et al.* (2002) also reported, with increasing radial growth indexes, a decrease of the constitutive resin flow, accompanied by a decrease in the cross sectional area of resin ducts and the initial monoterpenes content. However, the effects of vigor can depend on tree activity. Lombardero *et al.* (2000), modulating tree growth by combining thinning, dominance and fertilization, reported that the constitutive resin flow in *P. taeda* was least during the period of rapid tree growth (early wood production) but most during latewood production. Results seemed less variable for the parameters related to induced defence. The induced increase in resin flow after wounding was greatest in the fastest growing trees, even during their season of greatest growth (Lombardero *et al.*, 2000). After isolated fungus inoculations, the mean total monoterpenes content at the site of inoculation in grand fir was lower in suppressed trees than in dominant trees (Raffa and Berryman, 1982b) and reaction zone length in Scots pine was negatively correlated with productivity indexes (Lieutier *et al.*, 1993), results which have been interpreted as a lower induced resistance in suppressed or low productive trees. In *A. grandis*, resin production after fungus mass inoculations was greater in high-vigor trees (Filip *et al.*, 1989). In Norway spruce however, reaction zone length increased with increasing radial growth indexes (Baier *et al.*, 2002).

6.3.2. Stand density and diversity

Most studies on the effect of stocking and thinning on tree-bark beetle relationships have been carried out in North American pine forests (*P. contorta*, *P. taeda*, *P. echinata*). In all cases, dense stocking and absence of thinning were positively correlated to attack success or tree mortality by bark beetles (Belanger *et al.*, 1979; Mitchell *et al.*, 1983; Brown *et al.*, 1987; Bartos and Amman, 1989; Showalter and Turchin, 1993). Thinning has been reported to increase oleoresin flow rates and tree growth indexes over about 2 to 3 years when compared to unthinned plots (Mason, 1971; Waring and Pitman, 1985; Mitchell *et al.*, 1983; Matson *et al.*, 1987; Brown *et al.*, 1987). However, no information is available regarding the effect of thinning on tree resistance parameters other than oleoresin exudation, and thus no demonstration has been really provided that the decreases of beetle attacks and tree mortality after this treatment were caused by increases of tree resistance. On the other hand, in addition to acting on tree growth and dominance, thinning also induces significant modifications of the forest microclimate, which have been hypothesized to be the main factors linking beetle attacks and tree thinning (Amman *et al.*, 1988; Bartos and Amman, 1989; Bartos and Booth, 1994). In Europe, an integrated approach carried out in Norway spruce forests revealed that thinning increased the primary resin flow but did not show any effects on several other resistance parameters, such as the preformed monoterpenes content and the wound reaction development after low density inoculation with *C. polonica* (Baier *et al.*, 2002).

Very little information is available on the effects of stand diversity. In North America, hardwood trees mixed with pines seem to interfere with infestation growth and to decrease the mortality of pines following induced attacks by *D. frontalis* (Showalter and Turchin, 1993). No effect was observed on resin flow in that experiment. In Europe, Norway spruce trees exhibited higher primary resin flow, lower reaction zone length and lower relative increase of resin flow in response to low density inoculations, when growing in mixed species stands than when growing in pure stands (Baier *et al.*, 2002).

6.4. Relation with phytosanitary problems

The possibility that defoliators and pathogens can predispose trees to be overcome by bark beetle attacks has been proposed for a long time in Europe (Schwertfeger, 1944; Thalenhorst, 1958; Chararas, 1962), essentially according to empirical observations, suggesting that these primary aggressors weaken the trees, that is depress their natural resistance. Only relatively recently, in both North America and Europe, experiments have been conducted to quantify these observations. Among them, many refer to tree susceptibility to beetle attacks; some have investigated the tree resistance mechanisms themselves.

6.4.1. Mistletoe and pathogens

In North America, mistletoe, blister rust on branch and trunk, and root pathogens (*Armillaria mellea*) favor infestations by bark beetles in fir and pines (Ferrell, 1974; Tkacz and Schmitz, 1986; Rasmussen, 1987) at least for endemic populations. For epidemic populations however, Christiansen and Huse (1980) in Scandinavia did not find any relation between root infestation of Norway spruce by the butt rot *Heterobasidium annosum* and tree susceptibility to *I. typographus*.

In firs infested by mistletoe, successful beetle attacks were accompanied by very little or no resin secretions, while the only (failed) attack that occurred on healthy trees was filled of resin (Ferrell, 1974). In *P. resinosa*, root disease led to decreased resin flow (Raffa and Klepzig, 1996), to modifications of monoterpene ratios in tissues reacting to artificial inoculations by *Leptographium terebrantis*, but not to modifications of total monoterpene and phenol concentration in the unwounded tissues (Klepzig *et al.* 1995). No European study has dealt with these aspects.

6.4.2. Defoliating insects

Studies dealing with defoliations have generally suggested a significant increase of tree susceptibility to bark beetle attacks, only in heavily (90 % or more) defoliated trees. This is the case in North America for example in *Abies amabilis* defoliated by the sawfly *Neodiprion* sp. and then attacked by *Pseudohylesinus* spp. (McMullen *et al.*, 1981), and in *A. grandis* and *Pseudotsuga menziesii* defoliated by the moth *Orgyia pseudotsugata* and subsequently attacked by *S. ventralis* and *D. ponderosae* (Wright *et al.*, 1984). Similar conclusions have been drawn in Scandinavia for Scots pines defoliated by the sawfly *Diprion pini* and the moth *Bupalus piniaria* and attacked by *T. piniperda* and *T. minor* (Annila *et al.*, 1999; Långström *et al.*, 2001a;

Cedervind *et al.*, 2003) and in Eastern Europe for Norway spruce defoliated by the moth *Zeiraphera diniana* before attacks by *I. typographus*, *I. amitinus* and *P. chalcographus* (Grodska, 1997). Mass inoculations on trees defoliated by *B. piniaria* were also able to kill trees only when they suffered at least 90 % defoliation (Långström *et al.*, 2001b). Wallin and Raffa (2001) however, reported that colonization of *Pinus banksiana* by *Ips grandicollis* increased exponentially in relation to defoliation level by the moth *Choristoneura pinus*. In all cases where the delay was considered, tree susceptibility was maximum one to two years after the defoliation (Wright *et al.*, 1984; Raffa *et al.*, 1998; Cedervind *et al.*, 2003). In Northern Spain, Amezaga (1997) observed that the presence of pine processionary caterpillars (*Thaumetopoea pityocampa*) in *P. radiata* and *P. sylvestris* stands increased the rate of shoot pruning by *T. piniperda* in vigorous trees, but not in trees where dominance was taken by side shoots, thus suggesting an interference with the tree social status. Shoot damage during the maturation feeding of *Tomicus* spp. can be compared to defoliations. In Southwestern China, the critical threshold of bole attack density by *Tomicus* sp. on *Pinus yunnanensis* (that is tree resistance level to bole attacks) decreases when shoot damage increases, and a critical threshold of shoot damage (60 % damaged shoots) has been defined above which stem attacks always succeed in killing trees (Lieutier *et al.*, 2003c). Pruning was sometimes used to simulate defoliations and reduce photosynthesis in Scots pine and Norway spruce. It also increased susceptibility to bark beetles or their associated fungi (Långström and Hellqvist, 1993; Christiansen and Fjorne, 1993).

Parameters involved in various mechanisms of resistance to bark beetles, concerning both preformed and induced defences, can be affected by defoliations. Resin flow rate decreased significantly in *P. resinosa* moderately defoliated in controlled conditions (Raffa *et al.*, 1998), in *P. banksiana* and *P. sylvestris* heavily defoliated respectively by *C. pinus* and *D. pini* (Wallin and Raffa, 2001; Annila *et al.*, 1999), and in pruned Scots pines (Långström *et al.*, 1993). Opposite results have however been observed when the defoliation effect is compounded with fertilization (Kytö *et al.*, 1999). Monoterpene content of preformed resin can also be affected, as in *P. banksiana* defoliated by *C. pinus* (Wallin and Raffa, 1999). Results concerning the tree induced responses are more variable. In *Abies sibirica*, Vetrova *et al.* (1999) in Russia indicated that all defence parameters, histologically evaluated through the rate and intensity of response to inoculations with *Leptographium* sp. in phloem and xylem tissues, are affected by defoliation due to the moth *Dendrolimus superans sibiricus*. In Scots pine, no effect of defoliation or pruning was reported on reaction zone length, fungus performances, resin acid and phenol content after isolated inoculations with *L. wingfieldii* or *Ophiostoma ips*, or after attacks by *T. piniperda* and *T. minor* (Långström *et al.*, 1993, 2001b, Croisé *et al.*, 1998; Annila *et al.*, 1999). Results in North American conifers are more consistent. In *A. grandis*, the monoterpene concentration in the reaction zones induced by inoculations with *T. symbioticum* decreases in direct proportion to defoliation, and during two years after defoliation (Wright *et al.*, 1979). In *P. banksiana*, the phloem induced response to artificial inoculations with *O. ips* is affected in its extent, its rate of monoterpene accumulation, and the changes in monoterpene content, depending

on defoliation intensity and the time since defoliation (Wallin and Raffa, 1999, 2001).

6.5. Relation with water and nutrient availability

Because of observations by foresters and scientists, of coincidences between damage and climatic or locality factors, the roles of drought and bad soil quality as factors predisposing trees to bark beetle attacks has been asserted for a long time in Europe, (Schwertfeger, 1944; Thalenhorst, 1958; Chararas, 1962) and in North America as well (Keen, 1938; Rudinsky, 1962). In that manner, bark beetle outbreaks have often been explained by the existence of drought periods supposed to weaken trees (Pesson and Chararas, 1969; Lieutier *et al.*, 1988a, as examples for Europe). Most often, especially in experimental approaches, water stress and nutrient availability have been considered separately.

6.5.1. Water stress

Several approaches to demonstrate and understand the relationships between water stress and tree resistance to bark beetles have followed seasonal or diurnal variations of tree water status, in relation to variations in tree susceptibility or defence mechanisms. Others have attempted to experimentally manipulate water stress. Both preformed and induced defence mechanisms have been investigated, depending on the model of tree-bark beetle relationships that was considered. Some experiments have considered the general resistance level of trees to attacks.

Effects on preformed defence mechanisms. Nothing has been done in Europe in this field and the major part of the literature corresponds to studies carried out in Southern North America on loblolly pine with reference to its susceptibility to *D. frontalis*.

Studies of seasonal and daily variations in tree water status concluded that water availability accounts for a large part in resin flow variations (Mason, 1971), that water stress decreases it (Blanche *et al.*, 1992), and that oleoresin exudation pressure is related to soil and atmospheric moisture (Lorio and Hodges, 1968a). However, Lorio and Hodges (1968b) noticed that resin flow was not reduced until a severe soil and atmosphere moisture stress occurred. Lorio and Sommers (1986) even attributed the late summer increase in oleoresin yield [a phenomenon also reported by Barrett and Bengtson (1964) on *P. elliotti*] to moderate water deficits at this time. Lombardero *et al.* (2000) observed an increase of the oleoresin yield during the period of latewood formation in loblolly pine, when drought conditions were limiting tree growth. A study of rainfall conditions prevailing over 52 years in various southern States concluded, however, that there was no relation between rainfall and the end of epidemics of *D. frontalis* (King, 1972).

The first experimental attempt to manipulate tree water status and to quantify the effect of water stress on preformed defences, was done by Vité (1961) and Vité and Wood (1961) in California, in relation to the susceptibility of *P. ponderosa* to *I. confusus* and *D. brevicomis*. They manipulated water availability to trees through

sprinkling and concluded that oleoresin exudation pressure was directly and inversely related to water stress. In loblolly pine, several experiments were conducted by digging trenches around trees to diminish soil water reserves (Lorio and Hodges, 1977), by erecting shelters to prevent rain from reaching the soil (Dunn and Lorio, 1993), or by cooling the trunk of trees with dry ice, a process supposed to create an acute water stress (Lorio *et al.*, 1995). In all cases, the stressed trees showed a reduced resin flow, generally associated with a higher number of successful attacks by the southern pine beetle, compared to the control trees. However, in case of a mild stress, the rate of successful attacks was very low on all trees, which was attributed to the fact that trees could adjust their water regime (Dunn and Lorio, 1993). It was also suggested that attack success on artificially stressed trees could depend on the water conditions during the year and tree ontogeny (Lorio *et al.*, 1995). Indeed, although oleoresin yield was negatively affected in artificially stressed trees, during a wet year at the moment of earlywood formation, attacks failed on those trees as well as on control trees but, during a dry year at the period of latewood formation, attacks succeeded on stressed trees while they failed on control trees. This is also in favor of the hypothesis that mild water stress can enhance tree resistance while a severe stress can decrease it (Lorio, 1986). This hypothesis is corroborated by the observation that, in grand fir saplings, the constitutive terpene cyclase activity stayed unaltered during a moderate stress but was reduced significantly during a severe stress (Steele *et al.*, 1995).

Effects of water stress on preformed defence parameters others than resin flow rate have been poorly investigated. In loblolly pine, the proportion of resin acids in the xylem oleoresin of artificially stressed trees decreased (Hodges and Lorio, 1975), and soil moisture could influence the monoterpenes composition (Gilmore, 1977).

Effects on induced defence mechanisms. Few experiments have been carried out to directly measure the effects of water stress on the mechanisms of induced defence. In North America, Ferrell (1978) observed that attacks by *S. ventralis* caged on the trunk of severely water stressed *A. concolor* were successful and accompanied by little resinosis in the phloem, while similar attacks in the control trees failed due to extensive resinosis. Cooling the bole of *P. contorta* with dry ice caused the elimination of observable wound response after artificial inoculations with *Ophiostoma clavigerum* (Miller *et al.*, 1986). Steele *et al.* (1995) observed that wound-inducible terpene cyclase activity in *A. grandis* was significantly reduced after both a severe and a mild stress. In Europe, after a severe stress in Scots pine saplings, Croisé and Lieutier (1993) observed a decrease of the phloem reaction zone length and the total quantity of induced resin, in response to isolated inoculations with *L. wingfieldii* and *O. brunneo-ciliatum*. Similarly, a slight decrease in reaction zone length after isolated inoculations with *O. ips* was observed when inoculations took place during the period of maximum stress intensity, but no change was noticed in the phenol composition of the reaction zone, and fungal growth was not affected (Croisé *et al.*, 1998). After mass inoculations with *L. wingfieldii*, Croisé *et al.* (2001) did not report any change in the intensity of the

phloem induced response in 5-year-old severely stressed seedlings, although sapwood water conductivity decreased significantly and conspicuous damage were observed in the sapwood.

Effects on the tree resistance level itself. Such effects of water stress have already been presented above in some experiments where susceptibility to bark beetles had been considered simultaneously with tree defence mechanisms. They were mostly related to preformed defence and to susceptibility to *D. frontalis*. Other experiments investigated the effects of water stress directly on tree resistance level, without referring to defence mechanisms. However, because they mainly concerned bark beetles of which the success of attacks is thought to depend on the non efficacy of the induced defence mechanisms, one may suppose that these mechanisms were affected by water stress.

It has been generally reported that tree resistance (indicated by the critical threshold of inoculation density) increased with a mild stress and decreased with a severe stress. In Europe, the levels of resistance of *P. abies* to mass inoculations with *C. polonica*, and that of *P. sylvestris* to mass inoculations with *L. wingfieldii*, were higher in trees submitted experimentally to several months of mild stress than in the control trees (Christiansen and Glosli, 1996; Dreyer *et al.*, 2002). Similarly in Southwestern China where wet seasons alternate with dry seasons, an 18-month study of tree water status in two plots differing in their soil water availability revealed that *P. yunnanensis* resistance to mass inoculations with *Leptographium yunnanense* was higher during the dry periods and in the dry plots (Ye and Lieutier, 2001). At the other extreme, several successive cycles of severe stress decreased the level of resistance of Scots pine to mass inoculations with *L. wingfieldii* (Croisé *et al.*, 2001). These observations are in agreement with those reported for preformed defence (Lorio, 1986; Lorio and Sommers, 1986, Lorio *et al.*, 1995). However, no after effect of an artificial drought repeated three years consecutively was noticed in Norway spruce, which suggests that trees recover as soon as water is available in sufficient quantity (Christiansen, 1992).

6.5.2. Nutrient availability

Regarding fertilization effects on conifers – bark beetles relationships, experiments in North America have been concerned mostly with tree susceptibility to attacks, whereas European research was focused on the mechanisms of resistance themselves. The conclusions were generally that fertilization had no or a negative effect, while tree growth was largely stimulated.

No effect was observed on tree susceptibility in the case of *P. taeda* exposed to attacks by *D. frontalis* and *D. terebrans*, after N or NPK fertilization (Moore and Layman, 1978; Matson *et al.*, 1987) and for *A. grandis* facing *S. ventralis* attacks after NPK treatment (Filip *et al.*, 2002). In *P. contorta*, increasing N nutrition did not prevent attacks by *D. ponderosae* until growth improvement exceeded 100 g. of wood production per m² of foliage (Waring and Pitman, 1985). In Scots pine also, N fertilization did not modify the ability of *T. piniperda* to establish egg galleries and to cause stem damage (Löyttyniemi, 1978). However, the treatment stimulated

tree growth and increased shoot diameter, which resulted in an increase of shoot attack density during the beetle maturation feeding, because of more suitable sized shoots.

In Norway spruce and Scots pine, fertilization by N or other nutrients increased the number of resin ducts but tended to decrease their density, and had no effect or caused only a very slight decrease on the constitutive resin flow (Kytö *et al.*, 1996, 1998, 1999; Viiri *et al.*, 1999). In other situations however, a more important decrease of constitutive resin flow or stem resin content was reported, following fertilization with N, P or K, such as in *Picea sitchensis* (Wainhouse *et al.*, 1998b) and in *P. taeda* (Warren *et al.*, 1999). Results are not clear with phloem constitutive phenols, as fertilization was observed to cause no effect, a decrease or an increase of their total concentration (Kytö *et al.*, 1996, 1998; Viiri *et al.*, 1999; Wainhouse *et al.*, 1998b; Warren *et al.*, 1999). Little attention has been given to effects on induced defence mechanisms. In Norway spruce, no consequence of fertilization was observed on the induced resin flow and the length of the phloem lesion that develops in response to inoculation with *C. polonica* (Kytö *et al.*, 1996; Viiri *et al.*, 1999). Viiri *et al.* (2001) however, reported a decrease in the concentrations of total terpenes and stilbene aglycons in this reaction zone and suggested a possible decrease of the tree ability to defend itself against beetle attacks.

6.6. Effects of other damaging agents (Wind, lightning, fire, and pollution)

Research on effects of wind and lightning on conifer susceptibility to bark beetle attacks has been developed exclusively on *P. taeda* in Southern North America. A simulated wind stress including bending stems and pruning branches resulted in a decrease of oleoresin flow, probably because of the decrease of leaf area due to pruning (Fredericksen *et al.*, 1995). Although relatively low numbers of beetles were observed, *Dendroctonus* and *Ips* species tended to be trapped in higher numbers near the stressed trees, but no successful attacks were observed. After lightning, either natural or simulated, loblolly pine was also more susceptible to attacks by *D. frontalis* and various other bark beetle species (Hodges and Picard, 1971; Coulson *et al.*, 1986). Even small numbers of beetles were capable of overcoming host defences (Flamm *et al.*, 1993), thus demonstrating directly that the critical threshold of attack density was considerably lowered. Lightning decreased oleoresin pressure and flow rapidly (Hodges and Picard, 1971; Blanche *et al.*, 1985) but, 3 weeks after the strike, resin flow was restored while the monoterpene composition was changed (Blanche *et al.*, 1985).

Effects of fire have been studied in Europe after accidental fires and in North America after accidental or prescribed fires. In all situations, incidence of fire increases tree susceptibility to bark beetle attacks. In Spain, Amezaga (1997) reported an increased number of shoot attacks by *T. piniperda* in *P. radiata*. Bole attacks also are favored. In Scots pine, the fire-damaged trees were reported to be susceptible mostly during the first two years after fire (Ehnström *et al.*, 1995; Långström *et al.*, 1999) but after the big 1988 fire in Yellowstone Park, damage by bark beetles on several conifer species was high until 1992 (Rasmussen *et al.*, 1996). Susceptibility to bole attacks depended on the importance of fire injury to the crown

or the bole of the trees. *T. piniperda* successfully attacked Scots pines with less than 25 % foliage while all attacks failed when there was more than 50 % foliage left (Långström *et al.*, 1999). Colonization attempts by *Ips* and *Dendroctonus* species on fire-damaged *P. ponderosa* were also positively related to intensity of crown scorch (Wallin *et al.*, 2003). Pines with no crown damage can also be attacked by bark beetles when the bole has been scorched (Santoro *et al.*, 2001) and Rasmussen *et al.* (1996) observed that high levels of infestations were strongly correlated with the percentage of basal circumference of the tree that had been fire-killed. Among the possible mechanisms of resistance that could be affected, only the resin flow was investigated. Both constitutive and induced resin flow of *P. ponderosa* was negatively related to crown scorch intensity (Wallin *et al.*, 2003) but constitutive resin flow of *P. resinosa* increased in trees with scorch boles (Santoro *et al.*, 2001).

Pollution increased tree susceptibility to bark beetles in general but its effects seemed to vary depending on the nature of the pollutant, the tree or the beetle species. After photochemical oxidant injury, attacks by *D. ponderosae* and *D. brevicomis* on *P. ponderosa* were positively correlated to the injury (Stark *et al.*, 1968). Among the killed trees, beetle attack density was higher for the less affected trees than for the highly affected trees (Dahlsten and Rowney, 1980), which corresponds to a higher critical threshold of attack density in the former than in the latter ones. In Czechoslovakia, Norway spruce submitted to sulphur dioxide pollution was more susceptible, not to attacks by *I. typographus*, but to attacks by secondary bark beetles such as *Pityogenes chalcographus* (Christiansen, 1989). At the Polish/Czech border, in pollution-damaged Norway spruce stands, *P. chalcographus* was also the main pest and trees suffering from more than 60 % needle loss were predisposed to attacks (Lanz *et al.*, 1993). Regarding the resistance mechanisms, oleoresin flow decreased but no change was observed in the terpene composition in *P. ponderosa* submitted to oxidant injury (Cobb *et al.*, 1968; Miller *et al.*, 1968). Along a decreasing gradient of heavy metal pollution in Finland, constitutive resin flow of Scots pine increased until 4 km from the pollution source (Kytö *et al.*, 1998). No experiment was concerned with the effect of increased CO₂ concentrations on tree susceptibility to bark beetles.

6.7. Synthesis and conclusions on the role of environmental factors

Table 2 synthesizes the effects of the different environmental factors on the tree resistance level, tree susceptibility and different parameters of the preformed and induced defences, while separating the results obtained on European tree species from those obtained on trees growing outside Europe (mainly North America).

6.7.1. Remarks, gaps and particularities

Before commenting on table 2, it must be mentioned that certain parameters used to indicate the mechanisms of tree resistance should be considered with caution. This is the case for the absolute length of the induced reaction zone after isolated inoculations (see 2.1.2). Only the results mentioning the efficacy (e) of this reaction

Table 2: Summary of the effects of environmental factors on various parameters of conifer resistance to bark beetles and their associated fungi, at the whole tree level and for preformed defence mechanisms, according to studies carried out in Europe or outside Europe.

Environmental factors	R e g i o n	Resistance parameters					
		Whole tree		-----Preformed defenses-----			
		Resis- tance level (1)	Suscep- tibility (2)	Resin flow	Total terpe- nes	Terp. cyclase activity	Phen- ols
Tree vigour	E	+	-	-	-	-	-
	O	+	-	-	-	-	-
Stand density or no thinning	E			-	o		
	O		+	-			
Mixed stands	E			+			
	O		-	o			
Pathogens / Mistletoe	E		o (**)				
	O		+	-	o (m)		o
Defo- lation	L	o	o				
	E	o	o	-			
	H	-	+	- (f+)			
	O	-	+	-	-		
Water	M	+					
	O	+	o -	+		+	
stress	S	-	+				
	O		+	-			
Wind	U	+					
	O		+	-			
Fertilization	E		o	o -	-		o -
	O		o (-)	-	-		+
Lightning	E						
	O	-	+	- (m)			
Fire	L		o				
	E		o	o			
	H	+					
	O	+		-			
Pollution	L		o				
	O	o (-)	o (+)	-			
	E		+				
	O	-	+	-	o		

Levels of stress: L = light or low; H = heavy or high; M = moderate; S = severe; U = unknown intensity. Area: E = results from European tree species; O = results from trees growing outside Europe (mainly North America). 1 = critical threshold of attack or inoculation density; 2 = success of beetle attacks; Quantitative changes: + = increase; - = decrease; o = no change. Qualitative changes: m = modification of the composition; ** = epidemic populations. f+ = increase in case of interaction with fertilization

Table 2 (cont.): Summary of the effects of environmental factors on various parameters of conifer resistance to bark beetles and their associated fungi for induced defence mechanisms, according to studies carried out in Europe or outside Europe.

Resistance parameters					R	Environmental
-----Induced defenses-----					e	factors
Resin flow	Tree reaction (3)	Total terpenes	Terp. cyclase activity	Phe-nols	g I o n	
+	- +				E O	Tree vigour
	o	+			E O	Stand density or no thinning
-	-				E O	Mixed stands
					E O	Pathogens / Mistletoe
		m			E O	Défoliations
-(e)	o	- o		o	E H O	
-(e)	-				E O	
			-		E O	Water
-	- o	-		o	E S O	
	-(e)		-		E U O	stress
		m			E O	
o	o	-		- (*)	E O	Fertilization
					E O	Wind
					E O	Lightning
o					E L O	Fire
-					E H O	
					E L O	Pollution
					E H O	

Levels of stress: L = light or low; H = heavy or high; M = moderate; S = severe; U = unknown intensity. Area: E = results from European tree species; O = results from trees growing outside Europe (mainly North America). 3 = reaction zone length or efficacy of the reaction (e). Quantitative changes: + = increase; - = decrease; o = no change. Qualitative changes: m = modification of the composition; * = decrease of the stilbene aglycones.

should be regarded as reliable. Total concentration of phenols, especially in the induced reaction zone, has no relationship to tree defence ability. Indeed, both in spruce and pines, it has been demonstrated that the tree phenol response is not quantitative but rather qualitative, that is consists mostly in variations in the proportions of the constituents, the concentration of certain compounds decreasing, that of others increasing, while several others are neosynthesized (see 2.2.3). In this context, only the quantitative variations of particular compounds or families of compounds, those that have been demonstrated to be related to tree resistance or to have an effect on the aggressors, can be of interest. This is the case, for example, for stilbene aglycons, catechin, pinosylvin or pinocembrin (see 3 and 6.1).

Even regarding preformed defences, total phenol concentrations have a very limited interest, since toxicity in this chemical family varies largely from one compound to another (see 3). On the contrary, total monoterpenes concentrations have a meaning in terms of tree resistance, since all of them increase in response to attacks and have toxic effects on insects and fungi (see 3). Variations in relative content are thus less useful here. Unfortunately, in the attempts to try and connect the chemical characteristics of the tree to its defence mechanisms in relation to effects of environmental factors, qualitative variations have considered almost exclusively monoterpenes. In all cases but one, phenols were considered in relation to their total concentration.

In table 2, results are generally clear and coherent regarding the effects of environmental factors on tree susceptibility and the level of resistance itself, although additional information is needed for this latter parameter, especially concerning the silvicultural and fertilization effects. Fewer results are available regarding the effects on resistance mechanisms, i.e. the parameters involved in defence, but there is consistency if absolute reaction zone length and total phenol concentration are discarded. In general, except for water stress, defoliation, and fertilization effects, the mechanisms of induced defences have been very poorly investigated. Moreover, the effects of fertilization on induced defence mechanisms have been considered only in Europe, whereas North American studies have concentrated on water stress and defoliation effects. Even for the constitutive defences, little is known outside of resin flow variations, although terpenes and phenols certainly play a decisive role. For all environmental factors, studies of resin flow have been largely developed in Southern North America. European work on that parameter concerned only fertilization and silvicultural effects. In the present social and environmental context, the general lack of data concerning the effects of silviculture and pollution on tree defence mechanisms against bark beetles represents a dramatic gap. Even regarding tree susceptibility and resistance, almost nothing is known on the effects of silviculture and tree diversity.

The effect of tree vigor on resistance may be intriguing since an increase in resistance (or a decrease in tree susceptibility) due to high vigor, corresponds to a decrease of the preformed defences. The balance between vigor and preformed defence can be explained by the growth differentiation balance (GDB) hypothesis, especially during the period of rapid growth (Kytö *et al.*, 1999; Baier *et al.*, 2002; Lorio, 1986), but still the increase in resistance with vigor must be clarified. The stimulation of the induced defence mechanisms, which could become a priority over

growth in cases of wounding (Lombardero *et al.*, 2000) could be a reason. No effect of fertilization has been observed on tree susceptibility although both the preformed (resin flow and total terpenes) and induced (total terpenes and stilbene aglycons) defences are altered (table 2 and see references in 6.5.2). This alteration has been explained by the above mentioned hypothesis because fertilization stimulates tree growth (Viiri *et al.* (2001), but tree susceptibility should increase, the more because induced defence does not seem to be a priority over growth in that case.

6.7.2. General trends

In spite of the specific relationships reported above for some factors, there are general trends common to several environmental factors that can be drawn from table 2.

A dose effect is evident for several factors such as defoliation, water stress, fire and pollution. Defoliation, fire and pollution, have a depressive effect on tree resistance (or increase tree susceptibility), and this effect is proportional to the stress intensity. All three factors have in common an effect on tree vitality through foliage injury, and their intensity is quantified by the percentage of crown loss or crown scorch. In these conditions, a dose effect is not surprising because defence metabolism is conditioned by photosynthetic activity, through current photosynthesis or building of reserves. Moreover, photosynthetic activity of the remaining foliage is probably preferentially directed towards growth rather than defence metabolism, a priority which could also depend on the extent of foliage injury. Unfortunately, insufficient data are available to check if the effects on defence mechanisms are also proportional to the stress intensity, although this seems true at least for the effect of fire on the preformed and induced resin flows. Although many results are difficult to interpret because several experiments have been carried out without quantifying the stress intensity, it is also clear that a dose effect of water stress exists. It corresponds however to a completely different phenomenon, since mild stress increases tree resistance (or decreases tree susceptibility) whereas a severe stress decreases it. There is no proportionality between water stress intensity and tree resistance. On the contrary, a threshold of stress exists on each side of which the effects are opposite. Observations on the preformed but not the induced defence mechanisms agree with variations in tree resistance, but too little data are available to conclude definitely on this point. The GDB hypothesis can explain these results if we admit that tree growth stops very rapidly, and is affected by water stress before defence, and that photosynthesis continues until the above mentioned threshold is reached. Recent experiments suggest that the stress threshold could be linked to predawn needle water potential value of -1.2 MPa (Dreyer *et al.*, 2002). This value is below that observed during drought in temperate zones at the period of beetle flight, where generally only mild stresses occur. This means that the reason for many outbreaks may not be a decrease in tree resistance due to drought (Christiansen and Glosli, 1996; Dreyer *et al.*, 2002; Lieutier *et al.*, 2003a).

Preformed and induced defences can vary in opposite direction with the same factor, even under the same stress intensity. This has been mentioned above for the

effect of tree vigor (see 6.7.1). It has also been observed under a mild water stress in *A. grandis*, where constitutive terpene cyclase activity is stimulated while induced terpene cyclase activity is reduced (Steele *et al.*, 1995). In cases of severe stress, however, both activities are reduced. According to Lombardero *et al.* (2000), the fact that constitutive and induced defence can be differentially affected by environmental conditions could be one explanation for the existence of conflicting results regarding environmental effects on plant anti-herbivore defences in general.

Interference between factors can modify the characteristics of the tree defences against a given factor. For example, it has been mentioned above (see 6.3.2) that thinning can affect tree resistance through stimulation of growth and modification of social status, but it also modifies the forest microclimate which can have consequences on both insect biology and tree defences. More complex interactions may take place. Fertilization seems to be able to change the direction of the effects caused by other factors. In the absence of any treatment, it has often been reported that constitutive resin flow decreases when defoliation increases (see 6.4.2), but a positive relation between resin exudation and the intensity of defoliation by *D. pini* has been found in fertilized Scots pine, suggesting that defoliation stimulates resin production in the stem (Kytö *et al.*, 1999). Similarly, in a cross experiment combining drought and fertilization treatments, fertilization has been observed to moderate drought effects on tree resistance to mass inoculations of Scots pine with *O. brunneo-ciliatum* (Guérard *et al.*, 2000).

6.7.3. Explanatory theories

Several models have been proposed to explain the role of the environment on plant secondary metabolites and its involvement in resistance to attacks by plant-feeders: growth-differentiation balance (Loomis, 1932; Lorio, 1986; Herms and Mattson, 1992), carbon-nutrient balance (Bryant *et al.*, 1983), plant stress hypothesis (White, 1984; Mattson and Haack, 1987), optimal allocation (Tuomi *et al.*, 1991). All aim at defining general mechanisms, and conifer bark beetles and their associated fungi are only one component of a complex approach taking into consideration results from many experiments carried out separately with various species belonging to different guilds and submitted to different environmental factors. It is thus not surprising that none of these models has led to a general consensus (Koricheva *et al.*, 1998). It is however concluded generally that different models may apply to different guilds. In addition, only one environmental factor is generally considered in each experiment, and it is difficult to extrapolate to natural conditions where several factors interfere with each others. An interesting approach already considered in some experiments is to study only one insect guild with several environmental factors in combination.

Regarding bark beetles, I will only note that, compared to other groups of insects, bark beetles that attack living trees form a homogeneous guild although different life cycles and strategies can be distinguished. They have intimate relationship with their hosts because they spend the major part of their life cycle inside them, and because host resistance is the key factor of their population dynamics. They thus seem an insect model favorable to test the effects of environmental factors on tree resistance to attacks. However, the situation is

complicated by the important role played by the fungi in the relationships with the tree. Even for this group alone, many gaps, visible in table 2, need to be filled before trying to build a general theory. In addition, to progress in the understanding of the mechanisms by which environmental factors affect tree resistance, it will also be necessary to distinguish the effects that the modifications in the tree physiological parameters have on the insect itself from those that they have on its associated fungi. The effects resulting from the consideration of several environmental factors in combination in controlled conditions should also give interesting information on the mechanisms.

7. UTILIZATION OF RESISTANCE IN BARK BEETLE MANAGEMENT

This aspect has been presented recently both from a general point of view (Lieutier, 2002) and for possibilities of utilization in Central and Western Europe (Heidger and Lieutier, 2002). They will thus not be developed here. I will only reformulate the major ideas and underline, among the numerous potential applications of conifer resistance to bark beetles, the research topics that seem most likely to yield practical applications in the context of a modern forestry.

Tree selection for resistance is a classical but still promising application. The phenolic predictors of tree resistance that have already been proposed for Scots pine and Norway spruce (see 6.1) could be used as resistance markers in breeding programs, in addition to other desirable characteristics of the tree. Other predictors belonging to the same chemical family could certainly be discovered in other conifer species. This supposes research on the possibilities to use these predictors at the juvenile stage of the tree. Research on possible counter-adaptations by beetles and fungi are also needed, even if the chance for such adaptations may seem lower than with other insect guilds (Lieutier, 2002).

In the context of global change and biological invasions, bark beetles may encounter new hosts. Studies on factors that allow beetles and fungi to adapt to tree resistance mechanisms will also give useful information to evaluate the risk of damage and to help foresters to define options available for forest protection.

Regarding climatic change, detailed studies on the effects of environmental factors, such as water stress, pollution, and fire, on tree defence mechanisms will have practical applications in the field of risk prediction and physiological improvement of trees by adapted silvicultural methods. Research on effects of fertilization on tree resistance has demonstrated that this treatment can be beneficial to forestry when considering bark beetle problems, since it increases tree productivity without affecting the risk of damage (table 2). Similarly, clarifying the effects of thinning, and understanding the role of tree biodiversity on tree resistance, will also lead to improvements of silvicultural methods.

8. CONCLUSIONS

Knowledge of mechanisms of tree resistance to attacks by bark beetles and their associated fungi has improved considerably since the pioneer papers by Vité (1961),

Reid *et al.* (1967) and Berryman (1972), especially during the last 30 years in North America and the last 20 years in Europe. However, many aspects are still not understood and need to be investigated. Questions and research prospects have been listed and presented recently while considering the general state of knowledge of conifer resistance to bark beetles (Lieutier, 2002). Research in relation to environmental factors is particularly needed in the present environmental situation and some directions have been proposed above (see 6.7 and 7). This concluding section will provide a synopsis of the strengths and gaps in our understanding of the mechanisms of resistance of the European conifer species to European bark beetle species, through a comparison with the state of knowledge on the North American species.

Research really started in Europe in the early 80's with works developed on the resistance of *P. abies* to *I. typographus* and its associated fungus *C. polonica* (Christiansen and Horntvedt, 1983; Horntvedt *et al.*, 1983). Resistance of *P. sylvestris* to *Ips* and *Tomicus* species began to be studied later (Lieutier *et al.*, 1988b; Lieutier and Ferrell, 1988; Långström & Hellqvist 1988). Practically, among the native species, only these two conifers have been considered since. The species range considered in North America has not been much higher, the studies focusing mainly on *P. taeda* (sometimes associated with *P. echinata*), *P. ponderosa*, *P. contorta* and *A. grandis*. Much less attention has been given to *Pinus pinaster*, *Picea obovata* and *P. sitchensis* (introduced) in Europe, and to Douglas fir (*Pseudotsuga menziesii*), *A. concolor*, *Pinus elliottii*, *Pinus radiata* and *Picea glauca* in North America. However, considering that there are 31 species of Pinaceae in Europe (North Africa included) and 57 in North America (Mexico excluded) (Debazac, 1977), the ratio of species studied is about the same in both continents. Outside Europe and North America, at least 95 Pinaceae species live in Asia and 32 in Central or South America (Debazac, 1977). Among them, only *Pinus yunnanensis* in Southwestern China has been studied so far for the mechanisms of resistance to bark beetles. Little has been done in conifer families other than Pinaceae but they are not concerned with bark beetle damage, except some species of Cupressaceae in the Mediterranean areas. In hardwood trees, only elms (*Ulmus* spp.) have been studied, but only for resistance to the fungus (*Ophiostoma ulmi*) itself.

Regarding the beetle species, mainly *I. typographus*, *I. sexdentatus*, and *T. piniperda* have been considered in Europe with, to a lesser extent *D. micans* and *I. acuminatus*. In North America, the species concerned are mainly *D. frontalis*, *D. ponderosae*, and *S. ventralis*, with less frequently *D. brevicomis*, *D. pseudotsugae*, *D. terebrans*, *I. pini* and *I. confusus*. Similarly to tree species, the ratio of studied insect species to available species is similar on both sides of the Atlantic. However, a considerably higher number of North American papers is published each year, reflecting different research efforts in terms of number of scientists and institutions involved.

All tree resistance mechanisms that have been presented in this chapter (see 2.1) certainly exist in both regions. However, induced resin flow has been described only in loblolly pine, while the existence of delayed resistance has been clearly demonstrated in Norway spruce only. Hypersensitive reactions have, by far, been

much more studied than the other resistance mechanisms both in North America and in Europe, but preformed resistance has been studied mainly in North America. The reasons are that North America has economically important beetles both among those species where resin flow is a major resistance factor (*D. frontalis*) and in those species where induced resistance plays the main role (*D. ponderosae*). In Europe, except against *D. micans*, the major factor of conifer resistance to the economically important European bark beetles are induced defences (see 4).

In the field of the mechanisms involved in the hypersensitive reaction, research has depended on the topics considered and may have concentrated on either European or North American tree species. The relative role of beetle tunnelling activity and the associated fungi in the induction and stimulation of this reaction was demonstrated in Scots pine and was then extended to other conifers (see § 2.2.2). Collaboration between North American and European teams on Norway spruce established the essential role of the P.P. cells. This role was then extended to other kinds of defences (see § 2.2.2). The biochemical characteristics of the tree response have been investigated mainly in North American pines for terpenes, but in Norway spruce and Scots pine for phenols. However, little European research has dealt with the mode of action upon the aggressors. The mechanisms of tree death and the pathogenicity of beetle associated fungi have been studied in both areas, depending on the beetle species considered, but still no definite explanation is available for the former aspect.

The effects of environmental factors on tree resistance and defence mechanisms have been investigated largely on both North American and European species, but unequally depending on the factor considered (see 6.7 and table 2). For example, effects of water stress and defoliation have been studied about equally, but the fertilization effects were more thoroughly considered on Scots pine and Norway spruce. Models on the role of host resistance in bark beetle population dynamics have concerned almost exclusively North American species.

9. REFERENCES

- Amezaga, I. 1997. Forest characteristics affecting the rate of shoot pruning by the pine shoot beetle (*Tomicus piniperda* L.) in *Pinus radiata* D. Don and *P. sylvestris* L. plantations. *Forestry* 70, 129-37.
- Amman G.D., McGregor, M.D., Schmitz, R.F. & Oakes, R.D. 1988. Susceptibility of lodgepole pine to infestation by mountain pine beetles following partial cutting of stands. *Canadian Journal of Forest Research* 18, 688-95.
- Annila, E., Långström, B., Varama, M., Hiukka, R. & Niemela, P. 1999. Susceptibility of defoliated Scots pine to spontaneous and induced attack by *Tomicus piniperda* and *Tomicus minor*. *Silva Fennica* 33, 93-106.
- Baier P., Führer, E., Kirisits, T. & Rosner, S. 2002. Defence reactions of Norway spruce against bark beetles and the associated fungus *Ceratocystis polonica* in secondary pure and mixed species stands. *Forest Ecology and Management* 159, 73-86.
- Bakke, A., 1983. Host tree and bark beetle interaction during a mass outbreak of *Ips typographus* in Norway. *Zeitschrift für angewandte Entomologie*, 96, 118-25.
- Baradat, P., Bernard-Dagan, C., Pauly, G. & Zimmermann-Fillon, C. 1975. Les terpènes du Pin maritime : aspects biologiques et génétiques. III. Hérité de la teneur en myrcène. *Annales des Sciences Forestières*, 32, 29-54.

- Baradat, P., Marpeau, A. & Bernard-Dagan, C. 1978. Variation of terpenes within and between populations of maritime pine. In. Biochemical genetics of forest trees, D. Rudin (Ed.), Umea, Sweden.
- Barrett, J.P. & Bengston, G.W. 1964. Oleoresin yields for slash pines from seven seed sources. Forest Science, 10, 159-64.
- Bartos, D.L. & Amman, G.D. 1989. Microclimate: an alternative to tree vigor as a basis for mountain pine beetle infestations. USDA Forest Service Research Paper INT-400.
- Bartos, D.L. & Booth, G.D. 1994. Effects of thinning on temperature dynamics and mountain pine beetle activity in a lodgepole pine stand. USDA Forest Service Research Paper INT-RP-479.
- Belanger, R.P., Osgood, E.A. & Hatchell, G.E., 1979. Stand, soil, and site characteristics associated with southern pine beetle infestations in the southern Appalachians. USDA Forest Service Research Paper SE-198.
- Bernard-Dagan, C., Fillon, C., Pauly, G., Baradat, P. & Illy, G. 1971. Les terpènes du Pin maritime. I. Variabilité de la composition monoterpéniqne dans un individu, entre individus et entre provenances. Annales des Sciences Forestières, 28, 223-58.
- Berryman, A.A. 1972. Resistance of conifers to invasion by bark beetle fungus associations. BioScience 22,598-602.
- Berryman, A.A. 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. Environmental Entomology, 5,1225-33.
- Berryman, A.A. 1982. Population Dynamics of Bark Beetles. In. *Bark Beetles in North American Conifers*, J.B. Mitton, K.B. Sturgeon (Eds.). Austin: University of Texas.
- Berryman, A.A. & Ashraf, M. 1970. Effects of *Abies grandis* resin on the attack behavior and brood survival of *Scolytus ventralis* (Coleoptera: Scolytidae). The Canadian Entomologist, 102,1229-36.
- Blanche, C.A., Hodges, J.D. & Nebeker, T.E. 1985. Changes in bark beetle susceptibility indicators in a lightning-struck loblolly pine. Canadian Journal of Forest Research, 15, 397-99.
- Blanche, C.A., Lorio, P.L., Jr., Sommers, R.A., Hodges, J.D. & Nebeker, T.E. 1992. Seasonal cambial growth and development of loblolly pine: xylem formation, inner bark chemistry, resin ducts, and resin flow. Forest Ecology and Management, 49, 151-65.
- Bois, E. & Lieutier, F. 1997. Phenolic response of Scots pine clones to inoculation with *Leptographium wingfieldii*, a fungus associated with *Tomicus piniperda*. Plant Physiology and Biochemistry, 35, 819-25.
- Bois E., Lieutier F. & Yart, A. 1999. Bioassays on *Leptographium wingfieldii*, a bark beetle associated fungus, with phenolic compounds of Scots pine phloem. European Journal of Plant Pathology, 105, 51-60.
- Bordasch, R.P. & Berryman, A.A. 1977. Host resistance to the fir engraver beetle *Scolytus ventralis* (Coleoptera: Scolytidae). 2. Repellency of *Abies grandis* resins and some monoterpenes. The Canadian Entomologist, 109, 95-100.
- Bridges, J.R. 1987. Effects of terpenoid compounds on growth of symbiotic fungi associated with the southern pine beetle. Phytopathology, 77,83-85.
- Brignolas, F. 1995. Rôle des composés phénoliques dans l'efficacité de la réaction induite du liber de l'épicéa (*Picea abies*) à enrayer la progression d'*Ophiostoma polonicum*, champignon associé au Scolytide *Ips typographus*. Thèse Université d'Orléans: Physiologie et biologie des organismes, populations, interactions.
- Brignolas, F., Lacroix, B., Lieutier, F., Sauvard, D., Drouet, A., Claudot, A.-C., Yart, A., Berryman, A.A. & Christiansen, E. 1995b. Induced responses in phenolic metabolism in two Norway spruce clones after wounding and inoculations with *Ophiostoma polonicum*, a bark beetle-associated fungus. Plant Physiology, 109,821-27.
- Brignolas, F., Lieutier, F., Sauvard, D., Christiansen, E. & Berryman, A.A. 1998. Phenolic predictors for Norway spruce resistance to the bark beetle *Ips typographus* (Coleoptera: Scolytidae) and an associated fungus, *Ceratocystis polonica*. Canadian Journal of Forest Research, 28,720-28.
- Brignolas, F., Lieutier, F., Sauvard, D., Yart, A., Drouet, A. & Claudot, A.-C. 1995a. Changes in soluble phenol content of Norway spruce (*Picea abies* Karst.) phloem in response to wounding and inoculation with *Ophiostoma polonicum*. European Journal of Forest Pathology, 25,253-65.
- Brown, M.W., Nebeker, T.E. & Honea, C.R. 1987. Thinning increases loblolly pine vigor and resistance to bark beetles. Southern Journal of applied Forestry 11, 28-31.
- Bryant, J.P., Chapin, F.S., III & Klein, D.R. 1983. Carbon nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos, 40, 357-68.

- Buijtenen, J.P. & Van Santamour, F. 1972. Resin crystallization related to weevil resistance in white pine (*Pinus strobus*). *The Canadian Entomologist*, 104, 215-18.
- Cates, R.G. & Alexander, H. 1982. Host Resistance and Susceptibility. In. *Bark Beetles in North American Conifers*, J.B. Mitton, K.B. Sturgeson (Eds.). Austin: Univ. Texas.
- Cedervind, J., Pettersson, M. & Långström, B. 2003. Attack dynamics of the pine shoot beetle, *Tomicus piniperda* (Co., Scolytinae) in Scots pine stands defoliated by *Bupalus piniaria* (Lep. Geometridae). *Agricultural and Forest Entomology* 5, 253-61.
- Chararas C. 1962. *Scolytides des Conifères*. Paris, Lechevalier.
- Cheniclet, C., Bernard-Dagan, C. & Pauly, G. 1988. Terpene Biosynthesis Under Pathological Conditions. In. *Mechanisms of Woody Plant Defences Against Insects: Search for Pattern*, W.J. Mattson, J. Lévieux, C. Bernard-Dagan (Eds.). New York: Springer.
- Chiron, H., Drouet, A., Lieutier, F., Payer, H-D., Ernst, D. & Sandermann, H. Jr. 2000. Gene induction of stilbene biosynthesis in Scots pine in response to ozone treatment, wounding, and fungal infection. *Plant Physiology*, 124, 865-72.
- Christiansen, E. 1985a. *Ceratocystis polonica* inoculated in Norway spruce: Blue-staining in relation to inoculum density, resinosis and tree growth. *European Journal of Forest Pathology*, 15, 160-67.
- Christiansen, E. 1989. Bark beetles and air pollution. *Meddelelser fra det Norske Skogforsoksesen*, 42, 101-07.
- Christiansen, E. 1992. After-effects of drought did not predispose young *Picea abies* to infection by the bark beetle-transmitted blue-stain fungus *Ophiostoma polonicum*. *Scandinavian Journal of Forest Research*, 7, 557-69.
- Christiansen, E. & Ericsson, A. 1986. Starch reserves in *Picea abies* in relation to defence reaction against a bark beetle transmitted blue-stain fungus, *Ceratocystis polonica*. *Canadian Journal of Forest Research*, 16, 78-83.
- Christiansen, E. & Fjorøe, G. 1993. Pruning enhances the susceptibility of *Picea abies* to infection by the bark beetle-transmitted blue-stain fungus, *Ophiostoma polonicum*. *Scandinavian Journal of Forest Research* 8, 235-45.
- Christiansen, E., Franceschi, V.R., Nagy, N.E., Krekling, T., Berryman, A.A., Krokene, P. & Solheim, H. 1999b. Traumatic resin ducts formation in Norway spruce (*Picea abies* (L.) Karst.) after wounding or infection with a bark beetle-associated blue stain fungus, *Ceratocystis polonica* Siem. In. *Physiology and Genetics of Tree Phytophage Interactions*, F. Lieutier, W.J. Mattson, M.R. Wagner (Eds.). Versailles: INRA Editions.
- Christiansen, E. & Glosli, A.M. 1996. Mild drought enhances the resistance of Norway spruce to a bark beetle-transmitted blue-stain fungus. In: *Dynamics of Forest Herbivory: Quest for Pattern and Principle*, W.J. Mattson, P. Niemela, M. Rousi (Eds). USDA Forest Service General Technical Report NC-183, pp. 192-99.
- Christiansen, E. & Horntvedt, R. 1983. Combined *Ips/Ceratocystis* attack on Norway spruce and defensive mechanisms of the trees. *Zeitschrift für angewandte Entomologie*, 96, 110-18.
- Christiansen, E. & Huse, K. 1980. Infestation ability of *Ips typographus* in Norway spruce trees, in relation to butt rot, tree vitality and increment. *Meddelelser fra det Norske Skogforsoksesen*, 35, 469-82.
- Christiansen, E., Krokene P., Berryman, A.A., Franceschi, V.R., Krekling, T., Lieutier, F., Lönneborg, A. & Solheim, H. 1999a. Mechanical injury and fungal infection induce acquired resistance in Norway spruce. *Tree Physiology*, 19, 399-403.
- Christiansen, E., Waring, R.H. & Berryman A.A. 1987. Resistance of conifers to bark beetle attack: searching for general relationships. *Forest Ecology and Management*, 22, 89-106.
- Cobb, F.W. Jr., Kirstie, M., Zavarin, E. & Barber, H.W., Jr. 1968a. Inhibitory effects of volatile oleoresin components on *Fomes annosus* and four *Ceratocystis* species. *Phytopathology*, 58, 1327-35.
- Cobb, F.W., Jr., Wood, D.L., Stark, R.W. & Parmeter, J.R., Jr. 1968b. Photochemical oxidant injury and bark beetles (Coleoptera: Scolytidae) infestation of ponderosa pine. IV. Theory on the relationship between oxidant injury and bark beetle infestation. *Hilgardia*, 39, 141-52.
- Cook, S. P., Hain, F.P. & Nappen, 1986. Seasonality of the hypersensitive response by loblolly and shortleaf pine to inoculation with a fungal associate of the southern pine beetle (Coleoptera: Scolytidae). *Journal of Entomological Science*, 21, 283-85.
- Coulson, R.N. 1979. Population dynamics of bark beetles. *Annual Review of Entomology*, 24, 417-47.

- Coulson, R.N., Flamm, R.O., Pulley, P.E., Payne, T.L., Rykiel, E.J. & Wagner, T.L. 1986. Response of the southern pine bark beetle guild (Coleoptera: Scolytidae) to host disturbance. *Environmental Entomology*, 15, 850-58.
- Croisé, L., Dreyer, E. & Lieutier, F. 1998a. Effects of drought stress and severe pruning on the reaction zone induced by single inoculations with a bark beetle associated fungus (*Ophiostoma ips*) in the phloem of young Scots pines. *Canadian Journal of Forest Research* 28, 1814-24.
- Croisé, L. & Lieutier, F. 1993. Effect of drought on the induced defence reaction of Scots pine to bark beetle-associated fungi. *Annales des Sciences Forestières*, 50, 91-97.
- Croisé, L., Lieutier, F., Cochard, H. & Dreyer, E. 2001. Effects of drought stress and high density stem inoculations with *Leptographium wingfieldii* on hydraulic properties of young Scots pine trees. *Tree Physiology*, 21, 427-36.
- Croisé, L., Lieutier, F. & Dreyer, E. 1998b. Scots pine responses to number and density of inoculation points with *Leptographium wingfieldii* Morelet, a bark beetle-associated fungus. *Annales des Sciences Forestières*, 55, 497-506.
- Dahlsten, D.L. & Rowney, D.L. 1980. Influence of air pollution on population dynamics of forest insects and on tree mortality. Symposium on effects of air pollutants on Mediterranean and temperate forest ecosystems, Riverside, California, USA, June 22-27.
- DeAngelis, J.D., Nebeker, T.E., & Hodges J.D., 1986. Influence of tree age and growth rate on the radial resin duct system in loblolly pine (*Pinus taeda*). *Canadian Journal of Botany*, 64, 1046-49.
- Debazac, E.F. 1977. Manuel des conifères, ENGREF, Nancy.
- Delorme, L., & Lieutier, F. (1990). Monoterpene composition of the preformed and induced resins of Scots pine, and their effect on bark beetles and associated fungi. *Eur. J. For. Pathol.*, 20, 304-16.
- Dreyer, E., Guérard, N., Lieutier, F., Pasquier-Barré, F., Lung, B. & Piou, D. 2002. Interactions between nutrient and water supply to potted *Pinus sylvestris* trees and their susceptibility to several pests and pathogens. In. *Effects of water and nutrient stress on pine susceptibility to various pest and disease guilds*, Lieutier, F. (Ed), Final scientific report of the EU project FAIR 3 CT96-1854.
- Dunn, J.P. & Lorio, P.L., Jr. 1992. Effect of bark girdling on carbohydrate supply and resistance of loblolly pine to southern pine beetle (*Dendroctonus frontalis* Zimm.) attack. *Forest Ecology and Management*, 50, 317-30.
- Dunn, J.P. & Lorio, P.L., Jr. 1993. Modified water regimes affect photosynthesis, xylem water potential, cambial growth, and resistance of juvenile *Pinus taeda* L. to *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Physiological and Chemical Ecology*, 22, 948-57.
- Ehnström, B., Långström, B. & Hellqvist, C. 1995. Insects in burned forests – forest protection and faunal conservation (preliminary results). *Entomologica Fennica*, 6, 109-17.
- Evensen, P.C., Solheim, H., Hoiland, K. & Stenersen, J. 2000. Induced resistance of Norway spruce, variation of phenolic compounds and their effects on fungal pathogens. *Forest Pathology*, 30, 97-108.
- Everaerts, C., Grégoire, J.-C. & Merlin, J. 1988. Toxicity of Spruce Monoterpenes Against Bark Beetles and Their Associates . In. *Mechanisms of Woody Plant Defences Against Insects: Search for Pattern*, W.J. Mattson, J. Léveux, C. Bernard-Dagan (Eds.). New York: Springer.
- Fäldt, J., Martin, D., Miller, B., Rawat, S. & Bohlmann, J. 2003. Traumatic resin defence in Norway spruce (*Picea abies*): Methyl jasmonate-induced terpene synthase gene expression, and cDNA cloning and functional characterization of (+)-3-carene synthase. *Plant Molecular Biology*, 51, 119-33.
- Ferrell, G.T. 1974. Moisture stress and fir engraver (Coleoptera: Scolytidae) attack in white fir infected by true mistletoe. *Canadian Entomologist* 106, 315-18.
- Ferrell, G.T. 1978. Moisture stress threshold of susceptibility to fir engraver beetles in pole-size white firs. *Forest Science*, 24, 85-92.
- Ferrell, G.T. 1983. Host resistance to the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae): frequencies of attacks containing resin blisters and canals of *Abies concolor*. *The Canadian Entomologist*, 115, 1421-28.
- Ferrell G.T. & Otrosina W.J., 1996. Differential susceptibility of white fir provenances to the fir engraver and its fungal symbiont in Northern California. In. *Dynamics of forest herbivory; quest for pattern and principle*, W.J. Mattson, P. Niemela, M. Rousi (Eds), USDA Forest Service General Technical Report NC-183.
- Ferrell, G.T., Otrosina, W.J. & Demars, Jr, C.R. 1994. Predicting susceptibility of white fir during a drought-associated outbreak of the fir engraver, *Scolytus ventralis*, in California. *Canadian Journal of Forest Research* 24, 302-05.

- Filip, G.M., Christiansen, E., & Parks, C.A., 1989. Secondary resin production increases with vigor of *Abies grandis* inoculated with *Trichosporium symbioticum* in Northeastern Oregon. USDA Forest Service Research Note PNW-RN-489, 12 p.
- Filip, G.M., Ganio, L.M., Oester, P.T., Mason, R.R. & Wickman, B.E. 2002. Ten-year effect of fertilization on tree growth and mortality associated with *Armillaria* root disease, fir engravers, dwarf mistletoe, and western spruce budworm in Northeastern Oregon. Western Journal of Applied Forestry, 17, 122-128.
- Flamm, R.O., Pulley, P.E. & Coulson, R.N. 1993. Colonization of disturbed trees by the southern pine bark beetle guild (Coleoptera: Scolytidae). Environmental Entomology, 22, 62-70.
- Franceschi, V.R., Krekling, T., Berryman, A.A. & Christiansen, E. 1998. Specialized phloem parenchyma cells in Norway spruce (Pinaceae) bark are an important site of defence reactions. American Journal of Botany 85, 601-15.
- Franceschi, V.R., Krekling, T. & Christiansen, E. 2002. Application of methyl jasmonate on *Picea abies* (Pinaceae) stems induces defence-related responses in phloem and xylem. American Journal of Botany, 89, 578-86.
- Franceschi, V.R., Krokene, P., Krekling, T., Berryman, A.A. & Christiansen, E. 2000. Phloem parenchyma cells are involved in local and distant defence responses to fungal inoculation or bark beetle attack in Norway spruce (Pinaceae). American Journal of Botany, 87, 314-26.
- Fredericksen, T.S., Hedden, R.L. & Williams, S.A. 1995. Susceptibility of loblolly pine to bark beetle attack following simulated wind stress. Forest Ecology and Management, 76, 96-107.
- Gilbert, M., Vouland, G. & Grégoire J.C. 2001. Past attacks influence host selection by the solitary bark beetle *Dendroctonus micans*. Ecological Entomology, 26, 133-42.
- Gilmore, A.R. 1977. Effects of soil moisture stress on monoterpenes in loblolly pine. Journal of Chemical Ecology, 3, 667-76.
- Grégoire, J.C. 1988. The Greater European Spruce Beetle. In. *Dynamics of Forest Insect Populations: Patterns, Causes, Implications*, A.A. Berryman (Ed). New York: Plenum Press.
- Grégoire J.C., Braekman J.C. & Tondeur A., 1982. Chemical communication between larvae of *Dendroctonus micans* Kug. (Coleoptera: Scolytidae). Les colloques de l'INRA. 7. Les médiateurs chimiques: 16-20.
- Grodzki, W. 1997. Changes in the occurrence of bark beetles on Norway spruce in a forest decline area in the Sudety mountains in Poland. In. *Integrated cultural tactics into the management of bark beetles and reforestation pests*, J.C. Grégoire, A.M. Liebhold, F.R. Stephen, K.R. Day, S.M. Salom (Eds). USDA Forest Service General Technical Report NE-236.
- Guérard, N. 2001. Résistance du Pin sylvestre aux attaques de Scolytes et de leur champignons associés : interactions avec l'alimentation hydrique et minérale. Thèse Université de Tours, Biologie des populations, génétique et éco-éthologie.
- Guérard, N., Dreyer, E. & Lieutier, F. 2000a. Interactions between Scots pine, *Ips acuminatus* (Gyll.) and *Ophiostoma brunneo-ciliatum* (Math.): estimation of the critical thresholds of attack and inoculation densities and effects on hydraulic properties of the stem. Annals of Forest Sciences, 57, 681-90.
- Guérard, N., Dreyer, E. & Lieutier, F. 2000b. Influence of water and mineral nutrition on Scots pine resistance to bark-beetles and an associated blue-stain fungus. XXI IUFRO World Congress, 7.01.02 Working Party, «Mechanisms of tree resistance to phytophagous insects», 7-12 August, Kuala Lumpur (Malaysia).
- Hanover, J.A., 1975. Physiology of tree resistance to insects. Annual Review of Entomology, 20, 75-95.
- Hanover, J.W., 1966. Genetics of terpenes. 1. Gene control of monoterpenes levels in *Pinus monticola* Dougl. Heredity, 21, 73-84.
- Hard, J.S. 1985. Spruce beetle attacks slowly growing spruce. Forest Science, 31, 839-50.
- Harrington, T.C. 1993. Diseases of Conifers Caused by Species of *Ophiostoma* and *Leptographium*. In. *Ceratocystis and Ophiostoma. Taxonomy, Ecology, and Pathogenicity*, M.J. Wingfield, K.A. Seifert, J.F. Webber (Eds.). Saint Paul: APS Press.
- Hart, J.H. 1981. Role of phytostilbenes in decay and disease resistance. Annual Review of Phytopathology, 19, 437-58.
- Hart, J.H. & Shrimpton, D.M. 1979. Role of stilbenes in resistance of wood to decay. Phytopathology, 69, 1138-43.
- Heidger, C.M. & Lieutier, F. 2002. Possibilities to utilize tree resistance to insects in forest pest management in central and western Europe. In. *Mechanisms and Deployment of Resistance in Trees to Insects*, M.R. Wagner, K.M. Clancy, F. Lieutier, T.D. Paine (Eds), Dordrecht, Kluwer.

- Herms, D.A. & Mattson, W.J. 1992. The dilemma of plants: to grow or defend. Quarterly Review of Biology, 67, 283-335.
- Hodges, J.D. & Lorio, P.L., Jr. 1975. Moisture stress and composition of xylem oleoresin in loblolly pine. Forest Science, 21, 283-90.
- Hodges, J.D. & Picard, L.S. 1971. Lightning in the ecology of the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). The Canadian Entomologist, 103, 44-51.
- Horntvedt, R. 1988. Resistance of *Picea abies* to *Ips typographus*: tree response to monthly inoculations with *Ophiostoma polonicum*, a beetle transmitted blue-stain fungus. Scand. J. For. Res., 3, 107-114.
- Horntvedt, R., Christiansen, E., Solheim, H. & Wang, S. 1983. Artificial inoculation with *Ips typographus*-associated blue-stain fungi can kill healthy Norway spruce trees. Meddelelser fra det Norske Skogforskvesen, 38, 1-20.
- Hudgins, J.W., Christiansen, E. & Franceschi V. 2003a. Methyl jasmonate induces changes mimicking anatomical defences in diverse members of the Pinaceae. Tree Physiology, 23, 361-71.
- Hudgins, J.W., Krekling, T. & Franceschi V. 2003b. Distribution of calcium oxalate crystals in the secondary phloem of conifers: a constitutive defence mechanism? New Phytologist, 159, 677-690.
- Johnson, M.A. & Croteau, R. 1987. Biochemistry of Conifer Resistance to Bark Beetles and their Fungal Symbionts. In: *Ecology and Metabolism of Plant Lipids*, G. Fuller, W.D. Nes (Eds.). ACS Symposium Series N° 325. Washington DC: American Chemical Society.
- Karban, R. & Baldwin, I.T. 1997. *Induced Responses to Herbivory*. Chicago: The University of Chicago Press.
- Katoh, S. & Croteau, R. 1998. Individual variation in constitutive and induced monoterpene biosynthesis in grand fir (*Abies grandis*). Phytochemistry, 47, 577-82.
- Keen, F.P. 1938. *Insects enemies of western forests*. USDA Miscellaneous Publication 273.
- King, E.W. 1972. Rainfall and epidemics of the southern pine beetle. Environmental Entomology, 1, 279-85.
- Klepzig, K.D., Kruger, E.L., Smalley, E.B. & Raffa K.F. 1995. Effects of biotic and abiotic stress on induced accumulation of terpenes and phenolics in red pines inoculated with bark beetle-vectored fungus. Journal of Chemical Ecology 21, 601-26.
- Koricheva, J., Larsson, S. & Haukioja, E. 1998. Insect performance on experimentally stressed woody plants: a meta-analysis. Annual Review of Entomology, 43, 195-216.
- Krekling, T., Franceschi, V.R., Berryman, A.A. & Christiansen, E. 2000. The structure and development of polyphenolic parenchyma cells in Norway spruce (*Picea abies*) bark. Flora, 195, 354-69.
- Krokene, P., Christiansen, E. & Solheim, H. 2000. Induced disease resistance in Norway spruce and its implications for bark beetle population dynamics. Abstracts of the XXI International Congress of Entomology, August 20-26, Foz do Iguaçu, Brazil.
- Krokene, P., Christiansen, E., Solheim, H., Franceschi, V.R. & Berryman, A.A. 1999. Induced resistance to pathogenic fungi in Norway spruce. Plant Physiology, 121, 565-69.
- Krokene, P. & Solheim, H. 1999. What do low-density inoculations with fungus tell us about fungal virulence and tree resistance? In: *Physiology and Genetics of Tree-Phytophage Interactions*, F. Lieutier, W.J. Mattson, M.R. Wagner (Eds.). Versailles: INRA Editions.
- Krokene, P., Solheim, H. & Christiansen, E. 2001. Induction of disease resistance in Norway spruce (*Picea abies*) by necrotizing fungi. Plant Pathology, 50, 230-33.
- Krokene, P., Solheim, H., Krekling, T. & Christiansen, E. 2003. Inducible anatomical defence responses in Norway spruce stems and their possible role in induced resistance. Tree Physiology, 23, 191-97.
- Kytö, M., Niemela, P. & Annila, E. 1996. Vitality and bark-beetle resistance of fertilized Norway spruce. Forest Ecology and Management, 84, 149-57.
- Kytö, M., Niemela, P. & Annila, E. 1998. Effects of vitality fertilization on the resin flow and vigour of Scots pine in Finland. Forest Ecology and Management, 102, 121-30.
- Kytö, M., Niemela, P., Annila, E. & Varama, M. 1999. Effects of forest fertilization on radial growth and resin exudation of insect defoliated Scots pines. Journal of Applied Ecology, 36, 763-69.
- Långström, B., Annila, E., Hellqvist C., Varama, M. & Niemela, P. 2001a. Tree mortality, needle biomass recovery and growth losses in Scots pine following defoliation by *Diprion pini* (L.) and subsequent attack by *Tomicus piniperda* (L.). Scandinavian Journal of Forest Research 16, 342-53.
- Långström, B. & Hellqvist, C. 1988. Scots pine resistance against *Tomicus piniperda* as related to tree vitality and attack density. In: *Integrated control of scolytid bark beetles*, Payne, T.L., Saarenmaa, H. (eds), Proceedings of the IUFRO working party and XVII International congress of entomology symposium, Vancouver, B.C., Canada, July 4 1988.

- Långström, B. & Hellqvist, C. 1993a. Induced and spontaneous attacks by pine shoot beetles on young Scots pine trees: tree mortality and beetle performances. *Journal of Applied Entomology*, 115, 25-36.
- Långström, B. & Hellqvist, C. 1993b. Scots pine susceptibility to attack by *Tomicus piniperda* (L) as related to pruning date and attack density. *Annales des Sciences forestières* 50, 101-17.
- Långström, B., Hellqvist C. & Ehnström B., 1999. Susceptibility of fire-damaged Scots pine (*Pinus sylvestris* L.) to attack by *Tomicus piniperda* L. In. *Physiology and Genetics of Tree-Phytophage Interactions*, F. Lieutier, W.J. Mattson, M.R. Wagner (Eds). Versailles: INRA Editions.
- Långström, B., Hellqvist, C., Ericsson, A. & Gref, D. 1992. Induced defence reaction in Scots pine following stem attacks by *Tomicus piniperda* L. *Ecography*, 15, 318-27.
- Långström B., Solheim, H., Hellqvist, C. & Gref, R. 1993. Effects of pruning young Scots pines on host vigour and susceptibility to *Leptographium wingfieldii* and *Ophiostoma minus*, two blue-stain fungi associated with *Tomicus piniperda*. *European Journal of Forest Pathology* 23, 400-15.
- Långström, B., Solheim, H., Hellqvist, C. & Krokene, P. 2001b. Host resistance in defoliated Scots pine: effects of single and mass inoculations using bark beetle-associated blue-stain fungi. *Agricultural and Forest Entomology* 3, 211-16.
- Lanz, W., Skwara, P. & Grodski, W. 1993. Bark beetle attack on immission-damaged Norway spruce stands in Silesia. *Allgemeine Forst Zeitschrift*, 48, 670-73.
- Larsson, S., Oren, R., Waring, R.H. & Barrett, J.W., 1983. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. *Forest Science*, 29, 395-402.
- Lévieux, J. Jactel, H. & Lieutier, F. 1988. Preliminary study of variability in sap pressure of Scots pine clones in central France. *Annales des Sciences Forestières*, 45, 341-55.
- Lieutier, F. 1992. Les réactions de défense des conifères et stratégies d'attaques de quelques Scolytides européens. *Mémoires de la Société Royale Belge d'Entomologie*, 35, 529-39.
- Lieutier, F. 1993. Induced defence reaction of conifers to bark beetles and their associated *Ophiostoma* species. In. *Ceratocystis and Ophiostoma. Taxonomy, Ecology, and Pathogenicity*, M.J. Wingfield, K.A. Seifert, J.F. Webber (Eds.). Saint Paul: APS Press.
- Lieutier, F. 1995. Associated fungi, induced reaction and attack strategy of *Tomicus piniperda* (Coleoptera: Scolytidae) in Scots pine. In. *Behavior, Population Dynamics and Control of Forest Insects*, F.P. Hain, S.M. Salom, W.F. Ravlin, T.L. Payne, K.F. Raffa (Eds.). Proceedings International Union Forestry Research Organizations Joint Conference, 1994 February 6-11, Maui, Hawaï.
- Lieutier, F. 2002. Mechanisms of resistance in conifers and bark beetle attack strategies. In. *Mechanisms and Deployment of Resistance in Trees to Insects*, M.R. Wagner, K.M. Clancy, F. Lieutier, T.D. Paine (Eds), Dordrecht, Kluwer.
- Lieutier, F. & Berryman, A.A. 1988. Preliminary histological investigations on the defence reactions of three pines to *Ceratocystis clavigera* and two chemical elicitors. *Canadian Journal of Forest Research*, 18, 1243-47.
- Lieutier, F., Berryman, A.A. & Millstein, J.A. 1991a. Preliminary study of the monoterpene response of three pines to *Ophiostoma clavigerum* (Ascomycetes: Ophiostomatales) and two chemical elicitors. *Annales des Sciences Forestières*, 48, 377-88.
- Lieutier, F., Brignolas, F., Picron, V., Yart A. & Bastien, C. 1996a. Can Phloem Phenols Be Used as Markers of Scots Pine Resistance to Bark Beetles ? In. *Dynamics of Forest Herbivory: Quest for Pattern and Principle*, W.J. Mattson, P. Niemela, M. Rousi (Eds.). USDA Forest Service General Technical Report NC-183.
- Lieutier F., Brignolas F., Sauvard D., Yart A., Galet C., Brunet M. & Van de Sype H., 2003a. Intra- and inter-provenance variability in phloem polyphenols of *Picea abies* (L.) KARST. and relation with resistance to a bark-beetle-associated fungus. *Tree physiology*, 23, 247-56.
- Lieutier, F., Brignolas, F., Yart, A., Grodski, W., Jakus, R. & Sauvard, D. 2003b. Field validation of phenolics as predictors of Norway spruce resistance to *Ips typographus* attacks during a finishing outbreak. IUFRO Working Party meeting "Forest Insect Population Dynamics and Host Influences", September 14-19, Kanazawa, Japan.
- Lieutier, F., Cheniclet, C. & Garcia, J. 1989a. Comparison of the defence reactions of *Pinus pinaster* and *Pinus sylvestris* to attacks by two bark beetles (Coleoptera: Scolytidae) and their associated fungi. *Environmental Entomology*, 18, 228-34.
- Lieutier, F., Faure, T. & Garcia, J. 1988a. Les attaques de Scolytes et le dépérissement du pin sylvestre en Provence - Côte d'Azur. *Revue forestière française*, 40, 224-32.

- Lieutier, F. & Ferrell, G.Y. 1988. Relationships between indexes of tree vigour and the induced defence reaction of Scots pine to a fungus associated with *Ips sexdentatus* Boern. (Coleoptera: Scolytidae). In: *Integrated control of scolytid bark beetles*, Payne, T.L., Saarenmaa, H. (eds), Proceedings of the IUFRO working party and XVII International congress of entomology symposium, Vancouver, B.C., Canada, July 4 1988.
- Lieutier, F., Garcia, J., Romary, P. & Yart, A. 1995. Wound reactions of Scots pine (*Pinus sylvestris* L.) to attacks by *Tomicus piniperda* L. and *Ips sexdentatus* Boern. (Coleoptera: Scolytidae). Journal of Applied Entomology, 119, 591-600.
- Lieutier, F., Garcia, J., Romary, P., Yart, A., Jactel, H. & Sauvard, D. 1993. Inter-tree variability in the induced defence reaction of Scots pine to single inoculations by *Ophiostoma brunneo-ciliatum*, a bark beetle-associated fungus. Forest Ecology and Management, 59, 257-70.
- Lieutier, F., Långström, B., Solheim, H., Hellqvist, C. & Yart, A. 1996b. Genetic and Phenotypic Variation in the Induced Reaction of Scots Pine, *Pinus Sylvestris* L., to *Leptographium Wingfieldii*: Reaction Zone Length and Fungal Growth . . In. *Dynamics of Forest Herbivory: Quest for Pattern and Principle*, W.J. Mattson, P. Niemela, M. Rousi (Eds.). USDA Forest Service General Technical Report NC-183.
- Lieutier, F., Sauvard, D., Brignolas, F., Picron, V., Yart, A., Bastien, C. & Jay-Allemand, C. 1996c. Changes in phenolic metabolites of Scots-pine phloem induced by *Ophiostoma brunneo-ciliatum*, a bark-beetle-associated fungus. European Journal of Forest Pathology, 26, 145-58.
- Lieutier, F., Vouland, G., Pettinetti, M., Garcia, J., Romary, P. & Yart, A. 1992. Defence reactions of Norway spruce (*Picea abies* Karst.) to artificial insertion of *Dendroctonus micans* Kug. (Col. Scolytidae). Journal applied Entomology, 114, 174-86.
- Lieutier, F., Yart, A., Garcia, J. & Ham, M-C. 1990. Cinétique de croissance des champignons associés à *Ips sexdentatus* Boern. et à *Tomicus piniperda* L. (Coleoptera: Scolytidae) et des réactions de défense des pins sylvestres (*Pinus sylvestris* L.) inoculés. Agronomie, 10, 243-56.
- Lieutier, F., Yart, A., Garcia, J., Ham, M-C., Morelet, M. & Lévieux, J. 1989b. Champignons phytopathogènes associés à deux coléoptères scolytidae du pin sylvestre (*Pinus sylvestris* L.) et étude préliminaire de leur agressivité envers l'hôte. Annales des Sciences Forestières, 46, 201-16.
- Lieutier, F., Yart, A., Garcia, J., Poupinel, B. & Lévieux, J. 1988b. Do Fungi Influence the Establishment of Bark Beetles in Scots Pine ? In. *Mechanisms of Woody Plant Defences Against Insects: Search for Pattern*, W.J. Mattson, J. Lévieux, C. Bernard-Dagan (Eds.). New York: Springer.
- Lieutier, F., Yart, A., Jay-Allemand, C. & Delorme, L. 1991b. Preliminary investigations on phenolics as a response of Scots pine phloem to attacks by bark beetles and associated fungi. European Journal of Forest Pathology, 21, 354-54.
- Lieutier, F., Yart A., Ye H., Sauvard D. & Gallois V. 2004. Between-isolate variations in the performances of *Leptographium wingfieldii* Morelet, a fungus associated with the bark beetle *Tomicus piniperda* L. Annals of Forest Sciences, in press.
- Lieutier, F., Ye, H. & Yart, A. 2003c. Shoot damage by *Tomicus* sp. (Coleoptera: Scolytidae) and effect on *Pinus yunnanensis* resistance to subsequent reproductive attacks on the stem. Agricultural and Forest Entomology 5, 227-33.
- Lombardero, M.J., Ayres, M.P., Lorio, P.L., Jr. & Ruel, J.J. 2000. Environmental effects on constitutive and inducible resin defences of *P. taeda*. Ecology Letters, 3, 329-339.
- Loomis, W.E. 1932. Growth-differentiation balance vs carbohydrate-nitrogen ration. Proceedings of the American Society of Horticultural Science, 29, 240-45.
- Lorio, P.L., Jr. 1986. Growth-differentiation balance: a basis for understanding southern pine beetle-tree interactions. Forest Ecology and Management, 14, 259-73.
- Lorio, P.L., Jr. & Hodges, J.D. 1968a. Oleoresin exudation pressure and relative water content of inner bark as indicators of moisture stress in loblolly pines. Forest Science, 14, 392-98.
- Lorio, P.L., Jr. & Hodges, J.D. 1968b. Microsite effect on oleoresin exudation pressure of large loblolly pines. Ecology, 49, 1207-10.
- Lorio, P.L., Jr. & Hodges, J.D. 1977. Tree water status affects induced southern pine beetle attacks and brood production. USDA Forest Service Research Paper SO-135.
- Lorio, P.L., Jr. & Sommers, R.A. 1986. Evidence for competition for photosynthates between growth processes and oleoresin synthesis in *Pinus taeda* L. Tree physiology, 2, 301-06.
- Lorio, P.L., Stephen, F.M. & Paine, T.D. 1995. Environment and ontogeny modify loblolly pine response to induced acute water deficits and bark beetle attacks. Forest Ecology and Management, 73, 97-110.

- Löyttyniemi, K. 1978. (In Finnish) Effect of forest fertilization on pine shoot beetles (*Tomicus* spp., Col., Scolytidae). *Folia Forestalia*, 348, 1-19.
- Martin, D., Tholl, D., Gershenson, J. & Bohlmann, J. 2002. Methyl jasmonate induces traumatic resin ducts, terpenoid resin biosynthesis and terpenoid accumulation in developing xylem of Norway spruce (*Picea abies*) stems. *Plant Physiology*, 129, 1003-18.
- Mason R.R. 1971. Soil moisture and stand density affect oleoresin exudation flow in a loblolly pine plantation. *Forest Science*, 17, 170-77.
- Matson, P.A., Hain, F.P. & Mawby, W. 1987. Indices of tree susceptibility to bark beetles vary with silvicultural treatment in a loblolly pine plantation. *Forest Ecology and Management* 22, 107-18.
- Mattson, W.J. & Haack, R.A. 1987. The role of drought in outbreaks of plant-eating insects. *Bioscience*, 37, 110-118.
- McMullen, L.H., Fiddick, R.L. & Wood, R.O. 1981. Bark beetles, *Pseudohylesinus* spp. (Coleoptera: Scolytidae), associated with amabilis fir defoliated by *Neodiprion* sp. (Hymenoptera: Diprionidae). *Journal of the Entomological Society of British Columbia* 78, 43-45.
- Mergen, F., Hoekstra, P.E. & Echols, R.M. 1955. Genetic control of oleoresin yield and viscosity in slash pine. *Forest Science*, 1, 19-30.
- Miller, P.R., Cobb, F.W., Jr. & Zavarin, E. 1968. Photochemical oxidant injury and bark beetles (Coleoptera: Scolytidae) infestation of ponderosa pine. III. Effect of injury upon oleoresin composition, phloem carbohydrates, and phloem pH. *Hilgardia*, 39, 135-40.
- Miller, R.H. & Berryman, A.A. 1986. Nutrient allocation and mountain pine beetle attack in girdled lodgepole pines. *Canadian Journal of Forest Research*, 16, 1036-40.
- Miller, R.H., Whitney, H.S. & Berryman, A.A. 1986. Effects of induced translocation stress and bark beetle attack (*Dendroctonus ponderosae*) on heat pulse velocity and the dynamic wound response of lodgepole pine (*Pinus contorta* var. *latifolia*). *Canadian Journal of Botany*, 64, 2669-74.
- Mitchell, R.G., Waring, R.H. & Pitman, G.B. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *Forest Science*, 29, 204-11.
- Moore, G.E. & Layman, H.F. 1978. Attempts to increase resistance of loblolly pines to bark beetles by fertilization. *USDA Forest Service Research Note SE-260*.
- Müllck, D.B. 1977. The non-specific nature of defence in bark and wood during wounding, insect, and pathogen attack. *Recent advances in phytochemistry*, 11, 359-441.
- Mulock, P. & Christiansen, E. 1986. The threshold of successful attack by *Ips typographus* on *Picea abies*: a field experiment. *Forest Ecology and Management*, 14, 125-132.
- Nageleisen, L.M. 2002. Le point sur les attaques des Scolytes des résineux en fin d'année 2001 suite aux tempêtes de décembre 1999 et les mesures de lutte mises en œuvre. *Les Cahiers du DSF*, 1-2002 [La Santé des Forêts (France) 2000, 2001], Ministère de l'Agriculture, de l'Alimentation, de la Pêche et des Affaires Rurales (DERF), Paris.
- Nageleisen, L.M. 2003. Le point sur les attaques des Scolytes des résineux en fin d'année 2002 suite aux tempêtes de décembre 1999 et les mesures de lutte mises en œuvre. *Les Cahiers du DSF*, sous presse ,Ministère de l'Agriculture, de l'Alimentation, de la Pêche et des Affaires Rurales (DERF), Paris
- Nagy, N.E., Franceschi, V.R., Solheim, H., Krekling, T. & Christiansen, E. 2000. Wound-induced traumatic resin duct development in stems of Norway spruce (Pinaceae): anatomy, and cytological traits. *American Journal of Botany*, 87,302-13.
- Nebeker, T.E., Hodges, J.D., Honea, C.R. & Blanche, C.A. 1988. Preformed Defensive System in Loblolly Pine: Variability and Impact on Management Practices . In. *Integrated Control of Scolytid Bark Beetles*, T.L. Payne, H. Saarenmaa (Eds.). Blacksburg, VA: Virginia Polytechnic Institute Press.
- Nebeker, T.E., Hodges, J.D., Blanche, C.A., Honea, C.R. & Tisdale, R.A., 1992. Variation in the constitutive defensive system of Loblolly pine in relation to bark beetle attack. *Forest Science*, 38, 457-66.
- Nihoul, D., Nef. & Waterkeyn, L. 1989. Variability between and within individuals in some anatomical characteristics of the bark of Norway spruce (*Picea abies*) in the Belgian Ardennes. *Annales des Sciences Forestières*, 46, 85-95.
- Paine T.D., 1984. Seasonal response of ponderosa pine to inoculation of the mycangial from the western pine beetle. *Canadian Journal of Botany*, 62, 551-55.
- Paine T.D. & Hanlon, C.C. 1994. Influence of oleoresin constituents from *Pinus ponderosa* and *Pinus jeffreyi* on the growth of the mycangial fungi from *Dendroctonus ponderosae* and *Dendroctonus brevicomis*. *Journal of Chemical Ecology*, 20, 2551-63.

- Paine, T.D., Raffa, K.F. & Harrington, T.C. 1997. Interactions among scolytids bark beetles, their associated fungi, and live host conifers. Annual Review of Entomology, 42, 179-206.
- Paine T.D., Stephen F.M. & Cates R.G., 1993. Within and among tree variation in the response of loblolly pine to a fungus associated with *Dendroctonus frontalis* (Coleoptera: Scolytidae) and sterile wounding. The Canadian Entomologist, 125, 65-71.
- Pesson, P. & Chararas, C. 1969. Les Scolytides, insectes ravageurs mondiaux des forêts de conifères. L'année biologique, 8, 683-733.
- Raffa, K.F. 1991. Induced defensive reactions in conifer-bark beetle systems. In: *Phytochemical induction by herbivores*, D.W. Tallamy, M.J. Raupp (Eds), Wiley & Sons, New York.
- Raffa, K.F. & Berryman, A.A. 1982a. Physiological differences between lodgepole pines resistant and susceptible to the mountain pine beetle and associated microorganisms. Environmental Entomology, 11, 486-92.
- Raffa, K.F. & Berryman, A.A., 1982b. Accumulation of monoterpenes and associated volatiles following fungal inoculation of grand fir with a fungus transmitted by the fir engraver *Scolytus ventralis* (Coleoptera: Scolytidae). The Canadian Entomologist, 114, 797-810.
- Raffa, K.F. & Berryman, A.A. 1983a. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Ecological Monographs, 53, 27-49.
- Raffa, K.F. & Berryman, A.A. 1983b. Physiological aspects of lodgepole pine wound responses to a fungal symbiont of the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). The Canadian Entomologist, 115, 723-34.
- Raffa, K.F., Berryman, A.A., Simasko J., Teal W. & Wong B.L. 1985. Effects of grant fir monoterpenes on the fire engraver, *Scolytus ventralis* (Coleoptera: Scolytidae), and its symbiotic fungus. Environmental Entomology, 14, 552-56.
- Raffa, K.F. & Klepzig, K.D. 1996. Effects of root inhabiting insect-fungal complexes on aspects of tree resistance to bark beetles. In: *Dynamics of forest herbivory: quest for pattern and principle*, W.J. Mattson, P. Niemela, M. Rousi (Eds), USDA Forest Service General Technical Report NC-183.
- Raffa, K.F., Krause, S.C. & Reich, P.B. 1998. Long term effects of defoliation on red pine suitability to insects feeding on diverse plant tissues. Ecology 79, 2352-64.
- Raffa, K.F. & Smalley, E.B. 1995. Interaction of pre-attack and induced monterpene concentrations in host conifer defence against bark beetle-fungal complexes. Oecologia, 102, 285-95.
- Rasmussen, L.A. 1987. Mountain pine beetle selection of dwarf mistletoe and Comandra blister rust infected lodgepole pine. USDA Forest Service Research Note INT-367.
- Rasmussen, L.A., Amman, G.D., Vandygriff, J.C., Oakes, R.D., Munson, A.S. & Gibson, K.E. 1996. Bark beetle and wood borer infestation in the greater Yellowstone area during four postfire years. USDA Forest Service Research Paper INT-RP-487.
- Reid, R.W. & Gates H. 1970. Effect of temperature and resin on hatch of eggs of the mountain pine beetle (*Dendroctonus ponderosae*). The Canadian Entomologist, 102, 617-22.
- Reid, R.W. & Shrimpton, D.M., 1971. Resistant response of lodgepole pine to inoculation with *Europodium clavigerum* in different months and at different heights on stem. Canadian Journal of Botany, 49, 349-51.
- Reid, R.W., Whitney, H.S. & Watson, J.A. 1967. Reactions of lodgepole pine to attack by *Dendroctonus ponderosae* Hopkins and blue stain fungi. Canadian Journal of Botany, 45, 115-26.
- Rudinsky, J.A. 1962. Ecology of Scolytidae. Annual Review Entomology, 7, 327-48.
- Rudinsky, J.A., 1966. Host selection and invasion by the Douglas fir beetle, *Dendroctonus pseudotsugae* Hopkins, in coastal Douglas-fir forests. The Canadian Entomologist, 98, 98-111.
- Ruel, J.J., Ayres, M.P. & Lorio, P.L., Jr. 1998. Loblolly pine responds to mechanical wounding with increased resin flow. Canadian Journal of Forest Research, 28, 596-602.
- Safranyik, L., Shrimpton, D.M. & Whitney, H.S. 1975. An interpretation of the interaction between lodgepole pine, the mounain pine beetle and its associated blue stain fungi in western Canada. In: *Management of Lodgepole Pine Ecosystems*, D. Baumgartner (Ed.), Pullman: Washington State University Cooperative Extension Service.
- Sandness, A. & Solheim, H., 2002. Variation in tree size and resistance to *Ceratocystis polonica* in a monoclonal stand of *Picea abies*. Scandinavian Journal of Forest Research, 17, 522-28.
- Santoro, A.E., Lombardero, M.J., Ayres, M.P. & Ruel, J.J. 2001. Interactions between fire and bark beetles in an old growth pine forest. Forest Ecology and Management, 144, 245-54.
- Schroeder, M. 1990. Duct resin flow in Scots pine to the attack of the bark beetle *Tomicus piniperda* L. (Col., Scolytidae). Journal of applied Entomology, 109, 105-12.

- Schwertfeger, F. 1944. *Die Waldkrankheiten. Ein Lehrbuch der Forstpathologie und des Forstschatzes.* XVI, 479 p.
- Shrimpton, D.M. 1973a. Extractives associated with wound response of lodgepole pine attacked by the mountain pine beetle and associated microorganisms. Canadian Journal of Botany, 51, 527-34
- Shrimpton, D.M., 1973b. Age- and size-related response of lodgepole pine to inoculation with *Europhium clavigerum*. Canadian Journal of Botany, 51, 1155-60.
- Shrimpton, D.M. & Whitney H.S. 1968. Inhibition of growth of blue stain fungi by wood extractives. Canadian Journal of Botany, 46, 757-61.
- Showalter, T.D. & Turchin, P. 1993. Southern pine beetle infestation development: interaction between pine and hardwood basal area. Forest Science, 39, 201-10.
- Smith, R.H. 1963. Toxicity of pine resin vapors to 3 species of *Dendroctonus* bark beetles. Journal of Economic Entomology, 56, 827-31.
- Solheim, H. & Långström B. 1991. Blue stain fungi associated with *Tomicus piniperda* in Sweden and preliminary observation on their pathogenicity. Annales des Sciences forestières, 48, 149-56.
- Solheim, H., Långström, B. & Hellqvist, C. 1993. Pathogenicity of the blue-stain fungi *Leptographium wingfieldii* and *Ophiostoma minus* to Scots pine: effect of the tree pruning and inoculum density. Canadian Journal of Forest Research, 23, 1438-43.
- Stark, R.W., Miller, P.R., Cobb, F.W., Jr., Wood, D.L. & Parmeter, J.R., Jr. 1968. Photochemical oxidant injury and bark beetles (Coleoptera: Scolytidae) infestation of ponderosa pine. I. Incidence of bark beetle infestation in injured trees. Hilgardia, 39, 121-26.
- Steele, C.L., Lewinsohn, E. & Croteau, R. 1995. Induced oleoresin biosynthesis in grand fir as a defence against bark beetles. Proceedings National Academy of Sciences USA, 92, 4164-68.
- Stephen F.M., Paine T.D., 1985. Seasonal patterns of host resistance to fungal associates of the southern pine beetle. Zeitschrift für Angewandte Entomologie, 99, 113-22.
- Storer, A.J. & Speight, M.R. 1996. Relationships between *Dendroctonus micans* Kug. (Coleoptera: Scolytidae) survival and development and biochemical changes in Norway spruce, *Picea abies* (L.) Karst., phloem caused by mechanical wounding. Journal of Chemical Ecology, 22, 559-73.
- Thalenhorst W., 1958. Grundzüge der populationsdynamik des grössten Fichten-borkenkäfer *Ips typographus* L. Schriftenreihe der Forstlichen Fakultät der Universität Göttingen, 21.
- Tisdale, R.A. & Nebeker, T.E. 1992. Resin flow as a function of height along the bole of loblolly pine. Canadian Journal of Botany, 70, 2509-11.
- Tkacz, B.M. & Schmitz, R.F. 1986. Association of an endemic mountain pine beetle population with lodgepole pine infected by *Armillaria* root disease in Utah. USDA Forest Service Research Note INT-353.
- Tobolski, J.J. & Hanover, J.W., 1971. Genetic variations in the monoterpenes of Scotch pine. Forest Science, 17, 293-99.
- Tuomi, J., Fagerstrom, T. & Niemela, P. 1991. Carbon allocation, phenotypic plasticity, and induced defences. In: *Phytochemical induction by herbivores*, D.W. Tallamy, M.J. Raupp (Eds), Wiley & Sons, New York.
- Vetrova, V.P., Stasova, V.V. & Pashenova, N.V. 1999. Effect of defoliation on resistance response of *Abies sibirica* Ledeb. to inoculation with blue-stain fungi. In: *Physiology and genetics of tree phytophage interactions*, F. Lieutier, W.J. Mattson, M.R. Wagner (Eds), INRA, Versailles.
- Viiri, H., Annila, E., Kitunen, V. & Niemela, P. 2001. Induced responses in stilbenes and terpenes in fertilized Norway spruce after inoculation with blue-stain fungus, *Ceratocystis polonica*. Trees, 15, 112-22.
- Viiri, H., Kytö & Niemela, P. 1999. Resistance of fertilized Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.). In: *Physiology and Genetics of Tree-Phytophage Interactions*, F. Lieutier, W.J. Mattson, M.R. Wagner (Eds). Versailles: INRA Editions.
- Vité, J.P., 1961. The influence of water supply on oleoresin exudation pressure and resistance to bark beetle attack in *Pinus ponderosa*. Contribution Boyce Thompson Institute, 21, 37-66.
- Vité, J.P. & Wood, D.L. 1961. A study of the applicability of the measurement of oleoresin exudation pressure in determining susceptibility of second-growth ponderosa pine to bark beetle infestation. Contribution Boyce Thompson Institute, 21, 67-78.
- Vouland, G. 1991. Le Dendroctone de l'Epicea: *Dendroctonus micans* Kug. (Col.: Scolytidae) dans le Massif Central. Thèse Université Aix-Marseille III.
- Wainhouse, D., Cross, D.J. & Howell, R.S. 1990. The role of lignin as a defence against the spruce bark beetle *Dendroctonus micans*: effects on larvae and adults. Oecologia 85, 257-65.

- Wainhouse, D., Ashburner, R., Ward, E. & Boswell, R. 1997. The effect of lignin and bark wounding on susceptibility of spruce trees to *Dendroctonus micans*. *Journal of Chemical Ecology* 24, 1551-61.
- Wainhouse, D., Rose, D.R. & Pearce, A.J. 1998a. The influence of preformed defences on the dynamic wound response in Spruce bark. *Functional Ecology* 11, 564-72.
- Wainhouse, D., Ashburner, E., Ward, E. & Rose, J. 1998b. The effect of variation of light and nitrogen on growth and defence in young Sitka spruce. *Functional Ecology*, 12, 561-72.
- Wallin, K.F., Kolb, T.E., Skov, K.R. & Wagner, M.R. 2003. Effects of scorch on ponderosa pine resistance to bark beetles in northern Arizona. *Environmental Entomology*, 32, 652-61.
- Wallin, K.F. & Raffa, K.F. 1999. Altered constitutive and inducible phloem monoterpenes following natural defoliation of Jack pine: implications to host mediated interguild interactions and plant defence theories. *Journal of Chemical ecology* 25, 861-80.
- Wallin, K.F. & Raffa, K.F. 2001. Effects of folivory on subcortical plant defences: can defence theories predict interguild processes? *Ecology*, 82, 1387-1400.
- Waring, R.H. & Pitman, G.B. 1983. Physiological stress in lodgepole pine as a precursor for mountain pine beetle attack. *Zeitschrift für angewandte Entomologie*, 96, 265-70.
- Waring, R.H. & Pitman, G.B. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* 66, 889-97.
- Warren, J.M., Allen, H.L. & Booker, F.L. 1999. Mineral nutrition, resin flow and phloem phytochemistry in loblolly pine. *Tree Physiology*, 19, 655-63.
- Wong, B.L. & Berryman, A.A. 1977. Host resistance to the fir engraver beetle. 3. Lesion development and containment of infection in resistant *Abies grandis* inoculated with *Trichosporium symboticum*. *Canadian Journal of Botany*, 55, 1358-65.
- White, T.C.R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed foods. *Oecologia*, 63, 90-105.
- Wilkinson, R.C. 1979. Tunnelling in slash pine by *Ips calligraphus* (Germ.). *Florida Entomologist*, 62, 72-73.
- Witanachchi, J.P. & Morgan, F.D. 1981. Behavior of the bark beetle, *Ips grandicollis*, during host selection. *Physiological Entomology*, 6, 219-23.
- Wright, L.C., Berryman, A.A. & Gurusiddaiah, S. 1979. Host resistance to the fir engraver beetle, *Scolytus ventralis* (Coleoptera: Scolytidae) 4. Effect of defoliation on wound monoterpene and inner bark carbohydrate concentrations. *Canadian Entomologist* 111, 1255-62.
- Wright, L.C., Berryman, A.A. & Wickman, B.E. 1984. Abundance of the fir engraver, *Scolytus ventralis*, and the Douglas-fir beetle, *Dendroctonus pseudotsugae*, following tree defoliation by the Douglas-fir tussock moth, *Orgyia pseudotsugata*. *Canadian Entomologist* 116, 293-305.
- Ye, H. & Lieutier, F. 1997. Shoot aggregation by *Tomicus piniperda* (Col; Scolytidae) in Yunnan, southwestern China. *Annales des Sciences Forestières*, 54, 635-41.
- Ye H. & Lieutier F. 2001. Seasonal variations in *Pinus yunnanensis* natural resistance to artificial fungus inoculation, in relation with water stress. Final plenary workshop of the EU project ERBIC 18CT96 0057 "Definition of methods to protect conifers from insects compromising forest survival and regeneration in the mountain areas of Southwestern China". 27-31 May. Lijiang, China.

Chapter 10

FUNGAL ASSOCIATES OF EUROPEAN BARK BEETLES WITH SPECIAL EMPHASIS ON THE OPHIOSTOMATOID FUNGI

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1. INTRODUCTION

Fungi are common and well-known associates of bark beetles (Coleoptera: Scolytidae). The relationship between fungi and scolytids was recognized relatively long ago. Schmidberger (1836) described an “ambrosia” in the galleries of the wood-inhabiting bark beetle *Xyleborus dispar*, and Hartig (1844) discovered the fungal nature of this “ambrosia” lining the tunnels of the insects. Likewise, Hartig (1878) first recognized the interrelationships between insect damage, discoloration of wood and fungi, and during his studies on blue-stain in the sapwood of conifers, Münch (1907, 1908) observed that blue-stain in living trees and lumber is associated with attack by bark beetles. Since these early discoveries a large number of investigations on various aspects of the association of fungi with bark beetles have been carried out.

Scolytids are among the most economically important pests of the world’s forests, especially conifer forests in the boreal and temperate regions of the Northern hemisphere (Postner 1974; Schwerdtfeger 1981; Wood 1982; Wood and Bright 1992). A considerable number of fungal associates of bark beetles are known as forest pathogens in their own right, causing vascular wilt or vascular stain diseases (Webber and Gibbs 1989; Harrington 1993a, 1993b; Wingfield *et al.* 1993). Many other species give rise to discoloration in the sapwood of conifers and cause enormous losses to forestry and wood industry worldwide (Whitney 1982; Seifert 1993; Butin 1996).

Although the association between scolytids and fungi has been recognised for more than one century, many fundamental aspects of this relationship are still poorly

known. A key question pertaining to the symbiosis between bark beetles and fungi is that regarding the degree of dependence of the partners on each other. Many fungi are totally dependent on their associated insects for dissemination and they have not been found outside the bark beetle habitat (Mathiesen-Käärik 1953; Francke-Grosmann 1967; Whitney 1982; Kirschner 1998; Six 2003). Similarly, one group of scolytids, the ambrosia beetles, are obligatorily dependant on certain fungi, the ambrosia fungi, for nutrition (Francke-Grosmann 1967; Postner 1974; Norris 1979; Beaver 1989). However, the role of fungi associated with bark beetles that colonize the phloem of trees has been the subject of considerable debate, and arguments exist both for and against the view that the insects and the fungi they carry are mutualists (e. g. Francke-Grosmann 1967; Whitney 1982; Christiansen *et al.* 1987; Harding 1989; Harrington 1993a; Wingfield *et al.* 1995; Krokene 1996; Paine *et al.* 1997).

In this chapter a synthesis of the knowledge regarding the association of fungi with bark beetles is presented. This synthesis will focus on European scolytids and it deals mainly with fungal associates of conifer bark beetles. This is because they have been most intensively studied, in contrast to scolytids on hardwoods where much less knowledge is available. This review also highlights the ophiostomatoid fungi which include the ascomycete genera *Ceratocystis*, *Ceratocystiopsis* and *Ophiostoma* and related anamorph genera, causing tree diseases and blue-stain on trees and lumber. Fungal pathogens of bark beetles are treated by Wegensteiner (chapter 12) and are thus excluded here.

2. OVERVIEW OF THE ASSOCIATION OF FUNGI WITH BARK BEETLES IN RELATION TO BARK BEETLE ECOLOGY

The large majority of bark beetle species fulfil most of their life cycle in the wood or secondary phloem underneath the bark of conifer and deciduous trees (Postner 1974; Schwerdtfeger 1981; Wood 1982; Wood and Bright 1992; Pfeffer 1995). Two major groups, ambrosia beetles and phloeophagous bark beetles, are commonly distinguished based on their habitats and larval feeding habits (Francke-Grosmann 1966, 1967; Postner 1974; Beaver 1989; Wood 1982; Pfeffer 1995). These two groups differ greatly in their nutrition biology and also show fundamental differences in their association with fungi. Another group, the phloeomycetophagous bark beetles that feed both on phloem and on associated fungi are also considered (Francke-Grosmann 1952, 1966, 1967; see below and 6.2.2.).

One group of bark beetles, termed "ambrosia beetles" or "xylomycetophagous bark beetles" breeds in the wood of trees (Francke-Grosmann 1966, 1967; Postner 1974; Beaver 1989; Pfeffer 1995). The ambrosia beetles also include the platypodid beetles (Coleoptera: Platypodidae) with only one species, *Platypus cylindrus* occurring in Europe (Postner 1974; Pfeffer 1995). Wood is a poor substrate for nutrition of insects, since they are not able to digest lignin, cellulose and hemicelluloses, which are the main constituents of the xylem (Francke-Grosmann 1967; Graham 1967; Beaver 1989). Ambrosia beetles have overcome this problem through ectosymbiosis with nutritionally obligate fungi (Francke-Grosmann 1966, 1967; Graham 1967; Postner 1974; Beaver 1989; Berryman 1989; Six 2003). The

larvae of ambrosia beetles feed on specific fungi, known as "ambrosia fungi" that are transported to newly colonised trees and cultivated by the adult insects. Although ambrosia beetles can sometimes attack and kill living trees they usually breed on dying or recently killed trees and fresh logs and degrade timber (Postner 1974; Schwerdtfeger 1981).

The second, much larger group of bark beetles lives in the phloem of hardwood and conifer trees. They are referred to as "phloeophagous", "phloem-feeding" or "true bark beetles" (Postner 1974; Schwerdtfeger 1981; Wood 1982; Wood and Bright 1992; Pfeffer 1995). Phloem provides a nutrient-rich source of nutrition for the insects and in contrast to ambrosia beetles most phloem-feeding bark beetles are most likely not dependent on their fungal associates for nutrition (Francke-Grosmann 1967; Whitney 1982; Harding 1989). However, phloem-feeding bark beetles are commonly associated with various fungi, in particular blue-stain fungi belonging to the ascomycete genera *Ophiostoma* and *Ceratocystis* and their anamorphs (e. g. Mathiesen-Käärik 1953; Francke-Grosmann 1967; Whitney 1982; Beaver 1989; Raffa and Klepzig 1992; Krokene 1996; Paine *et al.* 1997; Kirschner 1998; Jacobs and Wingfield 2001; Six 2003).

Some phloem-feeding bark beetles, especially on conifers, are amongst the most economically important forest pests. Under certain circumstances these scolytids attack living trees and cause long-lasting and destructive outbreaks. In Europe, *Ips typographus* on Norway spruce is considered as the most aggressive and most economically important bark beetle species (Christiansen and Bakke 1988), but there are also many other scolytids that cause considerable damage to European forestry (Postner 1974; Schwerdtfeger 1981)

In order to utilize living trees for breeding, bark beetles must overcome the tree's defence systems and kill their hosts (Postner 1974; Christiansen *et al.* 1987; Raffa and Klepzig 1992; Krokene 1996; Paine *et al.* 1997; Lieutier 2002 and chapter 9). Overcoming the resistance of the host tree is accomplished by a co-ordinated mass attack of many individuals, which exhausts the anatomical and biochemical host defenses and is followed by tree death (Christiansen *et al.* 1987; Raffa and Klepzig 1992; Lieutier 2002 and chapter 9). For bark beetle species that attack living trees and kill them by this "cooperative strategy" (Lieutier 2002 and chapter 9) the association with pathogenic blue-stain fungi has always been suspected to be of great significance (Berryman 1972; Whitney 1982; Christiansen *et al.* 1987; Raffa and Klepzig 1992; Krokene 1996; Paine *et al.* 1997; Lieutier 2002 and chapter 9). Associated blue-stain fungi might help their insect vectors to overcome and kill their host trees by contributing to exhaust the tree's defense mechanisms (see 3.3.1. and 6.2.1.; Lieutier chapter 9). Among true bark beetles in Europe, one species, *Dendroctonus micans* is unusual, because it individually attacks trees and behaves like a true parasite that initially does not kill its host (Gregoire 1988; Lieutier 2002 and chapter 9). As part of the solitary, "defence-avoiding attack strategy" (Lieutier 2002 and chapter 9), associated blue-stain fungi do not play an important role in the successful breeding of *D. micans* in living trees (Lieutier *et al.* 1992; Lieutier 2002 and chapter 9).

Despite the traditional distinction between xylomycetophagous and phloeophagous bark beetles, some species seem to be intermediate between these

two groups. In Europe, two species on pine, *Tomicus minor* and *Ips acuminatus* share characteristics of both mycetophagous and phloeophagous scolytids and one may best refer to them as phloeomyctophagous bark beetles (Francke-Grosmann 1952, 1966, 1967; see 6.2.2.). Consequently, they are regularly associated with *Ambrosiella* species that are typical ambrosia fungi of xylomycetophagous scolytids and with blue-stain fungi in the genus *Ophiostoma* that are common associates of phloeophagous bark beetles (Mathiesen-Käärik 1953; Francke-Grosmann 1952, 1967).

One form of behaviour in some phloem-feeding bark beetles has important consequences regarding the transmission of virulent forest pathogens. Elm bark beetles in the genus *Scolytus* fulfil their maturation feeding requirements on twig crotches in the crown of trees and this leads to efficient transmission of the Dutch elm disease pathogens *Ophiostoma ulmi* and *Ophiostoma novo-ulmi* from diseased to healthy elm trees (Postner 1974; Webber and Brasier 1984; Webber and Gibbs 1989). *Scolytus intricatus* on *Quercus* spp. shows a similar behaviour and might thus be an efficient vector of the oak wilt pathogen *Ceratocystis fagacearum*, if it were accidentally introduced from North America into Europe (Webber and Gibbs 1989).

3. TAXONOMY, BIOLOGY AND ECOLOGY OF FUNGI ASSOCIATED WITH BARK BEETLES

Fungi associated with bark beetles have been grouped based on various characteristics. They have been classified as mycangial or non-mycangial, describing whether they are disseminated in mycangia (see 4.) or not (Paine *et al.* 1997; Six 2003). The term "ambrosia fungi" is used for those fungal associates of ambrosia beetles, which are cultivated in the galleries of the insects and on which the beetles depend for nutrition (Francke-Grosmann 1967; Norris 1979; Beaver 1989). Both classifications refer to the ecology of the fungi, but do not consider their taxonomy. The various fungi associated with bark beetles belong to the yeasts (3.1.), basidiomycetes (3.2.), ascomyctes (3.3.) and anamorphic fungi without sexual states (3.4.). Zygomycetes have occasionally also been reported as associates of bark beetles (Whitney 1982; Harding 1989; Kirschner 1998; Jankowiak 2004), but they are casual and inconsistent elements in this ecological niche and will not be treated in detail here.

3.1. Yeasts

Yeasts are commonly associated with phloeophagous bark and ambrosia beetles (Grosmann 1931; Siemaszko 1939; Callaham and Shifrine 1960; Francke-Grosmann 1967; Zimmermann 1973; Whitney 1971, 1982; Bridges *et al.* 1984; Harding 1989; Leufvén and Nehls 1986; Furniss *et al.* 1990; Six 2003). Very little is known about the taxonomy of yeasts associated with scolytids, the species assemblages occurring with bark beetles and the effects of yeasts on the insects. Taxonomically, all yeasts associated with bark beetles probably belong to the ascomyctes (Six 2003).

In many studies on the mycobiota of bark beetles yeasts have been recorded, but their identity has only rarely been determined (e. g. Grosmann 1931; Bramble and Holst 1940; Callaham and Shiffrine 1960; Zimmermann 1973; Bridges *et al.* 1984; Leufvén and Nehls 1986; Furniss *et al.*, 1990; Solheim 1992b; Krokene 1996; Six 2003). Species that are associated with ambrosia beetles have occasionally been reported as ambrosia fungi, thus being nutritionally important for the insects (Francke-Grosmann 1967). They are also suspected to be nutritionally important for phloeo-phagous bark beetles (Whitney 1982; Strongman 1986; Pignal *et al.* 1988; Harding 1989). Yeasts have been isolated from the outer surface of adult beetles and their immature stages as well as from the digestive tracts of larvae and mature insects (Grosmann 1931; Leufvén and Nehls 1986; Furniss *et al.* 1990; Six 2003). They are also common in the breeding galleries and pupal chambers of bark beetles (Bridges *et al.* 1984). In early stages of the breeding development of bark beetles, yeasts are among the most frequent micro-organisms that can be isolated from the phloem and xylem adjacent to the insect galleries (Bramble and Holst 1940; Käärik 1975; Bridges *et al.* 1984; Kirisits 1996), but they do not display pathogenicity to their host trees (Callaham and Shiffrine 1960). In isolations directly from bark beetles, yeasts occur more frequently than the blue-stain fungi, while the opposite is true for isolations from the wood of bark beetle-infested trees (Furniss *et al.* 1990; Solheim 1992b).

Individual bark beetle species often carry not only one, but two or several yeast taxa (Callaham and Shiffrine 1960; Whitney 1982; Leufvén and Nehls 1986; Six 2003). The yeasts associated with bark beetles are relatively unspecific and one fungal species is usually associated with several insect species (Callaham and Shiffrine 1960; Six 2003). Most bark beetle-associated yeasts belong to the genera *Candida*, *Pichia*, *Hansenula*, *Saccharomyces* and *Cryptococcus* (Callaham and Shiffrine 1960, Whitney 1982; Leufvén & Nehls 1986; Harding 1989; Six 2003). The most detailed study on yeasts associated with bark beetles in Europe was carried out by Leufvén and Nehls (1986) who studied the yeasts occurring with *I. typographus*. At least six different yeasts were recorded, with *Hansenula holstii* and *Candida diddensii* type yeasts being most prevalent (Leufvén and Nehls 1986).

3.2. Basidiomycetes

Basidiomycetes have only occasionally been mentioned as associates of bark beetles (Siemaszko 1939; Whitney 1982; Klepzig *et al.* 2001a, 2001b; Six 2003), but their diversity in this habitat may have been underestimated thus-far (Kirschner 1998, 2001). In Europe, *Gloeocystidium ipidophilum* was described from galleries of *I. typographus* on Norway spruce in Poland (Siemaszko 1939). This fungus was not mentioned again for a long time, but it was recently also found in Germany (Kirschner 1998) Poland (Jankowiak 2004) and Austria (Grubelnik 1998), in the same niche as the one originally reported for it. A hymenomycete similar, but not identical to *G. ipidophilum* was isolated from the sapwood of *Picea abies* infested by *I. typographus* in Norway (Solheim 1992b). *Heterobasidion annosum*, the causal agent of Annosum root rot (Butin 1996) has occasionally been found to be

associated with bark and ambrosia beetles on conifers (Bakshi 1950; Harding 1989; Kirschner 1998). The vector relationships between bark beetles and *H. annosum* are likely only casual.

Recently, knowledge on the association of basidiomycetes with bark beetles in Europe has been improved by Kirschner (1998, 2001) who isolated 20 kryptic basidiomycetes from the insects or from bark beetle galleries. Most of these basidiomycetes represent new taxa and at least some of them are suspected to be consistently associated with bark beetles. Their trophic roles may be diverse, and many of these newly detected basidiomycetes are likely mycoparasites or mycophilous fungi (Kirschner 1998). A few North American bark beetle species, particularly *Dendroctonus* species and *Ips avulsus* appear to be intimately associated with basidiomycetes, which is in contrast to the situation in Europe (Six 2003 and references therein). These basidiomycetes belong to the genus *Entomocorticium*, including five species known to be associated with bark beetles (Whitney *et al.* 1987; Klepzig *et al.* 2001a, 2001b; Six 2003 and references therein).

3.3. Filamentous ascomycetes

Filamentous ascomycetes have long been known as common associates of bark beetles. Fungi belonging to the genera *Ceratocystis*, *Ceratocystiopsis* and *Ophiostoma* are the most prevalent and most important associates of phloeoophagous bark beetles and they are also known to occur in the galleries of wood-inhabiting scolytids (Mathiesen-Käärik 1953; Francke-Grosmann 1967; Zimmermann 1973; Upadhyay 1981; Whitney 1982; Wingfield *et al.* 1993; Krokene 1996; Paine *et al.* 1997; Kirschner 1998; Six 2003). These principal fungal associates of phloem feeding bark beetles have received most attention, which is not surprising considering their economic importance as tree pathogens and agents of sapstain. However, it is worth mentioning that diverse assemblages of other ascomycetes with various tropic roles are associated with bark beetles, some of which seem to have a consistent relationship with the insects (Kirschner 1998, Malloch and Blackwell 1993). In this review, I focus on the ophiostomatoid fungi and refer to Kirschner (1998, 2001) and Malloch and Blackwell (1993) for an overview of other ascomycetes associated with bark beetles.

3.3.1 The ophiostomatoid fungi

Together with other ascomycetes, *Ophiostoma*, *Ceratocystis* and *Ceratocystiopsis* as well as related asexual fungi in the genera *Leptographium*, *Pesotum*, *Hyalorhinocladiella*, *Sporothrix* and *Thielaviopsis* are known as the “ophiostomatoid fungi” (Wingfield *et al.* 1993). This common name was introduced in the 1990s taking the similarities of these fungi into account. Ophiostomatoid fungi associated with bark beetles are also commonly known as “blue-stain fungi”, referring to the damage these fungi cause, namely blue, gray, brown or even black discoloration of the sapwood of trees, mostly on conifers (Münch 1907; Lagerberg *et al.* 1927; Seifert 1993; Butin 1996; Fig. 1).



Figure 1. Blue-stain in the sapwood of Norway spruce infested by the bark beetle *Ips typographus*.

Blue-stain is considered as serious problem in conifer trees (Seifert 1993; Butin 1996), however, hardwoods are also affected (Butin and Zimmermann 1972; Kowalski and Butin 1989; Kowalski 1991; Seifert 1993). On hardwoods, these fungi more often cause vascular wilt and vascular stain diseases (Kile 1993; Harrington 1993; Brasier 2000). Sap stain is caused by fungal hyphae, which are concentrated in the ray parenchyma cells and resin ducts of infected sapwood (Münch 1907; Liese and Schmid 1961; Ballard *et al.* 1984; Seifert 1993; Gibbs 1993). Tracheids are also colonized, especially at later stages of infection (Liese and Schmid 1961; Ballard *et al.* 1982; Seifert 1993; Gibbs 1993).

Blue-stain fungi utilise assimilates stored in the living ray parenchyma cells of the sapwood (Seifert 1993; Butin 1996). In contrast to decay fungi, they do not decompose the structural components of the wood (cellulose, lignin and hemicelluloses) (Münch 1908; Seifert 1993). The moisture content of the sapwood is important for the development of blue-stain. Most blue-stain fungi grow at moisture content between 30-40 % and 130-140 % of the dry weight, with different fungal species having different requirements (Münch 1908; Lagerberg *et al.* 1927; Butin 1996). Pathogenic blue-stain fungi that cause stain in living trees are able to infect fresh sapwood with high moisture content and low oxygen levels (Münch 1908; Lagerberg *et al.* 1927; Scheffer 1986; Solheim 1991).

Taxonomy of the phiomatoid fungi. *Ophiostoma* and *Ceratocystis* have many morphological characters in common, including perithecia with globose or pear-shaped bases and long perithecial necks (Fig. 2), evanescent ascii and hyaline, one-celled, small ascospores, which vary in their shape and possess or lack sheaths (Hunt 1956; Upadhyay 1981; De Hoog and Scheffer 1984; Wingfield *et al.* 1993;

Harrington and Wingfield 1998; Jacobs and Wingfield 2001). Based on their similarities *Ophiostoma* and *Ceratocystis* have been considered as synonyms for long periods of their taxonomic history. The third related genus, *Ceratocystiopsis* forms a morphologically well-defined group and is characterised by an unique combination of features, namely relatively small ascocarps, short perithecial necks with convergent ostiolar hyphae and sickle-shaped, sheathed ascospores (De Hoog and Scheffer 1984; Upadhyay and Kendrick 1975; Upadhyay 1981; Wingfield 1993). There are, however, various arguments relating to whether these fungi should be treated together with *Ophiostoma*.

It is now widely accepted that *Ceratocystis* is not closely related to *Ophiostoma* and *Ceratocystiopsis*, despite the similarities in their perithecial characteristics (De Hoog and Scheffer 1984; Wingfield *et al.* 1993; Jacobs and Wingfield 2001). Phylogenetic studies based on analyses of the rDNA sequence data placed *Ophiostoma* in a monophyletic group close to the Diaporthales, while *Ceratocystis* is closely related to taxa in the Microascales (Spatafora and Blackwell 1993; Hausner *et al.* 1993b; Paulin-Mahady *et al.* 2002). *Ceratocystiopsis*, though morphologically well defined, groups phylogenetically together with *Ophiostoma* and these genera have thus been synonymized (Hausner *et al.* 1993a). However, *Ceratocystiopsis* is still widely used as genus name and it is also treated as separate from *Ophiostoma* in the present review.



Figure 2. Perithecia of *Ceratocystis polonica*.

The similar ascocarps of *Ceratocystis*, *Ophiostoma* and *Ceratocystiopsis* evolved separately from each other, likely as adaptions to the bark beetle habitat. Besides molecular markers the separation of *Ceratocystis* from *Ophiostoma* and *Ceratocystiopsis* is supported by several lines of evidence. Most distinctively, these genera can be differentiated based on their asexual stages. *Ceratocystis* species have *Thielaviopsis* anamorphs (De Hoog and Scheffer 1984; until very recently known as

Chalara, Paulin-Mahady *et al.* 2002), with endogenous conidium development by “ring wall building” (Minter *et al.* 1983). In contrast, asexual stages of *Ophiostoma* belong to a variety of hyphomycete genera including *Leptographium*, *Pesotum* (until recently known as *Graphium*; Okada *et al.* 1998, 2000), *Sporothrix* and *Hyalorhinocladiella* (De Hoog and Scheffer 1984), and conidium development is always exogenic by “apical wall building” (Minter *et al.* 1982). Similarly, *Ceratocystiopsis* spp. have *Hyalorhinocladiella* and *Sporothrix* anamorphs, but not *Leptographium* and *Pesotum* states (Upadhyay 1981; De Hoog and Scheffer 1984; Wingfield 1993). Other than these characteristics *Ophiostoma* and *Ceratocystiopsis* are very similar, if not identical (De Hoog and Scheffer 1984; Wingfield 1993), and therefore, subsequent discussion will deal with *Ophiostoma* as including *Ceratocystiopsis*. There are also differences between *Ophiostoma* and *Ceratocystis* in the development of the ascospores and the arrangement and organisation of the asci in the peritheciium (Van Wyk and Wingfield 1990; Van Wyk *et al.* 1993).

Species of *Ophiostoma* and *Ceratocystis* also differ in the chemical composition of their cell walls (De Hoog and Scheffer 1984 and references therein). *Ophiostoma* spp. are unusual within the ascomycetes, since their cell walls contain besides chitin also cellulose and rhamnose (De Hoog and Scheffer 1984). In contrast, the cell walls of *Ceratocystis* consist mainly of chitin and do not contain any detectable amounts of cellulose and rhamnose (De Hoog and Scheffer 1984). In addition, *Ophiostoma* and *Ceratocystis* differ in their tolerance to the antibiotic cycloheximide that inhibits the protein synthesis in most eucaryotic organisms (Harrington 1981). While *Ceratocystis* is very sensitive to even low concentrations of cycloheximide, species of *Ophiostoma* tolerate high concentrations of this antibiotic (Harrington 1981; De Hoog and Scheffer 1984).

Ecology of the ophiostomatoid fungi. *Ceratocystis* and *Ophiostoma* also display differences in their ecology and their relationships with insects (Harrington 1987, 1993a; Kile 1993). *Ceratocystis* species colonize a variety of herbaceous and woody plants (Kile 1993). Many species are distributed in subtropical and tropical regions of the world and some others occur on woody plants in temperate and boreal regions, causing blue-stain in the sapwood of conifers (Harrington 1987; Kile 1993; Harrington and Wingfield 1998). Apart from bark beetles, a wide variety of insects such as flies (Diptera) or nitidulid beetles (Nitidulidae) are known as vectors of *Ceratocystis* spp. (Harrington 1987). Generally, *Ceratocystis* species have a relatively loose and unspecific relationship with insects. This is exemplified by the causal agent of oak wilt in North America, *C. fagacearum*, which is transmitted at low frequencies by nitidulid beetles (Juzwik and French 1983). However, there are also exceptions to this characteristic. There are three *Ceratocystis* species, which are consistently associated with conifer bark beetles (Solheim 1986; Redfern *et al.* 1987; Wingfield *et al.* 1997; Harrington and Wingfield 1998). Intriguingly, these three species are relatively virulent pathogens (Christiansen 1985; Redfern *et al.* 1987; Harrington and Wingfield 1998; Solheim and Safranyik 1997; Yamaoka *et al.* 1997; 1998).

Species of *Ophiostoma* and *Ceratocystiopsis* and their anamorphs are, in contrast to *Ceratocystis* spp., mainly distributed in temperate and boreal regions of the Northern hemisphere (Harrington 1987, 1993a; Jacobs and Wingfield 2001). Most of these fungi live in the phloem and in the sapwood of conifers and hardwoods and they rarely occur on other substrates such as herbaceous plants (Hunt 1956; Upadhyay 1981; Jacobs and Wingfield 2001). *Ophiostoma* spp. are predominantly known as fungal associates of phloeophagous bark beetles, with which they often form intimate and relatively specific relationships (Mathiesen-Käärik 1953; Whitney 1982; Paine *et al.* 1997; Kirschner 1998; Jacobs and Wingfield 2001). *Ophiostoma* species also occur in association with ambrosia beetles (Bakshi 1950; Mathiesen-Käärik 1953; Zimmermann 1973; Kirschner 1998), cerambycid beetles (Mathiesen-Käärik 1953; Jacobs and Wingfield 2001; Jacobs and Kirisits 2003; Jacobs *et al.* 2003a), weevils (Mathiesen-Käärik 1953; Jacobs and Wingfield 2001; Viiri, chapter 17) and phoretic mites carried by bark beetles (Bridges and Moser 1983, 1986; Lévieux *et al.* 1989; Moser *et al.* 1989, 1997). A number of ophiostomatoid fungi are not specifically associated with insects, but disseminated through the air or by rain-splash inoculum (Mathiesen-Käärik 1953; Kile 1993; Dowding 1969; Gibbs 1993). These species also occur in galleries of bark beetles, in particular at late stages of brood development, but their relationship with the insects is relatively loose and unspecific (Mathiesen-Käärik 1953; Kirisits 1996; Kirschner 1998).

The association of blue-stain fungi with bark beetles can easily be recognized on trees or logs infested by the insects, especially on conifers. At advanced stages of breeding activity, blue-stain can be seen in the phloem and in the sapwood (Fig. 1) around and underneath insect galleries. Perithecia and anamorph structures of the ophiostomatoid fungi develop in the phloem and sapwood in and around female and larval galleries and in pupal chambers (Fig. 3).

Blue-stain fungi are primary colonizers of the sapwood of dying and recently killed trees. A number of studies have treated the characteristic succession of colonization of the sapwood by blue-stain fungi, following attack by bark beetles (Bramble and Holst 1940; Käärik 1975; Solheim 1992a, 1992b). The most virulent blue-stain fungi are the first to grow into the fresh sapwood of trees that have been infested by the insects. Other, less virulent blue-stain fungi follow these primary invaders. During this temporal succession, primary and secondary invaders are rapidly replaced by other fungi, including wood-decay fungi and saprotrophic species (Solheim 1992b). In contrast to their pathogenic abilities, most blue-stain fungi are poorly adapted to live and survive saprophytically in host tissues (Gibbs and Inman 1991; Gibbs 1993; Solheim 1992b). They are thus quickly replaced by other fungi, which are better adapted to live saprophytically.

Pathogenicity of ophiostomatoid fungi. There are a considerable number of economically important plant and tree pathogens among the ophiostomatoid fungi (Wingfield *et al.* 1993; Kile 1993a; Harrington 1993a). Among these, the most aggressive tree pathogens are those that cause vascular wilt diseases. They are disseminated by insect vectors or abiotic agents, infect the vascular system of living trees, which leads to disruption of the water transport and finally to death of trees.



Figure 3. Larva of the spruce bark beetle *Ips typographus* prior to pupation in a pupal chamber. Plentiful sporulation of *Leptographium penicillatum* is seen along the walls of the gallery.

The best known examples of vascular wilt pathogens are *O. ulmi* and *O. novo-ulmi* that are effectively transmitted by elm bark beetles and have been responsible for various pandemics of Dutch elm disease in Europe, North America and parts of Asia (Brasier 1991, 2000; Webber and Gibbs 1989). Other examples of aggressive wilt pathogens within the ophiostomatoid fungi include *C. fagacearum*, the causal agent of oak wilt in North America (Webber and Gibbs 1989; Kile 1993), *Leptographium wageneri*, which is responsible for black stain root disease on conifers in western North America (Harrington 1993a; Viiri, chapter 17) and *Ceratocystis fimbriata*, which causes vascular stain and canker diseases on a wide range of economically important woody plants, including tree species of great economic importance (Kile 1993; Roux *et al.* 2000; Marin 2004). While the Dutch elm disease pathogens are consistently associated with insect vectors, the relationships of *C. fagacearum* and *C. fimbriata* with insects are loose and unspecific, and *L. wageneri* is probably intermediate between these two extremes (Webber and Gibbs 1989; Harrington 1993a; Kile 1993; Viiri, chapter 17).

Most ophiostomatoid fungi causing blue-stain in the sapwood of conifers are moderately or weakly virulent pathogens, or they are saprophytes that cause damage to stored logs, timber and other wood products (Seifert 1993; Gibbs 1993; Butin 1996). However, some species display relatively high levels of virulence to their hosts and can kill trees when inoculated at sufficiently high dosages (Horntvedt *et al.* 1983; Christiansen 1985; Christiansen *et al.* 1987; Harrington 1993a; Paine *et al.* 1997; Lieutier 2002, chapter 9). Generally, bark beetle-associated blue-stain fungi are much less virulent than the aforementioned aggressive wilt pathogens. In contrast to typical vascular wilt pathogens, pathogenic blue-stain fungi mainly

colonize the ray parenchyma cells of the sapwood which leads to disruption of the sap flow of infected trees (Ballard *et al.* 1982; Horntvedt *et al.* 1983; Webber and Gibbs 1989; Harrington 1993a; Paine *et al.* 1997; Kirisits and Offenthaler 2002). Colonization of xylem vessels or tracheids is very limited at early stages of pathogenesis and occurs extensively only at late stages of infection (Ballard *et al.* 1984; Webber and Gibbs 1989). Simultaneously to infection of the xylem the phloem of trees is also colonized by blue-stain fungi, which can lead to bark girdling of the host trees (Webber and Gibbs 1989). Due to the patterns of colonization of the xylem, pathogenic blue-stain fungi have been referred to as "vascular stain pathogens" (Webber and Gibbs 1989). The type of disease caused by these fungi has also been called "canker stain", because disease symptoms include both necrotic lesions in the phloem and stain in the sapwood (Wingfield *et al.* 1993; Fig. 4).

Systemic vascular wilt pathogens and non-systemic vascular stain pathogens differ substantially in the modes of inoculation and infection as well as in their pathogenesis. While infection of vascular wilt pathogens can start from a single inoculation point and progresses systemically, pathogenic blue-stain fungi are simultaneously inoculated into the host tissues during the mass attack of trees by bark beetles (Webber and Gibbs 1989). The host tree can always resist single or low numbers of inoculations of blue-stain fungi which lead to discrete necrotic lesions in the phloem and to limited desiccation or stain in the sapwood (Redfern *et al.* 1987; Lieutier *et al.* 1989a, 1989b; Krokene 1996; Lieutier 2002, chapter 9). However, it has been demonstrated in mass inoculation experiments that the defense mechanisms, in particular the induced, hypersensitive wound response of the host trees get exhausted, which can finally result in tree death (Horntvedt *et al.* 1983; Christiansen 1985; Christiansen *et al.* 1987; Croisé *et al.* 1998; Lieutier 2002, chapter 9). After mass inoculation, necrotic lesions develop in the phloem and the sapwood becomes blue-stained and dysfunctional (Fig. 4).

Examples of relatively virulent ophiostomatoid fungi associated with bark beetles in Europe include *Ceratocystis polonica* (associated with *Ips* spp. on *Picea* spp.; e. g. Horntvedt *et al.* 1983; Christiansen 1985; Solheim 1988; Harding 1989; Christiansen and Solheim 1990; Krokene and Solheim 1998; Kirisits 1998; Kirisits and Offenthaler 2002), *Ceratocystis laricicola* (associated with *Ips cembrae* on *Larix* spp.; Redfern *et al.* 1987; Kirisits *et al.* 2000) as well as *Leptographium wingfieldii* and *Ophiostoma minus* (associated with *Tomicus piniperda* on *Pinus* spp.; Solheim *et al.* 1993, 2001; Croisé *et al.* 1998). Other bark beetle-associated blue-stain fungi also display varying levels of virulence to their host trees. Most of them also stimulate the tree's defense reactions to some extent. However, they are less virulent as the aforementioned blue-stain fungi and can kill trees, if at all, only at very high inoculation dosages. Such less virulent bark beetle-associated blue-stain fungi in Europe include *Ambrosiella* sp., *Ophiostoma bicolor*, *O. penicillatum*, *O. piceaperdum*, *O. piceae* and *Pesotum* sp. on Norway spruce (Horntvedt *et al.* 1983; Solheim 1988, Harding 1989; Krokene and Solheim 1998; Kirisits 1996, 1998), *O. canum*, *O. ips* and *O. brunneo-ciliatum* on pine (Lieutier *et al.* 1989a, 1989b; Guérard *et al.* 2000; Solheim *et al.* 2001) as well as *Graphium laricis* and *O. brunneo-ciliatum* on European larch (Redfern *et al.* 1987; Kirisits *et al.* 2000). Within the fungal assemblages of particular bark beetles there are often one or

sometimes two relatively virulent fungal associates, while other associated fungi are less virulent. European scolytids with such patterns of virulence among fungal associates include *I. typographus*, *I. amitinus*, *I. cembrae*, *I. duplicatus* and *T. piniperda* (Horntvedt *et al.* 1983; Solheim 1988; Solheim *et al.* 1993, 2001; Kirisits *et al.* 2000; Krokene and Solheim 1996, 1998).



Figure 4. Necrotic lesions in the secondary phloem and blue-stain in the sapwood of a Norway spruce tree after mass inoculation with *Ceratocystis polonica*.

The results of various inoculation studies suggest that there is considerable variation in the virulence of different isolates of the same blue-stain fungus. Isolates of *L. wingfieldii* collected within the forest of Orléans varied greatly in their virulence to Scots pine (Lieutier *et al.* 2004). Likewise, low levels of virulence and loss of virulence have been described for isolates of *C. polonica* (Kirisits and Anglberger 1998; Krokene and Solheim 2001). Recently, hypovirulence caused by infections of dsRNA mycoviruses has been detected in isolates of *C. polonica* and *C. laricicola* (Marin 2004). This intriguing finding raises questions about the impact of the virus on the ecology and epidemiology of these pathogenic blue-stain fungi and also about possible indirect effects on the relationship between the fungi and their insect vectors.

Pathogenic blue-stain fungi are also known to be associated with North American bark beetles, but I will not treat them in detail here and refer to recent overviews provided by Krokene (1996) and Paine *et al.* (1997). In Asia, the best-

known examples of pathogenic blue-stain fungi associated with bark beetles are *C. polonica* (associated with *Ips typographus* f. *japonicus* on *Picea* spp. in Japan; Yamaoka *et al.* 2000), *C. laricicola* (associated with *Ips subelongatus* on *Larix kaempferi* in Japan; Yamaoka *et al.* 1998) and *Leptographium yunnanensis* (associated with *Tomicus piniperda* in China; Lieutier 2002).

3.4. Anamorphic Fungi

Among the anamorphic fungi associated with bark beetles almost all belong to the hyphomycetes (Francke-Grosmann 1967; Batra 1967; Beaver 1989; Whitney 1982; Kirschner 1998). Many asexual fungi have been known to be associated with bark beetles, but often the relationship between the insects and the fungi seem to be fortuitous and inconsistent (Zimmermann 1973; Whitney 1982; Kirschner 1998; Six 2003). However, some non-ophiostomatoid hyphomycetes are commonly associated with bark beetles (Kirschner 1998, 2001). The way, in which these more regularly associated hyphomycete taxa interact with their insect associates and with other fungi in the bark beetle habitat is unknown. But they may be significant, for example as antagonists and mycoparasites of more intimate associates such as ambrosia fungi and blue-stain fungi (Kirschner 1998; Six 2003).

For many ophiostomatoid species that are phylogenetically related to *Ophiostoma* no sexual state is known to occur and these taxa are thus known under the generic name of their anamorph state, *Leptographium*, *Pesotum*, *Sporothrix* and *Hyalorhinocladiella*. Among these, *Leptographium* species are probably best known (Jacobs and Wingfield 2001), but there are also numerous *Pesotum* species that are consistently associated with bark beetles (e. g. Mathiesen-Käärik 1953; Solheim 1992a, 1992b; Krokene and Solheim 1996; Kirisits *et al.* 2000). Synnematous anamorphs of *Ophiostoma* have until recently been classified in the genus *Graphium*, but phylogenetic studies based on sequence analyses of the rDNA placed *Graphium penicilliooides*, the type species of the genus *Graphium*, within the Microascales (Okada *et al.* 1998, 2000). *Graphium* is thus only distantly related to *Ophiostoma*, and consequently, synnematous anamorphs of *Ophiostoma* were transferred to *Pesotum* (Okada *et al.* 1998, 2000). In addition to *Pesotum* spp., a few *Graphium* species are closely associated with bark beetles (Kirschner 1998; Kirisits *et al.* 2000; Jacobs *et al.* 2003b).

Besides a few species where teleomorphs are known, ambrosia fungi generally belong to various genera of hyphomycetes. Major ambrosia fungi belong to the genera *Ambrosiella*, *Raffaelea* and *Fusarium* (Francke-Grosmann 1967; Batra 1967; Zimmermann 1973; Norris 1979; Beaver 1989). The principal ambrosia fungi of European xylomycetophagous bark beetles are *Ambrosiella* spp. (Table 1). Analyses of rDNA sequence data of *Ambrosiella* species have shown that this genus is polyphyletic, with two lineages closely related to *Ceratocystis* and *Ophiostoma*, respectively (Cassar and Blackwell 1996; Rollins *et al.* 2001, Paulin-Mahady *et al.* 2002). Three *Ambrosiella* species, including *A. xylebori* (the type species of the genus), *A. ferruginea* and *A. hartigii* are related to *Ceratocystis*, whereas eight other taxa, *A. brunnea*, *A. gnathotrichi*, *A. ips*, *A. macrospora*, *A. sulcati*, *A. sulfurea*, *A.*

tingens, and an *Ambrosiella* sp. associated with *Hylurgops palliatus* and *Polygraphus poligraphus* (Krokene and Solheim 1996) show affinities to *Ophiostoma* (Cassar and Blackwell 1996; Rollins *et al.* 2001). Similarly, *Raffaelea* species have proven to be closely related to *Ophiostoma* (Jones and Blackwell 1998). The close phylogenetic relationships of *Ambrosiella* and *Raffaelea* species to *Ophiostoma* and *Ceratocystis* clearly demonstrate that the most common associates of phloophagous and xylomycetophagous bark beetles share common ancestors.

A significant characteristic of the ambrosia fungi is their pleomorphism. In the breeding systems of the ambrosia beetles they form "ambrosial" layers along the gallery walls, representing the "ambrosia" first described by Schmidberger (1936). The "ambrosia" consists of a dense, palisade-like layer of hyphae, on the top of which numerous conidia are formed in chains (Francke-Grosmann 1967; Batra 1967; Zimmermann 1973; Beaver 1989). Beetles and larvae feed on this ambrosial layer and sporulation of the ambrosia fungi is greatly enhanced by the browsing activity of the insects (Mathiesen-Käärik 1953; Francke-Grosmann 1967; Beaver 1989). Likewise, ambrosial growth seems to be influenced by the physical contact between the insect and the fungus. The control of the growth form of the ambrosia fungi by the insects may be explained by secretions of the adult beetles and their larvae (Francke-Grosmann 1967; Beaver 1989). Slow "ambrosial" growth with intensive sporulation may also occur in culture, and can be stimulated by cultivation of the fungi on certain media (Francke-Grosmann 1967 and references therein; Batra 1967; Beaver 1989). However, in cultures ambrosia fungi often form fast-growing and sterile mycelia. A third growth form is commonly observed in the mycangium of the beetles, where ambrosia fungi form yeast-like stages (Francke-Grosmann 1967; Beaver 1989).

Ambrosia fungi are relatively sensitive to various environmental factors such as relative humidity, moisture content of the sapwood and extreme temperatures. Many ambrosia fungi including *Ambrosiella* species are extremely sensitive to desiccation as well as exposure to high and low temperatures (Zimmermann 1973; Zimmermann and Butin 1973). Ambrosia fungi and thus also ambrosia beetles have specific requirements on the moisture content of the sapwood of their host trees. Generally, this is one of the most decisive factors for establishment and successful breeding of the insects, since the fungus cannot grow when the moisture content is too low (Francke-Grosmann 1967). In the wood of their host trees ambrosia fungi usually penetrate only a few mm into the xylem and their growth is usually restricted to areas surrounding the galleries (Francke-Grosmann 1967; Zimmermann 1973). However, *Ambrosiella ferruginea*, the ambrosia fungus of *Xyloterus lineatus*, penetrates several cm into the sapwood of its conifer hosts and causes a reddish-brown discoloration in the xylem (Mathiesen-Käärik 1953; Francke-Grosmann 1956a).

4. TRANSMISSION OF FUNGI

Both bark beetles and their intimately associated fungi have evolved morphological adaptions to ensure maintainance of symbiosis from generation to generation. The

most obvious adaptions of the insects for consistent dispersal of certain fungi are specialized structures in the integument of the beetles associated with gland or secretory cells that are used for the storage, transport and transmission of fungi. These structures have been defined as mycangia or mycetangia (Batra 1963a; Francke-Grosmann 1967; Beaver 1989; Berryman 1989). In the strict sense, mycangia consist of more or less spacious tubes, pouches or cavities in the integument lined with glandular cells that produce secretions which protect and preserve the spores of associated fungi (Francke-Grosmann 1956a, 1956b, 1963a, 1963b, 1967; Batra 1963a; Beaver 1989; Léveillé *et al.* 1991; Six 2003). More broadly defined the term mycangium refers to any structure that functions in the transport and protection of fungi, regardless whether glandular cells are present or not (Whitney 1982; Six 2003).

Besides protecting fungal spores from detrimental environmental influences (e. g. drought, UV light) and effectively disseminating fungal associates to new habitats, mycangia also act selectively towards certain fungi, since spores of mutualistic species are favoured and detrimental or neutral symbionts are excluded (Batra 1963a; Francke-Grosmann 1967; Beaver 1989). The fungi consistently occurring in the mycangia (= mycangial fungi) are biologically highly or obligately significant for the insects. Probably all mycangial fungi have a decisive role for the nutrition of their associated insects (Francke-Grosmann 1967; Beaver 1989; Paine *et al.* 1997; Six 2003).

Mycangia are commonly classified on the basis of the location on the beetles and structural characteristics. There is a great diversity in the location, form, structure and size of mycangia in xylomycetophagous and phloeophagous bark beetles, which supports the view that these organs have evolved numerous times and independently in different scolytid genera and species (Batra 1963a; Francke-Grosmann 1967; Beaver 1989; Berryman 1989). Mycangia can be present on both sexes, only on the males or only on the females, depending on scolytid species (Francke-Grosmann 1967; Beaver 1989). Xylomycetophagous bark beetles generally possess mycangia, in which they disseminate their ambrosia fungi. Although mycangia play a primary role in dissemination of fungi by ambrosia beetles, other means of fungal dissemination, in particular through the gut, may also be important in this group of scolytids (Francke-Grosmann 1975; Beaver 1989).

Only a small number of the European xylomycetophagous bark beetles have thus-far been investigated for the type of mycangium that they bear. These include the economically important species, *Xyleborus dispar*, *X. monographus*, *X. saxeseni*, *Xyloterus domesticus*, *X. lineatus* and *X. signatus*, as well as the introduced *Xyleborus germanus* and *Gnathotrichus materiarius* (Table 1 and references therein). With exception of *G. materiarius* where the mycangium occurs in the male, only the females of European xyletomycetophagous scolytids possess a mycangium. There is a considerable variation in the types of mycangia present on European ambrosia beetles (Table 1 and references therein). In *Xyloterus* spp. the mycangium consists of a pair of glandular tubes in the prothorax (Francke-Grosmann 1956a, 1958, 1967). In *Xyleborus dispar* and *X. germanus* the mycangium is represented by intersegmental pouches located between the pro- and mesonotum (Francke-Grosmann 1956a, 1958, 1967), while in *X. monographus* it consists of membranous

pouches at the base of the mandibles (Schedl 1964, Francke-Grosmann 1967). Another type of mycangium is seen in *X. saxeseni* that possesses sclerotized pouches at the base of the elytra (Francke-Grosmann 1956a, 1967). Finally, the mycangium of *G. materiarius* consists of an enlargement of the precoxal cavity (Farris 1963; Francke-Grosmann 1966, 1967).

Mycangia are also known in a number of true bark beetles, although they occur only in a few species (Francke-Grosmann 1967; Whitney 1982; Beaver 1989; Paine *et al.* 1997; Six 2003). For example, various types of mycangia occur in some, but not all North American *Dendroctonus* species (Whitney 1982; Paine *et al.* 1997; Six 2003). In Europe, mycangia have been described for five true bark beetle species (Table 1 and references therein). In *I. acuminatus* which has a phloeomycetophagous feeding habit (Francke-Grosmann 1952; see 6.2.2.), females possess paired membranous pouches at the base of the mandibles (Francke-Grosmann 1963b, 1967). In the mycangium of *I. acuminatus* the nutritionally important fungus, *Ambrosiella macrospora* is transmitted. Primitive mycangia, consisting of secretion-filled punctures of the integument, especially on the elytra, have been described in both sexes of *Hylurgops palliatus*, *Hylastes ater* and *Hylastes cunicularius* (Francke-Grosmann 1956b, 1963a, 1967) Likewise, puncture pits on the mandibles, the pronotum and the elytra function as mycangia in *I. sexdentatus* (Lévieux *et al.* 1991).

For the majority of phloeophagous bark beetles that regularly carry particular fungi, mycangia have not been found. In these non-mycangial scolytid species dissemination of fungi is thus suspected to occur either epizoically by conidia and ascospores adhering to the insect's exoskeleton or endozoically through spores passing the gut undigested (Mathiesen-Käärik 1953; Francke-Grosmann 1967; Whitney 1982; Furniss *et al.* 1990; Paine *et al.* 1997). Apparently, this form of fungal transmission is as efficient as in scolytids which possess mycangia, since relatively specific and relatively constant assemblages of fungi also occur with non-mycangial bark beetles. However, it is also be possible that relatively simple, un conspicuous pit mycangia, similar to those of *Ips sexdentatus* (Lévieux *et al.* 1991) may also occur in other scolytids, but have so far not been recognized.

Phoretic mites often also play an important role in the transmission of ophiostomatoid fungi (Bridges and Moser 1983, 1986; Lévieux *et al.* 1989; Moser *et al.* 1989, 1997) Some mites in the genus *Tarsonemus* even possess specialized structures, called sporothecae which are organs for transmission of fungi (Moser 1985). Likewise, in some cases phoretic mites may even be more intimately associated with a particular fungus than the bark beetles themselves. The best known examples are *D. frontalis*, its hyperphoretic mites *Tarsonemus krantzi* and *T. ips* (which both have sporothecae) and *Ophiostoma minus* which is more closely associated with the mites than with the southern pine beetle (Bridges and Moser 1983; Moser 1985; Klepzig *et al.* 2001a, 2001b).

Fungi associated with bark beetles have also evolved adaptions to the symbiosis with their insect partners. Morphological features of *Ophiostoma*, *Ceratocystis* and *Ceratocystiopsis* such as long perithecial necks (Fig. 2) and sticky ascospores and conidia are viewed as adaptions to the bark beetle habitat (Francke-Grosmann 1967; Whitney 1982; Beaver 1989; Malloch and Blackwell 1993; Six 2003). Ascospores

Table 1. *Ambrosia fungi of European scolytids and types of mycangia occurring in European bark beetle species*

Bark beetle species	Principal ambrosia fungus ¹	Type of mycangium	References
<i>Ambrosia beetles (xylomyctophagous)²</i>			
<i>Gnathocerus materianus</i>	<i>Ambrosiina monospora</i> ³	Enlargement of precoxal cavity in male	Farris 1963; Francke-Grosmann 1966, 1967
<i>Xyleborus dispar</i>	<i>Ambrosiella hartigii</i>	Intersegmental pouches between pro- and mesonotum in female	Francke-Grosmann 1956a, 1958, 1967
<i>Xyleborus germanus</i>	<i>Ambrosiella hartigii</i>	Intersegmental pouches between pro- and mesonotum in female	Francke-Grosmann 1956a, 1958, 1967
<i>Xyleborus monographus</i>	Yellowish moniloid fungus [*]	Paired membranous pouches at base of mandible in female	Schedl 1964; Francke-Grosmann 1967
<i>Xyleborus sexdens</i>	<i>Ambrosiella sulfurea</i>	Sclerotized pouches in base of elytra in female	Francke-Grosmann 1956a, 1967
<i>Xylotenus domesticus</i>	<i>Ambrosiella ferruginea</i>	A pair of glandular tubes in prothorax of female	Francke-Grosmann 1956a, 1958, 1967
<i>Xylotenus lineatus</i>	<i>Ambrosiella ferruginea</i>	A pair of glandular tubes in prothorax of female	Francke-Grosmann 1956a, 1958, 1967
<i>Xylotenus signatus</i>	<i>Ambrosiella ferruginea</i>	A pair of glandular tubes in prothorax of female	Francke-Grosmann 1956a, 1958, 1967
True bark beetle (phloeophagous)			
<i>Hylastes aer</i>	-	Secretion-filled punctures of the integument, especially on the elytra	Francke-Grosmann 1956b, 1967
<i>Hylastes cunicularius</i>	-	Secretion-filled punctures of the integument, especially on the elytra	Francke-Grosmann 1956b, 1967
<i>Hyllurgops palliatus</i>	-	Secretion-filled punctures of the integument, especially on the elytra	Francke-Grosmann 1956b, 1967
<i>Ips acuminatus⁴</i>	<i>Ambrosiella macrospora</i>	Paired membranous pouches at base of mandible in female	Francke-Grosmann 1963b, 1967
<i>Ips sexdentatus</i>	-	Puncture pits on the proximal part of the mandible, the sides of the pronotum and the elytra	Léveillé <i>et al.</i> , 1991

Notes: ¹ See also table 2 and references therein. ² European scolytides with xylomyctophagous feeding habits (Postner 1974; Pfeffer 1995), for which neither the ambrosia fungus nor the type of mycangium has been investigated: *Xyleborus cryptographus*, *X. alni*, *X. eurygraphus*, *X. dryographus*, *X. pfeili*, *X. levae*. ³ references: Batra 1963b; Kischner 1998, 2001. ⁴ *I. acuminatus* is suggested to have a "phlocomycetophagous" feeding habit (Francke-Grosmann 1952).

and conidia easily adhere to the bodies of the insects. Ascospores often possess well developed sheaths, which may protect the spore from digestion in the gut of the beetles (Francke-Grosmann 1967; Malloch and Blackwell 1993). Ophiostomatoid fungi and ambrosia fungi are pleomorphic and show both mycelial and yeast-like growth forms. In the mycangium of the beetles the fungi are usually present in their slow-growing yeast stage (Francke-Grosmann 1967; Beaver 1989; Six 2003). The loss of the sexual stage in almost all known ambrosia fungi and in some ophiostomatoid fungi may also be viewed as extreme adaption to the symbiosis with bark beetles (Six 2003).

5. ASSEMBLAGES OF FUNGI ASSOCIATED WITH EUROPEAN BARK BEETLES

Since the discovery of the association of fungi with bark beetles numerous studies on the mycobiota associated with European scolytids have been carried out. An overview of the assemblages of fungi and especially the ophiostomatoid fungi associated with xylomycetophagous (5.1.) and phloeophagous bark beetles (5.2.) is presented.

5.1. Assemblages of fungi associated with xylomycetophagous bark beetles

For six xylomycetophagous beetles that are native in Europe and for two species that have been introduced into Europe their principal ambrosia fungi are known (Tables 1 and 2 and references therein). Their identity has not been determined for the other seven xylomycetophagous species in Europe (Table 1) that are economically less important. Most European scolytids with xylomycetophagous feeding habit are associated with species in the genus *Ambrosiella* (Tables 1 and 2) that includes taxa related to *Ceratocystis* or *Ophiostoma* (Cassar and Blackwell 1996; Rollins *et al.* 2001; Paulin-Mahady *et al.* 2002). *Xyleborus dispar* and the introduced *X. germanus* live in symbiosis with *A. hartigii*, whereas *X. domesticus*, *X. lineatus* and *X. signatus* are associated with *A. ferruginea*. Both *A. hartigii* and *A. ferruginea* are closely related to species in the genus *Ceratocystis* (Cassar and Blackwell 1996; Rollins *et al.* 2001). *Ambrosiella sulfurea*, which has affinities to the genus *Ophiostoma* (Cassar and Blackwell 1996; Rollins *et al.* 2001) is transmitted by *X. saxeseni*. The ambrosia fungus of *Xyleborus monographus* has been referred to as “yellowish moniloid fungus” (Francke-Grosmann 1967). A *Raffaelea* species has also been reported to be associated with this scolytid (Kowalski 1991). The introduced *G. materiarius* is associated with a non-ophiostomatoid ambrosia fungus, the yeast *Ambrosiozyma monospora* (Batra 1963b; Kirschner 1998). As seen in European ambrosia beetles the association between the insects and their principal ambrosia fungi is not species-specific, since several beetle species can be associated with the same *Ambrosiella* species.

In addition to their principal fungal associates, ambrosia beetles are also known to carry *Ophiostoma* species and other non-ambrosial ophiostomatoid fungi. These fungi have also been proposed to represent ambrosia fungi with nutritional

importance for the insects (Bakshi 1950), but most authors consider them as “weed fungi” that are ecologically insignificant for the beetles (Francke-Grosmann 1966, 1967; Beaver 1989). The spectrum of ophiostomatoid fungi occurring together with xylomycetophagous bark beetles comprises a considerable number of species, most of which are generalists that occur in association with a wide range of insects on several host trees (Table 2).

5.2. Assemblages of fungi associated with phloeophagous bark beetles

A synthesis of the numerous investigations on the assemblages of ophiostomatoid fungi associated with phloem-feeding bark beetles in Europe is provided in Table 2. Thus-far, 27 true bark beetle species, 23 on conifers and 4 on hardwoods have been examined for the ophiostomatoid fungi they carry. The best-studied European bark beetle regarding its fungal associates is *I. typographus* which has been included in many investigations within its distribution range in Europe (Table 2 and references therein) and also in Japan (Yamaoka *et al.* 1997). I will subsequently often refer to this species as example.

5.2.1. Overview about ophiostomatoid fungi associated with phloeophagous bark beetles

Ophiostomatoid fungi associated with true bark beetles in Europe mainly belong to the genus *Ophiostoma*, which is represented by a large number of species (Table 2). Several *Leptographium* and *Pesotum* species are also associated with phloeophagous bark beetles (Table 2). A few European bark beetles transmit *Ceratocystis* species, namely *C. polonica* and *C. laricicola*. *Ceratocystis polonica* is mainly associated with *I. typographus*, *I. amatinus* and *I. duplicatus* on Norway spruce, although it is occasionally also transmitted at low frequencies by other spruce bark beetles (Table 2). Likewise, *C. laricicola* is associated with *I. cembrae* on *Larix* spp. *Ceratocystis polonica* and *C. laricicola* are unusual, since they are among the few *Ceratocystis* species that are regularly transmitted by bark beetles. The only other known example is *C. rufipenni* that is associated with *D. rufipennis* on *Picea* spp. in North America (Wingfield *et al.* 1997). A few conifer bark beetles, including particularly *H. palliatus*, *I. acuminatus*, *I. sexdentatus* and *T. minor* transmit *Ambrosiella* species that are phylogenetically related to *Ophiostoma* (Table 2; see 3.4.). Species of *Graphium* as associates of bark beetles are also included in Table 2, despite the fact *Graphium* is not closely related to *Ophiostoma* and other ophiostomatoid fungi (Okada *et al.* 1998, 2000; Harrington *et al.* 2001). In particular, four *Graphium* species are common associates of European bark beetles. These include *G. pseudomititicum* associated with several pine bark beetles, *G. fimbriisporum*, associated with various spruce bark beetles, *G. laricis*, occurring with *I. cembrae* on larch and *G. penicillioides*, associated with *Taphrorychus bicolor* on beech and *Scolytus* spp. on elm (Kirschner 1998; Kirisits *et al.* 2000; Jacobs *et al.* 2003b; Table 2).

5.2.2. Intimacy of association between ophiostomatoid fungi and phloem-feeding bark beetles

Based on the intimacy of association with ophiostomatoid fungi, scolytids can broadly be divided into two groups. One of these groups includes bark beetle species that are relatively loosely associated with fungi, in the sense that only a low portion of individuals in a population carries fungi. The pine shoot beetle, *Tomicus piniperda* may be a typical example for a scolytid with a relatively loose relationship with blue-stain fungi. Although this bark beetle transmits numerous ophiostomatoid fungi (Table 2), none of these occur at consistently high frequencies in populations of the insect (Mathiesen-Käärik 1953; Lieutier *et al.* 1989b; Solheim and Långström 1991; Gibbs and Inman 1991). Even *L. wingfieldii*, *O. minus* and *Hormonema dematooides*, the most consistent associates of *T. piniperda* are usually isolated at relatively low frequencies, compared to other conifer bark beetle-fungus-systems (Lieutier *et al.* 1989b; Solheim and Långström 1991; Gibbs and Inman 1991). Other examples of conifer bark beetles with relatively loose association with fungi include the solitary *D. micans* on Norway spruce (Lieutier *et al.* 1992), *Cryphalus abietis* on Silver fir (Kirschner 1998), and *Pityogenes quadridens* on Scots pine (Mathiesen-Käärik 1953) (Table 2). Among bark beetle species on deciduous trees, *Leperisinus varius* on ash and *Scolytus intricatus* on oak infrequently disseminate unspecific *Ophiostoma* species (Kirschner 1998).

The second group of bark beetles comprises species that are intimately associated with blue-stain fungi, meaning that a large percentage of individuals (up to 100 %) carry spores of ophiostomatoid fungi. This does not necessarily mean that one particular blue-stain fungus is always present at such high frequencies, but that the majority of beetles usually carry at least one fungus out of the whole assemblage of fungi associated with a particular bark beetle species. For conifer bark beetles intensive association with blue-stain fungi is the rule rather than the exception. A typical example is *I. typographus* on Norway spruce. A diverse assemblage of fungi is associated with this economically extremely important bark beetle. Despite the fact that there is a great variation in the composition of the mycobiota reported in various investigations (see 5.2.5), all studies agree that *I. typographus* very consistently and regularly carries blue-stain fungi (Table 2). The same is true for many other conifer bark beetles, including *Crypturgus cinereus*, *Crypturgus pusillus*, *Dryocoetes autographus*, *Hylastes ater*, *Hylastes cunicularius*, *Hylurgops palliatus*, *Hylurgops glabratus*, *Ips acuminatus*, *Ips amitinus*, *Ips cembrae*, *Ips duplicatus*, *Ips sexdentatus*, *Orthotomicus laricis*, *Orthotomicus proximus*, *Pityogenes chalcographus*, *Polygraphus poligraphus* and *Tomicus minor* (Table 2).

Among bark beetles on hardwoods, *Scolytus* spp. on elm seem to be rather intimately associated with ophiostomatoid fungi, in particular with the introduced Dutch elm disease pathogens *O. ulmi* and *O. novo-ulmi* and with *G. penicilliooides* (Table 2). However, the different *Scolytus* species vary greatly in their efficiency as vectors of the Dutch elm disease pathogens, with *Scolytus scolytus* being the most effective vector (Webber and Brasier 1984; Webber and Gibbs 1989; Webber 1990, 2000). On beech, the secondary *Taphrorychus bicolor* may be relatively regularly associated with *G. penicilliooides* (Table 2).

5.2.3. Elements of the mycobiota of phloephagous bark beetles

The symbiosis between ophiostomatoid fungi and bark beetles is usually not a “one fungus – one insect” relationship. Hence, most bark beetle species are associated with an assemblage of several fungi. Typically, some fungal species occur at high frequencies and/or constantly together with a given bark beetle species, while others are rare and/or casual components of the mycobiota. For example, a very high number of fungi has been reported to occur together with *I. typographus* in Europe, but many of the recorded species are generally rare in this niche or have been found only by one or a few investigators (Table 2). Only a few species are mentioned as relatively constant associates in the majority of the studies on the mycobiota of *I. typographus*. Thus, despite different results of the various investigations (see 5.2.5.), *C. polonica*, *O. ainoae*, *O. bicolor*, *O. penicillatum* and *O. piceaperdum* are probably the most common and ecologically most significant fungi associated with *I. typographus* in Europe (Table 2). Very similar patterns also occur in many other bark beetle-fungus systems (Table 2).

Table 2: Ophiostomatoid fungi associated with bark beetles (Coleoptera: Scolytidae) in Europe. Species of *Graphium*, which were formerly known as anamorphs of *Ophiostoma* are also included.

Bark beetle (Host trees) ^a	Fungus ^b	References ^j
<i>Cryphalus abietis</i> ^{b,f} (Conifers [<i>Abies alba</i>])	<i>Ophiostoma piceae</i> (<i>Ophiostoma piceaperdum</i>)	Kirschner 1998, 2001 Kirschner 1998, 2001
<i>Crypturgus cinereus</i> ^{b,e} (Conifers [<i>Picea abies</i> , <i>Pinus sylvestris</i>])	<i>Ceratocystiopsis alba</i> <i>Ceratocystiopsis minima</i> <i>Ceratocystiopsis minuta</i> <i>Ophiostoma japonicum</i> (= <i>O. arborea</i> ?) <i>Ceratocystis leucocarpa</i> <i>Ophiostoma neglectum</i> <i>Ophiostoma piceae</i> <i>Ophiostoma cf. piceae</i> <i>Ophiostoma piceaperdum</i> <i>Ophiostoma stenoceras</i>	Kirschner 1998, 2001 Kirschner 1998, 2001 Kirschner 1998, 2001 Kirschner 1998, 2001 Kirschner 1998, 2001 Kirschner 1998, Kirschner and Oberwinkler 1999 Kirschner 1998, 2001 Kirschner 1998, 2001 Kirschner 1998, 2001 Kirschner 1998, 2001
<i>Crypturgus pusillus</i> ^{b,e} (Conifers [<i>Picea abies</i>])	<i>Ceratocystiopsis alba</i> <i>Ceratocystiopsis minima</i> <i>Ceratocystiopsis minuta</i> <i>Ceratocystis leucocarpa</i> <i>Graphium pseudomiticum</i> (= <i>G. fimbriisporum</i> ?) <i>Ophiostoma ainoae</i> <i>Ophiostoma araucariae</i> <i>Ophiostoma bicolor</i> <i>Ophiostoma japonicum</i> (= <i>O. arborea</i> ?) <i>Ophiostoma neglectum</i> <i>Ophiostoma piceae</i> <i>Ophiostoma cf. piceae</i>	Kirschner 1998, 2001 Kirschner 1998 Kirschner 1998, 2001 Kirschner 1998 Kirschner 1998, 2001 Kirschner 1998, Kirschner and Oberwinkler 1999 Kirschner 1998, 2001 Kirschner 1998

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ^j
	<i>Ophiostoma piceaperdum</i>	Kirschner 1998, 2001
	<i>Ophiostoma simplex</i>	Kirschner 1998
	<i>Ophiostoma stenoceras</i>	Kirschner 1998
	<i>Ophiostoma torulosum</i>	Kirschner 1998
<i>Dendroctonus micans</i> ^{b,f} (<i>Picea abies</i>)	<i>Ophiostoma camum</i> (<i>Ophiostoma penicillatum</i>) (<i>Ophiostoma minus</i>) (<i>Ophiostoma</i> sp.)	Lieutier <i>et al.</i> 1992 Lieutier <i>et al.</i> 1992 Lieutier <i>et al.</i> 1992 Lieutier <i>et al.</i> 1992
<i>Dryocoetes autographus</i> ^{b,e} (Conifers [<i>Picea abies</i> , <i>Pinus sylvestris</i>])	<i>Ceratocystiopsis alba</i> <i>Ceratocystiopsis minuta</i> <i>Ceratocystis autographa</i> <i>Graphium adustum</i> <i>Graphium fimbriisporum</i> <i>Graphium pseudomoriticum</i> (= <i>G. fimbriisporum</i> ?) <i>Leptographium guttulatum</i>	Kirschner 1998, 2001 Kirschner 1998, 2001 Bakshi 1951 Grosmann 1931 Kirisits <i>et al.</i> 2000; Jacobs <i>et al.</i> 2003b Kirschner 1998, 2001
	<i>Ophiostoma ainoae</i>	Kirisits <i>et al.</i> 2000; Jacobs and Wingfield 2001; Jacobs <i>et al.</i> 2001a
	<i>Ophiostoma araucariae</i>	Kirschner 1998, 2001
	<i>Ophiostoma cucullatum</i>	Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma galeiformis</i>	Bakshi 1951
	<i>Ophiostoma japonicum</i> (= <i>O. arborea</i> ?)	Kirschner 1998, 2001
	<i>Ophiostoma obscura</i>	
	<i>Ophiostoma neglectum</i>	Kirschner 1998; Kirschner and Oberwinkler 1999
	<i>Ophiostoma piceae</i>	Kirschner 1998, 2001 ; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma cf. piceae</i>	Kirschner 1998
	<i>Ophiostoma piceaperdum</i>	Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma simplex</i>	Kirschner 1998
	<i>Ophiostoma stenoceras</i>	Kirschner 1998
<i>Gnathotrichus materiarius</i> ^{d,e} (Conifers [<i>Larix decidua</i> , <i>Pinus sylvestris</i>])	<i>Leptographium</i> sp. <i>Ophiostoma araucariae</i> <i>Ophiostoma cucullatum</i> <i>Ophiostoma obscura</i> <i>Ophiostoma piceaperdum</i> <i>Ophiostoma piceae</i>	Kirschner 1998 Kirschner 1998 Kirschner 1998 Kirschner 1998 Kirschner 1998 Kirschner 1998
<i>Hylastes ater</i> ^{b,e} (<i>Pinus sylvestris</i>)	[<i>Graphium</i> (<i>Pesotum</i> ?) <i>aureum</i>] <i>Leptographium guttulatum</i> <i>Leptographium lundbergii</i> <i>Leptographium serpens</i> (<i>Ophiostoma ips</i>) <i>Ophiostoma minus</i>	Mathiesen-Käärik 1953 Wingfield and Gibbs 1991; Jacobs and Wingfield 2001 Dowding 1973; Mathiesen 1950; Mathiesen-Käärik 1953; Jacobs and Wingfield 2001 Wingfield and Gibbs 1991; Jacobs and Wingfield 2001 Mathiesen-Käärik 1953 Mathiesen 1950; Mathiesen-Käärik 1953

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^h	References ^j
	<i>Ophiostoma penicillatum</i>	Mathiesen 1950; Mathiesen-Käärik 1953, Jacobs and Wingfield 2001
	[<i>Ophiostoma penicillatum</i> f. <i>chalcographi</i>]	Mathiesen 1950
	[<i>Ophiostoma penicillatum</i> f. <i>pinii</i>]	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ophiostoma piceae</i> (<i>Ophiostoma piliferum</i>)	Mathiesen 1950; Mathiesen-Käärik 1953 Mathiesen-Käärik 1953
<i>Hylastes opacus</i> ^{b,g} (<i>Pinus sylvestris</i>)	<i>Graphium</i> (<i>Pesotum</i> ?) sp. <i>Leptographium guttulatum</i>	Wingfield and Gibbs 1991 Wingfield and Gibbs 1991; Jacobs and Wingfield 2001
	<i>Leptographium lundbergii</i>	Wingfield and Gibbs 1991; Jacobs and Wingfield 2001
	<i>Leptographium procerum</i>	Wingfield & Gibbs 1991; Jacobs and Wingfield 2001
	<i>Leptographium wingfieldii</i>	Wingfield & Gibbs 1991; Jacobs and Wingfield 2001
<i>Hylastes cunicularius</i> ^{b,e} (<i>Picea abies</i>)	<i>Ophiostoma galeiformis</i>	Mathiesen-Käärik 1953; Zhou <i>et al.</i> 2004
	<i>Ophiostoma olivaceum</i>	Mathiesen-Käärik 1953
	<i>Ophiostoma penicillatum</i>	Mathiesen-Käärik 1953; Jacobs and Wingfield 2001
	<i>Ophiostoma piceae</i>	Mathiesen-Käärik 1953
<i>Hylurgops palliatus</i> ^{b,e} (Conifers [<i>Picea abies</i> , <i>Pinus sylvestris</i> , <i>Larix kaempferi</i>])	<i>Ambrosiella</i> sp.	Krokene and Solheim 1996; Rollins <i>et al.</i> 2001
	<i>Ceratocystiopsis alba</i>	Kirschner 1998, 2001
	<i>Ceratocystiopsis minuta</i>	Kirschner 1998, 2001
	<i>Ceratocystis autographa</i>	Bakshi 1951
	<i>Ceratocystis polonica</i>	Krokene and Solheim 1996
	<i>Graphium fimbriisporum</i>	Kirisits <i>et al.</i> 2000; Jacobs <i>et al.</i> 2003b
	<i>Graphium pseudormiticum</i> (= <i>G. fimbriisporum</i> ?)	Kirschner 1998, 2001
	<i>Graphium</i> (<i>Pesotum</i> ?) <i>pyknocephalum</i>	Mathiesen 1950, Mathiesen-Käärik 1953
	<i>Graphium</i> (<i>Pesotum</i> ?) spp.	Wingfield and Gibbs 1991
	<i>Leptographium guttulatum</i>	Mathiesen 1950; Harding 1989; Wingfield and Gibbs 1991; Kirisits <i>et al.</i> 2000; Jacobs and Wingfield 2001; Jacobs <i>et al.</i> 2001b
	<i>Leptographium lundbergii</i>	Kotýnková-Sychrová 1966; Harding 1989 ; Wingfield and Gibbs 1991; Jacobs and Wingfield 2001
	<i>Leptographium procerum</i>	Wingfield and Gibbs 1991; Jacobs and Wingfield 2001
	<i>Leptographium wingfieldii</i>	Wingfield and Gibbs 1991; Jacobs and Wingfield 2001
	<i>Ophiostoma ainoae</i>	Kirisits <i>et al.</i> 2000
	<i>Ophiostoma bicolor</i>	Harding 1989; Kirschner 1998, 2001
	<i>Ophiostoma cucullatum</i>	Kirschner 1998 , Kirisits <i>et al.</i> 2000
	<i>Ophiostoma galeiformis</i>	Bakshi 1951
	<i>Ophiostoma japonicum</i> (= <i>O. arborea</i> ?)	Kirschner 1998, 2001
	<i>Ophiostoma neglectum</i>	Kirschner 1998, 2001 ; Kirisits,

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ^j
	<i>Ophiostoma penicillatum</i>	unpublished Mathiesen 1950; Mathiesen-Käärik 1953; Kirschner 1998; Jacobs and Wingfield 2001 Mathiesen 1950
	[<i>Ophiostoma penicillatum</i> f. <i>palliatum</i>] (= <i>Leptographium guttulatum</i>)	
	<i>Ophiostoma piceae</i>	Mathiesen 1950; Mathiesen-Käärik 1953; Harding 1989; Krokene and Solheim 1996; Kirschner 1998, 2001; Kirisits et al. 2000 Kirschner 1998
	<i>Ophiostoma cf. piceae</i>	Davidson et al. 1967; Harding 1989; Krokene and Solheim 1996; Kirschner 1998, 2001; Kirisits et al., 2000; Jacobs and Wingfield 2001
	<i>Ophiostoma piceaperdum</i>	Kirschner 1998
	<i>Ophiostoma simplex</i>	
	<i>Ophiostoma stenoceras</i>	Kirschner 1998
<i>Hylurgops glaberratus</i> ^{b,c} (Conifers [<i>Picea abies</i>])	<i>Graphium fimbriisporum</i>	Kirisits 1996; Kirisits et al. 2000; Jacobs et al. 2003b
	<i>Leptographium guttulatum</i>	Kirisits 1996; Kirisits et al. 2000; Jacobs and Wingfield 2001; Jacobs et al., 2001b
	<i>Ophiostoma ainoae</i>	Kirisits 1996; Kirisits et al. 2000
	<i>Ophiostoma cucullatum</i>	Kirisits 1996; Kirisits et al. 2000
	<i>Ophiostoma flexuosum</i>	Kirisits 1996; Kirisits et al. 2000
	<i>Ophiostoma floccosum</i>	Lin 2003
	<i>Ophiostoma piceae</i>	Kirisits 1996; Kirisits et al. 2000
	<i>Ophiostoma piceaperdum</i>	Kirisits 1996; Kirisits et al. 2000
<i>Ips acuminatus</i> ^{c,e} (<i>Pinus</i> spp.)	<i>Ambrosiella macrospora</i>	Mathiesen 1950; Francke-Grosmann 1952, 1963b; Cassar and Blackwell 1996
	<i>Ceratocystiopsis minima</i>	Lieutier et al. 1991
	<i>Ceratocystiopsis minuta</i>	Mathiesen 1951
	(<i>Ceratocystis coeruleascens</i>)	Mathiesen 1950; Mathiesen-Käärik 1953
	(<i>Graphium (Pesotum?) pyknocephalum</i>)	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Leptographium lundbergii</i>	Mathiesen 1950; Mathiesen-Käärik 1953; Jacobs and Wingfield 2001
	<i>Ophiostoma brunneociliatum</i>	Lieutier et al. 1991
	(<i>Ophiostoma canum</i>)	
	<i>Ophiostoma clavatum</i>	
	<i>Ophiostoma ips</i>	Mathiesen 1950; Mathiesen-Käärik 1953; Rennerfelt 1950; Mathiesen 1950, 1951; Mathiesen-Käärik 1953; Francke-Grosmann 1952, 1963b
	<i>Ophiostoma minus</i>	Lieutier et al. 1991; Mathiesen-Käärik 1953
	<i>Ophiostoma piceae</i>	Rennerfelt 1950; Mathiesen 1950; Mathiesen-Käärik 1953; Lieutier et al. 1991
	<i>Ophiostoma piliferum</i>	Mathiesen 1950; Mathiesen-Käärik 1953; Francke-Grosmann 1952, 1963
	<i>Ophiostoma sp.</i>	Lieutier et al. 1991
	<i>Ophiostoma spp.</i>	Rennerfelt 1950; Mathiesen 1950

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ^j
<i>Ips amitinus</i> ^{b,c} (<i>Picea abies</i> , <i>Pinus cembra</i>)	<i>Ceratocystiopsis cf. alba</i> <i>Ceratocystiopsis minuta</i> <i>Ceratocystis polonica</i> <i>Graphium fimbriisporum</i> <i>Graphium (Pesotum?) spp.</i> <i>Leptographium lundbergii</i> <i>Leptographium spp.</i> <i>Ophiostoma bicolor</i> <i>Ophiostoma brunneociliatum</i> <i>Ophiostoma cucullatum</i> <i>Ophiostoma minus</i> <i>Ophiostoma penicillatum</i> <i>Ophiostoma piceae</i> <i>Ophiostoma piceaperdum</i> <i>Ophiostoma cf. piceaperdum</i> <i>Ophiostoma piliferum</i>	Kirisits <i>et al.</i> 2000 Kirisits <i>et al.</i> 2000 Kirisits <i>et al.</i> 2000 Kirisits <i>et al.</i> 2000 ; Jacobs <i>et al.</i> 2003b Grosmann 1931 Grosmann 1931 Kirisits <i>et al.</i> 2000 Kirisits <i>et al.</i> 2000 Grosmann 1931
<i>Ips cembrae</i> ^{b,e} (<i>Larix decidua</i> , <i>Larix kaempferi</i>)	<i>Ceratocystiopsis cf. alba</i> <i>Ceratocystiopsis minuta</i> <i>Ceratocystis laricicola</i> <i>Graphium laricis</i> <i>Ophiostoma bicolor</i> <i>Ophiostoma brunneociliatum</i> (<i>Ophiostoma fusiforme</i>) (<i>Ophiostoma lunatum</i>) <i>Ophiostoma piceae</i> <i>Ophiostoma cf. piceaperdum</i>	Kirisits <i>et al.</i> 2000; Stauffer <i>et al.</i> 2001 Kirisits <i>et al.</i> 2000; Stauffer <i>et al.</i> 2001 Redfern <i>et al.</i> 1987; Redfern 1989; Kirisits <i>et al.</i> 2000; Stauffer <i>et al.</i> 2001 Kirisits <i>et al.</i> 2000; Stauffer <i>et al.</i> 2001; Jacobs <i>et al.</i> 2003b Kirisits <i>et al.</i> 2000; Stauffer <i>et al.</i> 2001 Redfern <i>et al.</i> 1987; Redfern 1989; Kirisits <i>et al.</i> 2000; Stauffer <i>et al.</i> 2001 Agayeva <i>et al.</i> 2004 Agayeva <i>et al.</i> 2004 Kirisits <i>et al.</i> 2000; Stauffer <i>et al.</i> 2001 Kirisits <i>et al.</i> 2000; Stauffer <i>et al.</i> 2001
<i>Ips duplicatus</i> ^{b,e} (<i>Picea abies</i>)	<i>Ceratocystis polonica</i> <i>Ophiostoma bicolor</i> <i>Ophiostoma penicillatum</i> <i>Ophiostoma piceae</i> <i>Ophiostoma piceaperdum</i> (<i>Ophiostoma</i> sp.) <i>Pesotum</i> sp.	Valkama 1995; Krokene and Solheim 1996 Valkama 1995; Krokene and Solheim 1996 Valkama 1995; Krokene and Solheim 1996 ; Jacobs and Wingfield 2001 Valkama 1995; Krokene and Solheim 1996 Krokene and Solheim 1996; Jacobs and Wingfield 2001 Mathiesen 1950 Krokene and Solheim 1996
<i>Ips sexdentatus</i> ^{b,e} (<i>Pinus</i> spp.)	<i>Ambrosiella ips</i> <i>Ambrosiella tingens</i> <i>Graphium pseudormiticum</i> <i>Ceratocystiopsis minuta</i> <i>Leptographium</i> sp. <i>Ophiostoma ainoae</i>	Siemaszko 1939; Mathiesen-Käärik 1953 Mathiesen-Käärik 1953 Kirschner 1998, 2001 ; Kirisits, unpublished Kirschner 1998, 2001 Lieutier <i>et al.</i> 1989 Kirschner 1998, 2001

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ^j
	(= <i>O. brunneo-ciliatum</i> ?)	Kirschner 1998, 2001
	<i>Ophiostoma araucariae</i>	Mathiesen-Käärik 1953; Lieutier <i>et al.</i> 1989, 1991; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma brunneo-ciliatum</i>	Mathiesen-Käärik 1953
	<i>Ophiostoma clavatum</i>	Siemaszko 1939; Francke-Grosmann 1952; Lieutier <i>et al.</i> 1989, 1991;
	<i>Ophiostoma ips</i>	Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma japonicum</i> (= <i>O. arborea</i> ?)	Kirschner 1998, 2001
	<i>Ophiostoma minus</i>	Siemaszko 1939; Lieutier <i>et al.</i> 1989
	<i>Ophiostoma obscura</i>	Kirschner 1998, 2001
	<i>Ophiostoma piceae</i>	Kirisits, unpublished
	<i>Ophiostoma piceaperdum</i>	Kirschner 1998, 2001
	<i>Ophiostoma</i> sp.	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Pesotum fragrans</i>	Mathiesen-Käärik 1953
<i>Ips typographus</i> ^{b,e} (<i>Picea abies</i>)	<i>Ceratocystiopsis alba</i>	Kirschner 1998, 2001; Kirisits, unpublished
	<i>Ceratocystiopsis minuta</i>	Siemaszko 1939; Mathiesen 1950, 1951, Kotýnková-Sychrová 1966; Käärik 1975; Solheim 1986, 1992a, 1992b, 1993; Harding 1989; Kirisits 1996; Grubelnik 1998; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000; Viiri and Lieutier 2004; Jankowiak 2004
	<i>Ceratocystis polonica</i>	Siemaszko 1939; Mathiesen 1950, 1951; Mathiesen-Käärik 1953; Käärik 1975; Solheim 1986, 1992a, 1992b, 1993; Harding 1985, 1989, 1995; Furniss <i>et al.</i> 1990; Krokene and Solheim 1996; Viiri and Weissenberg 1995; Kirisits 1996; Viiri 1997; Grubelnik 1998; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000; Viiri and Lieutier 2004, Salle <i>et al.</i> 2003; Jankowiak 2004
	<i>Graphium fimbriisporum</i>	Morelet 1995; Kirisits 1996; Grubelnik 1998; Kirisits <i>et al.</i> 2000; Jacobs <i>et al.</i> 2003b
	<i>Graphium pseudomititicum</i> (= <i>G. fimbriisporum</i> ?)	Kirschner 1998, 2001
	<i>Graphium</i> (<i>Pesotum</i> ?) <i>pycnocephalum</i>	Grosmann 1931; Siemaszko 1939, Mathiesen 1950; Mathiesen-Käärik 1953; Kotýnková-Sychrová 1966; Jankowiak 2004
	<i>Leptographium euphyes</i>	Jankowiak 2004
	<i>Leptographium lundbergii</i>	Harding 1989
	<i>Leptographium</i> spp.	Rennerfelt 1950; Kirschner 1998; Viiri and Weissenberg 1995; Viiri 1997; Viiri and Lieutier 2004
	<i>Ophiostoma ainoae</i>	Solheim 1986, 1992a, 1992b, 1993; Harding 1989; Viiri and Weissenberg 1995; Kirisits 1996; Viiri 1997; Grubelnik 1998; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000; Viiri and Lieutier

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^h	References ^j
	<i>Ophiostoma araucariae</i>	2004; Jankowiak 2004
	<i>Ophiostoma bicolor</i>	Kirschner 1998, 2001 Kotýnková-Sychrová 1966; Davidson <i>et al.</i> 1967; Käärik 1975; Solheim 1986, 1992a, 1992b, 1993; Harding 1985, 1989; Furniss <i>et al.</i> 1990; Viiri and Weissenberg 1995; Kirisits 1996; Krokene and Solheim 1996; Viiri 1997; Grubelnik 1998; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000; Viiri and Lieutier 2004; Salle <i>et al.</i> 2003; Jankowiak 2004
	<i>Ophiostoma cainii</i>	Harding 1989
	<i>Ophiostoma cucullatum</i>	Solheim 1986; Harding 1989; Kirisits 1996; Grubelnik 1998; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000; Viiri and Lieutier 2004; Jankowiak 2004
	<i>Ophiostoma flexuosum</i>	Solheim 1986; Harding 1989; Jankowiak 2004
	<i>Ophiostoma floccosum</i>	Mathiesen 1950, 1951; Mathiesen-Käärik 1953
	<i>Ophiostoma japonicum</i> (= <i>O. arborea</i> ?)	Kirschner 1998, 2001
	<i>(Ophiostoma minus)</i>	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ophiostoma neglectum</i>	Kirschner 1998, 2001
	<i>(Ophiostoma obscura)</i>	Kirschner 1998, 2001
	<i>Ophiostoma penicillatum</i>	Grosmann 1931, 1932; Goidánich 1936; Siemaszko 1939; Rennerfelt 1950; Mathiesen 1950; Mathiesen-Käärik 1953; Kotýnková-Sychrová 1966; Davidson <i>et al.</i> 1967; Käärik 1975; Solheim 1986; 1992a, 1992b, 1993; Harding 1985, 1989; Furniss <i>et al.</i> 1990; Viiri and Weissenberg 1995; Kirisits 1996; Krokene and Solheim 1996; Viiri 1997; Grubelnik 1998; Kirschner 1998; Kirisits <i>et al.</i> 2000; Jacobs and Wingfield 2001; Viiri and Lieutier 2004; Jankowiak 2004
	[<i>Ophiostoma penicillatum</i> f. <i>chalcographi</i>]	Mathiesen 1950
	<i>Ophiostoma piceae</i>	Grosmann 1931; Siemaszko 1939; Rennerfelt 1950; Mathiesen 1950; Mathiesen-Käärik 1953; Käärik 1975; Solheim 1986, 1992b, 1993; Harding 1985, 1989; Viiri and Weissenberg 1995; Kirisits 1996; Krokene and Solheim 1996; Viiri 1997; Grubelnik 1998; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000; Viiri and Lieutier 2004; Jankowiak 2004
	<i>Ophiostoma cf. piceae</i>	Kirschner 1998
	<i>Ophiostoma piceaperdum</i>	Kotýnková-Sychrová 1966; Solheim 1986, 1992b, 1993; Harding 1989, 1995; Viiri and Weissenberg 1995;

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^h	References ^j
<i>Leperisinus varius</i> ^{b,f} (<i>Fraxinus excelsior</i>)	(<i>Ophiostoma quercus</i>)	Kirschner 1998
<i>Orthotomicus laricis</i> ^{b,e} (<i>Pinus sylvestris</i>)	<i>Ceratocystiopsis falcata</i> <i>Ceratocystiopsis minuta</i> <i>Ceratocystis leucocarpa</i> <i>Graphium pseudomoriticum</i> <i>Leptographium</i> sp. <i>Ophiostoma ainoae</i> <i>Ophiostoma araucariae</i> <i>Ophiostoma bicolor</i> <i>Ophiostoma cucullatum</i> <i>Ophiostoma ips</i> <i>Ophiostoma japonicum</i> (= <i>O. arborea</i> ?) <i>Ophiostoma obscura</i> <i>Ophiostoma piceae</i> <i>Ophiostoma piceaperdum</i>	Kirschner 1998 Kirschner 1998, 2001 Kirschner 1998 Kirschner 1998, 2001 Kirschner 1998 Kirschner 1998, 2001 Kirschner 1998, 2001
<i>Orthotomicus proximus</i> ^{b,e} (<i>Pinus sylvestris</i>)	(<i>Ceratocstis coerulescens</i>) <i>Graphium</i> (<i>Pesotum</i> ?) <i>pynocephalum</i> (<i>Leptographium lundbergii</i>) (<i>Ophiostoma clavatum</i>) <i>Ophiostoma ips</i> <i>Ophiostoma minus</i> <i>Ophiostoma piceae</i> <i>Ophiostoma piliferum</i> (<i>Ophiostoma</i> sp.)	Mathiesen 1950; Mathiesen-Käärik 1953 Mathiesen-Käärik 1953 Mathiesen 1950; Mathiesen-Käärik 1953; Jacobs and Wingfield 2001 Mathiesen-Käärik 1953 Mathiesen 1950; Mathiesen-Käärik 1953 Mathiesen-Käärik 1953 Mathiesen-Käärik 1953 Mathiesen 1950

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b (<i>Pesotum fragrans</i>)	References ^j
<i>Pityogenes chalcographus</i> ^{b,c} (<i>Picea abies</i>)	<i>Ceratocystiopsis minuta</i> (<i>Ceratocystis coeruleescens</i>) <i>Ceratocystis polonica</i> <i>Graphium fimbriisporum</i> <i>Graphium pseudormiticum</i> (= <i>G. fimbriisporum</i> ?) <i>Graphium</i> (<i>Pesotum</i> ?) <i>pycnocephalum</i> <i>Leptographium</i> sp. <i>Ophiostoma ainoae</i> <i>Ophiostoma araucariae</i> <i>Ophiostoma bicolor</i> <i>Ophiostoma cucullatum</i> <i>Ophiostoma floccosum</i> <i>Ophiostoma neglectum</i> (<i>Ophiostoma obscura</i>) <i>Ophiostoma penicillatum</i> [<i>Ophiostoma penicillatum</i> f. <i>chalcographi</i>] <i>Ophiostoma piceae</i> <i>Ophiostoma cf. piceae</i> <i>Ophiostoma piceaperdum</i> <i>Ophiostoma serpens</i> <i>Ophiostoma stenoceras</i> <i>Pesotum</i> sp. <i>Pesotum</i> (<i>Graphium</i> ?) sp.	Mathiesen-Käärik 1953 Kirisits 1996; Kirschner 1998, 2001 ; Kirisits <i>et al.</i> 2000 Mathiesen 1950; Mathiesen-Käärik 1953 Krokene and Solheim 1996; Kirisits 1996, Kirisits <i>et al.</i> 2000 Kirisits 1996; Kirisits <i>et al.</i> 2000; Jacobs <i>et al.</i> 2003b Kirschner 1998, 2001 Mathiesen 1950; Mathiesen-Käärik 1953 Kirisits <i>et al.</i> 2000 Kirisits 1996 ; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000 ; Kirschner 1998, 2001 Krokene and Solheim 1996; Kirisits 1996; Kirschner 1998, 2001 ; Kirisits <i>et</i> <i>al.</i> 2000 Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000 Mathiesen 1950, 1951; Mathiesen- Käärik 1953; Lin 2003 Kirschner 1998; Kirscher and Oberwinkler 1999 Kirschner 1998, 2001 Grosmann 1931; Goidànic 1936; Mathiesen 1950; Mathiesen-Käärik 1953; Kirschner 1998; Jacobs and Wingfield 2001 Mathiesen 1950 Mathiesen 1950; Mathiesen-Käärik 1953; Krokene and Solheim 1996; Kirisits, 1996; Kirschner 1998, 2001 ; Kirisits <i>et al.</i> 2000 Kirschner 1998 Kotýnková-Sychrová 1966; Davidson <i>et</i> <i>al.</i> 1967; Kirisits 1996 ; Kirschner 1998, 2001 ; Kirisits <i>et al.</i> 2000 ; Jacobs and Wingfield 2001 Kotýnková-Sychrová 1966 Kirschner 1998 Kirisits 1996; Kirisits <i>et al.</i> 2000 Mathiesen 1950; Mathiesen-Käärik 1953 Mathiesen 1950, Mathiesen-Käärik 1953 Mathiesen-Käärik 1953; Jacobs and Wingfield 2001 Mathiesen 1950; Mathiesen-Käärik 1953 Mathiesen-Käärik 1953 Mathiesen 1950; Mathiesen-Käärik 1953 Mathiesen 1950; Mathiesen-Käärik 1953 Mathiesen 1950; Mathiesen-Käärik 1953
<i>Pityogenes quadridens</i> ^{b,g} (<i>Pinus sylvestris</i>)	(<i>Ambrosiella tingens</i>)	Mathiesen 1950, Mathiesen-Käärik 1953
	<i>Leptographium lundbergii</i>	Mathiesen-Käärik 1953; Jacobs and Wingfield 2001
	<i>Ophiostoma canum</i> (<i>Ophiostoma minus</i>)	Mathiesen 1950; Mathiesen-Käärik 1953
	[<i>Ophiostoma penicillatum</i> f. <i>pinii</i>] <i>Ophiostoma piceae</i>	Mathiesen 1950; Mathiesen-Käärik 1953 Mathiesen 1950; Mathiesen-Käärik 1953

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ^j
<i>Polygraphus poligraphus</i> ^{b,c} (<i>Picea abies</i>)	<i>Ambrosiella</i> sp.	Krokene and Solheim 1996; Rollins <i>et al.</i> 2001
	<i>Ceratocystiopsis minuta</i>	Kirschner 1998, 2001
	<i>Ceratocystis polonica</i>	Krokene and Solheim 1996
	<i>Graphium pseudormiticum</i> (= <i>G. fimbriisporum</i> ?)	Kirschner 1998
	<i>Ophiostoma bicolor</i>	Krokene and Solheim 1996; Kirschner 1998, 2001;
	<i>Ophiostoma penicillatum</i>	Krokene and Solheim 1996; Jacobs and Wingfield 2001
	<i>Ophiostoma piceae</i>	Kirschner 1998, 2001
	<i>Ophiostoma piceaperdum</i>	Kirschner 1998, 2001; Jacobs and Wingfield 2001
<i>Scolytus intricatus</i> ^{b,f} (<i>Quercus</i> spp.)	<i>Ophiostoma quercus</i>	Kirschner 1998
	<i>Ophiostoma stenoceras</i>	Kirschner 1998
<i>Scolytus</i> spp. ^{b,e} (<i>Ulmus</i> spp.)	<i>Ceratocystiopsis</i> cf. <i>falcata</i>	Kirisits and Konrad, unpublished
	<i>Graphium penicilliodes</i>	Brasier 1990; Kirisits <i>et al.</i> 2000;
	<i>Ophiostoma quercus</i>	Kirisits and Konrad, unpublished
	<i>Ophiostoma piceae</i>	Brasier 1990; Brasier & Kirk 1993;
	<i>Ophiostoma ulmi</i>	Kirisits <i>et al.</i> 2000; Kirisits, unpublished
	<i>Ophiostoma novo-ulmi</i>	Brasier and Kirk 1993; Lin 2003
		e. g. Siemaszko 1939; Webber and Brasier 1984; Webber and Gibbs 1989;
		Webber 1990, 2000; Brasier 1990, 1991
		e. g. Webber and Brasier 1984; Webber and Gibbs 1989; Webber 1990, 2000;
		Brasier 1990, 1991
<i>Taphrorychus bicolor</i> ^{b,c} (<i>Fagus sylvatica</i>)	<i>Graphium penicilliodes</i>	Kirschner 1998; Kirisits <i>et al.</i> 2000
	<i>Leptographium</i> sp.	Kirisits, unpublished
	<i>Ophiostoma</i> cf. <i>acericola</i>	Kirschner 1998; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma quercus</i>	Kirschner 1998; Kirisits <i>et al.</i> 2000; Lin 2003
	<i>Ophiostoma piceae</i>	Lin 2003
	<i>Ophiostoma</i> cf. <i>stenoceras</i>	Kirisits, unpublished
<i>Tomicus minor</i> ^{c,e} (<i>Pinus</i> spp.)	<i>Ambrosiella tingens</i>	Rennerfelt 1950; Mathiesen 1950; Francke-Grosmann 1952; Mathiesen-Käärik 1953; Rollins <i>et al.</i> 2001;
	<i>Ceratocystiopsis minuta</i>	Kirisits, unpublished
	<i>Graphium pseudormiticum</i>	Mathiesen 1950, 1951; Mathiesen-Käärik 1953
	<i>Leptographium guttulatum</i>	Jacobs <i>et al.</i> 2003b
	<i>Leptographium lundbergii</i>	Kirisits <i>et al.</i> 2000; Jacobs <i>et al.</i> 2001b;
	<i>Ophiostoma canum</i>	Jacobs and Wingfield 2001
		Mathiesen 1950; Mathiesen-Käärik 1953
		Rennerfelt 1950; Mathiesen 1950, 1951; Francke-Grosmann 1952; Mathiesen-Käärik 1953; Kotýnková-Sychrová 1966; Kirisits <i>et al.</i> 2000
	<i>(Ophiostoma floccosum)</i>	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ophiostoma minus</i>	Grosmann 1931; Rennerfelt 1950;
		Mathiesen 1950; Mathiesen-Käärik 1953

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ^j
	<i>Ophiostoma piceae</i>	Mathiesen 1950; Francke-Grosmann 1952; Mathiesen-Käärik 1953
	<i>Ophiostoma piliferum</i>	Grosmann 1931; Siemaszko 1939; Rennerfelt 1950; Mathiesen 1950; Francke-Grosmann 1952; Mathiesen-Käärik 1953
	(<i>Ophiostoma plurianulumatum</i>)	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ophiostoma</i> spp.	Rennerfelt 1950
<i>Tomicus piniperda</i> ^{b,f} (<i>Pinus</i> spp.)	<i>Ambrosiella tingens</i>	Rennerfelt 1950; Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ceratocystiopsis minuta</i>	Mathiesen-Käärik 1953; Kirisits <i>et al.</i> 2000
	<i>Ceratocystis autographa</i>	Kotýnková-Sychrová 1966
	<i>Graphium (Pesotum?)</i> spp.	Gibbs and Inman 1991; Wingfield and Gibbs 1991
	<i>Leptographium euphyes</i>	Jacobs <i>et al.</i> 2001a; Jacobs and Wingfield 2001
	<i>Leptographium guttulatum</i>	Jacobs <i>et al.</i> 2001b; Jacobs and Wingfield 2001
	<i>Leptographium lundbergii</i>	Mathiesen 1950; Mathiesen-Käärik 1953; Gibbs and Inman 1991; Jacobs and Wingfield 2001
	<i>Leptographium procerum</i>	Gibbs and Inman 1991; Jacobs and Wingfield 2001
	<i>Leptographium wingfieldii</i>	Morelet 1988; Piou <i>et al.</i> 1989; Lieutier <i>et al.</i> 1989; Solheim and Långström 1991; Gibbs and Inman 1991; Wingfield and Gibbs 1991; Kirisits <i>et al.</i> 2000; Jacobs and Wingfield 2001
	<i>Leptographium</i> sp.	Kirschner 1998
	<i>Ophiostoma canum</i>	Rennerfelt 1950; Mathiesen 1950; Mathiesen-Käärik 1953; Kirschner 1998
	(<i>Ophiostoma clavatum</i>)	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ophiostoma floccosum</i>	Lin 2003
	<i>Ophiostoma galeiformis</i>	Zhou <i>et al.</i> 2004
	<i>Ophiostoma huntii</i>	Gibbs and Inman 1991; Jacobs and Wingfield 2001
	<i>Ophiostoma ips</i>	Mathiesen-Käärik 1953
	<i>Ophiostoma minus</i>	MacCallum 1922; Grosmann 1931; Siemaszko 1939; Rennerfelt 1950; Mathiesen 1950; Mathiesen-Käärik 1953; Kotýnková-Sychrová 1966; Solheim and Långström 1991; Piou <i>et al.</i> 1989; Lieutier <i>et al.</i> 1989; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma piceae</i>	MacCallum 1922; Siemaszko 1939; Mathiesen 1950; Mathiesen-Käärik 1953; Solheim and Långström 1991; Gibbs and Inman 1991; Kirschner 1998; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma piceaperdum</i>	Solheim & Långström 1991; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma piliferum</i>	Siemaszko 1939; Rennerfelt 1950; Mathiesen 1950; Mathiesen-Käärik

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ^j
	<i>Ophiostoma</i> spp.	1953; Kotýnková-Sychrová 1966; Solheim and Långström 1991; Gibbs and Inman 1991; Kirisits, unpublished
		Rennerfelt 1950; Mathiesen 1950, Mathiesen-Käärik 1953
<i>Xyleborus dispar</i> ^{d,e} (Deciduous trees, rarely also conifers)	<i>Ambrosiella hartigii</i> ⁱ	Hartig 1844; Francke-Grosmann 1958, 1967; Batra 1967; Zimmermann 1973; Cassar and Blackwell 1996
	<i>Ceratocystis (Ophiostoma)</i> sp.	Zimmermann 1973
<i>Xyleborus dryographus</i> ^{d,e} (Deciduous trees)	<i>Ophiostoma verrucosum</i>	Gebhardt <i>et al.</i> 2002
<i>Xyleborus germanus</i> ^{d,e} (Deciduous trees and conifers)	<i>Ambrosiella hartigii</i> ⁱ	Francke-Grosmann 1958, 1967, Batra 1967; Cassar and Blackwell 1996
<i>Xyleborus monographus</i> ^{d,e} (Deciduous trees [Quercus sp.])	“Yellowish monilioid fungus” ⁱ <i>Ophiostoma grandicarpa</i> <i>Ophiostoma quercus</i> <i>Ophiostoma stenoceras</i> <i>Raffaelea</i> sp. ⁱ	Francke-Grosmann 1958; 1966, 1967; Kirschner 1998 Kirschner 1998 Kowalski 1991 Kirschner 1998 Kowalski 1991
<i>Xyleborus saxeseni</i> ^{d,e} (Deciduous trees and conifers)	<i>Ambrosiella sulfurea</i> ⁱ	Francke-Grosmann 1958, 1967; Batra 1967; Cassar and Blackwell 1996
<i>Xyloterus domesticus</i> ^{d,e} (Deciduous trees [Fagus sylvatica, <i>Quercus</i> sp., <i>Betula</i> sp.])	<i>Ambrosiella ferruginea</i> ⁱ <i>Graphium penicillioides</i> <i>Graphium (Pesotum?)</i> sp. <i>Ophiostoma ambrosia</i> (= <i>Ophiostoma piliferum</i>) <i>Ophiostoma bacillisorum</i> <i>Ophiostoma piceae</i> (<i>Ophiostoma quercus?</i>) <i>Ophiostoma torulosum</i>	Hartig 1872b; Francke-Grosmann 1956a, 1958, 1967; Batra 1967; Zimmermann 1973; Cassar and Blackwell 1996 Zimmermann 1973 Zimmermann 1973 Bakshi 1950 Butin and Zimmermann 1972; Zimmermann 1973 Zimmermann 1973 Butin and Zimmermann 1972; Zimmermann 1973; Kirisits, unpublished
<i>Xyloterus lineatus</i> ^{d,e} (Conifers [<i>Picea abies</i> , <i>Larix decidua</i> , <i>Larix kaempferi</i>])	<i>Ambrosiella ferruginea</i> ⁱ (<i>Ceratocystis autographa</i>) (<i>Graphium pseudormiticum</i>) <i>Leptographium lundbergii</i> (<i>Ophiostoma cucullatum</i>) (<i>Ophiostoma galeiformis</i>) <i>Ophiostoma neglectum</i>	Hartig 1872a; Mathiesen-Käärik 1953; Francke Grosmann 1956a, 1958, 1967; Batra 1967; Kirschner 1998, 2001 Bakshi 1951 Kirschner 1998, 2001 Bakshi 1950; Kotýnková-Sychrová 1966; Jacobs and Wingfield 2001 Kirschner 1998, 2001 Bakshi 1951 Kirschner 1998, 2001

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ^j
	<i>Ophiostoma penicillatum</i>	Oberwinkler 1999
	<i>Ophiostoma piceae</i>	Mathiesen-Käärik 1953; Jacobs and Wingfield 2001
	<i>Ophiostoma piceaperdum</i>	Bakshi 1950; Mathiesen-Käärik 1953; Kirschner 1998, 2001
	<i>Ophiostoma piliferum</i> (<i>Ophiostoma torulosum</i>)	Kotýnková-Sychrová 1966; Kirschner 1998, 2001
<i>Xyloterus signatus</i> ^{d,e} (Deciduous trees)	<i>Ambrosiella ferruginea</i> ⁱ	Bakshi 1950
		Kirschner 1998
		Francke Grosmann 1956a, 1958, 1967; Batra 1967

Notes: ^a Host trees of particular bark beetle species follow Postner (1974) and Pfeffer (1995). Hosts in brackets refer to the tree species, from which insects originated for the studies on the associated fungi and/or from which fungi were isolated. ^{b, c, d} Feeding habit of the respective bark beetle species: ^b phloeocephagous, ^c phloemycetophagous, ^d xylomycetophagous. ^{e, f, g} Level of intensity of association with ophiostomatoid fungi for the respective bark beetle species: ^e intimately associated, ^f loosely associated, ^g intensity of association not precisely known. Xylomycetophagous bark beetles have always been assigned to the group of scolytids with intimate association with fungi, since they nutritionally depend on ambrosia fungi. ^h Fungal species in bold font are appraised to be commonly associated with a given bark beetles species. Fungi in parenthesis are extremely rare elements of the mycobiota of a bark beetle species. Fungi in brackets are of doubtful taxonomic status. ⁱ Nutritionally important ambrosia fungus. ^j In the case of different reports by various authors regarding the abundance/importance of a particular fungus associated with a particular bark beetle species, the references, which reported the fungus as relatively common associate are printed in bold font.

Ophiostomatoid fungi vary greatly in the specificity of association with certain bark beetle species and the occurrence on different host trees. Some fungi are specifically associated with one or a few scolytid species on one host tree, while others occur with a wide range of insects and even on several host trees (Table 2). Originally, many blue-stain fungi were thought to be very specific in their association with bark beetles (Mathiesen-Käärik 1953; Francke-Grosmann 1967, Whitney 1982). As surveys of the mycobiota of scolytids have increased in number, it has become clear that strict specificity of fungi regarding their associated insects is rare and rather the exception than the rule (Table 2; Krokene and Solheim 1996; Kirisits 1996; Kirschner 1998; Kirisits *et al.* 2000; Jacobs and Wingfield 2001).

Despite the finding that some blue-stain fungi are less specific than previously believed, there are still fungal species showing a relatively narrow range of insect associates and host trees (Table 2). This is in clear contrast to other fungi, which are associated with a broad range of bark beetles and often occur on more than one host tree. Typical examples for the latter fungi are *Ceratocystiopsis minuta* and *O. piceaperdum*, which occur together with an extremely wide spectrum of European bark beetles on at least two conifer hosts (Table 2). Despite occurring in a wide range of niches, *C. minuta* and *O. piceaperdum* rely on their insect associates for transmission. However, another group of blue-stain fungi consists of unspecific species, which occur both in association with insects as well as on logs without insect attacks, indicating that they are both transmitted by bark beetles and by air-borne or rain-splash inoculum (Matiesen-Käärik 1953; Dowding 1969; Gibbs 1993).

Examples for such unspecific ophiostomatioid fungi include *Ophiostoma piceae*, *O. floccosum* and *O. piliferum* on conifers as well as *O. quercus* on hardwoods (Table 2).

5.2.4. Comparisons of the fungal assemblages of different bark beetle species

The synthesis presented in Table 2 allows for qualitative and quantitative comparisons of the differences in the whole mycobiota of different bark beetle species occurring on the same or on different host trees. This is a question, which is directly connected to the specificity of blue-stain fungi regarding their associated insects and hosts discussed above. Here, I also believe that specificity of the assemblages of fungi with individual bark beetles has previously been overestimated (e. g. Mathiesen-Käärik 1953; Francke-Grosmann 1967) and in many cases, differences of the mycobiota between scolytids occurring on the same host are relatively small and often mainly quantitative. For example, various spruce bark beetles have many elements of their mycobiota in common (Table 2). One major quantitative difference between the various bark beetles on Norway spruce refers to *C. polonica* that is more commonly associated with *I. typographus*, *I. duplicatus* and *I. amatinus*, while other spruce bark beetles rarely, if at all carry this blue-stain fungus (e. g. Solheim 1986; Harding 1989; Krokene and Solheim 1996; Kirschner 1998; Kirisits *et al.* 2000; Table 2 and references therein).

Certain elements of the fungal assemblages of bark beetles on pine also overlap between individual species, e. g. *Ophiostoma ips*, *O. brunneo-ciliatum*, *O. minus* and *C. minutula*, but there are also fungi that are relatively specific for individual scolytid species (Table 2). For example, the mycobiota of *T. minor* and *I. acuminatus* differ considerably, even though these two scolytids often occur together on thin-barked parts of the bole or branches of pines. Despite some overlap, the spectrum of fungi associated with bark beetles on different host trees (e. g. spruce, pine and larch; Table 2) generally shows large differences, which might suggest that the host tree is more important than the associated insects, in driving specificity and speciation of ophiostomatoid fungi.

5.2.5. Variation in the mycobiota of bark beetles

An intriguing aspect of the association of blue-stain fungi with phloem-feeding bark beetles is the variation of the assemblages of fungi associated with the same bark beetle species at different localities in Europe (Table 2 and references therein). Various factors might be responsible for this variation. Among these, the methodology employed in different studies may often be very important. Every method of fungal isolation is selective. Thus, the species spectrum and frequency of fungal associates of bark beetles can vary considerably depending on the sources and the methods of isolation employed by different researchers (e. g. Furniss *et al.* 1990; Krokene 1996; Yamaoka *et al.* 1997; Grubelnik 1998, Kirschner 1998). Methodological factors should be considered, when comparing results of different studies on the mycobiota of bark beetles (Table 2). In addition, mycological studies always have a strong "human component". Thus, the experience, skills and focus of the researcher can have a strong influence on the outcome of a study.

The investigations by Kirschner (1998, 2001) may be a good example to illustrate the influence of the isolation methods on the results of a study. Kirscher (1998, 2001) used a specific medium for isolation, consisting mainly of pieces of inner bark of *Picea abies* embedded in water agar, onto which adult, living bark beetles were placed individually. Such an isolation procedure was not used in any other study on the mycobiota of European bark beetles and this may be the reason that numerous fungi recorded by Kirschner (1998, 2001) have not been reported in any other investigation.

The variation of the mycobiota of bark beetles at different localities in Europe has been best-known for *I. typographus* and this scolytid is again used as an example to illustrate this phenomenon further, although variation in the spectrum of blue-stain fungi between different localities is also known for other bark beetle species (see Table 2 and references therein). An extremely diverse assemblage of blue-stain fungi is associated with *I. typographus* in Europe. A similar spectrum of fungi has been reported to occur together with this bark beetle in various parts of the continent, but remarkable qualitative and quantitative differences in the composition of the mycobiota of this insect between study sites have also been documented. Differences are most obvious for the most virulent fungal associate of *I. typographus*, *C. polonica*. Other differences in the mycobiota of *I. typographus* are also well-known, in particular for *O. piceaperdum* (Table 2), but they will not be discussed further here.

Thus-far, *C. polonica* only has been found as common associate of *I. typographus* in Poland (Siemaszko 1939), Norway (e. g. Solheim 1986, 1992a, 1992b; Krokene and Solheim 1996), in samples from Belgium (Harding 1989) and at some localities in Austria (Kirisits 1996, 2001; Grubelnik 1998; Kirisits *et al.* 2000). In contrast, it was not recorded at all in some studies (Rennerfelt 1950; Kotýnková-Sychrová 1966), or occurred rarely in investigations performed in Sweden (Mathiesen-Käärik 1953; Harding 1989), Denmark (Harding 1989), Finland (Viiri 1997), Germany (Harding 1989; Kirschner 1998) and France (Salle *et al.* 2003). It was also relatively rare in a recent study conducted in Southern Poland (Jankowiak 2004). In another French study, *C. polonica* occurred at moderately high frequencies (Viiri and Lieutier 2003). While it was the dominant fungal associate of *I. typographus* in South-Eastern Norway (Solheim 1986, 1992a, 1992b), *C. polonica* was less frequently isolated at six localities in Central Norway (Solheim 1993). Likewise, the fungus was rare or only moderately frequent in several study sites in Austria, in contrast to other localities where it was the dominant fungus associated with *I. typographus* (Kirisits 1996, 2001; Grubelnik 1998; Kirisits *et al.* 2000). It is particularly interesting that *C. polonica* is the most virulent blue-stain fungus associated with *I. typographus* (e. g. Horntvedt *et al.* 1983; Christiansen 1985; Solheim 1988; Krokene and Solheim 1998), which gives rise to speculation about the ecological consequences of the variation of the occurrence of *C. polonica* within the distribution range of *I. typographus* (Harding 1989; Solheim 1993).

There is no clear geographic pattern in the occurrence of *C. polonica* in Europe, since the fungus was both reported as frequent associate of *I. typographus* in some studies in Northern (e. g. Solheim 1986, 1992a, 1992b; Krokene and Solheim 1996) and Central Europe, while it occurred rarely or not at all in studies in adjacent

countries (e. g. Rennerfeldt 1950; Mathiesen-Käärik 1953; Kotýnková-Sychrova 1966; Harding 1989; Viiri 1997; Kirschner 1998). Furthermore, *C. polonica* has also been found together with *I. typographus* f. *japonicus* in Japan (Yamaoka *et al.* 1997; Marin 2004), which suggests that the fungus follows the distribution range of its vectors and host trees in Eurasia. Differences in the methodology between various studies might also explain some of the varying results concerning the mycobiota of *I. typographus* (see above), and in particular those regarding *C. polonica*. However, the conflicting results about the occurrence and frequency of fungi associated with *I. typographus* in Europe cannot be ascribed exclusively to differences in the methodology employed in the various studies.

It has been suggested that the population dynamics of *I. typographus* has a strong influence on the incidence and frequency of *C. polonica* or that *C. polonica* may even play a role in the initiation and development of outbreaks of *I. typographus* (Harding 1989; Solheim 1993). Following this hypothesis, *C. polonica* occurs at low frequencies during non-outbreak periods of *I. typographus*, but its frequency increases during the course of outbreaks. As increasing numbers of healthy trees are attacked, *C. polonica* gains a habitat, in which it is more competitive than other fungal associates of the spruce bark beetle (Harding 1989; Solheim 1993). This competitive advantage is probably due to its ability to maintain growth in the wet sapwood of healthy trees, which contains low levels of oxygen (Solheim 1991). Thus-far, there is only weak evidence supporting this hypothesis. Solheim (1993) developed this theory to explain differences in the frequency of *C. polonica* between South-Eastern Norway, where a severe outbreak of *I. typographus* occurred in the 1970s and Central Norway where the spruce bark beetle never caused large-scale damage. However, Harding (1989) did not find obvious differences in the frequency of *C. polonica* between sites varying in the outbreak status of *I. typographus*. Studies in Austria also provided no support for the view that the occurrence of *C. polonica* is related to damage levels by *I. typographus*. Here, *C. polonica* occurred at low frequencies in stands outside the natural range of Norway spruce, which have been suffering most severely during the outbreak of *I. typographus* since 1992 (Grubelnik 1998; Kirisits *et al.* 2000; Kirisits 2001). In these Austrian studies, *C. polonica* was more frequently recorded at localities within the natural range of Norway spruce. This pattern of diffusion could be due to climatic influences. *Ceratocystis polonica* has a relatively low temperature maximum around 31–32°C (Marin 2004) which may inhibit its vigour and give other fungi such as *O. bicolor* with higher growth maximum (Solheim 1991) competitive advantages at localities with high spring and summer temperatures, such as at the Austrian localities in the foothills of and outside the Alps. This hypothesis certainly requires thorough study.

Some authors have suggested that the vigour/vitality of Norway spruce may have a strong influence on the spectrum of fungi that are isolated from the phloem and sapwood following attack by *I. typographus* (Harding 1989; Solheim 1992b; Jankowiak 2004). According to this view, vigorous trees may favour the development of *C. polonica*, whereas other ophiostomatoid fungi are more competitive than *C. polonica* on low vigorous, wind-thrown and wind-broken trees as well as logs. This hypothesis is connected to the other hypothesis that *C. polonica* increases its frequency during outbreak periods of *I. typographus* (Harding 1989;

Solheim 1993; see above). Harding (1989) found no relationship between the occurrence of *C. polonica* and the health status of Norway spruce trees. In a recent study in Poland, *C. polonica* was relatively rare, but it occurred more frequently on healthy trees compared to weakened or dead trees as well as wind-thrown, wind-broken and trap trees (Jankowiak 2004). Despite a few hypotheses have been suggested to explain the variation of the frequency of *C. polonica* as associate of *I. typographus* at different localities in Europe, this phenomenon seems to be very complex and is not fully understood thus-far. This intriguing question, therefore, deserves continuing and careful study in the future.

6. SYMBIOSIS BETWEEN BARK BEETLES AND FUNGI

The term “symbiosis” has been used with different meanings in various scientific disciplines, either in a strict or broad sense. For the present discourse on fungal associates of bark beetles I follow the terminology of Whitney (1982). In its original definition symbiosis refers to the more or less continuous living together of different species, regardless of the benefits or disadvantages to the partners. This broad definition includes mutualism, antagonism and other symbiotic relationships. Mutualism, often referred to as symbiosis in its strict sense, is defined as relationship between two separate species where both partners benefit. In antagonistic relationships, one or both partners are detrimentally affected. The symbiotic relationships between xylomycetophagous bark beetles and ambrosia fungi (6.1) and between true bark beetles and fungi (6.2) are discussed below.

6.1. Symbiosis between xylomycetophagous bark beetles and ambrosia fungi

The relationship between xylomycetophagous bark beetles and ambrosia fungi clearly represents a symbiosis, since the two partners are in close physical contact with each other throughout their life and do not become separated at any stage of their life histories (Francke-Grosmann 1967; Beaver 1989; Berryman 1989). Moreover, beetles and fungi are mutualistic symbionts, which benefit from and obligately depend on each other (Francke-Grosmann 1967; Berryman 1989).

Ambrosia fungi mainly benefit from the association with ambrosia beetles by the consistent dissemination of fungal spores and their inoculation into new, suitable habitats (Francke-Grosmann 1967; Norris 1979; Beaver 1989). The fungi are also selectively protected and nourished in the beetle's mycangium. In the galleries, ambrosia beetles actively take care of their ambrosia fungi and protect them from other “weed” fungi which leads to the dominance of ambrosia fungi in the galleries of xylomycetophagous bark beetles (Francke-Grosmann 1967; Beaver 1989).

For the beetles the advantage of the association with their domesticated ambrosia fungi is obvious. The fungi provide the only source of food for the adult ambrosia beetles and their larvae (Francke-Grosmann 1967; Norris 1979; Beaver 1989; Berryman 1989). Ambrosia fungi derive nutrients from the wood of their host trees, concentrate them in their mycelium and make them available to the ambrosia beetles that feed on ambrosial layers formed along the galleries. Apart from converting

nutrients from the wood and providing them in a nutrient form (sugars and other carbohydrates, lipids and proteins) that can be digested by the beetles, fungi produce and concentrate nutrients essential for the beetles that are not at all or only at very low concentrations present in the wood. Nutritionally beneficial fungi provide a very rich source of protein, nitrogen and amino acids to the beetles (Beaver 1989; Six 2003 and references therein). Likewise, ambrosia fungi supply the beetles with sterols (especially ergosterol) that are very essential for growth, molting, and reproduction (Beaver 1989; Six 2003 and references therein). The fungal diet is probably also important for fulfilling some of the vitamin requirements of the insects (Beaver 1989). The total nutritional dependence of the xylem-cetophagous bark beetles on their associated fungi makes it possible to successfully rear the insects on artificial cultures of their ambrosia fungi (Francke-Grosman 1967; Beaver 1989; Norris 1979).

6.2. Symbiosis between phloeocephagous bark beetles and fungi

As in the ambrosia beetles and their associated ambrosia fungi, the relationship between phloeocephagous bark beetles and certain fungi, mainly ophiostomatoid fungi, yeasts and occasionally basidiomycetes, represents in many cases also a symbiosis, since the partners are more or less consistently and continuously associated with each other. Only for a short period of time, during some stages of larval development in the phloem, insects and fungi can physically become separated from each other, and the larvae feed ahead of the front of fungal colonization in the phloem (Whitney 1971; Yearian *et al.* 1972). Contact between them is re-established after pupation of the insects in the pupal chambers where the fungi often form dense layers of conidiophores and sometimes also ascocarps, and young adults become inoculated with conidia and ascospores (Whitney 1971; Webber and Gibbs 1989; Yearian *et al.* 1972) (see also Fig. 3).

While the association between phloeocephagous bark beetles and certain fungi clearly fulfills the criteria of a symbiosis, there is no unequivocal agreement whether their relationship represents mutualism (Whitney 1982; Harding 1989; Harrington 1993a; Paine *et al.* 1997). True bark beetles form a heterogenous group and various species differ considerably in their nutrition biology (phloeocephagous versus phloem-cetophagous), aggressiveness, attack strategies and range of vigour of host trees selected for breeding. It is thus reasonable to assume that there is no universal model describing the interactions between phloem-feeding bark beetles and associated fungi. Bark beetle species may vary considerably in their dependence on fungi and many different forms of symbiosis may be encountered in different bark beetle-fungal complexes.

Fungal associates of true bark beetles benefit in similar ways from the association with their insect partners as ambrosia fungi benefit from the relationship with xylomycetophagous scolytids (Whitney 1982; Krokene 1996; Paine *et al.* 1997; Six 2003). The fungi are transmitted and inoculated to new, appropriate habitats by the beetles. The insects not only disseminate fungal spores, but also create wounds in the bark, and enable blue-stain fungi and other fungal associates to infect the

tissues of their host trees. Many blue-stain fungi occur exclusively in association with bark beetles and obligately depend on the beetles to be transmitted to suitable habitats (Francke-Grosmann 1967; Krokene 1996; Paine *et al.* 1997; Upadhyay 1981; Kirschner 1998; Six 2003).

The ecological significance of the fungi for the bark beetles is less clear and in most cases still not fully understood. Different groups of fungi may be beneficial or inimical to the insects in various ways (Paine *et al.* 1997). I will discuss four modes of action how bark beetles can gain benefits from their associated fungi: involvement of fungi in tree killing and in exhaustion of the defense mechanisms of the host tree during bark beetle attack (6.2.1.), nutrition (6.2.2.), protection from detrimental fungi (6.2.3.), and involvement in pheromone production (6.2.4.).

6.2.1. Involvement of fungi in tree killing and in exhaustion of the defense mechanisms of the host during attack by bark beetles

Blue-stain fungi have long been suspected to play an important role in killing of conifer trees attacked by bark beetles (e. g. Nelson and Beal 1929; Nelson 1934; Bramble and Holst 1940). Many researchers considered the involvement of the fungi in tree killing and in exhaustion of the defence mechanisms of the host as the main mode of action from which bark beetles benefit from the association with fungi (e. g. Berryman 1972; Whitney 1982; Christiansen *et al.* 1987; Christiansen and Bakke 1988; Harding 1989; Raffa and Klepzig 1992; Krokene 1996; Paine *et al.* 1997). Association with phytopathogenic fungi has also been mentioned as an important characteristic of aggressive bark beetle species and even as a prerequisite for scolytids to display aggressive behaviour (Christiansen *et al.* 1987; Krokene 1996). The high level of virulence of some fungal associates to their host trees (see 3.3.1.) is the primary argument in support of the hypothesis that fungi are important components in the ability of bark beetles to kill trees (e. g. Berryman 1972; Whitney 1982; Christiansen *et al.* 1987; Raffa and Klepzig 1992; Krokene 1996).

However, the general importance of fungi to help bark beetles in overcoming the defense mechanisms of the host trees has also been questioned by several authors (e. g. Harrington 1993a; Wingfield *et al.* 1995; Paine *et al.* 1997; Lieutier 2002, chapter 9). This view is based on several lines of evidence. Here, I will mention only a few examples of the arguments that have been presented. Harrington (1993a) considers the virulence of ophiostomatoid fungi merely as adaption to the habitat of bark beetles on living trees that might have been evolved as result of interspecific competition between various ophiostomatoid fungi, but not primarily through coevolution with bark beetles. By their fast growth, tolerance against host chemicals and their ability to grow under anaerobic conditions in moist sapwood, pathogenic species gain competitive advantages over other fungal associates (Harrington 1993a). Other arguments refer to the intimacy of association between bark beetles and associated blue-stain fungi. For example, *T. piniperda* is so loosely associated with *L. wingfieldii* and other ophiostomatoid fungi that it is difficult to understand, how fungi could contribute to exhaust the defence mechanisms of pine trees during natural attack of the pine shoot beetle (Lieutier *et al.* 1989a; Lieutier 1993, 2002, chapter 9). In *I. typographus*, the pathogenic blue-stain fungus *C. polonica* has been

suggested to be essential to overcome the defense mechanisms of Norway spruce (Christiansen *et al.* 1987; Christiansen and Bakke 1988; Krokene 1996; Krokene and Solheim 1998). However, the frequency of *C. polonica* varies considerably between different localities and in many areas in Europe this pathogenic fungus is only rarely associated with *I. typographus* (see 5.2.5.). This clearly demonstrates that the spruce bark beetle does not obligately need *C. polonica* to successfully colonize living trees. Even in areas, where *C. polonica* occurs rarely, *I. typographus* is associated with numerous ophiostomatoid fungi, in particular *O. bicolor*, *O. penicillatum* and *O. piceaperdum* (Table 2). Thus, *I. typographus* always transmits fungi when attacking living host trees. However, these species are less virulent than *C. polonica* (Horntvedt *et al.* 1983; Harding 1989; Kirisits 1998) and probably less efficient to exhaust the defense systems of Norway spruce.

Apart from the few examples mentioned above, no attempt is made in this chapter to extensively review the role of ophiostomatoid fungi in tree killing and in exhaustion of the defense mechanism of the host during bark beetle attack. This is because this aspect of bark beetle-fungus relationship has recently been extensively treated by Lieutier (2002) and Lieutier (chapter 9) and I also refer to other recent reviews of this topic (Whitney 1982; Harding 1989; Harrington 1993a; Raffa and Klepzig 1992; Krokene 1996; Paine *et al.* 1997). I believe that the various lines of evidence justify to assume that bark beetle species greatly differ in the dependence on fungi to interfere with the defense mechanisms of their host trees. It is easy to predict that the debates on the role of fungi in overcoming the defense systems of host trees will continue in the future. Simultaneously, the conflicting views will likely stimulate research in various scolytid-fungus-host-systems, which will contribute to improve our current understanding of the intriguing interactions between bark beetles, fungi and live conifer trees.

The association of the Dutch elm disease pathogens *O. ulmi* and *O. novo-ulmi* with elm bark beetles represents a bark beetle-fungus relationship that differs from that of conifer bark beetles with blue-stain fungi. *Scolytus* species transmit *O. ulmi* and *O. novo-ulmi* during maturation feeding from diseased to healthy trees (Webber and Brasier 1984; Webber and Gibbs 1989). These healthy trees get infected, decline due to Dutch elm disease and become susceptible to attack by the next generation of elm bark beetles, which breed in the bark of diseased elm trees. The pandemics of Dutch elm disease since the early 20th century have created large amounts of susceptible host trees for the elm bark beetles and the fungi thus provided benefits to the populations of these scolytids (Webber and Brasier 1984; Webber and Gibbs 1989; Webber 2000). It should be considered, however, that the association of *O. ulmi* and *O. novo-ulmi* with *Scolytus* spp. is an untypical bark beetle-fungus-host relationship, since it is driven by an introduced pathogen that came in contact with highly susceptible host trees (Brasier 2000).

6.2.2. Nutrition

Concerning their nutritional biology, it is reasonable to further distinguish two groups within bark beetles colonizing the phloem of trees. One group of species feeds both on the phloem of the host trees, but also on associated fungi, and it is

probably justified to describe their feeding habit as "phloeomycetophagous" (Francke-Grosmann 1952, 1966, 1967). Some, but not all species in this group possess mycangia in which nutritionally relevant fungi are carried (Francke-Grosmann 1952, 1963b; Whitney 1982; Paine *et al.* 1997; Six 2003). These scolytids share characteristics of true bark beetles and xylomycetophagous bark beetles (Francke-Grosmann 1952, 1966, 1967; Six 2003 and references therein).

Within the European bark beetle fauna, two species on pine, *T. minor* and *I. acuminatus* have been reported to have a phloeomycetophagous feeding habit (Francke-Grosmann 1952, 1967). The larvae of these bark beetle species create very short galleries in the phloem and move later in the outer sapwood where they pupate. Initially the larvae feed in the phloem, but at later stages of their development they feed on conidia and mycelium of fungi, *I. acuminatus* on *Ambrosiella macrospora* and *T. minor* on *A. tingens*. The fungi form dense conidial layers in the larval galleries of *I. acuminatus* and *T. minor*, very similar to ambrosia fungi associated with ambrosia beetles. In *I. acuminatus* an oral mycangium has been detected in which the conidia of *Ambrosiella tingens* are transported (Francke-Grosmann 1963b). No mycangium has so far been found in *T. minor* (Francke-Grosmann 1952, 1963b). Scolytids with phloeomycetophagous feeding habit are probably more numerously represented in the North American bark beetle fauna. Although they have not explicitly referred to as phloeomycetophagous, *D. frontalis* and *D. ponderosae* likely belong to this group, since they both possess a mycangium and feed on phloem as well as on fungi, upon which they are largely dependent for nutrition (Barras 1973; Klepzig 2001a, 2001b; Six 2003).

Most bark beetle species that breed in the phloem of trees are truly phloeophagous and thus feed mainly on the phloem of their host trees, which is a nutrient-rich substrate. Typically, they do not possess a mycangium and are less - and in many cases not obligately - dependent on fungal associates for nutrition, although the fungi may provide an additional food source for larvae and teneral adults (Francke-Grosmann 1967; Harding 1989; Whitney 1982; Six 2003). Different groups of fungi may vary in their importance for the insects. Yeasts are suspected to be essential as suppliers of vitamins, especially B-group vitamins (Strongman 1986; Pignal *et al.* 1988; Beaver 1989; Harding 1989 and references therein), while non-mycangial ophiostomatoid fungi are generally thought to be less, if at all, important for nutrition of phloeophagous bark beetles (Grosmann 1931; Yearian *et al.* 1972; Whitney 1982; Harding 1989; Fox *et al.* 1993). Some blue-stain fungi even display antagonism against bark beetles (Barras 1970; Yearian *et al.* 1972; Klepzig *et al.* 2001a, 2001b).

The nutritional relevance of yeasts and blue-stain fungi for phloeophagous bark beetles in Europe is poorly known, but the few studies that have been conducted so far, suggest that the insects can be reared successfully in the absence of blue-stain fungi, while a positive influence of yeasts cannot be excluded (Grosmann 1931; Harding 1989; Colineau and Lieutier 1994; Simsek and Führer 1993; Simsek 1994). Grosmann (1931) concluded that yeasts and blue-stain fungi are not obligately needed for the development of *I. typographus*, since a single larva free of micro-organisms developed into an adult insect. This conclusion is questionable, however, due to the limited scope of the study and because the fecundity and behaviour of

progeny was not tested. Harding (1989) was able to rear *I. typographus* in the complete absence of blue-stain fungi through two generations, however, yeast were occasionally isolated from parent and offspring beetles. Simsek and Führer (1993) and Simsek (1994) successfully reared *I. typographus* from eggs to mature adults on a semi-artificial medium based on ground phloem, in which the development of associated fungi was suppressed by fungicides. Finally, *Ips sexdentatus* showed normal breeding behaviour and reproduced successfully in absence of its fungal associates, *O. brunneo-ciliatum* and *O. ips* (Colineau and Lieutier 1993). Besides these European studies, Yearian *et al.* (1972) successfully reared *I. avulsus*, *I. calligraphus* and *I. grandicollis* through 3 to 4 generations in the absence of *O. ips* on pine logs. In summary, the nutritional role of associated fungi for phloeophagous bark beetles has received relatively little attention in Europe thus-far, and this topic should, therefore, be investigated more intensively in the future.

Studies in North America have shown that certain blue-stain fungi are antagonists of bark beetles by making the phloem unsuitable for larval nutrition or inhibiting oviposition of adult beetles. In phloem colonized by *O. minus* larval development of *D. frontalis* was negatively affected in various ways, resulting in lower reproductive success (Barras 1970; Klepzig *et al.* 2001a, 2001b). Similarly, oviposition of *Ips avulsus*, *Ips calligraphus* and *Ips grandicollis* was almost totally inhibited in the phloem of pine logs that had been preinfected by *O. ips* (Yearian *et al.* 1972). Among conifer bark beetles in Europe it is generally not known, if blue-stain fungi could have negative effects on brood development, but Webber and Gibbs (1989) reported that larvae of elm bark beetles (*Scolytus* spp.) avoided areas of elm bark that had previously been colonized by *O. ulmi*. Possible antagonistic effects of blue-stain fungi on bark beetles in Europe form an uninvestigated area of research that deserves attention in the future.

6.2.3. Protection from detrimental fungi

The idea that mutualistic fungi protect bark beetle galleries from invasion by detrimental fungi originally comes from *D. frontalis* and its associated fungi and phoretic mites (Klepzig *et al.* 2001a, 2001b). In this system, the two mycangial fungi of *D. frontalis*, *Entomocorticium* sp. and *C. ranaculosus* compete with the nonmycangial and antagonistic fungus, *O. minus* for resources in the phloem of trees attacked by the southern pine beetle. The two mycangial fungi, especially *Entomocorticium* sp. and to a lesser extent *C. ranaculosus*, provide some protection from the detrimental *O. minus* to the developing larvae. Other examples of such competitive interactions are mentioned by Six (2003).

I speculate that protection of the developing broods from antagonists by associated fungi could be important in many beetle-fungus-systems. Blue-stain fungi quickly colonize the gallery systems and the adjacent phloem after attack by bark beetles and likely occupy this niche at least until the young insects have left their host trees. Thus, ophiostomatoid fungi might play a considerable role in preventing the establishment of fungi that are deleterious to the developing larvae. This postulate certainly requires confirmation by thorough studies.

6.2.4. Involvement in pheromone production

A few studies provided evidence that fungi may be involved in the production of pheromones (Whitney 1982 and references therein; Harding 1989 and references therein; Six 2003). The only investigation addressing this question in an European bark beetle-fungus system is that of Leufvén *et al.* (1984) who showed in laboratory assays that yeasts associated with *I. typographus* can convert cis/trans-verbenol, an aggregation pheromone of this bark beetle, to verbenone, which functions as an antiaggregation pheromone. The abundance of yeasts increased during later phases of bark beetle attack and this increase occurred at the same time as the increase of the amount of verbenone, which suggests that yeasts could be important in interfering with the chemical communication of *I. typographus* under field conditions (Leufvén and Nehls 1986).

Many species of *Ophiostoma* and *Ceratocystis* produce volatile metabolites that give fungal cultures characteristic odors (Hanssen 1993). These metabolites include short-chain alcohols and esters, mono- and sesquiterpenes as well as other miscellaneous compounds (Hanssen 1993). The production of intensive aromas by ophiostomatoid fungi and especially by *Ceratocystis* species is viewed as an adaption to attract various insects that are unspecifically involved in dissemination of these fungi (Kile 1993; Harrington and Wingfield 1998). It is attractive to think that volatiles produced by ophiostomatoid fungi might also play a role in the chemical communication of bark beetles, but so far this assumption is speculative and requires investigation (Hanssen 1993).

7. PERSPECTIVES FOR FUTURE RESEARCH

The association of fungi with bark beetles is a fascinating example of symbiosis that has received much attention in the past. It is easy to predict that the fungi transmitted by bark beetles and the relationship with their associated insects and host trees will continue to fascinate scientists in various disciplines. The fact that bark beetles are important forest pests and that many fungal associates of scolytids cause destructive tree diseases or are economically important agents of blue-stain, will likely help to justify allocation of research resources to continue studying these fungi thoroughly and in an interdisciplinary manner. Below I will present a few ideas for future research, from a personal, very subjective perspective.

Despite tremendous research efforts in the past I feel that we still can learn a lot about the diversity of fungi in the bark beetle habitat. So far, only a minor portion of the 154 European bark beetle species (Postner 1974) have been examined regarding the fungi they carry. It is, therefore, likely that a large number of ophiostomatoid fungi and other fungi associated with bark beetles remain to be discovered, even in a relatively well-studied region as Europe. Further surveys of ophiostomatoid species associated with bark beetles in Europe could greatly improve the knowledge on the taxonomy, ecology and biogeography of these fungi.

It is only a little more than a decade ago that the issue of "sibling species" within the ophiostomatoid fungi has started to receive considerable attention (Brasier and Kirk 1993). They represent morphologically similar or even indistinguishable fungi

that are ecologically and genetically isolated and represent different biological species. Examples of such sibling species in Europe are *O. quercus* and *O. piceae* as well as the bark beetle-vectored blue-stain fungi, *C. polonica* and *C. laricicola* (Brasier and Kirk 1993; Kirisits 2001; Harrington *et al.* 2002; Marin 2004). Due to the rapid progress in the development of reliable molecular markers, it is likely that many more sibling and kryptic species within the ophiostomatoid fungi will be identified in the near future. Genetic studies, mating experiments, studies on the host specialization of fungi and growth experiments can be effectively combined to provide several lines of evidence to distinguish "sibling species". These discoveries will also improve the understanding of speciation within the ophiostomatoid fungi and will provide new insights in their ecology and relationships with insects.

The synthesis of studies on the fungal assemblages of European bark beetles (Table 2) has clearly shown that remarkable variation in the composition of the mycobiota of the same bark beetle species at different localities in Europe can occur. *Ips typographus* has been mainly used as a model to illustrate this phenomenon, but it is also documented for other European scolytids. The factors, which drive the variation of the mycobiota of *I. typographus* as well as the resulting implications for the ecology and population dynamics of the spruce bark beetle still remain poorly known. Thus, further studies on the variation of the mycobiota of *I. typographus* in various parts of Europe will represent an intriguing area for future research. Although I have focussed on *I. typographus*, comparisons of the mycobiota of scolytids in various parts of Europe are certainly also of interest for other economically important bark beetle species. I also believe that the role of phoretic mites associated with bark beetles in transmission of blue-stain fungi should be further investigated, since mites have been shown to be very important in driving the transmission and frequency of ophiostomatoid fungi in bark beetle-fungus-mite-systems in North America (Bridges and Moser 1983, 1986; Klepzig *et al.* 2001a, 2001b).

The relationships between phloem-feeding bark beetles and fungi represent in most cases a "polysymbiosis". Typically, at least two, and often more fungal species are consistently associated with one scolytid species. It is reasonable to assume that different fungi interact in various ways with their bark beetle partners, with some fungi being beneficial for the insects, while others being neutral or antagonistic symbionts (Six 2003). Likewise, fungal associates strongly compete with each other for space and resources in the bark beetle habitat (Klepzig *et al.* 2001a, 2001b). These competitive interactions may influence the frequency of occurrence of fungal associates, which likely also has some consequences for the insect-fungal relationships. I think that we have presently just started to understand the interactions between various fungal associates of bark beetles at varying ecological situations (Klepzig *et al.* 2001a, 2001b; Six 2003). Therefore, the competitive interactions between fungi associated with scolytids *in vitro* and *in vivo* form a largely uninvestigated and highly intriguing area for future research that will provide essential information for characterizing the bark beetle-fungus symbiosis (Klepzig 1998; Klepzig and Wilkins 1997; Klepzig *et al.* 2001a, 2001b; Six 2003).

Although much is already known about the phytopathogenicity of bark beetle-associated blue-stain fungi, there is still a need for further studies. The pathogenicity

of some potentially important fungal species and the ability of these fungi to stimulate the defense reactions of their host trees should be tested, considering especially the variation of virulence displayed by different isolates of the same fungal species (see Lieutier *et al.* 2004). Likewise, the recently discovered mycovirus-mediated hypovirulence in *C. polonica* and *C. laricicola* (Marin 2004) offers many possibilities for future research. This includes the possible ecological implications of dsRNA mycovirus infections on populations of these *Ceratocystis* species and possible chances for implementation of biological control strategies. It may also be very intriguing to screen other pathogenic blue-stain fungi for the presence of dsRNA mycoviruses and to study the possible effects of the viruses on the pathogenicity and fitness of the fungi.

Pathogenic blue-stain fungi have been an invaluable tool to study the defense mechanisms of conifers against bark beetles and fungi (Lieutier 2002, chapter 9 and references therein) and I look forward to the progresses in the understanding of the resistance mechanisms of conifers that will be made in the future. In addition, studies should consider the processes of inoculation and infection of blue-stain fungi under natural conditions. For many conifer bark beetle species it is well established that they carry blue-stain fungi, however, the spore load of associated fungi transmitted by individual beetles is not known for most beetle-fungus-systems (but see Webber and Brasier 1984; Webber and Gibbs 1989; Webber 1990, 2000). For a few blue-stain fungi (*L. wingfieldii* and *O. brunneo-ciliatum*) a relationship between the number of spores inoculated and the intensity of the defense reaction has been established (Lieutier *et al.* 1989a; Lieutier 1993, 2002, chapter 9), but such a relationship has not been investigated for many other bark beetle-associated blue-stain fungi. Both the spore load carried by the beetles as well as possible relationships between the number of spores inoculated by the insects to the tree and the intensity of the tree's defense reactions are essential to understand inoculation and infection of blue-stain fungi by bark beetles under field conditions.

Recent reviews of the symbiosis between bark beetles and fungi, including the present one, have proposed that there may be great differences between various bark beetle-blue-stain fungus-systems in terms of the relevance of the fungi (Wingfield *et al.* 1995; Krokene 1996; Paine *et al.* 1997; Lieutier 2002, chapter 9; Six 2003). In order to improve our understanding of the relationship between bark beetles and blue-stain fungi, additional studies should be initiated aimed at investigating the direct effects of association with fungi for phloem-feeding bark beetles. Whitney (1982) proposed that the role of associated fungi for bark beetles could be revealed by production of aseptic, microbe-free insects and by comparing them in biological experiments with specifically fungus-inoculated insects or beetles from field populations. The production of microbe-free insects is extremely difficult to achieve and incudes the risk of failure. However, I believe that studies using aseptic bark beetles will be a main approach in the future to make progress in the understanding of the complex relationships between fungi, bark beetles and their host trees.

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9. REFERENCES

- Aghayeva, D.N., Wingfield, M.J., De Beer, W.Z. & Kirisits, T. 2004. Two new *Ophiostoma* species with *Sporothrix* anamorphs from Austria and Azerbaijan. *Mycologia*, in press.
- Bakshi, B.K. 1950. Fungi associated with ambrosia beetles in Great Britain. *Transactions of the British Mycological Society*, 33, 111-20.
- Bakshi, B.K. 1951. Studies on four species of *Ceratocystis*, with a discussion on fungi causing sap-stain in Britain. *Mycological Paper*, 35, 1-16.
- Ballard, R.G., Walsh, M.A. & Cole, W.E. 1982. Blue-stain fungi in xylem of lodgepole pine: a light-microscope study on extent of hyphal distribution. *Canadian Journal of Botany*, 60, 2334-41.
- Ballard, R.G., Walsh, M.A. & Cole, W.E. 1984. The penetration and growth of blue-stain fungi in the sapwood of lodgepole pine attacked by mountain pine beetle. *Canadian Journal of Botany*, 62, 1724-29.
- Barras, S.J. 1970. Antagonism between *Dendroctonus frontalis* and the fungus *Ceratocystis minor*. *Annals of the Entomological Society of America*, 63, 1187-90.
- Barras, S.J. 1973. Reduction of progeny and development in the southern pine beetle following removal of symbiotic fungi. *Canadian Entomologist*, 105, 1295-99.
- Batra, L.R. 1963a. Ecology of ambrosia fungi and their dissemination by beetles. *Transactions of the Kansas Academy of Science*, 66, 213-36.
- Batra, L.R. 1963b. Contributions to our knowledge of ambrosia fungi II. *Endomycopsis fasciculata* nom. nov. *American Journal of Botany*, 50, 481-87.
- Batra, L.R. 1967. Ambrosia fungi: A taxonomic revision, and nutritional studies of some species. *Mycologia*, 59, 976-1017.
- Beaver, R.A. 1989. Insect – Fungus Relationships in the Bark and Ambrosia Beetles. In. *Insect-Fungus Interactions. 14th Symposium of the Royal Entomological Society of London in collaboration with the British Mycological Society*, N. Wilding, N.M. Collins, P. M. Hammond, J.F. Webber (Eds.). London: Academic Press.
- Berryman, A.A. 1972. Resistance of conifers to invasion by bark beetle-fungus associations. *BioScience*, 22, 598-602.
- Berryman, A.A. 1989. Adaptive Pathways in Scolytid-Fungus associations. In. *Insect-Fungus Interactions. 14th Symposium of the Royal Entomological Society of London in collaboration with the British Mycological Society*, N. Wilding, N.M. Collins, P. M. Hammond, J.F. Webber (Eds.). London: Academic Press.
- Bramble, W.C. & Holst E.C. 1940. Fungi associated with *Dendroctonus frontalis* in killing shortleaf pines and their effect on conduction. *Phytopathology*, 30, 881-99.
- Brasier, C.M. 1990. China and the origin of Dutch elm disease: an appraisal. *Plant Pathology*, 39, 5-16.
- Brasier, C.M. 1991. *Ophiostoma novo-ulmi* sp. nov., causative agent of current Dutch elm disease pandemics. *Mycopathologia*, 115, 151-61.
- Brasier, C.M. 2000. Intercontinental spread and continuing evolution of the Dutch elm disease pathogens. In. *The Elms – Breeding and Conservation*, C.P. Dunn (Ed.). Dordrecht: Kluwer.
- Brasier, C.M. & Kirk, S.A. 1993. Sibling species within *Ophiostoma piceae*. *Mycological Research*, 97, 811-16.
- Bridges, J.R. & Moser, J.C. 1983. Role of two mites in transmission of the blue-stain fungus, *Ceratocystis minor*. *Ecological Entomology*, 8, 9-12.
- Bridges, J.R. & Moser, J.C. 1986. Relationship of phoretic mites (Acari: Tarsonemidae) to the bluestaining fungus, *Ceratocystis minor*, in trees infested by southern pine beetle (Coleoptera: Scolytidae). *Environmental Entomology*, 15, 951-53.

- Bridges, J.R., Marler, J.E. & McSparrin, B.H. 1984. A quantitative study of the yeasts associated with laboratory-reared *Dendroctonus frontalis* Zimm. (Coleopt., Scolytidae). Zeitschrift für Angewandte Entomologie, 97, 261-67.
- Butin, H. 1996. *Tree Diseases and Disorders. Causes, Biology and Control in Forest and Amenity trees.* Oxford: Oxford University Press.
- Butin, H. & Zimmermann, G. 1972. Zwei neue holzverfärbende *Ceratocystis*-Arten in Buchenholz (*Fagus sylvatica* L.). Phytopathologische Zeitschrift, 74, 281-87.
- Callaham, R.Z. & Shifrine, M. 1960. The yeasts associated with bark beetles. Forest Science, 6, 146-154.
- Cassar, S. & Blackwell, M. 1996. Convergent origins of ambrosia fungi. Mycologia, 88, 596-601.
- Christiansen, E. 1985. *Ceratocystis polonica* inoculated in Norway spruce: Blue-staining in relation to inoculum density, resinosis and tree growth. European Journal of Forest Pathology, 15, 160-67.
- Christiansen, E. & Bakke, A. 1988. The Spruce Bark Beetle of Eurasia. In: *Dynamics of Forest Insect Populations: Pattern, Causes, Implications*, A.A. Berryman (Ed.). New York, London: Plenum Press.
- Christiansen, E. & Solheim, H. 1990. The bark beetle-associated blue-stain fungus *Ophiostoma polonicum* can kill various spruces and Douglas fir. European Journal of Forest Pathology, 20, 436-46.
- Christiansen, E., Waring, R.H. & Berryman, A.A. 1987. Resistance of conifers to bark beetle attack: searching for general relationships. Forest Ecology and Management, 22, 89-106.
- Colineau, B. & Lieutier, F., 1994. Production of *Ophiostoma*-free adults of *Ips sexdentatus* Boern. (Coleoptera: Scolytidae) and comparison with naturally contaminated adults. Canadian Entomologist, 126, 103-10.
- Croisé, L., Lieutier, F. & Dreyer, E. 1998. Scots pine responses to number and density of inoculation points with *Leptographium wingfieldii* Morelet, a bark beetle-associated fungus. Annales des Sciences Forestières, 55, 497-506.
- Davidson, R.W., Francke-Grosmann, H. & Käärik, A. 1967. A restudy of *Ceratocystis penicillata* and report of two American species of this genus from Europe. Mycologia, 59, 928-32.
- De Hoog, G.S. & Scheffer, R.J. 1984. *Ceratocystis* versus *Ophiostoma*: a reappraisal. Mycologia, 76, 292-99.
- Dowding, P. 1969. The dispersal and survival of spores of fungi causing bluestain in pine. Transactions of the British Mycological Society, 52, 125-37.
- Dowding, P. 1973. Effects of felling time and insecticide treatment on the interrelationships of fungi and arthropods in pine logs. Oikos, 24, 422-29.
- Farris, S.H. 1963. Ambrosia fungus storage in two species of *Gnathotrichus* Eichhoff (Coleoptera: Scolytidae). Canadian Entomologist, 95, 257-59.
- Fox, J.W., Wood, D.L., Akers, R. P. & Parmeter, J.R. jr. 1993. Survival and development of *Ips paraconfusus* Lanier (Coleoptera: Scolytidae) reared axenically and with tree-pathogenic fungi vectored by cohabiting *Dendroctonus* species. Canadian Entomologist, 125, 1157-67
- Francke-Grosmann, H. 1952. Über die Ambrosiazucht der beiden Kiefernborkenkäfer *Myelophilus minor* Htg. und *Ips acuminatus* Gyll. Meddelanden från Statens Skogforskningsinstitut, 41, 1-52.
- Francke-Grosmann, H. 1956a. Hautdrüsen als Träger der Pilzsymbiose bei Ambrosiakäfern. Zeitschrift für Morphologie und Ökologie der Tiere, 45, 275-308.
- Francke-Grosmann, H. 1956b. Grundlagen der Symbiose bei pilzzüchtenden Holzinsekten. Verhandlungen der Deutschen Zoologischen Gesellschaft Hamburg (Leipzig), 112-118.
- Francke-Grosmann, H. 1958. Über die Ambrosiazucht der holzbrütenden Ipiden im Hinblick auf das System. Verhandlungen der Deutschen Gesellschaft für Angewandte Entomologie, 14, 139-44.
- Francke-Grosmann, H. 1963a. Some new aspects in forest entomology. Annual Review of Entomology, 8, 415-38.
- Francke-Grosmann, H. 1963b. Zur Übertragung der Pilzflora bei dem Borkenkäfer *Ips acuminatus*. Zeitschrift für Angewandte Entomologie, 52, 355-61.
- Francke-Grosmann, H. 1966. Über Symbiosen von xylo-mycetophagen und phloeophagen Scolytoidae mit holzbewohnenden Pilzen. Material und Organismen, Beiheft 1, 503-22.
- Francke-Grosmann, H. 1967. Ectosymbiosis in Wood-Inhabiting Insects. In: *Symbiosis*, Volume 2, S.M. Henry (Ed.). Academic, New York, London: Academic Press.
- Francke-Grosmann, H. 1975. Zur epizoischen und endozoischen Übertragung der symbiotischen Pilze des Ambrosiakäfers *Xyleborus saxeseni* (Coleoptera: Scolytidae). Entomologia Germania, 1, 279-92.

- Furniss, M.M., Solheim, H. & Christiansen, E. 1990. Transmission of blue-stain fungi by *Ips typographus* (Coleoptera: Scolytidae) in Norway spruce. Annals of the Entomological Society of America, 83, 712-16.
- Gebhardt, H., Kirschner, R. & Oberwinkler, F. 2002. A new *Ophiostoma* species isolated from the ambrosia beetle *Xyleborus dryographus* (Coleoptera: Scolytidae). Mycological Progress, 1, 377-82.
- Gibbs, J.N. 1993. The biology of ophiostomatoid fungi causing sapstain in trees and freshly cut logs. In. *Ophiostoma and Ceratocystis: Taxonomy, Ecology and Pathogenicity*, M.J. Wingfield, K.A. Seifert, J.F. Webber (Eds.). St.Paul, Minnesota: APS Press.
- Gibbs, J.N. & Inman, A. 1991. The pine shoot beetle *Tomicus piniperda* as a vector of blue-stain fungi to windblown pine. Forestry, 64, 139-249.
- Graham, K. 1967. Fungal-insect mutualism in trees and timber. Annual Review of Entomology, 12, 105-26.
- Gregoire, J.C. 1988. The Greater European Spruce Beetle. In. *Dynamics of Forest Insect Populations: Pattern, Causes, Implications*, A.A. Berryman (Ed.). New York, London: Plenum Press.
- Grosmann, H. 1931. Beiträge zur Kenntnis der Lebensgemeinschaft zwischen Borkenkäfern und Pilzen. Zeitschrift für Parasitenkunde, 3, 56-102.
- Grosmann, H. 1932. Über die systematischen Beziehungen der Gattung *Leptographium* Lagerberg et Melin zur Gattung *Ceratostomella* Sacc. nebst einigen Bemerkungen über *Scopularia venusta* Preuss und *Hantzschia phycomyces* Awd. Hedwigia 72, 180-98.
- Grubelnik, R. 1998. Untersuchungen über die Zusammensetzung der Mycoflora von *Ips typographus* auf ausgewählten Wald-Standorten in Österreich unter besonderer Berücksichtigung der pathogenen Art *Ceratocystis polonica*. Diplomarbeit, Universität für Bodenkultur Wien.
- Guérard, N., Dreyer, E. & Lieutier, F. 2000. Interactions between Scots pine, *Ips acuminatus* (Gyll.) and *Ophiostoma brunneo-ciliatum* (Math.): estimation of the critical thresholds of attack and inoculation densities and effects on hydraulic properties of the stem. Annales des Sciences Forestières, 57, 681-90.
- Hanssen, H.-P. 1993. Volatile metabolites produced by species of *Ophiostoma* and *Ceratocystis*. In. *Ophiostoma and Ceratocystis: Taxonomy, Ecology and Pathogenicity*, M.J. Wingfield, K.A. Seifert, J.F. Webber (Eds.). St.Paul, Minnesota: APS Press.
- Harding, S. 1985. Plantepatologiske aspekter ved barkbilleangrep på nåletræ - med særlig henblik på *Ips typographus*/rødgræn. Hovedopgave, Den Kongelige Veterinaer- og Landbohøjskole, København.
- Harding, S. 1989. The influence of mutualistic blue-stain fungi on bark beetle population dynamics. Ph.D thesis, Royal Veterinary and Agricultural University Copenhagen.
- Harding, S. 1995. Fungal associates of *Ips typographus* L. in Denmark – occurrence, frequency and pathogenicity. In. *Bark beetles, blue-stain fungi, and conifer defence systems*, E. Christiansen (Ed.). Proceedings from a symposium held at the Norwegian Forest Research Institute (NISK), 31 July - 2 August, 1995, Ås, Norway. Aktuelt fra Skogforsk, 6, 36.
- Harrington, T.C. 1981. Cycloheximide sensitivity as a taxonomic character in *Ceratocystis*. Mycologia, 73, 1123-29.
- Harrington, T.C. 1987. New combinations in *Ophiostoma* of *Ceratocystis* species with *Leptographium* anamorphs. Mycotaxon, 28, 39-43.
- Harrington, T.C. 1993a. Diseases of conifers caused by species of *Ophiostoma* and *Leptographium*. In. *Ophiostoma and Ceratocystis: Taxonomy, Ecology and Pathogenicity*, M.J. Wingfield, K.A. Seifert, J.F. Webber (Eds.). St.Paul, Minnesota: APS Press.
- Harrington, T.C. 1993b. Biology and taxonomy of fungi associated with bark beetles. In. *Beetle-Pathogen Interactions in Conifer Forests*, T.D. Schowalter, G.M. Filip (Eds.). New York: Academic Press.
- Harrington, T.C. & Wingfield, M.J. 1998. The *Ceratocystis* species on conifers. Canadian Journal of Botany, 76, 1446-57.
- Harrington, T.C., McNew, D., Steimel, J., Hofstra D. & Farrell R. 2001. Phylogeny and taxonomy of the *Ophiostoma piceae* complex and the Dutch elm disease fungi. Mycologia, 93, 111-36.
- Harrington , T.C., Pashenova, N.V., McNew, D.L., Steimel, J. & Konstantinov, M.Yu. 2002. Species delimitation and host specialization of *Ceratocystis laricicola* and *C. polonica* to larch and spruce. Plant Disease, 86, 418-22.
- Hartig, T. 1844. Ambrosia des *Bosstrichus dispar*. Allgemeine Forst- und Jagdzeitung, 13,73.
- Hartig, T. 1872a. Der Fichtensplintkäfer *Bostrychus (Xyloterus) lineatus*. Allgemeine Forst- und Jagdzeitung, 48, 181-83.

- Hartig, T. 1872b. Der Buchensplintkäfer *Bostrychus domesticus*. Allgemeine Forst- und Jagdzeitung, 48, 183-84.
- Hartig, R. 1878. *Die Zersetzungerscheinungen des Holzes der Nadelbäume und der Eiche in forstlicher, botanischer und chemischer Richtung*. Berlin: Julius Springer.
- Hausner, G., Reid, J. & Klassen, G.R. 1993a. *Ceratocystiopsis*: a reappraisal based on molecular criteria. Mycological Research, 97, 625-33.
- Hausner, G., Reid, J. & Klassen, G.R. 1993b. On the subdivision of *Ceratocystis* s.l., based on partial ribosomal DNA sequences. Canadian Journal of Botany, 71, 52-63.
- Horntvedt, R., Horntvedt, R., Christiansen, E., Solheim, H. & Wang, S. 1983. Artificial inoculation with *Ips typographus*-associated blue-stain fungi can kill healthy Norway spruce trees. Meddelelser fra Norsk institutt for skogforskning, 38, 1-20.
- Hunt, J. 1956. Taxonomy of the genus *Ceratocystis*. Lloydia, 19, 1-58.
- Jacobs, K. & Wingfield, M.J. 2001. *Leptographium species: Tree Pathogens, Insect Associates, and Agents of Blue-stain*. St.Paul, Minnesota: APS Press.
- Jacobs, K., & Kirisits, T. 2003. *Ophiostoma kryptum* sp. nov. from *Larix decidua* and *Picea abies* in Europe, similar to *O. minus*. Mycological Research, 107, 1231-42.
- Jacobs, K., Wingfield, M.J., Uzunovic, A. & Frisullo, S. 2001a. Three new *Leptographium* species from pine. Mycological Research, 105, 490-99.
- Jacobs, K., Wingfield M.J., Coetsee, C., Kirisits, T. & Wingfield, B.D. 2001b. *Leptographium guttulatum* sp. nov., a new species from spruce and pine in Europe. Mycologia, 93, 380-88.
- Jacobs, K., Seifert, K.A., Harrison, K.J. & Kirisits, T. 2003a. Identity and phylogenetic relationships of ophiostomatoïd fungi associated with invasive and native *Tetropium* spp. (Coleoptera: Cerambycidae) in Atlantic Canada. Canadian Journal of Botany, 81, 316-29.
- Jacobs, K., Kirisits, T. & Wingfield, M.J. 2003b. Taxonomic re-evaluation of three related species of *Graphium*, based on morphology, ecology and phylogeny. Mycologia, 95, 714-27.
- Jankowiak, R. 2004. Fungi associated with *Ips typographus* on *Picea abies* in Poland. I: Fungi associated with *Ips typographus* in relation to a different health condition of trees. Forest Pathology, accepted.
- Jones, K. G. & Blackwell, M. 1998. Phylogenetic analyses of ambrosial species in the genus *Raffaelea* based on 18S rDNA sequences. Mycological Research, 102, 661-65.
- Juzwik, J. & French, D.W. 1983. *Ceratocystis fagacearum* and *C. piceae* on the surfaces of free-flying and fungus-mat-inhabiting nitidulids. Phytopathology, 73, 1164-68.
- Kile, G.A. 1993. Plant diseases caused by species of *Ceratocystis sensu stricto* and *Chalara*. In. *Ophiostoma and Ceratocystis: Taxonomy, Ecology and Pathogenicity*, M.J. Wingfield, K.A. Seifert, J.F. Webber (Eds.). St.Paul, Minnesota: APS Press.
- Kirisits, T. 1996. Untersuchungen über die Vergesellschaftung von Bläuepilzen (*Ceratocystis/Ophiostoma* spp.) mit den rindenbrütenden Fichtenborkenkäfern *Ips typographus*, *Pityogenes chalcographus* und *Hylurgops glabratus* in Österreich. Diplomarbeit, Universität für Bodenkultur Wien.
- Kirisits, T. 1998. Pathogenicity of three blue-stain fungi associated with the bark beetle *Ips typographus* to Norway spruce in Austria. Österreichische Zeitschrift für Pilzkunde, 7, 191-201.
- Kirisits, T. 2001. Studies on the association of ophiostomatoïd fungi with bark beetles in Austria with special emphasis on *Ips typographus* and *Ips cembrae* and their associated fungi *Ceratocystis polonica* and *Ceratocystis laricicola*. Dissertation, Universität für Bodenkultur Wien.
- Kirisits, T. & Anglberger, H. 1999. Report on a strain of the pathogenic blue-stain fungus *Ceratocystis polonica* with low virulence. Österreichische Zeitschrift für Pilzkunde, 8, 157-67.
- Kirisits, T. & Offenthaler, I. 2002. Xylem sap flow of Norway spruce after inoculation with the blue-stain fungus *Ceratocystis polonica*. Plant Pathology, 51, 359-64.
- Kirisits, T., Grubelniuk, R. & Führer E. 2000. Die ökologische Bedeutung von Bläuepilzen für rindenbrütende Borkenkäfer. [The ecological role of blue-stain fungi for phloem-feeding bark beetles]. In. *Mariabrunner Waldbautage 1999 – Umbau sekundärer Nadelwälder*, F. Müller (Ed.). Vienna: Schriftenreihe der Forstlichen Bundesversuchsanstalt Wien, FBVA-Berichte, 111, 117-37.
- Kirschner, R. 1998. Diversität mit Borkenkäfern assoziierter filamentöser Mikropilze. Dissertation, Eberhard-Karls-Universität Tübingen.
- Kirschner, R. 2001. Diversity of filamentous fungi in bark beetle galleries in central Europe. In. *Trichomycetes and other fungal groups. Robert W. Lichtwardt Commemoration Volume*, J.K. Misra, B.W. Horn (Eds.). Enfield, Plymouth: Science Publishers, Inc.

- Kirschner, R. & Oberwinkler, F. 1999. A new *Ophiostoma* species associated with bark beetles infesting Norway spruce . Canadian Journal of Botany, 77, 247-52.
- Kotýnková-Sychrová, E. 1966. Mykoflóra chodeb kurovcu v Československu [The mycoflora of bark-beetle galleries in Czechoslovakia]. Ceska Mykologie, 20, 45-53.
- Kowalski, T. 1991. Oak decline: I. Fungi associated with various disease symptoms on overground portions of middle-aged and old oak (*Quercus robur* L.). European Journal of Forest Pathology 21, 136-51.
- Kowalski, T. & Butin, H. 1989. Taxonomie bekannter und neuer *Ceratocystis*-Arten an Eiche (*Quercus robur* L.). Phytopathologische Zeitschrift, 124, 236-48.
- Klepzig, K.D. 1998. Competition between a biological control fungus, *Ophiostoma piliferum*, and symbionts of the southern pine beetle. Mycologia, 90, 69-75.
- Klepzig, K.D. & Wilkins, R.T. 1997. Competitive interactions among symbiotic fungi of the southern pine beetle. Applied and Environmental Microbiology, 63, 621-27.
- Klepzig, K.D., Moser, J.C., Lombadero, M.J., Ayres, M.P., Hofstetter, R.W. & Walkinshaw, C.J. 2001a. Mutualism and antagonism: Ecological interactions among bark beetles, mites, and fungi. In: *Biotic interactions in plant-pathogen associations*, M.J. Jeger, N.J. Spence (Eds.). New York: CABI Publishing.
- Klepzig, K.D., Moser, J.C., Lombadero, F.J., Hofstetter, R.W. & Ayres, M.P. 2001b. Symbiosis and competition: complex interactions among beetles, fungi and mites. Symbiosis, 30, 83-96.
- Krokene, P. 1996. The role of blue-stain fungi in tree-killing by bark beetles. Dr. scient. Thesis, University of Oslo.
- Krokene, P. & Solheim, H. 1996. Fungal associates of five bark beetles species colonizing Norway spruce. Canadian Journal of Forest Research, 26, 2115-22.
- Krokene, P. & Solheim, H. 1998. Pathogenicity of four blue-stain fungi associated with aggressive and nonaggressive bark beetles. Phytopathology, 88, 39-44.
- Krokene, P. & Solheim, H. 2001. Loss of pathogenicity in the blue-stain fungus *Ceratocystis polonica*. Plant Pathology, 50, 497-502.
- Käärik, A. 1975. Succession of microorganisms during wood decay. In: *Biological transformation of wood by microorganisms*, W Liese (Ed.). Proceedings of the Sessions on Wood Products Pathology at the 2nd International Congress of Plant Pathology, September 10-12, 1973, Minneapolis/USA. Berlin, Heidelberg. New York: Springer-Verlag.
- Lagerberg, T., Lundberg, G. & Melin, E. 1927. Biological and practical researches into blueing in pine and spruce. Skogsvärdsföreningens Tidskrift, 25, 145-272, 561-739.
- Leufvén, A., Bergström, G. & Falsen, E. 1984. Interconversion of verbenols and verbenone by identified yeasts isolated from the spruce bark beetle *Ips typographus*. Journal of Chemical Ecology, 10, 1349-61.
- Leufvén, A. & Nehls, L. 1986. Quantification of different yeasts associated with the bark beetle, *Ips typographus*, during its attack on a spruce tree. Microbial Ecology, 12, 237-43.
- Lévieux, J., Lieutier, F., Moser, J.C. & Perry, T.J. 1989. Transportation of phytopathogenic fungi by the bark beetle *Ips sexdentatus* Boerner and associated mites. Zeitschrift für Angewandte Entomologie, 108, 1-11.
- Lévieux, J., Cassier, P., Guillaumin, D. & Roques, A. 1991. Structures implicated in the transportation of pathogenic fungi by the European bark beetle, *Ips sexdentatus* Boerner: Ultrastructure of a mycangium. Canadian Entomologist, 123, 245-54.
- Liese, W. & Schmid, R. 1961. Licht- und elektronenmikroskopische Untersuchungen über das Wachstum von Bläuepilzen in Kiefern- und Fichtenholz. Holz als Roh- und Werkstoff, 19, 329-37.
- Lieutier, F. 1993. Induced defense reaction of conifers to bark beetles and their associated *Ophiostoma* species. In: *Ophiostoma and Ceratocystis: Taxonomy, Ecology and Pathogenicity*, M.J. Wingfield, K.A. Seifert, J.F. Webber (Eds.). St.Paul, Minnesota: APS Press.
- Lieutier, F. 2002. Mechanisms of resistance in conifers and bark beetle attack strategies. In *Mechanisms and Deployment of Resistance in Trees to Insects*, M.R. Wagner, K.M. Clancy, F. Lieutier, T.D. Paine (Eds.). Dordrecht: Kluwer.
- Lieutier, F., Cheniclet, C. & Garcia, J. 1989a. Comparison of the defense reactions of *Pinus pinaster* and *Pinus sylvestris* to attacks by two bark beetles (Coleoptera: Scolytidae) and their associated fungi. Environmental Entomology, 18, 228-34.

- Lieutier, F., Yart, A., Garcia, J., Ham, M.C., Morelet, M. & Lévieux, J. 1989b. Champignons phytopathogènes associés à deux coléoptères scolytidae du pin sylvestre (*Pinus sylvestris*) et étude préliminaire de leur agressivité envers l'hôte. Annales des Sciences Forestières, 46, 201-16.
- Lieutier, F., Garcia, J., Yart, A., Vouland, G., Pettinetti, M. & Morelet, M., 1991. Ophiostomatales (Ascomycètes) associées à *Ips acuminatus* Gyll. (Coleoptera: Scolytidae) sur le pin sylvestre (*Pinus sylvestris* L.) dans le Sud-Est de la France et comparaison avec *Ips sexdentatus* Boern. Agronomie, 11, 807-17.
- Lieutier, F., Vouland, G., Pettinetti, M., Garcia, J., Romary, P. & Yart, A. 1992. Defence reactions of Norway spruce (*Picea abies* Karst.) to artificial insertion of *Dendroctonus micans* Kug. (Col., Scolytidae). Zeitschrift für Angewandte Entomologie, 114, 174-86.
- Lieutier, F., Yart, A., Ye, H., Sauvard, D., & Gallois, V. 2004. Variation in growth and virulence of *Leptographium wingfieldii*, a fungus associated with the bark beetle *Tomicus piniperda* L. Annals of Forest Science, in press.
- Lin, S. 2003. Untersuchungen über den *Ophiostoma piceae*-Artenkomplex in Österreich. Diplomarbeit, Universität für Bodenkultur Wien.
- MacCallum, B.D. 1922. Some wood-staining fungi. Transactions of the British Mycological Society, 7, 231-36.
- Malloch, D. & Blackwell, M. 1993. Dispersal biology of the ophiostomatoid fungi. In: *Ophiostoma and Ceratocystis: Taxonomy, Ecology and Pathogenicity*, M.J. Wingfield, K.A. Seifert, J.F. Webber (Eds.). St.Paul, Minnesota: APS Press.
- Marin, M. 2004. Phylogenetic and molecular population biology studies on *Ceratocystis* spp. associated with conifer and coffee diseases. Ph.D thesis, University of Pretoria.
- Mathiesen, A. 1950. Über einige mit Borkenkäfern assoziierte Bläuepilze in Schweden. Oikos, 2, 275-308.
- Mathiesen, A. 1951. Einige neue *Ophiostoma*-Arten in Schweden. Svensk Botanisk Tidskrift, 45, 203-32.
- Mathiesen-Käärik, A., 1953. Eine Übersicht über die gewöhnlichsten mit Borkenkäfern assoziierten Bläuepilze in Schweden und einige für Schweden neue Bläuepilze. Meddelanden från Statens Skogforskningsinstitutut, 43, 1-74.
- Minter, D.W., Kirk, P.M. & Sutton, B.C. 1982: Holoblastic phialides. Transactions of the British Mycological Society, 79, 75-93.
- Minter, D.W., Kirk, P.M. & Sutton, B. C. 1983. Thallic phialides. Transactions of the British Mycological Society, 80, 39-66.
- Moser, J.C. 1985. Use of sporothecae by phoretic *Tarsonemus* mites to transport ascospores of coniferous bluestain fungi. Transactions of the Brisish Mycological Society, 84, 750-53
- Moser, J.C., Perry, T.J. & Solheim, H. 1989. Ascospores hyperphoretic on mites associated with *Ips typographus*. Mycological Research, 93, 513-17.
- Moser, J.C. 1997. Phoretic mites and their hyperphoretic fungi associated with flying *Ips typographus japonicus* Niijima (Col., Scolytidae) in Japan. Journal of Applied Entomology 121, 425-28.
- Morelet, M. 1995. II. Travaux scientifiques. Notes de mycologie appliquée. Annales de la Société des Sciences Naturelles et d'Archéologie de Toulon et du Var, 47, 89-94.
- Münch, E., 1907. Die Blaufäule des Nadelholzes. I-II. Naturwissenschaftliche Zeitschrift für Land- und Forstwirtschaft, 5, 531-73.
- Münch, E. 1908. Die Blaufäule des Nadelholzes. III-IV. Naturwissenschaftliche Zeitschrift für Land- und Forstwirtschaft, 6, 32-47, 297-323.
- Nelson, R.M. 1934. Effect of bluestain fungi on southern pines attacked by bark beetles. Phytopathologische Zeitschrift, 7, 327-53.
- Nelson, R.M. & Beal, J.A. 1929. Experiments with bluestain fungi in southern pines. Phytopathology, 19, 1101-06.
- Norris, D.M. 1979. The mutualistic fungi of *Xyleborus* beetles. In: *Insect-Fungus Symbiosis*, L.R. Batra (Ed.). Montclair, NJ: Allanheld, Osmun & Co.
- Okada, G., Seifert, K.A., Takematsu, A., Yamaoka, Y., Miyazaki, S. & Tubaki, K. 1998. A molecular phylogenetic reappraisal of the *Graphium* complex based on 18S rDNA sequences. Canadian Journal of Botany, 76, 1495-1506.
- Okada, G., Jacobs, K., Kirisits, T., Louis-Seize, G.W., Seifert K.A., Sugita, T., Takematsu, A. & Wingfield, M.J. 2000. Epitypification of *Graphium penicilliooides* Corda, with comments on the phylogeny and taxonomy of *Graphium*-like synnematous fungi. Studies in Mycology, 45, 169-88.

- Paine, T.D., Raffa K.F., & Harrington T.C. 1997. Interactions among scolytid bark beetles, their associated fungi, and live host conifers. *Annual Review of Entomology*, 42, 179-206.
- Paulin-Mahady, A.E., Harrington, T.C. & McNew, D. 2002. Phylogenetic and taxonomic evaluation of *Chalara*, *Chalaropsis*, and *Thielaviopsis* anamorphs associated with *Ceratocystis*. *Mycologia*, 94, 62-72.
- Pfeiffer, A. 1995. *Zentral- und westpalearktische Borken- und Kernkäfer (Coleoptera: Scolytidae, Platypodidae)*. Basel, Schweiz: Pro Entomologia, c/o Naturhistorisches Museum Basel.
- Pignal, M.C., Chararas, C. & Bourgeay-Causse, M. 1988. Yeasts from *Ips sexdentatus* (Scolytidae). *Mycopathology*, 103, 43-48.
- Piou, D., Lieutier, F. & Yart, A. 1989. Observations symptomatologiques et rôles possibles d'*Ophiostoma minus* Hedg. (ascomycète: *Ophiostomatales*) et de *Tomicus piniperda* L. (Coleoptera: Scolytidae) dans le déperissement du pin sylvestre en forêt d'Orléans. *Annales des Sciences Forestières*, 46, 39-53.
- Postner, M. 1974. Scolytidae (Ipidae), Borkenkäfer. In. *Die Forstschädlinge Europas*, Band 2., W. Schwencke (Ed.). Hamburg, Berlin: Paul Parey Verlag.
- Raffa, K.F. & Klepzig, K.D. 1992. Tree Defense Mechanisms Against Fungi Associated with Insects. In. *Defense Mechanisms of Woody Plants Against Fungi*, R.A. Blanchette, A.R. Biggs (Eds.). New York, Berlin, Heidelberg: Springer.
- Redfern, D.B., Stoakley, J.T., Steele, H. & Minter, D.W. 1987. Dieback and death of larch caused by *Ceratocystis laricicola* sp. nov. following attack by *Ips cembrae*. *Plant Pathology*, 36, 467-80.
- Redfern, D.B. 1989. The roles of the bark beetle *Ips cembrae*, the woodwasp *Urocerus gigas* and associated fungi in dieback and death of larches. In. *Insect-Fungus Interactions. 14th Symposium of the Royal Entomological Society of London in collaboration with the British Mycological Society*, N. Wilding, N.M. Collins, P. M. Hammond, J.F. Webber (Eds.). London: Academic Press.
- Rennerfelt, E. 1950. Über den Zusammenhang zwischen dem Verblauen des Holzes und den Insekten. *Oikos*, 2, 120-37.
- Rollins, F., Jones, K.G., Krokene, P., Solheim, H. & Blackwell, M. 2001. Phylogeny of asexual fungi associated with bark and ambrosia beetles. *Mycologia*, 93, 991-96.
- Roux, J., Wingfield, M.J., Bouillet, J.-P., Wingfield, B.D. & Alfenas, A.C. 2000. A serious new wilt disease of *Eucalyptus* caused by *Ceratocystis fimbriata* in Central Africa. *European Journal of Forest Pathology*, 30, 175-84.
- Salle, A., Yart, A., Garcia, J., Romary, P. & Lieutier, F. 2003. Fungi associated with *Ips typographus* (L.) in France: Virulence and diversity in relation to bark beetle population levels. In. Book of Abstracts of a meeting of IUFRO working party S7.03.05 (Integrated Control of Scolytid Bark Beetles). Blodgett Forest Research Station, Georgetown, California, September 29 – October 2, 2003.
- Schedl, K. 1964. Biologie des gehöckerten Eichenholzbohrers, *Xyleborus monographus* Fab. (Scolytidae, Coleoptera). *Zeitschrift für Angewandte Entomologie*, 53, 411-28.
- Scheffer, T.C. 1986. O₂ requirements for growth and survival of wood-decaying and sapwood-staining fungi. *Canadian Journal of Botany*, 64, 1957-63.
- Schmidberger, J. 1836. Naturgeschichte des Apfelborkenkäfers *Apate dispar*. Beiträge zur Obstbaumzucht und zur Naturgeschichte der den Obstbäumen schädlichen Insekten, 4, 213-30.
- Schwerdtfeger, F. 1981. *Die Waldkrankheiten*. 4. Auflage. Hamburg, Berlin: Paul Parey Verlag.
- Seifert, K.A. 1993. Sapstain of commercial lumber by species of *Ophiostoma* and *Ceratocystis*. In. *Ophiostoma and Ceratocystis: Taxonomy, Ecology and Pathogenicity*, M.J. Wingfield, K.A. Seifert, J.F. Webber (Eds.). St.Paul, Minnesota: APS Press.
- Siemaszko, W. 1939. Zepoly grzybów towarzyszących kornikom polskim [Fungi associated with bark-beetles in Poland]. *Planta polonica*, 7, 1-54 + plates.
- Simsek, Z. 1994. Die Entwicklung eines halbsynthetischen Brut- und Nährmediums für Fichtenborkenkäfer (*Ips typographus* L. und *Pityogenes chalcographus* L.). Dissertation, Universität für Bodenkultur Wien.
- Simsek, Z. & Führer, E. 1993. Künstliches Nähr- und Brutmedium für *Ips typographus* L. (Col., Scolytidae). *Journal of Applied Entomology*, 116, 432-39.
- Six, D.L. 2003. Bark Beetle-Fungus Symbioses. In. *Insect Symbiosis. Contemporary Topics in Entomology Series*, K. Bourtzis, T.A. Miller (Eds.). Boca Raton, London, New York, Washington D.C.: CRC Press.
- Solheim, H. 1986. Species of Ophiostomataceae isolated from *Picea abies* infested by the bark beetle *Ips typographus*. *Nordic Journal of Botany*, 6, 199-207.

- Solheim, H. 1988. Pathogenicity of some *Ips typographus* associated blue-stain fungi to Norway spruce. *Meddelelser fra Norsk institutt for skogforskning*, 40, 1-11.
- Solheim, H. 1991. Oxygen deficiency and spruce resin inhibition of growth of fungi associated with *Ips typographus*. *Mycological Research*, 95, 1387-92.
- Solheim, H. 1992a. The early stages of fungal invasion in Norway spruce infested by the bark beetle *Ips typographus*. *Canadian Journal of Botany*, 70, 1-5.
- Solheim, H. 1992b. Fungal succession in sapwood of Norway spruce infested by the bark beetle *Ips typographus*. *European Journal of Forest Pathology*, 22, 136-48.
- Solheim, H. 1993. Fungi associated with the spruce bark beetle *Ips typographus* in an endemic area in Norway. *Scandinavian Journal of Forest Research*, 8, 118-22.
- Solheim, H. & Långström, B. 1991. Blue-stain fungi associated with *Tomicus piniperda* in Sweden and preliminary observations on their pathogenicity. *Annales des Sciences Forestières*, 48, 149-56.
- Solheim, H. & Safranyik L. 1997. Pathogenicity to Sitka spruce of *Ceratocystis rufipenni* and *Leptographium abietinum*, blue-stain fungi associated with the spruce bark beetle. *Canadian Journal of Forest Research*, 27, 1336-41.
- Solheim, H., Långström, B. & Hellqvist, C. 1993. Pathogenicity of the blue-stain fungi *Leptographium wingfieldii* and *Ophiostoma minus* to Scots pine: effect of tree pruning and inoculum density. *Canadian Journal of Forest Research*, 23, 1438-43.
- Solheim, H., Krokene, P. & Långström, B. 2001. Effects of growth and virulence of associated blue-stain fungi on host colonization behaviour of the pine shoot beetles *Tomicus minor* and *T. piniperda*. *Plant Pathology*, 50, 111-16.
- Spatafora, J.W. & Blackwell, M. 1994. The polyphyletic origins of ohiostomatoid fungi. *Mycological Research*, 98, 1-9.
- Stauffer, C., Kirisits, T., Nussbaumer, C., Pavlin, R. & Wingfield, M.J. 2001. Phylogenetic relationships between the European and Asian eight spined larch bark beetle populations (Coleoptera, Scolytidae) inferred from DNA sequences and fungal associates. *European Journal of Entomology*, 98, 99-105.
- Strongman, D.B. 1986. A method for rearing *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae) from eggs to pupae on host tissue with or without a fungal complement. *The Canadian Entomologist*, 118, 1309-11.
- Upadhyay, H.P., 1981. *A monograph of Ceratocystis and Ceratocystiopsis*. Athens: The University of Georgia Press.
- Upadhyay, H.P. & Kendrick, W.B., 1975. Prodromus for a revision of *Ceratocystis* (Microascales, Ascomycetes) and its conidial state. *Mycologia*, 67, 798-805.
- Valkama, H. 1995. Does *Ips duplicatus* transport sapwood staining fungi? In: *Bark beetles, blue-stain fungi, and conifer defence systems*, E. Christiansen (Ed.). Proceedings from a symposium held at the Norwegian Forest Research Institute (NISK), 31 July - 2 August, 1995, Ås, Norway. Aktuelt fra Skogforsk, 6, 44-45.
- Van Wyk, P.W.J. & Wingfield M.J. 1990. Ascospore development in *Ceratocystis sensu lato* (Fungi): a review. *Bothalia*, 20, 141-45.
- Van Wyk, P.W.J., Wingfield, M.J. & Van Wyk, P. S. 1993. Ultrastructure of centrum and ascospore development in selected *Ceratocystis* and *Ophiostoma* species. In: *Ophiostoma and Ceratocystis: Taxonomy, Ecology and Pathogenicity*, M.J. Wingfield, K.A. Seifert, J.F. Webber (Eds.). St.Paul, Minnesota: APS Press.
- Viiri H. 1997. Fungal associates of the spruce bark beetle *Ips typographus* L. (Col., Scolytidae) in relation to different trapping methods. *Journal of Applied Entomology*, 121, 529-33.
- Viiri, H. & Weissenberg, K. von 1995. *Ophiostoma* blue-staining fungi associated with *Ips typographus* in Finland. *Aktuelt fra Skogforsk*, 4/1995, 58-60.
- Viiri, H. & Lieutier, F. 2003. Ophiostomatoid fungi associated with the spruce bark beetle, *Ips typographus*, in post-epidemic areas in France. *Annals of Forest Science*, in press.
- Webber, J.F. 1990. Relative effectiveness of *Scolytus scolytus*, *S. multistriatus* and *S. kirschi* as vectors of Dutch elm disease. *European Journal of Forest Pathology*, 20, 184-92.
- Webber, J.F. 2000. Insect Vector Behaviour and the Evolution of Dutch Elm Disease. In: *The Elms – Breeding and Conservation*, C.P. Dunn (Ed.). Dordrecht: Kluwer.
- Webber J.F. & Brasier C.M. 1984. The transmission of Dutch elm disease: a study of the processes involved. In: *Invertebrate-microbial interactions. Joint symposium of the British Mycological Society and the British Ecological Society held at the University of Exeter, September 1982*, J.M. Anderson, A.D.M. Rayner, D.W.H. Walton (Eds.). Cambridge: Cambridge University Press.

- Webber J.F. & Gibbs J.N. 1989. Insect Dissemination of Fungal Pathogens of Trees. In. *Insect-Fungus Interactions. 14th Symposium of the Royal Entomological Society of London in collaboration with the British Mycological Society*, N. Wilding, N.M. Collins, P. M. Hammond, J.F. Webber (Eds.). London: Academic Press.
- Whitney, H.S. 1971. Association of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) with blue stain fungi and yeasts during brood development in lodgepole pine. Canadian Entomologist 103, 1495-1503.
- Whitney, H.S. 1982. Relationships between bark beetles and symbiotic organisms. In. *Bark Beetles in North American Conifers*, J.B. Mitton, K.B. Sturgeon (Eds.). Austin: University of Texas Press.
- Whitney, H.S., Bandoni, R.J. & Oberwinkler, F. 1987. *Entomocorticium dendroctini* gen. et sp. nov. (Basidiomycotina), a possible nutritional symbiote of the mountain pine beetle in lodgepole pine in British Columbia. Canadian Journal of Botany, 65, 95-102.
- Wingfield, M.J. 1993. Problems in delineating the genus *Ceratocystiopsis*. In. *Ophiostoma and Ceratocystis: Taxonomy, Ecology and Pathogenicity*, M.J. Wingfield, K.A. Seifert, J.F. Webber (Eds.). St.Paul, Minnesota: APS Press.
- Wingfield, M.J. & Gibbs, J.N. 1991. *Leptographium* and *Graphium* species associated with pine-infesting bark beetles in England. Mycological Research, 95, 1257-60.
- Wingfield, M., Seifert, K. A. & Webber, J. F. (Eds.) 1993. *Ophiostoma and Ceratocystis: Taxonomy, Ecology and Pathogenicity*. St.Paul, Minnesota: APS Press.
- Wingfield, M.J., Harrington, T.C. & Solheim, H., 1995. Do conifer bark beetles require fungi to kill trees? In *Bark beetles, blue-stain fungi, and conifer defence systems*, E. Christiansen (Ed.). Proceedings from a symposium held at the Norwegian Forest Research Institute (NISK), 31 July - 2 August, 1995, Ås, Norway. Aktuelt fra Skogforsk, 6, 6.
- Wingfield, M.J., Harrington, T.C. & Solheim, H. 1997. Two new species in the *Ceratocystis coerulescens* complex from conifers in western North America. Canadian Journal of Botany, 75, 827-34.
- Wood, S.L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Naturalist Memoirs, 6, 1-1359.
- Wood, S.L. & Bright, D.E., 1992. A catalog of Scolytidae and Platypodidae (Coleoptera), Part 2: Taxonomic Index. Great Basin Naturalist Memoirs, 13, 1-1553.
- Yamaoka, Y., Wingfield, M.J., Takahashi, I. & Solheim, H. 1997. Ophiostomatoid fungi associated with the spruce bark beetle *Ips typographus f. japonicus* in Japan. Mycological Research, 101, 1215-27.
- Yamaoka, Y., Wingfield, M.J., Ohsawa, M. & Kuroda, Y. 1998. Ophiostomatoid fungi associated with *Ips cembrae* in Japan and their pathogenicity to Japanese larch. Mycoscience, 39, 267-378.
- Yamaoka, Y., Takahashi, I. & Iguchi, K. 2000. Virulence of ophiostomatoid fungi associated with the spruce bark beetle *Ips typographus f. japonicus* in Yezo spruce. Journal of Forest Research, 5, 87-94.
- Yearian, W.C., Gouger, R.J. & Wilkinson, R.C. 1972. Effects of the bluestain fungus *Ceratocystis ips* on development of *Ips* bark beetles in pine bolts. Annals of the Entomological Society of America, 65, 481-87.
- Zhou, X.D., De Beer, Z.W., Harrington, T.C., McNew, D., Kirisits, T. & Wingfield, M.J. 2004. *Ophiostoma geleiformis* and phylogeny of species in the *O. galeiformis* complex. Mycologia, accepted.
- Zimmermann, G. 1973. Vergleichende ökologisch-physiologische Untersuchungen an Ambrosiapolypen, Assoziierten Bläuepilzen und Luftbläuepilzen. Dissertation, Georg-August-Universität Göttingen.
- Zimmermann, G. & Butin, H. 1973. Untersuchungen über Hitze- und Trockenresistenz holzbewohnender Pilze. Flora, 162, 393-419.

Chapter 11

RESEARCH ON PARASITOIDS AND PREDATORS OF SCOLYTIDAE – A REVIEW

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1. INTRODUCTION

Scolytidae are major forest pests in Europe. For example, *Ips typographus* (L.) is considered the main pest problem in forestry in many central and northern European countries. Consequently, there is a long tradition of forest entomology studying various aspects of bark beetle ecology, including their natural enemy complexes, with a view to developing control methods. In recent years, the need for the development of sustainable pest management methods, taking into account the whole forest ecosystem, has enhanced the interest in natural mortality factors.

Mills (1983) provided an extensive review of the natural enemies of conifer feeding bark beetles in Europe. In contrast, natural enemies of broadleaf-feeding species have never been reviewed. Furthermore, much research has been carried out in the last 20 years, in particular in fields such as host/prey location or tritrophic interactions. Other noteworthy reviews include two books by Hedqvist (1963; 1998) on chalcid and braconid parasitoids of Scolytidae in Sweden, and a publication by Nuorteva (1957) on parasitoids of bark beetles in Finland. Data are also available in general parasitoid and predator catalogues such as Thompson (1943), Herting (1973), and Noyes (2001), although these often repeat errors contained in primary publications.

This review will focus primarily on parasitoids and predators of bark beetle species considered to be pests of living trees in Europe, although it may also consider relevant research in other continents. A list of these European species is given in chapter 1. Pathogens of scolytids are reviewed in another chapter (Wegensteiner, chapter 12).

2. PARASITOIDS

2.1. Parasitoid complexes

Tables 1, 2 and 3 list the hymenopteran parasitoids of European Scolytidae living on Pinaceae, Cupressaceae and broadleaf trees, respectively. In addition to Hymenoptera, mites can also be parasitic on eggs, larvae or pupae of bark beetles. However, it is often difficult to properly assess the exact biology of mites, which may either be parasites, parasitoids, predators, saprophytes or commensals. In this review, mites will be reviewed in the predator section.

There is a large variation in the knowledge of the parasitoids of European bark beetles. As expected, the parasitoid complexes of the most important pests have been the target of specific studies. Parasitoids of *Ips typographus* have been studied, among others, by Sachtleben (1952), Bombosch (1954), Mills and Schlup (1989), and Weslien (1992) and those of *Tomicus piniperda* (L.) and *Ips acuminatus* (Gyll.) by Hérard and Mercadier (1996) and Balazy *et al.* (1987). *Scolytus* species have been investigated as well because of their importance as vectors of the Dutch elm disease (e.g. Beaver 1967a; Schroeder 1974; Maksimovic 1979; Merlin 1984, Manojlovic *et al.* 2000a, 2000b). *Phloeotribus scarabaeoides* (Bernard) was studied extensively by several authors for its importance in olive plantations (Russo 1938; González and Campos 1990a, 1991). Hintze-Podufal and Druschke (1988), Mills (1991) and Lozano and Campos (1991) provide significant data on the parasitoid complex of *Leperisinus varius* (F.) and Eichhorn and Graf (1974) on the ambrosia beetles *Trypodendron* spp. In addition, Nuorteva (1957), Hedqvist (1963, 1998), and Mendel (1986) provide numerous rearing records for bark beetles in Finland, Sweden, and Israel, respectively. For many European bark beetles, however, information on their parasitoid complex is usually restricted to parasitoid-host lists, catalogues and general studies which provide incomplete or erroneous records. No mention of parasitoids was found in the European literature for the following scolytid species: *Gnathotrichus materiarius* (Fitch), *Hylastes* spp., *Hylurgus ligniperda* (F.), *Trypodendron signatum* (F.) and *Xylosandrus germanus* (Blandford). Larvae of these species either live in the root system (*Hylastes* spp., *H. ligniperda*) or in the sapwood (*G. materiarius*, *T. signatum*, *X. germanus*) and are thus probably less susceptible to generalist larval parasitoids. In addition, *G. materiarius* and *X. germanus* are exotic species recently introduced into Europe, which may have not yet been adopted by European parasitoids.

The parasitoid complex of a particular scolytid host is difficult to evaluate because of the cryptic habit of bark beetle larvae and because a scolytid species usually shares the same breeding resource with a range of other insects. In most studies, parasitoids were reared from entire logs and attributed to the most abundant or most likely host, which resulted in many erroneous records. The most obvious mistakes are easily detected. For example, the braconid parasitoid *Eubazus semirugosus* (Nees) has often been associated with scolytids (Herting, 1973; Hedqvist, 1998) whereas it is a common egg-prepupal parasitoid of weevils of the genus *Pissodes* that cannot parasitize eggs of scolytids in galleries (Kenis and Mills, 1998). Similarly, most records of Ichneumonidae on Scolytidae are erroneous, with

the exception of the large spruce species *Dendroctonus micans* (Kug.), which is commonly attacked by the ichneumonid *Dolichomitus terebrans* (Ratzeburg) (Grégoire 1976). However, errors are often more difficult to trace, especially when two or more scolytid species occur simultaneously. Ideally, parasitism should be evaluated by the debarking of infested wood, observation and determination of host galleries and single rearing of parasitoid larvae, pupae or cocoons. Unfortunately, only few studies were based on log dissection and individual rearing (e.g. Schroeder 1974; Mendel 1986). Another method to study parasitoids and other natural enemies consists of the exposure of sentinel hosts for a short period of time, as was carried out by Weslien (1992) with *I. typographus*.

2.2. Parasitoid guilds and general biology

A parasitoid guild can be defined by the host stage attacked, the host stage killed, and the mode of parasitism (endo- or ectoparasitism) (Mills, 1994). Four parasitoid guilds are found on Scolytidae.

2.2.1. Egg parasitoids

Only one true hymenopteran egg parasitoid has been undoubtedly reared from scolytids in Europe. *Trichogramma semblidis* (Aurivillius) is a well-known parasitoid of the ash bark beetle *Leperisinus varius* (= *Hylesinus fraxini* Panzer = *H. orni* Fuchs) and the closely related ash species *Hylesinus crenatus* F. (e.g. Michalski and Seniczak 1974; Hintze-Podufal and Druschke 1988). It is also reported from 56 species of Lepidoptera, Diptera and Coleoptera (Noyes, 2001). However, the genus *Trichogramma* is a taxonomically difficult group, and sibling species within this complex with a narrower host range cannot be ruled out. *T. semblidis* was very common on ash bark beetles in Poland, with mean parasitism rates of 11-14% (Michalski and Seniczak 1974). Parasitoid females were found in galleries ovipositing in freshly laid beetle eggs.

2.2.2. Egg-larval endoparasitoids

The only confirmed egg-larval parasitoid of Scolytidae in Europe is the eulophid *Entedon ergias* Walker (= *leucogramma* (Ratzeburg)), one of the most abundant parasitoids of broad-leaf scolytids of the genus *Scolytus* (Hedqvist 1963; Schroeder 1974; Merlin 1984; Yates, 1984). Other *Entedon* spp. have been reported from bark beetles (Tables 1 and 3), but their biology is unknown. The biology of *E. ergias* has been described in detail by Beaver (1966a) on *Scolytus scolytus* (F.). The female enters the scolytid maternal gallery to oviposit in the egg. The parasitoid development occurs internally. Parasitised larvae are usually killed in the 4th, penultimate instar. Parasitism induces a modification of the behaviour of the parasitised larva, which moves to the outer bark before the unparasitised ones. Overwintering occurs as a larva in the host larva or as a pupa in the gallery. There are one or two generations per year. *E. ergias* has also been studied extensively in the

USA, where it was accidentally introduced and became established on the elm beetle, *Scolytus multistriatus* (Van Driesche *et al.* 1996)

2.2.3. Larval ectoparasitoids

Most of the parasitoids of Scolytidae belong to this guild. Two different strategies are observed. Larval ectoparasitoids can either enter bark beetle galleries to find and parasitize host larvae ("cryptoparasitoids"), or can locate and parasitise their host through the bark. The best known cryptoparasitoid is the holarctic *Roptrocerus xylophagorum* (Ratz.), a common and polyphagous parasitoid of conifer bark beetles. Its biology has been extensively studied, both in Europe and the USA (e.g. Hedqvist 1963; Samson 1984; Pettersson *et al.* 2000; Sullivan *et al.* 1999). Eggs are laid on bark beetle larvae and, occasionally, on pupae in the galleries. Two other species, *Roptrocerus mirus* (Walker) and *R. brevicornis* (Thomson), occur on conifers in Europe (Hedqvist 1963). They have never been studied in detail and have been cited much less frequently and from fewer hosts than *R. xylophagorum* (Table 1). However, this may result from identification errors since recent studies showed that *R. mirus* is nearly as frequent as *R. xylophagorum*, particularly on spruce (Wermelinger 2002; M. Kenis, unpublished). The pteromalid *Cerocephala ectoptogastri* Masi and several Bethylidae are mentioned as cryptoparasitoids of scolytid larvae and pupae by Mendel (1986), and seem to be particularly abundant in southern Europe and the Mediterranean region (Tables 2, 3) (Russo 1938; Mendel 1986). Other probable cryptoparasitoids are the species that attack ambrosia beetles in the sapwood, *Perniphora robusta* (Ruschka) and *Eurytoma polygraphi* (Ashmead), although their oviposition behaviour has never been clearly described.

The majority of the larval parasitoids attack their host through the bark. This biology is encountered mainly in Braconidae and Pteromalidae, but also in Ichneumonidae, Eurytomidae, Torymidae and Eupelmidae. Nuorteva (1957), Hedqvist (1963, 1998) and Mills (1983) provide general overviews of the biology of these parasitoids, but some species have been studied in greater detail, for example, *Coeloides bostrichorum* Giraud, *Rhopalicus tutela* (Walker) and *Dendrosoter middendorffii* (Ratzeburg) as parasitoids of *Ips typographus* (Sachtleben 1952; Bombosch 1954; Krüger and Mills 1990; Hougardy and Grégoire 2001), *Cheiropachus quadrum* (F.) and *Rhaphitelus maculatus* Walker on *Phloeotribus scarabaeoides* (Russo 1938; Campos and Gonzalez 1990, 1991; Gonzalez and Campos 1990b; Campos and Lozano 1994), and *Dendrosoter protuberans* (Nees), a parasitoid of *Scolytus* species (Kennedy, 1970). The general biology is similar for most species. Parasitoids usually locate their host by walking on the bark, paralysing the larvae or pupae by injecting venom, and laying a single egg on the paralysed host. Eggs and larvae develop quickly. Overwintering usually occurs as prepupae or pupae, in the host gallery. Braconids and ichneumonids build a cocoon in the gallery, whereas chalcids pupate directly in the host gallery. Several ectoparasitoids act as facultative or obligatory hyper- or cleptoparasitoids on other parasitoids of the same guild (see section 2.6 below).

2.2.4. Adult endoparasitoids

Adult parasitism is a relatively rare event in endopterygote insects. Bark beetles, however, are frequently parasitized in the adult stage by a range of Braconidae and Pteromalidae (Table 1). Interestingly, adult parasitism seems to be restricted to conifer bark beetles whereas there is no record from broadleaf species, apart from the dubious notification of *Centistes cuspidatus* Hal. on *Leperisinus varius* (Hintze-Podufal and Druschke 1988). The most studied adult parasitoid is the pteromalid *Tomicobia seitneri* (Ruschka), a frequent parasitoid of *Ips typographus* and, possibly, some other *Ips* spp. Faccoli (2000a, 2001a) provides a review of its biology. Females oviposit into adult beetles of various ages on the bark. Parasitized beetles are still able to bore into the bark and lay eggs, but fecundity is reduced by an average of 30% (Sachtleben 1952). The parasitoid kills its host and emerges from it in the gallery. It has usually two generations per year. Overwintering occurs as a larva in the host beetle. *T. seitneri* seems to be present in most *I. typographus* populations and parasitism rates vary from 20% to 100% (Faccoli 2000a). *T. seitneri* is often parasitized in the host beetle by another pteromalid, *Mesopolobus typographi* (Ruschka) (Balazy and Michalski 1962; Seitner, in Hedqvist 1963). Several other *Tomicobia* spp. are reported from conifer bark beetles in the world (Faccoli 2001a). In Europe, *T. acuminati* Hedqvist is found on *Ips acuminatus* and *T. pityophthori* (Boucek) on *Pityogenes chalcographus* (L.) (Hedqvist 1963; Lobinger and Feicht 1999).

Braconid adult parasitoids all belong to the sub-family Euphorinae. *Ropalophorus clavicornis* (Wesmael) is a frequently encountered parasitoid of *I. typographus* (Nuorteva 1957; Hedqvist 1998; Faccoli 2001a). Its biology has been poorly studied but seems to be very similar to that of *T. seitneri* (Bomboesch 1954; Nuorteva 1957; Faccoli 2001a). There is very little information on the level of parasitism by *R. clavicornis*, except from Bomboesch (1954) who mentions 18% parasitism in Bavaria. In a large collection of parasitoids from spruce infested by *I. typographus* in Switzerland, *R. clavicornis* was the main adult parasitoid, and the third most abundant species of the whole parasitoid complex (Wermelinger 2002). The genus *Cosmophorus* comprises several species apparently specialised on conifer bark beetles. Five of them occur in Europe. Hedqvist (1998) and van Achterberg and Quicke (2000) provide determination keys, host lists and general data on their biology, which is apparently similar to the other adult parasitoids. Finally, another euphorine braconid, *Cryptoxilos cracoviensis* (Capek and Capecki), has been reared from adults of *Cryphalus piceae* (Ratz.) in Poland (Capek and Capecki 1979).

2.3. Host specificity

Host range is among the most difficult characteristics to determine in parasitoid ecology (Shaw 1994). The literature is full of identification mistakes and erroneous host-parasitoid associations, especially in bark beetles and their parasitoids, which are usually associated merely because they emerge from the same logs. The most obvious errors were removed from Tables 1, 2 and 3, but these undoubtedly still contain many wrong associations. However, patterns in host specificity can emerge

from the most serious studies. For example, adult parasitoids and the egg-larval parasitoid *Entedon ergias* are probably more specific than the majority of the larval ectoparasitoids. *E. ergias* seems to be restricted to the genus *Scolytus*. *Tomicobia seitneri* and *Ropalophorus clavicornis* are usually associated with *I. typographus*, *Tomicobia acuminati* with *Ips acuminatus* and *Tomicobia pityophthori* with *Pityogenes chalcographus*. The host specificity of *Cosmophorus* spp. is less clear, and at least some species have been reared from several bark beetle hosts (Hedqvist 1998). The high specificity of parasitoids attacking eggs and adults could be explained by the fact that females probably locate their host by their aggregative pheromone, as shown for *T. seitneri* (Mills and Schlup 1989; Faccoli 2000a), *T. pityophthori* (Lobinger and Feicht 1999) and *R. clavicornis* (Faccoli 2001a). More generally, koinobiont endoparasitoids tend to be more specific than idiobiont ectoparasitoids because the former live in close interaction with the hormonal system of their host.

Larval ectoparasitoids of Scolytidae are thought to be rather more host-tree specific than host-specific, but this is highly variable. Few parasitoids are commonly found on conifer and broad-leaf species. The main examples include Eurytomidae (e.g. *Eurytoma morio* Boheman) and Eupelmidae (e.g. *Eupelmus urozonus* Dalman), which are known to be facultative or obligatory hyperparasitoids, but also some Pteromalidae such as *Heydenia pretiosa* Forster, *Dinotiscus colon* (L.), and the braconid *Ecphylus silesiacus* (Ratzeburg), although the existence of cryptic species cannot be ruled out. The pteromalid, *Perniphora robusta*, and the eurytomid *Eurytoma polygraphi* are specialised in ambrosia beetles living in the sapwood, but are found equally in conifers and broad-leaf trees. Other overlaps are probably the result of identification errors or accidental parasitism. Within conifers or broad-leaf trees, some parasitoids are reported to be polyphagous and to attack beetles on various tree genera (e.g. *Rhopalicus tutela*, *Roptrocerus* spp., *Dendrosoter middendorffii*), whereas others seem to be confined to a single tree genus (e.g. *Metacolus unifasciatus* Forster, *Coeloides abdominalis* (Zetterstedt) and *C. sordidator* (Ratzeburg) on pine, and *Coleoides bostrichorum*, on spruce). Some larval ectoparasitoids are strongly linked to a host species, such as *C. bostrichorum* with *I. typographus*, although other host records are sometimes found. However, it remains to be seen whether the apparent association between a parasitoid and a particular host tree is due to the tree itself or to the host beetle, or a combination of the two. Interestingly, when *I. typographus*, a typical spruce bark beetle, occasionally attacks pine, it is followed by its whole range of parasitoids, including those that are usually associated with spruce rather than pine, such as *C. bostrichorum*, *D. eupterus*, *T. seitneri* and *R. clavicornis* (Turcani and Capek, 2000; Turcani and Kenis, unpublished). Inversely, during an outbreak of the pine bark beetle *Ips sexdentatus* (Boern.) on oriental spruce (*Picea orientalis*) in Turkey, Schimitschek (1940) reared a parasitoid complex very similar to that usually observed on pine, including *C. abdominalis*, a species usually associated with various pine beetles.

Very few studies have focused on parasitoid host range in Scolytidae. A notable exception is Mendel (1986) who, in Israel, collected 26 parasitoid species from 15

bark beetle species on 17 different members of the Pinaceae, Cupressaceae and various broad-leaf families. He reared parasitoids singly from identified larval galleries, which prevented errors in host-parasitoid associations. Interestingly, there was little overlap between the parasitoid complexes in Pinaceae and other trees, but the overlap was much larger between Cupressaceae and broad-leaves. All levels of host specificity were found, from highly polyphagous species (e.g. *H. pretiosa*) to species specific to a single beetle (e.g. *Ecpylus caudatus* Rushka on *Hypoborus fucus* (Erichson), to a single genus (e.g. *Entedon ergias* on *Scolytus* spp.), or restricted to a single tree species but polyphagous within this tree (e.g. *D. middendorffii*, or *R. xylophagorum* in *Pinus*). The mechanisms leading to polyphagy or monophagy in larval ectoparasitoids are not clear, but probably include multiple factors such as host- and host tree location (both long range and short range), and physical constraints such as bark thickness and host size. Host location is the subject of the following section. The influence of bark thickness on host range has been investigated by Manojlovic *et al.* (2000a) in *E. silesiacus*, a parasitoid of *Scolytus* spp. on elm. *E. silesiacus*, the species living in the thickest bark, was the least parasitized and the least preferred host.

2.4. Host location

The topics of host location and, more generally, tri-trophic interactions, have provided some of the most interesting studies on bark beetle parasitoids in recent years. Host location mechanisms have been studied because they are supposed to be the key to understanding parasitoid host ranges, and also because their better understanding would allow the development of new control methods aiming at conserving and augmenting natural enemies in the field. In addition, Mills and his colleagues studied host location mechanisms in *Ips typographus* parasitoids to evaluate their potential as biological control agents against new hosts in North America (Mills and Krüger, 1989; Mills and Schlup, 1989; Mills *et al.*, 1991). The location of bark beetles by parasitoids involves two distinct steps. Firstly, the parasitoid must locate the host habitat, i.e. an infested tree (long-range host location). Secondly, the parasitoid must be able to locate a particular host at a suitable developmental stage (short-range host location).

The attraction of the adult parasitoid *Tomicobia seitneri* to the aggregation pheromone of *Ips typographus* was shown in field conditions by Mills and Schlup (1989) and Faccoli (2000a). Mills and Schlup also tested pheromones of American *Dendroctonus* spp., to which *T. seitneri* did not respond, suggesting that this host location mechanism involves specific interactions, and may be responsible for the higher specificity in adult parasitoids compared to larval parasitoids. Lobinger and Feicht (1999) showed that *Tomicobia pityophthori* was strongly attracted by the pheromone of its host, *Pityogenes chalcographus*. It is likely that other adult parasitoids also locate their hosts using the host pheromone as kairomone, as suggested by Faccoli (2001a) for *Ropalophorus clavicornis*. In contrast, it seems that aggregation pheromones do not attract larval ectoparasitoids, as shown by Mills and Schlup (1989) for *I. typographus* parasitoids. However, multistriatin, a

component of the aggregation pheromone of *Scolytus multistriatus* is known to be attractive for several larval ectoparasitoids of this elm-feeding scolytid (Kennedy, 1984; Gonzales *et al.*, 1999). The mechanisms and cues involved in long-range host location in larval ectoparasitoids are unclear. Mills and Schlup (1989) suggested that the cues could be emitted by the host-associated fungi. However, in a field experiment, *Rhopalicus tutela* was attracted by spruce logs and isolated bark infested with *I. typographus* larvae, but not by spruce wood containing the associated fungi alone.

In Spain, Lozano *et al.* (2000) showed that the larval ectoparasitoids *Dendrosoter protuberans* and *Cheiropachus quadrum* and their host, *Phloeotribus scarabaeoides* are attracted by the same compounds, alpha-pinene and 2-decanone. They suggest that these parasitoids could use these compounds to locate their host.

Mechanisms of short-range host location in larval ectoparasitoid have been studied more extensively, especially on *I. typographus* and its main parasitoids (Mills *et al.* 1991; Pettersson 2001a, 2001b; Pettersson *et al.* 2000, 2001a, 2001b). They followed interesting observations by Ryan and Rudinsky (1962) and Richerson and Borden (1972) on *Coeloides vancouverensis* (D.T.) (= *C. brunneri* Vier.) and its host *Dendroctonus pseudosugae* Hopkins in North America, providing evidence for the role of sound and infra-red radiation, respectively, as cues for locating host larvae beneath the bark. However, in a series of experiments on *I. typographus* parasitoids (*Coeloides bostrichorum*, *Dendrosoter middendorffii* and *Rhopalicus tutela*), Mills *et al.* (1991) rejected the role of sound, vibration and infrared radiation, and showed evidence that volatile cues play the major role. However, they were not able to isolate the source of these volatiles, nor the volatiles themselves. Pettersson and co-authors (Pettersson *et al.* 2000, 2001a, 2001b; Pettersson 2001a, 2001b) confirmed the role of volatiles in host location in *C. bostrichorum*, *R. tutela*, *Roptrocerus mirus* and *R. xylophagorum*. They revealed odour perceptive sensillae on antennae of *R. tutela* (Pettersson *et al.* 2001a), and showed that, for all parasitoids investigated, the attractive compounds were mainly oxygenated monoterpenes present in infested trees. These are probably involved in both short-range and long-range attraction, and seem not to arise from the insect hosts, but from the host-plant complex, including associated fungi.

2.5. Dispersal, longevity and feeding behaviour in the field

Most knowledge on the biology and ecology of parasitoid adults has been gathered from laboratory rearing (e.g. Kennedy 1970; Krüger and Mills 1990; Campos and Gonzales 1990; 1991; Gonzales and Campos 1990b, Manojlovic *et al.* 2000a), or from observations of adult behaviour on infested logs (e.g. Hedqvist 1963, Mills 1991). However, the ecology and biology of adults of bark beetle parasitoids remain largely unknown, especially in relation to dispersal capacities, longevity in natural conditions and feeding habits in the field. These characteristics, however, are essential in the development of new management methods taking into account the

roles and impacts of parasitoids and other natural mortality factors. Hougardy and Grégoire (2000) suggested that food sources such as nectar, pollen and honeydew are available in abundance in spruce forests and that searching for food is probably not time and energy consuming.

Dispersal behaviour could be studied using rubidium as an internal marker. Promising results were obtained by Hougardy *et al.* (2003) who marked larval parasitoids of *Ips typographus* by introducing rubidium chloride into spruce vascular systems. In another recent field study, Lobinger and Feicht (1999) used traps baited by the pheromone of *Pityogenes chalcographus* related to an electronic design to study the swarming behaviour of the adult parasitoid *Tomicobia pityophthori*.

2.6. Competitive interactions and other mortality factors in parasitoids

Larval ectoparasitoids are often subject to hyper- or cleptoparasitism. Antagonistic interactions between parasitoids of scolytids have been discussed by Mills (1991). *Eurytoma morio* and *Eurytoma arctica* Thomson, polyphagous parasitoids of conifer and broad-leaf tree scolytids, may act as primary parasitoids (e.g. Nuorteva 1957; Hedqvist 1963; Pettersen 1976a), cleptoparasitoids (Mills 1991) and hyperparasitoids through Braconidae and Pteromalidae (Sachtleben 1952; Nuorteva 1957). Eupelmidae of the genera *Calosota* and *Eupelmus* have been frequently reared from logs attacked by bark beetles (e.g. Hedqvist 1963, Pettersen 1976b; Mendel 1986) but the few data available on their biology suggest that they act mainly as hyperparasitoids (Hedqvist 1963). Kenis and Mills (1994) observed that *Calosota aestivalis* Curtis and *Eupelmus urozonus*, the most often cited eupelmid parasitoids of bark beetles in Europe, parasitized cocoons of *Dolichomitus terebrans* and *Coeloides* spp., respectively, in galleries of *Pissodes castaneus* De Geer (Col.: Curculionidae) in pine logs. Rarely, primary pteromalid parasitoids may also act as facultative hyperparasitoids of braconids, as observed with *Dinotiscus eupterus* on *Dendrosoter middendorffii* (Sachtleben 1952).

Cleptoparasitism is probably a common behaviour among parasitoids of bark beetles. Mills (1991) showed that females of *Cheiropachus quadrum* and *E. morio* commonly displaced females of *Coeloides filiformis* Ratz. ovipositing on the ash bark beetle *Leperisinus varius*. Hougardy and Grégoire (2003) observed that, on *Ips typographus*, *R. tutela* females were able to displace *C. bostrichorum* from the oviposition sites to steal the host previously located by the braconid. Hougardy (2003) also investigated the niche partitioning mechanisms in the main parasitoids of *I. typographus*, i.e. *Coeloides bostrichorum*, *Rhopalicus tutela*, and *Roptrocerus xylophagorum*. She analysed between-stand, between-tree and within-tree distributions, as well as habitat preferences and interactions with other species.

Competitive interactions among parasitoids of adults have been poorly studied. *Mesopolobus typographi* is known as a hyperparasitoid of *Tomicobia seitneri* (Seitner, in Hedqvist, 1963), but its biology is largely unknown.

Table 1. Parasitoids reared reared from scolytid species feeding on living Pinaceae in Europe and the Near East. xx = Particularly reliable association, i.e. mentioned in at least four different studies, or obtained by log dissection. x = other records. (x) = Association that appears dubious to the senior author because it comes from an unreliable study and the biology of the parasitoid makes this association unlikely. Totally unlikely associations are not mentioned in this table.

Table 1. (cont.).

Table 1. (cont.).

<i>T. lineatum</i>	-	-	-	-	-	-	-	-
<i>T. piniperda</i> ²	-	-	(x)	-	-	-	-	-
<i>T. minor</i>	-	-	-	-	(x)	(x)	-	-
<i>P. poligraphus</i>	-	-	-	-	-	-	-	-
<i>P. pityographus</i>	-	-	-	-	-	-	-	-
<i>P. vorontzovi</i>	-	-	-	-	-	-	-	-
<i>P. spinidens</i>	-	-	-	-	x	-	-	-
<i>P. curvidens</i>	-	-	-	-	-	-	-	-
<i>P. trepanatus</i>	-	-	-	-	-	-	-	-
<i>P. chalcographus</i>	-	-	-	-	-	-	-	-
<i>P. conjunctus</i>	-	-	-	-	-	-	-	-
<i>O. erosus</i>	-	-	-	-	-	-	-	-
<i>I. typographus</i>	-	(x)	-	-	-	-	-	-
<i>I. sexdentatus</i>	-	-	-	-	-	-	-	-
<i>I. duplicatus</i>	-	-	-	-	-	-	-	-
<i>I. cembrae</i>	-	-	-	-	-	-	-	-
<i>I. amitinus</i>	-	-	-	-	-	-	-	-
<i>I. acuminatus</i>	-	-	-	-	-	-	-	-
<i>D. micans</i>	-	-	-	xx	-	-	-	-
<i>C. piceae</i>	-	-	(x)	-	-	-	-	-
Ichnemonidae								
<i>Dolichomitus terebrans</i> (Ratzev.)	L.ec.	-	(x)	(x)	x	-	(x)	-
<i>Neoxorides collaris</i> (Gravenhorst)	L.ec.	-	(x)	-	-	-	-	(x)
<i>Xorides irrigator</i> (F.)	L.ec.	-	(x)	-	-	-	-	-
Pteromalidae								
<i>Chirotopachus quadrum</i> (F.)	L.ec.	-	(x)	(x)	-	-	-	-
<i>Dinotiscus aporioides</i> (Walker)	L.ec.	-	(x)	-	(x)	-	-	(x)
<i>D. colon</i> (L.)	L.ec.	-	xx	-	-	-	-	x
<i>Dinotiscus eupterius</i> (Walker)	L.ec.	x	x	x	-	xx	x	xx
<i>Hedenia pretiosa</i> Forster	L.ec.	-	x	-	-	xx	x	-
<i>Macromesma amphibia</i> Walker	L.ec. [?]	-	-	-	-	x	-	x

Table 1. (cont.).

Table 1. (cont.).

Parasitoid guilds: L.cc. = Larval ectoparasitoid; L.ec.c. = Larval endoparasitoid; (b) = Essentially hyperparasitoid. See text

Includes data often

Includes data of the cryptic species *T. minimorda* and *T. destryensis* of little details.

References: a: Noyes (2001); b: Herting (1973); c: Mills (1983); d: Hedqvist (1963); e: Thomson (1943); f: Hedqvist (1967); g: Faccioli (2000b); h: Hedqvist (1967); i: Capeck &apecki (1979); j: Grégoire (1976); k: Vooma (1986); l: Nuorteva (1957); m: Héraud & Mercadier (1996); n: Grodski (1997); o: Bombois (1954); p: Faccioli (2001a); q: Hwangmelliinger & Greco (2002); r: Mills & Schlip (1989); s: Petteuers (1976a); t: Sachtleben (1952); u: Mendel (1986); v: Eichhorn & Graf (1974); w: Westlin (1992); x: Capek (1955).

Predators and diseases are also responsible for mortality in bark beetle parasitoids. Many generalist predators, such as clerid beetles and dolichopodid flies, feed indiscriminately on both hosts and parasitoids (Mills 1983), but their impact on parasitoid populations has never been measured. Very little is known on pathogens of bark beetle parasitoids, although researchers often observe dead parasitoid larvae and pupae in galleries (M. Kenis, unpublished). Winter mortality is important. Faccoli (2002) measured mortality rates of 47-48 % in *C. bostrichorum* and *R. xylophagorum* in Italy. In Colorado, the winter mortality rate of *Dendrosopter protuberans* varied between 79 and 89 % (Hostetler and Brewer 1976). The mortality factors could not be firmly established, although low temperatures were suspected to play a major role, especially in *D. protuberans*.

Table 2. Parasitoids reared from scolytid species feeding on living Cupressaceae in Europe and the Near East. xx = Particularly reliable association, i.e. mentioned in at least four different studies, or obtained by log dissection. x = other records. Totally unlikely associations are not mentioned in this table. Records from Ruschka (1916), Lichtenstein and Picard (1920), Herting (1973), Mendel (1986), and Noyes (2001).

	Guild ¹	<i>Phloeosinus armatus</i>	<i>Phloeosinus bicolor</i>	<i>Phloeosinus thujae</i>
<u>Braconidae</u>				
<i>Dendrosopter protuberans</i> (Nees)	L.ec.	xx	xx	.
<i>Hecabolus sulcatus</i> Curtis	L.ec.	.	x	x
<i>Heterospilus incompletus</i> (Ratzeburg)	L.ec.	.	.	x
<u>Pteromalidae</u>				
<i>Cerocephala eccoptogastri</i> Masi	L.ec.c.	xx	xx	.
<i>Heydenia pretiosa</i> Forster	L.ec.c.	xx	xx	.
<i>Metacolus unifasciatus</i> Forster	L.ec.	xx	xx	x
<i>Rhaphitelus maculatus</i> Walker	L.ec.	xx	xx	x
<i>Rhopalicus quadratus</i> (Ratzeburg)	L.ec.	.	.	x
<u>Eulophidae</u>				
<i>Entedon ergias</i> Walker	E-L.en.	.	x	.
<u>Eupelmidae</u>				
<i>Calosota aestivalis</i> Curtis	L.ec. (h)	xx	xx	.
<u>Eurytomidae</u>				
<i>Eurytoma morio</i> Boheman	L.ec.	xx	xx	x
<u>Bethylidae</u>				
<i>Cephalonomia hypobori</i> Kieffer	L.ec.c.	.	xx	x

¹Parasitoid guilds: L.ec. = Larval ectoparasitoid; L.ec.c. = Larval ectoparasitoid, cryptoparasitoid; E-L.en. = Egg-larval endoparasitoid; (h) = Essentially hyperparasitoid. See text for more details.

Table 3. Parasitoids reared from scolytid species feeding on living broad-leaved trees in Europe and the Near East. XX = Particularly reliable association, i.e. mentioned in at least four different studies, or obtained by log dissection. X = other records. (X) = Association that appears dubious to the senior author because it comes from an unreliable study and the biology of the parasitoid makes this association unlikely.

Totally unlikely associations are not mentioned in this table.

Main references ³	Guild ¹	Xyleborus dispar															
		<i>Trypodendron domesticum</i>	<i>Scolytus scolytus</i>	<i>Scolytus ratzeburgi</i>	<i>Scolytus multistriatus</i>	<i>Scolytus laevis</i>	<i>Scolytus intricatus</i>	<i>Phloeotribus scarabaeoides</i>	<i>Leperesinus varius</i> ²	<i>Hylesinus crenatus</i>	f,u	a,b,c	a,b,d	a,b	a,b,e	a,b,f	d,u
<i>Bracon caudatus</i> Ratzeburg	L.ec.	.	(x)
<i>B. obscurator</i> Nees	L.ec.	.	(x)
<i>B. palpator</i> Ratzeburg	L.ec.	(x)
<i>B. ratzeburgii</i> Dalla Torre	L.ec.	.	(x)
<i>B. stabilis</i> Wesmael	L.ec.	xx	xx
<i>B. tenuicornis</i> Wesmael	L.ec.	.	x	x
<i>Centistes cuspidatus</i> (Haliday)	A.en. [?]	.	x	x
<i>Coeloides abdominalis</i> (Zetterstedt)	L.ec.	.	(x)	(x)	.	.	.
<i>C. filiformis</i> Ratzeburg	L.ec.	xx	xx
<i>C. melanous</i> Wesmael	L.ec.	x	xx	x	(x)	.	.	.
<i>C. scolyticida</i> Wesmael	L.ec.	.	x	xx	x	.	xx
<i>C. soridulator</i> (Ratzeburg)	L.ec.	.	.	.	(x)
<i>C. subconcolor</i> (Russo)	L.ec.	.	x	xx
<i>C. unicolor</i> Thomson	L.ec.	xx	.	.	.
<i>Dendrosolet ferrugineus</i> (Marshall)	L.ec.	.	x
<i>D. prothorans</i> (Nees)	L.ec.	xx	xx	xx	x	.	.	xx	x	x	x	xx	x	x	x	x	.

Table 3. (*cont.*).

Table 3. (cont.).

	Guild ¹	(x)
<i>Xyleborus dispar</i>		.
<i>Trypodendron domesticum</i> (= <i>Pseudopimpla anisandri</i> (Fairinger))		.
Pteromalidae		
<i>Acrocomus semifasciatus</i> Thomson	L.ec.?	.
<i>Agriocida ferrieri</i> Stephan	L.ec.?	.
<i>Cerocephala cornigera</i> Westwood	L.ec.c.?	.
<i>C. ectoptogastri</i> Masi	L.ec.c.	.
<i>Cheiropachus obscuripes</i> Brues	L.ec.	.
<i>C. quadratum</i> (F.)	L.ec.	.
<i>Cleonymus obscurus</i> (Walker)	L.ec.?	.
<i>Dinotisca aponius</i> (Walker)	L.ec.	.
<i>D. colon</i> (L.)	L.ec.	.
<i>Dinotisca euphorus</i> (Walker)	L.ec.	.
<i>Habrobyx brevicornis</i> (Raizeburg)	L.ec.?	.
<i>Heydenia pretiosa</i> Förster	L.ec.	.
<i>Perniphora robusta</i> Ruschka	L.ec.c.?	.
<i>Platynrhynchus ducalis</i> (Walker)	L.ec.?	.
<i>P. maculatus</i> Erdös	L.ec.?	.

Table 3. (*cont.*).

Table 3. (*cont.*).

Table 3. (cont.).

	Guild ¹
<i>Bethylidae</i>	
<i>Cephalonomia cursor</i> Westwood	L.ecc.?
<i>C. hypobori</i> Kieffer	L.ecc.
<i>Laelius elisae</i> (Russo)	L.ecc.?
<i>Plastanotus westwoodi</i> (Kieffer)	L.ecc.?
<i>Sclerodermus brevicornis</i> Kieffer	L.ecc.?
<i>S. domesticus</i> Latreille	L.ecc.
<i>Trypophloeidae</i>	
<i>Xyleborus dispar</i>	.
<i>Trypodendron domesticum</i>	.
<i>Scolytus scolytus</i>	.
<i>Scolytus ratzeburgi</i>	.
<i>Scolytus multistriatus</i>	.
<i>Scolytus laevis</i>	.
<i>Scolytus intricatus</i>	.
<i>Phloeotribus scarabaeoides</i>	.
<i>Leperesinus varius</i> ²	.
<i>Hylesinus crenatus</i>	.

¹Parasitoid guilds: E.en = Egg endoparasitoid; L.ec. = Larval ectoparasitoid; L.ecc. = Larval ectoparasitoid, cryptoparasitoid; E-L.en. = Egg-larval endoparasitoid; A.en. = Adult endoparasitoid; (h) = Essentially hyperparasitoid. See text for more details.

²Many records from *Hylesinus fraxini* Panzer, synonym with *Leperesinus varius* (F.)

References: a: Noyes (2001); b: Hertig (1974); c: Michałski and Seniczak (1974); d: Hedqvist, 1963; e: Hedqvist, 1998; f: Thomoson, (1943); g: Mills (1991); h: Hintze-Podhal and Druski (1988); i: Lozano and Campos (1991); j: Russo (1938); k: Mendel (1986); l: Gonzales and Campos (1990); m: Markovic and Slobjanovic (1996); n: Manohlović (2000); o: Maksimovic (1979); p: Merlin (1984); q: Schroeder (1974); r: Mendel (1986); s: Nuorteva (1957); t: Beaver (1967a); u: Eichhorn and Graf (1974); v: Yates (1984)

3. PREDATORS

Predators are defined as carnivorous organisms killing several prey during their development. Since most problems with bark beetles occur in conifers, most investigations on predators were carried out on conifers, and little information is available on predators of Scolytidae on broad-leaf trees. In general, predators have a larger range of prey species than parasitoids. They can be efficient antagonists because many species are more mobile and active during wintertime than their prey. Like parasitoids, many predators are known to locate their prey by semiochemicals, i.e. by bark beetle pheromones or tree volatiles. They are the first to arrive at newly infested trees - often concomitantly with their prey - while most parasitoids arrive later (Stephen and Dahlsten, 1976; Ohmart and Voigt, 1982; Linit and Stephen, 1983). Insect predators do not seem to prefer specific tree parts, but rather colonise the lower parts of bolts (Wermelinger 2002), in contrast to parasitoids, which often prefer the upper parts of a tree where the bark is thinner (Ball and Dahlsten 1973; Stephen and Dahlsten 1976; Gargiullo and Berisford 1981; Wermelinger 2002). Many insect predators produce only one generation per year (Nicolai 1996).

3.1. *The predatory taxa*

Many species have been found associated with bark beetle galleries but only a few are definitely known to forage on living eggs, larvae, pupae, or adults of bark beetles. Many species may be facultative predators, preying also on other subcortical taxa, and others may be solely scavengers. Most predatory species belong to the Coleoptera and Diptera. Some important coleopteran families include Cleridae, Rhizophagidae, and Trogossitidae (=Ostomidae). Many species of other families are also associated with bark beetles. Among the Diptera, the Dolichopodidae and Lonchaeidae are the most relevant families.

Furthermore, predatory bugs in the heteropteran family Anthocoridae suck on juvenile and adult scolytids. A few species of Raphidiidae (Neuroptera) live in their larval stage in the brood galleries of bark beetles and feed on scolytid larvae. There are also mite species that are predatory or parasitic on eggs and larvae of scolytids. The only relevant vertebrate group foraging on bark beetles is the woodpeckers.

Previous compilations of insect predators were provided by Herting (1973) and Mills (1983). The present synopsis mainly reviews the literature of the last five decades including also that on woodpeckers. The most important taxa are discussed in more detail below while a comprehensive list is given in Table 4.

3.1.1 *Coleoptera (beetles)*

Beetles are among the most important and most investigated predators of scolytids. Both their larvae and adults may feed on prey larvae or adults. They usually show less specificity for prey or tree species than parasitoids. Many predators are attracted by prey-emitted pheromones, modulated by tree volatiles (Erbilgin and Raffa 2001). Predaceous beetles in conifers often respond to alpha-pinene and ethanol (Schroeder and Weslien 1994). In addition, they can detect anti-aggregation pheromones such

as verbenone emitted by bark beetles. This is hypothesised to deter predators specialised on early successional scolytid species and to be indifferent or attractive to generalist predators (Lindgren and Miller, 2002). Among the most extensively investigated beetle species are *Thanasimus* spp. (Cleridae), *Rhizophagus* spp. (Rhizophagidae), and *Nemosoma elongatum* (L.) (Trogossitidae).

Cleridae (checkered beetles). This family includes two genera, among which three species of *Thanasimus* Latreille are known to be predators of bark beetles (Table 4). Among these, *T. formicarius* (L.) has been the most intensively studied. Experimental studies showed that it can reduce a brood of *Tomicus piniperda* by 81% (Schroeder 1997) and a brood of *Ips typographus* by 18% (Mills 1985). However, in field exclusion experiments involving *Ips typographus japonicus* Niijima, its impact was somewhat mixed with that of intraspecific competition (Lawson *et al.* 1997). *T. formicarius* starts flying early in the season, and forages throughout the summer, attacking a wide range of prey. In Germany, the females oviposit from early April to late August (Gauss 1954). This author mentions more than 20 species of bark-beetle prey in the following genera; *Ips*, *Pityogenes*, *Tomicus*, *Polygraphus*, *Hylesinus*, *Hylastes*, *Scolytus* and *Dendroctonus*. The predators are attracted to their prey by their aggregation pheromones (Bakke and Kvamme 1978, 1981; Köhnle and Vité 1984; Tømmerås 1988). Tømmerås (1985) observed that predator antennae have receptors keyed to a high number of prey pheromones [(+)- and (-)-ipsdienol, (S)-*cis*-verbenol, (-)-ipsenol, (+)-lineatin, (-)-verbenone, *exo*-brevicomin, frontalbin, etc] and host-tree volatiles [(+)- and (-)- \square -pinene, myrcene, terpineol, limonene, \square -pinene, camphor, pino-camphone, (+)- and (-)-linalool]. This sometimes resulted in high catches in pheromone traps (up to a 1:4 *T. formicarius* : *Ips typographus* ratio according to Bakke and Kvamme 1978). Responding to the pheromones and host-tree volatiles, the predators land on the attacked trees, feed on the attacking bark beetles and oviposit on the bark surface. *T. formicarius* was caught in equal numbers in pine stands attacked the previous year by *Tomicus piniperda* and in unattacked stands, suggesting that they are extremely mobile (Schroeder 1997). Their appearance early in the year and their response to aggregation pheromones allows them to be one of the first species to colonise bark-beetle broods (Lawson *et al.* 1997; Hérard and Mercadier 1996). *T. formicarius*' high impact can be explained by its high fecundity (106 eggs/female: Dippel *et al.* 1997), and high voracity; one adult consumes 3 adult *Ips typographus* per day (Gauss 1954), and each larva consumes 44 to 57 prey larvae during its whole larval life (Mills 1985; Hérard and Mercadier 1996; Dippel *et al.* 1997). Predator densities attacking *I. typographus* were estimated at 1.3 to 11 larvae/1000 cm² (Mills, 1985; Thalenhorst 1958). Combining these larval prey consumption figures with associated predator densities, we conclude that the larvae of *T. formicarius* kill 57 - 627 *I. typographus* larvae per 1000 cm². For comparison, *I. typographus* density has been estimated at 84 – 189 individuals/1000 cm² by Hougardy and Grégoire (2000) and 227/1000 cm² by Gonzalez *et al.* (1996). Adult *T. formicarius* live for 4-10 months and the life cycle takes one year (Gauss 1954) or two years in Scandinavia

(Schroeder 1999a). The beetles overwinter either as prepupae or as young adults in pupal niches within the bark.

Rhizophagidae (root-eating beetles). The family is represented among bark-beetle associates by the genus *Rhizophagus* Hrbst. Vogt (1966) lists 14 European species, most of which live under the bark of conifers or broadleaves. *R. depressus* (F.) and *R. dispar* (Payk.) are associated with *Trypodendron lineatum*, *Pityogenes chalcographus*, *Ips typographus*, *Ips acuminatus*, *Ips sexdentatus*, *Dendroctonus micans*, *Tomicus piniperda*, *T. minor* (Kolomiets and Bogdanova 1980) or respond to the pheromones of these species and/or to ethanol (Byers 1992; Kubisz 1992). They are probably only partly predacious, although there is documented evidence for predation. Hanson (1937) observed in the laboratory a single adult *R ferrugineus* (Payk.) consuming 79 eggs of *Hylastes* sp. Hérard and Mercadier (1986) found that the larvae of *R depressus* are partly mycetophagous or saprophagous, and partly predacious on *T. piniperda* (the larvae consumed 14 prey larvae, the adults 1 prey larva; all stages were also observed to feed on bark-beetle eggs). A similar observation was made by Merlin *et al.* (1986) on *Rhizophagus dispar* Gyll., which grew and developed either when reared on fungal cultures or when provided with living or dead bark beetle larvae. Schroeder (1996) found in an exclusion experiment that *R. depressus* reduced *T. piniperda* broods by 41%.

The biology and feeding habits of *Rhizophagus grandis*, one of the rare examples of a specific predator, are much clearer, because of the wide interest in this insect as a biological control agent against *Dendroctonus micans*. Except for specificity, the major features of *R. grandis*' life cycle are probably similar to those of the other species. The adults find the prey brood chambers using chemical clues (Wyatt *et al.* 1993; Tømmerås *et al.* 1984; Grégoire *et al.* 1992); this prey location mechanism is so finely tuned that a high proportion of the prey broods is eventually discovered (Fielding *et al.* 1991b; Vanaverbeke and Grégoire 1995). Oviposition is regulated both by chemical stimuli and inhibitors (Baisier 1990; Grégoire *et al.* 1991). Adults and larvae feed on the eggs, larvae, pupae and callow adults of the prey. The larvae aggregate on wounded prey but, when food is scarce, they become cannibalistic (Baisier *et al.* 1984; Baisier 1990). Merlin *et al.* (1984) observed that, during its whole larval life, each individual *R. grandis* consumes the equivalent of one fully grown *D. micans* larva. The prepupae become photopositive, leave the brood chambers and pupate in the ground or in the bark at the stem base of the trees. There is at least one generation per year (King *et al.* 1991).

Trogossitidae (bark-gnawing beetles). Most trogossitids live underneath the bark. However, there is only one species reported to be predatory on scolytids, i.e. *Nemosoma elongatum*. This is a well-known and widespread predator foraging on a wide range of bark beetles on both conifers and broadleaf trees (cf. Table 4). It is most often found associated with *Pityogenes chalcographus* in spruce and considered to be a very important predator of this bark beetle. The predator's biology and ecology have been investigated quite extensively (Baier 1991; Wigger 1994; Dippel 1995, 1996; Dippel *et al.* 1997). The adults are attracted by kairomonal cues

and boring dust of bark beetles. Its long-term abundance is, with a time lag, closely related to that of *P. chalcographus* (Kopf and Funke 1998) while its seasonal phenology shows much variation (cf. Baier 1991; Wigger 1996). However, in spring, oviposition of both prey and predator start at the same time. In *P. chalcographus* pheromone baited traps *N. elongatum* can reach up to 20 % of the total catches (Wigger 1996). Trogossitid predators of bark beetles respond to single kairomone compounds (Billings and Cameron 1984; Köhnle and Vité 1984).

Staphylinidae (*rove beetles*). A large number of species have been described associated with bark beetles, or were caught in bark beetle pheromone traps. However, they feed on a wide range of prey species and the precise biology is often unclear. The fact that they can be reared on bark beetles in the laboratory does not mean that they actually forage on bark beetles in the field. Some may also feed on tree sap (Nuorteva 1956). The most frequent staphylinid predators are *Nudobius latus* (Grav.) and *Placusa* spp. (Rauhut *et al.* 1993). They forage facultatively on bark beetles and their larvae. *N. latus* is frequently found in pheromone traps for spruce bark beetles.

Histeridae (*hister beetles*). The histerids most frequently associated with bark beetles in Europe are *Platysoma* spp. and *Plegaderus* spp. They are attracted to pheromone traps of spruce bark beetles (Rauhut *et al.* 1993) as well as to plant volatiles (Schroeder and Weslien, 1994). The foraging behaviour of *Eblisia minor* (Rossi) (= *Platysoma frontale* Paykull) was studied in more detail (Hérard and Mercadier 1996). During the three larval stages it consumed an average of 44 scolytid larvae. The adults are also predacious.

Nitidulidae (*sap beetles*). Various species of *Epuraea*, *Glischrochilus* and other genera are reported to be attracted to scolytid pheromones (Zumr 1983; Rauhut *et al.* 1993; Faccoli 2001b) or to plant volatiles (Schroeder and Weslien 1994). Both their adults and larvae may feed on eggs of bark beetles or other prey (Nuorteva 1956; Schroeder 1999). Many species are endangered and recorded on red lists.

Tenebrionidae (*darkling beetles*). Only a few tenebrionids exhibit a predatory feeding behaviour. Various *Corticeus* species are facultatively predacious on eggs and larvae of bark beetles (Nuorteva 1956; Goyer and Smith 1981; Smith and Goyer 1982; Hérard and Mercadier 1996). *Corticeus fraxini* (Kug.) was reared in the lab and some life history parameters were investigated (Hérard and Mercadier 1996). Both its larvae and adults are predacious. They respond to prey pheromones (Rauhut *et al.* 1993).

There are a few additional coleopteran families which include bark beetle predators. Within the Colydiidae, two *Aulonium* and one *Bitoma* species have been reported from European scolytids. Although the Carabidae are a large predatory group, only

Dromius and *Calodromius* species are frequently found associated with bark beetles. Various species from other predatory families are attracted by either prey- or host tree semiochemicals: *Salpingus planirostris* (F.) (Salpingidae) was found in high numbers in pheromone traps for spruce bark beetles (Rauhut *et al.* 1993). *Pytho depressus* (L.) (Pythidae) was strongly attracted by the host tree volatiles alpha-pinene and ethanol (Schroeder and Weslien 1994). Further coleopteran families with potential bark beetle predators are Laemophloeidae, Mycetophagidae, and Silvanidae (see Table 4).

3.1.2 Diptera (flies)

Most predatory Diptera feed on bark beetles in their larval stage. They often outnumber other subcortically living predatory taxa (Morge 1961). On the other hand, their prey consumption is usually lower than that of beetles. They do not feed exclusively on bark beetles but also on larvae of cerambycids, curculionids, other Diptera and Hymenoptera. The main families are described below. Other dipteran taxa occasionally associated with bark beetles are found in Table 4.

Dolichopodidae (long legged flies). The most relevant genus is *Medetera*. The adult flies are predatory on small insects with a soft integument (Nuorteva 1956; Lieutier 1979; Nicolai 1995a). Mating occurs on the infested trunks and the females deposit their eggs in bark crevices and under scales of bark beetle infested trees (Hopping 1947). *Medetera dendrobaena* Kowarz produces up to 120 eggs per female (Dippel *et al.* 1997). This species is mono- to bivoltine. The arrival of dolichopodids on infested logs occurs shortly after colonisation by bark beetles but their presence and oviposition extends through the summer (Stephen and Dahlsten 1976; Lieutier 1979; Nicolai 1995c).

Most species are known to prey on scolytid larvae, pupae, and teneral adults. They overwinter in the larval stage and emerge simultaneously with the bark beetles (Beaver 1966c; Lieutier 1979). Winter mortality in the maggots can be substantial (Hopping 1947; Nuorteva 1959; Beaver 1966c). *Medetera* has been found to be associated with many bark beetle species in different tree species (cf. Table 1; Capek 1957; Nuorteva 1959; Ounap 1992b). The genus is not necessarily restricted to scolytid diets but also feeds on other taxa. The prey consumption of *M. dendrobaena* showed a functional response, i.e. prey consumption increased with increasing bark beetle density (Nicolai 1995b). When prey is abundant, dolichopodids kill more prey than necessary (Beaver 1966c). With low prey supply they can act cannibalistically.

The impact of dolichopodid flies on scolytid survival is discussed controversially in the literature. Bark beetle mortality imposed by *Medetera* species was assessed to be minor (Mills 1986) and to be independent of *Medetera* densities (Mills 1985). At low densities the access of dolichopodid larvae to bark beetle larvae may be restricted by intact pieces of phloem (Nagel and Fitzgerald, 1975). However, they can reach densities of up to 10 larvae per 100 cm² (Dippel *et al.* 1997) and cause mortality rates of 70-90 % (Hopping 1947; Nuorteva 1959).

Lonchaeidae (lance flies). Among the Lonchaeidae, only the genus *Lonchaea* lives subcortically (Morge 1963). The feeding behaviour of these species is controversially discussed in the literature. They are often considered to be saprophagous or coprophagous (Lieutier 1979). Most species of this genus, however, have developed from saprophagous to predatory behaviour. Morge (1961, 1963) and Hérard and Mercadier (1996) investigated extensively the predatory behaviour of these species. They are specialised in colonising certain species and conditions of trees rather than in preying on specific species of bark beetles. More species live in broadleaves than in conifers. *Lonchaea* species occur in smaller numbers and feed on detritus rather than on living bark beetle larvae (Morge 1961). In conifers, however, some species are known to be obligatory predators, occurring in high numbers. They can feed on eggs, larvae, and adults as well (Morge 1967). Like the Dolichopodidae, they are very voracious, killing more prey individuals than they can eat. When prey individuals are rare, cannibalism occurs. (Hérard and Mercadier 1996).

Pallopteridae (painted-wing flies). *Toxoneura usta* (Meigen) is known to forage on scolytid larvae (Morge 1967; Martinek 1977; Chandler 1991). It is able to feed on eggs, larvae, pupae, and even adult bark beetles, killing many more prey than it can actually eat (Morge 1967). It is not specialised on any particular tree or prey.

Asilidae (robber flies). Asilid flies are not specialised predators of bark beetles. However, scolytids may be among their prey (Wichmann 1956; Dennis 1979). The adult flies insert their stylet before or behind the pronotum or between the elytra, inject paralysing saliva into the body and suck up the liquefied contents. Their larvae are predaceous on other subcortical insect larvae (Wichmann 1956).

3.1.3 Other insect groups

Among the Heteroptera, the predatory behaviour of *Scoloposcelis* species and *Xylocoris cursitans* (Fallén) (Anthocoridae) has been studied in some detail (Heidger 1994; Hérard and Mercadier 1996; Dippel *et al.* 1997). Both larvae and adults are very voracious, killing more prey than they can consume (Hérard and Mercadier 1996). *Scoloposcelis pulchella* can produce two generations per year. They respond to the same lures as their prey (Heidger 1994).

The larvae of some Raphidioptera prey on or underneath the bark. A few species of Raphidiidae are known to forage non-specifically on cerambycids, bark beetles and other subcortically living organisms (Schimitschek 1931; Wichmann 1957). They may be able to access scolytid galleries only after the bark is loosened, e.g. by maturation feeding of bark beetles or by woodpeckers (Wichmann 1957). For further predatory insects see Table 4.

3.1.4 Acari (mites)

Mites can be associated with bark beetles in two ways. The first group feeds on substrates other than living bark beetles, e.g. fungi or nematodes. Therefore, some of

these may even be beneficial to bark beetles (Hirschmann and Wisniewski 1983). These mites depend in a phoretic way on bark beetles, i.e. in a given stage they attach themselves to the emerging bark beetles and use them as transport vehicles to reach new habitats. The second group is parasitic or predacious on various scolytid stages. Adult females and deutonymphs may be phoretic as well.

In general, the ecology of acarine species associated with bark beetles is poorly understood. It may range from mutualistic to parasitic behaviour with all possible combinations of the two. Many mites are parasites rather than predators. A large number of mite species has been found associated with European bark beetles (Hirschmann 1971; Hirschmann and Wisniewski 1983; Kielczewski *et al.* 1983; Moser and Bogenschütz 1984; Moser *et al.* 1989), but only a few are known to actually feed on scolytids. In a study on *Ips typographus*, some 30 % of trapped beetles carried an average of 3 phoretic mites (Moser and Bogenschütz 1984). Common acarine predators such as *Iponemus* spp. and *Paracarophenax* spp. are known to be specialised on bark beetle eggs, whereas *Pyemotes* spp. and *Digamasellus* spp. feed on larvae and pupae. Some adults are commensals while their larvae feed on eggs (Hintze-Podufal and Druschke 1988). Adult bark beetles are not attacked (Moser 1975). The mites are transported to new habitats by adult beetles beneath their elytra or attached to the thorax or elytral declivity. Egg parasites seem to be more host specific than larval parasites (Lindquist 1969). Many species are specific in terms of habitats rather than in terms of hosts (Lindquist 1970). The impact of mites on bark beetle population dynamics is largely unexplored but often considered substantial. Mortality by *Pyemotes* spp. and *Iponemus* spp. reached up to 90 % (Gäbler 1947; Lipa and Chmielewski 1977; Kielczewski *et al.* 1983; Moser *et al.* 1989).

3.1.5 Aves (birds)

Among birds, the woodpeckers (Picidae) are the most important predators on scolytids. Most quantitative studies have been made in America, mainly in *Dendroctonus* spp. infestations. In Europe species like the black (*Dryocopus martius* L.), the great spotted (*Dendrocopos major* (L.)), and the three-toed woodpecker (*Picoides tridactylus* (Hemp. and Ehr)) are commonly observed foraging on bark beetles on conifers (Schimitschek 1931; Nuorteva 1956; Pechacek 1994) and on broadleaves (Yates 1984). In general, they seem to prefer larger prey species than scolytid larvae or beetles (Nuorteva and Saari 1980). In an American study, 89 % of

Table 4. List of European predatory species, their host trees, and their bark beetle preys. Observation type represents character of information: f= observed feeding on respective prey or prey found in faeces, a= associated in galleries or on bodies of respective prey, s= attracted to semiochemicals (pheromones or allelochemicals). Killing rate denotes prey consumption or killing by the respective predator (A= adult, L= larva), an asterisk indicates unclear feeding behaviour. For a summary of further older data see Herting & Simmonds (1973) and Mills (1983). Coleopteran taxonomy follows basically Freude *et al.* (1965-1998)

Table 4

Predator	Host tree	Observation type	Killing rate	References ¹
COLEOPTERA				
<u>Carabidae</u>				
<i>Calodromius spilotus</i> (Ill.) (= <i>Dromius quadrinotatus</i>)	<i>Pn</i>	.	.	22
<i>Dromius quadrivittatus</i> (L.)	<i>Pn</i>	.	x	22
<u>Carabidae</u> spp.*	<i>Pn</i>	.	.	36
<u>Cleridae</u>				
<i>Allonyx quadrimaculatus</i> (Sch.)	<i>Pn</i>	.	.	22
<i>Thanasimus femoralis</i> (Zett.)	<i>Pc, Fr</i>	x	.	77
<i>T. formicarius</i> (L.)		.	.	44-57 larvae/L 2.9 adults/A/day 74-109 adults/A 72,76
<i>T. rugifipes</i> (Braun)	<i>Pc</i>	.	x	63,76
<u>Colydiidae</u>				
<i>Aulonium ruficorne</i> (Ol.)	<i>Pn</i>	.	x	22, 40, 41
<i>A. trisutum</i> (Fourer.)	<i>Uf</i>	.	.	1
<i>Biota crenata</i> (F.)	<i>Pn</i>	x	.	22
<u>Histeridae</u>				
<i>Eblisia minor</i> (Rossi) (= <i>Platysoma frontale</i>)	<i>Pn</i>	.	x	44 larvae/L 1.5 larvae/A/day
<i>Paromatus parallelipipedus</i> (Hbst)	<i>Pn</i>	.	x	36, 37, 38, 63

Table 4 (cont.)

Table 4 (cont.)

Predator	Host tree						Spp	Obst ye	Killing rate	References ¹
<i>G. hortensis</i> (Fourcr.)*	<i>Pc</i>	.	.	.	x	.	.	x	.	63
<i>Ipidia binotata</i> (Rt.) (= <i>Quadrinotata</i> Quensel)	<i>Pn</i>	.	.	.	x	.	x	.	a	22
<i>Pityophagus ferrugineus</i> (L.)	<i>Pn,Fa</i>	.	.	x	.	.	x	x	.	36,53,57,77
Pyralidae										
<i>Pyrausta depresso</i> (L.)	<i>Pn</i>	x	.	s	67
Rhizophagidae (=Monotomidae)										
<i>Rhizophagus bipustulatus</i> F.	<i>Pc,Pn,Fr</i>	.	.	x	x	.	.	x	.	23,29,36,40,42
<i>R. cribraeus</i> Gyll.	<i>Pc,Pn</i>	.	x	.	x	x	.	.	x	27
<i>R. depressus</i> (F.)	<i>Pn,Pc</i>	x	x	x	x	x	.	x	a,f,s	18,22,27,29,38,55
<i>R. dispar</i> (Payk.)	<i>Pn,Pc</i>	x	x	x	x	.	x	x	a,f,s	14 larvae/L 1 larva/A/day 16 eggs/A/day 15 eggs/L/day
<i>R. ferrugineus</i> (Payk.)	<i>Pn,Pc</i>	x	x	x	x	.	x	x	79 eggs/A	7,19,22,55,67,77, 87
<i>R. grandis</i> Gyll.	<i>Pc,Pn</i>	x	a,f,s	1 larva/L
<i>R. nitidulus</i> (F.)	<i>Pn</i>	x	x	a,s	6,13,14,16,17,25, 26,27,33,73,74,84
<i>R. parvulus</i> Payk.	<i>Pc</i>	x	s	29,36,63,64
<i>R. perforatus</i> Er.	<i>Fr,Ul</i>	x	.	s	29
<i>R. puncticollis</i> Saalh.	<i>Pc</i>	x	.	s	29
Salpingidae										
<i>Rabocerus foveolatus</i> (Liungh)	<i>Pc</i>	.	.	x	a	76
<i>R. gabrieli</i> (Gehr.)	<i>Pc</i>	.	.	x	a	76
<i>Salpingus (Rhinosimus) planirostris</i> F.	<i>Pc</i>	.	.	x	s	63
<i>S. (Rhinosimus) ruficollis</i> (L)	<i>Pc</i>	.	.	x	.	.	x	.	s	63

Table 4 (cont.)

Predator	Host tree	T. lin.	Spp	Obst ye	Killing rate	References ¹
<i>Sphaeriestes (Salpingus) castaneus</i> Panz	Pc	.	x .	x .	x .	63
Silvanidae						
<i>Silvanus bidentatus</i> (F.)	Pn	.	x .	x .	x .	22
<i>S. unidentatus</i> (F.)	Pn	.	x .	x .	x .	22
Staphylinidae						
<i>Aleochara sparsa</i> Heer	Pc	.	x .	x .	x .	63
<i>Metoponcus brevicornis</i> (Er.)	Ab	.	x .	x .	x .	8
<i>Nudobius lenticus</i> (Grav.)	Pn,La,Pc	x .	x .	x .	x .	18,36,55,58,63,64
<i>Phloeonomus</i> spp.*	Pn,Pc	x .	x .	x .	x .	38,55,78
<i>Phlocoptora testacea</i> (Mannh.)	Pc,Pn	x .	x .	x .	x .	55,70
<i>Phlocoptiba lapponicus</i> (Zett.)*	Pc	x .	x .	x .	x .	55
<i>Placusa adsetta</i> Er.	Pn	x .	x .	x .	x .	22
<i>P. atrata</i> (Mannh.)	Pc,Be	x .	x .	x .	x .	55
<i>P. depressa</i> Mackl.	Pc	x .	x .	x .	x .	18,38,55,63
<i>P. tachyporoides</i> (Waltl.)	Pc	x .	x .	x .	x .	87
<i>Quedius laevigatus</i> Gyll.	Pc	x .	x .	x .	x .	55,87
<i>Q. plagiatus</i> Mannh.	Pc	x .	x .	x .	x .	78
<i>Staphylinidae</i> spp.*	Pn,Pc,La	.	x .	x .	x .	36,38,55,63,64,77
						78
Tenebrionidae						
<i>Corticeus fraxini</i> Kug	Pn	.	x .	x .	a,f	93 larvae/L 22
<i>C. (Hypophloeus) linearis</i> F.*	Pn	.	x .	x .	x .	1 larva/A/day
<i>C. longulus</i> Gyll.*	Pn	.	x .	x .	x .	18,22,63
<i>C. pini</i> Panz.*	Pn	.	x .	x .	x .	62
<i>C. suberis</i> (Luc.)* (= <i>rufiflus</i> Ros.)	Pn	.	x .	x .	a	42
						42

Table 4 (cont.)

Predator	Host tree		Obst ye	Killing rate	References ¹
<i>C. unicolor</i> * (Pilz, Mitt.)	<i>Pn</i>	.	.	a	42
Trogossitidae					
<i>Nemosoma elongatum</i> (L.)	<i>Pc, Al,</i> <i>Pn, Fa</i>	.	x .	x, a,f,s	2,3,10,11,20,28 30-45 larvae+pupae+ teneral beetles/L
D <small>ERMAPTERA</small>					
Forficulidae					
<i>Forficula auricularia</i> L.	.	x .	.	f	64
D <small>IPTERA</small>					
Asilidae					
<i>Laphria flavipes</i> (L.)	<i>Pc</i>	.	x .	.	79
<i>Choerades (Laphria) gilva</i> (L.)	<i>Pc</i>	.	x .	.	79
<i>Tolmerus (Machimus) atricapillus</i> (Fallén)	<i>Pc</i>	.	x .	.	79
Dolichopodidae					
<i>Dolichopus</i> sp.					
<i>Medetera ambigua</i> (Zett.)					
<i>M. adjaniae</i> (Goss.) (= <i>brevisepta</i> Par.)	<i>Pc, Pn</i>	.	x .	.	a
<i>M. dendrohaema</i> Kowarz	<i>Pc, Fa</i>	.	x .	.	a
<i>M. dichroera</i> Kowarz	<i>Pc, Pn</i>	.	x .	.	a,s
<i>M. excellens</i> Frey	<i>La, Pc</i>	.	x .	.	0.5-10 larvae/L/day
<i>M. impigra</i> Collin	<i>U, La, Fa</i>	.	x .	.	11,52,53,54
<i>M. infumata</i> Loew	<i>Pn, Pc</i>	.	x .	.	55,56
<i>M. melancholica</i> Lundb.*	<i>Al, Pn</i>	.	x .	.	64,76,78
<i>M. nitida</i> (Macqu.)	<i>Ul</i>	.	x .	.	4-7 larvae/L
<i>M. obscura</i> Zett.*	<i>Pn</i>	x .	x .	a,f	4,20
				.	55,77
				.	55
				.	4,66
				.	55

Table 4 (cont.)

Table 4 (cont.)

Predator	Host tree	Spp	Obst ye	Killing rate	References ^l
<i>T. lin.</i>					34
<i>T. spp.</i>					9,49,7,0,76
<i>T. bic.</i>					
<i>S. spp.</i>					
<i>S. int.</i>					
<i>P. pol.</i>					
<i>P. cha.</i>					
<i>P. cal.</i>					
<i>O. ero.</i>					
<i>I. typ.</i>					
<i>I. sex.</i>					
<i>I. cem.</i>					
<i>I. acu.</i>					
<i>H. pal.</i>					
<i>D. mic.</i>					
HETEROPTERA					
<u>Anthocoridae</u>					
<i>Lycocoris campestris</i> (F.)	<i>Pn</i>				22
<i>Scolopostelis obscurella</i> (Zett.)	<i>Pn</i>				22
<i>S. pulchella</i> (Zett.)	<i>Pn,Pc</i>				
<i>Axylocoris curvirostris</i> (Fallén)	<i>Pn</i>				
HYMENOPTERA					
<u>Fornicidae</u>					
<i>Fornicidae</i> spp.					39,83
<u>NEUROPTERA</u>					
<u>Chrysopidae</u>					
<i>Chrysoperla carnea</i> (Steph.)	<i>Pc</i>				
<u>ODONATA</u>					
<i>Anisoptera</i> spp.	<i>Pn</i>				76
RAPHIDIOPTERA					
<u>Raphidiidae</u>					
<i>Dichrostigma (Raphidia) flavipes</i> (Stein)	<i>Pc</i>				64,80
<i>Phaeostigma (Raphidia) notata</i> (F.)	<i>Pc</i>				64,80
<i>Phaeostigma</i> sp.	<i>Pn</i>				22

Table 4 (cont.)

Predator	Host tree	T. lin.	Spp	Obst ye	Killing rate	References ¹
	Pc	.	.	a		76
ACARI						
Acarophenacidae						
<i>Paracarophenax ipidarius</i> (Redik.)*	•	x	x	x	x	24,50,51
Ascidae						
<i>Lastoseius ometus</i> Oud.	•	•	•	•	x	a
<i>Proctolaelaps fischeri</i> (Vitzt.)	•	•	•	•	x	71
<i>P. pini</i> Hirsch.	•	•	•	•	x	71
<i>P. xyloperi</i> Sans.	•	•	•	•	x	71
Digamasellidae						
<i>Dendrolaelaps apophysosimilis</i>	•	•	•	•	x	71
Hirsch					a	
<i>Dendrolaelaps</i> spp.	•	•	•	•	x	71
Eumeniidae						
<i>Ptychopterus dryas</i> (Vitzt.)	•	•	x	x	x	a
<i>P. herfsi</i> (Oud.)	•	•	•	•	x	24
<i>P. scolyti</i> (Oud.)	•	•	•	x	x	5,12,24,33
Tarsostenidae						
<i>Iponemus gaehleri</i> (Schaar.)	•	x	x	x	x	24,50,51
Uropodidae						
<i>Trichouropoda bipilis</i> (Vitzt.)	Fr	•	•	•	x	23
ARANAEAE						
Erigonidae						
<i>Troxochrus nasutus</i> Schenkel	x	•	•	x	a	23
AVES						
Fringillidae						
<i>Fringilla coelebs</i> L.	•	•	x	•	f	72

Table 4 (cont.)

Predator	Host tree	<i>T. lin.</i>	<i>Spp.</i>	Obst ye	Killing rate	References ¹
<i>Picidae</i>						
<i>Dendrocopos major</i> (L.)	<i>La, Qu</i>	.	x	.	.	64,60
<i>Dryocopus martius</i> L.	<i>La</i>	.	x	.	.	64
<i>Picoides syriacus</i> (Hemp. & Elhr.)	<i>Pn, Ol, Pr</i>	.	x	x	x	39
<i>P. tridactylus</i> (L.)	<i>Cu, Ul</i>	.	x	.	x	
<i>Picoides</i> sp.	<i>Con</i>	.	x	.	x	1200 adults/day (estimate)
<i>Qu</i>						
References: 1 Allen (1975); 2 Baier (1991); 3 Baier (1994); 4 Beaver (1966); 5 Beaver (1967); 6 Bergmiller (1903); 7 Byers (1992); 8 Capek (1957); 9 Chandler (1991); 10 Dippel (1996); 11 Dippel <i>et al.</i> (1997); 12 Doberski (1980); 13 Fielding and Evans (1997); 14 Fielding <i>et al.</i> (1991b); 15 Gauß (1954); 16 Grégoire <i>et al.</i> (1991); 17 Grégoire <i>et al.</i> (1992b); 18 Grodzki (1997); 19 Hansson (1937); 20 Harz and Topp (1990); 21 Heidger (1994); 22 Herard and Mercadier (1990); 23 Hintze-Podula and Drusatka (1988); 24 Kielczewski <i>et al.</i> (1983); 25 King <i>et al.</i> (1991); 26 Kobakhidze (1965); 27 Kolomits and Bogdanova (1980); 28 Kopf and Funke (1998); 29 Kubisz (1992); 30 Labeledzi (1989); 31 Leveux <i>et al.</i> (1989); 32 Lieutier (1979); 33 Lipa and Chmielewski (1977); 34 Martinek (1977); 35 Matile (1993); 36 Mazur (1973); 37 Mazur (1975); 38 Mazur (1979); 39 Mendel (1985); 40 Mendel (1988); 41 Mendel <i>et al.</i> (1989); 42 Mendel <i>et al.</i> (1990); 43 Merlin <i>et al.</i> (1986); 44 Merlin <i>et al.</i> (1986); 45 Mills (1983); 46 Mills (1986); 47 Moor and Nyffeler (1983); 48 Mörge (1963); 49 Mörge (1967); 50 Moser and Bogsenschütz (1984); 51 Moser <i>et al.</i> (1989); 52 Nicolai (1995c); 53 Nicolai (1996); 54 Nicolai <i>et al.</i> (1992); 55 Naoitova (1959); 57 Ovres and Stark (1985); 58 Ounap (1992a); 59 Ounap (1992b); 60 Pavlik (1999); 61 Pavlack (1994); 62 Pischik (1980); 63 Rauthut <i>et al.</i> (1993); 64 Schmittschek (1993); 65 Schöpf and Köhler (1995); 66 Schröder (1974); 67 Schröder and Westien (1994); 68 Schröder (1996); 69 Schumacher and Pohns (2000); 70 Seiter (1924); 71 Strube and Benner (1984); 72 Thalenhorst (1958); 73 Tommerås <i>et al.</i> (1984); 74 Wainhouse <i>et al.</i> (1992); 75 Weganeiner and Führer (1991); 76 Wernelingen (2002); 77 Westien and Schroeder (1999); 78 Westien (1992); 79 Wichmann (1956); 80 Wicher (1957); 81 Wigger (1993); 82 Wigger (1990); 83 Wilkinson <i>et al.</i> (1993); 84 Wyatt <i>et al.</i> (1978); 85 Yates (1984); 86 Zinovjev (1957) [in Morge (1961)]; 87 Zumr (1983 ^a).						

²Host trees: Ab: *Abies*; Al: *Alnus*; Be: *Betulus*; Con: Conifers; Cu: *Cupressus*; Fa: *Fagus*; Fr: *Fraxinus*; La: *Larix*; Ol: *Olea*; Pe: *Picea*; Pn: *Pinus*; Pr: *Prunus*; Qu: *Quercus*; Ul: *Ulmus*

the prey in the gizzard of three-toed woodpeckers were larvae of buprestid beetles (Otvos and Stark 1985) while in a German study, the faeces of the same species consisted of 89 % of *I. typographus* (Pechacek 1994). When foraging on bark beetle broods, woodpeckers prefer the later and larger instars (Kroll and Fleet 1979). At the same time, they also devour predatory and parasitic insects living underneath the bark.

Indirect effects of woodpecker activity by puncturing, loosening and removing bark can cause more bark beetle mortality (due to desiccation, other predation, diseases) than direct woodpecker foraging (Moore 1972; Otvos 1979). They can debark large proportions of infested trunks (Hintze-Podufal and Druschke 1988). Only a fraction of the brood in bark flakes dropping to the ground survives to emergence (Kroll and Fleet 1979). Mortality imposed by woodpeckers may vary significantly among single trees, ranging from 5 to 70 % (Shook and Baldwin 1970; Moore 1972; Massey and Wygant 1973; Berryman 1976; Amman 1984; Pavlik 1999). They are most significant in endemic situations, in local outbreaks, or during the decline of an outbreak (Otvos 1979). Woodpecker impact is highest in the upper tree parts where bark beetle densities are highest, during winter and spring (Moore 1972). Woodpecker populations are positively influenced by bark beetle outbreaks.

4. QUANTITATIVE ASSESSMENT OF PARASITOIDS AND PREDATORS AND THEIR ROLES IN THE POPULATION DYNAMICS OF SCOLYTIDAE.

It is difficult to quantify the effects of predators on bark beetles. The consumption of prey in the field is hard to measure, and predators may not only forage on the target bark beetle, but also on other subcortical insects, including predators and parasitoids (Mendel *et al.* 1990) and therefore reduce the overall detrimental effect on a bark beetle population. For example, *Thanasimus formicarius* is an important mortality factor for *Medeterra* larvae (Nuorteva 1959).

In contrast, most studies on parasitoids of Scolytidae have provided some quantitative evaluations of parasitism, either as parasitism rates, or as relative abundance of parasitoid species. Parasitism rates varying from 0 to 100% have been found. However, parasitism rates and consumption rates are poor indicators of the real impact of natural enemies on bark beetle populations. Several authors state that natural enemies do not play an important role in regulating bark beetle populations (e.g. Sachtleben 1952; Bombosch 1954; Faccoli 2001a) whereas a few others affirm the contrary (e.g. Mendel 1987), but few of these statements are based on solid data. To better evaluate the impact of parasitoids and predators on bark beetle populations, various methods have been used, such as consumption rate based assessments (e.g. Dippel *et al.* 1997; Wermelinger 2002), life table analyses, and natural enemy exclusion experiments. Life tables are not easy to construct for bark beetles because of the problem of overlapping generations. On the other hand, their cryptic biology may facilitate population studies because the cause of death and the stage at which it occurs can usually be assessed through regular bark examination. Furthermore, the effect of population densities on mortality factors can be assessed easily because sample logs can be considered as separate populations, with different

beetle densities. In his study on *Scolytus scolytus* in the UK, Beaver (1966b, 1967b) was among the first to use a life table (or, better, population table) approach to assess the various mortality factors on bark beetles and their role in population regulation. He stated that populations are likely to be regulated by different mechanisms at different population densities. Among the main mortality factors were subcortical predators (mainly *Medetera* spp.) and larval ectoparasitoids (mainly *Coeloides scolyticida* Wesmael). Predators showed a density-dependent response at low beetle densities, but became inversely density-dependent at higher densities. In contrast, the ectoparasitoids showed a density-dependent response only above a certain host density. This suggests that subcortical predators have regulatory power at low beetle densities whereas ectoparasitoids compensate at high densities, together with other factors such as intraspecific competition. The roles of woodpeckers and the egg-larval endoparasitoid *Entedon ergias* were less clear. Similar studies on *Leperisinus varius* (Lozano *et al.* 1993, 1994) and *Phloeotribus scarabaeoides* (Lozano *et al.* 1996a, 1996b) showed that populations were regulated by density-dependent larval mortality, due to larval competition and ectoparasitism. However, in both bark beetles, larval parasitism alone tended to show an inversely density-dependent response. Other similar studies were made in North America. In a time-series analysis of populations and antagonists of the North American bark beetle *Dendroctonus frontalis* Zimmermann, delayed density dependency was shown (Turchin *et al.* 1999), suggesting that antagonists are more important during the decline phase of an outbreak than at the beginning. This is supported by another study on *Dendroctonus ponderosae* Hopk. that assigned predators (except clerids) and parasitoids a more significant role in epidemics than in endemic situations (Amman 1984). In a two-year study during an *Ips typographus* infestation in Switzerland, Wermelinger (2002) observed that predators were more abundant in the first year, at the peak of bark beetle density, whereas parasitoids dominated in the second year, when overall beetle mortality increased and populations collapsed.

Mills (1986) and Mills and Schlup (1989) produced basic partial life tables of *I. typographus* in Switzerland and Germany. They suggested that clerid predators *Thanatus* spp. and larval ectoparasitoids had a significant influence on brood survival. They showed that parasitism may vary with tree height (e.g. parasitism by braconids being much higher at the top of the tree), although the relation between parasitism and bark thickness was unclear. Wermelinger (2002) also found higher parasitism on *I. typographus* at the top of the tree than at the bottom.

Natural enemy exclusion experiments provide an elegant method to better assess the impact of natural enemies on bark beetle populations, but have rarely been carried out in Europe. Notable exceptions are the works by Weslien (1992) and Schroeder and Weslien (1994) who, in Sweden, observed a reduction of *I. typographus* and *Tomicus piniperda* populations of 83-89% compared to caged populations where parasitoids and predators were excluded. Related studies in North America also showed that parasitoids and predators can reduce bark beetle populations to a similar extent (e.g. Limit and Stephen 1983; Riley and Goyer 1986).

5. UTILISATION OF PARASITOIDS AND PREDATORS IN BIOLOGICAL CONTROL PROGRAMMES

Although the justification of most studies on parasitoids was their potential use in biological control strategies against scolytids, only few biological control programmes have been implemented. The most important has been the biological control of *Dendroctonus micans* in Georgia, Turkey, UK and France.

D. micans, originally a Siberian species, has been increasing its range continuously during the 20th century, and most of the time it was closely followed by *Rhizophagus grandis*. The impact of this predator was observed very early in Germany, after the establishment of both species (Bergmiller 1903). The first biocontrol programme involving *R. grandis* was developed in the Georgian SSR, after *Dendroctonus micans* invaded the region during the 1950s (Kobakhidze 1965). A small number of adult and larval predators was imported from Czechoslovakia, released in 1963 and established successfully in the local *D. micans* infestations. By 1970, 54,000 predators had been released (Tvaradze 1976), and by 1976 a series of rearing units was established, producing insects on logs infested with *D. micans*. From Georgia, *D. micans* progressed into Turkey, where a biocontrol programme has also been implemented.

In 1983, as *D. micans* was progressing through the French Massif Central, a Belgian-French programme was developed (Grégoire *et al.* 1985). Semi-artificial rearing methods using an artificial diet and oviposition stimulants were established and, in the period 1983-1991, 659 sites (12,275 ha; public as well as private forest) had been treated, usually with rather large releases (500-1000 pairs/site). The sites situated at the borders of the infested area were treated first, to take advantage of the lower pest density there, and to try limiting the spread of the pest. During 1983-99, a total of 530,000 insects were produced and released. Predator establishment and impact were closely followed in a series of permanent plots and in more temporary surveys. The predator releases were always followed by establishment and, within 6-8 years, by the collapse of the bark-beetle populations (see e.g. Vanaverbeke and Grégoire 1995). At present, *D. micans* is still expanding (Aveyron, Orne), justifying the need for further releases. A potential development is the monitoring of pest and predator movements using kairomone traps that attract *R. grandis* (Grégoire *et al.* 1992).

Also in 1983, following the discovery of *D. micans* in the north-west of England and in Wales (Bevan and King 1983), a rearing and release programme started in the UK (Fielding *et al.* 1991; Evans and Fielding 1994; Fielding and Evans 1997). Combined with internal quarantine procedures and the deployment of a pest-free zone around the infested area, predators were released in all sites. In order to cover as many sites as possible, release rates were adjusted to 10-50 pairs/site (average: 57 individuals/site). Between 1984 and 1995, 156,400 insects were released in 2,741 sites (public and private forest). Establishment of *R. grandis* and subsequent control of *D. micans* was observed at the same rates as elsewhere. As *D. micans* is still expanding, the biocontrol programme is continuing.

Finally, *R. grandis* is also being used in a neo-classical biological control programme against a close relative of *D. micans*, *D. valens*, a north-American

species which invaded China in the late 1990's. Following promising laboratory results (Miller *et al.* 1987), *R. grandis* is presently being mass-reared in China for releases in the Shanxi Province (Yang Zhong-qi, pers. comm.).

The programme against *D. micans* was the only classical biological control (i.e. the introduction and establishment of exotic natural enemies to control a pest), that has ever been carried out against scolytids in Europe, mainly because few exotic scolytids have invaded Europe, and these are, presently, not the most damaging species. Conversely, European parasitoids have often been considered for release against European scolytids that have established in other parts of the world. Several parasitoids of the European elm bark beetle, *Scolytus multistriatus*, vector of the Dutch elm disease, were introduced into North America, either accidentally (*Entedon ergias* and *Cheiropachus quadrum*) or intentionally (*Dendrosoter protuberans*, *Ecpylus silesiacus* and *Coeloides scolyticida*, but only *D. protuberans* became established) (Van Driesche *et al.* 1996). A full evaluation of the biological control programme was not made. The pteromalid parasitoid *Rhopalicus tutela* and several predators, *Thanasimus formicarius*, *Rhizophagus dispar*, *R. bipustulatus* and *R. ferrugineus*, were introduced against *Hylastes ater* in New Zealand, after its accidental introduction from Europe, despite the fact that these natural enemies were rarely, or never found in association with *H. ater* in Europe. Only *T. formicarius* became established, but its incidence appears limited. (Faulds 1989). *Metacolus unifasciatus*, *Dendrosoter chaenopachoides* and several predators were released against the European *Orthotomicus erosus* in South Africa (Kfir 1986). *D. chaenopachoides* became established and is now spreading (Tribe and Kfir 2001).

T. formicarius was sent from Germany to the US in 1882-83 against *Dendroctonus frontalis*, but this attempt did not succeed (Moeck and Safranyik 1984). Later, Mills and his colleagues (e.g. Mills 1985; Mills and Schlup 1989; Krüger and Mills 1990; Mills *et al.* 1991) studied the parasitoids and predators of European conifer bark beetles in relation to potential biological control of *Dendroctonus* spp. in North America. *T. formicarius* was sent to Canada for laboratory studies and rearing (Safranyik *et al.* 2002). It was decided not to release it because of its possible impact on other bark-beetle competitors of *D. ponderosae*, and because laboratory experiments had demonstrated that crossbreeding with the native *T. undatulus* to produce fertile hybrids was possible. Later on, in 1995-96, *T. formicarius* was again considered for classical biological control, against *Tomicus piniperda* in the US. However, its introduction was postponed because of its possible impact on non-target prey and the risk of competitive displacement of native predators (Haack *et al.* 1997). Interestingly, *T. formicarius* was also introduced in 1908 from Great-Britain into Sri Lanka against *Xyleborus fornicatus* on tea, but was never retrieved from the field (Clausen 1978).

Programmes to conserve or augment parasitoids and predators of scolytids have never been seriously attempted in Europe, with the notable exception of mass releases of parasitoids against the small elm bark beetle, *S. multistriatus*, in Granada, southern Spain, as part of integrated management of Dutch elm disease (González *et al.* 1999). Over 1 million specimens of seven parasitoid species were released from 1995 to 1997. Parasitism increased from 6 to 20 %, and, at the same time, the level

of tree infection and of bark beetle populations decreased substantially, but it is not clear whether the release of parasitoids played any role in these decreases.

In Sweden, Weslien (1992) observed that less than 10% of *Ips typographus* populations overwinter in logs, whereas the large majority of its natural enemies do. He suggested that log removal after the emergence of bark beetles in summer should be avoided, to preserve parasitoids and predators. Similarly, to control the olive beetle *Phloeotribus scarabaeoides*, in southern Spain, González and Campos (1991) suggested removal of infested wood in late June, just before the emergence of the beetle, when most of the parasitoids have already emerged.

Kairomones may be used to attract natural enemies and augment their impact. Schroeder and Weslien (1994) used logs baited with ethanol and alpha-pinene to attract antagonists of *T. piniperda*, and observed a significant reduction of beetle populations compared to unbaited logs. Grégoire *et al.* (1992) and Pettersson (2001a, 2001b) determined that oxygenated monoterpenes present in infested trees play an important role in host/prey location in *Rhizophagus grandis* on *Dendroctonus micans* and in parasitoids of *I. typographus*, respectively, and suggested the use of these compounds to enhance the role of natural enemies.

Control methods may be detrimental to parasitoids and predators and efforts should be made to limit these detrimental effects. Weslien and Schroeder (1999) observed that predators were more numerous in unmanaged than in managed spruce stands. Similarly, the application of pheromone traps may pose a problem in integrated bark beetle management. Since many predators and parasitoids react to the same semiochemicals as their prey or host, commercial pheromone traps may trap out significant amounts of these beneficials (Nebeker *et al.*, 1984). For pheromone traps against bark beetles it was calculated that the *Nemosoma elongatum* individuals caught in the traps would have eaten a multiple of the number of bark beetles caught in these traps (Baier 1991; Wigger 1993; Schumacher and Pohris 2000). Optimised blends of semiochemicals and application times may minimise such detrimental effects (Raffa 1991; Aukema *et al.* 2000).

6. CONCLUSIONS AND FUTURE RESEARCH

Parasitoids and predators have been studied more extensively in bark beetles than in any other forest insect pests in Europe, which illustrates the significance of Scolytidae in European forestry. Substantial progress was made in recent years in the understanding of various aspects of the ecology of parasitoids, such as host location, competitive interactions, etc. However, many gaps in our knowledge remain. First of all, most studies concentrated on a few scolytid species whereas the natural enemy complex of many others is largely unknown. This probably reflects the relative importance of the different pest species. However, most natural enemies are not host- or prey-specific and a better knowledge of the natural enemies of secondary pests would help in understanding the natural control of the primary pests, which can lead to the development of control strategies. Secondly, there is wide variation in knowledge of the different groups of natural enemies. In general, parasitoids have been more extensively studied than predators, although there is no

evidence suggesting that parasitoids are more important natural regulators than predators. Among parasitoids, adult parasitism has been much less investigated than parasitism on larvae. Most studies on predators focused on *Thanasimus formicarius* and *Rhizophagus grandis*, whereas the biology, ecology and impact of other species and groups remain largely unknown. More generally, the role of natural enemies in the population dynamics of scolytids needs to be better assessed, to evaluate their importance as regulatory factors and to develop strategies to enhance their impact.

Despite extensive research on the natural enemies of scolytids, few attempts have been made to use this knowledge in biological control strategies, with the notable exception of the *Dendroctonus micans/Rhizophagus grandis* programmes. Classical biological control (i.e. the introduction of an exotic natural enemy into a new area for permanent control) is better used against exotic species and, thus, is not targeted for the main scolytid pests in Europe. However, because of the increase of international wood trade, introductions of exotic bark- and wood boring insects are rising worldwide. New introductions are expected in Europe, both from other continents and other European regions (e.g. many European bark beetles, including *Ips typographus*, are still absent from the British Isles). Classical biological control could be envisaged as part of management strategies against new introduction. Biological control by augmentation (i.e. regular releases of laboratory reared-produced natural enemies) is technically possible, since many parasitoids and predators can be mass reared, but it will probably never be economically profitable in forestry, given the large areas involved and their low productivity. However, it may be considered for protection of particularly valuable trees, such as the elm trees of the Alhambra in Granada (González *et al.* 1999), or in orchards (e.g. *Phloeotribus scarabaeoides* and *Leperisinus varius* in olive groves). Biological control by conservation (i.e. the conservation and enhancement of native natural enemies already present on-site) is probably the most promising strategy against scolytid pests. Forestry practices could be modified to favour the action of native parasitoids and predators and to enhance the natural control of forest pests. Various techniques have been suggested, based on, for example, wood removal dates, use of kairomones, etc. (see section 5, above), and many more could be developed. These strategies, however, require an excellent knowledge of the biology and ecology of parasitoids and predators. More data still need to be gathered on many traits, such as natural enemy impact and population dynamics, host location mechanisms, biologies of adult parasitoids and predators in the field, specificity and interactions with alternative hosts and prey, etc. Furthermore, since such strategies would have to be adapted to particular regions and field situations, they would rely on the skills of foresters and other forest practitioners, who would have to be trained specifically for these tasks.

Taxonomy and identification of natural enemies is another field that would need more research. There is a serious lack of knowledge, particularly in the systematics of parasitoids attacking bark beetles. There are too few specialists in Europe, too many groups of parasitoids that are not properly covered, and the identification keys are not accessible for applied entomologists. A correct identification of natural enemies is an essential component of any biological control programme.

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8. REFERENCES

- Achterberg, C. van, & Quicke, D. 2000. The palaeotropical species of the tribe Cosmophorini Capek (Hymenoptera: Braconidae: Euphorinae) with descriptions of twenty-two new species. *Zoologische Mededelingen Leiden*, 74, 283-338.
- Allen, A.J.W. 1975. *Aulonium trisulcum* Fourc. (Col., Colydiidae) in Gloucestershire. *Entomologist's Monthly Magazine*, 111, 39.
- Amman, G.D. 1984. Mountain pine beetle (Coleoptera: Scolytidae) mortality in three types of infestations. *Environmental Entomology*, 13, 184-91.
- Aukema, B.H., Dahlsten, D.L., & Raffa, K.F. 2000. Exploiting behavioral disparities among predators and prey to selectively remove pests: maximizing the ratio of bark beetles to predators removed during semiochemically based trap-out. *Environmental Entomology*, 29, 651-60.
- Baier, P. 1991. Zur Biologie des Borkenkäferräubers *Nemosoma elongatum* (L.) (Col.: Ostomidae). *Zeitschrift für Angewandte Zoologie*, 78, 421-31.
- Baier, P. 1994. Untersuchungen zur abundanzdynamischen Relevanz der Beifänge von *Nemosoma elongatum* (L.) (Col., Ostomidae) in Chalcoprax® beköderten Flugbarrierefallen für *Pityogenes chalcographus* (L.) (Col., Scolytidae). *Journal of Applied Entomology*, 117, 51-57.
- Baisier, M. 1990. Biologie des stades immatures du prédateur *Rhizophagus grandis* Gyll. (Coleoptera: Rhizophagidae). Doctoral dissertation, Université Libre de Bruxelles.
- Baisier, M., Deneubourg, J.-L., & Grégoire, J.-C. 1984. Death due to interaction between *Rhizophagus grandis* larvae. A theoretical and experimental evaluation. In: *Biological Control of Bark Beetles (Dendroctonus micans.)*, J.-C. Grégoire, J.M. Pasteels (Eds.), Proceedings of the EEC Seminar, Brussels, 3-4/10/1984.
- Bakke, A., & Kvamme, T. 1978. Kairomone response by the predators *Thanasimus formicarius* and *Thanasimus rufipes* to the synthetic pheromone of *Ips typographus*. *Norwegian Journal of Entomology*, 25, 41-43.
- Bakke, A., & Kvamme, T. 1981. Kairomone response in *Thanasimus* predators to pheromone components of *Ips typographus*. *Journal of Chemical Ecology*, 7, 305-12.
- Balazy, S., & Michalski, J. 1962. Die parasitischen Hymenopteren der Borkenkäfer (Coleoptera Scolytidae) in Polen. *Prace Komisji Nauk Rolniczych i Lesnych*, Poznan, 13, 71-141.
- Balazy, S., Michalski, J., & Katajczak, E. 1987. Contribution to the knowledge of natural enemies of *Ips acuminatus* Gyll. (Coleoptera: Scolytidae). *Polskie Pismo Entomologiczne*, 57, 735-45.
- Ball, J.C., & Dahlsten, D.L. 1973. Hymenopterous parasites of *Ips paraconfusus* (Coleoptera: Scolytidae) larvae and their contribution to mortality I. Influence of host tree and tree diameter on parasitization. *Canadian Entomologist*, 105, 1453-64.
- Beaver, R.A. 1966a. The biology and immature stages of *Entedon leucogramma* (Ratzeburg) (Hymenoptera: Eulophidae), a parasite of bark beetles. *Proceedings of the Royal Entomological Society of London (A)*, 41, 37-41.
- Beaver, R.A. 1966b. The development and expression of population tables for the bark beetle *Scolytus scolytus* (F.). *Journal of Animal Ecology*, 35, 27-41.
- Beaver, R.A. 1966c. The biology and immature stages of two species of *Medetera* (Diptera: Dolichopodidae) associated with the bark beetle *Scolytus scolytus* (F.). *Proceedings of the Royal Entomological Society of London (A)*, 41, 145-54.
- Beaver R.A. 1967a. Hymenoptera associated with elm bark beetles in Wytham Wood, Berks. *Transactions of the British Entomological Society*, 17, 141-50.
- Beaver, R.A. 1967b. The regulation of population density in the bark beetle *Scolytus scolytus* (F.) *Journal of Animal Ecology*, 36, 435-51.

- Beaver, R.A. 1967c. Notes on the biology of the parasitic mite *Pyemotes scolyti* Oud. (Acar: Pyemotidae). Entomologist, 100, 9-12.
- Bergmiller, F. 1903. *Dendroctonus micans* und *Rhizophagus grandis*. Zentralblatt für das gesamte Forstwesen, 29, 252-56.
- Berryman, A.A. 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. Environmental Entomology, 5, 1225-33.
- Bevan, D., & King, C.J. 1983. *Dendroctonus micans* Kug., a new pest of spruce in U.K. Commonwealth Forestry Review 62 (1), 41-51.
- Billings, R.F., & Cameron, R.S. 1984. Kairomonal responses of Coleoptera, *Monochamus titillator* (Cerambycidae), *Thanasimus dubius* (Cleridae), and *Temnochila virescens* (Trogositidae), to behavioral chemicals of southern pine bark beetles (Coleoptera: Scolytidae). Environmental Entomology, 13, 1542-48.
- Bombosch, S. 1954. Zur Epidemiologie des Buchdruckers (*Ips typographus* L.). In. *Die Grosse Borkenkäferkalamität in Südwestdeutschland 1944-1951*. G. Wellenstein (Ed.). Ringingen, Germany: Forstschutzstelle Südwest.
- Byers, J.A. 1992. Attraction of Bark Beetles, *Tomicus piniperda*, *Hylurgops palliatus*, and *Trypodendron domesticum* and Other Insects to Short-Chain Alcohols and Monoterpenes. Journal of Chemical Ecology, 18, 2385-402.
- Campos, M., & González, R. 1990. Influence of breeding conditions on longevity and fecundity of *Rhaphitulus maculatus* (Hym.: Pteromalidae) reared under standard laboratory conditions. Entomophaga, 35, 411-20.
- Campos, M., & González, R. 1991. Effect of parent density on fecundity of two parasitoids (Hym., Pteromalidae) of the olive beetle, *Phloeotribus scarabaeoides* (Col., Scolytidae). Entomophaga, 36, 473-80.
- Campos, M., & Lozano, C. 1994. Observations on the reproductive biology of two parasites of *Hylesinus varius* and *Phloeotribus scarabaeoides* (Col.: Scolytidae): *Cheiropachus quadrum* (Hym.: Pteromalidae) and *Dendrosoter protuberans* (Hym: Braconidae). Entomophaga, 39, 51-59.
- Capek, M., & Capecki, Z. 1979. A new genus and a new species of Euphorinae (Braconidae, Hymenoptera) from Southern Poland. Polskie Pismo Entomologiczne, 49, 215-221 (in Polish).
- Capek, M. 1957. Beitrag zur Kenntnis der Entomophagen von *Pityokteines vorontzovi* Jac. und anderen Tannenborkenkäfern. Zeitschrift für Angewandte Entomologie, 41, 277-84.
- Chandler, P.J. 1991. Attraction of *Palloptera usta* Meigen (Diptera: Pallopteridae) to recently cut conifer wood and other notes on Pallopteridae. British Journal of Entomology and Natural History, 4, 85-86.
- Clausen, C.P. (Ed.) 1978. *Introduced parasites and predators of arthropod pests and weeds: A world review*. Agricultural Handbook No. 480. USDA Agricultural Research Service.
- Dennis, D.S. 1979. Ethology of *Holcocephala fusca* in Virginia (Diptera: Asilidae). Proceedings of the Entomological Society of Washington, 81, 366-78.
- Dippel, C. 1995. Zur Bionomie des Borkenkäferantagonisten *Nemosoma elongatum* L. (Col., Ostromidae). Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie, 10, 67-70.
- Dippel, C. 1996. Investigations on the life history of *Nemosoma elongatum* L. (Col., Ostromidae), a bark beetle predator. Journal of Applied Entomology, 120, 391-95.
- Dippel, C., Heidger, C., Nicolai, V., & Simon, M. 1997. The influence of four different predators on bark beetles in European forest ecosystems (Coleoptera: Scolytidae). Entomologia Generalis, 21, 161-75.
- Doberski, J.W. 1980. Mite populations on elm logs infested by European elm bark beetles. Zeitschrift für Angewandte Entomologie, 89, 13-22.
- Eichhorn, O., & Graf, P. 1974. Über einige Nutzholzborkenkäfer und ihre Feinde. Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz, 47, 129-35.
- Erbilgin, N. & Raffa, K.F. 2001. Modulation of predator attraction to pheromones of two prey species by stereochemistry of plant volatiles. Oecologia, 127, 444-53.
- Evans, H. F., & Fielding, N. J. 1994. Integrated management of *Dendroctonus micans* in the UK. Forest Ecology and Management, 65, 17-30.
- Faccoli, M. 2000a. Osservazioni bio-ecologiche relative a *Tomicobia seitneri* (Ruschka) (Hymenoptera Pteromalidae), un parassitoide di *Ips typographus* (L.) (Coleoptera Scolytidae). Frustula Entomologica, 23, 47-55.
- Faccoli, M. 2000b. Considerazioni bio-ecologiche sui coleotteri scolitidi dell'abete bianco (*Abies alba* Miller) in Italia. Redia, 83, 33-46.

- Faccoli, M. 2001a. *Tomicobia seitneri* (Ruschka), *Ropalophorus clavicornis* (Wesmael) and *Coeloides bostrychorum* Giraud: three hymenopterous parasitoids of *Ips typographus* (L.) (Col., Scolytidae) new to Italy. *Bollettino della Societa Entomologica Italiana*, 133, 237-46.
- Faccoli, M. 2001b. Catture di coleotteri "non-target" mediante alberi esca allestiti contro *Ips typographus* (L.) (Coleoptera Scolytidae). *Redia*, 84, 105-18.
- Faccoli, M. 2002. Winter mortality in sub-corticicolous populations of *Ips typographus* (Coleoptera, Scolytidae) and its parasitoids in the south eastern Alps. *Anzeiger für Schädlingskunde*, 75, 62-68.
- Faulds, W. 1989. *Hylastes ater* (Paykull), black pine bark beetle and *Hylurgus ligniperda* (Fabricius), golden haired bark beetle (Coleoptera: Scolytidae). In. *A Review of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874 to 1987*. Cameron, P.J., Hill, R.L., Bain, J. Thomas, W.P. (Eds.). CAB International Institute of Biological Control. Technical Communication.
- Fielding, N. J., Evans, H. F., Williams, J., & Evans, B. 1991a. Distribution and spread of the great European spruce bark beetle, *Dendroctonus micans*, in Britain - 1982 to 1989. *Forestry*, 64, 345-58.
- Fielding, N. J., O'Keefe, T., & King, C. J. 1991b. Dispersal and host-finding capability of the predatory beetle *Rhizophagus grandis* Gyll (Col, Rhizophagidae). *Journal of Applied Entomology*, 112, 89-98.
- Fielding, N.J., & Evans, H.F. 1997. Biological control of *Dendroctonus micans* (Scolytidae) in Great Britain. *Biocontrol News and Information*, 18, 51-60.
- Freude, H., Harde, K.W., & Lohse, G.A. 1965-1998. *Die Käfer Mitteleuropas Vol. 1-15*. Krefeld, Germany: Goecke and Evers Verlag.
- Gäbler, H. 1947. Milbe als Eiparasit des Buchdruckers. *Nachrichtenblatt des Deutschen Pflanzenschutzdienstes*, 1, 113-15.
- Gargiulo, P.M., & Berisford, C.W. 1981. Effects of host density and bark thickness on the densities of parasites of the southern pine beetle. *Environmental Entomology*, 10, 392-99.
- Gauss, R. 1954. Der Ameisenbunktkäfer *Thanasimus (Clerus) formicarius* Latr. als Borkenkäferfeind. In. *Die Grosse Borkenkäferkalamität in Südwest-Deutschland 1944-51*. G. Wellenstein [Ed.]. Ulm.
- González, R., & Campos, M. 1990a. Evaluation of natural enemies of the *Phloeotribus scarabaeoides* (Bern.) (Col: Scolytidae) in Granada Olive Groves. *Acta Horticulturae*, 286, 355-58.
- González, R., & Campos, M. 1990b. Rearing of *Cheiropachus quadrum* (Hym.: Pteromalidae) from the Olive beetle, *Phloeotribus scarabaeoides* (Col.: Scolytidae). Potential biological control agent. *Redia*, 73, 495-505.
- González, R., & Campos, M. 1991. Relaciones entre la fenología de *Phloeotribus scarabaeoides* (Col., Scolytidae) y sus parásitoides (Hym., Chalcidoidea). *Boletín de la Asociación Española de Entomología*, 15, 131-43.
- González, R., Gázquez, P., & Pajares, J.A. 1999. *La Grafiosis del Olmo, Programa de Control en la Alhambra (1994-1998)*. Jaén, Spain: Universidad de Jaén.
- Gonzalez, R., Grégoire, J.-C., Drumont, A., & De Windt, N. 1996. A sampling technique to estimate within-tree populations of preemergent *Ips typographus* (Coleoptera, Scolytidae). *Journal of Applied Entomology*, 120, 569-76.
- Goyer, R.A., & Smith, M.T. 1981. The feeding potential of *Corticeus glaber* and *Corticeus parallelus* (Coleoptera: Tenebrionidae), facultative predators of the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Canadian Entomologist*, 113, 807-11.
- Grégoire, J.C. 1976. Note sur deux ennemis naturels de *Dendroctonus micans* Kug. en Belgique (Col. Scolytidae). *Bulletin Annuel de la Société Royale d'Entomologie de Belgique*, 112, 208-12.
- Grégoire, J.-C., Merlin, J., Pasteels, J.M., Jaffuel, R., Vouland, G., & Schvester, D. 1985. Biocontrol of *Dendroctonus micans* by *Rhizophagus grandis* in the Massif Central (France). *Zeitschrift für angewandte Entomologie*, 99, 182-90.
- Grégoire, J.-C., Baisier, M., Drumont, A., Dahlsten, D.L., Meyer, H., & Francke, W. 1991. Volatile compounds in the larval frass of *Dendroctonus valens* and *Dendroctonus micans* (Coleoptera: Scolytidae) in relation to oviposition in the predator, *Rhizophagus grandis* (Coleoptera: Rhizophagidae). *Journal of Chemical Ecology*, 17, 2003-19.
- Grégoire, J.-C., Couillien, D., Drumont, A., Meyer, H., & Francke, W. 1992. Semiochemicals & the management of the predator *Rhizophagus grandis* for the biological control of *Dendroctonus micans*. *Zeitschrift für angewandte Entomologie*, 114, 110-12.
- Grégoire, J.-C., Couillien, D., Krebber, R., König, W. A., Meyer, H., & Francke, W. 1992. Orientation of *Rhizophagus grandis* (Coleoptera : Rhizophagidae) to oxygenated monoterpenes in a species-specific predator-prey relationship. *Chemoecology*, 3, 14-18.

- Grodzki, W. 1997. Parasitoids, predators & commensals of the cambiophagous insects on Norway spruce in the conditions of reduced biodiversity of forest ecosystems in the Sudety Mountains. Prace Instytutu Badawczego Lesnictwa, Seria A, 841, 193-213 (in Polish).
- Haack, R. A., Lawrence, R. K., McCullough, D. G., & Sadof ,C. S. 1997. *Tomicus piniperda* in North America: An Integrated Response to a New Exotic Scolytid. In. *Integrating cultural tactics into the management of bark beetle and reforestation pests*. J.C. Grégoire, A.M. Liebold, F.M. Stephen, K.R. Day, S.M. Salom (Eds.). USDA Forest Service General Technical Report NE-236.
- Hanson, H. S. 1937. Notes on the ecology and control of pine beetles in Great Britain. Bulletin of Entomological Research, 28, 185-241.
- Harz, B., & Topp, W. 1999. Totholz im Wirtschaftswald: eine Gefahrenquelle zur Massenvermehrung von Schadinsekten? Forstwissenschaftliches Centralblatt, 118, 302-13.
- Hedqvist, K.J. 1963. Die Feinde der Borkenkäfer in Schweden, 1. Erzwespen (Chalcidoidea) Studia Forestalia Suecica, 11, 1-176.
- Hedqvist, K.J. 1998. Bark beetle enemies in Sweden 2. Braconidae (Hymenoptera). Entomologica Scandinavica, Supplement, 52, 1-86.
- Heidger, C.M. 1994. Die Ökologie und Bionomie der Borkenkäfer-Antagonisten *Thanasimus formicarius* L. (Cleridae) und *Scolopocelis pulchella* Zett. (Anthocoridae): Daten zur Beurteilung ihrer prädatorischen Kapazität und der Effekte beim Fang mit Pheromonfallen. Dissertation Philipps-Universität Marburg.
- Hérard, F., & Mercadier, G. 1996. Natural enemies of *Tomicus piniperda* and *Ips acuminatus* (Col., Scolytidae) on *Pinus sylvestris* near Orléans, France: temporal occurrence and relative abundance, and notes on eight predatory species. Entomophaga, 41, 183-210.
- Herting, B. 1973. *A Catalogue of Parasites and Predators of Terrestrial Arthropods, Section A, Volume III, Coleoptera to Strepsiptera*. Farnham Royal, UK: Commonwealth Agricultural Bureaux.
- Hintze-Podufal, C., & Druschke, A. 1988. Untersuchungen zur Besiedlungsdichte und Parasitierung des kleinen bunten Eschenbastkäfers *Leperisinus varius* (F.) Mitteilungen der Schweizerischen Entomologischen Gesellschaft, 61, 241-45.
- Hirschmann, W. 1971. Gangsystematik der Parasitiformes. Teil 88. Subcorticale Parasitiformes, Biotop - Arten - Fundstellen. Acarologie, 15, 29-42.
- Hirschmann, W., & Wisniewski, J. 1983. Gangsystematik der Parasitiformes. Teil 30. Lebensräume der *Dendrolaelaps-* und *Longoseius*-Arten. Acarologie, 30, 21-33.
- Hopping, G.R. 1947. Notes on the seasonal development of *Medetera aldrichii* Wheeler (Diptera, Dolichopodidae) as a predator of the Douglas fir bark- beetle, *Dendroctonus pseudotsugae* Hopkins. Canadian Entomologist, 79, 150-53.
- Hostetler, B.B., & Brewer, J.W. 1976. Survival of *Dendrosoter protuberans*, a parasitoid of *Scolytus multistriatus* in Colorado. Annals of the Entomological Society of America, 69, 85-88.
- Hougardy, E. 2003. Host sharing in bark beetle parasitoids. Doctoral dissertation, Université Libre de Bruxelles.
- Hougardy, E., & Grégoire, J.-C. 2000. Spruce stands provide natural natural food sources to adult hymenopteran parasitoids of bark-beetles. Entomologia Experimentalis et Applicata, 96, 253-63.
- Hougardy, E., & Grégoire, J.-C. 2001. Bark beetle parasitoid population surveys following storm damage in spruce stands in the Vosges region (France). Integrated Pest Management Reviews, 6, 163-68.
- Hougardy, E., & Grégoire, J.-C. 2003. Cleptoparasitism increases host finding abilities in the polyphagous parasitoid species *Rhopalicus tutela* (Hymenoptera: Pteromalidae). Behavioural Ecology and Sociobiology, 55, 184-89.
- Hougardy, E., Pernet, P., Warnau, M., Delisle, J., & Grégoire, J.-C. 2003. Marking bark beetle parasitoids within the host plant with rubidium for dispersal studies. Entomologia Experimentalis et Applicata, 108, 107-14.
- Kenis, M., & Mills, N.J. 1994. Parasitoids of European species of the genus *Pissodes* (Coleoptera: Curculionidae) and their potential for biological control of *Pissodes strobi* (Peck) in Canada. Biological control, 4, 14-21.
- Kenis, M., & Mills, N.J. 1998. Evidence for the occurrence of sibling species in *Eubazus* spp. (Hymenoptera: Braconidae), parasitoids of *Pissodes* weevils (Coleoptera: Curculionidae). Bulletin of Entomological Research, 88, 149-63.
- Kennedy, B.H. 1970. *Dendrosoter protruberans* (Hymenoptera: Braconidae) an introduced larval parasitoid of *Scolytus multistriatus*. Annales of the Entomological Society of America, 63, 351-358.

- Kennedy, B.H. 1984. Effect of multilure and its components on parasites of *Scolytus multistriatus* (Coleoptera: Scolytidae). Journal of Chemical Ecology, 10, 373-85.
- Kfir, R. 1986. Release of natural enemies against the pine bark beetle *Orthotomicus erosus* (Wollaston) in South Africa. Journal of the Entomological Society of South Africa, 49, 391-92.
- Kielczewski, B., Moser, J.C., & Wisniewski, J. 1983. Surveying the acarofauna associated with Polish Scolytidae. Bulletin de la Société des Amis des Sciences et des Lettres de Poznan, Série D, 22, 151-59.
- King, C. J., Fielding, N. J., & O'Keefe, T. 1991. Observations on the Life-Cycle and Behaviour of the Predatory Beetle, *Rhizophagus grandis* Gyll (Col., Rhizophagidae) in Britain. Journal of Applied Entomology, 111, 286-96.
- Kobakhidze, D. N. 1965. Some results and prospects of the utilization of beneficial entomophagous insects in the control of insect pests in Georgian SSR (USSR). Entomophaga, 10, 323-30.
- Köhnle, U., & Vité, J.P. 1984. Bark beetle predators: strategies in the olfactory perception of prey species by clerid and trogositid beetles. Zeitschrift für Angewandte Entomologie, 98, 504-08.
- Kolomiets, N. G., & Bogdanova, D. A. 1980. *Parasites and Predators of Xylophagous Insects of Siberia* (in russian). Novosibirsk: Siberian Branch of the Ussr Akademy of Science, Sukachev Institute of Forest and Wood.
- Kopf, A., & Funke, W. 1998. Borkenkäfer und Borkenkäferfeinde. In. *Die Entwicklung von Wald-Biozönosen nach Sturmwurf*. A. Fischer (Ed.). Landsberg: Ecomed.
- Kroll, J.C., & Fleet, R.R. 1979. Impact of woodpecker predation on over-wintering within-tree populations of the southern pine beetle (*Dendroctonus frontalis*). In. *The role of Insectivorous Birds in Forest Ecosystems*. J.G. Dickson, R.N. Connor, R.R. Fleet, J.C. Kroll, J.A. Jackson (Eds.). London: Academic Press.
- Krüger, K., & Mills, N.J. 1990. Observations on the biology of three parasitoids of the spruce bark beetle, *Ips typographus* (Col., Scolytidae), *Coeloides bostrichorum*, *Dendrosoter middendorffii* (Hym., Braconidae) and *Rhopalicus tutela* (Hym., Pteromalidae). Journal of Applied Entomology, 110, 281-91.
- Kubisz, D. 1992. Occurrence of predators from the genus *Rhizophagus* Herbst (Col., Rhizophagidae) in pheromone traps. Journal of Applied Entomology, 113, 525-31.
- Labeledzki, A. 1989. Dragonflies (Odonata: Anisoptera) of Scots pine stands and their potential for regulating numbers of harmful forest insects. Prace Komisji Nauk Rolniczych I Komisji Nauk Lesnych, 68, 39-45 (in Polish).
- Lawson, S.A., Furuta, K., & Katagiri, K. 1997. Effect of natural enemy exclusion on mortality of *Ips typographus japonicus* Niijima (Col., Scolytidae) in Hokkaido, Japan. Journal of Applied Entomology, 121, 89-98.
- Léveillé, J., Lieutier, F., Moser, J.C., & Perry, T.J. 1989. Transportation of phytopathogenic fungi by the bark beetle *Ips sexdentatus* Boerner and associated mites. Journal of Applied Entomology, 108, 1-11.
- Lichtenstein, J.L., & Picard, F. 1920. Notes sur les Proctotrypides (Hym.). Bulletin de la Société Entomologique de France, 25, 54-55.
- Lieutier, F. 1979. Les diptères associés à *Ips typographus* et *Ips sexdentatus* (Coleoptera: Scolytidae) en région parisienne, et les variations de leurs populations au cours du cycle annuel. Bulletin d'Ecologie, 10, 1-13.
- Lindgren, B.S., & Miller, D.R. 2002. Effect of verbenone on attraction of predatory and woodboring beetles (Coleoptera) to kairomones in lodgepole pine forests. Environmental Entomology, 31: 766-73.
- Lindquist, E.E. 1969. Mites and the regulation of bark beetle populations. Proceedings of the 2nd International Congress of Acarology 1967, 389-99.
- Lindquist, E.E. 1970 Relationships between mites and insects in forest habitats. Canadian Entomologist, 102, 978-984.
- Linit, M.J. & Stephen, F.M. 1983. Parasite and predator component of within-tree southern pine beetle (Coleoptera: Scolytidae) mortality. Canadian Entomologist, 115, 679-88.
- Lipa, J.J., & Chmielewski, W. 1977. Parasitisation of *Scolytus pygmaeus* Fabr. (Coleoptera, Scolytidae) by a mite *Pyemotes scolyti* Oud. (Acarina, Pyemotidae). Polskie Pismo Entomologiczne, 47, 345-49 (in Polish).
- Lobinger, G., & Feicht, E. 1999. Schwarmverhalten und Abundanzdynamik der Erzwespe *Karpinskiella pityophthori* (Bouček) (Hym., Pteromalidae), eines Parasitoïden des Kupferstechers (*Pityogenes chalcographus* L., Col., Scolytidae). Anzeiger für Schädlingeskunde, 72, 65-71.

- Lozano, C., & Campos, M. 1991. Preliminary study about entomofauna of the bark beetle *Leperisinus varius* (Coleoptera, Scolytidae). *Redia*, 74, 241-43.
- Lozano, C., Kidd, N.A.C., & Campos, M. 1993. Studies on the population dynamics of the bark beetle *Phloeotribus scarabaeoides* (Col., Scolytidae) on European olives (*Olea europaea*). *Journal of Applied Entomology*, 120, 193-98.
- Lozano, C., Campos, M., Kidd, N.A.C., & Jervis, M.A. 1994. The role of parasitism and intra-specific competition in the population dynamics of the bark beetle *Leperisinus varius* (Fabr.) (Col., Scolytidae) on European olives (*Olea europaea*). *Journal of Applied Entomology*, 117, 182-89.
- Lozano, C., Campos, M., Kidd, N.A.C., & Jervis, M.A. 1996a. The role of parasitism in the population dynamics of the bark beetle *Phloeotribus scarabaeoides* (Col., Scolytidae) on European olives (*Olea europaea*). *Journal of Applied Entomology*, 120, 347-51.
- Lozano, C., Kidd, N.A.C., & Campos, M. 1996b. The population dynamics of the bark beetle *Leperisinus varius* (Fabr.) (Col., Scolytidae) on European olive (*Olea europaea*). *Journal of Applied Entomology*, 116, 118-26.
- Lozano, C., González, E., Pena, A., Campos, M., Plaza, M.T., Rodriguez, M., Izquierdo, I., & Tamayo, J. 2000. Response of parasitoids *Dendrosoter protuberans* and *Cheiropachus quadrum* to attractants of *Phloeotribus scarabaeoides* in an olfactometer. *Journal of Chemical Ecology*, 26, 791-99.
- Maksimovic, M. 1979. Influence of the density of bark beetles and their parasites on dieback of elm in some woods of Yugoslavia. *Zeitschrift für Angewandte Entomologie*, 88, 283-91.
- Manojlovic, B., Zabel, A., Stankovic, S., & Kostic, M. 2000a. *Ecpophylus silesiacus* (Ratz.) (Hymenoptera, Braconidae), an important elm bark beetle parasitoid. *Agricultural and Forest Entomology*, 2, 63-67.
- Manojlovic, B., Zabel, A., Kostic, M., & Stankovic, S. 2000b. Effect of nutrition of parasites with nectar of melliferous plants on parasitism of the elm bark beetles (Col., Scolytidae). *Journal of Applied Entomology*, 124, 155-61.
- Markovic, C., & Stojanovic, A. 1996. Parasitoid complex of *Scolytus intricatus* Ratz. (Coleoptera, Scolytidae) in the region of Serbia. *Zastita Bilja*, 47, 255-66 (in Serbian).
- Martinek, V. 1977. Species of genus *Palloptera* Fallen, 1820 (Dipt., Pallopteridae) in Czechoslovakia. *Studia Entomologica Forestalia*, 2, 203-20.
- Massey, C.L. & Wygant, N.D. 1973. Woodpeckers: most important predators of the spruce beetle. *Colorado Field Ornithologists*, 15, 4-8.
- Matile, L. 1993. *Les Diptères d'Europe occidentale Vol. I*. Paris: Société Nouvelle Éditions Boubée.
- Mazur, S. 1973. Contribution to the knowledge of the fauna of predatory beetles inhabiting feeding-places of *Tomicus =Blastophagus piniperda* L. *Sylwan*, 117, 53-59 (in Polish).
- Mazur, S. 1975. Appraisal of economic significance of predators: *Paromalus parallelepipedus* Herbst and *Plegaderus vulneratus* Panz. (Col., Histeridae) - persecutors of *Tomicus piniperda* L. *Sylwan*, 119, 57-60 (in Polish).
- Mazur, S. 1979. Beetle succession in feeding sites of the pine shoot beetle (*Tomicus piniperda* L., Coleoptera Scolytidae) in one-species and mixed pine stands. *Memorabilia Zoologica*, 30, 63-87.
- Mendel, Z. 1985. Predation of *Orthotomicus erosus* (Col., Scolytidae) by the Syrian woodpecker (*Picoides syriacus*, Aves, Picidae). *Zeitschrift für Angewandte Entomologie*, 100, 355-60.
- Mendel, Z. 1986. Hymenopterous parasitoids of bark beetles (Scolytidae) in Israel: Relationships between host and parasitoid size, and sex ratio. *Entomophaga*, 31, 127-37.
- Mendel, Z. 1987. Major pests of man-made forests in Israel: Origin, biology, damage and control. *Phytoparasitica*, 15, 131-37.
- Mendel, Z. 1988. Attraction of *Orthotomicus erosus* and *Pityogenes calcaratus* to a synthetic aggregation pheromone of *Ips typographus*. *Phytoparasitica*, 16, 109-17.
- Mendel, Z.; Podoler, H., & Livne, H. 1989. Establishment sequence and seasonal development of *Aulonium ruficorne* Olivier (Coleoptera: Colydiidae), a predator of bark beetles in pine plantations in Israel. *Acta Ecologica / Ecologia Applicata*, 10, 103-14.
- Mendel, Z.; Podoler, H., & Livne, H. 1990. Interactions between *Aulonium ruficorne* (Coleoptera: Colydiidae) and other natural enemies of bark beetles (Coleoptera: Scolytidae). *Entomophaga*, 35, 99-105.
- Merlin, J. 1984. Elm bark beetles and their main parasitoids in Belgium: emergence and some aspects of their ecological relations. *Mededelingen Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent*, 49/3a, 857-65.

- Merlin, J., Grégoire, J.-C., Baisier, M., & Pasteels, J. M. 1984. Some new data on the biology of *Rhizophagus grandis* (Col.: Rhizophagidae). In. *Biological Control of Bark Beetles*, J. -C. Grégoire, J. M. Pasteels (Eds.), Proceedings of the EEC Seminar, Brussels, October 3-4, 1984.
- Merlin, J., Parmentier, C., & Grégoire, J.-C. 1986. The feeding habits of *Rhizophagus dispar* (Col., Rhizophagidae), an associate of bark beetles. Mededelingen Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent, 51/3a, 915-23.
- Michalski, J., & Seniczak, S. 1974. *Trichogramma semblidis* (Chalcidoidea: Trichogrammatidae) as a parasite of the bark beetle eggs (Coleoptera: Scolytidae). Entomophaga, 19, 237-42.
- Miller, M., Moser, J. C., McGregor, M., Grégoire, J.-C., Baisier, M., Dahlsten, D. L., & Werner, R. A. 1987. Potential for biological control of native North American *Dendroctonus* beetles (Coleoptera: Scolytidae). Annals of the Entomological Society of America, 80, 417-28.
- Mills, N.J. 1983. The natural enemies of scolytids infesting conifer bark in Europe in relation to the biological control of *Dendroctonus* spp. in Canada. Biocontrol News and Information, 4, 305-28.
- Mills, N.J. 1985. Some observations on the role of predation in the natural regulation of *Ips typographus* populations. Zeitschrift für Angewandte Entomologie, 99, 209-15.
- Mills, N.J. 1986. A preliminary analysis of the dynamics of within tree populations of *Ips typographus* (L.) (Coleoptera: Scolytidae). Zeitschrift für Angewandte Entomologie, 102, 402-16.
- Mills, N.J. 1991. Searching strategies and attack rates of parasitoids of the ash bark beetle (*Leperisinus varius*) and its relevance to biological control. Ecological Entomology, 16, 461-70.
- Mills, N.J. 1994. Parasitoid guilds: Defining the structure of the parasitoid communities of Endopterygote insect hosts. Environmental Entomology, 23, 1066-83.
- Mills, N.J., & Krüger, K. 1989. Host location: an important factor in the use of exotic natural enemies for the biocontrol of native scolytids. In. *Integrated Control of Scolytid Bark Beetles*. T.L. Payne, H. Saarenmaa (Eds.). Blacksburg, USA: Virginia Polytechnic Institute and State University.
- Mills, N.J., & Schlup, J. 1989. The natural enemies of *Ips typographus* in Central Europe: Impact and potential use in biological control. In. *Potential for Biological Control of Dendroctonus and Ips Bark Beetles*. Kulhavy, D.L., Miller, M.C. (Eds.). Nacogdoches, Texas, USA: Cent. Appl. Study, School of For. S. F. Austin State Univ.
- Mills, N.J., Krüger, K., & Schlup, J. 1991. Short-range host location mechanisms of bark beetles parasitoids. Journal of Applied Entomology, 111, 33-43.
- Moeck, H. A., & Safranyik, L. 1984. *Assessment of predator and parasitoid control of bark beetles*. Environment Canada. Canadian Forestry Service, Pacific Forest Research Centre, Information Report BC-X-248.
- Moor, H., & Nyffeler, M. 1983. Eine Notiz über borkenkäfertötende Spinnen. Mitteilungen der Schweizerischen Entomologischen Gesellschaft, 56, 195-99.
- Moore, G. 1972. Southern pine beetle mortality in North Carolina caused by parasites and predators. Environmental Entomology, 1, 58-65.
- Morge, G. 1961. Die Bedeutung der Dipteren im Kampf gegen die Borkenkäfer. Archiv für Forstwesen, 10, 505-11.
- Morge, G. 1963. Die Lonchaeidae und Pallopteridae Österreichs und der angrenzenden Gebiete 1.Teil: Die Lonchaeidae. Naturkundliches Jahrbuch der Stadt Linz , 9, 123-312.
- Morge, G. 1967. Die Lonchaeidae und Pallopteridae Österreichs und der angrenzenden Gebiete 2.Teil: Die Pallopteridae. Naturkundliches Jahrbuch der Stadt Linz 13, 141-88.
- Moser, J.C. 1975. Mite predators of the southern pine beetle. Annals of the Entomological Society of America, 68, 1113-16.
- Moser, J.C., & Bogenschütz, H. 1984. A key to the mites associated with flying *Ips typographus* in South Germany. Zeitschrift für Angewandte Entomologie, 97, 437-50.
- Moser, J.C., Eidmann, H.H., & Regnander, J.R. 1989. The mites associated with *Ips typographus* in Sweden. Annales Entomologici Fennici, 55, 23-27.
- Nagel, W.P., & Fitzgerald, T.D. 1975. *Medetera aldrichi* larval feeding behavior and prey consumption (Dipt.: Dolichopodidae). Entomophaga, 20, 121-27.
- Nebeker, T.E., Mizell, R.F.I., Bedwell, N.J., Garner, W.Y., & Harvey, J.J. 1984. Management of bark beetle populations. Impact of manipulating predator cues and other control tactics. In. *Chemical and Biological Controls in Forestry*, Proceedings of a Conference Seattle.
- Nicolai, V. 1995a. Der Einfluss von *Medetera dendrobaena* (Diptera, Dolichopodidae) auf Borkenkäferpopulationen. Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie, 9, 465-69.

- Nicolai, V. 1995b. Ermittlungen der Totholzfauna mittels Borkenkälektoren. Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie, 9, 755-61.
- Nicolai, V. 1995c. The impact of *Medetera dendrobaena* Kowarz (Dipt., Dolichopodidae) on bark beetles. Journal of Applied Entomology, 119, 161-66.
- Nicolai, V. 1996. Bark beetles and their natural enemies at lowland stands of beech forests and of spruce forests in Central Europe. Zoologische Beiträge, N. F. 37, 135-56.
- Nicolai, V., Heidger, C., Dippel, C. & Strohmenger, T. 1992. Bark beetles and their predators in bark beetle pheromone traps. Zoologische Jahrbücher Systematik, 119, 315-38.
- Noyes, J.S. 2001. Interactive Catalogue of World Chalcidoidea 2001. CD Rom. Vancouver, Canada: Taxapad.
- Nuorteva, M. 1956. Über den Fichtenstamm-Bastkäfer, *Hylurgops palliatus* Gyll., und seine Insektenfeinde. Acta Entomologica Fennica, 13, 1-116.
- Nuorteva, M. 1957. Zur Kenntnis der parasitischen Hymenopteren der Borkenkäfer Finnlands. Annales Entomologici Fennici, 23, 118-21.
- Nuorteva, M. 1959. Untersuchungen über einige in den Frassbildern der Borkenkäfer lebende *Medetera*-Arten (Dipt., Dolichopodidae). Suomen Hyönteistieteellinen Aikakauskirja, 25, 192-210.
- Nuorteva, M., & Saari, L. 1980. Larvae of *Acanthocinus*, *Pissodes* and *Tomicus* (Coleoptera) and the foraging behaviour of woodpeckers (Picidae). Annales Entomologici Fennici, 46, 107-10.
- Ohmart, C.P., & Voigt, W.G. 1982. Temporal and spatial arrival of *Ips typographus maritimus* (Coleoptera: Scolytidae) and its insect associates on freshly felled *Pinus radiata* in California. Canadian Entomologist, 114, 337-48.
- Otvos, I.S. 1979. The effects of insectivorous bird activities in forest ecosystems: an evaluation. In: *The role of Insectivorous Birds in Forest Ecosystems*. J.G. Dickson, R.N. Connor, R.R. Fleet, J.C. Kroll, J.A. Jackson (Eds.). London: Academic Press, Inc.
- Otvos, I.S., & Stark, R.W. 1985. Arthropod food of some forest-inhabiting birds. Canadian Entomologist, 117, 971-90.
- Ounap, H. 1992a. Laboratory studies of the food selection of some predators of bark beetles (Coleoptera: Scolytidae). Eesti Teaduste Akadeemia Toimetised, Bioloogia, 41, 131-40.
- Ounap, H. 1992b. Species composition of the Diptera predators of bark beetles of conifers in Estonia. Metsanduslikud Uurimused, 24, 143-51.
- Pavlik, S. 1999. Predation of overwintering larvae of the European oak bark beetle (*Scolytus intricatus* Ratz.) by woodpeckers at logging residues in oak forests. Acta Facultatis Forestalis Zvolen-Slovakia, 41, 305-13 (in Slovak).
- Pechacek, P. 1994. Reaktion des Dreizehenspechts auf eine Borkenkäfergradation. Allgemeine Forst Zeitschrift, 49, 661.
- Pettersen, H. 1976a. Chalcid-flies (Hym., Chalcidoidea) reared from *Ips typographus* L. and *Pityogenes chalcographus* L. at some Norwegian localities. Norwegian Journal of Entomology, 23, 47-50.
- Pettersen, H. 1976b. Parasites (Hym., Chalcidoidea) associated with bark beetles in Norway. Norwegian Journal of Entomology, 25, 75-78.
- Pettersson, E.M. 2001a. Volatiles from potential hosts of *Rhopalicus tutela*, a bark beetle parasitoid. Journal of Chemical Ecology, 27, 2219-31.
- Pettersson, E.M. 2001b. Volatile attractants for three pteromalid parasitoids attacking concealed spruce bark beetles. Chemoecology, 11, 89-95.
- Pettersson, E.M., Sullivan, B.T., Anderson, P., Berisford, C.W., & Birgersson, G. 2000. Odor perception in bark beetle parasitoid *Roptrocerus xylophagorum* (Ratzeburg) (Hymenoptera: Pteromalidae) exposed to host associated volatiles. Journal of Chemical Ecology, 26, 2507-25.
- Pettersson, E.M., Birgersson, G., & Witzgall, P. 2001a. Synthetic attractants for the bark beetle parasitoid *Coeloides bostrichorum* Giraud (Hymenoptera: Braconidae). Naturwissenschaften, 88, 88-91.
- Pettersson, E.M., Hallberg, E., & Birgersson, G. 2001b. Evidence for the importance of odor-perception in the parasitoid *Rhopalicus tutela* (Walker) (Hymenoptera: Pteromalidae). Journal of Applied Entomology, 125, 293-301.
- Pishchik, A.A. 1980. An insect predator of *Blastophagus [Tomicus] piniperda* and *B. [T.] minor*. Lesnoe Khozyaistvo, 11, 55-57.
- Podoler, H., Mendel, Z. & Livne, H. 1990. Studies on the biology of a bark beetle predator, *Aulonium ruficorne* (Coleoptera: Colydiidae). Environmental Entomology, 19, 1010-16.

- Raffa, K.F. 1991. Temporal and spatial disparities among bark beetles, predators, and associates responding to synthetic bark beetle pheromones: *Ips pini* (Coleoptera: Scolytidae) in Wisconsin. *Environmental Entomology*, 20, 1665-79.
- Rauhut, B., Schmidt, G.H., & Schmidt, L. 1993. Das Coleopteren-Spektrum in Borkenkäfer-Pheromonfallen eines heterogenen Waldgebietes im Landkreis Hannover. *Braunschweiger Naturkundliche Schriften*, 4, 247-78.
- Richerson, J.V., & Borden, J.H. 1972. Host finding by heat perception in *Coeloides brunneri* (Hymenoptera: Braconidae). *Canadian Entomologist*, 104, 1877-81.
- Riley, M.A., & Goyer, R.A. 1986. Impact of beneficial insects on *Ips* spp. (Coleoptera: Scolytidae) bark beetles in felled loblolly and slash pines in Louisiana. *Environmental Entomology*, 15, 1220-24.
- Ruschka F. 1916. Hymenopteren - Parasiten istrianischer Borkenkäfer. *Entomologische Blätter für Biologie und Systematik der Käfer*, 11, 25-29.
- Russo, G. Z 1938. Contributto alla conoscenza dei Coleotteri Scolitidi Fleotribi: *Phloeotribus scarabaeoides* (Bern.) Fauv. II Biografia, simbionti, danni e lotta. *Bollettino del Laboratorio di Entomologia Agraria*, 2, 3-420.
- Ryan, R.B., & Rudinsky, J.A. 1962. Biology and habits of the Douglas-fir beetle parasite, *Coeloides brunneri* Viereck (Hymenoptera: Braconidae) in Western Oregon. *Canadian Entomologist*, 94, 748-63.
- Sachtleben, H. 1952. Die parasitischen Hymenopteren des Fichtenborkenkäfers *Ips typographus* L. *Beitrage zur Entomologie*, 2, 137-89.
- Safranyik, L., Shore, T.L., Moeck, H.A., & Whitney, H.S. 2002. *Dendroctonus ponderosae* Hopkins, Mountain Pine Beetle (Coleoptera: Scolytidae). In: *Biological Control Programmes against Insects and Mites, Weeds, and Pathogens in Canada 1981-2000*. P. Mason, J. Huber (Eds.). Wallingford, UK: CABI.
- Samson, P.R. 1984. The biology of *Roptrocerus xylophagorum* (Hym., Torymidae), with a note on its taxonomic status. *Entomophaga*, 29, 287-98.
- Schimitschek, E. 1931. Forstentomologische Untersuchungen aus dem Gebiete von Lunz. I. Standortsklima und Kleinklima in ihren Beziehungen zum Entwicklungsablauf und zur Mortalität von Insekten. *Zeitschrift für Angewandte Entomologie*, 18, 460-91.
- Schimitschek, E. 1940. Beiträge zur Forstentomologie der Türkei III. Die Massenvermehrung des *Ips sexdentatus* Boerner im Gebiete der orientalischen Fichte. *Zeitschrift für Angewandte Entomologie*, 27, 84-113.
- Schopf, R., & Köhler, U. 1995. Untersuchungen zur Populationsdynamik der Fichtenborkenkäfer im Nationalpark Bayerischer Wald. In: *Nationalpark Bayerischer Wald - 25 Jahre auf dem Weg zum Naturwald. Neuschönau, Nationalparkverwaltung Bayerischer Wald*.
- Schröder, D. 1974. Untersuchungen über die Aussichten einer biologischen Bekämpfung von Scolytiden an Ulmen als Mittel zur Einschränkung des "Ulmensterbens". *Zeitschrift für Angewandte Entomologie*, 76, 150-59.
- Schroeder, L. M. 1996. Interactions between the predators *Thanasimus formicarius* (Col.: Cleridae) and *Rhizophagus depressus* (Col.: Rhizophagidae), and the bark beetle *Tomicus piniperda* (Col.: Scolytidae). *Entomophaga*, 41, 63-75.
- Schroeder, L. M. 1997. Impact of natural enemies on *Tomicus piniperda* offspring production. In: *Integrating cultural tactics into the management of bark beetle and reforestation pests*, Vallombrosa, 1-4 September 1996. J.-C. Grégoire, A.M. Liebold, F.M. Stephen, K.R. Day, S.M. Salom (Eds.). Proceedings of the IUFRO conference, USDA, Forest Service General Technical Report NE-236.
- Schroeder, L. M. 1999a. Prolonged development time of the bark beetle predator *Thanasimus formicarius* (Col.: Cleridae) in relation to its prey species *Tomicus piniperda* (L.) and *Ips typographus* (L.) (Col.: Scolytidae). *Agricultural and Forest Entomology*, 1, 127-35.
- Schroeder, L.M., 1999b. Population levels and flight phenology of bark beetle predators in stands with and without previous infestations of the bark beetle *Tomicus piniperda*. *Forest Ecology and Management*, 123, 31-40.
- Schroeder, L.M. & Weslien, J. 1994. Reduced offspring production in bark beetle *Tomicus piniperda* in pine bolts baited with ethanol and alpha-pinene, which attract antagonistic insects. *Journal of Chemical Ecology*, 20, 1429-44.
- Schumacher, J., & Pohris, V. 2000. Der Kleine Buchenborkenkäfer als relevanter Rindenbrüter in Schwarzerlen-Beständen. *Allgemeine Forst Zeitschrift/Der Wald*, 55, 760-63.

- Seitner, M., 1924. Beobachtungen und Erfahrungen aus dem Auftreten des achtzähnigen Fichtenborkenkäfers *Ips typographus* L. in Oberösterreich und Steiermark in den Jahren 1921 bis einschl. 1923. 5. Parasiten und Räuber. Centralblatt für das Gesamte Forstwesen, 50, 2-23.
- Shaw, M.R. 1994. Parasitoid host ranges. In *Parasitoid Community Ecology*. B.A. Hawkins, W. Sheehan (Eds.). New York: Oxford University Press.
- Shook, R.S., & Baldwin, P.H. 1970. Woodpecker predation on bark beetles in Engelmann spruce logs as related to stand density. Canadian Entomologist, 102, 1345-54.
- Smith, M.T., & Goyer, R.A. 1982. The life cycle of *Corticeus glaber* (Coleoptera: Tenebrionidae), a facultative predator of the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). Canadian Entomologist, 114, 535-37.
- Stephen, F.M., & Dahlsten, D.L. 1976. The arrival sequence of the arthropod complex following attack by *Dendroctonus brevicomis* (Coleoptera: Scolytidae) in ponderosa pine. Canadian Entomologist, 108, 283-304.
- Strube, H.G.R., & Benner, A. 1984. Über die mit dem Gestreiften Nutzholzborkenkäfer *Trypodendron lineatum* Olivier (Coleoptera, Ipidae) vergesellschafteten Milben (Acaria). Zeitschrift für Angewandte Entomologie, 98, 103-09.
- Sullivan, B.T., Seltmann, K.C. & Berisford, C.W. 1999. A simple continuous-rearing technique for the bark beetle parasitoid, *Roptrocerus xylophagorum* (Ratzeburg). Journal of Entomological Science, 34, 260-64.
- Thalenhorst, W. 1958. Grundzüge der Populationsdynamik des grossen Fichtenborkenkäfers *Ips typographus* L. Schriftenreihe der Forstliche Fakultät der Universität Göttingen und Mitteilungen der Niedersächsisches Forstliches Versuchsanstalt, 21, 1-126.
- Thompson, W.R. 1943. *A catalogue of the parasites and predators of insect pests. Section 1 Parasite host catalogue. Part 1 Parasites of the Arachnida and Coleoptera*. Belleville, Canada: Imperial Parasite Service.
- Tømmerås, B. A. 1985. Specialization of the olfactory receptor cells in the bark beetle *Ips typographus* and its predator *Thanasimus formicarius* to bark beetle pheromones and host tree volatiles. Journal of Comparative Physiology A, 15, 335-41.
- Tømmerås, B. A. 1988. The Clerid beetle, *Thanasimus formicarius*, is attracted to the pheromone of the ambrosia beetle, *Trypodendron lineatum*. Experientia, 44, 536-37.
- Tømmerås, B. A., Mustaparta, H. & Grégoire, J.-C. 1984. Electrophysiological recordings from olfactory receptor cells in *Dendroctonus micans* and *Rhizophagus grandis*. In: *Biological Control of Bark Beetles*, J. -C. Grégoire, J.M. Pasteels (Eds.), Proceedings of the EEC seminar, Brussels, October 3-4, 1984.
- Tribe, G.D., & Kfir, R. 2001. The establishment of *Dendrosoter caenopachoides* (Hymenoptera: Braconidae) introduced into South Africa for the biological control of *Orthotomicus erosus* (Coleoptera: Scolytidae), with additional notes on *D. sp. nr. labdacus*. African Entomology, 9, 195-98.
- Turcani, M. & Capek, M. 2000. "The results of study of parasitoids and insect predators of bark beetles in native Scotch pine (*Pinus sylvestris* L.) stands in Slovensky raj Mts." Lesnický Casopis – Forestry Journal, 46, 381-92 (in Slovak, English summary).
- Turchin, P. Taylor, A.D., & Reeve, J.D. 1999. Dynamical role of predators in population cycles of a forest insect: an experimental test. Science, 285, 1068-71.
- Tvaradze, M. S. 1976. On the acclimatisation of *Rhizophagus grandis* for control of *Dendroctonus micans* (in Russian). Sb. Nauch. Rabot po Izuch. B. E. Luboeda v Gruzii, Tbilisi, 2, 76-90.
- Van overbeke, A., & Grégoire, J.-C. 1995. Establishment and spread of *Rhizophagus grandis* Gyll (Coleoptera: Rhizophagidae) six years after release in the Forêt domaniale du Mézenc (France). Annales des Sciences Forestières, 52, 243-50.
- Van Driesche, R.G., Healy, S., & Reardon, R.C. 1996. *Biological Control of Arthropod Pests of the Northeastern and North Central Forests in the United States: a Review and Recommendations*. Morgantown, WV, USA: Forest Health Technical Enterprise Team.
- Vogt, H. 1966. Rhizophagidae. Pp. 80-83. In: *Die Käfer Mitteleuropas Vol. 9*. Freude H., Harde K.W., Lohse, G.A. (Eds.). Krefeld, Germany: Goecke and Evers Verlag.
- Voolma, K. 1986. "Entomophages of *Dendroctonus micans* in Estonia" Metsabuduslikud Uurimused, Estonian SSR 21, 89-97 (in Russian).

- Wainhouse, D., Beech-Garwood, P. A., Howell, R. S., Kelly, D., & Orozco, M. P. 1992. Field Response of Predator *Rhizophagus grandis* to Prey Frass and Synthetic Attractants. *Journal of Chemical Ecology*, 18, 1693-1705.
- Wegensteiner, R., & Führer, E., 1991. Zur höhenabhängigen Aktivitätsdynamik einiger Nadelholz-Borkenkäfer (Coleoptera, Scolytidae). *Anz. Schädl.kd. Pflanzenschutz Umweltschutz*, 64, 25-34.
- Wermelinger, B., 2002. Development and distribution of predators and parasitoids during two consecutive years of an *Ips typographus* (Col., Scolytidae) infestation. *Journal of Applied Entomology*, 126, 521-27.
- Weslien, J., 1992. The arthropod complex associated with *Ips typographus* (L.) (Coleoptera, Scolytidae): species composition, phenology, and impact on bark beetle productivity. *Entomologica Fennica*, 3, 205-13.
- Weslien, J., & Schroeder, L.M. 1999. Population levels of bark beetles and associated insects in managed and unmanaged spruce stands. *Forest Ecology and Management*, 115, 267-75.
- Wichmann, H.E. 1956. Untersuchungen über *Ips typographus* L. und seine Umwelt - Asilidae, Raubfliegen. *Zeitschrift für Angewandte Entomologie*, 39, 58-62.
- Wichmann, H.E. 1957. Untersuchungen an *Ips typographus* L. und seiner Umwelt - Die Kamelhalsfliegen. *Zeitschrift für Angewandte Entomologie*, 40, 433-40.
- Wigger, H. 1993. Ökologische Bewertung von Räuber-Beifängen in Borkenkäfer-Lockstofffallen. *Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz*, 66, 68-72.
- Wigger, H. 1994. Die Reaktion der Frasskapazität des Borkenkäferräubers *Nemosoma elongatum* L. (Col., Oستomidae) im Imaginalstadium auf unterschiedliches Beuteangebot in künstlichen Gängen. *Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz*, 67, 8-13.
- Wigger, H. 1996. Populationsdynamik und Räuber-Beute-Beziehung zwischen dem Borkenkäfer-Räuber *Nemosoma elongatum* und dem Kupferstecher *Pityogenes chalcographus* (Coleoptera: Oستomidae, Scolytidae). *Entomolia Generalis*, 21, 55-67.
- Wilkinson, R.C., Bhatkar, A.P., Kloft, W.J., Whitcomb, W.H., & Kloft, E.S. 1978. *Formica integra* - Feeding, trophallaxis, and interspecific confrontation behavior. *Florida Entomologist*, 61, 179-87.
- Wyatt, T. D., Phillips, A. D. G., & Grégoire, J.-C. 1993. Turbulence, trees and semiochemicals: wind-tunnel orientation of the predator, *Rhizophagus grandis*, to its barkbeetle prey, *Dendroctonus micans*. *Physiological Entomology*, 18, 204-10.
- Yates, M.G. 1984. The biology of the oak bark beetle, *Scolytus intricatus* (Ratzeburg) (Coleoptera: Scolytidae), in southern England. *Bulletin of Entomological Research*, 74, 569-79.
- Zumr, V. 1983. Effect of synthetic pheromones Pheroprax on the coleopterous predators of the spruce bark beetle *Ips typographus* (L.). *Zeitschrift für Angewandte Entomologie*, 95, 47-50.

Chapter 12

PATHOGENS IN BARK BEETLES

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1. INTRODUCTION

Insect pathology is the science of diseases in all kind of insects, including pests, beneficials or indifferent species. Knowledge of pathogen occurrence in useful insects, like honeybees or silk worms, and in insect vectors of human disease, provided the impetus for the development of insect pathology. The scope of insect pathology covers the whole field of diseases in insects including aetiology, symptomatology, epizootiology, and the structural, chemical and functional alterations that result from diseases.

Comprehensive information is given by several authors on morphological features and action of different entomopathogens (Weiser, 1961a; Müller-Kögler, 1965; Weiser, 1966, 1977; Krieg, 1986; Levine, 1988; Adams and Bonami, 1991; Entwistle *et al.*, 1993; Tanada and Kaya, 1993; Hunter-Fujita *et al.*, 1998; Boucias and Pendland, 1998; Becnel and Andreadis, 1999; Butt *et al.*, 2001). But, entomopathogens are also known to play a major role in the population dynamics of many important forest insects. Outbreaks of phytophagous forest insects are very often terminated by pathogens, and they are responsible for rapid decline and collapse of local insect populations. Therefore, entomopathogens have potential for microbial control programmes through inoculative, inundative or augmentative releases (Lacey and Goettel, 1995).

2. PATHOGENS AND THEIR ACTION

In microbial insect diseases, pathogens invade and multiply in insects and spread to infect other specimens. Pathogens can be transmitted to insects horizontally by contact, ingestion, and by vectors, and vertically from parents to their offspring

(transovum transmission). Pathogens can be non-cellular, infectious agents: viruses, prokaryotic forms: bacteria and eukaryotic forms: fungi and protozoa. All these pathogens may cause infections. They can be separated into potential pathogens (incapable of invading the host without assistance of external factors) and facultative pathogens (do not require an insect weakened by external factors), they need a certain medium for replication, and most of them are bacteria and fungi. Obligate pathogens require live insect hosts for survival and replication (which occurs intracellularly), e.g. viruses, some fungi and microsporidia (protozoa). Some pathogens are able to release exotoxins which open the host for infections (catabolic and anabolic substances; of. bacteria and fungi), others produce endotoxins confined to the infectious unit (e.g. *Bacillus thuringiensis*) with the same function. The method of entry of pathogens varies with the type of pathogen. Fungi generally invade through the integument (contact insecticides), whereas viruses, bacteria and protozoa enter their host primarily through the mouth (peroral).

Infectivity is the ability of a pathogen to produce an infection, whereas virulence is the disease producing power of a pathogen to overcome the host defense mechanisms and to kill the host. The infection in insects may vary from latent or inapparent (no signs of disease), chronic (symptoms are possible, but no mortality) and acute (symptoms most obvious, mortality). Chronic and latent infections can become acute infections by the action of stressors. The course of infection by pathogens after invasion of an insect host up to the time of death is described by the "incubation period" (period from invasion of pathogen to the development of first symptoms), then by the beginning and height of disease (clearly visible symptoms), followed by death. Many pathogens continue to grow and reproduce (form spores or persistent cysts) after the death of an insect (e.g. bacteria and fungi). However, definite symptoms allowing indication of disease are not visible in all cases. In addition, the termination of a chronic disease may involve the recovery of an insect due to its immune responses. Several different pathogens (and non-pathogenic organisms) can occur within the same host insect and they may interact with each other. The interaction may result in independent coexistence, complementarity or interference.

Preliminary diagnosis (cursory examination of a dead insect) is normally followed by a tentative diagnosis (macroscopic and microscopic examinations of the diseased specimen), both lead to a definite diagnosis of pathogens, based on laboratory and field data and comparison with information from the literature. Physical examinations by use of optical and electron microscopes and molecular studies of pathogens are the basis for all further studies. After this laboratory studies must be conducted to isolate, culture and study the biology of pathogens. Completing all these steps allows evaluation of impact of pathogens on their hosts, and extensive bioassays are necessary before use of pathogens in biological control.

3. TAXONOMY, SYSTEMATICS AND BIOLOGY OF PATHOGENS

3.1. Viruses

Virus particle (virion) morphology is an important character in assigning a virus to a taxonomic group. A virion is composed of a protein shell (capsid) that surrounds the nucleic acid. The capsid provides the virion with morphological and functional properties, the nucleic acid with the genetic constituent, and both together form the nucleocapsid. Each virus has only one type of nucleic acid, either DNA or RNA. In some groups (Baculoviridae, Entomopoxviridae, Reoviridae) the nucleocapsids are occluded in a crystalline protein matrix (occlusion body). This occlusion body contributes to the stability and persistence of the virions when they are released from the host into the environment. When a host consumes the occlusion body, the protein matrix dissolves in the midgut, releasing the virions which attach to the membranes of the microvilli and cross these membranes. The virions are taken in by a process of fusion, they begin to replicate viral RNA or DNA in the cytoplasm, e.g. entomopoxviruses (EPV) or cytoplasmic polyhedrosis virus (CPV), or in the nucleus, e.g.: nuclear polyhedrosis virus (NPV) or granulosis virus (GV). One important feature of insect viruses is that they are obligate pathogens and most of them are relatively host specific. Virus infections are usually very contagious and cause mortality.

3.2. Bacteria

Bacteria are unicellular organisms but lack of defined nucleus (Prokaryotes). They may have rigid cell walls or they are without cell walls. Some species produce resistant endospores. Bacteria are the most common microorganisms associated with insects, most of them developing extracellularly except for the pathogenic *Rickettsia*. Many cause no diseases to insects, but a significant number are important pathogens. Bacterial infections in insects can be classified as bacteremia (bacteria multiply in the insect's haemolymph without production of toxins), septicemia (bacteria multiply in the insect haemocoel and produce toxins) and toxemia (bacteria produce toxins killing the insect and are confined to the gut lumen). Bacteria infect insects mostly through the mouth and digestive tract (taken in together with food). Within the digestive tract, the bacteria produce enzymes. These enzymes may damage the cells of the gut wall and enable the bacteria to enter the haemocoel and may act on tissues in the haemocoel. The majority of non-sporeforming bacteria are facultative pathogens whose pathogenicity depends on stress conditions affecting the insect host.

Many of the insect pathogenic bacteria occur in the family Bacillaceae; *Bacillus thuringiensis* in particular, has received considerable attention as a microbial control agent. Members of the family Bacillaceae produce endospores and are gram-positive, motile or nonmotile rods. They are aerobic or facultatively aerobic and usually produce a catalase. They multiply as vegetative cells. The vegetative cell,

when it begins to produce a spore, is called a sporangium. During sporulation they produce parasporal bodies within the sporangium containing an endotoxin.

Different subspecies of *B. thuringiensis* are known to be pathogenic to different insect orders . One type is known to be pathogenic to Lepidoptera, another one to (aquatic) Diptera and a third one to Coleoptera, and they are classified in different serotypes.

3.3. Fungi

Entomopathogenic fungi can be found within the Zygomycota, Ascomycota and Deuteromycota. Up to now, mainly species of the Deuteromycota (can be grown on artificial media) were tested with regard to their efficacy to pest insects.

Most of the Entomopathogenic fungi form superficial growth on the surface of their hosts where they produce conidia. Their growth and development are limited mainly by the external environmental conditions, in particular, high humidity or moisture and adequate temperatures for sporulation and spore germination. The infectious units are the conidia (and hyphal bodies). The fungi gain access to the insect mainly through the integument. The development of a mycosis can be separated into three phases: 1. adhesion and germination of the spore on the insect's cuticle, 2. penetration of the integument into the haemocoel and 3. development of the fungus, which generally results in death of the insect, ending with sporulation on the surface of the cadaver. Host specificity of entomopathogenic fungi varies considerably, some of them infecting a broad range of insect hosts (e.g. *Beauveria bassiana* infects at least 100 different insect species). Virulence of isolates may also have a high degree of specificity.

3.4. Protozoa

Entomopathogenic protozoa are minute unicellular organisms, they are members of the protozoan phyla: Rhizopoda, Apicomplexa, Microspora, Zoomastigina and Ciliophora . The highly pathogenic forms occur in the protozoan phylum Microspora, particularly those that invade the haemocoel and different tissues and develop intracellularly. They may cause severe acute infections in insects, but some produce only inapparent or chronic infections, which nonetheless may play an important role in regulating insect populations.

The majority of the protozoa enter the insect by the way of the mouth and digestive tract. The infective stage is generally a spore or a cyst. Those protozoa that remain in the lumen of the digestive tract are attached to the midgut epithelium or enter appendages associated with the digestive tract (gregarines). Others penetrate into the haemocoel and develop within cells of various tissues and organs (e.g. apicomplexa and microspora). Microsporidia possess unicellular spores, containing a uninucleate or binucleate sporoplasm, and an extrusion apparatus always with a polar filament and a polar cap; they do not have mitochondria. They are obligate pathogens and multiply only in living cells, causing economically serious diseases in beneficial and pest insects. Therefore, microsporidia are the most promising

protozoa for use in microbial control. But, the rest of protozoa, other Apicomplexa, (Neogregarina and Coccidia) are also efficient pathogens of insects.

4. PATHOGENS IN BARK BEETLES

Many pathogens have been described from different insect species, whereas pathogens in bark beetles are still not very well investigated and there are only a few articles summarizing the current knowledge (Postner, 1974; Mills, 1983; Bathon, 1991; Nierhaus-Wunderwald, 1993; Stephen *et al.*, 1993; Fuxa *et al.*, 1998). Furthermore, there is a great lack in knowledge of the action of pathogens in bark beetles worldwide in spite of the presumed potential of pathogens in controlling bark beetle populations.

4.1. Viruses

The *Ips typographus* Entomopoxvirus was the first record of a virus disease in the most important European spruce bark beetle species, *Ips typographus*, occurring in the cells of the midgut epithelium (Weiser and Wegensteiner, 1994; Wegensteiner and Weiser, 1995). Information on the prevalence of the ItEPV in different *I. typographus* populations (varying from 0.0 to 3.6%) is presented by Wegensteiner *et al.* (1996). This virus is presumed to be different from all former described entomopoxvirus type A (Zizka *et al.*, 2001). Discoidal inclusion bodies are released with faeces and the infection appears in adult beetles where it destroys the gut epithelium. The virus seems to be absent in America. Only from Northern China there are two reports of an entomopoxvirus in *Dendroctonus armandi* (Fan *et al.*, 1987; Tang and Fan, 1990). In North America Sikorowski *et al.* (1996) found five different virus-like particles in *Dendroctonus frontalis* which were not connected with evident disease and similar to different virus types but no entomopoxvirus. Haidler (1998) found the ItEPV in *I. typographus* from a locality in the Austrian central Alps, Händel (2001) found the ItEPV not only in *I. typographus* but also in *I. amitinus*; furthermore, he found indications of a Baculovirus (in the nuclei of midgut epithelium) and of entomopoxvirus-like spheroids in the cytoplasm of the midgut epithelium of *Polygraphus poligraphus*. The common occurrence of ItEPV in *I. typographus* was reported from different sampling plots in a planned national park area in Austria (Gasperl, 2002).

Up to now, there are no papers concentrating on the efficacy of these virus infections on their hosts. Preliminary field experiments showed successful introduction of the ItEPV in an *Ips typographus* field population (Pultar and Weiser 1999). Experiments infecting *Scolytus scolytus* larvae with the *Oryctes* baculovirus produced inexplicable results on the presence of virus particles which were different from those inoculated, but in any case infections had no significant influence on mortality of beetles (Arnold and Barson, 1977). At the moment, there is no evidence of transmission of the *Ips typographus* Entomopoxvirus to *Scolytus* spp. or other bark beetle species of deciduous trees.

4.2. Bacteria

Relatively few papers deal with entomopathogenic bacteria in bark beetles. Chararas (1955, 1962) and Pesson *et al.* (1955) were the first to report bacteria in bark beetles from Europe; some of the bacteria (*Aerobacter scolyti* and *Escherichia klebsiellaeformis*) were found to cause high mortality (up to 100%) in *Scolytus multistriatus* within 72 hours (Pesson *et al.*, 1955). Lysenko (1959) found bacteria in *Ips curvidens* (*Serratia marcescens*) and in *Xyloterus lineatus* (*Pseudomonas caviae*, *Pseudomonas septica*, *Cloaca cloacae* and *Bacillus coagulans*). Novak (1960) found *Pseudomonas septica* in *Trypodendron lineatum*. Balazy (1966) reports the occurrence of several bacteria in different bark beetle species from Poland, without precise identification. Later some of these bacteria (*Bacillus subtilis*, *Bacillus pumilus*, *Enterobacter cloacae*, *Enterobacter aerogenes*, *Flavobacterium* sp., *Corynebacterium* sp.) were found to occur in *Scolytus multistriatus* in Australia (French *et al.*, 1984). Inspection of *Anisandrus dispar* produced evidence of numerous bacteria (*Enterobacter agglomerans*, *Pseudomonas chlororaphis*, *Xanthomonas maltophilia*, *Staphylococcus lentus*, *Vibrio alginolyticus*, *Bacillus subtilis*, *Pseudomonas cepacia*, *Erwinia rhamontici*, *Erwinia rubrifaciens*, *Pasteurella haemolytica*, *Bacillus megaterium*, *Pseudomonas alcaligenes*, *Pseudomonas paucimobilis*, *Bacillus thuringiensis*, *Acinetobacter calcoacetus*) and other microorganisms (Canganella *et al.*, 1994). Even in North America there are few records dealing with bacteria in bark beetles, from laboratory colonies (Wood 1961) and from field populations (Doane, 1960; Jouvenaz and Wilkinson, 1970; Moore, 1971, 1972). *Serratia marcescens* caused high mortality in *S. multistriatus* larvae within a four day period and was highly correlated with the number of larvae, which was interpreted as a crowding effect (Doane, 1960). In one population of adult *I. calligraphus* from Florida the incidence of *S. marcescens* was high (45.7%) due to ingestion of contaminated phloem in old logging debris or to contact between crowded adults during the predispersal, maturation-feeding period (Jouvenaz and Wilkinson, 1970). Most of these reports refer to isolates from beetles dead in their galleries in the bark. There is no evidence of any transmission of bacterial infections with eggs and in larvae. Most cases were characterised by a multiple mixed bacterial flora, without evidence of any specific strain.

The occurrence of *Bacillus thuringiensis* in *Ips typographus* and *Dendroctonus micans* is reported from Georgia, where activity of the bacterium is thought to correlate with the activity of β -exotoxin in the bacterial preparation Bitoxibacillin used (Imnadze, 1978). Infection experiments with *Bacillus thuringiensis* var. *insectus* against *Ips subelongatus* worked partly, but most probably also as a consequence of exotoxins (Gusteleva, 1982a, b). Tomalak *et al.*, (1988) found Gram-negative bacteria in the fat body of all inspected *Hylurgopinus rufipes* from Canada, but with no apparent pathological effects in the host. Testing different bacteria (*Bacillus thuringiensis* var. *thuringiensis*, *Bacillus alvei*, *Bacillus cereus*, *Pseudomonas syringae*) against *Scolytus scolytus*- and *S. multistriatus*- larvae worked partly, with mortality up to 91.3% depending on inoculation dose (Jassim *et al.*, 1990). Further experiments confirmed possible contaminations during laboratory

evaluation, because *Bacillus thuringiensis* was not effective against *Ips calligraphus* and *Dendroctonus frontalis*, but a bacterial metabolite alone was very effective (Cane *et al.*, 1995) when applied to laboratory colonies. *Bacillus thuringiensis* var. *tenebrionis* caused no significant mortality in adult *Ips typographus* in field tests, spraying bark surface of spruce logs before beetles colonised the log sections respectively after beetles colonisation (Novotny and Turciani, 2000).

4.3. Fungi

In a similar extent as bacteria, pathogenic and saprophytic fungi are common in dead beetles, in many cases this development is without growth of fungi on surface of dead beetles.

In comparison with other pathogens, many records can be found dealing with entomopathogenic fungi in bark beetles, first reviewed by Müller-Kögler (1965). A number of investigations show the occurrence of fungi in bark beetle field populations, several different fungal species were found, including *Beauveria bassiana* and *Spicaria (Paecilomyces)* sp. which are those mentioned most frequently.

As a consequence of numerous references the occurrence of different entomopathogenic (mainly Deuteromycete) fungi in different bark beetle species is listed in chronological order.

Beauveria bassiana in: *Hylastes ater* (Petch, 1932), *Ips typographus*, *Ips duplicatus* (Karpinski 1935), *Ips typographus* (Siemaszko, 1939), *Ips typographus* (Neuzilova, 1956), *Scolytus multistriatus* (Doane, 1959), *Scolytus ratzeburgi*, *Scolytus multistriatus*, *Scolytus scolytus*, *Scolytus laevis*, *Polygraphus poligraphus*, *Hylurgops palliatus*, *Hylastes ater*, *Hylastes opacus*, *Dryocoetes autographus*, *Leperesinus fraxini*, *Ips typographus*, *Ips amitinus* (Balazy, 1962, 1965, 1966; Balazy *et al.*, 1967), *Blastophagus piniperda* (Nuorteva and Salonen, 1968), *Hylastes ater* (Leatherdale, 1970), *Trypodendron lineatum* (Magema *et al.*, 1981), *Ips acuminatus* (Balazy *et al.*, 1987), *Ips typographus* (Landa *et al.*, 2001), *Leperesinus varius* (Kirschner, 2001).

Beauveria caledonica in: *Crypturgus pusillus*, *Dryocoetes autographus*, *Gnathotrichus materiarius*, *Hylurgops palliatus*, *Ips typographus*, *Orthotomicus laricis*, *Pityogenes chalcographus*, *Polygraphus poligraphus* (Kirschner, 2001).

Paecilomyces farinosus in: *Ips typographus* (Neuzilova, 1956), *Ips typographus* (Balazy *et al.*, 1967), *Trypodendron lineatum* (Kirschner, 2001), *Ips typographus* (Landa *et al.*, 2001).

Paecilomyces fumosoroseus in: *Ips typographus* (Landa *et al.*, 2001).

Paecilomyces variotii in: *Leperesinus varius* (Chararas, 1957), *Dryocoetes autographus* (Chararas, 1962).

Verticillium lecanii in: *Crypturgus pusillus* (Balazy, 1962), *Polygraphus poligraphus* (Balazy, 1963), *Scolytus intricatus*, *Scolytus kirschii*, *Polygraphus poligraphus*, *Hylesinus crenatus*, *Ips typographus* (Balazy, 1973; Landa *et al.*, 2001).

Mucor hiemalis in: *Trypodendron lineatum* (Magema *et al.*, 1981).

Tolypocladium cylindrosporum in: *Pityogenes chalcographus* (Kirschner, 2001).

In all cases cited it is evident that Deuteromycete fungi are able to kill all stages of bark beetles when the fungus has free access to the cuticle, but do not interfere with the developmental stages (eggs, larvae, pupae, callow adults) during their development in sterile conditions of galleries in fresh bark (in the tree).

Infections with other fungi are rare, there is one case of an Ascomycete, *Metschnikowia typographi* in *Ips typographus* (Weiser and Wegensteiner, 1998), *Ips typographus* and *Ips amitinus* (Händel, 2001; Weiser *et al.*, 2003), the infection is under further investigation.

The importance of high humidity for infection of bark beetles (larvae and adults) with Deuteromycetes and for growth of conidia on cadavers is mentioned by several authors (Doane, 1959; Schwester, 1957; Balazy, 1963). The possible role of vectors (e.g. predators, parasitoids) in spread of infection through transmission of fungal spores within bark beetle galleries was mentioned in early investigations (Karpinski, 1935; Doane, 1959). Many fungi were found in galleries of bark beetles (31 different species) from different tree species, and even if beetles were not present in their galleries, several of them were known as entomopathogenic fungi (*Beauveria bassiana*, *Beauveria caledonica*, *Conidiobolus coronatus*, *Paecilomyces farinosus*, *Tolypocladium cylindrosporum* and *Verticillium lecanii*). *B. bassiana*, *B. caledonica* and *P. farinosus* were the most abundant species (Kirschner, 1998, 2001; Landa *et al.*, 2001).

Novak and Samsinakova (1962) performed laboratory and field tests with *B. bassiana* against *Trypodendron lineatum* and they were able to show high efficacy of laboratory isolates especially to larvae (100% mortality in 6 to 8 days) but also to adults (100% mortality in 12 days).

Several studies have focused on efficacy comparison of different fungal species in bark beetles. Artificial infection was successful with *Verticillium lecanii* in *Scolytus scolytus* larvae (Balazy, 1963). Action of *Verticillium lecanii* was also tested in the laboratory against *Scolytus scolytus* larvae by Barson (1976), but especially high mortality was caused in *S. scolytus* larvae by *Beauveria bassiana* (Barson, 1977), an inoculum of 1×10^6 spores was determined as the LD₅₀ after 5 days (at 23°C and 100% relative humidity). Comparison of the efficacy of *B.*

bassiana and *P. farinosus* in adult *I. typographus* and in *S. ratzeburgi* larvae revealed better infections using *B. bassiana* (Balazy, 1966). Nuorteva and Salonen (1968) found *B. bassiana* infection rates in *B. piniperda* up to 62.5%, but infection rates decreased with increasing time of exposure of conidia on the bark surface.

All developmental stages of *Pityogenes chalcographus* (larvae, pupae, adults) were sensitive to *B. bassiana* infections in a laboratory study (especially larvae and pupae) depending on inoculation dose (in 3 to 10 days up to 100% mortality). In addition, abiotic conditions favouring efficacy of *B. bassiana* were higher temperature (especially 25°C), bark humidity (45%) in breeding systems and particularly air humidity in incubation vessels (especially 91%). Furthermore, horizontal transmission of the infection was observed within breeding systems, and the number of eggs laid was significantly reduced in infected females (Wulf, 1979, 1983).

Doberski (1981a, b) tested the pathogenic effects of different strains of *Beauveria bassiana*, *Metarhizium anisopliae* and *Paecilomyces farinosus* to *Scolytus scolytus* larvae, with *B. bassiana* being the most virulent species. Indirect inoculation of adult beetles via treated bark was found to be successful for *B. bassiana* and *M. anisopliae*. Successful infections in larvae were found at temperatures down to 2°C with *B. bassiana* and *P. farinosus*. In the case of *M. anisopliae* the minimum temperature for infection was 10°C; *B. bassiana* and *M. anisopliae* were successful even at low humidities (from 100% to 51%), and *P. farinosus* only from 100% to 86% humidity. Unknown factors essential for germination of *B. bassiana* on the cuticle of *Dendroctonus ponderosae* were presumed by Hunt *et al.* (1984). Gusteleva (1984) reports controversially the high sensitivity of adult *Ips subelongatus* to *Beauveria bassiana* (89% mortality) but observed no effect on larvae.

Matha and Weiser (1985) tested a commercial *B. bassiana* preparation (Boverol) via indirect inoculation of beetles exposing them to spore treated filter paper and were able to show that this method caused 100% mortality in *I. typographus*. In addition, they were able to transfer the infection from dead beetles overgrown with fungus to healthy ones by accidental contact, but mortality was not as high as through contact with preparation on filter paper.

When Houle *et al.* (1987) tested different fungal species and different fungal strains against *Scolytus multistriatus*, they found *B. bassiana*, *M. anisopliae* and *Paecilomyces fumoso-roseus* produced 100% mortality at high inoculation dosages, whereas other fungal species tested were not as effective (*Cordyceps militaris*, *Hirsutella thompsonii*, *Nomuraea rileyi*, *Verticillium lecanii*, *Paecilomyces farinosus*).

Temperature, humidity, spore formulation and spore dose dependent effects of *Beauveria bassiana* to *Trypodendron lineatum* were tested in the laboratory, and the results were similar to those from tests with other bark beetle species (Prazak, 1988, 1991, 1997). Different test conditions caused 36% to 55% mortality in most cases, while only a few experiments lead to mortality rates higher than 80%. Transmission of *B. bassiana* from inoculated male beetles to healthy female beetles was successful and caused 20% reduction of egg laying. Treatment of the bark surface resulted in

reduced number of egg niches (up to 44%) depending on applied spore concentration. Treatment of soil resulted in high mortality of hibernating offspring beetles (88% to 100% mortality). In additional tests, infection rates were high in *P. chalcographus* and *Hylastes cunicularius*, but relatively low in *Hylurgops palliatus* (Prazak, 1988).

Testing pathogenic effects of *Beauveria bassiana*, *Beauveria brongniartii* and of one more *B. brongniartii* strain (syn. *B. tenella*) to *Ips typographus* showed high virulence particularly of *B. bassiana* (4.8 days mean life span); even contact of *I. typographus* with *B. bassiana* treated bark for one minute caused 60% mortality, or contact of healthy beetles with cadavers of *I. typographus* with fungal conidia on their surface caused high infection rates (98.6%). Infection rates differed at three test temperatures (13°, 23° and 33°) but were always high (78% to 100%) (Wegensteiner, 1992). Inoculation dose and temperature were also shown to be very important factors for the action of *B. bassiana* in *I. typographus* (up to 100% infection), and even contact of *I. typographus* with *B. bassiana* treated bark led to infection rates up to 97% (Wegensteiner, 1996). Laboratory tests exposing *Polygraphus poligraphus* to *B. bassiana* or *B. brongniartii* treated bark pieces showed that *B. bassiana* caused higher infection rates (72%-100%) than *B. brongniartii* (69.6%-81.4%). Furthermore, testing th. effects of temperature and *B. bassiana* inoculation dose in *P. poligraphus* brought similar results as found in *I. typographus* (87% to 100% infection) (Wegensteiner, 2000).

The efficacy of *Metarhizium anisopliae* was tested against adult *Pityogenes chalcographus*, when direct inoculation of beetles caused high mortality (95.3%), and inoculation via treated bark resulted in 26.8% infection (Pehl and Kehr, 1994). Markova (2000) tested the effects of *B. bassiana*, *M. anisopliae*, *P. farinosus* and *V. lecanii* to *I. typographus*; the most pathogenic species was *M. anisopliae* (100% mortality in 4 days) and the least pathogenic one was *V. lecanii* (still causing 90% mortality).

However, *B. brongniartii* and *Metarhizium anisopliae* were never identified from field collected bark beetles.

In field populations the importance of entomopathogenic fungi is mentioned, especially for *P. farinosus* and *B. bassiana* (Balazy, 1968). Fungal pathogens were found in all developmental stages even if the percentage of infection and the proportion of reduction of beetle population was estimated to be relatively low. Bychawska and Swiezynska (1979) performed field experiments spraying *B. bassiana* on trap logs to infect *Tomicus piniperda*; this treatment caused no significant infection in *T. piniperda*, and different abiotic conditions (rain, snow, insolation) were identified as major problems reducing viability of germs in field conditions. In a further experiment infested trap logs were sprayed with *B. bassiana* suspension then covered with a polyethylene foil to improve climatic conditions and to infect the emerging callow adults of *T. piniperda* with *B. bassiana*; this procedure was successful and resulted in 71 to 100% infection (Lutyk and Swiezynska, 1984).

In all reported cases there is no mention of mortality in larvae during their development in fresh phloem of trees.

Some special laboratory experiments were performed simulating hibernation of *I. typographus* in litter, which caused 70% mycosis at 20°C, 17°C and 12°C after 28 days, 35 days and 41 days respectively. Furthermore, field experiments were carried out with the special aim of using *B. bassiana* against *I. typographus* during hibernation in litter, and these resulted in promising infections (Hallet *et al.*, 1994). These results were confirmed by a further study, but *B. bassiana*-infection rates were high even in the control group, due to the natural presence of *B. bassiana* in the soil of all experimental plots (Arbesleitner, 2002) similar to the observations of Hallet *et al.* (1994). Kreutz (1995) found only *B. bassina* in *I. typographus* after hibernation in the soil.

Testing the virulence of *B. bassiana* against *I. typographus* by the way of inoculative release via *B. bassiana*-containing pheromone traps (catch – inoculate – release technique) were very promising, since this inoculation mode caused high infection rates (70.7 to 96.7%) and a significantly reduced life span of beetles (several beetles died within the nuptial chamber) plus a reduction of length of maternal galleries (Vaupel and Zimmermann, 1996; Kreutz *et al.*, 2000a, b; Kreutz, 2001).

4.4. Protozoa

Fuchs (1915) was the first to describe protozoan diseases in *Ips typographus*, with the identification of two protozoan species, *Telosporidium typographi* and *Gregarina typographi*. In most of the investigations adult beetles were inspected, in the majority of cases from field collected specimens.

Weiser (1954, 1955, 1961a, 1966, 1977) was the first to summarize the knowledge on protozoa in bark beetles. Purrini and Führer (1979) were the first who tested laboratory infections of bark beetles with protozoa. Sprague (1977) and Levine (1988) included the protozoan species described from bark beetles in their systematic compendium of microsporidia.

Rhizopoda, Amoebina

The occurrence of a rhizopodan species was mentioned, first determined as a variety of *Malamoeba locustae* (Purrini, 1978a, b), and later described as *Malamoeba scolyti*, in the cells of the midgut epithelium and of the Malpighian tubules of *Dryocoetes autographus* (Purrini, 1980). Purrini and Führer (1979) were able to show that *Malamoeba scolyti* is also infective to *Pityogenes chalcographus* (6.0% to 26.0% infection of tested beetles). Kirchhoff (1982) and Kirchhoff and Führer (1985) found *M. scolyti* in *Hylurgops palliatus* field populations too and they investigated the effects of this pathogen by artificial infection in the lab. Kirchhoff and Führer (1990) found a significant reduction of life span of infected *D. autographus* (at 20°C, time to death: 5 to 7 weeks post infection, compared with 3 to 4 months in control beetles), and successfully transferred the infection to several other bark beetle species (*Hylurgops palliatus*, *Hylastes ater*, *Tomicus piniperda*, *Polygraphus poligraphus*, *Pityogenes chalcographus*, *Pityogenes bidentatus*, *Pityogenes calcaratus*, *Ips typographus*, *Ips laricis*, *Ips acuminatus*, *Ips sexdentatus*); but they also mentioned that it can be some inhibition in manifestation

of disease in case of nematode presence in the gut of *I. typographus* and *D. autographus* (Kirchhoff, 1982; Kirchhoff and Führer, 1990). The whole life cycle of *M. scolyti* in *D. autographus* was described by Purrini and Zizka (1983). Wegensteiner (1994), Wegensteiner *et al.* (1996) and Händel *et al.* (2001) found *Malamoeba scolyti* in the gut of *Ips typographus* from different localities in Austria. *M. scolyti* was found in *Dryocoetes autographus* and *Ips typographus*, but also in *Hylurgops glabratus* from a locality in the Austrian Alps, even if in a small number of beetles (Haidler, 1998). Händel (2001) mentioned in his study the occurrence of *M. scolyti* in *Ips typographus*, *Hylurgops palliatus*, *Dryocoetes autographus* and for the first time in *Hylastes cunicularius* from several localities in Austria. Totally new was the observation of *Malamoeba scolyti* in *Ips acuminatus* from Austria (Zitterer, 2002).

Besides this species, there is only one more passing mention of an *Endamoeba* sp. in *Pityogenes calcaratus* (Purrini and Halperin, 1982).

4.5. Apicomplexa, Eugregarinida

Fuchs (1915) first described *Gregarina typographi* occurring in the midgut lumen of *Ips typographus*. Theodorides (1960) found *Gregarina typographi* occurring in *Ips sexdentatus*. Different gregarines are mentioned from several bark beetle species in the compendium of Geus (1969): *Gregarina piktyokteinidis* in *Pityokteines curvidens* (Rauchalles i. litt., in Geus 1969), *Gregarina hylastidis* in *Hylastes ater*, *Hylastes cunicularius* and *Hylastes opacus* (Rauchalles i. litt., in Geus, 1969), *Gregarina typographi* in *Dryocoetes autographus* (Geus, 1969), *Gregarina pityogenidis* in *Pityogenes bidentatus* (Rauchalles i. litt., in Geus, 1969) and *Acanthospora crypturgi* in *Crypturgus pusillus* (Geus, 1969).

Inspecting *Ips typographus* in Austria brought evidence of *Gregarina typographi* in the beetles from some of the different localities (Wegensteiner, 1994). A further study, including more sites, showed that *G. typographi* can be found in *I. typographus* from many localities in Austria and the Czech Republic, in some cases at high prevalence (up to 43.8%) (Wegensteiner *et al.*, 1996). Inspecting the pathogens of bark beetles living associated on spruce brought evidence of *Gregarina hylastidis* in *Hylastes cunicularius* and most probably of *Gregarina cf. typographi* in *Hylurgops glabratus*, in *Pityogenes chalcographus* and in *Ips amatinus* (Haidler, 1998; Händel, 2001); in addition, they also found *G. typographi* in *I. typographus* and in *D. autographus*. An undescribed *Gregarina* sp. was observed in the midgut lumen of *Tomicus minor* from Austria (Kohlmayr, 2001). *Gregarina typographi* could be found frequently in *I. typographus* from a national park area, and partly in a very high proportion of inspected beetles (up to 63.9%) (Gasperl, 2002). During inspection of *Ips acuminatus* a *Gregarina* sp. was found in the gut lumen of adult beetles from Austria and Norway (Zitterer, 2002).

4.6. Apicomplexa, Neogregarinida

The first to report a neogregarinid species, *Telosporidium typographi*, in *Ips typographus* was most probably Fuchs (1915) who argued that the impact of this infection on the beetles can be an important mortality factor.

Weiser (1955) first described the occurrence of *Menzbieria chalcographi* in *Pityogenes chalcographus*. Purrini and Führer (1979) performed infection experiments with *M. chalcographi* in *P. chalcographus* and showed that beetles from different localities were not in all cases sensitive to this infection (0.0% to 12.0% infection), and artificial infection worked only in beetles without nematodes in the gut. *Ophryocystis dendroctoni* was found in the Malpighian tubules of *Dendroctonus pseudotsugae* (Weiser, 1970). *Mattesia schwenkei* was described from the adipose tissue of *Dryocoetes autographus* (Purrini, 1977) and of *Hylurgops glabratus* (Purrini, 1978b). Purrini (1978b, 1980) found *Menzbieria chalcographi* in *Dryocoetes autographus*, in *H. glabratus* and in *Hylurgops palliatus*. *Ophryocystis hylesini* was found in the Malpighian tubules of *Hylesinus fraxini* (Purrini and Ormieres, 1981). A first indication of the occurrence of *Ophryocystis* sp. in the Malpighian tubules of *Pityogenes calcaratus* is given by Purrini and Halperin (1982). The presence of spores of a new neogregarine in the adipose tissue was recorded for *Ips typographus* from a nature reserve in Germany (Wegensteiner and Weiser, 1996a), the spores were identified as similar to those spores which Fuchs (1915) described as *Telosporidium typographi*. Morphological features of this neogregarinid species indicated that it is most probably a *Mattesia* sp. (Zizka *et al.*, 1997, 1998). This *Mattesia* sp. was found only in very few *I. typographus* from a national park area in Austria (Gasperl, 2002). Not concise data are given on the occurrence of an unidentified neogregarinid species in *Pityophthorus pityographus* (Haidler, 1998) and in *Pityogenes chalcographus* (Händel, 2001). Another neogregarinid species, similar to *Mattesia* sp. in *I. typographus*, was found in *Ips acuminatus* from one locality in Norway (Zitterer, 2002).

4.7. Microspora

Three types of microsporidia are represented in bark beetles of conifers: *Chytridiopsis* sp. with thick walled spherical pansporoblasts filled with 16 or more spherical spores, infecting the cells of the midgut epithelium. *Nosema typographi* with single binucleate spores mainly in the fat body and Malpighian tubules, and *Unikaryon* sp. respectively *Canningia* sp. with single uninucleate spores mainly in the cells of the midgut epithelium, the Malpighian tubules and the ovarioles of adult beetles. The genera *Stempellia* and *Pleistophora* are infecting scolytids of deciduous trees, they have ovoid spores connected in groups of 8 – 16 or in irregular masses in the cells of the midgut epithelium and other tissues.

Weiser (1954a, b) was the first to describe *Chytridiopsis typographi* (formerly *Haplosporidium typographi*) from the gut epithelium of *Ips typographus*, and in the American species *Dendroctonus pseudotsugae* (Weiser, 1970); in the same paper *Nosema dendroctoni* is described for *D. pseudotsugae*. *Nosema typographi* was described by means of light microscopy from the adipose tissue of *Ips typographus* (Weiser, 1955), and later this investigation was completed by an electron

microscopy study (Weiser *et al.*, 1997). *Nosema typographi* was also found in *Hylurgops palliatus* (Purrini, 1978b). Furthermore, Weiser (1961b) described a microsporidium, *Nosema curvidentis*, from *Pityokteines curvidens*, which occurred mainly in the adipose tissue, the hypodermis and connective tissues.

Stempellia scolyti was found by Weiser (1966) mainly in the midgut of *Scolytus scolytus*, *S. multistriatus*, *Scolytus pygmaeus* and *Scolytus ensifer*. Lipa (1968) found *Nosema scolyti* in the same four *Scolytus* species (in the midgut, in Malpighian tubules and in haemocytes). Weiser (1968) described *Plistophora scolyti* in *Scolytus scolytus* and mentioned a double infection with *Nosema curvidentis* in the gut wall and in oenocytes. A microsporidium similar to *Stempellia scolyti* in size, but different in development was found in *Scolytus scolytus* from Kosovo (Purrini, 1975).

There are only two mentions of the occurrence of *Unikaryon minutum* in an American bark beetle, *Dendroctonus frontalis* (Knell and Allen, 1978), and later it was found again in different populations occasionally at high prevalence (4.3% to 55.0% infection) in the same host (Bridges, 1987).

Nosema typographi and *Helicosporidium parasiticum* were mentioned briefly to occur in *Hylurgops palliatus* (Purrini, 1980).

Pleistophora xyloteri was described as occurring in the gut wall of *Trypodendron domesticum*, and *Nosema dryocoetes* in the adipose tissue of *Dryocoetes autographus* (Purrini and Ormieres, 1981). *Nosema calcarati* was found in the gonads of *Pityogenes calcaratus* (Purrini and Halperin, 1982).

In further investigations *Chytridiopsis typographi* was found to infect *Hylastes cunicularius* too (20% infection) (Purrini and Weiser, 1984). Dates on spore dimorphism of *Chytridiopsis typographi* from *I. typographus* are mentioned in the study of Purrini and Weiser (1985); in the same paper there is a passing mention (without precise data) that *Chytridiopsis typographi* was also found in *Ips laricis* and in *Hylurgops glabratulus* from Germany. A study concentrating on the pathogens in *Ips typographus* brought evidence of several microsporidia in this species, *Chytridiopsis typographi* was found in many localities in Austria and the Czech Republic in prevalence up to 27.7% (Wegensteiner, 1994; Wegensteiner *et al.*, 1996; Skuhravy, 2002). Considerable distinctions were found in infection rates of *I. typographus* field populations (from pheromone trap catch), varying in different years depending upon date of sampling within a year (1.0% to 80.0% infection), in comparison with several consecutive laboratory generations (22.1% to 67.5% infection) (Wegensteiner and Weiser, 1996b.). *Chytridiopsis typographi* and *Nosema typographi* were found in *Ips typographus* from a nature reserve in Germany (Wegensteiner and Weiser, 1996a). Laucius and Zolubas (1997) found *Chytridiopsis typographi* also in *Ips typographus* from Lithuania. Studies on associated spruce bark beetles from a site in the central Alps of Austria showed that *Ch. typographi* also can be found in *Hylastes cunicularius*, *Hylurgops glabratulus*, *Pityophthorus pityographus*, *Pityogenes chalcographus*, *Ips typographus* and *Ips amitinus* (Haidler, 1998), results which were confirmed in a further study for the species *Pityogenes chalcographus*, *Ips typographus* and *Ips amitinus* (Händel,

2001). *Chytridiopsis* sp. seems to be a non-specific pathogen infecting several bark beetle species of conifers.

Canningia spinidentis was described from the adipose tissue, the Malpighian tubules, muscles and connective tissues of *Pityokteines spinidens* (Weiser *et al.*, 1995). *Unikaryon montanum* was found in the adipose tissue, the Malpighian tubules and the ovaries of *Ips typographus* (Weiser *et al.*, 1998).

Host specificity of *Nosema typographi* and *Unikaryon montanum* is unclear at the moment especially with regard to associated (in the same tree) living bark beetles. Not identified microsporidia were mentioned by Haidler (1998) for *Hylurgops glabratus*, *Hylurgops palliatus*, *Dryocoetes autographus*, *Pityogenes chalcographus* and *Ips amitinus*. Händel (2001) was able to find *Nosema typographi* in *Ips typographus* and a *Nosema* sp. in *Hylurgops palliatus*, and *Unikaryon montanum* in *Ips typographus*, respectively undescribed *Unikaryon* spp. in *Pityogenes chalcographus*, *Ips amitinus* and in *Polygraphus poligraphus*. The *Unikaryon* sp. in *Polygraphus poligraphus*, found in the midgut cells, in gut muscles and in Malpighian tubules was described later as *Unikaryon polygraphi* (Weiser *et al.*, 2002). Analysis of *Ips typographus* from different sampling plots in a planned national park in Austria brought evidence of *Chytridiopsis typographi* in the beetles of most plots, but *Nosema typographi* and *Unikaryon montanum* were found only in the beetles from one sampling plot (Gasperl, 2002). *Chytridiopsis* sp. (probably *Chytridiopsis typographi*) was found in *Ips acuminatus* from Austria, Czech Republic and from Norway (Zitterer, 2002).

Kohlmayr (2001) and Kohlmayr *et al.* (2003) report the occurrence of *Canningia tomici* in the cells of the midgut epithelium, the adipose tissue and in the gonads of *Tomicus piniperda* from Austria, Czech Republic, Poland, Finland and from USA.

5. CONCLUSIONS

Until recently, the numerous reports of the occurrence of pathogens in bark beetles were mostly confined to morphological description of the pathogens. Relatively few papers concentrated on the effects of natural or artificial infections in the hosts. Horizontal transmission of pathogens is likely to be promising only between female and male beetles of the parental generation, especially in polygamous species, simply because of a bark beetle's life pattern. Vertical pathogen transmission from beetles of the parental generation to beetles of the filial generation is also conceivable (trans ovum or in the course of maturation feeding). Infections transmitted in eggs evidently remain unapparent till maturation of beetles into adults. However, all efforts to find progressing infections in larvae and callow adults failed. Natural per os infection in larval stage most probably doesn't occur because all the economically most important bark beetle species normally feed in a sterile, not contaminated medium (phloem or xylem), and larvae of most of these species avoid contact with other individuals. Investigations of the occurrence or prevalence of pathogens in a bark beetle population vary widely due to the sampling period (time of the year), host generation (parental or filial generation), and mode of sampling (collecting beetles out of logs by hand, collecting beetles from a

pheromone trap or collecting beetles emerging through a longer period from logs), and thus may influence the significance of results of infection data.

The evaluation of pathogenic effects in bark beetles can be tentatively only, there are no precise records of numbers of dead beetles in the field (with regard to natural mortality). Infections in bark beetles are not manifested by the way of deformation, change of colour or surface, or of behaviour of infected animals; only fungal infections are forming surface covers on dead animals.

There is uncertainty in indication of mortality of bark beetles with different infections, but infected animals must have a loss of expectation of life even dead bark beetles are not present in high numbers in the galleries, maybe they die during swarming.

For microbial control it is necessary to inoculate the target insects sufficiently (per os, via cuticle or trans ovum) to ensure successful infection. The time window for this process, especially for artificial infection, is normally very short for bark beetles, due to the relatively short swarming periods of beetles. After this, beetles live hidden in the bark and are "protected" against inoculation, with the exception of horizontal transmission between the breeding partners or of vertical pathogen transmission. One possibility could be the use of pheromone traps, attracting beetles to the traps and inoculating them with infectious material. Furthermore, use of microbials against bark beetles can raise similar questions as in other cases, concerning the possible side effects of pathogens in other insects, especially natural enemies. Till now, there is no knowledge on non target infectivity of pathogens of bark beetles to other insects including their predators and parasites, and there is no knowledge of ability of migrating nematodes or mites to provide transport for any bark beetle pathogen. In addition, the type of pathogen and control strategy can be aimed at short term control or can fulfil a longer term regulatory effect. In case of entire absence of one pathogen species in the bark beetle population of a region, an inoculative release of such a pathogen could be a good option.

Viruses could be very interesting for microbial control measures, especially from the point of selectivity and effectiveness, as known from other insect species. At the moment there is a lack of knowledge on infection process and efficacy of viral infections, but the distribution of propagules in faecal pellets, could be useful for field application (autodissemination). Even though several reports deal with bacteria in bark beetles, no bacterium is known at the moment to act effectively in bark beetles. Fungal pathogens look to be very promising candidates for microbial control of bark beetles. A large number of pathogenic fungi have been described in bark beetles and several were found to cause rapid mortality in laboratory experiments, and may act as very efficient control agents. However, some of the entomopathogenic fungi have the disadvantage that they act rather non-specifically. Protozoa, especially microsporidia are known for their relatively slow action, but as obligatory pathogens and as occasional vertically transmitted pathogens, this group may be very important for long term regulation strategies.

Evaluating the efficacy of single pathogens is relatively easy based on laboratory tests, but it is more of a problem to estimate actions of pathogens under field conditions, and interactions between different pathogens and of pathogens with

other natural enemies (predators, parasitoids) is equally problematic. Survival of resistant stages of pathogens in the environment of the host's habitat is an important point. Furthermore, most of the pathogens have a limited capacity to disperse by their own action and must rely on physical and biotic factors for their dispersal.

Even if the number of pathogens isolated from bark beetles is relatively high, few studies have dealt with practical control aspects using microbials in bark beetle field populations. Therefore, there remains a great need to identify and measure the scope of pathogens influencing bark beetle populations.

6. REFERENCES

- Adams J.R. & J.R. Bonami 1991. *Atlas of Invertebrate Viruses*. CRC Press.
- Arbesleitner G. 2002. Der insektenpathogene Pilz *Beauveria bassiana* – seine Wirkung auf den Borkenkäfer *Ips typographus* bei der Überwinterung im Boden und Überprüfung der keimungs- und wachstumshemmenden Wirkungen unterschiedlicher Substanzen. Diploma thesis, Universität für Bodenkultur Wien.
- Arnold M.K. & G. Barson 1977. Occurrence of Virus like Particles in Midgut Epithelial Cells of the Large Elm Bark Beetle, *Scolytus scolytus*. *Journal of Invertebrate Pathology* 29, 373-81.
- Balazy S. 1962. Observations on appearing of some entomogenous fungi of fungi imperfecti group of forest insects. *Polskie Pismo Entomologiczne* (Bulletin Entomologique de Pologne), Ser. B, 3-4, 149-64.
- Balazy S. 1963. The fungus *Cephalosporium (Acrostalagmus) lecanii* Zimm., a pathogen of beetle larvae. *Acta Societatis Botanicorum Poloniae* 32, 69-80.
- Balazy S. 1965. Entomopathogenous fungi from the order Hyphomycetes damaging forest insects in Poland. *Roczniki Wydziału Rolniczej w Poznaniu* 27, 21-30.
- Balazy, S. 1966. Living organisms regulating population density of bark beetles in spruce forests, with special reference to entomopathogenic fungi. *Poznańskie Towarzystwo Przyjaciół Nauk Wydział Nauk Rolniczych I Lesnych* XXI, 1, 3-50.
- Balazy S. 1968. Analysis of bark beetle mortality in spruce forests in Poland. *Ekologia Polska - Ser. A*, XVI, 33, 657-87.
- Balazy S. 1973. A review of entomopathogenic species of the genus *Cephalosporium* Corda (Mycota, Hyphomycetales). *Bulletin de la societe des Amis des Sciences et des Lettres de Poznan*, Ser. D 14, 101-137. In: Schuler T., M. Hommes, H.-P. Plate & G. Zimmermann 1991. *Verticillium lecanii* (Zimmermann) Viegas (Hyphomycetales: Moniliaceae): Geschichte, Systematik, Verbreitung, Biologie und Anwendung im Pflanzenschutz. *Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft*, Berlin-Dahlem 269, P. Parey.
- Balazy S., J. Michalski & E. Ratajczak 1987. Materials to the knowledge of natural enemies of *Ips acuminatus* Gyll. (Coleoptera; Scolytidae). *Polskie Pismo Entomologiczne* (Bulletin Entomologique de Pologne) 57, 735-45.
- Balazy S., J. Bargielski, G. Ziolkowski & C. Czerwinska 1967. Mortality of mature beetles *Ips typographus* (L.) (Col., Scolytidae) in the galleries and its causes *Polskie Pismo Entomologiczne* (Bulletin Entomologique de Pologne) XXXVII/1, 201-05.
- Barson G. 1976. Laboratory studies on the fungus *Verticillium lecanii*, a larval pathogen of the large elm bark beetle (*Scolytus scolytus*). *Annals of Applied Biology* 83, 207-14.
- Barson G. 1977. Laboratory evaluation of *Beauveria bassiana* as a pathogen of the larval stage of the large elm bark beetle, *Scolytus scolytus*. *Journal of Invertebrate Pathology* 29, 361-66.
- Bathon H. 1991. Möglichkeiten der biologischen Bekämpfung von Borkenkäfern. *Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft*, Berlin-Dahlem 267, 111-17.
- Becnel J.J. & T.G. Andreadis 1999. Microsporidia in Insects. In: *The Microsporidia and Microsporidiosis*, M. Wittner, L.M. Weiss (Eds), ASM Press.
- Boucias D.G. & Pendland J.C. 1998. *Principles of Insect Pathology*. Kluwer Academic Publishers, Norwell, USA, 537 pp.

- Bridges J.R. 1987. Prevalence of *Unikaryon minutum* (Microsporidia: Nosematidae) Infection in Outbreak Populations of the Southern Pine Beetle (Coleoptera: Scolytidae). Journal of Invertebrate Pathology 49, 334-35.
- Butt T.M., C. Jackson & N. Magan 2001. *Fungi as Biocontrol Agents*. CABI Publ.
- Bychawska S. & H. Swiezynska 1979. Attempts of *Myelophilus piniperda* L. control with the use of entomopathogenous fungus *Beauveria bassiana* (Bals.) Vuill. Sylwan 12, 59-64.
- Cane J.H., H.E. Cox & W.J. Moar 1995. Susceptibility of *Ips calligraphus* (Germar) and *Dendroctonus frontalis* (Zimmermann) (Coleoptera: Scolytidae) to coleopteran-active *Bacillus thuringiensis*, a *Bacillus* metabolite, and avermectin B1. The Canadian Entomologist 127, 831-37.
- Canganella F., B. Paparatti & V. Natali 1994. Microbial species isolated from the bark beetle *Anisandrus dispar* F. Microbiological Research 149, 123-28.
- Chararas C. 1955. Ann. Epiph. 3, 315-28; cit.: Postner, M. (1974): *Scolytidae (=Ipidae), Borkenkäfer*. In: Die Forstschädlinge Europas, Bd. 2. W. Schwenke (Ed), P. Parey.
- Chararas C. 1957. Rev.Path.Veg.d'Ent.Agr.Fr. 36, 145-155; cit.: Postner, M. (1974): *Scolytidae (=Ipidae), Borkenkäfer*. In: Die Forstschädlinge Europas, Bd. 2.W. Schwenke (Ed), P. Parey.
- Chararas C. 1962. Encyclopedie Entomologique A, 38, Lechevalier, Paris; cit.: Postner, M. (1974): *Scolytidae (=Ipidae), Borkenkäfer*. In: Die Forstschädlinge Europas, Bd. 2. W. Schwenke (Ed), P. Parey.
- Doane C.C. 1959. *Beauveria bassiana* as a pathogen of *Scolytus multistriatus*. Annals Entomological Society of America 52, 109-11.
- Doane C.C. 1960. Bacterial Pathogens of *Scolytus multistriatus* Marsham as related to crowding. Journal of Insect Pathology 2, 24.29.
- Doberski J.W. 1981a. Comparative laboratory studies on three fungal pathogens of the elm bark beetle, *Scolytus scolytus*: Pathogenicity of *Beauveria bassiana*, *Metarrhizium anisopliae*, and *Paecilomyces farinosus* to larvae and adults of *S. scolytus*. Journal of Invertebrate Pathology 37, 188-94.
- Doberski J.W. 1981b. Comparative laboratory studies on three fungal pathogens of the elm bark beetle, *Scolytus scolytus*: effects of temperature and humidity on infection by *Beauveria bassiana*, *Metarrhizium anisopliae*, and *Paecilomyces farinosus*. Journal of Invertebrate Pathology 37, 195-200.
- Entwistle P.F., J.S. Cory, M.J. Bailey & S. Higgs 1993. *Bacillus thuringiensis*, an Environmental Biopesticide: Theory and Practice. J. Wiley & Sons.
- Fan, M.; C. Kuo & X. Lu 1987. Tentative study on entomopoxvirus of *Dendroctonus armandi* Tsai et Li. Journal Disinsectional Microorganism 1, 140-41.
- French J.R.J., P.J. Robinson, G. Minko & P.J. Pahl 1984. Response of the European elm bark beetle, *Scolytus multistriatus*, to host bacterial isolates. Journal of Chemical Ecology 10, 1133-49.
- Fuchs G. 1915. Die Naturgeschichte der Nematoden und einiger anderer Parasiten 1. des *Ips typographus* L. 2. des *Hylobius abietis* L. Zoologische Jahrbücher, Abteilung für Systematik 38, 109-222.
- Führer E. & K. Purini 1981. Protozoan Parasites of bark beetles – a vacancy in research work as to population dynamics. Proc. XVII IUFRO World Congress Japan 1981, Div. 2, 501-11.
- Fuxa J.R., R. Ayyappath & R.A. Goyer 1998. *Pathogens and Microbial Control of North American Forest Insect Pests*. USDA, Forest Health Technology Enterprise Team, Morgantown.
- Gasperl H. 2002. Grundlegende Erhebungen zum Borkenkäferaufreten an Fichten-Fangbäumen und zum Pathogenaufreten in Borkenkäfern aus dem geplanten Nationalpark Gesäuse. Diploma thesis, Universität für Bodenkultur Wien.
- Geus A. 1969. Sporentierchen, Sporozoa. Die Gregarinida. In: *Die Tierwelt Deutschlands*, 57. Teil, F. Dahl, F.G. Peus (Eds), G. Fischer, Jena.
- Gusteleva L.A. 1982a. Prospects for using microbial preparations against *Ips subelongatus*. Lesnoe Khozyaistvo 9, 67.
- Gusteleva L.A. 1982b. The interaction of wood decomposing insects with microorganisms. In: Konsortivnye svyazi dereva i dendrofil nykh nasekomykh, ed.: A.S. Isaev, 56-67.
- Gusteleva L.A. 1984. Virulence of *Beauveria bassiana* (Bals.) Vuill to the larvae of the bark beetle *Ips subelongatus* Motsch. (Coleoptera, Scolytidae). Revue d'Entomologie de l'Urss 63, 40-42.
- Händel U. 2001. Untersuchungen zum Gegenspielerkomplex assoziiert lebender Fichtenborkenkäfer (Col., Scolytidae) aus naturnahen und sekundären Fichtenbeständen unter besonderer Berücksichtigung der Pathogene. PhD thesis, Universität für Bodenkultur Wien.

- Händel U., M. Kenis & R. Wegensteiner 2001. Untersuchungen zum Vorkommen von Pathogenen und Parasiten in Populationen überwinternder Fichtenborkenkäfer (Col., Scolytidae). Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie 13, 423-28.
- Haidler B. 1998. Pathogene und Parasiten von Fichtenborkenkäfern in einem Fichtenbestand am Achner Kogel bei Tamsweg. Diploma thesis, Formal- und Naturwissenschaftliche Fakultät der Universität Wien.
- Hallet S., J.C. Gregoire & J. Coremans-Pelseneer 1994. Prospects in the use of the entomopathogenous fungus *Beauveria bassiana* (Bals.) Vuill. (Deuteromycetes: Hyphomycetes) to control the spruce bark beetle *Ips typographus* L. (Coleoptera: Scolytidae). Mededelingen Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen Universiteit Gent 59, 379-83.
- Houle C., G.C. Hartmann & S.S. Wasti 1987. Infectivity of eight species of entomogenous fungi to the larvae of the elm bark beetle, *Scolytus multistriatus* (Marsham). Journal of the New York Entomological Society 95, 14-18.
- Hunt D.W.A., J.H. Borden, J.E. Rahe & H.S. Whitney 1984. Nutrient-Mediated Germination of *Beauveria bassiana* Conidia on the Integument of the Bark Beetle *Dendroctonus ponderosae* (Coleoptera: Scolytidae). Journal of Invertebrate Pathology 44, 304-14.
- Hunter-Fujita F.R., P.F. Entwistle, H.F. Evans & N.E. Crook 1998. *Insect Viruses and Pest Management*. J. Wiley & Sons.
- Imnadze T.S. 1978. Characteristics of strains of *Bacillus thuringiensis* serotype I isolated from bark beetles in Georgia. Soobshcheniya Akademii Nauk Gruzinskoi SSR 92, 457-60. In: Review of Applied Entomology, Ser. A, Vol. 68, 1980, no. 2616, p. 328.
- Jassim H.K., H.A. Foster & C.P. Fairhurst 1990. Biological control of Dutch elm disease: *Bacillus thuringiensis* as a potential control agent for *Scolytus scolytus* and *S. multistriatus*. Journal of Applied Bacteriology 69, 563-68.
- Jouvenaz D.P. & R.C. Wilkinson 1970. Incidence of *Serratia marcescens* in Wild *Ips calligraphus* Populations in Florida. Journal of Invertebrate Pathology 16, 295-96.
- Karpinski J.J. 1935. Les causes qui limitent la reproduction de Bostryches typographes (*Ips typographus* L. et *Ips duplicatus* Sahlb.) dans la foret primitive. Inst.Rech.Forets doman., Trav., Compt.rend., Ser. A, Warszawa 15, 1-86, cit in: Müller-Kögler E. 1965. Pilzkrankheiten bei Insekten. P. Parey.
- Kirchhoff J.-F. 1982. Die insektenpathogene Amöbe *Malamoeba scolyti* Purrini als Krankheitserreger bei verschiedenen Borkenkäfern. PhD thesis, Georg August Universität, Göttingen.
- Kirchhoff J.-F. & E. Führer 1985. Häufigkeit und Verbreitung von *Malamoeba scolyti* Purrini bei *Dryocoetes autographus* in einigen Gebieten Nord- und Nordwestdeutschlands. Forstwissenschaftliches Centralblatt 104, 373-80.
- Kirchhoff J.-F. & E. Führer 1990. Experimentelle Analyse der Infektion und des Entwicklungszyklus von *Malamoeba scolyti* in *Dryocoetes autographus* (Coleoptera: Scolytidae). Entomophaga 35 (4), 537-44.
- Kirschner R. 1998. Diversität mit Borkenkäfern assoziierter filamentöser Mikropilze. PhD thesis, Fakultät für Biologie, Eberhard-Karls-Universität Tübingen.
- Kirschner R. 2001. Diversity of Filamentous Fungi in Bark Beetle Galleries in Central Europe. In: Trichomycetes and Other Fungal Groups: Professor Robert W. Lichtwardt Commemoration Volume, Editors-J. K. Misra and Bruce W. Horn, Science Publishers, Inc., Enfield (NH), USA, 175-96.
- Knell J.D. & G.E. Allen 1978. Morphology and Ultrastructure of *Unikaryon minutum* sp.n. (Microsporidia: Protozoa), a Parasite of the Southern Pine Beetle, *Dendroctonus frontalis*. Acta Protozoologica 17, 271-78.
- Kohlmayr B. 2001. Zum Auftreten von Krankheitserregern in den Europäischen Waldgärtnerarten *Tomicus piniperda*, *Tomicus minor* und *Tomicus destruens* (Coleoptera; Scolytidae). PhD thesis, Universität für Bodenkultur Wien.
- Kohlmayr B., J. Weiser, R. Wegensteiner, U. Händel & Z. Zizka 2003. Infection of *Tomicus piniperda* (Col., Scolytidae) with *Canningia tomi* sp.n. (Microsporidia, Unikaryonidae). Journal of Pest Science 76, 65-73.
- Kreutz J. 1995. Untersuchungen zur Überwinterung des Buchdruckers, *Ips typographus* (L.) (Scolytidae) im Boden. Diploma thesis, Mathem.-Naturwiss.Fakult. d. Saarlandes.
- Kreutz J. 2001. Möglichkeiten zur biologischen Bekämpfung des Buchdruckers, *Ips typographus* L. (Col., Scolytidae), mit insektenpathogenen Pilzen in Kombination mit Pheromonfallen. PhD-thesis, University of Saarbrücken.

- Kreutz J., G. Zimmermann, H. Marohn, O. Vaupel & G. Mosbacher 2000a. Möglichkeiten des Einsatzes von *Beauveria bassiana* (Bals.) Vuill. und anderen Kontrollmethoden zur biologischen Bekämpfung des Buchdruckers *Ips typographus* L. (Col., Scolytidae) im Freiland. Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie 12, 119-25.
- Kreutz J., G. Zimmermann, H. Marohn, O. Vaupel & G. Mosbacher 2000b. Preliminary investigations on the use of *Beauveria bassiana* (Bals.) Vuill. and other control methods against the bark beetle *Ips typographus* (Col., Scolytidae) in the field. IOBC/wprs Bulletin 23 (2), 167-73.
- Krieg A. 1986. *Bacillus thuringiensis*, ein mikrobielles Insektizid. Acta Phytomedica 10, P. Parey.
- Lacey L.A. & M.A. Goettel 1995. Current developments in microbial control of insect pests and prospects for the early 21st century. Entomophaga 40, 3-27.
- Landa Z., P. Hornak, L.S. Osborne, A. Novakova & E. Bursova 2001. Entomogenous fungi associated with spruce bark beetle *Ips typographus* L. (Coleoptera, Scolytidae) in the Bohemian Forest. Silva Gabreta 6, 250-72.
- Laucius S. & P. Zolubas 1997. Spruce bark beetle (*Ips typographus* L.) dynamics in forest reserve in 1995-1996. Miskininkyste 1 (39), 84-92.
- Leatherdale D. 1970. The arthropod hosts of entomogenous fungi in Britain. Entomophaga 15, 419-35.
- Levine N.D. 1988. *The protozoan phylum Apicomplexa*. Vol. I, II. CRC Press, Boca Raton.
- Lipa J.J. 1968. *Stempellia scolyti* Weiser com.nov. and *Nosema scolyti* n.sp. microsporidian parasites of four species of *Scolytus* (Coleoptera). Acta Protozoologica 6, 69-78.
- Lutyk P. & H. Swiezynska 1984. Trials to control the larger pine-shoot beetle (*Tomicus piniperda* L.) with the use of the fungus *Beauveria bassiana* (Bals.) Vuill. on piled wood. Sylwan, 9, 41-45.
- Lysenko, O. 1959. Report on diagnosis of bacteria isolated from insects (1954-1958). Entomophaga 4, 15-22.
- Magema N., C. Verstraeten & C. Gaspar 1981. Les ennemis naturels du scolyte *Trypodendron lineatum* (Olivier, 1795) (Coleopatra, Scolytidae) dans la forest de Hazeilles et des Epioux. Annales de la Societe Royale Zoologique de Belgique 111, 89-95.
- Markova, G. 2000. Pathogenicity of several entomogenous fungi to some of the most serious forest insect pests in Europe. IOBC/wprs Bulletin 23, 231-39.
- Matha V. & J. Weiser 1985. Effect of the fungus *Beauveria bassiana* on adult bark beetles *Ips typographus*. Conference Biological and Biotechnical Control of Forest Pests, Tabor (CSFR).
- Mills N.J. 1983. The natural enemies of scolytids infesting conifer bark in Europe in relation to the biological control of *Dendroctonus* spp. in Canada. CAB Biocontrol News and Information 4, 305-28.
- Moore G.E. 1971. Mortality Factors Caused by Pathogenic Bacteria and Fungi of the Southern Pine Beetle in North Carolina. Journal of Invertebrate Pathology 17, 28-37.
- Moore G.E. 1972. Microflora from the Alimentary Tract of Healthy Southern Pine Beetles, *Dendroctonus frontalis* (Scolytidae), and Their Possible Relationship to Pathogenicity. Journal of Invertebrate Pathology 19, 72-75.
- Müller-Kögler E. 1965. *Pilzkrankheiten bei Insekten*. P. Parey.
- Neuzilova A. 1956. Ein Beitrag zur Kenntnis der parasitischen Pilze bei *Ips typographus* L. Preslia 28, 273-75.
- Nierhaus-Wunderwald, D. 1993. Die natürlichen Gegenspieler der Borkenkäfer. Wald und Holz 1/93, 8-14.
- Novak V. 1960. Die natürlichen Feinde und Krankheiten des gemeinen Nutzholzborkenkäfers *Trypodendron lineatum* Oliv. Zoologicke Listy, Folia Zoologica IX (XXIII), 4, 309-22.
- Novak V. & A. Samsinsakova 1962. Les essais d'application du champignon parasite *Beauveria bassiana* (Bals.) Vuill. dans la lutte contre les parasites en agriculture et sylviculture en CSSR. Colloques Internationaux de Pathologie des Insectes, Paris, 133-35.
- Novotny J. & M. Turcani 2000. The results of experimental treatment of biopreparation on the basis of *Bacillus thuringiensis* var. *tenebrionis* Berl. for control of *Ips typographus* L. (Col., Scolytidae). Lesnický casopis (Forestry Journal) 46, 303-10.
- Nuorteva M. & M. Salonen 1968. Versuche mit *Beauveria bassiana* (Bals.) Vuill. gegen *Blastophagus piniperda* L. (Col., Scolytidae). Annales Entomologici Fennici 34, 49-55.
- Pehl L. & R. Kehr 1994. Biologische Bekämpfung von Borkenkäfern. Allgemeine Forst Zeitschrift 19, 1065-67.

- Pesson P., C. Toumonoff & C. Chararas 1955. Étude des épidémies bactériennes observées dans les élevages d'insectes xylophages. Annales Épiphyties 6, 315-28.
- Petch T. 1932. A list of the entomogenous fungi of Great Britain. Transactions of the British mycological Society 17, 170-78.
- Postner M. 1974. Scolytidae (=Ipidae), Borkenkäfer. In: *Die Forstschädlinge Europas*, Bd. 2, W. Schwenke (Ed), P. Parey.
- Prazak R. 1988. Die Wirkung des insektenpathogenen Pilzes *Beauveria bassiana* (Bals.) Vuill. auf den Gestreiften Nutzholzborkenkäfer *Trypodendron lineatum* Oliv. (Coleoptera: Scolytidae). PhD thesis, Universität für Bodenkultur Wien.
- Prazak R. 1991. Studies on indirect infection of *Trypodendron lineatum* Oliv. with *Beauveria bassiana* (Bals.) Vuill. Journal of Applied Entomology 111, 431-41.
- Prazak R. 1997. Laboratory evaluation of *Beauveria bassiana* (Bals.) Vuill. (Deuteromycotina: Hyphomycetes) against *Trypodendron lineatum* Oliv. (Coleoptera: Scolytidae). Journal of Plant Diseases and Protection 104, 459-65.
- Pultar O. & J. Weiser 1999. Infection of *Ips typographus* with entomopoxvirus in the forest. Poster at 7th IOBC/wprs meeting in Vienna.
- Purrini K. 1975. Zur Kenntnis der Krankheiten des Großen Ulmensplintkäfers, *Scolytus scolyti* F. im Gebiet von Kosovo, Jugoslawien. Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz 48, 154-56.
- Purrini K. 1977. Über eine neue Schizogregarinen-Krankheit der Gattung *Mattesia* Naville (Sporozoa, Dischizae) des Zottigen Fichtenborkenkäfers, *Dryocoetes autographus* Ratz (Coleoptera, Scolytidae). Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz 50, 132-35.
- Purrini K. 1978a. Über *Malamoeba locustae* King and Taylor (Protozoa, Rhizopoda, Amoebidae) beim Zottigen Fichtenborkenkäfer, *Dryocoetes autographus* Ratz (Col.: Scolytidae). Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz 51, 139-41.
- Purrini K. 1978b. Protozoen als Krankheitserreger bei einigen Borkenkäferarten (Col., Scolytidae) im Königsee-Gebiet, Oberbayern. Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz 51, 171-75.
- Purrini K. 1980. *Malamoeba scolyti* sp.n. (Amoebidae, Rhizopoda, Protozoa) parasitizing the bark beetles *Dryocoetes autographus* Ratz. and *Hylurgops palliatus* Gyll. (Scolytidae, Col.). Archiv für Protistenkunde 123, 358-66.
- Purrini K. & E. Führer 1979. Experimentelle Infektion von *Pityogenes chalcographus* L. (Col.: Scolytidae) durch *Malamoeba scolyti* Purrini (Amoebina, Amoebidae) und *Menzbieria chalcographi* Weiser (Neogregarina, Ophryocystidae). Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz 52, 167-73.
- Purrini K. & R. Ormieres 1981. On three new sporozoan parasites of bark beetles (Scolytidae, Coleoptera). Zeitschrift für angewandte Entomologie 91, 67-74.
- Purrini K. & J. Halperin 1982. *Nosema calcarati* n.sp. (Microsporidia), a new parasite of *Pityogenes calcaratus* Eichhoff (Col., Scolytidae). Zeitschrift für angewandte Entomologie 94, 87-92.
- Purrini K. & J. Weiser 1984. Light- and electron microscopic studies of *Chytridiopsis typographi* (Weiser 1954) Weiser 1970 (Microspora), parasitizing the bark beetle *Hylastes cunicularius* Er. Zoologischer Anzeiger, Jena 212, 369-76.
- Purrini K. & J. Weiser 1985. Ultrastructural study of the microsporidian *Chytridiopsis typographi* (Chytridiopsida: Microspora) infecting the bark beetle *Ips typographus* (Scolytidae: Coleoptera), with new data on spore dimorphism. Journal of Invertebrate Pathology 45, 66-74.
- Purrini K. & Z. Zizka 1983. More on the life cycle of *Malamoeba scolyti* (Amoebidae: Sarcomastigophora) parasitizing the bark beetle *Dryocoetes autographus* (Scolytidae, Coleoptera). Journal of Invertebrate Pathology 42, 96-105.
- Schvester D. 1957. Contribution à l'étude écologique des Coléoptères Scolytides. Essai d'analyse des facteurs de fluctuation des populatins chez *Ruguluscolytus rugulosus* Müller 1818. Annales Epiphyties, Paris, 8 np. Hors ser.
- Siemaszko W. 1939. Fungi associated with bark beetles in Poland. Planta Polonica 7, 1-54.
- Sikorowski P.P., A.M. Lawrence, T.E. Nebeker & T.S. Price 1996. Virus and Virus-like Particles Found in Southern Pine Beetle Adults in Mississippi and Georgia. Mississippi Agricultural & Forestry Experiment Station Technical Bulletin 212, 1-9.

- Skuhravy V. 2002. *Lykozrout smrkovy a jeho kalamity* (The Norway spruce bark beetle and its outbreaks). Agrospoj, Praha.
- Sprague V. 1977. Annotated list of species of microsporidia. (p. 31-334). The zoological distribution of microsporidia. (p. 335-385). In: *Comparative Pathobiology, Vol. 2, Systematics of microsporidia*. L.A. Bulla, T.C. Cheng (Eds.) Plenum Press.
- Stephen F.M., C.W. Berisford, D.L. Dahlsten, P. Fenn & J.C. Moser 1993. Invertebrate and Microbial Associates. In: *Beetle-Pathogen Interactions in Conifer Forests*, T.D. Schowalter, G.M. Filip (Ed), Academic Press.
- Tanada Y. & H.K. Kaya 1993. *Insect pathology*. Academic Press.
- Tang X. & M. Fan 1990. Study on DNA and polypeptides of a smallpox virus in *Dendroctonus armandi* Tsai et Li. *Microbiology of Insects* Beijing 17, 258-61.
- Theodorides J. 1960. Parasites et phoretiques de coleopteres et de myriapodes de Richelieu (Indre-et-Loire). *Annales de Parasitologie* XXXV, 488-581.
- Tomalak M., H.E. Welch & T.D. Galloway 1988. Interaction of Parasitic Nematode *Parasitaphelenchus oldhami* (Nematoda: Aphelenchoidae) and a Bacterium in Dutch Elm Disease Vector, *Hyllurgopinus rufipes* (Coleoptera: Scolytidae). *Journal of Invertebrate Pathology* 52, 301-08.
- Vaupel O. & G. Zimmermann 1996. Orientierende Versuche zur Kombination von Pheromonfallen mit dem insektenpathogenen Pilz *Beauveria bassiana* (Bals.) Vuill. gegen die Borkenkäferart *Ips typographus* L. (Col., Scolytidae). *Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz* 69, 175-79.
- Wegensteiner R. 1992. Untersuchungen zur Wirkung von *Beauveria*-Arten auf *Ips typographus* (Coleoptera, Scolytidae). Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie 8, 104-06.
- Wegensteiner R. 1994. *Chytridiopsis typographi* (Protozoa, Microsporidia) and other pathogens in *Ips typographus* (Coleoptera, Scolytidae). IOBC/wprs Bulletin Vol. 17 (3), 39-42.
- Wegensteiner R. 1996. Laboratory evaluation of *Beauveria bassiana* (Bals.) Vuill. against *Ips typographus* (Coleoptera, Scolytidae). IOBC/wprs -Bulletin 19 (9), 186-89.
- Wegensteiner R. 2000. Laboratory evaluation of *Beauveria bassiana* (Bals.) Vuill. and *Beauveria bronniartii* (Sacc.) Petch against the four eyed spruce bark beetle, *Polygraphus poligraphus* (L.). (Coleopatra, Scolytidae). IOBC/wprs Bulletin 23 (2), 161-66.
- Wegensteiner R. & J. Weiser 1995. A new Entomopoxvirus in the bark beetle *Ips typographus* (Coleoptera: Scolytidae). *Journal of Invertebrate Pathology* 65, 203-05.
- Wegensteiner R. & J. Weiser 1996a. Untersuchungen zum Auftreten von Pathogenen bei *Ips typographus* (Coleoptera, Scolytidae) aus einem Naturschutzgebiet im Schwarzwald (Baden-Württemberg). *Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz* 69, 162-67.
- Wegensteiner R. & J. Weiser 1996b. Occurrence of *Chytridiopsis typographi* (Microspora, Chytridiopsida) in *Ips typographus* L. (Coleoptera, Scolytidae) field populations and in a laboratory stock. *Journal of Applied Entomology* 120, 595-602.
- Wegensteiner R. & J. Weiser 1998. Infection of *Ips typographus* from Finland with the Ascomycete *Metschnikowia cf. bicuspidata*. Poster, 6th European Congress of Entomology, Ceske Budejovice, CR, 23.-29.08.1998, Abstracts vol. 2, 667.
- Wegensteiner R., J. Weiser & E. Führer 1996. Observations on the occurrence of pathogens in the bark beetle *Ips typographus* L. (Coleoptera, Scolytidae). *Journal of Applied Entomology* 120, 199-204.
- Weiser J. 1954a. Beitrag zur Kenntnis der Parasiten des Borkenkäfers *Ips typographus*. I. *Vestnik Ceskoslovenske Zoologicke Spolecnosti* (Acta Societatis Zoologicae Bohemosloveniae; Transactions of the Czechoslovak Zoological Society) 18, 217-27.
- Weiser J. 1954b. Príspovek k systematizaci Schizogregarin. *Ceskoslovenske Parasitologie* 1, 179-212.
- Weiser J. 1955. Beitrag zur Kenntnis der Parasiten des Borkenkäfers *Ips typographus*. II. *Vestnik Ceskoslovenske Zoologicke Spolecnosti* (Acta Societatis Zoologicae Bohemosloveniae; Transactions of the Czechoslovak Zoological Society) 19, 374-80.
- Weiser J. 1961a. *Die Mikrosporidien als Parasiten der Insekten*. Monographien zur angewandten Entomologie 17, P. Parey, Hamburg und Berlin.
- Weiser J. 1961b. A new microsporidian from the bark beetle *Pityokteines curvidens* Germar (Col. Scolytidae) in Czechoslovakia. *Journal of Insect Pathology* 3, 324-29.
- Weiser J. 1966. *Nemoci hmyzu*. Academia Prag.

- Weiser J. 1968. *Plistophora scolyti* sp.n. (Protozoa, Microsporidia) a new parasite of *Scolytus scolytus* F. (Col., Scolytidae). *Folia Parasitologica* 15, 11-14.
- Weiser J. 1970. Three new pathogens of the Douglas Fir Beetle, *Dendroctonus pseudotsugae*: *Nosema dendroctoni* n.sp., *Ophryocystis dendroctoni* n.sp. and *Chytridiopsis typographi* n.comb. *Journal of Invertebrate Pathology* 16, 436-41.
- Weiser J. 1977. *An Atlas of Insect Diseases*. 2nd ed. Academia, Prague
- Weiser J. & R. Wegensteiner 1994. A new Entomopoxvirus in the bark beetle *Ips typographus* (Coleoptera, Scolytidae) in Czechoslovakia. *Zeitschrift für angewandte Zoologie* 80, 425-34.
- Weiser J., R. Wegensteiner & Z. Zizka 1995. *Canningia spinidentis* gen. et sp.n. (Protista: Microspora), a new pathogen of the fir bark beetle *Pityokteines spinidens*. *Folia Parasitologica* 42, 1-10.
- Weiser J., R. Wegensteiner & Z. Zizka 1997. Ultrastructures of *Nosema typographi* Weiser 1955 (Microspora: Nosematidae) of the bark beetle *Ips typographus* (Coleoptera: Scolytidae). *Journal of Invertebrate Pathology* 70, 156-60.
- Weiser J., R. Wegensteiner & Z. Zizka 1998. *Unikaryon montanum* sp.n., (Protista, Microspora), a new pathogen of the spruce bark beetle, *Ips typographus* (Coleoptera: Scolytidae). *Folia Parasitologica* 45, 191-95.
- Weiser J., U. Händel, R. Wegensteiner & Z. Zizka 2002. *Unikaryon polygraphi* sp.n. (Protista: Microspora), a new pathogen of the four-eyed spruce bark beetle, *Polygraphus poligraphus* (Col., Scolytidae). *Journal of Applied Entomology* 126, 148-54.
- Weiser J., R. Wegensteiner, U. Händel & Z. Zizka 2003. Infections with the Ascomycete *Metschnikowia typographi* n.sp. in the bark beetle *Ips typographus* and *Ips amitinus* (Col., Scolytidae.). *Folia Microbiologica* 47, (in press).
- Wood D.L. 1961. The occurrence of *Serratia marcescens* Bizio in laboratory populations of *Ips confusus* (LeConte) (Coleoptera, Scolytidae). *Journal of Insect Pathology* 3, 330-31.
- Wulf A. 1979. Der insektenpathogene Pilz *Beauveria bassiana* (Bals.) Vuill. als Krankheitserreger des Kupferstechers *Pityogenes chalcographus* L. (Col., Scolytidae). PhD thesis, Georg-August-Universität Göttingen.
- Wulf A. 1983. Untersuchungen über den insektenpathogenen Pilz *Beauveria bassiana* (Bals.) Vuill. als Parasit des Borkenkäfers *Pityogenes chalcographus* L. (Col., Scolytidae). *Zeitschrift für angewandte Entomologie* 95, 34-46.
- Zitterer P.M. 2002. Antagonists of *Ips acuminatus* (Gyllenhall) with special consideration of pathogens. Diploma thesis, Universität für Bodenkultur Wien.
- Zizka Z., J. Weiser & R. Wegensteiner 1997. Ultrastructures of Oocysts of *Mattesia* sp. in *Ips typographus*. *Journal of Eukaryotic Microbiology* 44, 25A, no. 98.
- Zizka Z., J. Weiser & R. Wegensteiner 1998. Ultrastructures of syzygies and gametocysts of *Mattesia* sp. in the bark beetle *Ips typographus*. *Journal of Eukaryotic Microbiology* 45, 8A, no. 42.
- Zizka Z., J. Weiser & R. Wegensteiner 2001. Ultrastructures of the Entomopoxvirus Ab in the bark beetle *Ips typographus*. In: Cells III., ed.: J. Berger, Kopp Publ., Ceske Budejovice, 214-15.

Part 2

Bark Weevils

Chapter 13

TAXONOMY AND SYSTEMATICS OF BARK WEEVILS

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1. RECENT STATUS OF THE FAMILY CURCULIONIDAE

The family Curculionidae includes the majority of species described from the Curculionoidea and it can be considered as the most derived taxonomic group of the super-family which is also part of the most derived group among the Coleoptera. During the second half of the last century, the concept of the Curculionidae family changed with Crowson (1955) including a large number of taxa which are now omitted from the group ; however he first formally mentioned the Scolytidae and Platypodidae as sub-families. Later on, the use of cladistic methods further clarified relationships between different groups of weevils.

Entire groups were then separated from the Curculionidae. It was the case for the Dryophthoridae (=Rhynchophoridae) (Morimoto, 1962a, 1962b, 1976), and the Ithyiceridae that form a monospecific group (Morimoto, 1976; Sanborne, 1981). After a study using the male genitalia, the Erirhinidae, Brachyceridae, Cryptolaryngidae and Raymondionymidae were separated from the Curculionidae Thompson, 1992). At the present time, only species that present male genitalia with a gonatocera type are considered as Curculionidae. In the Curculionidae *sensu stricto*, males have a manubrium which is smaller than the spiculum gastrale. If the spiculum gastrale is absent, then the rostrum is also absent. The Platypodinae do not follow this pattern because in this group, the sclerification of genitalia is very thin and the spiculum gastrale is not visible. This new way of looking at Curculionidae has been used by Alonso-Zarazaga and Lyal (1999) in their world catalogue of families and genera of Curculionoidea.

2. EXTERNAL MORPHOLOGY

A fundamental feature of the Curculionidae is the absence of specific external characters and the only apomorphism that allows definition of the Curculionidae clade is based on a single character of the male genitalia. However, the Curculionidae have a very unique shape.

The head is produced into a rostrum of very variable length and form. It can be long and pointed in the genus *Curculio* or short and wide in the *Otiorrhynchus*. The rostrum can be turned-down on the prosternum in the Cryptorhynchinae. The antennae are located on the rostrum and are geniculate after the scape and have a variable number of articles between 9 and 11. Eyes are present except for the *Torneuma* that live in the soil or in cavities or caves.

The thorax: the prothorax is variable and can present a furrow to screen the rostrum. The mesothorax is also variable with a scutellum which can be visible or not and the elytra that are dorsally attached to this segment. The metathorax is hidden by the elytra and the membranous wings are attached to it. Its ventral part shows furrows that can vary according to the sex. Legs are also variable and tarsi are usually cryptopentamere with four visible articles.

The abdomen consists of 9 segments with segments 8 and 9 modified and forming the sclerified parts of the sexual organs. On the dorsal part, 7 segments are visible under the elytra. On the ventral part, only 5 segments are visible, the two missing segments being reduced and included in the metathorax. The first two visible segments are more or less joined.

3. INTERNAL MORPHOLOGY

The digestive system is divided into three parts: the stomodeum with the oesophagus including the crop and the proventricule, the mesenteron and the proctodeum. The mesenteron often shelters symbiotic bacteria that have a cellulolytic role (Buchner, 1933). The proctodeum is connected to the excretory system which is composed of the Malpighian tubules. There are six Malpighian tubules in the Curculionidae. The classic respiratory system is composed of tracheae with access to the environment through spiracles located on the thorax and the abdomen. The circulatory system does not show real vessels and the « blood » fills up the general cavity and is put in motion by a dorsal propulsive vessel. The nervous system is divided into a central, a visceral and a peripheral system (Hoffmann 1950). The central system is formed by a brain composed of three pairs of ganglia that innervate the eyes, the antennae and the labrum and a double chain of ventral ganglia. The visceral system includes dorsal ganglia that innervate the dorsal vessel, the genitalia and the spiracles. The peripheral nervous system consists of hypodermic cells located at the base of sensory hairs that cover the tegument. The muscles are well developed and complex. Cephalic and thoracic muscles connected with mandibles for the first and legs and wings for the second are very strong. There are also muscles in the abdomen that are used during oviposition. Male genitalcopulatory sacs are composed of two testicles,

the accessory glands, the *vas deferens*, the seminal vesicles, the ejaculatory duct and the *aedeagus* with the *spiculum gastrale*, tegmen and penis. Female genitals include ovaries, acrotrophic ovarioles, the oviduct, the copulatory sac, the spermatheca, the uterus, the vagina and the genitalia (ovipositor, *spiculum ventrale* and 8th abdominal tergite).

4. PHYLOGENETIC ANALYSIS

Most recent works on the phylogeny of Curculionidae (Farell *et al.* 2002 ; Marvaldi *et al.* .2002) using molecular analysis and new morphological data (larval characters, internal morphology) and including a large number of samples of Curculionidae in the analysis, show a weak resolution of the relationships within the family.

For instance, it is not certain that the traditional Adelognatha and Phanerognatha groups are monophyletic (Marvaldi, 1997).

The species of weevils listed as BAWBILT (Bark and Wood Boring Insects in Living Trees) belong to the family Curculionidae. Recent work on the phylogenetic relationships in weevils (Wink *et al.*, 1997) mentions the two subfamily groups Adelognatha and Phanerognatha for the species of Curculionidae. They have male genitalia of the gonatocere type. Those species belong to the following six subfamilies Cossoninae Schoenherr 1825 (genus *Brachytemnus*), Cryptorhynchinae Schoenherr 1825 (genus *Cryptorhynchus*), Curculioninae Latreille 1802 (genus *Anthonomus*), Mesoptiliinae Lacordaire 1863 (genus *Magdalais*) and Molytinae Schoenherr 1823 (genera *Hylobius*, *Pissodes*, *Trachodes*) for the Phanerognatha clade and Entiminae Schoenherr 1823 (genus *Otiorrhynchus*, *Strophosoma*) for the Adelognatha clade (Lacordaire 1866). This last group is probably monophyletic with several synapomorphies based on larval characters (Marvaldi, 1997) as well as molecular characters (Wink *et al.*, 1997) or a combination of both (Marvaldi *et al.*, 2002). It is one the subfamilies of Curculionidae which is strongly supported phylogenetically.

Curculioninae and Hylobiinae are heterogenous groups and their position in the Curculionidae is not yet resolved.

The following status for the list of species could be proposed as below:

- Adelognatha

- Subfamily: Entiminae Schoenherr 1823

- Tribe: Otiorrhynchini Schoenherr 1826

- Genus: *Otiorrhynchus* Germar 1822 (type species:*Curculio rhacusensis* Germar 1822)

- Synonymies: *Pachygaster* Germar, 1817 non Meigen,1803;

Loborhynchus Dejean, 1821; *Panaphilis* Dejean,1821;

Loborhynchus Schoenherr, 1823 non Dejean, 1821 ;

Otiorrhynchus Germar, 1824 non Germar, 1822.

- Sub-genera: *Otiorrhynchus* (s.st.) Germar 1824

Dorymerus Seidlitz, 1890

Tourniera Stierlin, 1861

Postaremus Reitter, 1912

- Species:

- *O. (s.st.) arcticus* Germar 1824

- Synonymy: *O. (s.st.) monticola* Germar 1824

- *O. (s.st.) niger* Fab. 1775

- *O. (Postaremus) nodosus* MÅller 1764

- Synonymy: *O. dubius* Strîm, 1783; the name *dubius* is still valid.

It is now among the sub-genus (*Postaremus*) Reitter, 1912.

- *O. (Tourniera) ovatus* L. 1758

- *O. (Dorymerus) singularis* L. 1767

- Tribe: Brachyderini Schoenherr, 1826

- Genus: *Strophosomus* Schoenherr, 1823 (type species: *Curculio melanogrammus* Forster, 1771). *Strophosomus* is not the valid name for this species and *Strophosoma* Bilberg, 1820 must be used.

- Synonymies: *Judolus* Dejean, 1821; *Strophosomus* Schoenherr, 1823; *Bryssus* Dejean, 1821; *Strophosomum* Gistel, 1856.

- Species:

- *S. (s.st.) melanogramma* Forster 1771

- Synonymies: *S. (s.st.) coryli* F., 1775; *S. (s.st.) illibata*

Boh., 1833; *S. (s.st.) obesa* Thoms., 1868 non Marsham,

1802; *S. (s.st.) fagi* Chevrolat, 1865.

- Species:

- *S. (s.st.) capitata* De Geer 1775

- Synonymies: *S. (s.st.) obesa* (Marsham, 1802); *S. (s.st.) coryli* Boh. 1840 non Fabricius 1775; *S. (s.st.) fulvicornis* Walton, 1846; *S. (s.st.) desbrochersi* Tournier, 1876; *S. (s.st.) grisea* Tournier, 1876

- Phanerognatha

- Subfamily: Cossoninae Schoenherr, 1825

- Tribe: Onycholipini Wollaston, 1873

- Genus: *Brachytemnus* Wollaston, 1873 (type species: *Rhyncolus porcatus* Germar, 1824).

- Species:

- *B. porcatus* Germar, 1824

- Tribe: Rhyncolini Gistel, 1856

- Species:

- *R. (s.st.) ater* (Linnaeus, 1758)

- Subfamily: Cryptorhynchinae Schoenherr, 1825

- Tribe: Cryptorhynchini Schoenherr, 1825

- Genus: *Cryptorhynchus* Illiger, 1807 (type species: *Curculio lapathi*

Linnaeus, 1758

- Synomynies: *Aracnipus* Dejean, 1821; *Arachnipes* Villa & Villa, 1833; *Cryptorhynchidius* Pierce, 1919; *Eupterus* Fiedler, 1941; *Cryptorrhynchobius* Voss, 1965

- Species:

- *C. lapathi* Linnaeus, 1758

- Subfamily: Curculioninae Latreille, 1802

- Tribe: Anthonomini Thomson, 1859

- Genus: *Furcipes* Bedel, 1884 (type species: *Curculio rectirostris* Linnaeus, 1758). This name is not valid. It is a replacing name for the genus *Furcipes* Desbrochers, 1868 which is valid. *Furcipes* Bedel is then a synonym of *Furcipes* Desbrochers which has a priority as being older. *Furcipes* is a subgenus of the genus *Anthonomus* Germar, 1817.

- Genus: *Anthonomus* Germar, 1817

- Synomyny: (*Furcipes*) Bedel, 1884

- Species:

- *A. rectirostris* L., 1758

- Subfamily: Mesoptiliinae Lacordaire, 1863

- Tribe: Magdalini Pascoe, 1870

- Genus: *Magdalalis* Germar 1817 (type species: *Curculio violaceus* L., 1758)

- Subgenera: - *Magdalalis* Germar, 1817

- *Aika* Barrios, 1984

- *Dagmalis* Kino & Morimoto, 1960

- *Edo* Germar, 1819

- *Laemosaccidius* Smreczynski 1972

- *Odontomagdalalis* Barrios, 1984

- *Panopsis* Daniel, 1903

- *Panus* Schoenherr, 1823

- *Porrothus* Dejean, 1821

- Synomynies: *Thamnophilus* Schoenherr, 1823; *Magdalinus* Germar, 1843; *Scaradamycetes* Gistel, 1848.

- Species:

- *M. violaceus* L., 1758.

- Subfamily: Molytinae Schoenherr 1823

- Tribe: Hylobiini Kirby, 1837

- Sub-tribe: Hylobiina Kirby, 1837

- Genus: *Hylobius* Germar, 1817 (type species: *Curculio piceus* De Geer, 1875)

- Subgenera: - *Hylobius* Germar, 1817

- Synonymy: *Hypomolyx* LeConte, 1876,

- *Callirus* Dejean, 1821 (type species: *Curculio abietis* L., 1758)
 - Synomynies: *Hylobitelus* Reitter, 1923; *Polyaunbus* Kino, 1934.
 - Species:
 - *H. abietis* L.1758
 - *H. pinastri* Gyll.1813
- Tribe: *Pissodini* Gistel, 1856
- Sub-tribe: *Pissodina* Gistel, 1856
 - Genus: *Pissodes* Germar, 1817 (type species: *Curculio pini* L.1758)
 - Synonymy: *Piniphilus* Dejean, 1821
 - Subgenera: *Pissodes* Germar, 1817 *Epipissodes* Voss, 1956
 - Species:
 - *P. castaneus* (DeGeer, 1775)
 - *P. harcyniae* (Herbst, 1795)
 - *P. piceae* (Illiger, 1807)
 - *P. pini* (L.1758)
 - *P. piniphilus* (Herst.1797)
 - *P. scabricollis* Miller, 1859
- Tribe: *Acicnemidini* Lacordaire, 1866
 - Genus: *Trachodes* Germar, 1824 (type species: *Curculio squamifer* Paykull, 1800)
 - Synonymies: *Blastophila* Gistel, 1856; *Metrachodes* Marshall, 1948
 - Subgenera: - *Trachodes* Germar, 1824
 - Species:
 - *T. hispidus* (L., 1758)
 - *Atrachodes* Morimoto, 1962

The names and synonymies of the species as well as the names of authors together with the dates have to be clearly and carefully mentioned and identified in order to avoid any misinterpretation as recently observed in evolutionary works on bark beetles (Kelley *et al.*, 1999).

5. GEOGRAPHICAL DISTRIBUTION

With 9 genera and 22 species, the BAWBILT weevils are among the largest beetle families recorded in Europe. The geographical distribution of most species has not been fully covered and information is fragmentary for the majority of them.

5.1. *Adelognatha*

5.1.1. Genus *Otiorrhynchus*:

This is one of the largest weevil genera in Europe and it is represented in the BAWBILT list with 5 species.

O. (s.st.) arcticus is known to be a subalpine or alpine species with records from the Pyrenees and the Massif Central (Hoffmann, 1958). Adult weevils live under mosses and stones and the larvae feed on the roots of various herbaceous plants and sometimes on the roots of young seedlings as recently mentioned on larch in Iceland (Halldorsson *et al.*, 2000).

O. (s.st.) niger and *O. (Postaremus) nodosus* are mentioned as pests in forest nurseries, specially on spruce and pine seedlings in central and eastern Europe and in Sicily (Hoffmann, 1958). More recently *O. (s.st.) niger* has been recorded in northern Europe (Lunderstadt, 1981) while *O. (Postaremus) nodosus* was causing problems to natural regenerations of Scots pine in Lapland (Suoheimo, 1984).

O. (Tourniera) ovatus is also a pest of forest nurseries. This species is polyphagous and widely distributed throughout Europe and present in North America. Damage has been mentioned in the past on spruce plantations and in forest nurseries in Czechoslovakia (Srot, 1979) and in the German Democratic Republic (Bogs and Braaschd, 1988). Adult weevils feed on flowers of various plants.

O. (Dorymerus) singularis larvae are rhizophagous (Schauermann, 1977). Adult weevils are polyphagous and feed on beech, alder, walnut, spruce, pines. This species is recorded from western and Central Europe, in Baden-Wurtemberg for instance where it has damaged young oak and lime plantations (Bogenschutz, 1982).

5.1.2. Genus *Strophosoma*:

There are 6 species in Europe all parthenogenetic. Two of them are harmful to forestry.

The larvae of *S. melanogramma* feed on roots of various herbaceous plants and also on beech and oak while the adults feed on leaves, shoots and buds of various plants including oak, walnut, maple, hawthorn, pine.

Recent damage has been recorded in forest nurseries and reforestation sites, in the UK (Parry, 1983; Parry *et al.*, 1990; Stork *et al.*, 2001), but also in southern Sweden on beech, oak and Norway spruce (Lif, 2000; Prieme *et al.*, 2000), in the mountain regions of Germany (Biernath *et al.*, 1996), in central France (Lemperiere pers obs.). Outbreaks of the weevil were mentioned in the Czech Republic in 1995 on beech, Norway spruce and *Sorbus aucuparia* (Urban, 1995).

The larvae of *S. capitata* feed on the roots of heather and ericaceous plants and the adults on oak, beech, arbutus, hornbeam.

Damage is recorded from central France on oak (Rougon *et al.*, 1995), from Norway on Scots pine planted after forest fires (Solbraa, 1983). In Poland, several observations mention damage on young Scots pines (Szmidt and Stachowiak, 1980, Stachowiak, 1991, 1992) but also on hazelnuts (Gantner, 2001) and birch plantations (Korcynski, 2001).

5.2. *Phanerognatha*

5.2.1. Genus *Brachytemnus*

Adults and larvae of *B. porcatus* live on firs, spruces and pines like *Pinus maritima*, *P. laricio*, *P. halepensis* of the Mediterranean area. The insect is also mentioned from central Europe (Hoffmann, 1958).

5.2.2. Genus *Cryptorhynchus*

The poplar weevil *C. lapathi* is the only species of the genus in northern and central Europe. It is also found in Siberia and Japan (Hoffmann, 1958).

Larvae and adults live in the wood of Salicaceae and Betulaceae : *Salix caprea*, *S. viminalis*, *S. purpurea*, *S. triandra*, *S. fragilis* ; *Populus alba*, *P. canadensis*, *P. virginiana*, *P. nigra*, *P. tremula*.

Adults feed on the bark while larvae tunnel in the inner bark. Damage is recorded on young trees as well as mature stands all over Europe with records from Italy on poplars (Allegro 1989, 1990, 1997; Arru, 1977; Cavalcaselle and Allegro, 1986; Giorcelli and Allegro, 1999; Lapietra and Allegro, 1987, 1990; Montermini *et al.*, 1998; Pollini, 1990; Verenini, 1984), from Spain on *Salix* (Anton, 1979; Sabate and Rojo, 1982), from south-east and south-west France on poplar plantations (Attard, 1978, 1979), from Croatia (Jodal, 1987) and Hungary (Prenner *et al.*, 1983; Szontagh, 1985). In central Europe the weevil is more polyphagous with records on *Salix* in Poland (Czerniakowski, 2001) and southern Russia (Maksimenko *et al.*, 2001) on *Alnus* (Chlodny, 1982) in Poland and on Norway spruce in Czechoslovakia (Kristek, 1989). In the north west of Europe the weevil was observed on poplar in the Netherlands (Moraal, 1996) and *Salix viminalis* in Ireland (Neeman and Kennedy, 1989).

5.2.3. Genus *Anthonomus*

A. rectirostris is found in northern and central Europe and also found in Siberia and Japan. Larvae feed in the kernel of many wild and cultivated cherry trees : *Cerasus padus*, *C. avium*, *C. vulgaris* (Holighaus and Dahlbender, 1995).

5.2.4. Genus *Magdalisa*

M. violaceus is known from Central and 'boreal' Europe, Switzerland, the Italian Alps and Belgium and live on *Picea excelsa* and *Abies pectinata*. It could be considered as a saproxylic weevil as living on dying or dead trees and/or dead parts of trees (branches).

Pupal chambers penetrate deep in the wood as in *Pissodes* species (Hoffmann, 1958).

5.2.5. Genus *Hylobius*

Of the four species of the genus found in Europe, *H. abietis* and the somewhat smaller *H. pinastri* are very hard to tell apart. They feed on the cambium and bark of many conifers. *H. abietis* is very common in Europe from Siberia to northern Spain and its distribution and spread are referred to sylvicultural practices (clear cuttings and reforestation programmes). It is considered as the worst pest of young conifers. There are numerous records of the presence of the insect in its distribution zone,

from Siberia (Gourov, 1994), Russia (Charitonova, 1965, Lur'e, 1966), the nordic countries (Bejer-Petersen *et al.*, 1962), including Norway (Christiansen 1971), Sweden (Eidmann, 1964 , 1971, 1981; Langström, 1982; Nordenhem, 1989), Finland (Langström, 1985), Eastern Europe including Bulgaria (Cankov, 1970), the Czech Republic (Zumr and Stary, 1994), Poland (Sierpinski, 1972; Szmidt and Korczynski, 1983) , the north west of Europe with the Netherlands (Elton, 1964), the United Kingdom (Stoakley, 1968; Bevan, 1987), Belgium (Nef, 1992), France (Hoffmann, 1958; Malphettes, 1966),

H.pinastri is less abundant and has a more Nordic distribution (Eidmann, 1974, Lindelow *et al.*, 1993; Langström, 1982). *H.piceus* is observed on larch and Scots pine, in Siberia, northern Europe, (Eidmann, 1974; Langström, 1982). This rare species is known from the Alps in the region of the Queyras (Lemperiére, pers. obs.).

5.2.6. Genus *Pissodes*

The genus is represented by 8 species in Europe. This genus comprises some forestry pests.

P.castaneus is known from southern France (Lieutier *et al.*, 1997), Turkey (Tozlu, 2001), Moldova (Poiras, 1991) and Russia (Kulinich and Orlinskii, 1998) on different pine species as a secondary pest.

P.harcyniae was recorded as a secondary pest on *Pinus silvestris*, *Picea excelsa*, *Abies pectinata*. It is mentioned as rare in eastern and southern France (Hoffmann, 1954) but is more common in central Europe (Kula and Zabecki, 1997, 2000).

P.piceae lives on silver firs and sometimes on spruce and is primarily a montane species. It is common in all the mountains of continental Europe where it can cause damages on ailing and weaken trees. It is mentioned in Italy (Tiberi, 1997, Moriondo and Tiberi, 2000), in the eastern part of the Carpathian mountains in Romania (Simionescu, 1995; Simionescu *et al.*, 1998), in Poland (Podlaski, 1996, 2002; Starzyk, 1996), in Bulgaria (Tsankov, 1994) and central France (Lemperiére, 1987).

P.pini is common in central and southern Europe, in the Alps on Scots pines where it feeds on the top of trees. It is also mentioned on *Pinus uncinata* in the Pyrenees (Hoffmann 1954) and in Germany (Habermann and Geibler, 2001)

P.piniphilus is known from central Europe, in Germany (Habermann and Geibler, 2001), in Austria (Cecht and Tomiczek, 1996), in Poland (Kurowska and Falencka-Jablonska, 1994, Witrylak, 1995) and northern Europe, in Estonia (Luik, 1994; Voolma, 2001), Finland (Pappinen and Weissenberg, 1996) and also Russia and Siberia (Bogdanova, 1998; Demakov, 1994, 1996, 1998; Maslov *et al.*, 1999) on Scots pine and *Abies nordmanniana*. The insect develops on dying trees (Karoles, 1992) and is considered as rare in France (Hoffmann, 1954).

P.scabricollis is known as a secondary pest on spruce in central Europe (Oppermann, 1985).

5.2.7. Genus *Trachodes*

This genus holds half a dozen of not very well known species. *T. hispidus* lives in the thin and dry branches of oak, beech and birch. They are recorded from Northern Europe, Switzerland and Belgium (Hoffmann 1958).

REFERENCES

- Allegro, G. 1989. La difesa contro gli insetti parassiti del pioppo: un aggiornamento tecnico. *Informatore Agrario*, 45, 93-96.
- Allegro, G. 1990. Lotta meccanica contro i principali insetti xilofagi del pioppo mediante impiego di sbarramenti sui tronchi. *Informatore Agrario*, 46, 91-95.
- Allegro, G. 1997. Conoscere e combattere il punteruolo del pioppo *Cryptorhynchus lapathi* L.). Sherwood - Foreste ed Alberi Oggi, 3, 33-38.
- Alonso-Zarazaga, M. & Lyal, C.H.C. 1999. *A world catalogue of families and genera of Curculionoidea (Insecta: Coleoptera) (excepting Scolytidae and Platypodidae)*. Barcelona: Entomopraxis.
- Arru, G.M. 1977. *Populus deltoides* Bartr. and insect problems in Italy. In: *Symposium on Eastern Cottonwood and Related Species*, B.A. Thielges and S.B. Land (Eds.). Baton Rouge, La. (USA). Louisiana State University and Agricultural and Mechanical College. Division of Continuing Education.
- Attard, G. 1979. Principales insectos del chopo en el sureste de Francia. *Boletin del Servicio de Defensa contra Plagas e Inspección Fitopatológica*, 5, 25-29.
- Bejer-Petersen, B., Jutinen, P., Kangas, E., Bakke, A., Butovitsch, B., Eidmann, H.H., Hedqvist, K.-J. & Lekander, B. 1962. Studies on *Hylobius abietis* L. - Development and life cycle in the Nordic countries. *Acta Entomologica Fennica*, 17, 6-106.
- Bejer-Petersen, B. 1975. Length of development and survival of *Hylobius abietis* as influenced by silvicultural exposure to sun light. *Kongelige Veterinaer og Landbohøjskole*, 111-20.
- Biernath, M., Messing, M., Pohris, V. & Lunderstadt, J. 1996. Arthropoden an Jungbuchen (*Fagus sylvatica* L.) in Naturverjüngungen und Voranbauten des Erzgebirges und des Harzes. In: *Schriften aus der Forstlichen Fakultät der Universität Göttingen und der Niedersächsischen Forstlichen Versuchsanstalt*, (Eds.). Göttingen: Universität Göttingen.
- Bogdanova, D.A. 1998. Foci of *Heterobasidion annosum* and xylophagous insects in Scots pine forests of the Upper Ob region. *Lesovedenie*, 2, 80-85.
- Bogenschutz, H. 1982. Schaden durch Russelkaferfrass in einer Laubholz-Pflanzung. *Allgemeine Forstschrift*, 28, 855.
- Bogs, D. & Braasch, D. 1988. Dickmaulrüssler als Schadlinge der Baumschule und Staudengartnerei und ihre rationelle Bekämpfung. *Nachrichtenblatt für den Pflanzenschutz in der DDR*, 42, 233-36.
- Calder, A.A. 1989. The alimentary canal and nervous system of Curculionoidea (Coleoptera): gross morphology and systematic significance. *Journal of Natural History*, 23, 1205-65.
- Calder, A.A. 1990. Gross morphology of the soft parts of the male and female reproductive systems of Curculionoidea (Coleoptera). *Journal of Natural History*, 24, 453-505.
- Cankov, G. 1970. Biologie, Ökologie und Bekämpfungsmethoden des grossen braunen Rüsselkäfers (*Hylobius abietis* L.) in Bulgarien. *Deut. Akad. Landwirtschaftswiss., Tagungsbericht*, 110, 109-15.
- Cavalcaselle, B. & Allegro, G. 1986. Phytosanitary situation of poplar plantations in Italy during the period 1985-1986. In: *Compte rendu des réunions des groupes de travail entomologie et technologie de la Commission Internationale belge du Peuplier*, L. Nef, A. Leclercq (Eds.). 1986 September Bruxelles, Belgium.
- Cech, T. & Tomiczek, C. 1996. Zum Kiefernsterben in Niederösterreich. *Forstschutz Aktuell*, 17/18, 12-13.
- Chłodny, J. 1982. Uwagi o zagrożeniu przez szkodliwe owady drzewostanów i zadrzewień GOP w latach 1976-1980. *Sylwan*, 126, 19-26.
- Crowson, R.A. 1955. *The natural classification of the families of Coleoptera*. London: Lloyd and Co.
- Czerniakowski, Z.W. 2001. Praktyczne uwagi o sygnalizacji i zwalczaniu krytoryjka olszowca (*Cryptorhynchus lapathi* L.) na plantacjach wikliny amerykanki. *Progress in Plant Protection*, 41, 439-41.
- Demakov, Y.P. 1994. Effect of the pine weevil *Pissodes piniphilus* on the mortality pattern in Scots pine stands. *Lesovedenie*, 4, 54-60.

- Demakov, Y.P. 1996. The pine weevil in the forests of the Marii El republic. *Lesnoe Khozyaistvo*, 2, 47-49.
- Demakov, Y.P. 1998. The structure of xylophilous entomological complexes during a mass outbreak of *Pissodes piniphilus* Herbst. *Lesovedenie*, 4, 43-51.
- Eidmann, H.H. 1964. Studien über die Entwicklung von *Hylobius abietis* L. im Freiland und in Laboratoriumversuchen. *Zeitschrift für Angewandte Entomologie*, 54, 140-49.
- Eidmann, H.H. 1971. Selected literature on *Hylobius abietis* L. and related species. *Skogshöskolan*, Ra o. Upps., 9, 1-22.
- Eidmann, H.H. 1981. Pine weevil research for better reforestation. In: *Proc. I.U.F.R.O Congr.*, (Eds.). Japan, Tokyo.
- Elton, E.T., Blankwaardt, H.F.H., Burger, H.C., Steemers, W.F. & Tichelman, L.G. 1964. Insect communities in barked and unbarked pine stumps, with special reference to the large pine weevil (*Hylobius abietis* L., Coleoptera: Curculionidae). *Zeitschrift für Angewandte Entomologie*, 55, 1-54.
- Erichson, W.F. 1842. Die Larven des Coleopterorum. *Archiv für Naturgeschichte*, 8, 373-75.
- Fabricius, J.C. 1792. *Entomologia systematica emendata et aucta. Secundum classes, ordines, genera, species adjectis synonymis, locis, observationibus, descriptionibus. Vol. 1.*
- Farrell, B.D. 1998. Inordinate Fondness Explained: Why Are There So Many Beetles? *Science*, 281, 555-59.
- Gantner, M. 2001. Occurrence of hazelnut pests in Southeastern Poland. *Acta Horticulturae*, 556, 469-77.
- Geoffroy, E.L. 1762. *Histoire abrégée des insectes qui se trouvent aux environs de Paris dans laquelle ces animaux sont rangés suivant un ordre méthodique*. Paris: Durand.
- Giorcelli, A. & Allegro, G. 1999. I trattamenti per una corretta difesa fitosanitaria del pioppeto. Sherwood - Foreste ed Alberi Oggi,
- Gourov, A. 1994. Distributional patterns and behaviour of *Hylobius spp* adults during the additional feeding on conifers in Siberia. In: *I.U.F.R.O Eur. Hylobius Meet.*, (Eds.). France, Sainte-Eulalie.
- Habermann, M. & Geibler, A.V. 2001. Regenerationsfähigkeit von Kiefern (*Pinus sylvestris* L.) und Befall durch rindenbrütende Sekundarschadlinge nach Frass der Nonne (*Lymantria monacha* L.). Forst und Holz, 56, 107-11.
- Halldorsson, G., Sverrisson, H., Eyjolfsdottir, G.G. & S., O.E. 2000. Ectomycorrhizae reduce damage to Russian larch by *Otiorrhynchus* larvae. *Scandinavian Journal of Forestry Research*, 15, 354-58.
- Herbst, J.F.W. 1793. Natursystem aller bekannten in- und ausländischen Insekten, als eine fortsetzung der von Buffonschen Naturgeschichte. In: *Der Käfer*, NC (Eds.). Berlin:
- Hoffmann, A. 1950. *Coleoptères Curculionides (Première partie)*. Paris: Lechevalier.
- Hoffmann, A. 1954. *Coleoptères Curculionides (Deuxième partie)*. Paris: Lechevalier.
- Hoffmann, A. 1958. *Coleoptères Curculionides (Troisième partie)*. Paris: Lechevalier.
- Holigaus, F. & Dahlbender, W. 1995. Der Kirschkernstecher - ein vergessener Schaedling? *Obstau*, 20, 70-71.
- International Commission on Zoological Nomenclature 1991. *Curculio viridicollis* Fabricius, 1792 (currently *Phyllobius viridicollis*; insecta, Coleoptera): specific name conserved, and *Rhyncolus Germar*, 1817: *Curculio ater* Linnaeus, 1758 designated as the type species. *Bulletin of Zoological Nomenclature*, 48, 268-69.
- Karoles, K. 1998. *Sustainable forest management in Estonia. Ministry of the environment of Estonia, Estonian forest board*, Tallin, Estonia.
- Kelley, S.T. & Farrell, B. 1998. Is specialization a dead end? The phylogeny of host use in *Dendroctonus*. *Evolution*, 52, 1731-43.
- Kristek, J. 1989. Die Populationsdynamik der Forstschansekten als Grundlage des integrierten Forstschutzes gegen sie. *Acta Universitatis Agriculturae, Facultas Silviculturae*, 58, 47-83.
- Kula, E. & Zabecki, W. 1997. Vliv socialnho postaveni stromu na faunu kambioxylafagu smrku. Lesnictvi - Forestry, 43, 269-78.
- Kula, E. & Zabecki, W. 2000. Struktura kambioxylagni fauny smrku pri ruzne vycetni tloustce a socialnim postaveni stromu. *Lesnický Casopis*, 46, 257-71.
- Kulinich, O.A. & Orlinskii, P.D. 1998. Distribution of conifer beetles (Scolytidae, Curculionidae, Cerambycidae) and wood nematodes (*Bursaphelenchus* spp.) in European and Asian Russia. *Bulletin OEPP*, 28, 39-52.
- Kurowska, B. & Falencka-Jablonska, M. 1994. Analiza zmian wystepowania szkodnikow wtornych w strefach zagrozenia wokol Elektrowni 'Kozienice'. *Sylwan*, 138, 67-78.
- Kuschel, G. 1995. A phylogenetic classification of Curculionoidea to families and subfamilies. *Memoirs*

- of the Entomological Society of Washington, 14, 5-33.
- Lacordaire, T. 1863. *Histoire Naturelle des Insectes - Genera des Coleoptera*. Paris: Roret.
- Lacordaire, T. 1866. *Histoire Naturelle des Insectes. Genera des Coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes*. Paris: Roret.
- Lapietra, G. & Allegro, G. 1987. Nuove possibilità di lotta contro il punteruolo del pioppo nel periodo autunno-invernale. Quaderni di Ricerca - Centro di Sperimentazione Agricola e Forestale/Istituto di Sperimentazione per la Pioppicoltura, (16), 9.
- Lapietra, G. & Allegro, G. 1990. Insects damaging poplars in Italy during 1987-89, control strategies and future perspectives. In. *Proc. FAO International Poplar Commission*, FAO (Eds.). Working Party on Insects and Other Animal Pests 1990 March 19-23 Buenos Aires, Argentina.
- Latreille, P.A. 1806. *Genera Crustaceorum et Insectorum, secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata*. Parisiis et Argentorati: Koenig.
- Långström, B. 1982. Abundance and seasonal activity of adult *Hylobius*-weevils in reforestation areas during first years following final felling. *Communications Instituti Forestalis Fenniae*, 106, 23.
- Långström, B. 1985. Damage caused by *Hylobius abietis* in Finland in the years 1970-1971; Results from the Finnish part of a joint Nordic study. *Folia For.*, 612, 1-11.
- Lempérière, G. & Malphettes, C.B. 1987. Observations sur une infestation de *Pissodes piceae* Illiger - Le pisseode du Sapin - dans le Limousin. *Revue Forestière Française*, 29, 39-44.
- Lieutier, F., Vouland, G. & Pettinetti, M. 1997. Test de choix de pins méditerranéens par les Scolytides et autres insectes xylophages en conditions naturelles. *Revue Forestière Française*, 49, 215-24.
- Linnaeus, C. 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum caracteribus, differentiis, synonymis*. Salvii, Holmiae:
- Löf, M. 2000. Influence of patch scarification and insect herbivory on growth and survival in *Fagus sylvatica* L., *Picea abies* L. Karst. and *Quercus robur* L. seedlings following a Norway spruce forest. *Forest Ecology and Management*, 134, 111-23.
- Luik, A. 1994. Some aspects of the life history and population dynamics of *Pissodes piniphilus* Hrbst. (Coleoptera, Curculionidae). *Eesti Teaduste Akadeemia Toimetised, Bioloogia*, 43, 27-36.
- Lunderstadt, J. 1981. Ernährungsphysiologische Gesichtspunkte für die Systembindung von forstlich wichtigen Phytophagen. *Zeitschrift für Angewandte Entomologie*, 92, 510-20.
- Lyal, C.H.C. & King, T. 1996. Elytro-tergal stridulation in weevils (Insecta: Coleoptera: Curculionoidea). *Journal of Natural History*, 30, 703-73.
- Maksimenko, A.P., Fedchenko, A.V., Yaroshenko, V.A. & Titarenko, L.N. 2001. Alder or poplar snout beetle. *Zashchita i Karantin Rastenii*, 8, 38.
- Marvaldi, A.E. 1997. Higher level phylogeny of Curculionidae (Coleoptera: Curculionoidea) based mainly on larval characters, with special reference to broad-nosed weevils. *Cladistics*, 13, 285-312.
- Marvaldi, A.E., Sequeira, A.S., O'Brien, C.W. & Farrell, B. 2002. Molecular and morphological phylogenetics of weevils (Coleoptera, Curculionoidea): Do niche shifts accompany diversification? *Systematic Biology*, 51, 761-85.
- Maslov, A.D., Gunev, A.G. & Matusevich, L.S. 1999. Mass outbreak of *Lyda nemoralis* in the Tver' region of Russia. *Lesnnoe Khozyaistvo*,
- Montermini, A., Vai, N., Barani, A., Nanni, C., Boselli, M., Scaravelli, P., Marchetti, L., Pacchiarini, L., Oliva, G. & Vezzadini, S. 1998. Messa a punto di un modello di informazione per la difesa fitosanitaria ragionata del pioppo. In. *Atti, Giornate fitopatologiche, Scicli e Ragusa*, (Eds.). Maggio
- Moraal, L.G. 1996. Aantastingen door insecten en mijten in 1995: in bossen, natuurgebieden en wegbeplantingen. *Nederlands Bosbouwtijdschrift*, 68, 111-20.
- Moriondo, F. & Tiberi, R. 2000. Aspetti fitopatologici delle abetine di Vallombrosa. *Italia Forestale e Montana*,
- Moritomo, K. 1962. Comparative morphology, phylogeny and systematics of the superfamily Curculionoidea of Japan I. *Journal of the Faculty of Agriculture of the Kyushu University*, 11, 331-73.
- Moritomo, K. 1962. Key to families, subfamilies, tribes and genera of the superfamily Cuculionoidea of Japan excluding Scolytidae, Platypodidae and cossoninae. *Journal of the Faculty of Agriculture of the Kyushu University*, 12, 21-66.
- Moritomo, K. 1976. Notes on the family characters of Apionidae and Brentidae (coleoptera), with key to the related families. *Kontyu*, 44, 469-476.
- Moritomo, K. 1978. Cherk-list of the family Rhynchophoridae (Coleoptera) of Japan, with description of a new genus and five new species. *Esakia*, 12, 103-18.

- Neenan, M. & Kennedy, T.F. 1989. *Cryptorhynchus lapathi* (L.), a potential pest of willow plantations. Irish Naturalists' Journal, 23, 32.
- Nordenhem, H. 1989. Age, sexual development, and seasonal occurrence of the pine weevil *Hylobius abietis* (L.). Journal of Applied Entomology, 108, 206-70.
- Oppermann, T.A. 1985. Bark and wood insect pests of pollution-damaged spruce and pine. Forstzool. Inst. Univ. Freiburg: Br., German Fed.-Rep.
- Pappinen, A. & Weissenberg, K.v. 1996. Weevil feeding on Scots pine affects germination of *Endocronartium pini*. European Journal of Forest Pathology, 26, 225-34.
- Parry, W.H. 1982. The overwintering of adult *Strophosoma melanogrammum* (Coleoptera: Curculionidae) in forest soils. In: *Intl Colloquium of Soil Zoology*, P. Lebrun, H.M. André, A. De Medts, C. Grégoire-Wibo, G. Wauthy (Eds.). New Trends in Soil Biology Louvain-la-Neuve (Belgium).
- Podlaski, R. 2002. Relationship between the microhabitat and trophic conditions and the numbers of *Pissodes piceae* (III.) (Col., Curculionidae) in stumps of *Abies alba* Mill. in the Swietokrzyski National Park (Poland). Journal of Applied Entomology, 126, 207-11.
- Pollini, A. 1990. I nemici del pioppeto specializzato. Vita in Campagna, 8, 49-51.
- Prenner, J., Palfy, C., Nagy, L. & Molnar, J. 1983. Erdeszeti novenyvedelmi technologiak. Novenyvedelem, 19, 508-15.
- Prieme, A., Knudsen, T.B., Glasius, M. & Christensen, S. 2000. Herbivory by the weevil, *Strophosoma melanogrammum*, causes severalfold increase in emission of monoterpenes from young Norway spruce (*Picea abies*). Atmospheric Environment, 34, 711-18.
- Rougon, C., Roques, A., Rougon, D. & Levieux, J. 1995. Impact of insects on the regeneration potential of oaks in France. I. Action of phytophagous Curculionidae (Coleoptera) on female flowers prior to fecundation. Journal of Applied Entomology, 119, 455-63.
- Sabate, P. & Rojo, M. 1982. *Cryptorhynchus lapathi*, L., gorgojo perforador del chopo. Experiencias de lucha en Cataluna. Agricultura, 605, 999-1001.
- Sanborne, M. 1981. Biology of *Ithyicerus noveboracensis* (Forster) (Coleoptera) and weevil phylogeny. Evolutionary Monograph, 4, 1-80.
- Schoenherr, C.J. 1823. Curculionides. Isis von Onken, 10, 1132-46.
- Schoenherr, C.J. 1833-1845. *Genera et species curculionidum, cum synonymia hujus familiae. Species novae aut hactenus minus cognitae, descriptionibus a Dom. Leonardo Gyllenhal, C. H. Boheman et entomologis aliis illustratae*. Paris: Roret.
- Sierpinski, Z. 1972. Insect pests in stands of *Pinus silvestris* in Poland. Folia Entomologica Hungarica, 25, 263-69.
- Simionescu, A. 1995. Protectia rasinoaselor din nordul Carpatilor Orientali calamitate de vint si zapada. Revista Padurilor, 110, 16-25.
- Simionescu, A., Negura, A. & Cucos, V. 1998. Inmulirea, preventarea si combaterea gandacilor de scoarta ai rasinoaselor in anii 1993-1996 din nordul Carpatilor Orientali. Revista Padurilor,
- Solbraa, K. 1983. Pests and diseases on pine planted after wildfires in Norway. Freiburger Waldschutz-Abhandlungen, 4, 247-58.
- Srot, M. 1979. Prispevok k bionomii lalokonosce vejciteho (*Otiorrhynchus ovatus* L.). Lesnictvi - Forestry,
- Stachowiak, P. 1991. Liczebnosc i szkodliwosc foliofagicznych chrzaszczy (Coleoptera) w roznowiekowych uprawach i mlodnikach sosnowych. Trudy Zoologiczescii Institut, Akademii Nauk SSSR, 221, 173-83.
- Stachowiak, P. 1992. Badania nad zerami imagines zmiennika brudnego (*Strophosoma capitatum* Deg.) i choinka szarego (*Brachyderes incanus* L.) (Coleoptera, Curculionidae). Prace z Zakresu Nauk Lesnych, 74, 107-11.
- Starzyk, J.R. 1996. Bionomics, ecology and economic importance of the fir weevil, *Pissodes piceae* (III.) (Col., Curculionidae) in mountain forests. Journal of Applied Entomology, 120, 65-75.
- Stoakley, J.T. 1968. Control of the pine weevil, *Hylobius abietis* L., and of *Hylastes* species. Forestry, 41, 182-88.
- Stork, N.E., Hammond, P.M., Russell, B.L. & Hadwen, W.L. 2001. The spatial distribution of beetles within the canopies of oak trees in Richmond Park, UK. Ecological Entomology, 26, 302-11.
- Suoheimo, J. 1984. Isokorvakarsakkaan aikuissten esintyminen ja merkitys manbyn luontaiselle uudistamiselle Pohjois-Lapissa. Silva Fennica, 18, 255-59.
- Szmidt, A. & Stachowiak, P. 1980. *Strophosoma capitatum* Deg. (Coleoptera, Curculionidae). Nasilenie

- wystepowania chrzaszczy, ich wybiorczosc zerowa oraz szkodliwosc. Prace Komisji Nauk Rolniczych i Komisji Nauk Lesnych, 50, 145-53.
- Szmidt, A. & Korczynski, I. 1983. Population density of *Hylobius abietis* L. beetles and thier feeding intensity as the prognosis indexes. Pr. Kom. roln. lesn., 54, 137-44.
- Thompson, R.T. 1992. Observations on the morphology and classification of weevils (Coleoptera, Curculionoidea) with a key to major groups. Journal of Natural History, 26, 835-91.
- Tiberi, R. 1997. I principali insetti fitofagi della foresta di Vallombrosa. Italia Forestale e Montana, 52, 274-83.
- Tozlu, G. 2001. Sarikamis (Kars) Ormanlarinda Saricam (*Pinus sylvestris* L.)'da zarar yapan Elateridae, Buprestidae, Cerambycidae, Curculionidae (Coleoptera) ve Diprionidae (Hymenoptera) familyalarina bagli turler uzerinde calismalar. Turkiye Entomoloji Dergisi, 25, 193-204.
- Tsankov, G., Mirchev, P. & Ovcharov, D. 1994. Insect pests and their role in the decline and dying of silver fir (*Abies alba*) in Bulgaria. Nauka za Gorata, 31, 23-33.
- Urban, J. 1999. Listopas sedy: opomijeny skudce mladych listnacu a jehlicnanu. Lesnicka Prace, 78, 73-75.
- Voolma, K. & Luik, A. 2001. Outbreaks of *Bupalus piniaria* (L.) (Lepidoptera, Geometridae) and *Pissodes piniphilus* (Herbst) (Coleoptera, Curculionidae) in Estonia. Journal of Forest Science, 47 (Special Issue 2, 171-73.
- Wink, M., Mikes, Z. & Rheinheimer, J. 1997. Phylogenetic relationships in weevils (Coleoptera: Curculionoidea) inferred from nucleotids sequences of mitochondrial 16S rDNA. Naturwissenschaften, 84, 318-21.
- Witrylak, M. 1995. Biologia, ekologia i znaczenie gospodarcze wgryzonja jodlowca *Cryphalus piceae* (Ratz.) (Coleoptera, Scolytidae) w gorskich drzewostanach Lesnego Zakladu Doswiadczałnego w Krynicach. Sylwan, 139, 51-66.
- Woods, S.L. 1986. A reclassification of the genera of Scolytidae (Coleoptera). Great Basin Naturalist Memoirs, 10, 1-126.
- Zumr, V. & Stary, P. 1992. The occurence of the large pine weevil *Hylobius abietis* L., in individual forest zones. Forest Ecology and Management, 51, 251-58.

Chapter 14

GENERAL BIOLOGY AND LIFE CYCLES OF BARK WEEVILS

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1. INTRODUCTION

The large pine weevil, *Hylobius abietis* (L.) is the single most important insect pest of reforestation in northern and western Europe. The number of scientific papers published annually on this insect continues to increase in response to the need to find long-term solutions to the problems it causes. Its common name in English suggests that it is one of the larger weevils found feeding on conifers. Adults are about 8-14mm long (Eidmann 1974). The large pine weevil breeds in conifer stumps but feeds on conifer seedlings, so its reputation as a pest is greatest in countries which employ clear-cut plantation forestry.

Other species of *Hylobius*, *H. pinastri* Gyll. and *H. piceus* De G. occur in large parts of Europe (Eidmann 1974; Långström 1982). The biology of *H. pinastri* is similar to that of *H. abietis* (Nordlander 1990), although *H. pinastri* appears to prefer moist areas dominated by spruce (Långström 1982; Nordlander 1990). *Hylobius pinastri* is moderately abundant in Scandinavia and makes up about a quarter of the weevil population (with *H. abietis*) in Estonia (Luik and Voolma 1989). *Hylobius piceus* is less common and mostly found in moist forests, almost never on clear-cuttings. It breeds in the root collar of living conifer trees and the adults are seldom observed feeding on seedlings (Eidmann 1974; Å. Lindelöw pers. comm.). A fourth European species, *Hylobius transversovittatus* (Goeze), lives in the roots of a perennial plant *Lythrum salicaria*, and is hence of no interest in this

context, but is used for biological control of its introduced host in the United States (Kok *et al.* 1992).

Several other economically important species of the genus *Hylobius* occur outside Europe (*H. assimilis* Boheman, *H. congener* Dalla Torre *et al.*, *H. pales* (Herbst), *H. radicis* Buchanan, *H. warreni* Wood, and *H. xiaoi* Zhang). Lynch (1984) reviews the biology of the pales weevil (*H. pales*) and Cerezke (1994) the biology of *H. warreni* in North America. There are clearly differences between members of the genus according to where they breed. *H. radicis*, *H. warreni* and *H. xiaoi* breed in the root collar region or lower stem of healthy hosts and *assimilis* in small, living lateral roots, whereas *H. pales* and *H. congener* breed in roots of dying or recently dead trees, just as *H. abietis* does.

Eight *Pissodes* species occur in Europe (Kudela, 1974). *Pissodes castaneus* De Geer (= *notatus* F.), *P. pini* (L.) and *P. piniphilus* (Herbst) attack pine stems. They are widely distributed in Europe and, for *P. castaneus*, in North Africa. *Pissodes piceae* (Illiger) is a pest of fir stems and occurs throughout the distribution of its host, *Abies alba*. Three species feed on spruce stems; *P. harcyniae* (Herbst) is distributed from France to Siberia and Scandinavia, *P. scabricollis* (Miller) occurs in Central and eastern Europe, and *P. gyllenhali* (Sahlberg) is found mainly in Northern Europe. The eighth species, *P. validirostris* (Sahlberg) attacks pine cones and will not be included in this review.

Kudela (1974) provides a review of the knowledge on the biology and ecology of the eight *Pissodes* spp. until the late 1960's. Since then, new information has been provided for *P. castaneus*, mainly in Southern France (Carle, 1967, 1973, 1974; Alauzet, 1972a, 1972b, 1973, 1977, 1984, 1985, 1986; Lauga and Alauzet, 1983). Observations were made also on *P. piceae* in France (Lempérière and Malphettes, 1987; Lévieux *et al.*, 1994) and Poland (Starzyk, 1996; Podlaski, 2002), and on *P. piniphilus* in Estonia (Riis, 1975; Luik, 1994). In the last 30 years, no research has been published that specifically focused on the biology of *P. pini* and the three spruce *Pissodes* spp., which demonstrates their minor importance as forest pests.

The genus *Otiorrhynchus* is a homogenous group divided into four subgenera and includes around a thousand species throughout the world. The distribution of the genus is related to cold and temperate climates in both hemispheres (Lempérière, 1999). The weevils are wingless and nocturnal and most species are parthenogenetic. The larvae are serious pests in agriculture and forestry in many countries in Europe (Dolmans 1992). Four *Otiorrhynchus* species: *O. arcticus* (Fabr.), *O. nodosus* (Müller), *O. singularis* (L.) and *O. sulcatus* (Fabr.) are recognised as BAWBILT species. The black vine weevil, *Otiorrhynchus sulcatus*, which is a pest in nurseries, the clay coloured weevil, *O. singularis*, which is a pest in nurseries and forest regeneration and *O. arcticus* and *O. nodosus* which are pests in afforestation (Bejer-Petersen 1979; Bevan 1987; Van Tol 1993; Harding *et al.* 1998; Halldórrsson *et al.* 2000). There exists an extensive literature on the black vine weevil, especially the biology of the larvae, (Montgomery and Nielsen 1979; Stenseth 1976, 1979), whereas the other species have received much less attention. Much of the information, given below, on the biology of these insects is therefore based on existing knowledge of the black vine weevil.

2. HYLOBIUS ABIETIS

2.1 Adult feeding

The adult pine weevil feeds on the young stem of a conifer transplant where there is no competition with *Hylastes* species, which mainly feed from the root collar down (Scott and King 1974). While this represents the sole source of economic damage from the weevil, conifer seedlings do not constitute its main food supply. Extensive feeding also occurs in the crowns of mature coniferous trees and on their roots (Örlander *et al.* 2000, 2001). Where such trees are present as shelterwood, this reduces the attention weevils give to seedlings (Örlander *et al.* 2001; Nordlander *et al.* 2003a, b). Seedlings with a stem diameter of 3-8mm at planting are more vulnerable to damage by pine weevils than larger seedlings (Thorsén *et al.* 2001). Irrespective of stem diameter, mortality due to pine weevil feeding is generally higher for seedlings than for cuttings (Hannerz *et al.* 2002). Previous damage on seedlings strongly increases the risk of subsequent attack by pine weevils due to the release of attractive host volatiles (Nordlander 1991; Björklund *et al.* 2003). The likelihood of attack is also strongly affected by the environment immediately around the seedling. Both humus and vegetation provide cover for pine weevils and encourage feeding in their presence, whereas seedlings in bare mineral soil are largely avoided as food sources (Christiansen and Bakke 1971, Björklund *et al.* 2003; Örlander and Nordlander 2003).

A pine weevil eats about 0.2 cm² of bark per day (Pohris 1983; Bylund *et al.* 2004), but this depends on the species of conifer, the depth of bark and temperature. Given twigs of *Pinus sylvestris*, a preferred host, a pine weevil may consume an average of 0.36 cm² per day at 20°C, five times as much bark surface area as at 10 °C, nearly twice as much as *Picea abies* (at 20°C) and more than ten times the bark of *Fraxinus excelsior* (Leather *et al.* 1994). Although the weevil may consume bark of broadleaved trees (Manlove *et al.* 1997), they are usually ignored when an alternative conifer is available. Different conifer species provide food of varying quality, e.g. the preoviposition period has been shown to vary between 11.8 and 15.5 days at 20°C depending on the conifer species consumed by the females (Wainhouse *et al.* 2001). The feeding rate and amount of bark removed depend upon weevil size and total nitrogen content of bark (lower N means more bark is consumed). Also, not all bark material removed is consumed (Wainhouse *et al.* in press).

2.2 Behaviour and dispersal

The pine weevil is strongly affected by air temperature, humidity and light (Christiansen and Bakke 1971; Havukkala and Selander 1976). The activity of weevils is stimulated by increases in temperature up to 25 °C (Christiansen and Bakke 1968; Pohris 1983). This may affect their feeding rate in parts of the forest environment which are differentially shaded (Örlander *et al.* 2000; Nordlander *et al.* 2003b). Light and humidity reactions are largely dependent on the physiological (reproductive) stage of *H. abietis* (Havukkala and Selander 1976). Female weevils avoid both high and low humidities, but are generally hygronegative and more so

than males (Havukkala 1979). In areas with high humidity, spatial displacement is brought about by an increase in walking speed and decrease in the amount of turning per unit time (Havukkala 1980). Under uniform humidity and temperature conditions pine weevils move faster on mineral soil (sand) than on organic humus (Kindvall *et al.* 2000), possibly to avoid being exposed to excessive solar radiation (Björklund *et al.* 2003) or to the increased risk of predation during daylight hours. In the field, a stable diurnal rhythm of locomotor activity is maintained, but modified by weather conditions. Sibul *et al.* (1999) found that weevils were relatively passive at noon but increased their activity in late afternoon. The periods of greatest activity were correlated with high relative humidity (85-95%) and a moderately warm temperature (17-21°C) which generally corresponded to twilight periods (Sibul *et al.* 1999). During a hot period, the activity of weevils in an exposed site was limited to twilight and dark hours (Christiansen and Bakke 1971).

Migration by flight is an important way in which the pine weevil moves within large forest mosaics, where clear-cut patches appear regularly as part of the forest exploitation regime. In Scandinavia, weevils leave overwintering sites in spring at temperatures $> 8\text{-}9^{\circ}\text{C}$ and the flight period occurs during late May and early June (Eidmann 1968; Solbreck and Gyldberg 1979). The proportion of male and female weevils with well-developed flight muscles is already high at the beginning of May in field populations and flight muscle development is completed ahead of sexual maturation (Nordenhem 1989). Eggs start to develop in the oviducts during the spring migration period (Christiansen 1971a), and after a short time of feeding all females are in the reproductive phase (Örlander *et al.* 2000).



Figure 1. Adult *Hylobius abietis* in flight (photographed by Niklas Björklund)

Under good conditions for migratory flight (Fig 1), individual weevils will undertake most of their flight activity, including their longest flights, in the first 10

days of their migratory period (Solbreck 1980). They respond positively to light and readily climb upwards to initiate flights. There seems to be quite a range of variation in flight duration among individuals, so that some may fly for half an hour and others not at all. Weevils are able to fly when temperatures exceed 18-19 °C and at low wind velocity of 3-4 m s⁻¹ (Solbreck and Gyldberg 1979). It appears that at take-off, pine weevils head into the prevailing wind, then turn to fly downwind continuing to fly upwards, thus reaching heights of 30-50m, above the canopy of the forest. Most flight is undertaken at wind speeds of < 3 m s⁻¹. Indirect estimates of flight distance, deduced from knowledge of flight duration and direction in relation to air movement, have been made by Solbreck (1980). The estimates for an experimental population form a frequency distribution which suggests that 50% fly 1.5 km during the entire flight period, while some individuals are capable of covering 80 km. Nilssen (1984) trapped *H. abietis* in Finland at least 30km from its nearest source, and possibly a source 85km away, from whence it may have arrived with wind assistance.

During the migratory phase, host volatiles are used by weevils to locate areas with an abundance of freshly felled coniferous trees (Nordlander *et al.* 1986; Nordenhem and Eidmann 1991). Flight muscle degeneration follow the flight period, so that most older weevils lack flight muscles (Nordenhem 1989). As the migratory phase ends, weevils tend to become photonegative.

2.3 Reproduction and oviposition

The pine weevil is synovigenic. Reproductive maturation in female weevils is signalled by a progression and later a demise in the status of the reproductive system (Christiansen 1971a). Recognisable stages in the reproductive cycle are:

- 1a Juvenile (prereproductive) – short ovarioles, no oocytes
 - 1b Developing juvenile – extended ovarioles, developing oocytes
 - 2 Fertile – large ovarioles, oocytes in oviducts, *corpora lutea* present
 - 3 Senile – extended ovarioles, no oocytes, *corpora lutea* present
 - 4 Redeveloping - extended ovarioles, developing oocytes, *corpora lutea* present
- These stages are illustrated in Christiansen (1971a) and Nordenhem (1989).

Pine weevils meet and copulate often (Nordlander *et al.* 1986; Tilles *et al.* 1988). No sex pheromone that bring the sexes together have been found in the pine weevil (Nordlander *et al.* 1986; Tilles *et al.* 1986; Zagatti *et al.* 1997), but there is a close-range mating stimulant present on the body surface of females and young males (Tilles *et al.* 1988). In courtship, these function in concert with stridulation and tactile signalling by the male (Selander and Jansson 1977; Selander 1978).

Eggs are reported to be laid singly or in irregular groups in niches excavated in the bark below ground level (Eidmann 1974; Scott and King 1974). However, Nordlander *et al.* (1997) show that eggs are laid in the bark of roots mainly when the surrounding soil is likely to dry out. More consistently, eggs are laid in the soil and first instar larvae migrate to the bark of conifer roots. Two explanations for this behaviour are 1) that eggs avoid conspecific cannibalism or predation, or 2) newly

hatched larvae are better than adults at locating suitable larval feeding sites (Nordlander *et al.* 1997).

Under laboratory conditions, most eggs were laid near the surface of the soil (moist sand) to depths of 10cm, with only 8% laid at depths of 40-60 cm (Pye and Claesson 1981). In peat soil in the field a considerable proportion of the eggs were found under the main roots at about 20-30cm below the surface (Nordlander *et al.* 1987). However, in a hard-packed substrate found in the field, oviposition occurred entirely within 5cm of the surface (Pye and Claesson 1981). Larval populations have been found mostly within 5cm of the surface, with only 2% below 15cm (Henry and Day, 2001).

The following terminology (Bejer-Petersen *et al.* 1962; Nordenhem 1989) is used to denote the age of clear-cuttings in which breeding occurs. (A) is the growing season immediately following cutting, and (A+1), (A+2) etc. are subsequent years. Oviposition by migrant weevils on first year (A) breeding substrate occurs in the summer months, between June and August (Lekander *et al.* 1985). The preferred temperature for oviposition is 22°C (Christiansen and Bakke 1968). The frequency of eggs laid is unimodal during this period with a peak in late June (Nordlander *et al.* 1997) or somewhat earlier or later depending on prevailing climate. Reproduction ceases in August, coincides with a sudden drop in weevils caught by traps (Nordenhem 1989), and is probably induced by decreasing daylength (Örlander *et al.* 1997). No eggs are found in the oviducts in autumn and the oocytes that are present in the ovarioles are smaller than those in early summer (Christiansen 1971a). Such weevils, if they survive winter hibernation, are destined to resume vitellogenesis and ovulation in the following year. Fat reserves may be lower, and therefore fertility may also be lower, in the second season.

The realised fecundity of female pine weevils during the first season has been estimated to be approximately 70 eggs (Bylund *et al.* 2004). The fecundity of weevils depends on female size and the bark species on which adult feeding has taken place. Three or fourfold differences in fecundity (22-71 eggs) were reported by Wainhouse *et al.* (2001). Both subsequent egg and larval size and egg shape were also affected by conifer species; egg volume varied between 0.405 – 0.470 mm³. Feeding by larval stages and particularly maturation feeding by adult female weevils are key factors in reproductive success.

2.4 Larval feeding

Pine weevil larvae feed under the bark of roots of recently killed or dying conifer trees and in fresh stumps. Their rate of development and mortality is dependent on the conifer species acting as host (Thorpe and Day 2002). The effects of host species are discussed in Chapter 16.

Freshly hatched larvae migrate from oviposition sites in soil to suitable feeding sites in bark (Nordenhem and Nordlander 1994, Nordlander *et al.* 1997). Older larvae can also move between roots (Nordenhem and Nordlander 1994), a behaviour which represents a trade-off between improved larval food and the risks of predation by ground beetles (Salisbury and Leather, 1998).

The larva makes a long tunnel with irregular orientation, and which increases in diameter with larval size (Schwerdtfeger 1970). Feeding occurs in the cambial region and the larva constructs ventilation ducts to the surface (Scott and King 1974). In thick-barked roots pupal chambers may be found in the bark, but where the bark is thin, the larva excavates an oval chamber inside the wood, and closes the entrance hole with a plug of small chips resulting from its boring activity. The fully grown larva may be 9.5–16 mm in length (Kangas 1959). Generally, the larvae tunnel downwards after hatching where they may be better protected for overwintering (Pye and Claesson 1981) although the depth to which they go may depend on substrate and climate (Henry and Day 2001).

2.5 Duration of development and longevity

There are five larval instars (Bejer-Petersen *et al.* 1962; Christiansen 1971b). The rate of development from egg to pupa varies with temperature; in warm dry conditions, an egg laid in the spring (A) may become a fully developed final instar larva by late autumn in the UK (Scott and King 1974). This developmental schedule may produce an adult weevil by late May in the following year (A+1), although cooler temperature commonly delay emergence until July to September. In the Nordic countries most affected by the pine weevil (Denmark, Sweden, Norway and Finland), the duration of development tends to be longer than in the UK, but usually the time between generations is two years (Bejer-Petersen *et al.* 1962). Three or four year life cycles are associated with cooler climates of northern Scandinavia. The time of oviposition (earlier or later in the summer) is partly responsible for the pattern of subsequent larval development and whether the life cycle is completed in one, two or three years (Lekander *et al.* 1985). Temperature of the breeding substrate ultimately determines the length of the developmental period. Whether a breeding site is shaded or insulated can result in the developmental time being amplified to two years rather than one (Bakke and Lekander 1965; Bejer-Petersen 1975; Kuziemyska-Grzeczka 1984). Shelterwood can significantly prolong larval development. Von Sydow and Örlander (1994) found earlier emergence of pine weevils on sites with less than 80 shelter trees ha⁻¹ than on sites with denser shelter trees.

Facultative pre-pupal diapause experienced by larvae in pupal chambers, is induced when final instar larvae are exposed to temperatures below a threshold of 21°C (Eidmann 1963, 1964; Christiansen 1971b). Termination of diapause has not been studied in detail, but diapause of larvae developing at 12 °C appears to be broken 6 months after oviposition (Christiansen 1971b).

It is alleged that adult weevils of the new generation may appear and reproduce already in year A+1 in the UK (Scott and King 1974). In southern Scandinavia the new generation weevils either emerge and feed in late summer year A+1 or they remain in the pupal chamber until spring A+2 (Nordenhem 1989). In both cases they remain prereproductive until just after migration to new sites in year A+2 (Örlander *et al.* 2000). As oviposition occur also on year A+1 by weevils of the parent generation that have overwintered, new generation weevils appear also in late

summer year A+2 and in spring year A+3 (Nordlander 1987; Nordenhem 1989). Adult abundance varies throughout the year according to these patterns of emergence and migration to sites with fresh breeding material (Örlander *et al.* 1997). Typically, weevils are most abundant during the summer year A, in summer and autumn year A+1, and in spring year A+2. Due to oviposition year A+1 and delayed development of part of the population pine weevils are often abundant on clear-cuttings until year A+3 (Örlander *et al.* 1997)

2.6 Overwintering

Diapause occurs in the final larval instar and its incidence depends on the temperature experienced during this stage (Eidmann 1963, 1964). Larvae that have reached the final instar before autumn will overwinter in diapause. Younger larvae hibernate in a quiescent state and reach the final instar in the following summer (A+1) when pupal development is completed. In northern Scandinavia the larvae may pass through yet another winter in diapause. Overwintering larvae tolerate temperatures of -12 °C on average, and can survive temperatures as low as -19 °C (Luik and Voolma 1989). The supercooling point is generally higher than that for bark beetles and they do not survive prolonged periods at -15 °C (Luik and Voolma 1989). However, with a snow covering on the ground for insulation, there is generally likely to be little mortality in their natural environment in most regions.

Overwintering of adults takes place either in the pupal chamber or in the litter by those adults that have left the pupal chamber already in late summer and spent some time feeding before hibernation (Nordenhem 1989). Adults that have already been reproductive for one season may overwinter in the litter several times and reach an age of up to four years (Eidmann 1979).

2.7 Monitoring and Population Studies

There have been no published studies of pine weevil population dynamics, although frequent attempts have been made to monitor populations of adults at clear-cut sites during the period of conifer transplant vulnerability to attack. Freshly cut billets of coniferous trees have proved successful in attracting weevils in proportion to their abundance (Långström 1982; Wilson and Day 1995, 1996; Wilson *et al.* 1996; Zumr and Stary 1993). Örlander *et al.* (1997) argue that there are drawbacks with this method; natural host material can vary in its attraction to weevils, weevils are not arrested permanently, and standardisation of recorded weevils is problematic. To overcome these problems, Nordlander (1987) has introduced a more standardised approach based on a chemically-baited, covered pitfall trap (Nordlander 1990; Zumr and Stary 1994; Lindelöw *et al.* 1993). The use of this bait also has a drawback in that pre-reproductive weevils emerging in late summer are not attracted to the traps (Nordenhem and Eidmann, 1991). However, it appears that this can be advantageous in enabling separate monitoring of a parent population in decline at a time when it is present alongside a new generation of adults (Örlander *et al.* 1997). To catch pine weevils in all phases in a fairly well standardized manner one may use the covered

pitfall traps baited with equally-sized stem or branch pieces taken from one tree individual (Nordenhem and Eidmann 1991; Nordlander 1991).

An emergence trap devised specifically for use with pine weevils emerging from stumps on spruce clear-cuttings, provides a method for monitoring temporal patterns of emergence and for estimating on-site overwintering densities of weevil populations (Moore 2001). The trap is highly efficient at capturing weevils, regardless of their age, and has been used as an alternative to stump excavation for the estimation of emergent adult population density (Moore *et al.* 2003).

Relative measures to estimate larval population density have been devised and calibrated by examining bark on excavated stumps (Henry 1995; Henry and Day 2001). Samples of bark of known surface area within 10 cm of the soil surface and within 70 cm of the trunk, could be used to estimate a known fraction of the larval population (Henry and Day 2001). More recently absolute estimates of larval populations have been made (Moore *et al.*, 2003) and time of year and time of felling were both shown to influence population size, spatial distribution and development in stumps, as well as emergence from stumps. In this study 'potential' adult emergence was estimated to be between 46,400 and 170,825 *H.abietis* ha⁻¹. This is in close agreement with other estimates of adult population density on clear-cuttings in the UK, reaching levels between 150,000 ha⁻¹ (Heritage 1996) to 220,000 ha⁻¹ (Leather *et al.* 1995) Absolute estimates of immigrant weevil populations on a fresh clear-cutting and an adjacent shelterwood (A+1) in Sweden, have resulted in much lower densities, about 14,000 weevils ha⁻¹ (Nordlander *et al.* 2003a).

3. *PISSODES* spp.

3.1 Host range and host tree preference

All European *Pissodes* spp. are restricted to a single host tree genus, unlike some North American species, e.g. *P. strobi* (Peck) or *P. nemorensis*, which commonly attack pine and spruce species (O'Brien, 1989). There are, however, single reports of *P. castaneus* on spruce and larch, and of *P. pini* on spruce (Kudela 1974). Within the host genus, *Pissodes* spp. are usually rather polyphagous. For example, although *P. piceae* was originally restricted to silver fir, *Abies alba*, it is now commonly found on introduced fir species, *A. grandis*, *A. nordmanniana* and *A. nobilis*. *P. castaneus* and *P. pini* are found on nearly all pine species within their distribution range. Nevertheless, Carle (1973) and Alauzet (1984) found significant differences in the reproductive performance of *P. castaneus* fed and reared on different pine species. *P. piniphilus* seems to be restricted to Scots pine, *Pinus sylvestris* and, occasionally, to white pine, *P. strobus*. The natural host of the three spruce-feeding *Pissodes* spp. is the Norway spruce, *Picea abies*, but it is not known whether they also attack introduced spruce species.

Very little is known of the chemical interactions between *Pissodes* spp. and their host trees in Europe. Blanc and Blanc (1975) studied the effects of pine extracts on *P. castaneus* behaviour. They showed that feeding behaviour was stimulated by phenolic substances contained in the xylem and bark. Host selection and host

resistance mechanisms have been much more studied in North America on *P. strobi* (e.g. Mehary *et al.* 1994; Sahota *et al.* 1998). Since these studies have important implications in the development of IPM strategies against *P. strobi*, similar investigations should be carried out for European species.

Pissodes spp. also show preferences in the age of the host tree. *P. castaneus* is known to prefer young (4-15 year old) pine trees, *P. piniphilus* is mainly found on 30-40 year old pine trees, and *P. piceae* and *P. harcyniae* prefer old trees (Kudela 1974). However, for each *Pissodes* sp. trees of various ages are commonly attacked. It is generally agreed that European *Pissodes* spp. are secondary pests, i.e. they prefer weakened or freshly-killed trees. For example, *P. castaneus* outbreaks are usually associated with pine decline in combination with other insects or pathogens. It was shown that it prefers to attack trees previously weakened by the scale *Matsucoccus feydauti* Duc (Carle 1973, 1974) and the rust *Cronartium flaccidum* (Alauzet 1972a, 1984). *Pissodes piceae*, *P. pini* and *P. piniphilus* are known to attack mainly weakened trees or trees previously attacked by bark beetles (Kudela 1974; Riis 1975; Luik 1994). *Pissodes piniphilus* and *P. harcyniae* are particularly abundant in stands affected by air pollution (Kudela 1974). However, there are consistent observations of *Pissodes* spp. attacking apparently healthy trees, in particular *P. castaneus*, *P. piniphilus*, *P. piceae*, and *P. harcyniae*, especially when present in high density (Kudela 1974; Alauzet 1984; Starzyk 1996). More studies should focus on the real pest status of *Pissodes* spp., and in their exact role in the decline of conifers in Europe.

3.2 Adult biology

The biology and ecology of *Pissodes* adults have been poorly studied, especially in the field. In the laboratory, freshly emerged *P. castaneus* adults feed first on the bark of twigs (maturation feeding) (Carle 1967). Branches and stems are used by older adults. Sexes are morphologically similar, but can be distinguished by the structure of the abdomen and the snout (Carle 1967; Starzyk 1996). Mating is frequently observed, including during oviposition. Adults are believed to be long-lived (e.g. Hierholzer 1954; Bukzeeva 1965), but field data on survival are lacking. Carle (1973) kept adults alive for up to 587 days in natural conditions in southern France. Carle (1967, 1973), Blanc and Blanc (1975) and Alauzet (1984), provide data on various other aspects of the biology of *P. castaneus* adults in laboratory conditions, such as temperature resistance, feeding habits, fecundity, etc. These data are not available for the other *Pissodes* spp.

3.3 Oviposition and fecundity

Pissodes spp. lay their eggs in holes bored in the bark by the female. Ovipositor holes are often found in wounds or cracks in the bark. In most species, eggs are laid in groups of one to five (Kudela 1974) although broods of *P. piceae* are usually larger. In Poland, Starzyk (1996) observed up to 35 eggs per hole, with an average of 13, whereas, in Germany, Haeselbarth (1962) found a maximum of 15 eggs, with

an average of 4.1 eggs per hole. Fecundity was investigated for *P. castaneus* only. Lauga and Alauzet (1983) and Alauzet (1984) measured a mean potential fecundity of over 500 eggs per female. The fecundity was influenced by rearing temperature and food quality. The ecological optimum for fecundity was calculated at 16–17°C. In constant rearing conditions, *P. castaneus* females showed two egg-laying cycles, a short one (4–8 days) and a long one (20–60 days), with temperature-dependent durations.

3.4 Larval and pupal stage

All weevils of the genus *Pissodes* for which larval stages have been studied have four larval instars. This includes the European *P. castaneus* (Carle 1967; Alauzet 1984), *P. piceae* (Haeselbarth 1962) and *P. validirostris* (Roques 1976) and several American species (listed in Alauzet 1984). Hierholzer (1954) and Bukzeeva (1965) mention five larval instars in *P. piceae* and *P. castaneus*, respectively, on the basis of head capsule measurements showing five distinct peaks. In fact the last two peaks represent healthy fourth instar larvae and larvae parasitized by *Eubazus* spp. (Hym.: Braconidae), which tends to have a strongly reduced size (Haeselbarth 1962; M. Kenis, unpublished data). Carle (1967), Alauzet (1984), and Hierholzer (1954) provide measurements of the head capsule width and duration in rearing, for each instar of *P. castaneus* and *P. piceae*, respectively.

Pissodes larvae burrow feeding tunnels in phloem and cambium. At the end of the fourth larval instar, the larvae excavate a pupal cell in the surface of the wood. The pupal cell is covered with shredded wood fibre, and is typical for *Pissodes* spp. Sometimes, the pupal cell is built more deeply in the sapwood, particularly in *P. pini* in pine trunks, or in *P. castaneus* when this latter attacks the top of young pine trees, where the bark is very thin. Larvae parasitized by *Eubazus* spp. tend to build their pupal chamber in the bark, closer to the surface, in particular in fir or pine trunks with a thick bark (M. Kenis, unpublished data).

3.5 Life cycle

The phenology of *Pissodes* spp. varies with species and climatic conditions. The stem-feeding European species usually develop without obligatory diapause, as shown in laboratory rearing (Carle 1967 and Alauzet 1984 for *P. castaneus*; Kenis, 1994 and unpublished data for *P. castaneus*, *P. pini*, and *P. piniphilus*). However, in the field, Carle (1974) and Alauzet (1986) observed a facultative diapause in the fourth instar larvae of *P. castaneus*, possibly induced by temperature and photoperiod conditions. Kenis (1994) showed intraspecific variations in *P. pini* in Switzerland. Lowland populations developed without diapause, both in the field and in the laboratory, whereas mountain populations from the Alps had more than 80% of their individuals entering into an obligatory diapause in the last larval instar when reared in the laboratory. When larvae were collected in the field in autumn and incubated in the laboratory, nearly 100% of the larvae remained in diapause. This

diapause in mountain populations was considered as an adaptation to the particular climatic conditions in cold areas, where *P. pini* has a two-year cycle.

P. castaneus shows the largest variability in phenology, probably due to its wide ecological and geographic distribution in Europe and North Africa. The most complete studies on *P. castaneus* phenology are from Carle (1973, 1974) and Alauzet (1977, 1984) in southern France. They describe life cycles that vary from site to site and year to year. In general, however, there are overlapping generations, and from one to two generations a year, with adults and last instar larvae as the main overwintering stages. Other studies in southern Europe are reviewed by Alauzet (1984), which also describe various phenological patterns. In other European regions, *P. castaneus* has usually one generation per year, or even one per two years in northern Europe, with either young adults or mature larvae overwintering (see Kudela 1974, Carle 1974, and Alauzet 1984, for review). However, observations in central Europe showed that, in single populations, overlapping generations is the rule and both larvae and adults overwinter (M. Kenis, unpublished data).

The life cycle of *P. piceae* is less variable, probably because it is strictly confined to silver fir, a European tree with a rather limited ecological and climatic range. In central France (Lempière and Malphettes 1987) and Bavaria (Haeselbarth 1962), the life cycle is as follows. Eggs are laid in spring or early summer. The final instar overwinters in its pupal cell and pupates in spring, and adults emerge in late spring and in summer, but will oviposit in the following year only. However, Lévieux *et al.* (1994) in Central France, and Starzyck (1996) in Poland state that pupation and adult emergence can also occur in late summer and autumn, if eggs are laid early in the year, suggesting that *P. piceae* does not have an obligatory diapause in the larval stage.

There is no detailed study on the phenology of other stem-feeding *Pissodes* spp. in Europe. *P. pini*, *P. piniphilus* and the three spruce-feeding species are believed to be usually univoltine, but the life-cycle can last two years at high latitudes (Kangas 1938; Kudela 1974) or altitudes (Kenis 1994). Both adults and larvae can overwinter, and generations partly overlap.

4. OTIORRHYNCHUS SPP.

4.1 Adult biology

Otiorrhynchus adults feed for 5-8 weeks before oviposition starts and feeding is most extensive during the pre-oviposition and early oviposition periods (Stenseth 1976; Moorhouse *et al.* 1992; Palm 1996). Adults are known to be even more polyphagous than the larvae. They feed on the leaves and bark of trees and plants. Leaf notching by black vine weevil (*O. sulcatus*) adults is of concern for ornamental plant growers (Bevan 1987; Van Tol 1993) and ring-barking by clay coloured weevil (*O. singularis*) adults is a significant problem in reforestation (Bejer-Petersen 1979; Bevan 1987). All species, except *O. arcticus*, are predominantly parthenogenetic, but males of all the other species are known from the southernmost part of the distribution area.

4.2 Oviposition and fecundity

Otiorrhynchus spp. deposit their eggs in the soil or leaf litter at the base of their host plants (Palm 1996). Oviposition is mostly in mid or late summer, but may continue until there is a hard frost (Nielsen 1989). Oviposition usually lasts for several weeks and is broken into distinct oviposition cycles (Moorhouse *et al.* 1992). Fecundity is dependent upon temperature, photoperiod food quality and the age of the weevils (Evenhuis 1978; Garth and Shanks 1978; Moorhouse *et al.* 1992). Overwintering weevils start laying eggs earlier than newly emerged adults and lay more eggs (Tanigoshi *et al.* 1999), however, reduced egg viability of overwintering black vine weevil females has been recorded (Stenseth 1976). Fecundity of weevils seems to be related to host nutritional quality (Moorhouse *et al.* 1992) as well as to host plant type. Hanula (1988) observed that black vine weevils reared on *Taxus* produce more eggs than weevils on a different diet. The egg production is normally in the range of 150-300 eggs/weevil, but an individual black vine weevil has been recorded laying as many as 2101 eggs (Nielsen and Dunlap 1981; Moorhouse *et al.* 1992).

4.3 Larval and pupal stage

The eggs hatch in 2-3 weeks, i.e. in the late summer or autumn, and the young larvae burrow into soil where they can be found throughout the plant root zone feeding on the fine roots (Evenhuis 1978). A drop in the soil temperature, signals them to move deeper into the soil where they overwinter. The larvae overwinter in the soil and resume feeding on roots in the early spring. At this stage they cause the heaviest damage as the overwintering larvae prefer larger roots and may girdle the main stem killing the plants. The larvae are polyphagous; more than 100 plant species have been identified as potential host plants of black vine weevil larvae and the other species are also known to be polyphagous (Wagner and Negley 1976; Masaki *et al.* 1984; Palm 1996). Larvae pupate in May and June and adults emerge in June and July (Garth and Shanks 1978; Stenseth 1976). However, the larvae of *O. nodosus* and *O. arcticus* continue their development throughout the summer after the first overwintering and pupate in the early summer after a second overwintering (Larsson and Gígja 1959). The exact number of larval instars is uncertain. The larvae pupate inside an earthen chamber and the adults emerge from the pupae after 2-3 weeks (Nielsen 1989; Moorhouse *et al.* 1992; Palm 1996).

4.4 Life cycle

The black vine weevil *Otiorrhynchus sulcatus* and the clay coloured weevil *O. singularis* are univoltine, whereas *O. arcticus* and *O. nodosus* are perennial at least in the northernmost part of the distribution area (Larsson and Gígja 1959; Bevan 1987; Van Tol 1993). All species overwinter as larvae in the soil, but the adult weevils also overwinter to some extent. After a period of feeding in the spring or early summer the larvae pupate and the adults emerge about two weeks later. The larvae of the black vine weevil and the clay coloured weevil pupate in early spring and adult clay coloured weevils start to emerge in March-April, whereas adult black

vine weevils start to emerge in May-June (Stenseth 1976; Nielsen 1989; Garth and Shanks 1978). The larvae of *O. arcticus* and *O. nodosus* pupate in the early summer and the weevils emerge in late June (Larsson & Gígja 1959; Halldórsson 1994). Egg laying is generally in mid or late summer, following a period of pre-ovipositional feeding.

REFERENCES

- Alauzet, C. 1972a. Etude de la localisation des pontes de *Pissodes notatus* (Coléoptère, Curculionidae) sur pin maritime, en présence de *Cronartium flaccidum* (Basidio-, Phragmobasidiomycète, Urédinale, Cronartiacée). Bulletin de la Société d'Histoire Naturelle de Toulouse, 108, 341-48.
- Alauzet, C. 1972b. Mise en évidence d'un stade de repos facultatif dans le développement de *Pissodes notatus* (F.) (Coléoptère, Curculionidae) dans la nature. Bulletin de la Société Entomologique de Toulouse, 108, 514-19.
- Alauzet, C. 1973. Etude de la zone préférentielle de ponte de *Pissodes notatus* (F.) (Coléoptère, Curculionidae) sur *Pinus maritima*, en l'absence de tout autre parasite. Bulletin d'Ecologie, 4, 144-50.
- Alauzet, C. 1977. Cycle biologique de *Pissodes notatus* (Coleoptera, Curculionidae) dans la région toulousaine (France). Canadian Entomologist, 109, 597-603.
- Alauzet, C. 1984. Bioécologie de *Pissodes notatus* (Coleoptera, Curculionidae). Thèse d'Etat. Université Paul Sabatier, Toulouse, France.
- Alauzet, C. 1985. Développement sous-cortical d'un ravageur des pins: *Pissodes notatus* F. (Col.: Curculionidae). I Exigences thermiques du développement dans la nature. Bulletin d'Ecologie, 16, 265-68.
- Alauzet, C. (1986) Développement sous-cortical d'un ravageur des pins: *Pissodes notatus* F. (Col.: Curculionidae). II Mise en évidence d'une diapause facultative. Journal of Applied Entomology, 101: 134-40.
- Bakke, A. & Lekander, B. 1965. Studies on *Hylobius abietis* L. II. The influence of exposure on the development and production of *Hylobius abietis*, illustrated through one Norwegian and one Swedish experiment. Meddelelser fra det Norske Skogforsoksvesen, 20, 117-35.
- Bejer-Petersen, B. 1975. Length of development and survival of *Hylobius abietis* as influenced by silvicultural exposure to sunlight. Årsskrift, Kongelige Veterinaer og Landbohøjskole, 1975, 111-20
- Bejer-Petersen, B. 1979. *Forstzoologi*, 2. udgave. Nucleus-Biologilærerforeningens forlag Aps. København.
- Bejer-Petersen, B., Juutinen, P., Kangas, E., Bakke, A., Butovitsch, V., Eidmann, H., Heqvist, K.J. & Lekander, B. 1962. Studies on *Hylobius abietis* L. 1. Development and life cycle in the Nordic countries. Acta Entomologica Fennica, 17, 1-107.
- Bevan, D. 1987. *Forest Insects*. Forestry Commission, Handbook 1. London: HMSO Books.
- Björklund, N., Nordlander, G. & Bylund, H. 2003. Host-plant acceptance on mineral soil and humus by the pine weevil *Hylobius abietis* (L.). Agricultural and Forest Entomology, 5, 61-65.
- Bukzeeva, O.N. 1965. Duration of generations of the pine weevil, *Pissodes notatus* F. (Coleoptera, Curculionidae) in the Voronezh region. Entomological Review, 44, 22-24.
- Bylund, H., Nordlander, G. & Nordenhem, H. 2004. Feeding and oviposition rates in the pine weevil *Hylobius abietis* (Coleoptera: Curculionidae). Bulletin of Entomological Research (accepted).
- Carle, P. 1967. Contribution à l'étude biologique de *Pissodes notatus* F. Revue de Zoologie Agricole et Appliquée, 10-12, 139-51.
- Carle, P. 1973. Le Dépérissement du Pin Mésogén en Provence. Thèse d'Etat, Bordeaux I.
- Carle, P. 1974. Le dépérissement du pin mésogén en Provence. (Condensé de thèse) Annales des Sciences Forestières, 31, 1-26.
- Cerezke, H.F. 1994. Warren root collar weevil, *Hylobius warreni* Wood (Coleoptera: Curculionidae), in Canada: ecology, behavior, damage relationships and management. Canadian Entomologist, 126, 1383-1442.
- Christiansen, E. 1971a. Developmental stages in ovaries of pine weevils, *Hylobius abietis* L. (Coleoptera: Curculionidae), present in reforestation areas during the first years after the final felling. Meddelelser fra det Norske Skogsforstksvesen, 28, 393-415.

- Christiansen, E. 1971b. Laboratory study on factors influencing pre-imaginal development in *Hylobius abietis* L. (Col., Curculionidae). Norsk Entomologisk Tidsskrift, 18, 1-8.
- Christiansen, E. & Bakke, A. 1968. Temperature preference in adults of *Hylobius abietis* L. (Coleoptera Curculionidae) during feeding and oviposition. Zeitschrift für angewandte Entomologie, 62, 83-89.
- Christiansen, E. & Bakke, A. 1971. Feeding activity in the pine weevil, *Hylobius abietis* L. (Col., Curculionidae), during a hot period. Norsk Entomologisk Tidsskrift, 18, 109-11.
- Dolmans, N. 1992. *Diseases and disorders in forest nurseries*. Cost 813. Brussels: Commission of European Community.
- Eidmann, H.H. 1963. Zur Diapause einiger Forstinsekten. Zeitschrift für angewandte Entomologie, 52, 362-67.
- Eidmann, H.H. 1964. Studien über die Entwicklung von *Hylobius abietis* L. im Freiland und in Laboratoriumversuchen. Zeitschrift für angewandte Entomologie, 54, 140-49.
- Eidmann, H.H. 1968. Invasion of conifer plantations by radioactively labelled *Hylobius abietis* L. Proceedings of the IAEA/FAO Symposium Isotopes and radiation in Entomology, 1967, 75-84. Wien.
- Eidmann, H.H. 1974. *Hylobius* Schönh. In. *Die Forstschädlinge Europas*, Vol 2, W. Schwenke, (Ed.), Hamburg/Berlin: Paul Parey.
- Eidmann, H.H. 1979. *Integrated management of pine weevil (*Hylobius abietis* L.) populations in Sweden. Current topics in forest entomology* in. USDA Forest Service General Technical Report WO-8.
- Evenhuis, H. H. 1978. Bionomics and control of the black vine weevil, *Otiorrhynchus sulcatus*. Mededelingen Faculteit Landbouwwetenschappen RijksUniversiteit Gent, 43, 607-11.
- Garth, S. & Shanks Jr. C. H. 1978. Some factors affecting infestation of strawberry fields by the black vine weevil in Western Washington. Journal of Economic Entomology, 71, 443-48.
- Haeselbarth, E. 1962. Zur Biologie, Entwicklungsgeschichte und Ökologie von *Brachistes atricornis* Ratz. als eines Parasiten von *Pissodes piceae*. Zeitschrift für Angewandte Entomologie 49, 233-89.
- Halldórsson, G. 1994. Weevils. The Annual Journal of the Icelandic Forestry Association 1994, 53-58.
- Halldórsson, G., Sverrisson, H., Eyjólfssdóttir G.G. & Oddsdóttir, E.S. 2000. Ectomyorrhizae reduce damage of Russian larch by *Otiorrhynchus* larvae. Scandinavian Journal of Forest Research, 15, 354-58.
- Hannerz, M., Thorsén, Å., Mattsson, B. & Weslien, J. 2002. Pine weevil (*Hylobius abietis*) damage to cuttings and seedlings of Norway spruce. Forest Ecology and Management, 160, 11-17.
- Hanula, J. L. 1988. Oviposition preference and host recognition by the black vine weevil, *Otiorrhynchus sulcatus* (Coleoptera: Curculionidae). Environmental Entomology, 17, 694-98.
- Harding, S., Annila, E., Ehnström, B., Halldorsson, G. & Kvamme, T. 1998. Insect pests in forests of the Nordic countries 1987-1990. Rapport fra skogforskningen – Supplement, 3, 1-21.
- Havukkala, I. 1979. The humidity reactions of the large pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae), during three stages of its life cycle. Annales Entomologici Fennici, 45, 58-64.
- Havukkala, I. 1980. Klinokinetic and klinotactic humidity reactions of the beetles *Hylobius abietis* and *Tenebrio molitor*. Physiological Entomology, 5, 133-40.
- Havukkala, I. & Selander, J. 1976. Reactions of the large pine weevil, *Hylobius abietis* L. (Col., Curculionidae), to various light and humidity stimuli during three stages of its life cycle. Annales Entomologici Fennici, 42, 54-62.
- Henry, C.J. 1995. The role of *Bracon hylobii* and other parasitoids in the population dynamics of *Hylobius abietis*, the large pine weevil. DPhil Thesis Univ. of Ulster, Coleraine, UK.
- Henry, C.J. & Day, K.R. 2001. Biocontrol of the large pine weevil: structure of host (*Hylobius abietis* [L.]) and parasitoid (*Bracon hylobii* Ratz.) populations in felled stumps of Sitka spruce. In. *Protection of World Forests from Insect Pests: Advances in Research*. RI Alfaro, K. Day, S Salom, KSS Nair, H Evans, A Liebhold, F Lieutier, M Wagner, K Futai, K Suzuki (Eds.) IUFRO World Series, Vol. 11.,Vienna: IUFRO Secretariat.
- Heritage, S. 1996. Protecting plants from damage by the large pine weevil and black pine beetles. Forestry Commission Research Information Note, 268, 1-8.
- Hierholzer, O. 1954. Ein Beitrag zur Kenntnis des Weißstannenrüsslers *Pissodes piceae* Ill.. In. *Die Große Borkenkäferkalamität in Südwestdeutschland 1944-1951*. Wellenstein, G. (Ed.) Ringingen, Germany.
- Kangas, E. 1938. Zur Biologie und Verbreitung der *Pissodes* Arten (Col., Curculionidae) Finnlands. Annales Entomologici Fennici, 4, 1-46, and 73-98.

- Kangas, E. 1959. Systematische Untersuchungen über die Larven der *Hylobius piceus* DeG., *abietis* L. und *pinastri* Gyll. (Col., Curculionidae). Annales Entomologici Fennici, 25, 110-18.
- Kenis, M. 1994. Variations in diapause among populations of *Eubazus semirugosus* (Nees) (Hym.: Braconidae), a parasitoid of *Pissodes* spp. (Col.: Curculionidae). Norwegian Journal of Agricultural Sciences, Supplement 16, 77-82.
- Kindvall, O., Nordlander, G. & Nordenhem, H. 2000. Movement behaviour of the pine weevil *Hylobius abietis* in relation to soil type: an arena experiment. Entomologia Experimentalis et Applicata, 95, 53-61.
- Kok, L.T., McAvoy, J.T., Malechi, R.A., Hight, S.D., Drea, J.J. & Coulson, J.R. 1992. Host specificity tests of *Hylobius transversovittatus* Goeze(Coleoptera; Curculionidae), a potential biological control agent of purple loosestrife, *Lythrum salicaria* L. (Lythraceae). Biological Control, 2, 1-8.
- Kudela, M. 1974. Curculionidae, Pissodini. In: *Die Forstschädlinge Europas. 2 Band.* Schwenke, W. (Ed.). Hamburg: Paul Parey.
- Kuziemyska-Grzeczka, G. 1984. Badania nad mozliwoscia I szybkoscia rozwoju szeliniaka sosnowca (*Hylobius abietis* L.) (Col.; Curculionidae) na roznych gatunkach drzew na powierzchni laslonecznionej i ocienionej. Folia Forestalia Polonica, A, 27, 49-57.
- Långström, B. (1982) Abundance and seasonal activity of adult *Hylobius*-weevils in reforestation areas during first years following final felling. Communicationes Instituti Forestalis Fenniae, 106: 1-22.
- Larsson, S.G. & Gíðja, G. (1959) Coleoptera 1. Synopsis. In: *The Zoology of Iceland*, Volume III, Part 46_a. Ejnar Munksgaard, Copenhagen and Reykjavík.
- Lauga, J. & Alauzet, C. 1983. Dynamique des populations d'un ravageur du pin: *Pissodes notatus* (Coleoptera, Curculionidae). Optimum écologique de ponte et modèle de fécondité. Acta Oecologica, Oecologia Applicata, 4, 151-61.
- Leather, S.R., Ahmed, S.I. & Hogan, L. 1994. Adult feeding preferences of the large pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae). European Journal of Entomology, 91, 385-389.
- Leather, S.R., Small, A.A. & Bogh, S. 1995. Seasonal variation in local abundance of adults of the large pine weevil, *Hylobius abietis* L. Journal of Applied Entomology, 119, 511-13.
- Lekander, B., Eidmann, H.H., Bejer, B. & Kangas, E. 1985. Time of oviposition and its influence on the development of *Hylobius abietis* (L.) (Col., Curculionidae). Zeitschrift für angewandte Entomologie, 100, 417-21.
- Lempérière, G. 1999. A taxonomic overview of the genus *Otiorrhynchus*. 3rd International Workshop on Vine Weevil. 9-11 June 1999, Angers France.
- Lempérière, G. & Malphettes, C.B. 1987. Observations sur une infestation de *Pissodes piceae* Illiger le pisseude du sapin dans le Limousin. Revue Forestière Française, 39, 39-44.
- Lévieux, J., Monestier, C., & Cassier, P. 1994. The fir weevil *Pissodes piceae* Ill. (Coleopt. Curculionidae) life cycle in central France. A possible vector of phytopathogenic fungi. Bulletin de la Société Entomologique de France, 119, 5-14.
- Lindelöw, H., Eidmann, H.H. & Nordenhem, H. 1993. Response on the ground of bark beetle and weevil species colonising conifer stumps and roots to terpenes and ethanol. Journal of Chemical Ecology, 19, 1393-1403.
- Luik, A. 1994. Some aspects of the life history and population dynamics of *P. piniphilus* Hrbst. (Coleoptera, Curculionidae). Eesti Teaduste Akadeemia Toimetised, Bioloogia, 43, 27-36
- Luik, A. and Voolma, K. (1989) Some aspects of the occurrence, biology and cold-hardiness of *Hylobius* weevils. In *Insects affecting reforestation: biology and damage*. Alfaro, R.I. and Glover, S.G. (Eds.) Victoria, Canada, Pacific and Yukon Region, Forestry Canada.
- Lynch, A.M 1984. The pales weevil, *Hylobius pales* (Herbst): a synthesis of the literature. Journal of the Georgia Entomological Society, 19, 1-34.
- Manlove, J.D., Styles, J. & Leather, S.R. 1997. Feeding of adults of the large pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae). European Journal of Entomology, 94, 153-56.
- Masaki, M., K. Omura, & F. Ichinohe. 1984. Host range studies of the black vine weevil, *Otiorrhynchus sulcatus* (Fabricius) (Coleoptera: Curculionidae). Applied Entomology and Zoology, 19, 95-106.
- Mehary, T., Gara, R.I., & Greenleaf, J. 1994. Host selection behavior of *Pissodes strobi* and implications to pest management. In: *The White Pine Weevil: Biology, Damage and Management*. Proceedings of a symposium held January 19-21, 1994 in Richmond, British Columbia. . R.I. Alfaro, G. Kiss, R.G. Fraser (Eds.) FRDA Report. Canadian Forest Service and British Columbia Ministry of Forestry.
- Montgomery, M. E. & D. G. Nielsen. 1979. Embryonic development of *Otiorrhynchus sulcatus*: effect of temperature and humidity. Entomologia experimentalis et applicata, 26, 24-32.

- Moore, R. 2001. Emergence trap developed to capture adult large pine weevil *Hylobius abietis* L. (Coleoptera: Curculionidae) and its parasite *Bracon hylobii* (Hymenoptera: Braconidae). Bulletin of Entomological Research, 91, 109-15.
- Moore, R., J.M. Brixey, & A.D. Milner 2003. The effect of time of year on the development of immature stages of the Large Pine Weevil (*Hylobius abietis* L.) in stumps of Sitka spruce (*Picea sitchensis* Carr.) and the influence of felling date on their growth, density and distribution. Journal of Applied Entomology, (in press).
- Moorhouse, E. R., A. K. Charnley, & A. T. Gillespie. 1992. A review of the biology and control of the vine weevil *Otiorrhynchus sulcatus* (Coleoptera: Curculionidae). Annals of Applied Biology, 121, 431-54.
- Nielsen, D.G. 1989. Minimizing *Otiorrhynchus* root weevil impact in conifer nurseries. In. *Insects Affecting Reforestation: Biology and Damage*. R.I. Alfaro, S.G. Glover, (Eds.). Proceedings of a meeting of the IUFRO working group on Insects Affecting Reforestation (S2.07-03) held under the auspices of the XV III International Congress of Entomology, July 3-9, 1988, Vancouver, British Columbia, Canada..
- Nielsen, D. G. & M. J. Dunlap 1981. Black vine weevil reproductive potential on selected plants. Annals of the Entomological Society of America, 74, 60-65.
- Nilssen, A.C. 1984. Long-range aerial dispersal of bark beetles and bark weevils (Coleoptera, Scolytidae and Curculionidae) in northern Finland. Annales Entomologici Fennici, 50, 37-42.
- Nordenhem, H. 1989. Age, sexual development, and seasonal occurrence of the pine weevil *Hylobius abietis* (L.). Journal of Applied Entomology, 108, 260-70.
- Nordenhem, H. & Eidmann, H.H. 1991. Response of the pine weevil *Hylobius abietis* L. (Col., Curculionidae) to host volatiles in different phases of its adult life cycle. Journal of Applied Entomology, 112, 353-58.
- Nordenhem, H. & Nordlander, G. 1994. Olfactory oriented migration through soil by root-living *Hylobius abietis* (L.) larvae (Col., Curculionidae). Journal of Applied Entomology, 120, 397-403.
- Nordlander, G. 1987. A method for trapping *Hylobius abietis* (L.) with a standardised bait and its potential for forecasting seedling damage. Scandinavian Journal of Forest Research, 2, 199-213.
- Nordlander, G. 1990. Limonene inhibits attraction to α -pinene in the pine weevils *Hylobius abietis* and *H. pinastri*. Journal of Chemical Ecology, 16, 1307-20.
- Nordlander, G. 1991. Host finding in the pine weevil *Hylobius abietis*: effects of conifer volatiles and added limonene. Entomologia Experimentalis et Applicata, 59, 229-37.
- Nordlander, G., Bylund, H., Örländer, G. & Wallertz, K. 2003a. Pine weevil population density and damage to coniferous seedlings in a regeneration area with and without shelterwood. Scandinavian Journal of Forest Research, 18: 438-48.
- Nordlander, G., Eidmann, H.H., Jacobsson, U., Nordenhem, H. & Sjödin, K. 1986. Orientation of the pine weevil *Hylobius abietis* to underground sources of host volatiles. Entomologia Experimentalis et Applicata, 41, 91-100.
- Nordlander, G., Nordenhem, H. & Bylund, H. 1997. Oviposition patterns of the pine weevil, *Hylobius abietis*. Entomologia Experimentalis et Applicata, 85, 1-9.
- Nordlander, G., Örländer, G. and Langvall O. 2003b. Feeding by the pine weevil *Hylobius abietis* in relation to sun exposure and distance to forest edges. Agricultural and Forest Entomology, 5, 191-98.
- O'Brien, L.B. 1989. A catalog of the Coleoptera of America north of Mexico. Family Curculionidae, subfamily Pissodinae Bedell 1988. Agriculture Handbooks, 529-143d, 1-8.
- Örländer, G., Nilsson, U. & Nordlander, G. 1997. Pine weevil abundance on clear-cuttings of different ages: a 6-year study using pitfall traps. Scandinavian Journal of Forest Research, 12, 225-40.
- Örländer, G., Nordlander, G., Wallerz, K. & Nordenhem, H. 2000. Feeding in the crowns of Scots pine trees by the pine weevil *Hylobius abietis*. Scandinavian Journal of Forest Research, 15, 194-201.
- Örländer, G., Nordlander, G. & Wallerz, K. 2001. Extra food supply decreases damage by the pine weevil *Hylobius abietis*. Scandinavian Journal of Forest Research, 16, 450-54.
- Örländer, G. & Nordlander, G. 2003. Effects of field vegetation control on pine weevil (*Hylobius abietis*) damage to newly planted Norway spruce seedlings. Annals of Forest Science, 60, (in press).
- Podlaski, R. 2002. Relationship between the microhabitat and trophic conditions and the numbers of *Pissodes piceae* (Ill.) (Col., Curculionidae) in stumps of *Abies alba* Mill. in the Swietokrzyski National Park (Poland). Journal of Applied Entomology, 126, 207-11.

- Pohris, V. 1983. Untersuchungen zur Frassaktivität des Grossen braunen Russelkäfers, *Hylobius abietis* L. (Coleoptera: Curculionidae) in Abhängigkeit von Licht, Temperatur und Luftfeuchtigkeit im Phytotron-Versuch. Wissenschaftliche Zeitschrift Technische Universität Dresden, 32, 211-15.
- Pye, A.E. & Claesson, R. 1981. Oviposition of the large pine weevil, *Hylobius abietis* (Coleoptera, Curculionidae), in relation to the soil surface. Annales Entomologici Fennici, 47, 21-24.
- Riis, A. 1975. *Pissodes piniphilus* in Estonia. Metsanduslikud Uurimused, 12, 294-314.
- Roques, A. (1976) Observations sur la biologie et l'écologie de *Pissodes validirostris* Gill (Coléoptère, Curculionidae) en forêt de Fontainebleau. Annales de Zoologie et d'Ecologie Animale, 8: 523-42.
- Sahota, T.S., Manville, J. F., Peet, F.G., White, E.E., Ibaraki, A., & Nault, J. R. 1998. Resistance against white pine weevil: effects on weevil reproduction and host finding. Canadian Entomologist, 130, 337-47.
- Salisbury, A.N. & Leather, S.R. 1998. Migration of larvae of the large pine weevil, *Hylobius abietis* L. (Col., Curculionidae): possible predation a lesser risk than death by starvation? Journal of Applied Entomology, 122, 295-99.
- Schwerdtfeger, F. 1970. Die Waldkrankheiten. Ein Lehrbuch der Forstpathologie und des Forstschatzes. Parey-Verlag, Hamburg-Berlin.
- Scott, T.M. & King, C.J. 1974. The large pine weevil and black pine beetles. Forestry Commission Leaflet, 58, 2-12. London: HMSO.
- Selander, J. 1978. Evidence of pheromone-mediated behaviour in the large pine weevil, *Hylobius abietis* (Coleoptera, Curculionidae). Annales Entomologici Fennici, 44, 105-12.
- Selander, J. & Jansson, A. 1977. Sound production associated with mating behaviour of the large pine weevil, *Hylobius abietis* (Coleoptera, Curculionidae). Annales Entomologici Fennici, 43, 66-75.
- Sibul, I., Merivee, E. & Luik, A. 1999. On diurnal locomotor activity of *Hylobius abietis* L. (Coleoptera, Curculionidae). Proceedings of the XXIV Nordic Congress of Entomology, Tartu, Estonia, 163-66.
- Solbreck, C. 1980. Dispersal distances of migrating pine weevils, *Hylobius abietis*, Coleoptera: Curculionidae. Entomologia Experimentalis et Applicata, 28, 123-31.
- Solbreck, C. & Gyldberg, B. 1979. Temporal flight pattern of the large pine weevil, *Hylobius abietis* L. (Coleoptera, Curculionidae), with special reference to the influence of weather. Zeitschrift für angewandte Entomologie, 88, 532-36.
- Starzyk, J.R. 1996. Bionomics, ecology and economic importance of the fir weevil, *Pissodes piceae* (Ill.) (Col., Curculionidae) in mountain forests. Journal of Applied Entomology, 120, 65-75.
- Stenseth, C. 1976. Some aspects of the biology of *Otiorrhynchus sulcatus* (Coleoptera: Curculionidae). Forsknig og forsøk i landbruket, 27, 133-44.
- Stenseth, C. 1979. Effects of temperature on development of *Otiorrhynchus sulcatus* (Coleoptera: Curculionidae). Annals of Applied Biology, 91, 179-85.
- Tanigoshi, L., Menzies, G., Bathe, R., Youngquist, D., Dahlqvist, S. & Murray, T., 1999. Root weevil egg laying studies. WSU Vancouver, Lynden Satellite Research Station.
- Thorpe, K.V. & Day, K.R. 2002. The impact of host plant species on the larval development of the large pine weevil, *Hylobius abietis* L. Agricultural and Forest Entomology, 4, 187-94.
- Thorsén, Å., Mattsson, S. & Weslien, J. 2001. Influence of stem diameter on the survival and growth of containerized Norway spruce seedlings attacked by pine weevils (*Hylobius* spp.). Scandinavian Journal of Forest Research, 16, 54-66.
- Tilles, D.A., Eidmann, H.H. & Solbreck, B. 1988. Mating stimulant of the pine weevil *Hylobius abietis* (L.). Journal of Chemical Ecology, 14, 1465-1503.
- Tilles, D.A., Nordlander, G., Nordenhem, H., Eidmann, H.H., Wassgren, A.-B. & Bergström, G. 1986. Increased release of host volatiles from feeding scars: a major cause of field aggregation in the pine weevil *Hylobius abietis* (Coleoptera: Curculionidae). Environmental Entomology, 15, 1050-54.
- Van Tol, R.W.H.M. 1993. Efficacy of control of the Black Vine Weevil (*Otiorrhynchus sulcatus*) with strains of *Heterohabditis* sp. and *Steinernema* sp. and the fungus *Metarhizium anisopliae* in nursery stock. Med. Fac. Landbouww. Univ. Gent, 58/2a.
- von Sydow, F. & Örländer, G. 1994. The influence of shelterwood density on *Hylobius abietis* (L.) occurrence and feeding on planted conifers. Scandinavian Journal of Forest Research, 9, 367-75.
- Wagner, R. E. & Negley, F. B. 1976. The genus *Otiorrhynchus* in America north of Mexico (Coleoptera: Curculionidae). Proceedings of the Entomological Society of Washington, 78, 240-62.
- Wainhouse, D., Ashburner, R. & Boswell, R. 2001. Reproductive development and maternal effects in the pine weevil *Hylobius abietis*. Ecological Entomology, 26, 655-61.

- Wainhouse, D., Boswell, R.. & Ashburner, R Maturation feeding and reproductive development in adult pine weevil, *Hylobius abietis*. Bulletin of Entomological Research, in press.
- Wilson, W.L. & Day, K.R. 1995. The comparative effectiveness of chemical traps, and fir, spruce and larch billets, for the estimations of pine weevil (*Hylobius abietis* L.) density indices. Journal of Applied Entomology, 119, 157-60.
- Wilson, W.L. & Day, K.R. 1996. Variation in the relative abundance of the large pine weevil among Sitka spruce plantation sites. Forestry, 69,169-71.
- Wilson, W.L., Day, K.R. & Hart, E.A. 1996. Predicting the extent of damage to conifer seedlings by the pine weevil (*Hylobius abietis* L.): a preliminary risk model by multiple logistic regression. New Forests, 12, 203-22.
- Zagatti, P., Lempérière, G. & Malosse, M. 1997. Monoterpene emitted by the large pine weevil, *Hylobius abietis* (L.) feeding on Scots pine, *Pinus sylvestris* L. Physiological Entomology, 22, 394-400.
- Zumr, V. & Stary, P. 1993. Baited pitfall and flight traps in monitoring *Hylobius abietis* (L.) (Col. Curculionidae). Journal of Applied Entomology, 115, 454-61.
- Zumr, V. & Stary, P. 1994. Seasonal occurrence of *Hylobius abietis* (L.) (Col., Curculionidae) in different forest environments of a model area. Journal of Applied Entomology, 118, 361-64.

Chapter 15

SEMIOCHEMICALS IN THE LIFE OF BARK FEEDING WEEVILS

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1. INTRODUCTION

There is a strong taxonomic bias and limitation in the literature on the BAWBILT group of bark feeding weevils in general and on the reactions to semiochemicals in particular. All are conifer feeding species.

Of the 11 species of weevils on the BAWBILT list, only one species, the large pine weevil *Hylobius abietis*, has been studied in regard to host selection and the chemical signals mediating the orientation to and selection of the host plant for feeding, sex-recognition, and egg-laying. In addition, recent work on anti-feedants has focused entirely on this species. Thus, while there is some information on the Palearctic *H. pinastri* and *Pissodes* spp and from the Nearctic on *Pissodes* spp and *H. pales* and other root-weevils, this chapter will deal almost exclusively with the large pine weevil, *Hylobius abietis* (L.).

2. ORIENTATION BY ADULTS AND LARVAE TO THE HOST

The orientation on different scales in the life of pine weevils relates to different resources –ecological entities depending on the life-cycle (Trädgårdh 1913; Bejer-Petersen *et al.* 1962). The orientation of pine weevils could be seen as a series of behavioural steps on different spatial scales. The steps span from orientation over the landscape towards habitat by flying adults at km-scale to the larval feeding migrations at cm-scale (Fig. 1). Migration to new patches by adults is mandatory as the larval feeding destroys the substrate (bark of conifer roots) in one or a few years. The steps are discussed below in sequence in relation to stimuli from habitat, breeding trees, feeding patches, mates etc.

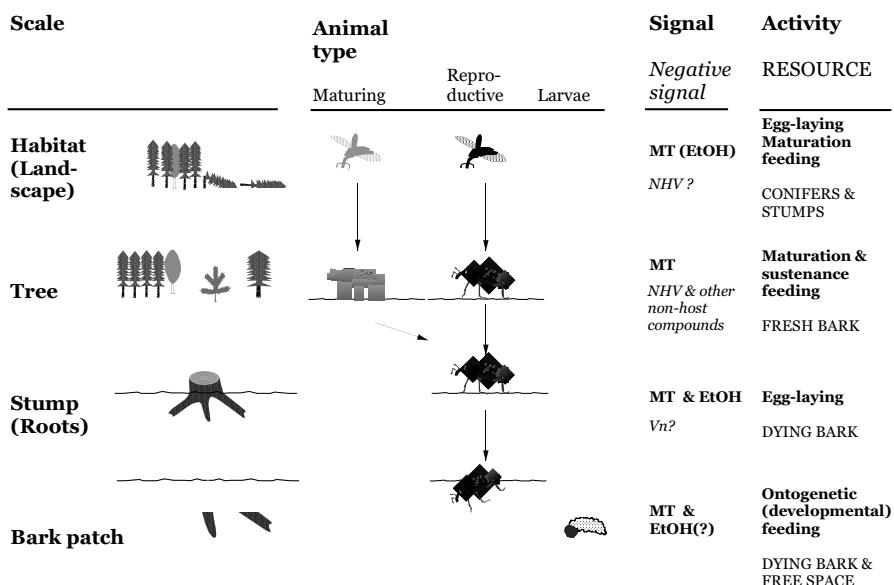


Figure 1 – Level of behavioural steps at different scales in *Hylobius abietis*. MT) Monoterpene hydrocarbons (like α -pinene, see Figure 2), EtOH) ethanol (and probably other stress-induced volatiles), NHV) Non-host Volatiles. See text for references.

2.1. Breeding adults: Habitat

At the largest scale (1–10 km), the weevil needs to navigate the forest landscape when migrating to find a habitat suitable for breeding (Fig. 1). The suitable habitat is patches of conifer forest where dying roots are available as part of trees or as fresh stumps (felling areas in modern forestry).

In Scandinavia this migration is done by long distance flights (Solbreck 1980) guided by olfactory cues. That the long distance orientation in fact occurs towards odour sources, rather than to general landscape features, is evidenced by the large numbers of weevils observed in the artificial industrial landscapes of large sawmills processing conifer logs (Solbreck and Gyldberg 1979). Interestingly, this evidence is strong only in North and East Europe.

Fresh, uninfested spruce and pine logs are by themselves attractive to flying *H. abietis*, proving a wide sense primary attraction to the host plants (*sensu* Schlyter & Birgersson 1999; attraction to volatiles from healthy hosts, stress-induced volatiles like ethanol need not be present) (Tunset *et al.*; 1993, Brattli *et al.* 1998). It is not clear how important ethanol is at this larger scale, but it probably play some role as it is active in flight traps (Lindelöw *et al.* 1992). Early on, Mustaparta (1973) conclusively showed the existence of neurones in single sensilla on the antenna that physiologically respond to host volatiles and their relation to behaviour (Mustaparta 1975). Wibe and co-authors (Wibe and Mustaparta 1996; Wibe *et al.* 1996, 1997,

1998) showed neurones in single sensilla with high specificity to many host volatiles (Wibe *et al.* 1998; Mustaparta 2002), mostly monoterpene hydrocarbons like α -pinene (Fig. 2). A more comprehensive study of behavioural responses to attractant candidates (Muller and Gunther 1991) is under way (Roten *et al.* 2002).

2.2. Breeding adults: Adult feeding patches (trees) by odour and other modalities

At the next step of scale (1–100s m) when the insect is present in the suitable habitat, adults must find spaced large mature trees (10–100m scale) or densely planted small seedlings (1–10 m scale) for feeding. After landing in the suitable habitat or emerging from the breeding substrate (for most individuals today: the clear-cuts of modern forestry) the adults need not only to locate the egg-laying sites. They also need live host-plants for maturation and sustenance feeding to fill their demand for the long egg-laying and mating period (Fig. 1).

The adults feed mostly in the crown of mature trees in and nearby felling areas – recently quantified by Örlander *et al.* (2000). This feeding on larger trees causes little or no harm as it is small in relation to the bark biomass of mature trees. Unfortunately for forestry production, the adults feed not only on the mature trees but as well on the small seedlings (transplants) planted in the clear-cuts. The feeding of a single weevil at a seedling stem base may consume a large part of bark of the stem and may easily ring-bark the transplant. This is where their economic damage occurs.

Insects normally integrate olfactory, visual and tactile cues for the purpose of finding (mainly) host plants for feeding (Finch 1986; Chapman and deBoer 1995; Schoonhoven *et al.* 1998). Apart from olfaction, visual cues are indicated for *H. pales* (Hunt and Raffa 1991). Probably, the large trees are located on the larger scale (felling area vs. edge, 10–100 m) by visual cues, possibly directly in flight when coming into the habitat (Örlander *et al.* 2000), and the feeding sites found by tactile cues. The densely planted small seedlings might be encountered to a large degree by random walks (Björklund *et al.* 2002), but host odour, enhanced by feeding scars effluvia, aids the adults in finding the transplants for feeding (Tilles *et al.* 1986b; Nordlander 1991). Furthermore, there is an effect on beetle movement in orientation to seedlings if they stand surrounded by mineral soil or humus (Kindvall *et al.* 2000). A pure mineral soil makes weevil movements faster and the animal less likely to stay on a mineral soil patch (Kindvall *et al.* 2000), interfering with host finding. However, also host acceptance at very close range is interfered with and in the field the mineral soil partly protects transplants from feeding (Björklund *et al.* 2002).

2.3. Breeding adults: Breeding patches and mate recognition

Location by reproductive adults of breeding patches like stumps and roots takes place on a m–dm-scale, while mate recognition occurs on the smallest scale of mm to cm. While the physical scale and the chemical compounds differ, the chemical senses, mainly olfaction, is the modality for these steps.

2.3.1. Long distance

The longer distance orientation to breeding patches does not seem to differ from that of many other bark- and wood-living beetles. In particular, some root infesting bark beetles can be attracted to and sampled by the same signals (*Hylastes* spp: Eidmann *et al.* 1991; Erasmus and Chown 1994; Erbilgin *et al.* 2001). The weevil breeds in dying roots of conifers, such as those of storm-felled or cut trees, and does not appear to have a long-distance pheromone (Tilles *et al.* 1988; Zagatti *et al.* 1997) in spite of some early indications to that effect (Mustaparta 1974, 1975). As in *Tomicus piniperda* bark beetles (Byers *et al.* 1985), feeding beetles on Scots pine (*Pinus sylvestris*) logs enhance attraction somewhat over uninfested logs, but no more than can be explained by the increased release of host odours (Tilles *et al.* 1986b; Zagatti *et al.* 1997). The attraction of long-horn beetles (cerambycids), bark weevils (curculionids), and non-aggressive bark beetles to combinations of conifer volatiles and ethanol is well established (Fig. 2, Moeck 1970; Klimetzek *et al.* 1986; Schroeder 1988; Byers 1992; Lindelöw *et al.* 1992; Erasmus and Chown 1994). Attraction to ethanol alone or in combination with odours from stressed hosts occurs also in long-horns and bark beetles living in hardwoods (Montgomery and Wargo 1983; Dunn and Potter 1991). In dying stems, roots, or logs the release of ethanol (Moeck 1970) and other low-molecular products is due to anaerobic stress (Graham 1968; Davies 1980; Kimmerer and Kozolowski 1982; Kelsey 1996; Kelsey and Joseph 1997; Kelsey 2001) or decay fungi (Gara *et al.* 1993). These stress signals make the host material more attractive. It should be noted that the stress reaction in living tissue in stumps (vonSydow and Birgersson 1997) is the key ethanol production mechanism, while the microbial degradation of killed tissue is less important (Kelsey 2001).

A stress-induced primary attraction seems active in the pine weevil, shown by the synergism between ethanol and conifer host volatiles (Tilles *et al.* 1986a; Nordlander 1987). A study in Scandinavia by Lindelöw *et al.* (1992) showed that *H. abietis* was the only species attracted consistently not only to combinations of host monoterpenes and ethanol, but also to ethanol itself, indicating a preference for strongly stressed (dying) host roots (Fig. 1). This is proof of stress-induced primary attraction (*sensu* Schlyter and Birgersson 1999), agreeing well with the status of the dying breeding substrate. Ecologically similar weevils and scolytids –breeding in conifer roots– have broadly similar responses to turpentine, α -pinene, ethanol, and their combinations (Fig. 2). A combination of turpentine and ethanol is generally attractive (Lindelöw *et al.* 1993). Among weevils, only *H. abietis* was attracted to ethanol alone, whereas *H. pinastri* was the only species not significantly attracted to ethanol plus spruce turpentine (Lindelöw *et al.* 1993).

2.3.2. Final location

At the final step in location of breeding patches, a short distance orientation (dm-scale) occurs to individual roots (of stumps) for egg-laying (Fig. 1). Weevils walk on the forest floor (litter) and dig through the soil towards the stress signals from roots, as described in laboratory studies by Nordlander *et al.* (1986). Older stumps will release not only hydrocarbon monoterpenes and ethanol, but also oxygenated

monoterpene like verbenone, which in larger doses inhibits attraction to host material (Lindgren *et al.* 1996). Whereas breeding success differs among conifer hosts both for *Hylobius abietis* (Thorpe & Day 2002) and for Nearctic *Hylobius* (Hunt *et al.* 1993), attraction to different host by reproductives have been little studied.

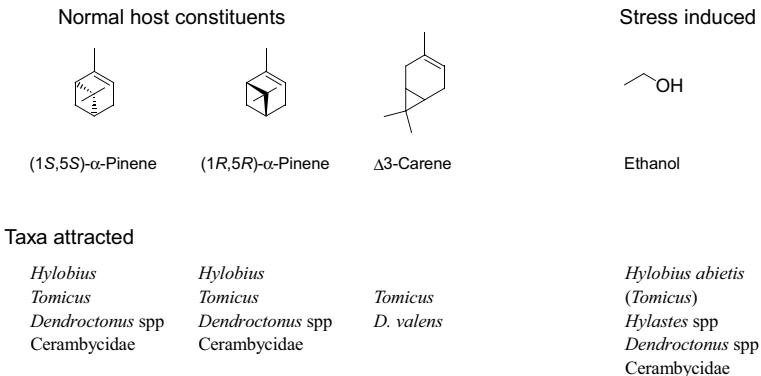


Figure 2 – Kairomonal attractants in weevils and other BAWBILTs. Figure redrawn from Schlyter and Birgersson (1999). For most root feeding beetles, like *Hylobius* and *Hylastes*, and those breeding in substrates of dying host tissue there is a synergism between monoterpene and ethanol.

2.3.3. Mate recognition

Another type of final step is the recognition by males of their female sex partners at close distance (cm- or mm-scale). The short-range contact sex-recognition pheromone is partly characterised as a long-chain, low volatile extractable compound from the female cuticle (Tilles *et al.* 1988).

2.4. Larval orientation to feeding patches

A basic piece of the biology, the normal egg-laying site, was only recently discovered in Swedish studies. Most of egg-laying is in fact not directly on the host bark but in the soil near roots (field: Nordlander *et al.* 1997). Even the small 1st instar larvae may migrate for 5 cm through soil to the feeding substrate (lab: Nordenhem and Nordlander 1994). Larger larvae may also leave over-crowded sites and migrate through soil to other parts of the root (Nordenhem and Nordlander 1994), which may increase survival in spite of an increased risk of predation (Salisbury and Leather 1998). The signal used by the larvae is the same as for adults orienting to dying roots; monoterpenes (α -pinene) and ethanol (Fig. 1, Nordenhem and Nordlander 1994).

2.5. Non-breeding adults

The responses to olfactory stimuli in the phases of the adult life cycle reflect the seasonal needs, egg-laying plus food or food only, respectively (Nordenhem and Eidmann 1991). The non-breeding (pre-reproductive) adults are more attracted to fresh host material or monoterpene mixtures with no ethanol added, whereas breeding adults require older material with ethanol emission (Nordenhem and Eidmann 1991; Malphettes *et al.* 1994; Zumr *et al.* 1995). A similar pattern was found in the Nearctic *Hylobius radicis* Buchanan, *H. assimilis* Boheman, *H. pales* (Herbst), and *Pachylobius picivorus* (Germar). The non-reproducing animals were found only in passive traps, while reproductively mature individuals of all species were found in terpene + ethanol traps (Hoffman *et al.* 1997).

3. HOST ACCEPTANCE IN ADULT FEEDING

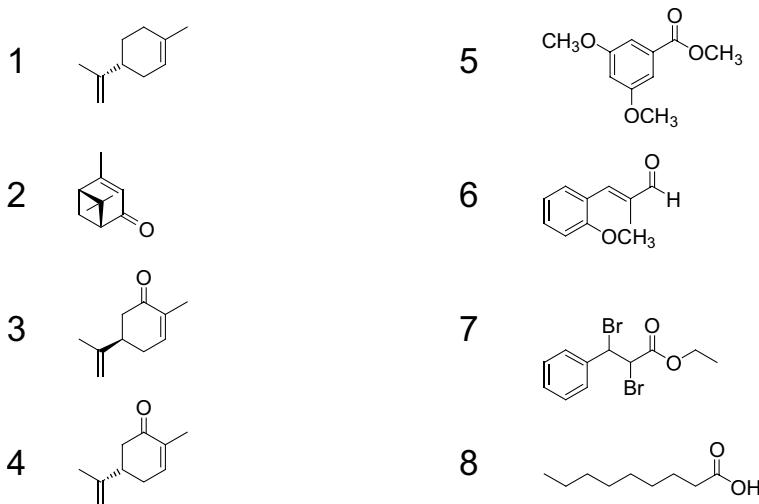
The preference for conifers is far from absolute, the adults have been observed feeding on both coniferous and broad-leaved tree species (Scott and King 1974) and appear to be more an oligophagous than a monophagous species. The insects have been presented to a number of woody plant species where they showed a preference in the order: *P. sylvestris* >> *B. pendula* >> *P. abies* >> *F. excelsior* > *A. pseudoplatanus* (Leather *et al.* 1994; Manlove *et al.* 1997). Recently, Måansson & Schlyter (2003) showed in no-choice tests that the outer bark was contacted and removed in 35 of 38 spp offered from 25 plant families. However, in 17 spp the inner bark was not accepted for feeding, indicating that while regarded as food by the insects, these species had anti-feedant qualities in their inner bark causing the weevils to starve rather than to feed for 48 h. Also in the field, feeding on non-conifer seedlings like *Fagus* and *Quercus* occurs frequently (Löf 2000). Such feeding damage may, however, be intermixed with damage from short-snouted weevils (*Otiorrhynchus scaber* L. and *Strophosoma melanogramma* Forst.), that feed predominantly on angiosperm seedlings (Löf 2000). At the weevil densities prevailing today in forestry, there is also evidence for a strong random component in the contact of the weevils with seedlings. Judging from frequent catches in traps surrounding intact spruce seedlings, most seedlings will be visited within 2.5 cm by a weevil once a week (Björklund *et al.* 2002). Such random plant contacts may partly explain the feeding on non-hosts (Löf 2000).

Several single components from *Pinus* host bark have, somewhat surprisingly, been implicated as anti-feedants or repellents (Dethier *et al.* 1960) for adult pine weevil feeding (Fig. 3). Nordlander (1990, 1991) reported limonene, a monoterpene hydrocarbon, as inhibitor of attraction to the host. Lindgren *et al.* (1996) quantified the inhibition of feeding in response to the oxygenated monoterpene verbenone as did Klepzig and Schlyter (1999) for carvone, another monoterpene ketone. Bratt *et al.* (2001) reported anti-feedant activity of a new natural product, ethyl 2,3-dibromo-3-phenylpropanoate, –a halogenated phenylpropanoid derivative from *P. contorta*. The fact that these and several other components coming from host tissue (Klepzig and Schlyter 1999) are active as negative signals for feeding is puzzling. It could be explained by the testing at unnaturally high doses and/or by the testing alone without the full complimentary blend of other host signals. Non-host bark

may, naturally, yield more of anti-feedant compounds (Månnsson 2001, Månnsson & Schlyter 2003, Månnsson et al. 2004)

A type of deterrent pheromone found in the faeces laden material added by the ovipositing female over the egg and egg-niche, in cases where egg-laying occurs directly on the bark, has been tentatively reported (Nordlander 1999). An anti-feedant component (methyl-3,5-dimethoxybensoate) from the faeces material has been reported as field active (Nordlander *et al.* 2000a; Nordlander 2001).

However, not only strict semiochemicals may be active chemicals in weevil host selection. Sahota *et al.* (2001) showed negative post-ingestive effects, probably toxic, on ovarian growth in *Pissodes strobi* of extracts from resistant *Picea sitchensis*.



*Figure 3 – Molecules with reported anti-feedant activity of different origin: Left column those found in host *Pinus sylvestris* tissue (1: (R)-Limonene, Nordlander 1990; 2: Verbenone, Lindgren *et al.* 1996; 3 & 4: (R)-(+)- and (S)-(-)-Carvone, Klepzig and Schlyter 1999). Right column from other sources (5: Beetle faeces, Aromatic ester, Nordlander *et al.* 2000, 6: Non-hosts, Aromatic aldehyde, Eriksson *et al.* 2002; 7: *Pinus contorta*, halogenated phenylpropanoid, Bratt *et al.* 2001 8: Non-host *Tilia cordata*, Nonanoic acid, Månnsson *et al.* 2004). [FS1]*

4. OPTIONS FOR CONTROL BY SEMIOCHEMICALS

The actual problem for production forestry occurs during the subsistence feeding by older adults and maturation feeding by young adults on seedlings. Direct control must aim at either diminishing weevil populations or preventing feeding on the small transplants. A control program will also need accurate forecasting or monitoring of weevil distribution and abundance to predict damage.

4.1. Pheromones and kairomone attractants

Conventionally, semiochemical attractants have had three major applications; monitoring, mass-trapping, and mating-disruption. For the boll weevil (*Anthonomus grandis* Boh.) and for *K*-selected palm weevils (*Rhynchophorus* and *Metamasius* spp) a mass-trapping with aggregation pheromones have been reported as efficient (Plato *et al.* 2000, Oehlschlager *et al.* 2002). As the pine weevil has no long-range pheromone, the options for a competitive attractant useful in mass-trapping or disruption are bleak. Pheromones are species-specific signals produced only by the insect, often multi-component and active at very low levels. In contrast, a kairomone (host odour) signal is especially in conifer-inhabiting species not very specific and field-active only at rather high rates of release (Byers *et al.* 1985; Tilles *et al.* 1986a, b). These rates can never compete with the same compounds, released en masse from host materials that are abundant in the suitable habitat, in attracting any major proportion of the population. The short-range sex-recognition pheromone found in adult females (Tilles *et al.* 1988) will, due to the short range of action (mm–cm) be of little use for a conventional semiochemical usage.

Only for the monitoring trapping has kairomone bait and walk-in traps for use in clear-cuts been developed (Nordlander 1987). The synergistic bait of α -pinene and ethanol (Tilles *et al.* 1986a) is, however, best suited for mature (egg-laying period) weevils only (Nordenhem and Eidmann 1991; Malphettes *et al.* 1994). For North American root weevils (Fettig *et al.* 1998, Rieske 2000) as well as for *H. abietis* (Zumr and Stary 1992, Wilson and Day 1995), an increase of catch or attraction is reported of fresh host logs or bark over synthetic monoterpenes alone.

However, the relation between weevil damage and weevil catch in pitfall traps is not straightforward and may only exist at the end of the season (Nordlander 1987). In a large and well-replicated long-term study, problems existed in relating insect catches to feeding damage over a 6-year period, and only at 2 years was the correlation significant (Örlander *et al.* 1997).

4.2. Allomonal antifeedants and repellents

Schlyter and Löfqvist (1998) and Leather *et al.* (1999) suggested that deterrents and pre-ingestive anti-feedants (*sensu* Måansson 2001) could be used, relying on techniques developed for several other insects (Koul 1993, Frazier and Chyb 1995). So far, there are few formal papers published on laboratory tests of European *Hylobius* in spite of intensive research efforts (Beitzenheineke and Hofmann 1992; Klepzig and Schlyter 1999; Bratt *et al.* 2001). The use of 'neem' formulations (Schmutterer 1995) has been tested in *Hylobius* spp (Beitzenheineke and Hofmann 1992; Salom *et al.* 1994, 1996; Klepzig and Schlyter 1999, Sibul *et al.* 2001), but with the exception of Sibul *et al.* (2001) there is little success. Several papers in 'grey literature' report more or less successful applications in the field of a few compounds (Schlyter 1998, 2001; Schlyter *et al.* 2000, 2004b; Fojtik *et al.* 2000; Nordlander *et al.* 2000b; Nordlander 2001; Sibul *et al.* 2001). The compounds reported are rather diverse but mostly volatiles (Fig. 3).

Whereas satisfactory efficacy has been reported in several cases, a major problem seems to be the formulation for extended field activity (Sjödin *et al.* 2001; Löfqvist *et al.* 2002a). Nevertheless, patents have now been granted or applied for a number of anti-feedants/repellents and the formulation of these (Nordlander *et al.* 2000a; Löfqvist *et al.* 2002b).

CONCLUSIONS

Two very general conclusions can be made based on the available literature:

- Signals for orientation (kairomone volatiles) are relatively well known and practically useful in the field. Even so, work remains on the behavioural activity of several host monoterpenes.
- Host acceptance signals in adult feeding (both feeding stimulants and inhibitors) are little known, in spite of work in several applied projects with allomonal anti-feedants (Nordlander *et al.* 2000b; Smitt 2002).

Several specific future research issues include:

- 1- Why are young conifer seedlings so little resistant to adult weevil attacks, which seem so important in modern forestry? One reason might be that the selection pressures (predation) over the life of the seedling are quite diverse and the weevil defence is not the only concern. Nystrand and Granström (2000) showed several other mortality factors: seed predation by carabids (*Pterostichus*, *Calathus*) and predation by slugs (*Arion*) as the most important factors for young – juvenile (weeks) seedlings. Mortality of juvenile seedlings was not related to catches of pine weevils in their study. Are these small trees physiologically incapable of resistance or are selection pressures too variable during the life of the tree to affect traits expressed during the seedling period?
- 2- Direct control by population reduction by semiochemical mass-trapping is not possible. Monitoring by kairomone baited walk-in traps could be more accurate in regions that have less dispersal by flight than in Scandinavia.
- 3- Adult feeding decisions is partly by contact chemoreception and can be redirected. Research on the anti-feedants structure-activity and formulations may well provide a key element for seedling protection.
- 4- Compared to the well-studied kairomone responses of predatory Coleoptera (e.g. Erbilgin and Raffa 2001; Schroeder 2003) and parasitoid Hymenoptera (Pettersson 2001) attacking conifer bark beetles, essentially nothing is known about semiochemical responses in bark weevil predators or parasitoids.
- 5- Sex recognition pheromone identification would allow new avenues of testing a low-volatile compound for behavioural modification. How would males and females react to a small host plant that smells like a sexually active female?

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REFERENCES

- Beitzenheineke, I. & Hofmann, R. 1992. Experiments on the Effect of an Azadirachtin-Containing, Formulated Preparation Azt-Vr-Nr on *Hylobius abietis* L., *Lymantria monacha* L., and *Drino inconspicua* Meig. Journal of Plant Diseases and Protection, 99, 337-48.
- Bejer-Petersen, B., Juutinen, P., Kangas, E., Bakke, A., Butovitsch, V., Eidmann, H., Hedqvist, K.J. & Lekander, B. 1962. Studies on *Hylobius abietis* L. Development and life cycle in the Nordic Countries. Acta Entomologica Fennica, 17, 1-17.
- Björklund, N., Nordlander, G. & Bylund, H. 2002. Host-plant acceptance on mineral soil and humus by the pine weevil *Hylobius abietis* (L.). Agricultural and Forest Entomology, 5, 61-65.
- Bratt, K., Sunnerheim, K., Nordenhem, H., Nordlander, G. & Långström, B. 2001. Pine weevil (*Hylobius abietis*) antifeedants from lodgepole pine (*Pinus contorta*). Journal of Chemical Ecology, 27, 2253-62.
- Brattli, J.G., Andersen, J. & Nilssen, A.C. 1998. Primary attraction and host tree selection in deciduous and conifer living Coleoptera : Scolytidae, Curculionidae, Cerambycidae and Lymexylidae. Journal of Applied Entomology, 122, 345-52.
- Byers, J.A. 1992. Attraction of bark beetles, *Tomicus piniperda*, *Hylurgops palliatus*, and *Trypodendron domesticum* and other insects to short-chain alcohols and monoterpenes. Journal of Chemical Ecology, 2385-2402, 2385-402.
- Byers, J.A., Lanne, B.S., Schlyter, F., Löfqvist, J. & Bergström, G. 1985. Olfactory recognition of host-tree susceptibility by pine shoot beetles. Naturwissenschaften, 72, 324-26.
- Chapman, R.F. & deBoer, G. 1995. Regulatory Mechanisms in Insect Feeding. Chapman & Hall.
- Davies, D.D. 1980. Anaerobic metabolism and the production of organic acids. In. P.K. Stumpf Conn, E.E. (Eds.), The Biochemistry of Plants Vol. 2. Academic press, pp. 581-611.
- Dethier, V.G., Browne, L.B. & Smith, C.N. 1960. The designation of chemicals in terms of the responses they elicit from insects. Journal of Economic Entomology, 53, 134-36.
- Dunn, J.P. & Potter, D.A. 1991. Synergistic Effects of Oak Volatiles with Ethanol in the Capture of Saprophagous Wood Borers. Journal of Entomological Science, 26, 425-29.
- Eidmann, H.H., Kula, E. & Lindelöw, A. 1991. Host Recognition and Aggregation Behaviour of *Hylastes cunicularius* Erichson (Col, Scolytidae) in the Laboratory. Journal of Applied Entomology, 112, 11-18.
- Erasmus, M.J. & Chown, S.L. 1994. Host Location and Aggregation Behavior in *Hylastes angustatus* (Herbst) (Coleoptera, Scolytidae). African Entomology, 2, 7-11.
- Erbilgin, N. & Raffa, K.F. 2001. Kairomonal range of generalist predators in specialized habitats: responses to multiple phloophagous species emitting pheromones vs. host odors. Entomologia Experimentalis & Applicata, 99, 205-10.
- Erbilgin, N., Szele, A., Klepzig, K.D. & Raffa, K.F. 2001. Trap type, chirality of α -pinene, and geographic region affect sampling efficiency of root and lower stem insects in pine. Journal of Economic Entomology, 94, 1113-21.
- Eriksson, C., Smitt, O., Schlyter, F., Sjödin, K., & Höglberg, H.-E. 2002. Searching for pine weevil antifeedants, strategy and synthesis. 19th annual meeting of International Society of Chemical Ecology, p. 217.
- Fettig, C.J., Salom, S.M. & Platt, J.O. 1998. Mark and recapture studies of *Hylobius pales* (Herbst) (Col., Curculionidae) for measuring bait and trap efficacy. Journal of Applied Entomology, 122, 423-30.
- Finch, S. 1986. Assessing host-plant finding by insects. In. *Insect-Plant Interactions* J.R. Miller Miller, T.A. (Eds.), Springer.
- Fojtík, P., Schlyter, F., Vrkoc, J. & Vrkocova, P. 2000. The large pine weevil, *Hylobius abietis* L.: Control by non-host repellents. 17th Annual Meeting of International Society of Chemical Ecology, p. PO26.

- Frazier, J.L. & Chyb, S. 1995. Use of feeding inhibitors in insect control. In. *Regulatory Mechanisms in Insect Feeding*, R.F. Chapman deBoer, G. (Eds.), Chapman & Hall.
- Gara, R.I., Little, W.R. & Rhoades, D.F. 1993. Emission of Ethanol and Monoterpenes by Fungal Infected Lodgepole Pine Trees. *Phytochemistry*, 34, 987-90.
- Graham, K. 1968. Anaerobic induction of primary chemical attractancy for ambrosia beetles. *Canadian Journal of Zoology*, 46, 905-08.
- Hoffman, G.D., Hunt, D.W.A., Salom, S.M. & Raffa, K.F. 1997. Reproductive readiness and niche differences affect responses of conifer root weevils (Coleoptera: Curculionidae) to simulated host odors. *Environmental Entomology*, 26, 91-100.
- Hunt, D.W.A. & Raffa, K.F. 1991. Orientation of *Hylobius radicis* and *Pachyllobius picivorus* (Coleoptera, Curculionidae) to Visual Cues. *Great Lakes Entomologist*, 24, 225-30.
- Hunt, D.W.A., Lintereur, G., Salom, S.M. & Raffa, K.F. 1993. Performance and Preference of *Hylobius radicis* Buchanan, and *H. pales* (Herbst) (Coleoptera, Curculionidae) on Various *Pinus* Species. *Canadian Entomologist*, 125, 1003-10.
- Kelsey, R.G. 1996. Anaerobic induced ethanol synthesis in the stems of greenhouse-grown conifer seedlings. *Trees-Structure and Function*, 10, 183-88.
- Kelsey, R.G. 2001. Chemical indicators of stress in trees: Their ecological significance and implication for forestry in eastern Oregon and Washington. *Northwest Science*, 75, 70-76.
- Kelsey, R.G. & Joseph, G. 1997. Ambrosia beetle host selection among logs of Douglas fir, western hemlock, and western red cedar with different ethanol and α -pinene concentrations. *Journal of Chemical Ecology*, 23, 1035-51.
- Kimmerer, T.W. & Kozolowski, T.T. 1982. Ethylene, ethane, acetaldehyde and ethanol production by plants under stress. *Plant Physiology*, 69, 840-47.
- Kindvall, O., Nordlander, G. & Nordenhem, H. 2000. Movement behaviour of the pine weevil *Hylobius abietis* in relation to soil type: an arena experiment. *Entomologia Experimentalis Et Applicata*, 95, 53-61.
- Klepzig, K.D. & Schlyter, F. 1999. Laboratory evaluation of plant-derived antifeedants against the pine weevil *Hylobius abietis* (Coleoptera : Curculionidae). *Journal of Economic Entomology*, 92, 644-50.
- Klimetzek, D., Köhler, J., Vité, J.P. & Kohnle, U. 1986. Dosage response to ethanol mediates host selection by "secondary" bark beetles. *Naturwissenschaften*, 73, 270-72.
- Koul, O.B.K. 1993. Plant allelochemicals and insect control: An antifeedant approach. In. *Chemical ecology of phytophagous insects*. T.N. Ananthakrishnan Raman, A. (Eds.), International Science Publisher.
- Leather, S.R., Ahmed, S.I. & Hogan, L. 1994. Adult Feeding Preferences of the Large Pine Weevil, *Hylobius abietis* (Coleoptera, Curculionidae). *European Journal of Entomology*, 91, 385-89.
- Leather, S.R., Day, K.R. & Salisbury, A.N. 1999. The biology and ecology of the large pine weevil, *Hylobius abietis* (Coleoptera : Curculionidae): a problem of dispersal? *Bulletin of Entomological Research*, 89, 3-16.
- Lindlöw, Å., Risberg, B. & Sjödin, K. 1992. Attraction During Flight of Scolytids and Other Bark-Dwelling and Wood-Dwelling Beetles to Volatiles from Fresh and Stored Spruce Wood. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 22, 224-28.
- Lindlöw, Å., Eidmann, H.H. & Nordenhem, H. 1993. Response on the Ground of Bark Beetle and Weevil Species Colonizing Conifer Stumps and Roots to Terpenes and Ethanol. *Journal of Chemical Ecology*, 19, 1393-403.
- Lindgren, B.S., Nordlander, G. & Birgersson, G. 1996. Feeding deterrence of verbenone to the pine weevil, *Hylobius abietis* (L) (Col, Curculionidae). *Journal of Applied Entomology*, 120, 397-403.
- Löf, M. 2000. Influence of patch scarification and insect herbivory on growth and survival in *Fagus sylvatica* L., *Picea abies* L. Karst. and *Quercus robur* L. seedlings following a Norway spruce forest. *Forest Ecology and Management*, 134, 111-23.
- Löfqvist, J., Schlyter, F. & Höglberg, H.-E. 2002a. *Anti-feedants -a seedling protection method against damage by the Pine weevil* (In Swedish: Gnaghämmare - en metod för plantskydd mot snyttbaggeskador). Årsrapport 2001. Feromoner och Kairomoner för bekämpning av skadeinsektar, ett MISTRA finansierat forskningsprogram,,.
- Löfqvist, J., Smitt, O., Höglberg, H.-E., Schlyter, F. & Sjödin, K. 2002b. Composition for inhibiting feeding of weevils. PCT Patent Application WO0200022.

- Malphettes, C.B., Fourgeres, D. & Saintonge, F.X. 1994. Study of the Sexual Development of Large Pine Weevil Females (*Hylobius abietis* L) (Coleoptera, Curculionidae) Caught in Kairomones Baited Pitfall Traps. Anzeiger für Schadlingskunde Pflanzenschutz Umweltschutz, 67, 147-55.
- Manlove, J.D., Styles, J. & Leather, S.R. 1997. Feeding of the adults of the large pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae). European Journal of Entomology, 94, 153-56.
- Moek, H.A. 1970. Ethanol as the primary attractant for the ambrosia beetle *Trypodendron lineatum* (Coleoptera: Scolytidae). Canadian Entomologist, 102, 985-95.
- Montgomery, M.E. & Wargo, P.M. 1983. Ethanol and other host-derived volatiles as attractants to beetles that bore into hardwoods. Journal of Chemical Ecology, 9, 181-90.
- Muller, M. & Gunter, H. 1991. The Response of the Large Pine Weevil, *Hylobius abietis* L (Coleoptera, Curculionidae), to Certain Chemical-Compounds of Its Host Plants. Archives of Phytopathology and Plant Protection, 27, 299-306.
- Mustaparta, H. 1973. Olfactory sensilla on the antennae of the Pine weevil, *Hylobius abietis*. Zeitschrift für Zellforschung, 144, 559-71.
- Mustaparta, H. 1974. Response of the Pine weevil, *Hylobius abietis* L., to bark beetle pheromones. Journal of Comparative Physiology, 88, 395-98.
- Mustaparta, H. 1975. Behavioural responses of the Pine weevil *Hylobius abietis* L (Col. : Curculionidae) to odours activating different groups of receptor cells. Journal of Comparative Physiology, 102, 57-63.
- Mustaparta, H. 2002. Encoding of plant odour information in insects: peripheral and central mechanisms. Entomologia Experimentalis Et Applicata, 104, 1-13.
- Månnsson, P.E. 2001. The role of anti-feedants in host selection of herbivorous insects. Introductory essay No. 5. Chemical Ecology, Crop Science. Swedish University of Agricultural Sciences, Alnarp.
- Månnsson, P.E., and Schlyter, F. 2003. *Hylobius* pine weevils adult host selection and antifeedants: feeding behaviour on host and non-host woody Scandinavian plants. Agricultural and Forest Entomology, 4, in press.
- Månnsson, P.E. et al. Antifeedants in *Hylobius abietis* Pine Weevils: Finding an active compound in extract from *Tilia cordata* Mill., Linden/Lime tree *in prep for J. Chem. Ecol.*
- Nordenhem, H. & Eidmann, H.H. 1991. Response of the Pine Weevil *Hylobius abietis* L (Col, Curculionidae) to Host Volatiles in Different Phases of Its Adult Life-Cycle. Journal of Applied Entomology, 112, 353-58.
- Nordenhem, H. & Nordlander, G. 1994. Olfactory Oriented Migration through Soil by Root-Living *Hylobius abietis* (L) Larvae (Col, Curculionidae). Journal of Applied Entomology, 117, 457-62.
- Nordlander, G. 1987. A method for trapping *Hylobius abietis* (L.) with a standardized bait and its potential for forecasting seedling damage. Scandinavian Journal of Forest Research, 2, 199-213.
- Nordlander, G. 1990. Limonene Inhibits Attraction to α -Pinene in the Pine Weevils *Hylobius abietis* and *H pinastri*. Journal of Chemical Ecology, 16, 1307-20.
- Nordlander, G. 1991. Host Finding in the Pine Weevil *Hylobius abietis* - Effects of Conifer Volatiles and Added Limonene. Entomologia Experimentalis & Applicata, 59, 229-37.
- Nordlander, G. 1999. Faecal matters gave hints for seedling protection (In Swedish: Toalettbestyr gav tips om plantskydd). Skogseko, pp. 8-9.
- Nordlander, G. 2001. Feeding repellent could became seedling protection of the future (In Swedish: Gnagavskräckande ämne kan bli framtidens plantskydd). Plantaktuellt, p. 16.
- Nordlander, G., Eidmann, H.H., Jacobsson, U., Nordenhem, H. & Sjödin, K. 1986. Orientation of the Pine Weevil *Hylobius abietis* to Underground Sources of Host Volatiles. Entomologia Experimentalis et Applicata, 41, 91-100.
- Nordlander, G., Nordenhem, H. & Bylund, H. 1997. Oviposition patterns of the pine weevil *Hylobius abietis*. Entomologia Experimentalis et Applicata, 85, 1-9.
- Nordlander, G., Örländer, G., Petersson, M., Bylund, H., Wallertz, K., Nordenhem, H. & Långström, B. 2000a. Pine weevil control without insecticides -final report of a TEMA research program (In Swedish: Snytbaggebekämpning utan insekticider - slutrapport för ett TEMA-forskningsprogram). Asa Forest Research Station, pp. 1-77.
- Nordlander, G., Nordenhem, H., Borg-Karlsson, A.-K. & Unelius, R. 2000b. Use for sapling protection. Swedish and PCT Patent Application WO0056151A1.
- Nystrand, O. & Granström, A. 2000. Predation on *Pinus sylvestris* seeds and juvenile seedlings in Swedish boreal forest in relation to stand disturbance by logging. Journal of Applied Ecology, 37, 449-63.

- Oehlschlager, A.C., Gonzalez, L., Gomez, M., Rodriguez, C. & Andrade, R. 2002. Pheromone-based trapping of West Indian sugarcane weevil in a sugarcane plantation. *Journal of Chemical Ecology*, 28, 1653-64.
- Pettersson, E.M. 2001. Volatile attractants for three Pteromalid parasitoids attacking concealed spruce bark beetles. *Chemoecology*, 11, 89-95.
- Plato, T.A., Plato, J.C., Plato, J.S. & Plato, S.E. 2000. The use of attract and control technologies in the control, prevention, suppression and eradication of the cotton boll weevil. XXI International Congress of Entomology, August 20-26, #0611. International Congress of Entomology.
- Rieske, L.K. 2000. Pine weevil (Coleoptera : Curculionidae) population monitoring in Christmas trees using volatile host compounds. *Journal of Entomological Science*, 35, 167-75.
- Roten, Ø.O., Borg-Karlson, A.-K., Andersson, J. & Mustaparta, H. 2002. Behavioural responses by the pine weevil *Hylobius abietis* to odors produced by host and non-host plants. 19th Annual meeting of International Society of Chemical Ecology, August 3-7 I
- Sahota, T.S., Manville, J.F., Hollmann, J., Leal, I., Ibaraki, A. & White, E. 2001. Resistance against *Pissodes strobi* (Coleoptera : Curculionidae) in severed leaders and in a water-soluble bark extract of *Picea sitchensis* (Pinaceae): evidence for a post-ingestive mode of action. *Canadian Entomologist*, 133, 315-23.
- Salisbury, A.N. & Leather, S.R. 1998. Migration of larvae of the large Pine Weevil, *Hylobius abietis* L. (Col., Curculionidae): Possible predation a lesser risk than death by starvation? *Journal of Applied Entomology*, 122, 295-99.
- Salom, S.M., Carlson, J.A., Ang, B.N., Grosman, D.M. & Day, E.R. 1994. Laboratory Evaluation of Biologically-Based Compounds as Antifeedants for the Pales Weevil, *Hylobius pales* (Herbst) (Coleoptera, Curculionidae). *Journal of Entomological Science*, 29, 407-19.
- Salom, S.M., Gray, J.A., Alford, A.R., Mulesky, M., Fettig, C.J. & Woods, S.A. 1996. Evaluation of natural products as antifeedants for the pales weevil (Coleoptera: Curculionidae) and as fungitoxins for *Leptographium procerum*. *Journal of Entomological Science*, 31, 453-65.
- Schlyter, F. 1998. Anti-feedants - a new seedling protection against the Pine weevil (In Swedish: Gnaghämmare - ett nytt plantskydd mot snytbaggen). Årsrapport 1997. Feromoner och Kairomoner för bekämpning av skadeinsekter, ett MISTRA finansierat forskningsprogram, pp. 12-14.
- Schlyter, F. 2001. Anti-feedants as plant protection against *Hylobius* pine weevils (In Swedish: Gnaghämmare som skydd mot snytbaggar). Växtskyddsnotiser, 65, 47-53.
- Schlyter, F. & Löfqvist, J. 1998. Kan insekticider mot snytbaggen ersättas med naturliga eller syntetiska "anti-feedants"? K. Skogs-o. Lantbr. akad. Tidskr., 137, 51-58.
- Schlyter, F. & Birgersson, G. 1999. Forest Beetles. In: *Pheromone in Non-Lepidopteran Insects Associated with Agricultural Plants*, J. Hardie Minks, A.K. (Eds.), CAB International.
- Schlyter, F., Marling, E., Måansson, P.E. & Löfqvist, J. 2000. Non-host signals inhibiting feeding in *Hylobius* pine weevils: Laboratory assays and field tests. XXI International Congress of Entomology, August 20-26, #1966. International Congress of Entomology.
- Schlyter, F., Löfqvist, J., Smitt, O., Sjödin, K. & Höglberg, H.-E. 2004a. Carvone and less volatile analogues as repellent and deterrent antifeedants against the pine weevil, *Hylobius abietis* (L.). *J. Chem. Ecol.*, (submitted).
- Schlyter, F., Örländer, G., Peterson, M., Birgersson, G., Zhang, Q.-H., Löfqvist, J., Streintz, L. & Vrkoc, J. 2004b. Field test of carvone and coumarine antifeedant formulations for pine weevil *Hylobius abietis* on spruce seedlings, combining biological effect and chemical release. *J. Chem. Ecol.*, (in prep.).
- Schmutterer, H. 1995. The Neem Tree. Source of Unique Natural Products for Integral Pest Management, Medicine, Industry and Other Purposes. VCH Verlagsgesellschaft.
- Schoonhoven, L.M., Jermy, T. & van Loon, J.J.A. 1998. *Insect-Plant Biology: From Physiology to Evolution*. Chapman & Hall.
- Schroeder, L.M. 1988. Attraction of the Bark Beetle *Tomicus piniperda* and Some Other Bark-Living and Wood-Living Beetles to the Host Volatiles α -Pinene and Ethanol. *Entomologia Experimentalis et Applicata*, 46, 203-10.
- Schroeder, L.M. 2003. Differences in responses to α -pinene and ethanol, and flight periods between the bark beetle predators *Thanatus femoralis* and *T. formicarius* (Col.: Cleridae). *Forest Ecology and Management*, 177, 301-11.
- Scott, T.M. & King, C.L. 1974. *The Large Pine Weevil and Black Pine Weevil*. HMSO.

- Sibul, I., Luik, A. & Voolma, K. 2001. Possibilities to influence maturation feeding of the large pine weevil *Hylobius abietis* L., with plant extracts and neem preparations. Practice oriented results on the use of plant extracts and pheromones in pest control; Proceedings of the international workshop
- Sjödin, K., Smitt, O. & Schlyter, F. 2001. How do we formulate a plant protection against the pine weevil? (In Swedish: Hur formulerar vi ett plantskydd mot snytbaggen?). Årsrapport 2000. Feromoner och Kairomoner för bekämpning av skadeinsekter, ett MISTRA finansierat forskningsprogram, pp. 17-19.
- Smitt, O. 2002. *Syntheses of Allelochemicals for Insect Control*. Dept. Organic Chemistry. Royal Institute of Technology.
- Solbreck, C. 1980. Dispersal distances of migrating pine weevils, *Hylobius abietis* (Coleoptera, Curculionidae). Entomologia Experimentalis & Applicata, 28, 123-31.
- Solbreck, C. & Gyldberg, B. 1979. Temporal flight pattern of the large pine weevil, *Hylobius abietis* L. (Coleoptera, Curculionidae), with special reference to the influence of weather. Zeitschrift für Angewandte Entomologie, 88, 532-53.
- Thorpe, K.V. & Day, K.R. 2002. The impact of host plant species on the larval development of the large pine weevil *Hylobius abietis* L. Agricultural and Forest Entomology, 4, 187-94.
- Tilles, D.A., Sjödin, K., Nordlander, G. & Eidmann, H.H. 1986a. Synergism between Ethanol and Conifer Host Volatiles as Attractants for the Pine Weevil, *Hylobius abietis* (L) (Coleoptera, Curculionidae). Journal of Economic Entomology, 79, 970-73.
- Tilles, D.A., Nordlander, G., Nordenhem, H., Eidmann, H.H., Wassgren, A.B. & Bergström, G. 1986b. Increased Release of Host Volatiles from Feeding Scars - a Major Cause of Field Aggregation in the Pine Weevil *Hylobius abietis* (Coleoptera, Curculionidae). Environmental Entomology, 15, 1050-54.
- Tilles, D.A., Eidmann, H.H. & Solbreck, B. 1988. Mating Stimulant of the Pine Weevil *Hylobius abietis* (L). Journal of Chemical Ecology, 14, 1495-503.
- Trädgårdh, I. 1913. On the chemotropism of insects and its significance for economic entomology. Bulletin of Entomological Research, 4, 113-17.
- Tunset, K., Nilssen, A.C. & Andersen, J. 1993. Primary Attraction in Host Recognition of Coniferous Bark Beetles and Bark Weevils (Col, Scolytidae and Curculionidae). Journal of Applied Entomology, 115, 155-69.
- Wibe, A. & Mustaparta, H. 1996. Encoding of plant odours by receptor neurons in the pine weevil (*Hylobius abietis*) studied by linked gas chromatography electrophysiology. Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology, 179, 331-44.
- Wibe, A., Borg-Karlsson, A.-K., Norin, T. & Mustaparta, H. 1996. Identification of plant volatiles activating the same receptor neurons in the pine weevil, *Hylobius abietis*. Entomologia Experimentalis & Applicata, 80, 39-42.
- Wibe, A., Borg-Karlsson, A.K., Norin, T. & Mustaparta, H. 1997. Identification of plant volatiles activating single receptor neurons in the pine weevil (*Hylobius abietis*). Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology, 180, 585-95.
- Wibe, A., Borg-Karlsson, A.-K., Persson, M., Norin, T. & Mustaparta, H. 1998. Enantiomeric composition of monoterpene hydrocarbons in some conifers and receptor neuron discrimination of α -pinene and limonene enantiomers in the pine weevil, *Hylobius abietis*. Journal of Chemical Ecology, 24, 273-87.
- Wilson, W.L. & Day, K.R. 1995. The Comparative Effectiveness of Chemical Traps, and Fir, Spruce and Larch Billets, for the Estimations of Pine Weevil (*Hylobius abietis* L) (Col, Curculionidae) Density Indexes. Journal of Applied Entomology, 119, 157-60.
- vonSydow, F. & Birgersson, G. 1997. Conifer stump condition and pine weevil (*Hylobius abietis*) reproduction. Canadian Journal of Forest Research, 27, 1254-62.
- Zagatti, P., Lemperiere, G. & Malosse, C. 1997. Monoterpenes emitted by the large pine weevil, *Hylobius abietis* (L.) feeding on Scots pine, *Pinus sylvestris* L. Physiological Entomology, 22, 394-400.
- Zumr, V. & Stary, P. 1992. Field Experiments with Different Attractants in Baited Pitfall Traps for *Hylobius abietis* L (Col, Curculionidae). Journal of Applied Entomology, 113, 451-55.
- Zumr, V., Stary, P. & Dostalkova, I. 1995. Comparison of Seasonal Responses of *Hylobius abietis* (L) (Col, Curculionidae) to Chemical and Natural Lures in Baited Pitfall Traps. Anzeiger Fur Schadlingskunde Pflanzenschutz Umweltschutz, 68, 166-68.
- Örlander, G., Nilsson, U. & Nordlander, G. 1997. Pine weevil abundance on clear-cuttings of different ages: A 6- year study using pitfall traps. Scandinavian Journal of Forest Research, 12, 225-40.
- Örlander, G., Nordlander, G., Wallertz, K. & Nordenhem, H. 2000. Feeding in the crowns of Scots pine trees by the pine weevil *Hylobius abietis*. Scandinavian Journal of Forest Research, 15, 194-201.

Chapter 16

HYLOBIUS ABIETIS – HOST UTILISATION AND RESISTANCE

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1. INTRODUCTION

The pine weevil, *Hylobius abietis*, breeds predominantly in the bark of roots of felled conifers and occasionally in moribund trees or in logs in contact with the soil. In unmanaged forests, these resources are unpredictable in time and space and usually scarce, except after relatively rare events such as extensive windblow. *H. abietis* is therefore, expected to occur at low density in its natural habitat. In managed forests, where clearfelling at the end of a rotation is the silvicultural norm, high weevil populations develop on the abundant root-stumps left in the ground. *Hylobius abietis* is therefore a ‘silvicultural’ pest whose population size is determined to a large extent by the availability of breeding sites (Eidmann 1979). The size of weevil populations is one of the main factors determining the extent of mortality of young conifers planted after clearfelling in central and northern Europe. But emphasis on the quantitative aspects of root-stump availability as a determinant of population size tends to obscure possible qualitative variation, both between and within host species, in their ‘suitability’ for larval development. The ‘quality’ of the resource is also likely to change over time, depending on such site-related factors as rainfall, temperature and rate of fungal decay. Weevil population dynamics and abundance could therefore be influenced by qualitative as well as quantitative variation in their breeding resource.

The young conifers used in replanting clearfell sites are vulnerable to attack by adult weevils that emerge from the root-stumps. Weevils are large relative to the transplants and because they feed on the bark of the main stem, relatively small amounts of damage can be lethal. Mortality of unprotected young conifers on reafforestation sites is normally high (Långström & Day, chapter 19), giving the impression that most plants are very susceptible to weevil attack. However, because weevil population densities and therefore rates of attack on transplants are so high,

any underlying differences in susceptibility, both within and between species are likely to be obscured. This is an important point because even relatively low levels of resistance can be of value in pest management, allowing for example a reduction in the amount of insecticide needed to protect plants (van Emden 1991). In the following sections of this Chapter, evidence for 'residual' resistance in root-stumps affecting the survival and development of larvae and for resistance in seedlings affecting the amount of adult feeding is reviewed.

2. 'RESISTANCE' OF ROOT-STUMPS TO LARVAE

In conifer bark, preformed defences such as resin and lignified stone-cell-masses, as well as the induced dynamic wound response can be highly effective in preventing colonisation of the bark of living trees by bark beetles and weevils (Christiansen and Horntvedt 1983; Grégoire 1988; Phillips and Croteau 1999; Raffa and Berryman 1987; Wainhouse *et al* 1990). In the intact root-stump left in the ground after felling, preformed and possibly also induced defences could remain effective and reduce establishment success of *H. abietis* larvae for a period after felling. Evidence for the residual effects of resistance mechanisms present in the living tree comes from both field and laboratory experiments showing that there are within and between species differences in the quality of stumps as a breeding resource for weevils. Because it is difficult to work with root-stumps, most experiments have been done with logs cut from the lower stem of mature trees. It is a reasonable assumption however, that the bark of these logs is similar to that on the main body of the root-stump which contains most of the bark resource on which larvae feed.

Pine, the presumed natural host, is generally more favourable for larval development than spruce. Larvae develop more slowly on buried logs of Norway spruce than of Scots pine (Bejer-Petersen *et al* 1962), more weevils tend to emerge from root-stumps of pine than spruce (von Sydow and Birgersson 1997) and adults from spruce appear to have a lower fecundity and a shorter adult life span than those emerging from pine (Guslits 1970). Species such as larch appear to be highly unfavourable for larval development (Wainhouse *et al* 2001; Thorpe and Day 2002).

The flow of resin from bark has been suggested as a cause of larval mortality especially in pines (Wainhouse *et al* 2001) and in Sitka spruce, physical defence in the form of lignified stone-cell-masses within the bark can reduce the growth rate of larvae (Fig 1).

Indirect evidence for the importance of 'residual' resistance comes from the observation that larval size influences survival on different conifer hosts. Egg size in *H. abietis* is influenced both by female size and by the quality of the food resource during maturation feeding (Wainhouse *et al* 2001). The large larvae that hatch from large eggs survive better than smaller ones when inoculated onto logs of different conifer species (Fig 2). This suggests that preformed defences in the bark were still active after felling and that small larvae were most susceptible to their effects. Competitive interactions between larvae in root-stumps may be an additional cause of mortality of small larvae (Nordenhem and Nordlander 1994).

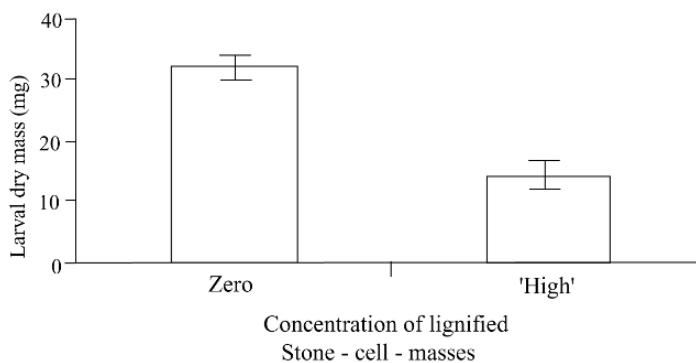


Figure 1. Mass of *Hylobius abietis* larvae developing on logs of *Sitka spruce* for 106 days. Larvae feeding in bark that contained high concentrations of lignified stone-cell-masses were much smaller than those from bark which contained no stone-cell-masses (From Thorpe and Day, 2002).

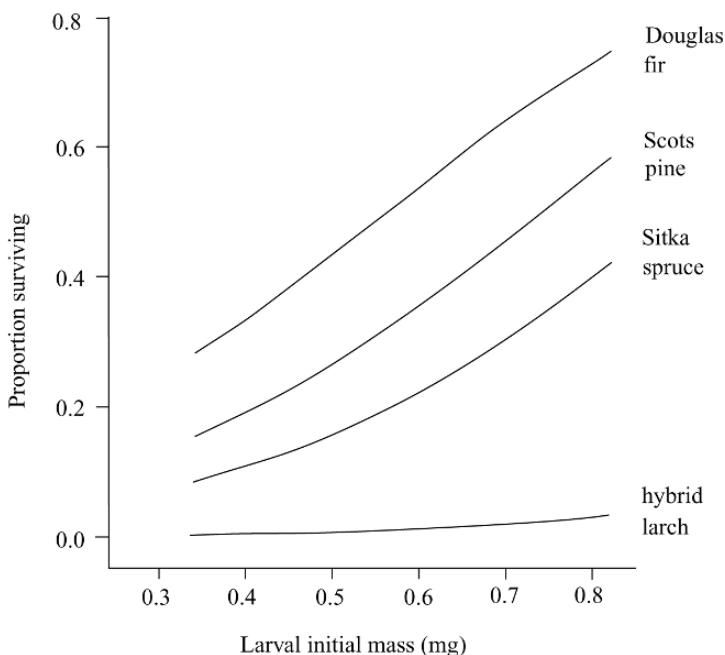


Figure 2. Predicted survival of larvae of *Hylobius abietis* of different initial mass when inoculated into the bark of logs of different conifer species (From Wainhouse et al 2001).

These different experiments show that conifer root-stumps are not simply a 'passive' breeding resource. They suggest that the number of weevils emerging from clearfell sites for a given level of initial attack is likely to be affected not only by the

tree species previously occupying the site but also by the 'age' of the root-stump i.e. the time since felling. During the early phase of root-stump colonisation, when 'residual' resistance is most likely to be effective, larval mortality could be relatively high. Field experiments are however, needed to verify this.

3. RESISTANCE OF YOUNG CONIFERS TO ADULT FEEDING

Female weevils emerge from root-stumps with undeveloped ovaries in which eggs develop only after a period of maturation feeding (Fig 3) (Munro 1928; Nordenhem 1989; Leather *et al* 1999; Örlander *et al* 2000). Initial feeding is likely to be on the bark of transplants, although weevils also feed on the bark of branches and twigs within the crown of mature conifers and on the bark of logs and brash left on site after felling operations. In the laboratory, this period of maturation feeding can be relatively short. For example, when weevils fed on the bark of different seedling conifers, the first mature eggs were formed after 12-16 days (Wainhouse *et al* 2001). In this study, variation in the rate of reproductive development was most likely due to differences in the nitrogen content of the bark of the different conifer species.

To be of practical value, resistance in young conifers would need to be expressed through a reduction in the amount of feeding or an increase in the ability of the plants to tolerate and recover from a given level of feeding damage. Most methods for quantifying the amount of feeding have been developed for field use where the emphasis has been on visual estimation of damage categories (Eidmann and Lindelöw 1997 and references therein). In quantifying attack, there has naturally been much emphasis on lethal damage estimated by simple methods that allow large sample sizes. Methods that classify damage as absent, moderate or heavy can be subjective however, and make it difficult to compare different studies where plants may vary in size and age or where the differences in the amount and distribution of feeding are relatively small.

3.1. Variation in damage to young conifers

Nearly all studies on variation in feeding damage on young conifers have concentrated on the role of plant phenotype or on the influence of the local environment. However, a number of different factors can interact to determine damage levels (Eidmann and Lindelöw 1997). Factors that have been reported to affect the amount of feeding on transplants include the method of nursery production (Selander *et al* 1990; Selander 1993; von Sydow 1997), plant size (Eidmann 1969; Selander 1993; Thorsén *et al* 2001), scarification of soil around the transplants (Långström 1985; von Sydow 1997), insolation (von Sydow and Örlander 1994) and the presence of branches and other felling residues around the plants (Selander 1993). It is also possible that factors referred to collectively as transplant 'stress' could influence susceptibility to weevil attack (Kauppi 1984; McKay 1997; South & Zwolinski 1997). This can make it difficult not only to identify resistance traits but also to compare field studies in which different species, plant age, plant production systems, insecticide treatment and planting sites have been used. Results exclusively

from field assessments of damage can therefore be difficult to interpret in terms of plant resistance.

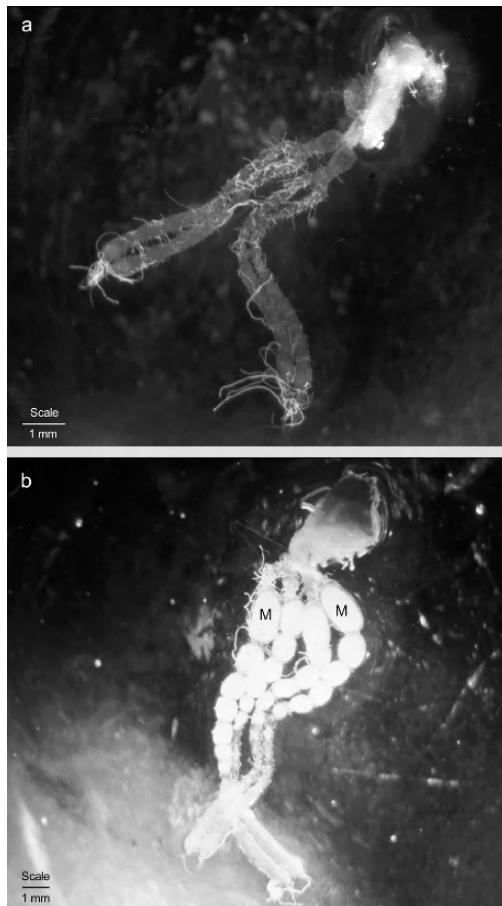


Figure 3. Ovaries dissected from (a) a recently emerged, immature female and (b) one containing two mature eggs (m) ready for laying. Note difference in approximate scale. (See Nordenhem (1989) for discussion)

3.1.1. Species differences and the influence of nursery production method

There have been few comparative studies of species susceptibility to attack, but in a trial of three-year-old bare-rooted spruce and pine of similar lower stem diameter, von Sydow and Örlander (1994) found no differences between them in feeding rate or damage. However, some laboratory experiments with seedling plants suggest that pine may be more tolerant of attack (section 3.2.2., Fig. 7)

Plants that are mass-produced for use in reafforestation programmes are usually 'containerised' or cell-grown under protected cultivated or are open-grown bare-rooted plants. Comparing attack rates on these different plant types is not straightforward, because they can vary in physical characteristics such as stem diameter, amount or distribution of foliage or bark thickness as well as in their response to site conditions and transplantation stress due to differences in root-shoot ratio.

Conifer transplants are sometimes assumed to be more susceptible to weevil attack than naturally regenerated plants but again, there have been few detailed comparisons. Selander *et al* (1990) demonstrated that nursery-produced Scots pine seedlings planted close to naturally occurring ones of similar size were more frequently attacked, had higher mortality and tended to recover less well from sublethal damage. However, none of the natural seedlings were lifted and replanted so it is not possible to determine whether the differences were due to 'nursery production method' or to a 'transplantation effect'. The effects of transplantation are known to be complex, affecting in particular the water relations of the plant (Burdett 1990; Margolis and Brand 1990) but there is also evidence of effects on secondary chemicals. In 3-year-old pines that had recently been replanted, terpene concentration in needles and stems initially increased by around 30% compared with similar 'control' pines that had been planted one year earlier. By the end of the growing season however, concentrations were lower than in controls (Sallas *et al* 1999). The initial effects were attributed to the negative influence of planting on photosynthesis, which reduced the overall carbon budget, and to possible effects of drought stress.

When methods of nursery production are compared, several studies have indicated that in both spruce and pine, bare-rooted transplants have higher survival rates than containerised ones (Selander *et al* 1990; Selander 1993; von Sydow 1997) (Fig 4). In an interesting comparison between containerised cuttings and seedlings of Norway spruce of similar stem diameter, seedlings were in general, more frequently attacked, were more likely to be girdled and had higher mortality rates than cuttings (Hannerz *et al* 2002) (Fig 5). These differences were attributed in part to the thicker bark and presence of needles on the stem base of cuttings.

The effect of fertilisation on levels of attack has been investigated by Selander and Immonen (1991). In transplanted fertilised or unfertilised 2-yr-old containerised Scots pine seedlings, the area of wounded bark on those fertilised with NPK was approximately three times higher than seedlings fertilised with PK, N or those left unfertilised. This variation in response to fertiliser composition is difficult to interpret without some analysis of the nutritional or secondary chemical 'quality' of the bark on which the weevils were feeding. As well as altering the nitrogen concentration in the bark of young conifers, nitrogen fertilisation also reduces the concentration of preformed carbon-based defences such as resin and polyphenols (Wainhouse *et al* 1998). These effects are broadly explained by resource-availability theories of plant defence that predict that nitrogen fertilisation stimulates growth and so limits the amount of carbon available for synthesis of secondary chemicals. In

general therefore, fertilised plants are expected to be less well defended in the short term (Herms and Mattson 1992).

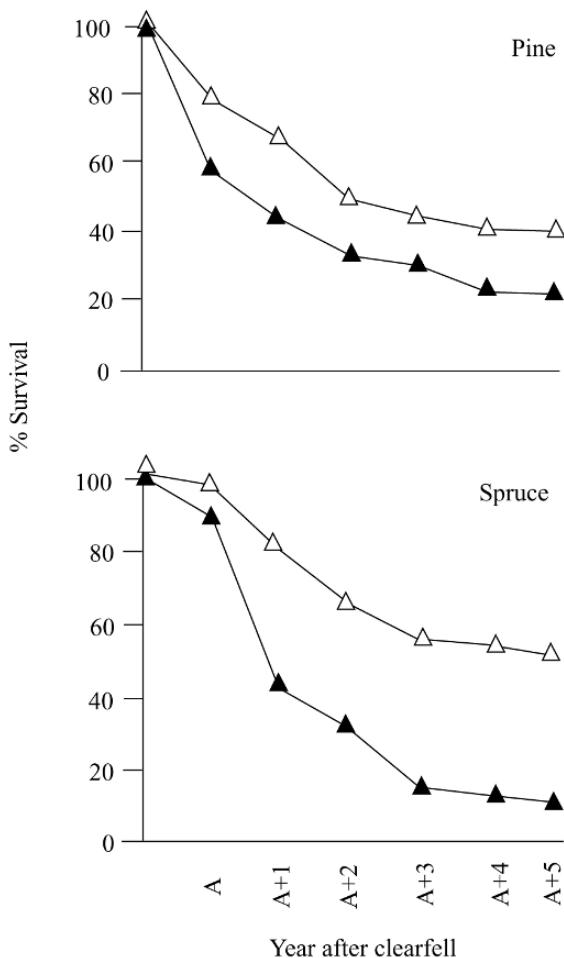
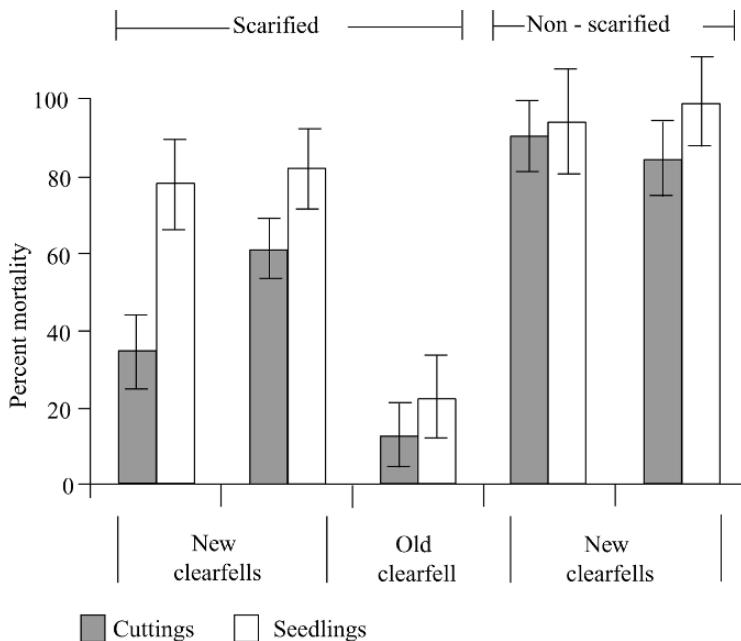


Figure 4. Survival of bare-rooted (Δ) and containerised (\blacktriangle) Scots pine and Norway spruce planted after felling without an intervening fallow period. The young trees had been treated with insecticide at planting. A was the first growing season after felling (From von Sydow 1997).

3.1.2 Effect of plant size

Larger plants, i.e. those with a bigger stem diameter, are in general less likely to be killed by weevil attack. One of the main reasons for this is that the probability of girdling is lower in larger plants (Selander 1993; Örlander and Nilsson 1999; Thorsén *et al* 2001). Larger plants however, tend to accumulate more feeding

damage (Eidmann 1969), but appear to be able to recover from it more readily than small plants. In one extensive study, thousands of containerised Norway spruce seedlings were planted out in southern Sweden and their fate monitored for up to 7 years (Thorsén *et al* 2001). Prior to planting, experimental plants had been grown for different lengths of time at different densities and in different sized containers so



*Figure 5. Mortality of Norway spruce cuttings and seedlings on clearfalls of different age located in southern Sweden. Some of the sites were scarified before planting (From Hannerz *et al* 2002).*

that when planted out, they differed in stem diameter, height and age. It was clear from this study that mortality caused by weevil feeding was reduced as stem diameter increased, independently of other effects. Seedlings of 8–10 mm diameter suffered the least damage and there was also evidence that faster growing transplanted seedlings suffered only light damage.

3.2. Resistance mechanisms

Resistance mechanisms are usually considered in relation to their effects on the survival, development or behaviour of insects, or in relation to the plants ability to tolerate attack (Painter 1951, 1958; Kogan and Ortman 1978). Most studies of ‘resistance’ to weevil feeding in young conifers have examined the effect of phenotypic variation on damage levels. There have been no systematic studies of

genetic variation in resistance and only a few studies have investigated possible resistance mechanisms. With some knowledge of the underlying mechanisms of resistance to feeding by *H. abietis* in young conifers, it would be easier to interpret the observed variation in attack in relation to plant phenotype.

3.2.1 Effects of preformed defences on orientation and feeding behaviour

The ability of weevils to detect components of resin has been demonstrated in several electrophysiological studies in which olfactory receptors responsive to different monoterpenes and sesquiterpenes have been described (Mustaparta 1975a, b; Wibe and Mustaparta 1996; Wibe *et al* 1996, 1997, 1998). For most of these chemicals, the behavioural response of weevils and their possible role in finding and accepting hosts is generally unknown. Where behavioural studies have been done, interpretation is complicated by the likely role of monoterpenes in both adult maturation feeding and location of root-stumps for oviposition and also by apparent changes in responsiveness during the reproductive cycle (Nordenhem and Eidmann 1991; Lindelöw *et al* 1993). The monoterpene, α -pinene, which is released from both root-stumps and transplants is attractive to weevils (Selander *et al* 1973, 1974; Kalo *et al* 1974; Mustaparta 1974; Mustaparta 1975b (but see Müller and Haufe 1991)). The response to α -pinene released from root-stumps however, is synergised by ethanol which is released naturally from host material under anaerobic conditions (Nordlander *et al* 1986; Tilles 1986a; Nordlander 1987, 1990; Lindelöw *et al* 1993; Kelsey 1994). The fact that ‘wounding’ of bark either mechanically or through active feeding by weevils, increases its attractiveness to *H. abietis*, is further evidence of the important role of volatile monoterpenes in host finding (Tilles 1986b; Nordlander 1991; Zagatti *et al* 1997).

Some monoterpenes however, may be repellent or inhibitory. Limonene and myrcene for example have been found to inhibit the attractive response to α -pinene (Nordlander 1990, 1991; Zumr and Starý 1992) and limonene is known to be toxic or repellent to bark beetles and weevils (Raffa *et al* 1985; Werner 1985; Lindgren *et al* 1996). Monoterpene composition in conifers is under genetic control (Phillips and Croteau 1999) and the concentration of limonene is known to vary among pine and spruce populations (Yazdani and Nilsson 1986; Nerg *et al* 1994). This suggests the possibility that monoterpene composition could play a role in resistance by affecting the behavioural response of weevils to transplants. However the high intraspecific variation in monoterpene composition and strong environmental influence on concentration in young conifers (Kalo *et al* 1974; Nerg *et al* 1994) suggests that resistance mechanisms affecting weevil host finding are likely to be of little practical significance.

Once plants have been located, weevil feeding behaviour could be affected by resin or other secondary chemicals within the bark. Several host and non-host chemicals have been observed to affect the feeding behaviour of weevils (Table 1), but in general, there is little evidence of the natural occurrence of feeding inhibitors or repellents in the bark of young conifers.

Table -1. The effect of some chemicals on the feeding behaviour of adult *Hylobius abietis*

<i>Chemicals affecting adult feeding behaviour</i>	<i>Origin</i>	<i>Response</i>	<i>Reference</i>
Acetophenone glycoside	ramets of <i>Pinus sylvestris</i> clones	negative correlation with feeding damage	Lieutier <i>et al</i> 1996
Ethyl- <i>trans</i> -cinnamate, Ethyl 2,3-dibromo-3-phenyl-propanoate	bark of lodgepole pine	antifeedants	Bratt <i>et al</i> 2001
Verbenone	commercial or microbial breakdown of host tissues	feeding deterrent	Lindgren <i>et al</i> 1996
Coumarin, carvone, verbenone, limonin, borneol, 4-allylanisole	commercial	feeding deterrent	Klepzig & Schlyter 1999

3.2.2. Induced resistance, wound repair and tolerance.

The effect of induced changes in bark on resistance to further feeding and the ability of transplants to recover from sublethal damage has been examined in several studies of artificial wounding. Mechanical wounding of the stems of 1-year-old *Pinus sylvestris* seedlings causes an increase in the overall concentration of resin acids in areas immediately adjacent to the wound within about 3 days, apparently as a result of *de novo* synthesis in affected tissues (Gref and Ericsson 1985). In further experiments, Ericsson *et al* (1988) wounded pine seedlings on one side of the main stem and waited until it was almost completely healed by formation of callus tissue before exposing the plants to weevils in a bioassay. Where weevils had access to both wounded and unwounded seedlings, wounded seedlings were attacked first, apparently because weevils were attracted to monoterpenes released from the incompletely closed wounds. However on the wounded plants, most feeding occurred on the unwounded side suggesting that the risk of girdling had been reduced (Fig 6). Reduced feeding on the wounded side was attributed to the higher induced concentration of resin acids. Some feeding however, occurred above the wound on the wounded side of the stem apparently due to the higher concentration of carbohydrates and other nutrients that accumulated because the wound blocked downward transport. These results indicate that weevils are sensitive both to the nutritional and defensive status of the bark on which they feed.

Evidence of species variation in tolerance of attack also comes from laboratory experiments with wounded seedlings. When one year old Scot's pine and Norway

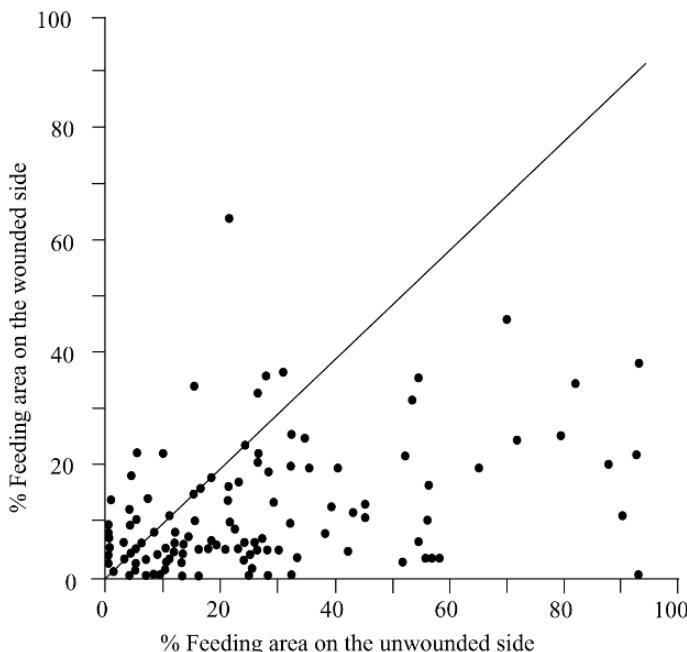


Figure 6. The effect of mechanical stem wounding on subsequent feeding damage by *Hylobius abietis*. The wounds made on one side of the stem had largely callused over at the start of the experiment but weevils feed most on the unwounded side. Data summed over two experiments (From Ericsson et al., 1988).

spruce seedlings were partially girdled on the lower stem by a mechanical wound, mortality was found to be much higher in spruce than in pine (Långström and Hellqvist 1989) (Fig. 7). If the tolerance observed in this experiment could be demonstrated under field conditions and the main factors influencing it identified, this resistance trait could be of considerable practical significance.

4. HOST PLANT RESISTANCE IN THE MANAGEMENT OF PINE WEEVIL

Several studies of larval development suggest that 'residual' resistance contributes to between and within species variation in larval survival and growth rate. If root-stumps are most 'resistant' immediately after felling, the offspring of weevils attacking immediately after a spring clearfell may have lower survival than those of weevils attacking root-stumps of trees felled some months earlier. Field experiments are therefore needed to determine whether for a given level of attack, the total population emerging from spring clearfells is less than that from sites clearfelled when weevil attack does not occur for several months.

Most mass-produced conifer transplants appear to be generally susceptible to high levels of attack by *H. abietis*. Different methods of nursery production and in

particular, plant size affect the survival of transplants on clearfell sites. Studies of resistance mechanisms indicate a possible role for induced resistance and tolerance but further studies are needed to confirm this and to show how plant phenotype influences resistance expression. With increasing restrictions on insecticide application in forests, the use of plants able to resist at least moderate levels of weevil attack will be essential for the development of an effective Integrated Pest Management programme against this important European pest.

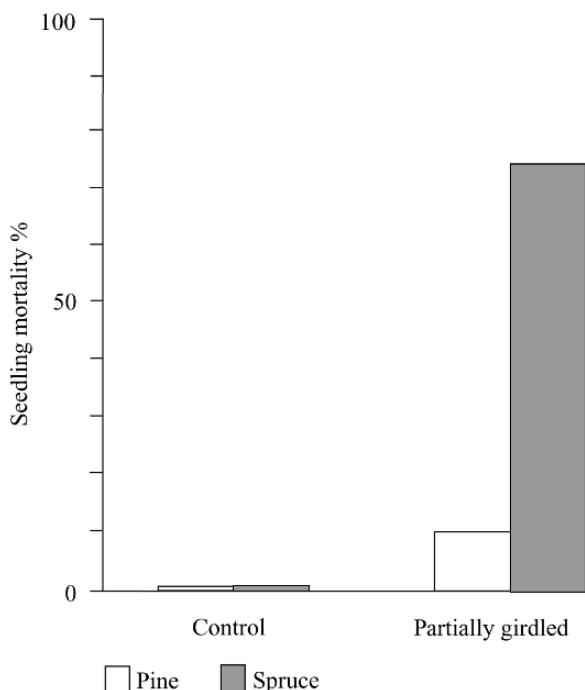


Figure 7. Mortality of pine and spruce seedlings planted out for one year after partial girdling of the stem. Plants were two years old at the end of the experiment, with stem diameters ranging from 3-3.9 mm (From Långström and Hellqvist 1989).

5. REFERENCES

- Bejer-Petersen, B., Juutinen, P., Kangas, E., Bakke, A., Butovitsch, V., Eidman, H., Heqvist, K.L. & Lekander, B. 1962 . Studies on *Hylobius abietis*, L. 1. Development and life cycle in the Nordic countries. *Acta Entomologica Fennica*, 17, 1-106.
- Bratt, K., Sunnerheim, K., Nordenhem, H., Nordlander, G. & Långström, B. 2001. Pine weevil (*Hylobius abietis*) antifeedants from lodgepole pine (*Pinus contorta*). *Journal of Chemical Ecology*, 27, 2253-62.
- Burdett, A.N 1990. Physiological processes in plantation establishment and the development of specifications for forest planting stock. *Canadian Journal of Forest Research*, 20, 415-27.
- Christiansen, E. & Horntvedt, R. 1983. Combined *Ips/Ceratocystis* attack on Norway spruce, and defensive mechanisms of the trees. *Zeitschrift fur angewandte Entomologie*, 96, 110-18.

- Eidmann, H.H. 1969. Rüsselkäferschäden an verschiedenen Nahrungspflanzen. Anzeiger f. Schädlingeskunde u. Pflanzenschutz, 42, 22-6.
- Eidmann, H.H. 1979. Integrated management of pine weevil (*Hylobius abietis* L.) populations in Sweden. In. *Current topics in forest entomology*. Forest Service General Technical Report WO-8 USDA.
- Eidmann, H.H. & Lindelöw, Å. 1997. Estimates and measurements of pine weevil feeding on conifer seedlings: their relationships and application. Canadian Journal of Forest Research, 27, 1068-73.
- Ericsson, A., Gref, R., Hellqvist, C. & Långström, B. 1988. Wound response of living bark of Scots pine seedlings and its influence on feeding by the weevil, *Hylobius abietis*. In. *Mechanisms of woody plant defenses against insects*, W.J. Mattson, J. Levieux, C. Bernard-Dagan (Eds.). Springer-Verlag, New York.
- Gref, R. & Ericsson, A. 1985. Wound-induced changes of resin acid concentrations in living bark of Scots pine seedlings. Canadian Journal of Forest Research, 15, 92-6.
- Grégoire, J-C. 1988. The greater European spruce bark beetle. In. *Dynamics of forest insect populations. Patterns, causes, implication*, A.A. Berryman (Ed.), Plenum Press, New York.
- Guslits I.S. 1970. The effects of feeding conditions on the fecundity and vital activities of the adults of the pine weevil - *Hylobius abietis* (in Russian) Zoologicheskii Zhurnal, 49, 862-8.
- Hannerz, M., Thorsén, Å., Mattsson, S. & Weslien, J. 2002. Pine weevil (*Hylobius abietis*) damage to cuttings and seedlings of Norway spruce. Forest Ecology and Management, 160, 11-17.
- Herms, D.A. & Mattson, W.J. 1992. The dilemma of plants: to grow or defend. The Quarterly Review of Biology, 67, 283-335.
- Kalo, P., Selander, J., Kangas, E. & Perttunen, V. 1974. The chemical composition of volatiles produced by the host of *Hylobius abietis* L. (Col., Curculionidae) I. The terpene composition of pine seedlings. Annales Entomologici Fennici, 40, 86-95.
- Kauppi, P. 1984. Stress, strain, and injury: Scots pine transplants from lifting to acclimation on the planting site. Acta Forestalia Fennica, 185, 1-49.
- Kelsey, R.G. 1994. Ethanol synthesis in Douglas-fir logs felled in November, January, and March and its relationship to ambrosia beetle attack. Canadian Journal of Forest Research, 24, 2096-104.
- Klepzig, K.D. & Schlyter, F. 1999. Laboratory evaluation of plant-derived antifeedants against the pine weevil *Hylobius abietis* (Coleoptera: Curculionidae). Journal of Economic Entomology, 92, 644-50.
- Kogan, M. & Ortman, E.F. 1978. Antixenosis – a new term proposed to define Painter's 'nonpreference' modality of resistance. Bulletin of the Entomological Society of America, 24, 175-6.
- Långström, B. 1985. Damage caused by *Hylobius abietis* in Finland in the years 1970-1971. Results from the Finnish part of a joint Nordic study. Folia Forestalia, 612, 1-11.
- Långström, B. & Hellqvist, C. 1989. Effects of defoliation, decapitation, and partial girdling on root and shoot growth of pine and spruce seedlings. In. *Insects affecting reforestation: biology and damage*, R.I. Alfaro, S.G. Glover. Forestry Canada, Victoria B.C.
- Leather, S.R., Day, K.R. & Salisbury, A.N. 1999. The biology and ecology of the large pine weevil, *Hylobius abietis* (Coleoptera : Curculionidae): a problem of dispersal? Bulletin of Entomological Research, 89, 3-16.
- Lieutier, F., Garcia, J., Yart, A., Geraud, L., Malphettes, C-B. & Romary, P. 1996. Preliminary investigations on the relationships between phloem phenolic content of Scots pine and maturation feeding of the pine weevil *Hylobius abietis*. In *Integrating cultural tactics into the management of bark beetle and reforestation pests*, J.-C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, S.M. Salom. USDA Forest Service Northeastern Forest Experiment Station General Technical Report NE-236.
- Lindelow, A., Eidmann, H.H. & Nordenhem, H. 1993. Response on the ground of bark beetle and weevil species colonizing conifer stumps and roots to terpenes and ethanol. Journal of Chemical Ecology, 19, 1393-1403.
- Lindgren, B.S., Nordlander, G. & Birgersson, G. 1996 Feeding deterrence of verbenone to the pine weevil, *Hylobius abietis* (L) (Col, Curculionidae). Journal of Applied Entomology, 120, 397-403.
- Margolis, H.A. & Brand, D.G. 1990. An ecophysiological basis for understanding plantation establishment. Canadian Journal of Forest Research, 20, 375-90.
- McKay, H.M. 1997. A review of the effect of stresses between lifting and planting on nursery stock quality and performance. New Forests, 13, 369-99.
- Mustaparta, H. 1974. Response of the pine weevil *Hylobius abietis* L. (Col., Curculionidae), to bark beetle pheromones. Journal of Comparative Physiology, 88, 395-98.

- Mustaparta, H. 1975a. Response of single olfactory cells on the pine weevil *Hylobius abietis* L. (Col., Curculionidae). *Journal of Comparative Physiology*, 97, 271-90.
- Mustaparta, H. 1975b. Behavioural responses of the pine weevil *Hylobius abietis* L. (Col.: Curculionidae) to odours activating different groups of receptor cells. *Journal of Comparative Physiology*, 102, 57-63.
- Müller, M. & Haufe, G. 1991. Das Verhalten des Grossen braunen Rüsselkäfers, *Hylobius abietis* L. (Coleoptera, Curculionidae), gegenüber Inhaltsstoffen seiner Wirspräflanzen. *Archiv für Phytopathologie und Pflanzenschutz*, 27, 299-306.
- Munro, J.W. 1928. The biology and control of *Hylobius abietis* L. *Forestry*, 2, 31-39.
- Nerg, A., Kainulainen, P., Vuorinen, M., Hanso, M., Holopainen, J.K. & Kurkela, T. 1994. Seasonal and geographic variation of terpenes, resin acids and total phenolics in nursery grown seedlings of Scots pine (*Pinus sylvestris* L.). *New Phytologist*, 128, 703-13.
- Nordenhem, H. 1989. Age, sexual development, and seasonal occurrence of the pine weevil *Hylobius abietis* (L.). *Journal of Applied Entomology*, 108, 260-70.
- Nordenhem, H. & Eidmann, H.H. 1991. Response of the pine weevil *Hylobius abietis* L. (Col., Curculionidae) to host volatiles in different phases of its adult life cycle. *Journal of Applied Entomology*, 112, 353-58.
- Nordenhem, H. & Nordlander, G. 1994. Olfactory oriented migration through soil by root-living *Hylobius abietis* (L.) larvae (Col., Curculionidae). *Journal of Applied Entomology*, 117, 457-62.
- Nordlander, G. 1987. A method for trapping *Hylobius abietis* (L.) with a standardized bait and its potential for forecasting seedling damage. *Scandinavian Journal of Forest Research*, 2, 199-213.
- Nordlander, G. 1990. Limonene inhibits attraction to α -pinene in the pine weevils *Hylobius abietis* and *H. pinastri*. *Journal of Chemical Ecology*, 16, 1307-20.
- Nordlander, G. 1991. Host finding in the pine weevil, *Hylobius abietis*: effects of conifer volatiles and added limonene. *Entomologia Experimentalis et Applicata*, 59, 229-38.
- Nordlander, G., Eidmann, H., Jacobsson, U., Nordenhem, H. & Sjödin, K. 1986. Orientation of the pine weevil *Hylobius abietis* to underground sources of host volatiles. *Entomologia Experimentalis et Applicata*, 41, 91-100.
- Örlander, G. & Nilsson, U. 1999. Effect of reforestation methods on pine weevil (*Hylobius abietis*) damage and seedling survival. *Scandinavian Journal of Forest Research*, 14, 341-54.
- Örlander, G., Nordlander, G., Wallertz, K. & Nordenhem, H. 2000. Feeding in the crowns of Scots pine trees by the pine weevil *Hylobius abietis*. *Scandinavian Journal of Forest Research*, 15, 194-201.
- Painter, R.H. 1951. *Insect resistance in crop plants*, The Macmillan Company, New York.
- Painter, R.H. 1958. Resistance of plants to insects. *Annual Review of Entomology*, 3, 267-90.
- Phillips, M.A. & Croteau, R.B. 1999. Resin-based defences in conifers. *Trends in Plant Science*, 4, 184-90.
- Raffa, K.F. & Berryman, A.A. 1987. Interacting selective pressures in conifer-bark beetle systems: a basis for reciprocal adaptations?. *American Naturalist*, 129, 234-62.
- Raffa, K.F., Berryman, A.A., Simasko, J., Teal, W. & Wong, B. L. 1985. Effects of grand fir monoterpenes on the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae) and its symbiotic fungus. *Environmental Entomology*, 14, 552-56.
- Sallas, L., Vuorinen, M., Kainulainen, P. & Holopainen, J.K. 1999. Effects of planting on concentrations of terpenes, resin acids and total phenolics in *Pinus sylvestris* seedlings. *Scandinavian Journal of Forest Research*, 14, 218-26.
- Selander, J. 1993. Survival model for *Pinus sylvestris* seedlings at risk from *Hylobius abietis*. *Scandinavian Journal of Forest Research*, 8, 66-72.
- Selander, J. & Immonen, A. 1991. Effect of fertilization on the susceptibility of Scots pine seedlings to the large pine weevil, *Hylobius abietis* (Coleoptera, Curculionidae). *Folia Forestalia*, 771, 1-21.
- Selander, J., Immonen, A. & Raukko, P. 1990. Resistance of naturally regenerated and nursery-raised Scots pine seedlings to the large pine weevil, *Hylobius abietis* (Coleoptera, Curculionidae). *Folia Forestalia*, 766, 1-19.
- Selander, J., Kangas, E., Perttunen, V. & Oksanen, H. 1973. Olfactory responses of *Hylobius abietis* L. (Col. Curculionidae) to substances naturally present in pine phloem or their synthetic counterparts. *Annales Entomologici Fennici*, 39, 40-45.
- Selander, J., Kalo, P., Kangas, E. & Perttunen, V. 1974. Olfactory behaviour of *Hylobius abietis* L. (Col. Curculionidae). I. Response to several terpenoid fractions isolated from Scots pine phloem. *Annales Entomologici Fennici*, 40, 108-15.

- South, D.B. & Zwolinski, J.B. 1997. Transplant Stress Index: A proposed method of quantifying planting check. *New Forests*, 13, 315-28.
- Thorpe, K.V. & Day, K.R. 2002. The impact of host plant species on the larval development of the large pine weevils *Hylobius abietis*. *Agricultural and Forest Entomology*, 4, 187-94.
- Thorsén, Å., Mattsson, S. & Weslien, J.-O. 2001. Influence of stem diameter on the survival and growth of containerized Norway spruce seedlings attacked by pine weevils (*Hylobius* spp.). *Scandinavian Journal of Forest Research*, 16, 54-66.
- Tilles, D.A., Sjödin, K., Nordlander, G. & Eidmann, H.H. 1986a. Synergism between ethanol and conifer host volatiles as attractants for the pine weevil, *Hylobius abietis* (L.) (Coleoptera: Curculionidae). *Journal of Economic Entomology*, 79, 970-73.
- Tilles, D.A., Nordlander, G., Nordenhem, H., Eidmann, H.H., Wassgren, A.-B. & Bergström, G. 1986b. Increased release of host volatiles from feeding scars: A major cause of field aggregation in the pine weevil *Hylobius abietis* (Coleoptera: Curculionidae). *Environmental Entomology*, 15, 1050-54.
- van Emden, H. F. 1991. The role of the host plant in insect pest mis-management. *Bulletin of Entomological Research*, 81, 123-26.
- von Sydow, F. 1997. Abundance of pine weevils (*Hylobius abietis*) and damage to conifer seedlings in relation to silvicultural practices. *Scandinavian Journal of Forest Research*, 12, 157-67.
- von Sydow, F. & Örländer, G. 1994. The influence of shelterwood density on *Hylobius abietis* (L.) occurrence and feeding on planted conifers. *Scandinavian Journal of Forest Research*, 9, 367-75.
- von Sydow, F. & Birgersson, G. 1997. Conifer stump condition and pine weevil (*Hylobius abietis*) reproduction. *Canadian Journal of Forest Research*, 27, 1254-62.
- Wainhouse, D., Cross, D.J. & Howell, R.S. 1990. The role of lignin as a defence against the spruce bark beetle *Dendroctonus micans*: effect on larvae and adults. *Oecologia*, 85, 257-65.
- Wainhouse, D., Ashburner, R. & Boswell, R. 2001. Reproductive development and maternal effects in the pine weevil *Hylobius abietis*. *Ecological Entomology*, 26, 655-61.
- Wainhouse, D., Ashburner, R., Ward, E., Rose, J. 1998. The effect of variation in light and nitrogen on growth and defence in young Sitka spruce. *Functional Ecology*, 12, 561-72.
- Werner, R.A. 1995. Toxicity and repellency of 4-allylanisole and monoterpenes from white spruce and tamarack to the spruce beetle and eastern larch beetle (Coleoptera: Scolytidae). *Environmental Entomology*, 24, 372-79.
- Wibe, A. & Mustaparta, H. 1996. Encoding of plant odours by receptor neurons in the pine weevil (*Hylobius abietis*) studied by linked gas chromatography-electrophysiology. *Journal of Comparative Physiology A*, 179, 331-44.
- Wibe, A., Borg-Karlsson, A.-K., Norin, T. & Mustaparta, H. 1996. Identification of plant volatiles activating the same receptor neurons in the pine weevil, *Hylobius abietis*. *Entomologia Experimentalis et Applicata*, 80, 39-42.
- Wibe, A., Borg-Karlsson, A.-K., Norin, T. & Mustaparta, H. 1997. Identification of plant volatiles activating single receptor neurons in the pine weevil (*Hylobius abietis*). *Journal of Comparative Physiology A*, 180, 585-95.
- Wibe, A., Borg-Karlsson, A.-K., Persson, M., Norin, T. & Mustaparta, H. 1998. Enantiomeric composition of monoterpene hydrocarbons in some conifers and receptor neuron discrimination of α -pinene and limonene enantiomers in the pine weevil, *Hylobius abietis*. *Journal of Chemical Ecology*, 24, 273-87.
- Yazdani, R. & Nilsson, J.-E. 1986. Cortical monoterpene variation in natural populations of *Pinus sylvestris* in Sweden. *Scandinavian Journal of Forest Research*, 1, 85-93.
- Zagatti, P., Lemprière, G. & Malosse, C. 1997. Monoterpenes emitted by the large pine weevil, *Hylobius abietis* (L.) feeding on Scots pine, *Pinus sylvestris* L. *Physiological Entomology*, 22, 394-400.
- Zumr, V. & Starý, P. 1992. Field experiments with different attractants in baited pitfall traps for *Hylobius abietis* L. (Col., Curculionidae). *Journal of Applied Entomology*, 113, 451-55.

Chapter 17

FUNGI ASSOCIATED WITH *HYLOBIUS ABIETIS* AND OTHER WEEVILS

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1. INTRODUCTION

Many weevils (Coleoptera: Curculionidae) carry fungal spores to their host trees. According to Leach (1940), an insect can be considered to be a vector if it 1) is consistently associated with an infected plant in the field, 2) visits healthy host plants under conditions when infection is possible, 3) carries pathogen inoculum with it in the field, and 4) is able to transmit the pathogen to a healthy plant under controlled conditions. Most of the well-known weevil-fungus associations are from North American species carrying root-rot or staining fungi. The association of European weevils with fungi has so far not been reviewed extensively, and research focused solely on transmission of fungi is scarce. In many cases associations between weevils and fungi have been found as extra information in investigations set up to study different topics, e.g. spread of the pathogenic root-rot fungus *Heterobasidion annosum coll.* (Fr.) Bref.

In weevils, association with fungi is closely connected with the phloophagous feeding guild, which involves feeding on the fresh, highly nutritive phloem and inner bark. The weevils that make large patches of feeding scars with their chewing mouthparts are the possible inoculum agents of harmful fungi. During their emergence from pupal chambers and galleries, most weevils are contaminated both internally and externally with fungal spores.

Generally, for transmitting fungi, bark beetles are more important than weevils (Whitney 1982; Harrington 1988; Beaver 1989). Very few true Curculionidae have developed a mutualistic association with fungi (Bright 1993). Consequently, none of the weevils have mycangia or similar structures for transporting fungi. This suggests that primitive Curculionidae did not require fungi to aid in host discovery and utilisation and thus followed a different evolutionary pathway (Bright 1993). The most harmful European weevil, the large pine weevil *Hylobius abietis* L., feeds on seedlings but breeds mainly in stumps and roots. Overall, it is questionable whether

there are any direct benefits for large pine weevil about fungal associates, as they compete for the same resources.

Disparate genera of ophiostomatoid fungi have evolved similar structures as adaptations to insect dispersal. From the standpoint of fungi, reliable spore dispersal and inoculation to a suitable habitat are crucial. Further, direct penetration through the cell walls is an effective method of dispersal. Most fungi associated with European weevils seem to be only slightly or moderately pathogenic and are introduced to stressed trees. Among the few exceptions are the highly pathogenic *H. annosum* (Jørgensen and Beier Petersen 1951; Laine 1977) and the causal agent of resin-top disease *Peridermium pini* (Pers.) Lév (Pappinen and von Weissenberg 1994a, b, 1996). The prevalence of insects and fungi varies, and in European weevils it seems that the opportunity for contact with pathogenic fungi is occasional and occurs when population density is high.

In Europe the number of pathogenic weevil-disseminated root diseases in pole-size and mature conifers is lower than in North America. It appears that the root-collar zone, used e.g. by *Hylobius warreni* Wood (Cerezke 1994) and *Hylobius pinicola* (Couper) in the boreal forest in Canada, seem to be used less effectively in Europe than in North America. The unique type of wilting disease, black-stain root disease, spread by root-feeding insects and caused by the fungus *Leptographium wageneri* (Kendrick) Wingfield has limited occurrence in Europe compared to Western North America where the disease commonly occurs (Morelet 1986). Further, in the genus *Hylobius* there are seven species in North America, whereas in Europe there are only four species, of which only three live on conifers. In Europe, we have no harmful species of the genus *Stereonius* or *Pachylobius*. Nevertheless, among the European curculionids there are some potential fungal vector candidates (Table 1).

2. BLUE-STAIN FUNGI ASSOCIATED WITH EUROPEAN WEEVILS

2.1. *Hylobius abietis*

Species of *Leptographium* are anamorphs of *Ophiostoma* H. & P. Sydow (Ascomycetes). Although some of these species are associated with transmission by specific bark beetles, most of them are associated with a broad group of bark beetles and curculionids. *Leptographium procerum* (W.B. Kendr.) Wingf. is known to be distributed worldwide, mostly in pines and spruce. It has been isolated e.g. from Canada, Croatia, England, Finland, France, New Zealand, Norway, Poland, South Africa, Sweden, and the USA (Kendrick 1962; Hallaksela 1977; Halambek 1976; Jacobs and Wingfield 2001). The fungus, when inoculated into two-year-old *Pinus strobus* L. seedlings, caused mortality (Halambek 1976).

In Europe, the fungus does not have a well-recognized insect vector; but both sexes of the large pine weevil have been found to carry *L. procerum* (Lévieux *et al.* 1994a). Fungal spores are located on the dorsal and lateral sides of the pronotum, especially anteriorly. Sticky masses of spores are situated in cuticular depressions associated with the pronotal setae. According to Piou (1993), 3-47% of the emerging

large pine weevils and 18 % of the seedlings killed by pine weevil were infected with *L. procerum*. In addition, in France the staining fungi *Leptographium wingfieldii* Morelet (7%), *Ophiostoma canum* (Münch) H. & P. Sydow (2%) and *O. piliferum* (Fries) H. & P. Sydow (1-3%) have been detected in low frequencies on emerging pine weevils (Piou 1993). Furthermore, *Leptographium alethinum* Jacobs, Wingf. & Uzunovic has been isolated from the galleries of the pine weevil in England and Scotland. This species has recently been distinguished from *L. procerum* by the absence of rhizoids (Jacobs *et al.* 2001). The pathogenicity, distribution and overall significance of *L. alethinum* or the other possible stain-fungi associates of pine weevil are not known. The structural variation of the conidiophores, however, suggests the presence of various fungi (Lévieux 1994a).

2.2. *Pissodes* weevils

In France, about 10 % of the *Pissodes piceae* Illiger individuals carry *O. canum* and *O. ips* (Rumb.) Nannf., indicating a low rate of infestation on fir (Lévieux 1994b). The largest patches of spores were located on the sides of the pronotum and sometimes on the elytra and rostrum. *Ophiostoma minus* (Hedgcock) H. & P. Sydow, *Ophiostoma pini*, *Ceratocystiopsis minuta* (Siem.) Upad. Kendrick, *O. piceae* (Münch) H. & P. Sydow, *O. pluriannulata* (Hedgcock) H. & P. Sydow, *O. stenoceras* (Robak) Melin & Nannf. and *Aureobasidium pullulans* (de Bary) Arnaud have sometimes been found associated with *Pissodes pini* L. (Mathiesen-Käärik 1953, 1960). *O. minus* is found sporadically with a number of bark beetles and thus its association with *P. pini* cannot be included among the specific associations (Mathiesen-Käärik 1960.).

According to Löyttyniemi and Uusvaara (1977), *Pissodes* larvae found in pine and spruce logs did not cause discoloration during six weeks of storage. If the logs were felled in southern Finland at the beginning of July or earlier, some logs became partly blue by the end of September, especially in the vicinity of the pupal chip cells. In the same study, most of the weevil individuals caught in window traps were *P. pini*; only a few specimens of *P. piniphilus* (Herbst) and *P. harcyniae* (Herbst) were trapped, but there is no direct evidence of specific fungal transmission.

3. VECTORS OF DECAY FUNGI

Larvae of the large pine weevil have been detected in the roots of Scots pine infected with the root-rot fungus *H. annosum* (Jørgensen and Beier Petersen 1951; Laine 1977). In the field, seedlings killed by root-rot are often wounded by the gnawing of pine weevils. Even small fruiting bodies are sometimes found around feeding scars made by the pine weevil (Laine 1977). *H. annosum* has been isolated from the excrement of large pine weevils collected in the field in Czech Republic (Kadlec *et al.* 1992). Furthermore, both the mycelium and the conidia of *H. annosum* have survived in viable condition through the digestive tract of the large pine weevil (Nuorteva and Laine 1972; Dušin 1979). However, on the basis of these experiments, it is unclear whether mycelium actually survived through the pine

Table 1. Root- and phloem-feeding weevils (Coleoptera: Curculionidae) and associated fungi.

Insect	Fungus	References
<i>Hylobius</i> sp.	<i>Leptographium procerum</i>	Jacobs <i>et al.</i> 2001
<i>Hylobius abietis</i>	<i>Heterobasidion annosum</i>	Nuorteva & Laine 1968; Laine 1977; Kadlec <i>et al.</i> 1992
	<i>Leptographium alethium</i>	Jacobs <i>et al.</i> 2001
	<i>Leptographium procerum</i>	Piou 1993; Lévieux <i>et al.</i> 1994a
	<i>Leptographium wingfieldii</i>	Piou 1993
	<i>Graphium canum</i>	Piou 1993
	<i>Ophiostoma piliferum</i>	Piou 1993
<i>Hylobius pales</i>	<i>Leptographium procerum</i>	Lackner & Alexander 1982; Wingfield 1983; Lewis & Alexander, 1986; Alexander <i>et al.</i> 1988; Klepzig <i>et al.</i> 1991; Nevill & Alexander, 1992a,b,c
	<i>Ophiostoma ips</i>	Klepzig <i>et al.</i> 1991
	<i>Ophiostoma piceae</i>	Nevill & Alexander 1992a,c
	<i>Graphium</i> sp.	Klepzig <i>et al.</i> 1991; Nevill & Alexander 1992a
<i>Hylobius radicus</i>	<i>Ophiostoma ips</i>	Klepzig <i>et al.</i> 1991
	<i>Leptographium procerum</i>	Wingfield 1983; Alexander <i>et al.</i> 1988; Klepzig <i>et al.</i> 1991
	<i>Leptographium terebrantis</i>	Wingfield 1983; Klepzig <i>et al.</i> 1991
	<i>Graphium</i> sp.	Klepzig <i>et al.</i> 1991
	<i>Leptographium procerum</i>	Wingfield 1983; Alexander <i>et al.</i> 1988
	<i>Leptographium terebrantis</i>	Wingfield 1983
	<i>Leptographium procerum</i>	Wingfield 1983; Klepzig <i>et al.</i> 1991
	<i>Ophiostoma ips</i>	Klepzig <i>et al.</i> 1991
	<i>Leptographium procerum</i>	Livingston & Wingfield 1982; Lewis & Alexander 1986
	<i>Armillaria mellea</i>	Livingston & Wingfield 1982

Table 1. (continuation)

Insect	Fungus	References
<i>Pissodes approximatus</i>	<i>Leptographium procerum</i>	Lackner & Alexander 1982; Alexander <i>et al.</i> 1988
<i>Pissodes castaneus</i>	<i>Armillaria</i> spp.	Ehnström & Axelsson 2002
	<i>Cronartium flaccidum</i>	Alauzet 1972
	<i>Ophiostoma</i> spp.	Lévieux <i>et al.</i> 1994b
	<i>Leptographium wagneri</i>	Witcosky & Hansen 1985; Witcosky <i>et al.</i> 1986a; Witcosky 1989
<i>Pissodes fasciatus</i>	<i>Leptographium procerum</i>	Lackner & Alexander 1982; Nevill & Alexander 1992a,b,c
<i>Pissodes nemorensis</i>	<i>Ophiostoma piceae</i>	Nevill & Alexander 1992a,c
	<i>Graphium</i> sp.	Nevill & Alexander 1992a
<i>Pissodes piceae</i>	<i>Ophiostoma canum</i>	Lévieux <i>et al.</i> 1994b
	<i>Ophiostoma ips</i>	Lévieux <i>et al.</i> 1994b
<i>Pissodes pini</i>	<i>Ophiostoma minus</i>	Mathiesen-Käärik 1953, 1960
	<i>Heterobasidion annosum</i>	Kangas 1938; Jørgensen & Beier Petersen 1951; Nuorteva & Laine, 1968; Laine 1977
	<i>Leptographium procerum</i>	Kendrick 1962; Livingston & Wingfield 1982
	<i>Leptographium landbergii</i>	Mathiesen-Käärik 1953
	<i>Aureobasidium pullulans</i>	Mathiesen-Käärik 1960
<i>Pissodes piniphilus</i>	<i>Peridermium pini</i>	Kangas 1934; Pappinen & von Weissenberg 1994a,b
	<i>Lachnellula pini</i> (Brunch.) Dennis	Kangas 1938
	<i>Ceratocystiopsis minuta</i>	Mathiesen 1951
	<i>Leptographium wagneri</i>	Witcosky & Hansen 1985; Witcosky <i>et al.</i> 1986a; Witcosky 1989
<i>Stereomnius carinatus</i>		

weevil digestive tract or whether the mycelium was originally contaminated with the conidia.

It has been suggested that a succession of fungi in roots wounded by *Hylobius* begins with the hyphomycetes or by other fungi usually not considered capable of causing extensive decay in wood and that later succession is followed by the decay fungi (Whitney 1961). Thus, in the Great Lakes region, *H. annosum* and *Armillaria* spp. have not been isolated from declining red pine, *Pinus resinosa* Ait. stands associated with the complex of scolytids, curculionids, *Leptographium* and *Ophiostoma* fungi (Klepzig *et al.* 1991; Erbilgin and Raffa 2002). Most decay fungi (except for *Armillaria* and some others) infect the stump from a cut surface. They grow relatively slowly down to the roots and in the early phases of colonization probably do not affect the suitability of the substrate for insect breeding. Nor are the larger roots, where the pine weevil breeds, reached rapidly by the soil fungi that penetrate the thin roots (von Sydow 1993). Consequently, it seems that the large pine weevil and most weevils breed without fungal interaction.

In Finland, larvae and pupae of *Pissodes pini* have been detected at the stem base of *H. annosum*-infected Scots pine (Nuorteva and Laine 1968). Fruiting bodies of *H. annosum* have also been found near the feeding wounds of *P. pini* (Nuorteva and Laine 1968; Laine 1977). In Denmark, Jørgensen and Beier Petersen (1951) have found *P. pini* gnawing trees infected by *H. annosum*. However, in all these cases it is unclear whether *P. pini* attacked trees weakened by root rot or whether the weevil fed first and root rot came later. Of the European *Pissodes* species, on some occasions *P. pini* has been speculated to be a primary pest on mature conifers.

4. VECTORS OF RESIN TOP DISEASE

The pine-top weevil, *P. piniphilus*, is considered to be an important pest in Europe. However, the primacy of *P. piniphilus* has not yet been solved. *Tomicus piniperda* and *Tomicus minor* often attack trees where *P. piniphilus* has been breeding in a previous year (Ehnström and Axelsson 2002). The pine-top weevil and the small-banded pine weevil, *Pissodes castaneus* (De G.), often breed in pines that are weakened by resin-top disease caused by a rust pathogen *Peridermium pini* (Kangas 1934; Kudela 1974). On *Pinus pinaster* Ait. the association of *P. castaneus* with resin top disease caused 62% mortality, whereas mortality was lower in trees infected by the fungus alone (Alauzet 1972). However, also in all these cases it is unsure whether host trees were weakened by the fungus before weevil breeding or whether the fungus was disseminated after the weevil arrived.

Pappinen and von Weissenberg (1994a) found a positive correlation between *P. piniphilus* pupal chambers and disease frequency. The weevils were associated with stands that were heavily infected by the resin-top disease. The presence of canker favoured the breeding of *P. piniphilus*, while the number of pupal chambers was largest in the region of the canker. *P. piniphilus* has been found to carry spores in both field and laboratory conditions (Pappinen and von Weissenberg 1994b). Weevils were able to carry spores and infect healthy trees with spores while the time

of weevil emergence and the development of new aecia were overlapping (Pappinen and von Weissenberg 1994a, b).

In a feeding test, *P. piniphilus* preferred diseased branches significantly more than healthy branches (Pappinen and von Weissenberg 1996). Furthermore, weevil feeding increased the germination of *P. pini* aeciospores on pine phloem and needle extracts. Especially in rust fungi, insect transfer leads to cross-fertilization, brings one mating type to another and results in high levels of local genetic diversity (Hunt 1985; Webber and Gibbs 1989; Hamelin 1996). Thus the migration and breeding habits of weevils may affect the incidence of disease on host trees.

5. ROOT DISEASES IN NORTH AMERICA

5.1. Black-stain root disease

Leptographium wageneri, which causes black-stain root disease, is characterized by dark staining in the roots and lower stem of mature conifers. *L. wageneri* colonizes a tree tangentially along the growth rings and thus only along the actively conducting xylem tracheids of the roots and stems, whereas radial growth is minor (Harrington and Cobb 1983). The disease fulfils the requirements of wilting disease by blocking water transport and finally leading to a decrease in the terminal growth of infected trees (Witcosky and Hansen 1985). Black-stain root disease is thought to be a native disease of Douglas-fir *Pseudotsuga menziesii* (Mirb.) Franco in western North America. There are three recognized host-specialized varieties, *L. wageneri* var. *wageneri* M.J. Wingf., which is pathogenic to pinions, the variety *ponderosum* T.C. Harr. & F.W. Cobb, which specializes on western hard pines, and the variety *pseudotsugae* T.C. Harr. & F.W. Cobb, which causes black-stain on Douglas-fir and hemlock species (Harrington and Cobb 1986; Zambino and Harrington 1989).

A root-feeding bark-beetle, *Hylastes nigrinus* (Mannerheim), and the root-feeding weevils *Steremnius carinatus* (Boheman) and *Pissodes fasciatus* LeConte are among the primary vectors (Harrington *et al.* 1985; Witcosky and Hansen 1985; Witcosky *et al.* 1986a; Hansen *et al.* 1988). In infected areas, apparently low numbers of vector insects, up to 5%, may be infested with *L. wageneri* during emergence and dispersal (Harrington *et al.* 1985; Witcosky *et al.* 1986a). *S. carinatus* causes, in particular, the tree-to-tree spread of the pathogen around established infections, while wounds caused by *P. fasciatus* are encountered less frequently on diseased trees (Hansen *et al.* 1988). Adults of *S. carinatus* are flightless, and *P. fasciatus* feeds only on dead and dying trees, which restricts their ability to spread root pathogens. However, both weevils carry *L. wageneri* in the field, transmit the fungus to host trees, and feed or oviposit on susceptible hosts under conditions suitable for transmission of *L. wageneri*, thus fulfilling the postulates of the vector hypothesis (Leach 1940; Witcosky and Hansen 1985; Witcosky *et al.* 1986a).

Black-stain root disease is most often found in 5- to 30-year-old plantations that have been pre-commercially thinned (Harrington *et al.* 1983, 1985; Hansen *et al.* 1988; Witcosky *et al.* 1986a, b). Clear cutting and thinning activities increase weevil

populations at such sites (Harrington *et al.* 1985; Witcosky *et al.* 1986a, b). Even in the absence of vector activity, the fungus can cause mortality of seedlings and large trees through root graft transmission (Hessburg and Hansen 1986; Harrington 1988). In areas with high risk of black-stain root disease, thinning should be avoided or done immediately after the flight period so that the host material can age and lose much of its attractiveness (Witcosky *et al.* 1986b; Witcosky 1989). Forest management has created favourable conditions for root-feeding insects and for the fungus causing black-stain root disease.

Damage due to the black-stain root disease in thinned stands has been suggested to be a result of the behavioural preferences of its insect vectors. Large areas of young susceptible stands have increased the occurrence of root disease. The fungus *L. wageneri* does not have cellobolytic enzymes for penetration of cell walls. Different host-specialized varieties of black-stain fungi attack Douglas-fir and lodgepole pine *Pinus contorta* Dougl. ex Loud. All these features together indicate that the fungus is able to adapt to different habitats; and they make black-stain root disease extremely harmful, if it manages to spread into managed forests in Europe.

5.2. *Leptographium terebrantis*

Leptographium terebrantis Barras and Perry is, together with *L. procerum*, among the causal agents of red pine decline on *P. resinosa* in the United States. *L. terebrantis* causes the black-staining of primary roots, lesions in the phloem and resin-soaking areas in the lower stem and root-collar (Harrington and Cobb 1983; Raffa and Smalley 1988). The typical symptoms in a forest are openings formed by dead and diseased trees in various stages of decline. This fungus is weakly pathogenic and colonizes, in particular, stressed or wounded conifers. *L. terebrantis* and *L. wageneri* are more virulent than *L. procerum* (Harrington and Cobb 1983; Wingfield 1983, 1986).

The fungus is associated with various bark beetles, *D. terebrans* Oliver, *D. valens* LeConte and *Hylurgops porosus* (LeConte) (Harrington and Cobb 1983; Owen *et al.* 1987); but it has also been isolated from trees infested by the root-collar weevil *H. radicis* Buchanan (Wingfield 1983; Klepzig *et al.* 1991). However, in the absence of *L. procerum* Wingfield (1983) could not isolate *L. terebrantis* from any of the trees infested by the root-collar weevil. Thus, the role of the fungus in this disease is speculative – neither of the abovementioned fungal agents have been shown to cause the disease independently.

5.3. *Procerum* root disease

Leptographium procerum is common on pines and is speculated to cause white pine root decline on *P. strobus*. The symptoms are presence of resinous streaks from roots to stem base, sapwood discoloration, decreased shoot growth and needle wilting. The weevils and bark beetles transmit the fungus from infected trees to the roots of healthy but stressed trees. *L. procerum* is considered to be a weak wound pathogen that is unable to kill seedlings when wound-inoculated into a stem

(Harrington and Cobb 1983; Wingfield 1983). The pathogenicity of this species has been a matter of substantial debate (Jacobs and Wingfield 2001). The discrepancy may be caused by different inoculation methods, variation in the pathogenicity of fungal strains or simply that the fungus is not a primary pathogen.

Leptographium procerum is associated with several root and root-collar infesting insects in the eastern parts of North America. Mainly the pine-reproducing weevils, *Hylobius pales* Herbst, *H. radicis*, *H. assimilis* (Bohemann) (*H. rhizophagus* M., B. & W.), *Pachylobius picivorus* (Germar) and *Pissodes nemorensis* Germar, carry *L. procerum* (Wingfield 1983; Lewis and Alexander 1986; Alexander *et al.* 1988; Raffa and Smalley 1988; Nevill and Alexander 1992b, c). Furthermore, *L. procerum* is found in the galleries of *Pissodes approximatus* Hopkins (Herbst) on pine (Wingfield 1983; Alexander *et al.* 1988). Under controlled conditions, weevils seem to transmit *L. procerum* to fresh white pine bolts more effectively than bark beetles do (Lewis and Alexander 1986). In addition, *L. procerum* is commonly isolated from surface-sterilized *H. radicis*, *H. pales* and *P. picivorus*, and less frequently from *D. valens* (Wingfield 1983).

As the pathogen spreads throughout the root collar, the infected tissue becomes more suitable for weevil oviposition and breeding. *H. pales* and *P. nemorensis* normally oviposit in stressed or diseased trees, not on healthy ones, as *H. radicis* does. *H. radicis* causes symptoms on pines similar to those associated with white pine root decline, although it seldom infests five-needle pines (Wingfield 1983, 1986). Wingfield (1983) isolated *L. procerum* from roots that had been recently damaged by weevils, but not from roots damaged during previous years and already decaying. Furthermore, the low recovery of the fungus from the soil suggests dissemination by the insect (Lewis *et al.* 1987). Leach's postulates about the vectorship are fulfilled when weevils transmit *L. procerum*. At first, weevils are associated with diseased trees (Leach 1940; Lackner and Alexander 1982; Wingfield 1983, Nevill and Alexander 1992b). Secondly, weevils are found with their host trees during their whole life cycle (Raffa and Klepzig 1996). Furthermore, *H. pales* and *P. nemorensis* weevils carry *L. procerum* in the field (Wingfield 1983) and finally, weevils are able to transmit the fungus to a healthy plant (Lackner and Alexander 1982; Lewis and Alexander 1986; Nevill and Alexander 1992c). It is important to note that Leach's postulates relate to the vectorship – but Koch's postulates are a prerequisite to show primary pathogenicity – for *L. procerum* and *L. terebrantis* (in the field) this has never been achieved.

6. CONCLUSIONS

The ecological role of root-feeding weevils and the fungi with which they are associated is obscure. If weevils are associated with fast-growing pathogenic fungi, they compete for the same nutrient resources. This points out what Berryman (1989) has suggested that co-adaptation of the weevils with fungal pathogens is not an evolutionarily stable strategy.

In *L. wageneri*, the sexual state of *Ophiostoma wageneri* (Goheen and F.W. Cobb) T.C. Harr. has been found only in the galleries of *Hylastes*; thus it is possible

that the fungus needs root-inhabiting insects to bring the compatibility types together (Goheen and Cobb 1978). Whether lack of a functional sexual state is an indication that the weevils play some role in dissemination of root-infecting pathogens, is a highly speculative idea.

On white pine it has been demonstrated that adult weevils locate and oviposit on trees with roots diseased by *L. procerum* in advance of bark beetles (Nevill and Alexander 1992b). Whether European root-feeding weevils play a special role in inhabiting weakened seedlings and trees before the bark beetles remains to be solved.

The phrase “out of sight, out of mind” describes well the role of subterranean and sub-cortical insects in many ecosystems (Hunter 2001). In many cases, delimitation of species for instance within *Leptographium* is difficult and requires studies on the ultra-structure of fungal spores. Difficulties in identification may have inhibited detection of associated fungi. Both in the assessment of root-feeding insect abundance and their possible fungal associates, there is a clear gap in our knowledge.

7. REFERENCES

- Alauzet, C. 1972. Étude de la localisation des pontes de *Pissodes notatus* (Coléoptère, Curculionidae) sur pin maritime en présence de *Cronartium flaccidum* (Basidio-, Phragmobasidiomycète, Urédinale, Cronartiacée). Bulletin de la Société d'Histoire Naturelle de Toulouse, 108, 341–348.
- Alexander, S.A., Horner, W.E., & Lewis, K.J. 1988. *Leptographium procerum* as a Pathogen of Pines. In. *Leptographium Root Diseases on Conifers*, T.C. Harrington, F.W. Jr. Cobb (Eds.). St. Paul, Minnesota: APS Press.
- Beaver, R.A. 1989. Insect-Fungus Relationship in the Bark and Ambrosia Beetles. In. *Insect-Fungus Interactions*, N. Wilding, N.M. Collins, P.M. Hammond, J.F. Webber (Eds.). London: Academic Press.
- Berryman, A.A. 1989. Adaptive Pathways in Scolytid-Fungus Associations. In. *Insect-Fungus Interactions*, N. Wilding, N.M. Collins, P.M. Hammond, J.F. Webber (Eds.). London: Academic Press.
- Bright, D.E. 1993. Systematics of Bark Beetles. In. *Beetle-Pathogen Interactions in Conifer Forests*, T.D. Schowalter, G.M. Filip (Eds.). San Diego: Academic Press.
- Cerezke, H.F. 1994. Warren rootcollar weevil, *Hylobius warreni* Wood (Coleoptera: Curculionidae), in Canada: Ecology, behaviour, damage relationships, and management. The Canadian Entomologist, 126, 1383–1442.
- Dušin, N.G. 1979. K voprosu o rasprostranenii kornevoi gubki nekotoryimi nasekomymi stvolovoi gruppy. [The spreading of *Heterobasidion annosum* by insects living in the stem of pines]. Záštita lesa, 4, 24–26.
- Ehnström, B., & Axelsson, R. 2002. *Insekts gnag i bark och ved*. Uppsala: SLU ArtDatabanken.
- Erbilgin, N., & Raffa, K.F. 2002. Association of declining red pine stands with reduced populations of bark beetle predators, seasonal increases in root colonizing insects, and incidence of root pathogens. Forest Ecology Management, 164, 221–36.
- Goheen, D.J., & Cobb, F.W. Jr. 1978. Occurrence of *Verticicladiella wagenerii* and its perfect state, *Ceratocystis wageneri* sp. nov., in insect galleries. Phytopathology, 68, 1192–1195.
- Hallaksela, A.-M. 1977. Kuusen kantojen mikrobilajisto. [Microbial flora isolated from Norway spruce stumps]. Acta Forestalia Fennica, 158, 1–48.
- Halambek, M. 1976. Dieback of eastern white pine (*Pinus strobus* L.) in cultures. Poljoprivredna znanstvena smotra – Agriculturae Conspectus Scientificus, 39, 495–98.
- Hamelin, R. 1996. Genetic diversity between and within cankers of the white pine blister rust. Phytopathology, 86, 875–79.

- Hansen, E.M., Goheen, D.J., Hessburg, P.F., Witcosky, J.J., & Schowalter, T.D. 1988. Biology and Management of Black-Stain Root Disease in Douglas-fir. In. *Leptographium Root Diseases on Conifers*, T.C. Harrington, F.W. Jr. Cobb (Eds.). St. Paul, Minnesota: APS Press.
- Harrington, T.C. 1988. *Leptographium* Species, Their Distributions, Hosts and Insect Vectors. In. *Leptographium Root Diseases on Conifers*, T.C. Harrington, F.W. Jr Cobb (Eds.). St. Paul, Minnesota: APS Press.
- Harrington, T.C., & Cobb, F.W. Jr. 1983. Pathogenicity of *Leptographium* and *Verticicladiella* spp. isolated from roots of Western North American conifers. *Phytopathology*, 73, 596–99.
- Harrington, T.C., & Cobb, F.W. Jr. 1986. Varieties of *Verticicladiella wageneri*. *Mycologia*, 78, 562–67.
- Harrington, T.C., Cobb, F.W. Jr, & Lownsberry, J.W. 1985. Activity of *Hylastes nigrinus*, a vector of *Verticicladiella wageneri*, in thinned stands of Douglas-fir. *Canadian Journal of Forest Research*, 15, 519–23.
- Harrington, T.C., Reinhart, C., Thornburgh, D.A., & Cobb, F.W. Jr. 1983. Association of black-stain root disease with precommercial thinning of Douglas-fir. *Forest Science*, 29, 12–14.
- Hessburg, P.F., & Hansen, E.M. 1986. Mechanisms of intertree transmission of *Ceratocystis wageneri* in young Douglas-fir. *Canadian Journal of Forest Research*, 16, 1250–54.
- Hunt, R.S. 1985. Experimental evidence of heterothallism in *Cronartium ribicola*. *Canadian Journal of Botany*, 63, 1086–88.
- Hunter, M.D. 2001. Out of sight, out of mind: the impacts of root-feeding insects in natural and managed systems. *Agricultural and Forest Entomology*, 3, 3–9.
- Jacobs, K., & Wingfield, M.J. 2001. *Leptographium species, Tree pathogens, Insect Associates and Agents of Blue-Stain*. St. Paul, Minnesota: APS Press.
- Jacobs, K., Wingfield, M.J., Uzunovic, A., & Frisullo, S. 2001. Three new species of *Leptographium* from pine. *Mycological Research*, 105, 490–99.
- Jørgensen, E., & Beier Petersen, B. 1951. Angræb af *Fomes annosus* (Fr.) Cke, og *Hylesinus piniperda* L. på *Pinus sylvestris* i Djurslands plantager. *Dansk Skovforenings Tidsskrift*, 9, 453–79.
- Kadlec, Z., Starý, P., & Zumr, V. 1992. Field evidence for the large pine weevil, *Hylobius abietis* as a vector of *Heterobasidion annosum*. *European Journal of Forest Pathology*, 22, 316–18.
- Kangas, E. 1934. Tutkimuksia Punkaharjun männiköiden hyönteistuhoista. *Metsätieteellisen tutkimuslaitoksen julkaisuja*, 19, 1–68.
- Kangas, E. 1938. Zur Biologie und Verbreitung der *Pissodes*-Arten (Col., Curculionidae) Finnlands. *Annales Entomologici Fennici*, 4, 73–98.
- Kendrick, W.B. 1962. The *Leptographium* complex, *Verticicladiella* Hughes. *Canadian Journal of Botany*, 40, 771–97.
- Klepzig, K.D., Raffa, K.F., & Smalley, E.B. 1991. Association of an insect-fungal complex with Red Pine Decline in Wisconsin. *Forest Science*, 37, 1119–39.
- Kudela, M. 1974. *Pissodes* Germar. In. *Die Forstschädlinge Europas*. 2. Band. W. Schwenke (Ed.). München.
- Lackner, A.L., & Alexander, S.A. 1982. Occurrence and pathogenicity of *Verticicladiella procera* in Christmas tree plantations in Virginia. *Plant Disease*, 66, 211–12.
- Laine, L. 1977. Juurikääpä puuvartisilla kasveilla Suomessa ja sen levitämisen hyönteisten välityksellä. *Helsingin yliopiston kasvitieteen laitoksen julkaisuja* 3.
- Leach, J.G. 1940. *Insect Transmission of Plant Diseases*. New York & London: McGraw Hill Book Company.
- Lévieux, J., Piou, D., Cassier, P., André, M., & Guillaumin, D. 1994a. Association of phytopathogenic fungi for the Scots pine (*Pinus sylvestris* L.) with the European pine weevil *Hylobius abietis* (L.) (Col. Curculionidae). *The Canadian Entomologist*, 126, 929–36.
- Lévieux, J., Monestier, C., & Cassier, P. 1994b. The fir weevil *Pissodes piceae* Ill. (Coleopt. Curculionidae) life cycle in Central France. A possible vector of phytopathogenic fungi. *Bulletin de la Societe Zoologique de France*, 119, 5–14.
- Lewis, K.J., & Alexander, S.A. 1986. Insects associated with the transmission of *Verticicladiella procera*. *Canadian Journal of Forest Research*, 16, 1330–33.
- Lewis, K.J., Alexander, S.A., & Horner, W.E. 1987. Distribution and efficacy of propagules of *Verticicladiella procera* in soil. *Phytopathology*, 77, 552–56.
- Livingston, W.H., & Wingfield, M.J. 1982. First report of *Verticicladiella procera* on pines in Minnesota. *Plant Disease*, 66, 260–61.

- Löyttyniemi, K., & Uusvaara, O. 1977. Insect attack on pine and spruce sawlogs felled during the growing season. *Communicationes Instituti Forestalia Fenniae*, 89, 1–48.
- Mathiesen, A. 1951. Einige neue *Ophiostoma*-arten in Schweden. *Svensk Botanisk Tidskrift*, 45, 203–32.
- Mathiesen-Käärik, A. 1953. Eine Übersicht über die gewöhnlichsten mit Borkenkäfern assoziierten Bläuepilze in Schweden und einige für Schweden neue Bläuepilze. *Meddelanden från Statens skogsforskningsinstitut*, 43, 1–74.
- Mathiesen-Käärik, A. 1960. Studies on the ecology, taxonomy and physiology of Swedish insect-associated blue stain fungi, especially the genus *Ceratocystis*. *Oikos*, 11, 1–25.
- Morelet, M. 1986. Les *Verticillidiella* des pins en liaison avec les phénomènes de dépérissement. *Bulletin OEPP/EPPO Bulletin*, 16, 473–77.
- Nevill, R.J., & Alexander, S.A. 1992a. Pathogenicity of three fungal associates of *Hylobius pales* and *Pissodes nemorensis* (Coleoptera: Curculionidae) to eastern white pine. *Canadian Journal of Forest Research*, 22, 1438–40.
- Nevill, R.J., & Alexander, S.A. 1992b. Root- and stem-colonizing insects recovered from eastern white pines with procerum root disease. *Canadian Journal of Forest Research*, 22, 1712–16.
- Nevill, R.J., & Alexander, S.A. 1992c. Transmission of *Leptographium procerum* to eastern white pine by *Hylobius pales* and *Pissodes nemorensis* (Coleoptera: Curculionidae). *Plant Disease*, 76, 307–10.
- Nuorteva, M., & Laine, L. 1968. Über die Möglichkeiten der Insekten als Überträger des Wurzelschwamms (*Fomes annosus* (Fr.) Cooke). *Annales Entomologici Fennici*, 34, 113–35.
- Nuorteva, M., & Laine, L. 1972. Lebensfähige Diasporen des Wurzelschwamms (*Fomes annosus* (Fr.) Cooke) in den Exkrementen von *Hylobius abietis* L. (Col., Curculionidae). *Annales Entomologici Fennici*, 38, 119–21.
- Owen, D.R., Lindahl, K.Q. Jr, Wood, D.L. & Parmeter, J.R. Jr. 1987. Pathogenicity of fungi isolated from *Dendroctonus valens*, *D. brevicomis*, and *D. ponderosae* to ponderosa pine seedlings. *Phytopathology*, 77, 631–36.
- Pappinen, A., & von Weissenberg, K. 1994a. Association of the pine-top weevil with *Endocronartium pini* on Scots pine. *European Journal of Forest Pathology*, 24, 249–57.
- Pappinen, A., & von Weissenberg, K. 1994b. The ability of the pine-top weevil to carry spores and infect Scots pine with *Endocronartium pini*. *European Journal of Forest Pathology*, 24, 258–63.
- Pappinen, A., & von Weissenberg, K. 1996. Weevil feeding on Scots pine affects germination of *Endocronartium pini*. *European Journal of Forest Pathology*, 26, 225–34.
- Piou, D. 1993. Rôle d'*Hylobius abietis* (L) (Col, Curculionidae) dans le transport de *Leptographium procerum* (Kendr) Wing et son inoculation au pin sylvestre. *Annales des Sciences Forestières*, 50, 297–308.
- Raffa, K.F., & Klepzig, K.D. 1996. Effects of root inhabiting insect-fungal complexes on aspects of tree resistance to bark beetles. In: *Dynamics of Forest Herbivory: Quest for Pattern and Principle*, W.J. Mattson, P. Niemelä, M. Rousi (Eds.). USDA Forest Service. General Technical Report NC-183.
- Raffa, K.F., & Smalley, E.B. 1988. Host resistance to invasion by lower stem and root infesting insects of pine: response to controlled inoculations with the fungal associate *Leptographium terebrantis*. *Canadian Journal of Forest Research*, 18, 675–81.
- von Sydow, F. 1993. Fungi occurring in the roots and basal parts of one- and two-year-old spruce and pine stumps. *Scandinavian Journal of Forest Research*, 8, 174–84.
- Webber, J.F., & Gibbs, J.N. 1989. Insect Dissemination of Fungal Pathogens of Trees. In: *Insect-Fungus Interactions*. N. Wilding, N.M. Collins, P.M. Hammond, J.F. Webber (Eds.). London: Academic Press.
- Whitney, R.D. 1961. Root wounds and associated root rots of white spruce. *Forestry Chronicle*, 37, 401–11.
- Whitney, H.S. 1982. Relationships between Bark Beetles and Symbiotic Organisms. In: *Bark Beetles in North American Conifers. A System for the study of Evolutionary Biology*. J.B. Mitton, K.B. Sturgeon (Eds.). Austin: University of Texas Press.
- Wingfield, M.J. 1983. Association of *Verticillidiella procera* and *Leptographium terebrantis* with insects in the Lake States. *Canadian Journal of Forest Research*, 13, 1238–45.
- Wingfield, M.J. 1986. Pathogenicity of *Leptographium procerum* and *L. terebrantis* on *Pinus strobus* seedlings and established trees. *European Journal of Forest Pathology*, 16, 299–308.
- Witcosky, J.J. 1989. Root Beetles, Stand Disturbance, and Management of Black-Stain Root Disease in Plantations of Douglas-fir. In: *Insects Affecting Reforestation: Biology and Damage*, R.I. Alfaro, S.G. Glover (Eds.). Victoria: Forestry Canada.

- Witcosky, J.J., & Hansen, E.M. 1985. Root-colonizing insects recovered from Douglas-fir in various stages of decline due to black-stain root disease. *Phytopathology*, 75, 399–402.
- Witcosky, J.J., Schowalter, T.D., & Hansen, E.M. 1986a. *Hylastes nigrinus* (Coleoptera: Scolytidae), *Pissodes fasciatus*, and *Sterenius carinatus* (Coleoptera: Curculionidae) as vectors of black-stain root disease of Douglas-fir. *Environmental Entomology*, 15, 1090–95.
- Witcosky, J.J., Schowalter, T.D., & Hansen, E.M. 1986b. The influence of time of precommercial thinning on the colonization of Douglas-fir by three species of root-colonizing insects. *Canadian Journal of Forest Research*, 16, 745–49.
- Zambino, P.J., & Harrington, T.C. 1989. Isozyme variation within and among host-specialized varieties of *Leptographium wageneri*. *Mycologia*, 81, 122–33.

Chapter 18

PARASITOIDS, PREDATORS, NEMATODES AND PATHOGENS ASSOCIATED WITH BARK WEEVIL PESTS

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1. INTRODUCTION

Among the main bark weevil pests in Europe, *Hylobius abietis* L. and *Pissodes* spp. have been the subject of several major studies regarding the biology, impact and use of their natural enemies. In particular, parasitoids and nematodes of *H. abietis*, and parasitoids of pine and fir *Pissodes* spp. have been extensively studied. In contrast, very little has been done on *Cryptorhynchus lapathi* L., and nothing on *Hylobius pinastri* (Gyllenhal), or on *Otiorrhynchus* spp. in the forest environment, probably reflecting their lower importance in forest protection.

2. HYLOBIUS ABIETIS

2.1. Parasitoids

Compared to other bark and wood boring insects, *H. abietis* has a very limited parasitoid complex. Eight to ten parasitoid species are recorded from the weevil, but no single study on the life history of *H. abietis* mentioned more than three parasitoids (e.g. Munro 1929; Hanson 1943; Elton *et al.* 1964; Gerdin and Hedqvist 1985; Henry 1995) (Table 1). This restricted parasitoid complex is probably due to the fact that larvae are concealed beneath soil and thick bark and, thus, are not accessible to polyphagous parasitoids attacking other bark weevils or bark beetles in conifers.

Table 1. Parasitoids recorded in the literature from *Hylobius abietis* and their biology.
Names in bold refer to frequent parasitoids reported from at least three different studies.
Other names were mentioned in only one study. References are in the text..

	Biology
Hym. Braconidae	
<i>Allodorus lepidus</i> (Haliday)	Egg-larval koinobiont endoparasitoid ?
<i>Aspilota</i> sp.	Adult endoparasitoid, very unlikely record. See text
<i>Bracon hylobii</i> Ratzeburg¹	Larval idiobiont ectoparasitoid
<i>Perilitus areolaris</i> Gerdin & Hedqvist²	Adult endoparasitoid
Hym. Ichneumonidae	
<i>Dolichomitus tuberculatus</i> (Geoffroy)	Larval (and pupal?) idiobiont ectoparasitoid
<i>Stenarella gladiator</i> (Scopoli)	Unknown, but very unlikely record. See text
Hym. Pteromalidae	
<i>Tomicobia</i> sp.	Adult endoparasitoid
Dipt. Phoridae	
<i>Megaselia plurispinulosa</i> Zetterstedt	Larval koinobiont endoparasitoid ?

¹ Some records as *Bracon brachycerus* Thomson, probably a misidentification

² Some records as *Perilitus rutilus* (Nees), probably a misidentification

Adults are commonly attacked by *Perilitus areolaris* Gerdin and Hedqvist (Hym.: Braconidae) (Gerdin and Hedqvist 1985; Starý *et al.* 1988). Earlier studies mentioned *Perilitus rutilus* (Nees) as parasitoid of *H. abietis* adults (e.g. Schindler 1964; Novák 1965; Slizynski 1969), but recent taxonomic studies (Starý *et al.* 1988; Haeselbarth 1999) suggested that *P. rutilus* was a misidentification of *P. areolaris*, which is known only from *H. abietis*, whereas *P. rutilus* is a parasitoid of weevils of the genera *Sitona* and *Phytonomus*. Schindler (1964) provides data on the life cycle of *P. areolaris* (as *P. rutilus*) in Germany. The parasitoid has two generations per year on *H. abietis*. It overwinters as a larva, in the adult weevil or in a cocoon. One to nine specimens emerge from a single host. Impact on beetle populations is difficult to measure for adult parasitoids. Schindler (1964) found 1-4% parasitism in field-collected samples in Germany, and Novák (1965) 15-16% in Czechoslovakia but, given the long life span of beetles, the short life of parasitized beetles and the two generations per year of parasitoids, the percentage of beetles eventually killed by the parasitoid is probably much higher. Further details on the biology of *P. areolaris*, such as larval development, mating and oviposition behaviour, are given in Slizynski (1969) and Gerdin and Hedqvist (1985). Schindler (1964) mentions *Aspilota* sp. (Hym.: Braconidae) as a rare parasitoid of adult *H. abietis*, but this record is very dubious because *Aspilota* species are known to parasitise Phoridae (Diptera). Långström (1972) also observed two parasitoids of adult *H. abietis* in Finland, *Pygostolus* sp. (Hym.: Braconidae) and *Tomicobia* sp. (Hym.: Pteromalidae). Since only larvae were obtained, *Pygostolus* sp. may be a

misidentification for *Perilitus areolaris*. *Tomicobia* spp. are known parasitoids of Scolytidae and Curculionidae, but have not been reported elsewhere from *H. abietis*.

H. abietis larvae are attacked by at least two parasitoids, *Dolichomitus tuberculatus* (Geoffroy) (Hym.: Ichneumonidae) and *Bracon hylobii* Ratzeburg (Hym.: Braconidae). *D. tuberculatus* has often been reared from *H. abietis*, but always at low level (e.g. Munro 1929; Hanson 1943). Little is known of the biology of this parasitoid on *H. abietis*. It has also been reared from the weevil *C. lapathi* (see below) and from Cerambycidae (Fitton *et al.* 1988; Kenis and Hilszczanski, chapter 21) and, as other *Dolichomitus* species, it is most certainly an idiobiont ectoparasitoid of mature larvae or pupae.

B. hylobii is by far the most important and the most studied parasitoid of *H. abietis*. It is a gregarious ectoparasitoid of *H. abietis* larvae. Females lay four to 12 eggs on the weevil larvae. Laboratory experiments showed that females laid more eggs and spent much more time on larger larvae than on smaller larvae. Only larvae heavier than 100 mg were parasitized (Henry and Day 2000). In the laboratory, females gave rise to a maximum of 93 offspring and up to 17 host larvae were parasitised by a single female (Henry 1995). *B. hylobii* has five larval instars (Munro, in Hedqvist 1958). The last larval instar builds a cocoon in which it overwinters. Pupation and adult emergence occur in spring. In the UK, it was observed causing 30% parasitism in pine (Munro 1929) and an average of 47 % in Sitka spruce (Henry and Day 2001), but has a non-uniform distribution within sites. It was long assumed that *B. hylobii* is able to attack only larvae that occur at the level of the ground (Hedqvist 1958) and, therefore, would be incapable of parasitizing the majority of larvae that live under the bark deeper in the soil. However, a recent study (Henry and Day 2001) showed that, on Sitka spruce in the UK, most host larvae were reachable by *B. hylobii*. Parasitized larvae were found at depths of up to 15 cm and, on average, occurred at greater depth than healthy larvae.

B. hylobii seems to be rather specific. The only other hosts known are weevils of the genus *Pissodes* (Hedqvist 1958). A closely related species, *Bracon brachycerus* Thomson has been reported from *H. abietis* (see Hedqvist 1958; Herting 1973,) but Hedqvist (1958) supposes that these were misidentifications for *B. hylobii*.

The use of *B. hylobii* as a biological control agent has often been discussed. Munro (in Hedqvist 1958) was the first to suggest its use as a mean of control. More recently, Henry and Day (2000, 2001) proposed and tested several control methods involving augmentation or conservation of *B. hylobii*. Some 40,000 adult parasitoids were reared in the laboratory and released onto forest clear fells in their first two summers. Parasitism in these plots was three times higher than in control plots (Henry and Day, 2001). However, the prospects of using *B. hylobii* in inundative releases are limited by the high costs usually related to mass production of specific parasitoids. Henry and Day (2000, 2001) also suggest sylvicultural methods to increase the impact of *B. hylobii*, which could be used in combination with other control methods. For example, *B. hylobii* will lay fewer eggs on smaller larvae, thus parasitizing higher numbers of small larvae than large larvae. Therefore, they anticipate that increasing resistance in the larval weevils' feeding substrate may have not only a direct effect on weevil mortality but also an indirect effect through an

increase in parasitism rate. Provision of food for parasitoid adults has also been suggested. Finally, some forest site conditions known to reduce the level of parasitism, such as brash heaped on site after felling and needle litter lying over bark, could be easily modified to favour the activity of *B. hylobii*. However, more studies are needed, particularly on host-location behaviour and on reproduction in the field, to properly assess the possible impact of these methods.

A few other larval parasitoids were mentioned on single occasions in the literature. *Allodorus lepidus* Haliday (Hym.: Braconidae) was cited by Györfi (in Herting 1973), but we have found nothing on the status and biology of this species. Bramanis (1930) mentions *Steranella gladiator* (Scopoli) (as *Mesostenus gladiator*) (Hym.: Ichneumonidae) on *H. abietis* larvae or pupae in pine stumps in Latvia, with a parasitism rate of 3.5%. This record is also doubtful because *Steranella* species are usually parasitoids of aculeate Hymenoptera. In Sweden, Trägardh (1931) observed *Megaselia plurispinulosa* Zetterstedt (Dipt.: Phoridae) on *H. abietis* larvae in spruce stumps. Up to 54% of the larvae were found parasitized in one sample, with about 8 to 10 phorid larvae per host. It remains to be seen, however, whether it is a true parasitoid or a scavenger, as are the great majority of Phoridae. However, it belongs to a genus which is known to include several parasitoids of various insect orders (Disney 1994). Furthermore, the structure of its mouthparts suggests a truly parasitic behaviour (Trägardh 1931).

2.2. Predators

Little is known of predators of *H. abietis*. Reviews by Escherich (1923), Eidmann (1974) and Leather *et al.* (1999) provide lists of possible vertebrate and invertebrate predators, but nothing is known of their actual impact. Several birds have been observed feeding on larvae and adults, among which woodpeckers seem to be the most important (Eidmann 1974). Many insect predators were encountered in and around pine stumps attacked by *H. abietis* (list in Leather *et al.* 1999) but only few were observed feeding on the weevil. Notable exceptions are *Laphria* sp. (Dipt.: Asilidae), which was observed attacking adults, several Carabidae and Elateridae (Coleoptera), feeding on larvae and adults, and fly larvae, possibly of the genus *Brachyopa* (Dipt.: Syrphidae) found beside cadavers in larval galleries (Escherich 1923). The feeding habit of *H. abietis* larvae probably protects them against generalist predators. However, larvae may be caught when migrating from one food source to another. Experiments showed that, during migration, larvae are vulnerable to carabid predators (Salisbury and Leather 1998). But the real impact of predators in the field still needs to be evaluated.

2.3. Pathogens

Up to now the occurrence of pathogens in *Hylobius abietis* and closely related *Hylobius* species has been poorly studied, in spite of the importance of these forest pest insects. In Europe some reports have focused on the occurrence and action of entomopathogenic fungi in *H. abietis* but few authors have reported the occurrence

of Protozoa. Pathogens have not been better studied in other species of the genus *Hylobius*, including the North America species. A few papers have focused on entomopathogenic fungi, and only one on a protozoan disease (in *H. pales* (Herbst): Walstad *et al.* 1970, Walstad and Anderson 1971, Schabel 1976, 1978, Schabel and Taft 1988; in *H. rhizophagus* Millers: Goyer and Benjamin 1971).

The results of early attempts to use the entomopathogenic fungus *Beauveria bassiana* (Bals., Vuill.) against *H. abietis* in laboratory and field tests were not always in agreement, and some of them were not very promising (Novák and Samsinakova 1964, Samsinakova and Novák 1967, Waldenfels 1975). Investigations on the occurrence of entomopathogenic fungi in field populations of *H. abietis* showed that *B. bassiana* can be found in *H. abietis* adults (Gerdin, 1977). In laboratory experiments, *B. bassiana* was tested against adult *H. abietis* and it was shown that high temperatures ($> 30^{\circ}\text{C}$) were unfavourable (compared to 13° and 23°C). Inoculation with spore suspension led to higher infection rates compared to inoculation with dry spore powder (Wegensteiner and Führer 1988). The same study showed that sustained contact with *B. bassiana*-treated spruce bark caused high infection rates, and even limited contact of beetles with *B. bassiana*-treated bark for three days resulted in 100% infection, but with a long survival time of beetles (81.8 days). A comparative study of the efficacy of *B. bassiana* and two *Beauveria brongniartii* (Sacc., Petch.) strains showed differences in incubation time but high infection rates with all tested isolates (Wegensteiner 1989). Inoculation of *H. abietis* via fortuitous contact with spores of *B. bassiana* or *B. brongniartii* on fungus-overgrown beetles resulted in short survival time and high infection rates. This observation indicates the importance of a host passage, which is known to increase virulence (Wegensteiner 1992).

Metarhizium anisopliae (Metschn., Sorokin) has been reported to be very effective against *H. abietis*, achieving 100% mortality within 9 days, but significant strain-dependent differences were found in *H. abietis*, as well as differences in susceptibility of *H. abietis* compared to other insect species (Markova and Samsinakova 1990, Markova 2000). Some of these authors have mentioned that the tough, thick cuticle of *H. abietis* can be an exceptional problem for the effectiveness of entomopathogenic fungi, at least in prolonging the time to host death.

Pathogens other than fungi are reported from adult beetles. *Gregarina hylobii* (Fuchs) was found in the midgut lumen of *H. abietis*, and *Ophryocystis hylobii* (Purrini & Ormieres) in the Malpighian tubules (Fuchs 1915, Geus 1969, Purrini and Ormieres 1982). *Nosema hylobii* (Purrini) was described from the cells of the midgut epithelium of *H. abietis* (Purrini 1981). All those investigations were basic studies and concentrated on populations in Germany. Nothing is known of the effects of these pathogens on their hosts.

2.4. Nematodes

There is little evidence that parasitic nematodes are an important cause of natural mortality of forest weevils, but entomopathogenic nematodes (Rhabditida:

Heterorhabditidae and Steinernematidae) have potential as inundative biological control agents of *Hylobius abietis*.

Nematodes from three orders (Tylenchida, Diplogasterida and Rhabditida) have been reported from *Hylobius abietis* larvae. Up to 10% of insects collected in Denmark harboured *Allantonema miribile* Leuckart (Tylenchida: Allantonematidae), a parasite of the body cavity (Bovien 1937), but Wüller (1923) reported that *A. miribile* was not particularly pathogenic to pine weevils. *Dirhabdilaimus leuckarti* Fuchs (Diplogasterida: Diplogasteroididae) was isolated from dead or moribund "white, flaccid" larvae of *H. abietis* in Sweden, but when cultured and tested in the laboratory was unable to cause disease in *H. abietis* larvae (Pye and Burman, 1977). *Diplogaster* sp. (Diplogasterida: Diplogasteridae) was found in almost half of the dead *H. abietis* larvae field-collected in Sweden, but could not be confirmed as the cause of death (Gerdin 1977). Most members of the genus feed on dead material.

Entomopathogenic nematodes (*Steinernema* spp. and *Heterorhabditis* spp.) are parasites of insects that normally kill the host and develop in the resulting cadaver. Their natural hosts include the soil-dwelling stages of many insect species. They are also in commercial use for the control of several insect pests worldwide. *Steinernema feltiae* Filipjev was isolated from *H. abietis* in the Czech republic (Mracek *et al.* 1993); both adult and larval weevils were infected (Z. Mracek, pers. comm.). Entomopathogenic nematodes may in certain circumstances result in epizootics (Peters 1996). Epizootics have not been reported in *H. abietis*, but up to 30% of *Hylobius pales* sampled in North Carolina were infected with a *Steinernema* sp. (Thomas 1970).

Due largely to their mutualistic association with entomopathogenic bacteria (*Xenorhabdus* spp. and *Photorhabdus* spp., respectively), *Steinernema* spp. and *Heterorhabditis* spp. can result in rapid death of their insect hosts, and mass production is possible on a large scale for inundative application (Burnell and Stock 2000; Gaugler 2002). They have several other attributes that make them suitable as biological control agents, including safety to humans, plants and non-target organisms, and active host finding by the infective juvenile (making cryptic hosts, such as pine weevil larvae in tree stumps, potential targets). Entomopathogenic nematodes are applied inundatively, and recycling in the host environment is of secondary importance.

Field trials against adult *Hylobius abietis* in Sweden and *H. congener* in Canada showed that treating young seedlings with *Steinernema* spp. reduced damage due to adult weevils (Pye and Pye 1985; Eidt *et al.* 1995). However, extensive field trials in Scotland by the Forestry Commission using nematodes on containerised and bare root planting stock did not produce significant reduction in *H. abietis* feeding damage to the plants (Brixey 1997). Inadequate control of adult weevils might be due to failure of nematodes to survive at adequate numbers throughout the *Hylobius* feeding season, or may be accounted for by poor susceptibility of the adult weevils to entomopathogenic nematodes (a dose of 8,800 infective juvenile nematodes/insect was required to kill 50% of adult weevils (Collins 1993).

Early work in Sweden demonstrated the susceptibility of pine weevil larvae to *Steinernema carpocapsae* Weiser (Pye and Burman 1978) and preliminary field

trials showed that application of this nematode had the potential to suppress numbers of weevils in stumps (Burman *et al.* 1979). In Scottish field trials, up to 70% of the population within treated stumps were infected and killed by nematodes (Brixey 1997). More extensive area-wide trials conducted in Scotland by the Forestry Commission confirm that *S. carpocapsae*, applied as a spot treatment to stumps, shows promise for area-wide suppression of *H. abietis* populations (S. Heritage, pers comm. 2002). Both the Swedish and Scottish work has concentrated largely on a single species of nematode, *S. carpocapsae*. In recent trials in Ireland, *Heterorhabdites downesi* Stock, Griffin and Burnell was the most successful of four nematode species tested in reducing numbers of adult pine weevil emerging from treated pine stumps (Dillon 2003). Stumps treated with this nematode produced an average of 8 adult weevils compared to 146 emerging from untreated stumps. Entomopathogenic nematodes on their own are unlikely to provide adequate control of pine weevil populations, but they may form an important component of an integrated pest management system for this pest.

3. *Pissodes* spp.

3.1. Parasitoids

In the last 40 years, several extensive studies have been published on parasitoids of five of the eight European *Pissodes* spp. The pine trunk species *Pissodes castaneus* De Geer was studied by Alauzet (1982, 1987), Mills and Fisher (1986), Kenis and Mills (1994, 1998), Kenis *et al.* (1996) and Kenis (1996, 1997). Parasitoids of the two other pine trunk species, *P. pini* (L.) and *P. piniphilus* (Herbst) were investigated by Mills and Fisher (1986), Kenis and Mills (1994, 1998) and Kenis *et al.* (1996). The parasitoid complex of the fir trunk species *P. piceae* (Illiger) was studied by Haeselbarth (1962), Mills and Fisher (1986), Kenis and Mills (1994, 1998) and Kenis *et al.* (1996). *P. validirostris* (Salhberg), inhabiting pine cones, was the target of important studies by Annila (1975), Roques (1975), Mills and Fisher (1986), Kenis and Mills (1994, 1998), Kenis *et al.* (1996) and Kenis (1996, 1997). In contrast, very little has been done on the parasitoid complex of spruce trunk species, *P. harcyniae* (Herbst), *P. scabricollis* Miller and *P. gyllenhali* Gyllenhal, apart from some old parasitoid records (e.g. Lovaszy 1941; Zinovev 1958). However, unpublished data on parasitoids of *P. harcyniae* are provided in Table 2.

Table 2 shows the parasitoid complex of *Pissodes* spp. in Europe. *P. validirostris*, a pest of pine cones, is included in this review for comparison with congeneric species attacking conifer trunks. Only larval or pupal parasitoids are known. In all *Pissodes* spp., parasitism is usually dominated by braconids of the genera *Eubazus* and, to a lesser extent, *Coeloides*. In *Pissodes castaneus* however, the ichneumonid *Dolichomitus terebrans* (Ratzeburg) or the pteromalids *Rhopalicus tutela* (Walker) and *R. guttatus* (Ratzeburg) are occasionally more abundant than the braconids (Kenis and Mills, 1994). In general, parasitism on *Pissodes* spp. is higher than in other bark and wood boring beetles. Parasitism rates above 50% are common, whereas such high levels are rarely observed in Scolytidae, Cerambycidae

or *Hylobius abietis*. These high rates can be explained by the accessibility of *Pissodes* eggs and larvae. Most parasitism is due to the egg-larval koinobiont parasitoids *Eubazus* spp. which have easy access to eggs in *Pissodes* feeding holes. Such egg-larval parasitism rarely afflicts Scolytidae, the eggs of which are hidden in galleries. The other parasitoids are all larval idiobiont ectoparasitoids and are usually also known from other bark and wood beetles. However, larvae of *Pissodes* weevils are particularly accessible because of their large size -compared to other bark beetles- and their proximity to the bark surface -compared to wood boring beetles.

The biology, ecology and taxonomy of the braconids *Eubazus* spp. and *Coeloides* spp. have been the focus of several studies. *Eubazus* spp. were investigated in detail by Haeselbarth (1962) on *P. piceae*, by Alauzet (1987) on *P. castaneus*, by Annila (1975), by Roques (1975) on *P. validirostris* and by Kenis *et al.* (1996) and Kenis and Mills (1998) on all *Pissodes* spp. *Eubazus* spp. attacking *Pissodes* spp. are specific to this genus and, perhaps, to the genus *Magdalalis* (Achterberg and Kenis, 2000). They lay their eggs in *Pissodes* eggs, develop inside the host larva, and kill their host in the prepupal stage. Then, they build a cocoon in which to pupate under the bark or in the cone. Until recently, the taxonomy of the genus *Eubazus* was confusing. Several species had been described in the past, in many genera (*Eubadizon*, *Brachistes*, *Allodorus*, *Calyptus*), but many studies on *Pissodes* parasitoids had suggested that a single species attacks all European *Pissodes* spp. (Haeselbarth 1962; Annila 1975; Roques 1975; Alauzet 1982; Mills and Fisher 1986). Very recently, Kenis and his co-workers (Kenis *et al.* 1996; Kenis and Mills 1998) used morphometric, molecular and bio-ecological characters to show the occurrence of three sibling species, each of them being largely specialised in different hosts and microhabitats. *E. semirugosus* (Nees) is a parasitoid of those *Pissodes* spp. which develop in pine and spruce trunks, *E. robustus* (Ratzeburg) primarily attacks *P. validirostris* in pine cones and is occasionally found attacking *Pissodes* spp. in pine trunks, and the newly described species *E. abieticola* Achterberg and Kenis attacks only *P. piceae* in fir trunks. The taxonomy of the *Eubazus* spp. attacking *Pissodes* spp. throughout the world was revised by Achterberg and Kenis (2000). Interesting intraspecific variability in developmental responses was found in *Eubazus* spp. Mountain biotypes of *E. semirugosus* and *E. robustus* were found to have an obligatory diapause, in contrast to lowlands biotypes of the same species that were reared on the same hosts without diapause (Kenis *et al.* 1996). This variation is regarded as an adaptation to the phenology of their hosts in different climatic conditions. Indeed, the phenology of *Eubazus* populations is usually well synchronized with that of the corresponding *Pissodes* populations.

Three *Coeloides* spp. are found on *Pissodes* spp. (Haeselbarth 1967; Kenis and Mills 1994). *C. sordidator* (Ratzeburg), synonymous with *C. melanostigma* Strand and *C. stigmaticus* Hellén, is a major parasitoid of all pine-feeding *Pissodes* spp. It is also known from pine scolytids, cerambycids and buprestids (Haeselbarth 1967), but records from *Pissodes* spp. are much more frequent. In contrast, *C. abdominalis* (Zetterstedt) is a well-known parasitoid of pine bark beetles (Haeselbarth 1967; Mills 1983), but it has also been reared in sizeable numbers from *P. castaneus* and *P. pini* (Alauzet 1982, 1987; Kenis and Mills 1994). Finally, *C. forsteri* Haeselbarth

is a rarer species, which has been reared exclusively from *P. pini*, *P. piceae*, *P. piniphilus* and *P. harcyniae* (Haeselbarth 1967; Kenis and Mills 1994). Details on the biology of *C. sordidator* are given in Annila (1975), Roques (1975), Alauzet (1987) and Kenis (1996, 1997). *C. abdominalis* was studied by Alauzet (1987) on *P. castaneus* and by Nuorteva (1957) on Scolytidae. The biology of *C. forsteri* on *P. piceae* was described by Haeselbarth (1962) as *Coelooides* sp. All *Coelooides* spp. are idiobiont ectoparasitoids of late instar larvae in feeding galleries. They paralyse and oviposit on *Pissodes* larvae through the bark. Parasitoid larvae develop quickly and build a cocoon in which they overwinter. One or two generations per year are recorded by most authors, although Alauzet (1987) counted up to four generations in southern France. True diapause in *C. sordidator* was observed in the cocoon stage and was induced by short day photoperiod on the mother and by low temperature on larvae (Kenis 1997). In an attempt to develop rearing methods for *C. sordidator*, Kenis (1996) analysed the factors affecting sex ratio in laboratory rearing. Three factors were found to influence sex ratio: the host age, the age of ovipositing females, and the host of origin. Male-biased sex ratios were observed with young hosts, young females and with *C. sordidator* strains originally from *P. castaneus*. Female-biased sex-ratios were observed with older hosts, older females and with strains from *P. validirostris*. Competitive interactions between *C. sordidator* and *E. semirugosus* were studied by Kenis (1997). *C. sordidator* did not discriminate between healthy larvae and larvae containing *E. semirugosus* larvae suggesting that *C. sordidator*, and probably other ectoparasitoids, have a negative impact on *E. semirugosus* populations. Haeselbarth (1962) made similar observations with *Eubazus abieticola* and *Coelooides forsteri*.

Other braconids have occasionally been reported from *Pissodes* spp. *Bracon* spp. were reared from *P. piceae*, *P. pini* and *P. castaneus*. (Frediani, 1957, Haeselbarth 1962, Alauzet 1982; Kenis and Mills 1994). *B. palpebrator* Ratzeburg, *B. praetermissus* Marshall and *B. hylobii* have been mentioned as species, but the genus is in need of revision. Another species, *Spathius rubidus* (Rossi), was also reared in low numbers from *P. castaneus*, *P. pini* and *P. validirostris* (Annila 1975; Roques 1975; Alauzet 1982; Kenis and Mills 1994, M. Kenis, unpublished).

The ichneumonid *Dolichomitus terebrans* (Ratzeburg) is frequently associated with *P. castaneus* and has also been reared from *P. harcyniae*, *P. pini*, *P. piniphilus* and *P. piceae*. The few observations available on the parasitoid complex of *P. harcyniae* suggest that *D. terebrans* is a dominant species in this complex. It is also known from the scolytid *Dendroctonus micans* (Kugelann) (Gregoire 1976) as well as from several microlepidoptera (Aubert 1969), but several of these records may result from identification errors. In North America, a sub-species, *D. terebrans nubilipennis* (Viereck), occurs, which seems to be restricted to *Pissodes* spp. (Carlson 1979). *D. terebrans* is an ectoparasitoid attacking larvae, prepupae or pupae in pupal cells. In *P. validirostris*, it is replaced by three other pimpline ichneumonids, *Exeristes ruficollis* (Gravenhorst), *Scambus sudeticus* (Glowacki) and *S. sagax* (Hartig) (Roques 1975; Kenis and Mills 1994). A recent paper (Starzyk 1996) provides a list of ichneumonids supposedly reared from *P. piceae* in Poland: *Baranisobas ridibundus* (Gravenhorst), *Coleocentrus caligatus* (Gravenhorst),

Scambus brevicornis (L.) and *Atractodes* sp. Since none of these species are known to attack Curculionidae, these records have to be considered cautiously.

The pteromalids *Rhopalicus tutela* (Walker), *R. guttatus* (Ratzeburg) and *Metacolus unifasciatus* Foerster are ectoparasitoids on larvae in galleries and are frequently found on *P. castaneus*. *R. tutela* has also been occasionally found on *P. pini*, *P. piniphilus*, and *P. harcyniae* (Kenis and Mills 1994, Kenis, unpublished). *R. guttatus* was sometimes reared from pine cones (Hedqvist 1963; Roques 1975), suggesting that it also attacks *P. validirostris*. However, Roques (1975) found it mainly in cones attacked by *Dioryctria mutatella* Fuchs (Lep.: Pyralidae). *M. unifasciatus* is usually associated with pine scolytids whereas *R. tutela* is a polyphagous species attacking a large number of bark beetle species (Mills 1983) and its abundance on *Pissodes* spp. probably depends on the density of its alternate hosts in the environment. Its biology, particularly host location mechanism, has been intensively studied on the scolytid beetle *Ips typographus* (L.) (e.g. Krüger and Mills 1990; Pettersson 2001; Pettersson et al. 2001).

Two species of *Eurytoma* spp. are reared from *Pissodes* spp. *Pissodes validirostris* is often heavily attacked by *E. annilai* Hedqvist (Annila 1975; Roques 1975). Roques (1976) showed that *E. annilai* (in Roques mentioned as *E. waachli*) is a cleptoparasitoid of the ichneumonids *Scambus* spp. *E. annilai* and *E. wachli* Mayr are occasionally reared from *P. castaneus*, but their biology is not known. Kenis and Mills (1994) suggest that they may act as clepto- or hyperparasitoids. An unidentified *Eurytoma* sp. has been reared in high numbers from *P. harcyniae* in Poland (M. Kenis, unpublished).

Two eupelmids, *Calosota aestivalis* Curtis and *Eupelmus urozonous* Dalman were reared from *P. castaneus* by Frediani (1957) (as *C. vernalis* Curtis) and Kenis and Mills (1994). Whereas Frediani describes them as primary parasitoids, Kenis and Mills reared them from cocoons of *D. terebrans* and *Coeloides* spp., respectively.

Finally, Alauzet (1982) mentions the tarsonemid mite *Pediculoides ventricosus* Newport as a parasite of *P. castaneus* pupae in southern France. However, its biology and incidence on *P. castaneus* have not been fully assessed.

High rates of parasitism observed in nearly all studies suggest an important impact on weevil populations. However, most studies on parasitoids were rather descriptive and no serious attempt has been made to evaluate the real impact of these parasitoids on the population dynamics of their hosts, or to develop methods to conserve or augment parasitoids. This perhaps reflects the relatively low importance of *Pissodes* spp. in European forestry compared to, e.g., bark beetles or *Hylobius abietis*. Ironically, the largest study on parasitoids of *Pissodes* spp. in Europe was carried out for the biological control project against the North American *Pissodes strobi*, a pest that is far more serious than any of its eight European congeners (Kenis and Mills 1994; Hulme and Kenis 2002). Only two authors briefly explore the potential of parasitoids for the control of *Pissodes* spp. in Europe. Haeselbarth (1962) suggests that fir trees infested by *P. piceae* be cut in spring, between the emergence period of the parasitoids and that of the weevil. Annila (1975) suggests strategies to conserve parasitoids of *P. validirostris* in pine seed orchards in Finland.

*Table 2. Parasitoids of *Pissodes* spp. in Europe, with level of abundance: xxx = Dominant in at least two studies or samples, and present in >50% of the studies/samples; xx = Dominant in at least one study/sample or present in >50% of the studies/samples; x = Present in at least two studies/samples or reared from *Pissodes* sp. by M. Kenis. Based on reviews by Mills and Fisher (1985), Kenis and Mills (1994) and unpublished surveys by M. Kenis from 1993-1998.*

Parasitoid species	Biology ¹	<i>castaneus</i>	<i>pini</i>	<i>piniphilus</i>	<i>validirostris</i>	<i>piccae</i>	<i>harcyniae</i>
Hym.: Ichneumonidae							
<i>Dolichomitus terebrans</i> (Ratzeburg)	L. ec.	xxx	x	x		x	xxx
<i>Exeristes ruficollis</i> (Gravenhorst)	L. ec.				x		
<i>Scambus sagax</i> Hartig	L. ec				x		
<i>Scambus sudeticus</i> (Glowacki)	L. ec.				xx		
Hym.: Braconidae							
<i>Bracon hylobii</i> Ratzeburg	L. ec.			x		x	
<i>Bracon praetermissus</i> Marshall	L. ec.		x				
Undetermined <i>Bracon</i> spp.	L. ec.	x	x	x			
<i>Coeloides abdominalis</i> (Zetterstedt)	L. ec.	x	x				
<i>Coeloides forsteri</i> Haeselbarth	L. ec.		x	x		x	xx
<i>Coeloides sordidator</i> (Ratzeburg)	L. ec.	xxx	xx	xxx	xx		
<i>Eubazus abieticola</i> Achterberg & Kenis	E.-L. en.					xxx	
<i>Eubazus robustus</i> (Ratzeburg)	E.-L. en.	x		x	xxx		
<i>Eubazus semirugosus</i> (Nees)	E.-L. en.	xxx	xxx	xxx			xxx
<i>Spathius rubidus</i> (Rossi)	L. ec.	x	x		x		
Hym.: Pteromalidae							
<i>Metacolus unifasciatus</i> Foerster	L. ec.	xx					
<i>Rhopalicus guttatus</i> (Ratzeburg)	L. ec.	xx	x		x	x	
<i>Rhopalicus tutela</i> (Walker)	L. ec.	xx	x	x			xx
Hym.: Eupelmidae							
<i>Calosota aestivalis</i> Curtis	L. ec. (h)	x					
<i>Eupelmus urozonius</i> Dalman	L. ec. (h)	x					
Hym.: Eurytomidae							
<i>Eurytoma annilai</i> Hedqvist	L. ec.	x			x		
<i>Eurytoma wachtli</i> Mayr	L. ec.	x					
Undetermined <i>Eurytoma</i> spp.	L. ec.			x			xx
Acar: Tarsonemidae							
<i>Pediculoides ventricosus</i> Newport	<i>P. ec.</i>		x				

¹ Biology: L. ec. = Larval idiobiont ectoparasitoid; E.-L. en. = Egg-larval koinobiont endoparasitoid; P. ec. = Pupal ectoparasite; h = Facultative hyperparasitoid.

Should new control methods against *Pissodes* spp. be needed, the biology and ecology of *Pissodes* parasitoids are sufficiently known to apply this knowledge to the development of control methods. Similarly, this knowledge could be useful in case a European *Pissodes* species becomes invasive in another part of the world, such as *P. castaneus* which was introduced into Uruguay and Argentina (Abgrall *et*

al. 1999). Then, some parasitoids, in particular the specific *Eubazus* spp., could be considered as valuable control agents.

3.2. Predators, nematodes and pathogens

Other natural enemies of *Pissodes* spp. have been studied in much less details than parasitoids. Undoubtedly, the most important predators are woodpeckers. These are particularly important for the large species *P. piceae* and *P. pini* attacking mature fir and pine trees. Quantifying their impact is difficult, but Haeselbarth (1962) suggests that, often, over 50% of overwintering larvae of *P. piceae* are destroyed by woodpeckers. Nuorteva and Saari (1980) observed similar damage on *P. pini* larvae overwintering in their pupal cell. Fir, pine and spruce trunks debarked by woodpeckers are a good indication of the presence of *Pissodes* spp. (M. Kenis, unpublished).

Insect predators are not considered important mortality factors in European *Pissodes* spp. in contrast to North America, where *Lonchaea corticis* Taylor (Dipt.: Lonchaeidae) is the main natural enemy of *Pissodes strobi* (Peck) (Hulme and Kenis 2002). Alauzet (1982) mentions *Thanasimus formicarius* (L.) feeding occasionally on young, emerging adults, whereas eggs and feeding larvae are difficult to reach. *T. formicarius* has been extensively studied as a predator of bark beetles (Kenis, Wermelinger and Grégoire, chapter 11). Lonchaeid flies (Haeselbarth 1962), *Nudobius latus* (Gravenhorst) (Col.: Staphylinidae) and *Xylophagus cinctus* (De Geer) (Dipt.: Xylophagidae) (Starzyk 1996) were found attacking *P. piceae*, but nothing is known of their importance.

Tylenchid nematodes of the genera *Sphaerulariopsis* (Sphaerulariidae) and *Neoparasitylenchus* (Allantonematidae) (Siddiqui 2000) are associated with *Pissodes* spp. It is notable that these genera also parasitise bark beetles, in which they may cause pathological effects (Kaya 1984). Other authors reported nematodes in *Pissodes* larvae and adults (e.g. Haeselbarth 1962), but nothing is known of the impact of these nematodes. The potential of entomopathogenic nematodes as a biological control agent for European *Pissodes* species has received little attention, but Laumond *et al.* (1979) showed that *Pissodes castaneus* larvae and pupae were very susceptible to *Steinernema carpocapsae* in the laboratory.

Dead larvae, pupae and teneral adults are sometimes found covered by fungi (Haeselbarth 1962; M. Kenis, unpublished), but their identity and role in weevil mortality has never been investigated. In contrast, dead larvae have often been observed enveloped in the growing mycelium of *Armillaria* spp., in particular in *P. piceae* (Starzyk 1996) and *P. castaneus* (M. Kenis, unpublished). Inundative biological control using pathogens has never been tested against *Pissodes* spp. in Europe.

4. CRYPTORHYNCHUS LAPATHI

To our knowledge, no specific studies have focused on the natural enemy complex of *C. lapathi*. Old parasitoid records are summarised in Szalay-Marzsó (1962) but,

among the dozen parasitoid species listed in this publication, most are impossible to accept as parasitoids of *C. lapathi*. The only investigations on the life history of *C. lapathi* and its parasitoids are found in Strojny (1951), who described the oviposition behaviour of the ichneumonid *Dolichomitus tuberculatus* (Geoffroy) on *C. lapathi* larvae in willow branches, and in Szalay-Marszó (1962), who briefly described parasitism by the ichneumonid *Perosis* sp. (probably, but not certainly, *Schreineria* sp.) on 5th instar larvae. But there is no information on the abundance of these parasitoids. Since the review of Szalay-Marzsó (1962), only Schimitschek (1964) mentioned the braconid *Bracon immutator* Nees, var. *austriaca* Fahringer, as a larval parasitoid, but does not provide any data on its abundance and biology.

Szalay-Marzsó (1962) also briefly mentions predation by tits on adults, and by woodpeckers on larvae. Nothing is known about pathogens or nematodes under natural conditions; however, the potential of entomopathogenic nematodes for the control of *Cryptorhynchus lapathi* was tested by Cavalcaselle and Deseo (1984).

5. OTIORRHYNCHUS SPP.

No studies have focused on natural enemies of *Otiorrhynchus arcticus* Germar and *O. nodosus* (Müller), the two species of this large genus considered as seedling pests in northern Europe. However, information on their potential natural enemy complex can be gathered from the numerous data on natural enemies of other *Otiorrhynchus* spp. in horticulture. Lists of parasitoids are found in Herting (1973), Tschorsnig and Herting (1994) and Noyes (2001). Parasitoids of adult weevils belong to the genera *Perilitus* and *Pygostolus* (Hym.: Braconidae), *Dirhicnus* and *Tomicobia* (Hym.: Pteromalidae), *Pandelleia*, and *Rondania* (Dipt.: Tachinidae), and *Megaselia* (Dipt.: Phoridae). Predators are reviewed by Herting (1973) and include the genera *Cerceris* (Hym.: Sphecidae), *Broscus* and *Carabus* (Col.: Carabidae), *Hister* (Col.: Histeridae) and *Formica* (Hym.: Formicidae). In general, the parasitoid and predator complexes of *Otiorrhynchus* spp. are rather limited, and no attempt has been made to use these natural enemies as biological control agents.

In contrast, parasitic nematodes are important natural enemies of *Otiorrhynchus* spp. In Finland, natural populations of *Steinernema feltiae* killed 20% of *Otiorrhynchus dubius* (Ström) and *O. ovatus* (L.) larvae in strawberries (Vainio and Hokkanen 1993). Natural infections of *O. sulcatus* by entomopathogenic nematodes (*Steinernema carpocapsae* S. *feltiae* and *Heterorhabditis megidis* Poinar, Jackson and Klein have also been reported (Poinar 1986; Peters 1996). Numerous trials have demonstrated the success of entomopathogenic nematodes for the control of *Otiorrhynchus* spp. (particularly *O. sulcatus* (F.)) infesting hardy ornamentals and soft fruits (e.g. Klingler 1988; Landi 1990; Deseo and Costanzi 1987; Mracek *et al.* 1993; Fitters *et al.* 2001), and several nematode-based products are sold for this purpose. Trials in Ontario demonstrated the potential of heterorhabditids for control of *O. sulcatus* and *O. ovatus* in forest nurseries, provided soil temperatures were adequate (Rutherford *et al.* 1987). Considering the success of parasitic nematodes against *Otiorrhynchus* spp. in horticulture, it would be highly desirable to evaluate

their potential against *O. arcticus* and *O. nodosus* in nurseries and plantations in northern Europe.

The main pathogens reported from *Otiorrhynchus* species (*O. ligustici* (L.), *O. ovatus*, *O. dubius*, *O. sulcatus*) are entomopathogenic fungi, which can be found in both larvae and adults of field populations, in some cases at high incidence (Marchal 1977, 1989). Therefore, the potential of such fungi to control *Otiorrhynchus* was tested: *Metarhizium anisopliae* and *Beauveria brongniartii* caused highest mortality of weevil larvae in laboratory and field tests (Workshop of the IOBC Study Group "Insect Pathogens and Insect-parasitic Nematodes" 1987 in Versailles 1989). *B. brongniartii* was reported to cause high mortality (up to 100%) of *O. sulcatus* in the lab and in the greenhouse (Coremanns-Pelseneer and Nef 1986, Tillemans *et al.* 1987). Various *M. anisopliae* strains were found to be effective (62% to 100% mortality) against *O. sulcatus* larvae in ornamentals (Zimmermann 1981, Sellenschlo 1984, Gillespie and Moorehouse 1989, Moorhouse *et al.* 1993a, 1993b). In addition, *M. anisopliae* was found to be also very effective under field conditions against *O. ovatus* and *O. dubius* larvae, whereas *B. bassiana* was less effective (Vainio and Hokkanen 1993). All of these results indicated the potential of entomopathogenic fungi for control of pest weevils in ornamentals, nurseries and various agricultural crops; today there are several commercial products on the market.

6. CONCLUSIONS

The information available on natural enemies of bark weevil pests in Europe varies with pest species and natural enemy category. The best studied systems are parasitoids of *Hylobius abietis* and *Pissodes* spp. The parasitoid complex of these insects is well known and the biology and ecology of their main parasitoids have been extensively studied. However, the role of parasitoids and other natural enemies in regulating weevil populations remains unclear. The impact of parasitoids is likely to be higher in *Pissodes* spp. than in *H. abietis*. *Pissodes* weevils are unusual among bark and wood-boring insects by suffering from high rates of parasitism. This is largely due to the specific egg-larval parasitoids *Eubazus* spp. Predators and pathogens have been less investigated. Even for the best studied systems, however, the impact and role of natural enemies on pest populations are not clearly understood.

Until now, little effort has been made to use these natural enemies in biological control programmes. Classical biological control, i.e. the introduction and establishment of an exotic natural enemy, has little prospect of success because the best targets for classical biological control are exotic pests whereas the main bark weevils in Europe are native. Inundative and conservation biological control are more promising strategies. Entomopathogenic nematodes and entomopathogenic fungi are used as biological pesticides against weevils in horticulture, and the techniques could be adapted to related forest pests. Particularly good targets would be *Otiorrhynchus* species and *H. abietis*. Promising results have already been achieved against *H. abietis* using entomopathogenic nematodes, but more research is

needed before obtaining commercially competitive products. Parasitoids and predators show little prospects as inundative biological control agents because of the high production costs and the large areas involved in forestry. In contrast, silvicultural methods could be developed, or modified, to enhance natural populations of parasitoids and predators, and increase their impact on the target pests. Such methods have already been suggested, in particular against *H. abietis*, but, so far, they have not been implemented.

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8. REFERENCES

- Abgrall, J.F., Villén González, V., & Porcile, J.F. 1999. Estudios de investigación sobre gorgojo de los pinos (I parte). Peligro a la vista. Chile Forestal, 24, 9-13.
- Achterberg, C. van, & Kenis, M. 2000. The Holarctic species of the subgenus *Allodorus* Foester s.s. of the genus *Eubazus* Nees (Hymenoptera: Braconidae). Zoologische Mededelingen Leiden, 73, 427-55.
- Alauzet, C. 1982. Bioécosse de *Pissodes notatus* F. ravageur des pins maritimes en forêt de Bouconne (Haute-Garonne: France). Nouvelle Revue d'Entomologie, 12, 81-89.
- Alauzet, C. 1987. Bioécologie de *Eubazus semirugosus*, *Coeloides abdominalis* et *C. sordidator* (Hym. : Braconidae) parasites de *Pissodes notatus* (Col. : Curculionidae) dans le sud de la France. Entomophaga, 32, 39-47.
- Annila, E. 1975. The biology of *Pissodes validirostris* Gyll. (Col., Curculionidae) and its harmfulness, especially in Scots pine seed orchards. Communications Instituti Forestalis Fenniae, 85, 1-95.
- Aubert, J.F. 1969. *Les Ichneumonides Ouest-Palearctiques et leur Hôtes*, I. *Pimplinae, Xoridinae, Acaenitinae*. Alfortville, France: Quatres Feuilles Editeur.
- Bovien, P. 1937. Some types of association between nematodes and insects. Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København, 101, 1-114.
- Bramanis, L. 1930. Die Bedeutung der Kiefernstubben auf den Kahlschlägen für die Entwicklung des Rüsselkäfers *Hylobius abietis* L. Folia zoologica et Hydrobiologica 1, 168-77. (Abstract in Review of Applied Entomology, 18, 695-96).
- Brixey, J. 1997. The potential for biological control to reduce *Hylobius abietis* damage. Forestry Commission Research Information Note, 273.
- Burman, M., Pye, A.E., & Nojd N.O. 1979. Preliminary field trial of the nematode *Neoplectana carpocapsae* against larvae of the pine weevil, *Hylobius abietis* (Coleoptera, Curculionidae). Annales Entomologici Fennici, 45, 88.
- Burnell, A.M., & Stock, S.P. 2000. *Heterorhabditis, Steinernema* and their bacterial symbionts - lethal pathogens of insects. Nematology, 2, 31-42.
- Carlson, R.W. 1979. Ichneumonidae. In: *Catalog of Hymenoptera in America North of Mexico* 1. K.V. Krombein, P.D. Hurd, D.R. Smith, B.D. Burks (Eds.). Washington, D.C.: Smithsonian Institution Press.
- Cavalcaselle, B., & Deseo, K.V. 1984. Prove di lotta contro le larve di insetti xilofagi del pioppo con nematodi entomopatogeni. Atti Giornate Fitopatologiche, 2, 393-402.
- Collins, S. 1993. The potential of entomopathogenic nematodes to reduce damage by *Hylobius abietis* L. Ph.D Thesis, University of London, UK.
- Coremanns-Pelseneer, J. & Nef, L. 1986. *Otiorrhynchus sulcatus* (Coleoptera): Larval control by the fungus *Beauveria* (first results). Mededelingen Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent, 51 (3a), 1049-56.
- Deseo, K., & Costanzi, M. 1987. Impiego di nematodi entomoparassiti contro larve di curculionidi dannosa a colture floricolle ornamentali. *Difesa delle piante*, 10, 127-32.

- Disney, R. H. L. 1994. *Scuttle Flies: the Phoridae*. Cambridge, UK: Cambridge University..
- Dillon, A., 2003. Biological control of the large pine weevil, *Hylobius abietis* L., (Coleoptera, Curculionidae) using entomopathogenic nematodes. Ph.D Thesis, National University of Ireland, Maynooth, Ireland.
- Eidmann, H.H. 1974. *Hylobius* Schönh. In. *Die Forstschädlinge Europas II. Käfer*. W. Schwenke (Ed.). Berlin: Paul Parey.
- Eidt, D.C., Zervos S., Pye, A.E., & Finney Crawley, J.R. 1995. Control of *Hylobius congener* Dalle Torre, Shenkling, and Marshall (Coleoptera: Curculionidae) using entomopathogenic nematodes. Canadian Entomologist, 127, 431-38.
- Escherich, K. 1923. *Die Forstinsekten Mitteleuropas, Band II*. Berlin: Paul Parey.
- Elton, E.T.G., Blankwaardt, H.E.H., Burger, H.C., Steemers, W.F., & Tichelman, L.G. 1964. Insect communities in barked and unbarked pine stumps with special reference to the large pine weevil (*Hylobius abietis* L., Col., Curculonidae). Zeitschrift für Angewandte Entomologie, 55, 1-53.
- Fitters, P.F.L., Dunne R., & Griffin C.T. 2001. Vine weevil control in Ireland with entomopathogenic nematodes: optimal time of application. Irish Journal of Agricultural and Food Research, 40, 199-213.
- Fitton, M.G., Shaw, M.R., & Gauld, I.D. 1988. Pimpline Ichneumon-flies. Hymenoptera, Ichneumonidae (Pimplinae). Handbooks for the Identification of British Insects, 7 (1), 1-110.
- Frediani, D. 1957. Su alcuni imenotteri pariti del *Pissodes notatus* F. nella Toscana litoranea. Bollettino della Società Entomologica Italiana 87, 92-97.
- Fuchs, G. 1915. Die Naturgeschichte der Nematoden und einiger anderer Parasiten 1. des *Ips typographus* L., 2. des *Hylobius abietis* L. Zoologisches Jahrbuch, Abteilung für Systematik, 38, 109-222.
- Gaugler, R. (Ed.) 2002. *Entomopathogenic nematology*. Wallingford, UK: CABI.
- Gerdin, S. 1977. Observations on Pathogens and Parasites of *Hylobius abietis* (Coleoptera: Curculionidae) in Sweden. Journal of Invertebrate Pathology, 30, 263-64.
- Gerdin, S., & Hedqvist, K.J. 1985. *Perilitus areolaris* sp. n. (Hymenoptera: Braconidae), an imago parasitoid of the large pine weevil, *Hylobius abietis* (Linnaeus) and its reproductive behaviour. Entomologica Scandinavica, 15, 363-69.
- Goyer, R.A., & Benjamin, D.M. 1971. Infection of a Pine root weevil, *Hylobius rhizophagus*, by two muscardine fungi. Journal of Economic Entomology, 64 (2), 562.
- Geus, A. 1969. Sporen tierchen, Sporozoa. Die Gregarinida. In. *Die Tierwelt Deutschlands und der angrenzenden Meeresteile*, 57. Teil. Jena, Germany: G. Fischer.
- Gillespie, A., & Moorehouse, E. 1989. *Metarhizium anisopliae*: a promising biological control agent for black vine weevil, *Otiorrhynchus sulcatus*. IOBC/WPRS Bulletin, 14 (1), 53.
- Grégoire, J.C. 1976. Note sur deux ennemis naturels de *Dendroctonus micans* Kug. en Belgique (Col. Scolytidae). Bulletin Annuel de la Société Royale d'Entomologie de Belgique, 112, 208-12.
- Haeselbarth, E. 1962. Zur Biologie, Entwicklungsgeschichte und Oekologie von *Brachistes atricornis* Ratz. als eines Parasiten von *Pissodes piceae*. Zeitschrift für Angewandte Entomologie, 49, 233-89.
- Haeselbarth, E. 1967. Zur Kenntnis der paläarktischen Arten der Gattung *Celooides* Wesmael (Hymenoptera, Braconidae). Mitteilungen der Münchner Entomologischen Gesellschaft, 57, 20-53.
- Haeselbarth, E. 1999. Zur Braconiden-Gattung *Perilitus* Nees, 1818. 2. Beitrag: Die Arten mit ausgebildetem ersten Cubitus-Abschnitt. Mitteilungen der Münchner Entomologischen Gesellschaft, 89, 11-46.
- Hanson, H.S. 1943. The control of bark beetles and weevils in coniferous forests in Britain. Scottish Forestry Journal, 57, 19-45.
- Hedqvist, K.J. 1958. Notes on *Bracon hylobii* Ratz. (Hym. Braconidae), a parasite of the pine weevil (*Hylobius abietis*). Annales Entomologici Fennici, 24, 73-83
- Hedqvist, K.J. 1963. Die Feinde der Borkenkäfer in Schweden, 1. Erzwespen (Chalcidoidea). Studia Forestalia Suecica, 11, 1-176.
- Henry, C.J. 1995. The effect of a braconid ectoparasitoid, *Bracon hylobii* Ratz., on larval populations of the large pine weevil, *Hylobius abietis* L. PhD thesis, University of Ulster, Coleraine, UK.
- Henry, C.J., & Day, K.R. 2000. Egg allocation by *Bracon hylobii* Ratz., the principal parasitoid of the large pine weevil (*Hylobius abietis* L.) and implications for host suppression. Agricultural and Forest Entomology, 3, 11-18.
- Henry, C.J., & Day, K.R. 2001. Biocontrol of the large pine weevil: structure of host (*Hylobius abietis* (L.)) and parasitoid (*Bracon hylobii* Ratz.) populations in felled stumps of Sitka spruce. IUFRO World Series Vol. 11, 1-12.

- Herting, B. 1973. *A Catalogue of Parasites and Predators of Terrestrial Arthropods, Section A, Volume III, Coleoptera to Strepsiptera*. Farnham Royal, UK: Commonwealth Agricultural Bureaux.
- Hulme, M.A., & Kenis, M. 2002. *Pissodes strobi* (Peck), White Pine Weevil (Coleoptera: Curculionidae). In *Biological Control Programmes against Insects and Mites, Weeds, and Pathogens in Canada 1981-2000*. P. Mason, J. Huber (Eds.). Wallingford, UK: CABI.
- Kaya, H.K. 1984. Nematode parasites of bark beetles. In *Plant and insect nematodes*. W.R. Nickle (Ed.). New York: Marcel Dekker.
- Kenis, M. 1996. Factors affecting sex ratio in rearing of *Coeloides sordidator* (Hymenoptera: Braconidae). *Entomophaga*, 41, 217-24.
- Kenis, M. 1997. Biology of *Coeloides sordidator* (Hymenoptera: Braconidae), a possible candidate for introduction against *Pissodes strobi* (Coleoptera: Curculionidae) in North America. *Biocontrol Science and Technology*, 7, 157-64.
- Kenis, M., Hulme, M.A., & Mills, N.J. 1996. Comparative developmental biology of populations of three European and one North American *Eubazus* spp. (Hymenoptera: Braconidae), parasitoids of *Pissodes* spp. weevils (Coleoptera: Curculionidae). *Bulletin of Entomological Research*, 86, 143-53.
- Kenis, M., & Mills, N.J. 1994. Parasitoids of European species of the genus *Pissodes* (Coleoptera: Curculionidae) and their potential for biological control of *Pissodes strobi* (Peck) in Canada. *Biological control*, 4, 14-21.
- Kenis, M., & Mills, N.J. 1998. Evidence for the occurrence of sibling species in *Eubazus* spp. (Hymenoptera: Braconidae), parasitoids of *Pissodes* weevils (Coleoptera: Curculionidae). *Bulletin of Entomological Research*, 88, 149-63.
- Klingler, J. 1988. Investigations on the parasitism of *Otiorrhynchus salicicola* and *O. sulcatus* [Col.: Curculionidae] by *Heterorhabdites* sp. [Nematoda]. *Entomophaga*, 33, 325-31.
- Krüger, K., & Mills, N.J. 1990. Observations on the biology of three parasitoids of the spruce bark beetle, *Ips typographus* (Col., Scolytidae), *Coeloides bostrichorum*, *Dendrosoter middendorffii* (Hym., Braconidae) and *Rhopalicus tutela* (Hym., Pteromalidae). *Journal of Applied Entomology*, 110, 281-91.
- Landi, S., 1990. Possibilità di controllo biologico di *Otiorrhynchus* spp. su piante ornamentali in vivaio. *Redita*, 73, 261-73.
- Långström, B. 1972. Snytbaggarnas (*Hylobius* spp., Col., Curculionidae) uppträdande på hyggen av varierande ålder och skogstyp i Finland 1970-1971. Licentiate-thesis at the Faculty of Forestry at the University of Helsinki, Finland. (In Swedish)
- Laumond C., Mauléon H., & Kermarrec A. 1979. Données nouvelles sur le spectre d'hôtes et le parasitisme du nématode entomophage *Neoaplectana carpocapsae*. *Entomophaga*, 24, 13-27.
- Leather, S.R., Day, K.R., & Salisbury, A.N. 1999. The biology and ecology of the large pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae): a problem of dispersal? *Bulletin of Entomological Research*, 89, 3-16.
- Lovasz, P. 1941. Zur Kenntnis der Schlupfwespen einiger schädlicher Rüsselkäfer. *Annales Entomologici Fennici*, 7, 194-204.
- Marchal, M. 1977. Fungi imperfecti isolés d'une population naturelle d'*Otiorrhynchus sulcatus* Fabr. (Col., Curculionidae). *Revue de Zoologie Agricole et Pathologie Végétale*, 76, 101-08.
- Marchal, M. 1989. Endémisme des mycoses à *Beauveria bassiana* et *Metarhizium anisopliae* dans de populations naturelles d'*Otiorrhynchus sulcatus*. *OILB/WPRS Bulletin*, 12, 35.
- Markova, G. 2000. Pathogenicity of several entomogenous fungi to some of the most serious forest insect pests in Europe. *IOBC wprs Bulletin* 23, 231-39.
- Markova, G., & Samsinakova, A. 1990. Laboratory studies on the effect of the entomopathogenic fungus *Beauveria bassiana* on larvae of *Lymantria dispar*. *Nauka za Gorata*, 27, 81-84.
- Mills, N.J. 1983. The natural enemies of scolytids infesting conifer bark in Europe in relation to the biological control of *Dendroctonus* spp. in Canada. *Biocontrol News and Information*, 4, 305-28.
- Mills, N.J., & Fischer, P. 1986. The entomophage complex of *Pissodes* weevils, with emphasis on the value of *P. validirostris* as a source of parasitoids for use in biological control. In *Proceedings of the 2nd. International Conference IUFRO Cone and Seed Insects Working Party, Briançon, September 1986*. A. Roques (Ed.) Olivet, France: INRA.
- Moorehouse, E., Gillespie, A., & Charnley, A. 1993a. The development of *Otiorrhynchus sulcatus* (Fabricius)(Coleoptera: Curculionidae) larvae on a range of ornamental pot-plant species and the potential for control using *Metarhizium anisopliae*. *Journal of Horticultural Science*, 68, 627-35.

- Moorehouse, E., Gillespie, A., & Charnley, A. 1993b. Application of *Metarhizium anisopliae* (Metsch.) Sor. conidia to control *Otiorrhynchus sulcatus* (F.) (Coleoptera: Curculionidae) larvae on glasshouse plants. Annals of Applied Biology, 122, 623-36.
- Mräcek, Z., Jiskra K., & Kahouna L., 1993. Efficiency of steiner nematid nematodes (Nematoda: Steinernematidae) in controlling larvae of the black vine weevil, *Otiorrhynchus sulcatus* (Coleoptera: Curculionidae) in laboratory and field experiments. European Journal of Entomology, 90, 71-76.
- Munro, J.W. 1929. The biology and control of *Hylobius abietis* L. Part II. Forestry, 3, 61-65.
- Novák, V. 1965. Beitrag zur Kenntnis der Fruchtbarkeit des brauen Rüsselkäfers (*Hylobius abietis* L.). P. 711. In: *Proceedings of the XII International Congress of Entomology, London 1964*. London UK.
- Novák, V., & Samsinakova, A. 1964. Les essais d'application du champignon parasite *Beauveria bassiana* dans la lutte contre les parasites en agriculture et sylviculture en CSSR. Colloque International de Pathologie des Insectes, Paris 1962, 133-35.
- Noyes, J.S. 2001. *Interactive Catalogue of World Chalcidoidea 2001*. CD Rom. Vancouver, Canada: Taxapad.
- Nuorteva, M. 1957. Zur Kenntnis der parasitischen Hymenopteren der Borkenkäfer Finnlands. Annales Entomologici Fennici, 23, 47-71.
- Nuorteva, M., & Saari, L. 1980. Larvae of *Acanthocinus*, *Pissodes* and *Tomicus* (Coleoptera) and the foraging behaviour of woodpeckers (Picidae). Annales Entomologici Fennici, 46, 107-10.
- Peters, A., 1996. The natural host range of *Steinerinema* and *Heterorhabdites* spp. and their impact on insect populations. Biocontrol Science and Technology, 6, 389-402.
- Pettersson, E.M. 2001. Volatiles from potential hosts of *Rhopalicus tutela*, a bark beetle parasitoid. Journal of Chemical Ecology, 27, 2219-31.
- Pettersson, E.M., Hallberg, E., & Birgersson, G. 2001. Evidence for the importance of odor-perception in the parasitoid *Rhopalicus tutela* (Walker) (Hymenoptera: Pteromalidae). Journal of Applied Entomology, 125, 293-301.
- Poinar, G.O. Jr. 1986. Recognition of *Neoaplectana* spp. (Steiner nematidae: Rhabditida). Proceedings of the Helminthological Society of Washington, 53, 121-29.
- Purrini, K. 1981. *Nosema hylobii* n.sp. (Nosematidae, Microsporidia), a new microsporidian parasite of *Hylobius abietis* L. (Curculionidae, Coleoptera). Zeitschrift für angewandte Entomologie, 92, 1-8.
- Purrini, K., & Ormieres R. 1982. *Gregarina hylobii* and *Ophryocystis hylobii* n.sp. (Ophryocystidae, Neogregarinida) Parasitizing *Hylobius abietis* (Curculionidae, Coleoptera). Journal of Invertebrate Pathology, 39, 164-73.
- Pye, A.E., & Burman M. 1977. Pathogenicity of the nematode *Neoaplectana carpocapsae* (Rhabditida, Steinernematidae) and certain microorganisms towards the large pine weevil, *Hylobius abietis* (Coleoptera, Curculionidae). Annales Entomologici Fennici, 43, 115-19.
- Pye, A.E., & Burman M. 1978. *Neoaplectana carpocapsae*: infection and reproduction in large pine weevil larvae, *Hylobius abietis*. Experimental Parasitology, 46, 1-11.
- Pye, A.E., & Pye N.L. 1985. Different applications of the insect parasitic nematode *Neoaplectana carpocapsae* to control the large pine weevil, *Hylobius abietis*. Nematologica, 31, 109-16.
- Roques, A. 1975. Etude de la méroscénose des cônes de pin sylvestre en forêt de Fontainebleau. Thèse 3ème cycle, Paris VI. France.
- Roques, A. 1976. Observations on the biology and cleptoparasitic behaviour of *Eurytoma waachtli* (Chalc. Eurytomidae) a parasite of *Pissodes validirostris* (Col. Curcul.) in the cones of Scots pine at Fontainebleau. Entomophaga, 21, 289-95.
- Rutherford, T.A., Trotter D., & Webster J.M. 1987. The potential of heterorhabditid nematodes as control agents of root weevils. Canadian Entomology, 119, 67-73.
- Salisbury, A.N., & Leather, S.R. 1998. Migration of larvae of the large pine weevil, *Hylobius abietis* L. (Col.: Curculionidae): Possible predation a lesser risk than dead by starvation? Journal of Applied Entomology, 122, 299-299.
- Samsinakova, A., & Novák, V. 1967. Eine Methode zur integrierten Bekämpfung des Rüsselkäfers (*Hylobius abietis* L.). Anzeiger für Schädlingskunde Pflanzenschutz Umweltschutz, 40, 22-27.
- Schabel, H.G. 1976. Green muscardine disease of *Hylobius pales* (Herbst) (Coleoptera: Curculionidae). Zeitschrift für angewandte Entomologie, 81, 413-21.
- Schabel, H.G. 1978. Percutaneous infection of *Hylobius pales* by *Metarrhizium anisopliae*. Journal of Invertebrate Pathology, 31, 180-87.

- Schabel, H.G., & Taft S.J. 1988. *Gregarina hylobii* (Sporozoa: Eugregarinida) in American pine reproduction weevils (Coleoptera: Curculionidae). Transactions of the American Microscopical Society, 107, 269-76.
- Schimitschek, E. 1964. Liste der 1934-1936 und 1940-1953 gezogenen Parasiten und ihrer Wirte. Zeitschrift für angewandte Entomologie, 53, 320-41.
- Schindler, U. 1964. Zur Imaginalparasitierung forstlicher Curculionidae. Zeitschrift für angewandte Zoologie, 51, 501-07.
- Sellenschlo, U. 1984. Der gefürchtete Dickmaulrüssler (*Otiorrhynchus sulcatus* (F., 1775)(Col.Curc.)), ein gefürchteter Schädling an Zierpflanzen. Praktische Schädlingsbekämpfer, 36, 22-24.
- Siddiqui, M.R., 2000. *Tylenchida: Parasites of Plants and Insects*. 2nd ed. Wallingford, UK: CABI.
- Slizinski, K. 1969. *Perilitus rutilus* Nees (Hym., Braconidae) – the parasite of imago of *Hylobius abietis* L. (Col., Curculionidae), new for the Polish fauna. Polskie Pismo Entomologiczne, 39 : 407-16.
- Starý, P., Sterba, J., & Soldan, T. 1988. *Perilitus areolaris* G. & H. (Hymenoptera, Braconidae), a parasitoid of the pine weevil *Hylobius abietis* (L.) in Czechoslovakia. Acta Entomologica Bohemoslavaca, 85, 428-33.
- Starzyk, J.R. 1996. Bionomics, ecology and economic importance of the fir weevil, *Pissodes piceae* (Ill.) (Col., Curculionidae) in mountain forests. Journal of Applied Entomology, 120, 65-75.
- Strojny, W. 1951. Some observations on the egg-laying process of *Ephialtes tuberculatus* Fourcr. (Hym. Ichn.) – parasite of the larva of *Cryptorrhynchus lapathi* L. (Col. Curc.). Polskie Pismo Entomologiczne, 21, 140-43.
- Szalay-Marzsó, L. 1962. Zur Morphologie, Biologie und Bekämpfung des Erlenwürgers *Cryptorrhynchus lapathi* L. (Col. Curculionidae) in Ungarn. Zeitschrift für angewandte Entomologie, 49, 163-194.
- Thomas, H.A. 1970. Neoaplectanid nematodes as parasites of the pales weevil larva, *Hylobius pales*. Entomological News, 81, 91.
- Tillemans, F., & Coremans-Pelseneer J. 1987. *Beauveria brongniartii* (Fungus moniliiale) as control agent against *Otiorrhynchus sulcatus* (Coleoptera, Curculionidae). Mededelingen Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent, 52, 379-84.
- Trägardh, I. 1931. Zwei forstentomologisch wichtige Fliegen. Zeitschrift für angewandte Entomologie, 18, 672-90.
- Tschorsnig, H.-P., & Herting, B. 1994. Die Raupenfliegen (Diptera: Tachinidae) Mitteleuropas: Bestimmungstabellen und Angaben zur Verbreitung und Ökologie der Einzelnen Arten. Stuttgarter Beiträge zur Naturkunde Serie A (Biologie), 506: 1-170.
- Vainio, A., & Hokkanen H.M.T. 1993. The potential of entomopathogenic fungi and nematodes against *Otiorrhynchus ovatus* L. and *O. dubius* Strom (Col., Curculionidae) in the field. Journal of Applied Entomology, 115, 379-87.
- Waldenfels, J. 1975. Versuche zur Bekämpfung von *Hylobius abietis* L. (Coleopt., Curculionidae). Anzeiger für Schädlingskunde Pflanzenschutz Umweltschutz, 48, 21-25.
- Walstad, J.D., Anderson, R.F., & Stambaugh, W.J. 1970. Effects of Environmental Conditions on two species of Muscardine Fungi (*Beauveria bassiana* and *Metarrhizium anisopliae*). Journal of Invertebrate Pathology, 16, 221-25.
- Walstad, J.D. & Anderson, R.F. 1971. Effectiveness of *Beauveria bassiana* and *Metarrhizium anisopliae* as control agents for the pales weevil. Journal of Economic Entomology, 64 (1), 322-23.
- Wegensteiner, R. 1989. The efficacy of *Beauveria bassiana*, *B. brongniartii* and *B. tenella* against *Hylobius abietis* (Col., Curcul.). Proceedings of the International Conference on Biopesticides, Theory and Practice, 25.-28.09.1989, Ceske Budejovice, Czechoslovakia. 238-42.
- Wegensteiner, R. 1992. Possibilities and efficacy of infection of *Hylobius abietis* (Col., Cuculionidae) with *Beauveria bassiana* and *Beauveria brongniartii*. Poster Abstract, XXV Annual Meeting of the Society for Invertebrate Pathology, Heidelberg, 16-21.08.1992. 225.
- Wegensteiner, R. & Führer, E. 1988. Zur Wirksamkeit von *Beauveria bassiana* (Bals.) Vuill. gegen *Hylobius abietis* L. (Col.: Curculionidae). Entomophaga 33, 339-48.
- Workshop of the IOBC Study Group "Insect Pathogens and Insect-parasitic Nematodes" 1987 in Versailles (1989): Control of weevils (Curculionidae) - b) Use of fungi. WPRS Bulletin, 12, 25-60.
- Wükler, G. 1923. Ueber Fortpflanzung und Entwicklung von *Allantonema* und verwandte Nematoden. Ergebnisse und Fortschritte der Zoologie, 5, 389-507.
- Zimmermann, G. 1981. Gewächshausversuche zur Bekämpfung des gefürchteten Dickmaulrüsslers, *Otiorrhynchus sulcatus* F., mit dem Pilz *Metarrhizium anisopliae* (Metsch.) Sorok. Nachrichtenblatt für den Deutschen Pflanzenschutzdienst 33, 103-08.

Zinovev, G.A. 1958. On the structure, dynamics and topology of the nuclei of bark beetle outbreaks. *Zoologiceskij Zurnal*, 37, 379-94.

Chapter 19

DAMAGE, CONTROL AND MANAGEMENT OF WEEVIL PESTS, ESPECIALLY *HYLOBIUS ABIETIS*

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1. INTRODUCTION

This part of the BAWBILT synthesis deals with bark feeding weevils that cause damage and mortality, mainly to newly planted conifer seedlings in Europe. The species listed in the damage & control database are summarised in Table 1 giving their estimated aggressiveness and extent for the reporting countries. The large pine weevil, *Hylobius abietis* (L.) (Col., Curculionidae) is the most important species in this group. The weevil breeds in fresh conifer stumps and feeds on young seedlings, and consequently this or related species have become major pests wherever clear-felling and subsequent replanting is practiced in forestry. In Europe, *H. abietis* is sometimes accompanied by the lesser pine weevil *Hylobius pinastri* (Gyll.), but this species is considered much less important than *H. abietis*, and little is known about its feeding behaviour. Hence, all pine weevil damage is normally attributed to *H. abietis*, and this will be the case in this overview as well. There is also a third and fairly rare conifer-related species, *Hylobius piceus* (DeG.) that occasionally may attack seedlings, but this species is not related to clear-fellings as it mainly lives in the roots of senescent conifers.

Within the genus *Pissodes*, several species also damage the bark of conifers, but in contrast to *Hylobius* where the adult is the damage-causing agent, either larvae or adults may feed on the bark of live seedlings (or young trees). The most destructive species in this group is the white pine weevil, *Pissodes strobi* (Peck.) in North America (Alfaro *et al.* 1995), but there is nothing similar, which occurs in Europe, neither in biology nor destructiveness. *Pissodes pini* (L.), and especially *Pissodes castaneus* (DeG.) may occasionally kill young conifer saplings by their adult feeding activity, but this damage is negligible compared to the *Hylobius* problem. These *Pissodes*-weevils may, however, cause substantial mortality to weak or senescent

pine trees by ovipositing into the lower stem, whereafter the developing brood colonizes the phloem and eventually kills the tree. Thus, this damage physiologically resembles that of bark beetles, and there is a third and possibly more aggressive species on pine, *Pissodes piniphilus*, attacking the upper stem in the same way. Similarly, *Pissodes harcyniae* (Hrbst.) attacks dying Norway spruce trees and *P. piceae* (Hrbst.) occurs on true firs (*Abies* sp.).

Weevil larvae of the genus *Otiorrhynchus* are well known pests on garden crops like strawberries, but a few species also attack conifer seedlings. Problems have mainly occurred in conifer nurseries, where e.g. *O. nodosus* (Müller) has devastated seedling crops on several occasions in Scandinavia (Harding *et al.* 1998). Damage reports from forest sites are rare except from Iceland, where the same species together with *O. arcticus* (Fabr.) has caused substantial mortality to planted larch seedlings (Halldorsson *et al.* 2000).

In contrast to all the above-mentioned species which all are related to conifers, *Cryptorhyncus lapathi* is the only weevil attacking broad-leaved trees that has been included in the BAWBILT database. The reported aggressiveness varies between countries from low to high, and so too does the reported extension of damage. A summary of the information included in the database for all these weevils is given in Table 1.

The substance of this review will entirely focus on the damage, control and management of the large pine weevil, *H. abietis*.

2. HYLOBIUS DAMAGE HISTORY

Linneaus (1767) described the large pine weevil as *Curculio abietis* in 1758, but did not recognise it as a pest (in contrast e.g. to *Tomicus piniperda*), as forests were not really managed at that time. During the 19th century, and with the advent of commercial forestry, *H. abietis* became established as a major forest pest in Germany (Ratzeburg 1839), Sweden (Holmgren 1856), Finland (Blomqvist 1883) and England (Ormerod 1890). In Escherich's book "Forstinsekten Mitteleuropas" (1923), 38 pages are devoted to discussing the damage and control of this species. At that time, much attention was given to different trapping methods used to reduce the number of weevils and hence to reduce seedling mortality. Physical seedling protection using barriers were in use, and different, mainly badly-smelling, chemicals were tested to deter weevils from feeding on the seedlings. Toxic substances for seedling protection were tested but not much used.

Nearly fifty years later, Eidmann (1974) summarized the *Hylobius* problem in Schwenke's "Die Forstschädlinge Europas", and gave a comprehensive review of the countermeasures that are totally dominated by the use of insecticides for seedling protection. In the 1950s, DDT became the main way to control pine weevil damage and was routinely used in most European countries until the late 1970s. DDT was banned for seedling protection and other uses in forestry, first in Sweden in 1975, and soon many countries followed. In most countries another chlorinated hydrocarbon, lindane or gamma-cyclohexane, soon replaced DDT for seedling protection. During the 1980s, permethrin and later other synthetic pyrethroids

replaced the chlorinated hydrocarbons for *Hylobius* control. In addition, some countries also used (and still use) systemic insecticides for seedling protection, whereas this practice has never been permitted in most countries.

The cheap and efficient *Hylobius* control provided by insecticides has inhibited the development of other control strategies. After the DDT ban in 1975, Sweden temporarily invested in the development of alternatives (Eidmann 1979). As lindane was never registered for seedling protection in Sweden, a 2-4 year fallow period, that was known previously to reduce weevil damage, was adopted as the main strategy to avoid excessive seedling damage. Soil scarification was also found to reduce seedling damage besides its other beneficial effects, but nobody understood why seedlings in mineral soil suffered less damage than seedlings in humus. During these years, feeding deterrents were tested but with poor results, whereas physical barriers preventing the weevils from reaching the seedlings were more successful. Two concepts, the TENO collar (Lindström *et al.* 1986) and the stocking (Eidmann and von Sydow 1989) were made commercially, and several other ideas developed and tested. Thus, there was an integrated pest management approach based on replacing insecticides with physical barriers and silvicultural countermeasures. These attempts to replace insecticides in seedling protection, as well as research plans to improve seedling resistance aspects against weevil damage for inclusion into the IPM system, all collapsed when permethrin was registered for seedling protection in 1980, as reviewed by Långström (1998).

During the 1990s there has been an increasing public concern about the use of insecticides in forestry, mainly but not exclusively, in northern Europe. In Sweden, the situation is getting acute (again!) as the registration of permethrin will end in 2003. Despite ambitious research (see below), no alternatives can fully replace insecticides in *Hylobius*-control yet, and hence cypermethrin was recently (April 2003) registered for the period until the end of 2005 to bridge the gap between permethrin and control techniques not involving insecticides. A similar concern about insecticides in forestry is growing in the rest of Scandinavia and UK although the situation is less acute than in Sweden. In 2002, a decision was taken in Denmark to refrain from protecting seedlings with insecticides in state forests (H.P. Ravn, pers. comm.). During the last decades, there has also been a lot of debate throughout Europe about the practice of clear-felling, and with increasing pressure and FSC-certification of forest products, the chemical protection of seedlings is now part of a much bigger issue. Hence, the research needs for a necessary development of integrated pest management strategies without chemical insecticides are the focus of recent review papers on the large pine weevil problem (Långström 1998; Leather *et al.* 1999; Fjelstad-Pedersen and Ravn 2000).

Facing the threat of loosing insecticides for *Hylobius* control again, the Swedish forestry and research agencies have in recent years funded research for *Hylobius* control that is not based on insecticides. Two major programs, one aiming at replacing insecticides with antifeedants (Schlyter and Löfqvist 1998), and the other aimed at taking the above-mentioned silvicultural IPM concept further by testing and combining different countermeasures in order achieve good seedling survival at acceptable costs (Nordlander 2001). In the UK, a similar environmental concern has lead to large research investments in biological control of *Hylobius* using pathogenic

nematodes for suppression of weevil populations (Brixey 1997). Another line of biological control of *Hylobius*, also aimed at population suppression, is pursued in Poland where positive results have been obtained by treating stumps with the fungus *Phlebiopsis gigantea*, which is antagonistic to the root rot *Heterobasidion annosum*, and also deprives the pine weevil larvae of their food (Skrzecz 1996).

Altogether, the *Hylobius* situation in Europe is serious, as acceptable seedling protection against weevil damage is an absolute imperative for efficient forest management. From an economic point of view, there is, at least not for Scandinavian forestry with slow growth rates and long rotation periods, no room for costly seedling protection. If planting costs become excessively high, modern forestry practice will have to be abandoned and replaced with low-intensity forestry relying

Table 1. Aggressiveness and extension (A/E) of BAWBILT weevils in different countries according to the reported information in the damage & control database

Country	<i>H abi</i>	<i>H pin</i>	<i>P sp.</i>	<i>P cas</i>	<i>P pin</i>	<i>P pph</i>	<i>P pic</i>	<i>P har</i>	<i>O sul</i>	<i>O sin</i>	<i>C lap</i>
Aus	***/**			**/*	**/*	***/**					
Bel	**/**				*/*	*/*					*/*
Est	***/***	***/**			*/*	*/*	***/**				
Fra	*/***							*/***			*/***
Ger	***/**							**/***			
Hun	***/**				***/**						***/***
Ire	***/***				*/*						*/**
Ita							*/*	*/*			*/*
Lit	***/**										
Pol	***/***				***/**						***/**
Por	*/*				*/*						*/*
Rom	***/***					*/*	*/*				*/*/**
Slo	***/***					*/*					*/*
Spa	*/**						**/**				
Swe	***/***										
Swi	*/*										*/*
Net	*/*				*/*						*/**
UK	***/***				*/*	*/*					*/*

Aus=Austria, Bel=Belgium, Est=Estonia, Fra=France, Ger=Germany, Hun=Hungary, Ire=Ireland, Ita=Italy, Lit=Lithuania, Pol=Poland, Por=Portugal, Rom=Romania, Slo=Slovakia, Spa=Spain,

Swe=Sweden, Swi=Switzerland, Net=The Netherlands, UK=The United Kingdom

H abi=*Hylobius abietis*, *H pin*=*Hylobius pinastri*, *P sp.*=*Pissodes* sp., *P can*=*Pissodes castaneus*, *P pin*=*Pissodes pini*, *P pph*=*Pissodes piniphilus*, *P pic*=*Pissodes piceae*, *P har*=*Pissodes harcyniae*, *O sul*=*Otiorrhynchus sulcatus*, *O sin*=*Otiorrhynchus singularis*, *C lap*=*Cryptorhynchus lapathi*

on natural regeneration and small-scale operations. This will have detrimental effects on the national income in countries like Finland and Sweden.

3. CURRENT *HYLOBIUS*-DAMAGE IN EUROPE

Compiled data in the BAWBILT damage & control database clearly show that *Hylobius abietis* is one of the highest ranked forest pests in Europe. Only Estonia has given information on the pest status and control of *Hylobius pinastri*, in addition to that given for *H. abietis*. We know, however, that *H. pinastri* causes some damage at least in Germany (Escherich 1923), Latvia (Ozols 1967), Finland (Långström 1982), Sweden (Nordlander 1990), and Estonia (Sibul 2000). In the following text, however, no attempt is made to separate the damage by the two species, and everything is attributed to *H. abietis*.

In the BAWBILT database, many countries rank the aggression as high and the geographical extent of damage as high (Table 1). There are, however, some inconsistencies between these rankings and the reported control measures indicating that a deeper analysis of the *Hylobius*-problem was needed. Hence, a request for more details on the damage and control of this pest was sent out to the BAWBILT community in early 2002. Most countries replied and a more detailed and consistent pattern emerged, as summarized in Table 2.

Today, *Hylobius abietis* is mainly a problem in northern and eastern parts of Europe. Typically, countries using clear felling and planting as their main forest management strategy are reporting the worst pine weevil problems. This finding is not new, but it is interesting that countries that have abandoned this practice, like Germany and the Netherlands, report that *Hylobius* used to be a problem. In Switzerland, *Hylobius* is not a problem as forestry there has long since been based on dimensional cutting and natural gap regeneration. *Hylobius* is not a problem in southern Europe either, but the reasons for this are not clear.

The extent of the *Hylobius*-problem is difficult to assess from the database as figures are not comparable. When the host area available for the weevils is given, it may mean the total conifer forest area in the country or the annual cutting area, or anything in between. It is, however, evident that the situation differs tremendously between countries, as the annual reforestation area threatened by *Hylobius* ranges from a few hundred (Hungary) to more than 100 000 hectares in Finland and Sweden. The damage estimates are also confusing as they reflect the present situation with the widespread use of insecticides for seedling protection. For example, France reports small problems but is treating 15 million seedlings with insecticides (of 65 million planted), whereas the UK reports 30-100% mortality unless seedlings are properly protected. In Finland, ca 150 million conifer seedlings are planted annually on ca 100 000 ha of which approximately 70-80 million seedlings are protected with insecticides and even then the estimated *Hylobius*-related mortality is ca 10 % (valued at ca 5-10 million Euro per annum). The figures for Sweden are even higher: ca 100 million seedlings are chemically protected out of ca 300 million planted. Without proper protection seedling mortality in southern Sweden would approach 100%, whereas in northern Sweden, losses can be kept at

Table 2. Known and estimated damage and economic losses (Millions of Euro) caused by *Hylobius abietis* in Europe

Country	BAWBIL-T		Annual host area planted		Seedlings protected		Mortality (%) if no with		Annual loss (ME)		Main control strategy	Alternat. Monitor. Strateg.	Reference
	Agr.	Extent	1000 ha	(millions)	(millions)	protect.	insect.	pyr	pyr	fp, pb			
Austria	***	**	16	80	15	40-60	15						H.Krehan
Belgium	**	**											BAWBIL-T
Czech Repub.	***	**	15	50	25	<50	2-3?	0.4	2				M.Knizek
Denmark	***	**	5	1	0.7	50-100	5	0.2	3				HP.Ravn
Estonia	***	***	27	14	?								K.Voolma
Finland	***	***	150	150	80		10	6					H.Viiri
France	*	***			65	0-70	1	0.3					FX.Saintonge
Germany	***	**	2	few									H.Niemeyer
Hungary	***	**	0.1	12	5	10-30?	<10	<0.05	0.05-0.2				F.I.Lakatos
Iceland	No <i>Hylobius</i>												
Ireland	***	***	8	20	20	50-90	10	3.2	?				D.Ward
Italy	*	*	small										M.Faccoli
Lithuania	***	**	7										BAWBIL-T
Norway	***	***	20	40	25-30	0-80	0-20	2	7				E.Christiansen
Poland	***	***	30	240	100-150	<60	<10	0.1-0.5					I.Skrzecz
Portugal	*	*	small	8	none	variab							M.Branco
Romania	***	***	6	25	25	50-80	10-15	<0.1	0.5				N.Olenici
Slovakia	***	***	15										BAWBIL-T
Spain	**	**	100										BAWBIL-T
Sweden	***	***	200	300	100	20-100	<20	15-20					B.Längström
Switzerland	**	*	v. small	1	none	small		0	0				B.Forster
The Netherl.	*	*	small										L.Moraal
U.K.	***	***	15	4	4?	30-100	2	17	pyr, car	none			R.Moore

pyr = pyretroids; car = carbamates; NR = natural regeneration; ss = soil scarification, mounding; fp = fallow period 1-3 years; pb = physical barrier

tolerable levels (<20%) by using silvicultural countermeasures (see below). A conservative estimate of replanting and other costs relating to *Hylobius*-damage is in the range 15-30 million Euro annually in Sweden (Weslien 1998). Recently, the Swedish National Forest Board estimated that the annual cost for the Swedish forest industry for refraining from the use of insecticides for pine weevil control would be ca 60 million Euro per year (Thuresson *et al.* 2003). In Poland, as many as 240 million seedlings are planted on 30 000 ha, and half of these are treated. The cost estimates differ, however, largely between counties as Poland reports much lower losses than Finland and Sweden despite similar planting activity. In relation to the above-mentioned facts, no reliable economic loss estimates can be made for the BAWBILT community unless we get better data input here. However, current best estimates of the total costs incurred by the BAWBILT community, if insecticides were not employed for plant protection, might be in the region of 140 million Euro per year.

4. CURRENT CONTROL METHODS IN USE IN EUROPE

In the BAWBILT damage & control database, control strategies are grouped into different categories with several subheadings. This is a general system for the whole database and many options are not relevant for the *Hylobius*-problem. The grouping of the options is questionable in some cases, e.g. using a fallow period is clearly a silvicultural management option, but here it is classified as "other control strategy". Also, most countermeasures against the large pine weevil are preventative, i.e. applied prior to the damage occurrence, and hence very little is direct control in the real sense of the word. The available information for *Hylobius* control is compiled in Table 2.

4.1 Use of insecticides

In most countries practicing forestry based on clear-felling and planting, chemical protection of conifer seedlings prior to planting is the main way to control the pine weevil problem. In Finland, Poland and Sweden, ca 300 million seedlings altogether are treated annually, and this constitutes the major part of all treated seedlings planted within the BAWBILT area. Countries like Austria, Czech Republic, France, Ireland, Norway and Romania constitute a second group with 15-25 million seedlings treated, whereas countries like Estonia, Hungary, Lithuania and UK plant a few million seedlings, but protect most of them with insecticides. Most of the chemical seedling protection is in fact damage prevention, as it is applied routinely prior to planting. Direct control by treating planted seedlings at the planting site in cases of heavy weevil attack (top-up treatment) occurs occasionally at least in Sweden and in Ireland, but is not the main method of insecticide application. In Austria, seedlings are often treated twice in two consecutive years, as the protective effect does not last long enough (Rudolf Wegensteiner, pers comm). The same practice is common in Ireland too (Declan Ward, pers comm).

Synthetic pyrethroids are mostly used but systemic insecticides (carbosulfan) are also occasionally used in some countries although they are forbidden in others (Table 3). As was mentioned above, only permethrin has been allowed for seedling protection in Sweden and that use is coming to an end in 2003. Recently, cypermethrin and imidacloprid were registered for seedling protection in Sweden, but only for a two-year-period. Hitherto Ireland, Norway and UK have also relied on permethrin although carbosulfan is also registered, but not much used, in the UK. The same applies to bensultap (Bancol) in Norway. In the other countries, two or more pyrethroids are used, and Poland and the Netherlands also allow carbosulfan to be used for seedling protection.

*Table 3. Insecticides registered for control of damage caused by *Hylobius abietis* in Europe*

Country	Synthetic pyrethroids							Carbamates	Other
	perm	cyperm	a-cyperm	esfen	delta	lambda	pyr		
Austria			yes		yes			yes	
Belgium									
Czech rep.									
Denmark		yes	yes	yes					
Estonia			yes		yes				
Finland	yes		yes		yes				
France	yes				yes				Mar-Susc
Germany		yes	yes			yes			
Hungary							yes		Dimecron
Iceland									
Ireland		yes							
Italy									
Lithuania									
Norway		yes							
Poland				yes		yes	yes		Mar-Susc
Portugal									
Romania				yes			yes		
Slovakia									
Spain									
Sweden	yes	yes							Merit
Switzerland									
The Netherlands	yes				yes				
United Kingdom	yes							Mar-Susc	

4.2 Physical protection

As the weevils approach the seedlings by walking (see e.g. Björklund *et al.* 2003), prevention of the weevils' access to the seedlings by physical barriers is an old idea (for different concepts, see Escherich 1923). With the ban of DDT in 1975 in Sweden, these old ideas gained a revival resulting in the TENO-collar and the plant stocking that for a few years were semi-commercially produced (Lindström *et al.*

1986; Eidmann and von Sydow 1989) but they became obsolete with the registration of permethrin in 1980. During the 1990s a multitude of new and old concepts for physical protection have been tested. Some of these, like the idea of covering the lower stem with a waxy coating ("Bugstop") have reached semi-commercial scale, but there are still application problems related to phytotoxic effects due to heating. Another approach based on a paper cylinder covered with slippery *Fluon®*-coating gives good protection (Eidmann *et al.* 1996), but is difficult to mechanise. Several other concepts of physical protective "shelters" have been developed and tested with variable results (Hagner and Jonsson 1995; Örlander and Petersson 1998; Petersson *et al.* 2004). The barrier concept is still a viable idea providing that the application can be mechanised, and the current work in this field is reported below.

Elsewhere in Europe, there has been little interest in physical barriers for seedling protection, but some of the Swedish concepts have been tried on a small scale in several countries (Beitzen-Heineke and Kolbe 1987; Zumr and Stary 1995). In Austria, another old concept has been taken up again resulting in "*Hylobex*", a stem-coating containing stone meal, which is on the market and used to some extent.

4.3 Trapping-out and population suppression

For more than 100 years, different ways of suppressing the weevil population have been tried, generally with poor results. Escherich (1923) reports a number of approaches based on trap logs, trap ditches, and bark pieces all of which, it is claimed, attract large numbers of weevils. Some of these techniques are still useful either as tools to monitor weevil populations (Långström 1982; Voolma 1994; Wilson and Day 1995), or in combination with insecticides to suppress weevil numbers. Nordlander (1987) developed an efficient weevil trap baited with host odours, but simultaneously concluded that trapping out weevils would require an unrealistic trapping effort. Nevertheless, some countries like Poland (Skrzecz 2003) and Romania (Olenici and Olenici 1994) include trapping-out in their control strategy.

Debarking of stumps was also practiced as a weevil suppression technique, but is now abandoned as laborious and inefficient (Elton *et al.* 1964). Stump pulling was tried in Sweden during the 1980s, mainly for reasons other than *Hylobius*-control, but the remaining thin roots were found to support a substantial weevil population so the effect on *Hylobius* was small (Anon. 1978). Other stump treatment approaches are dealt with below.

An unanswered but interesting question in this context is whether the current large-scale use of insecticides is having an effect on the local weevil populations. If so, we can expect even larger problems in a future without chemical seedling treatment. This topic will be addressed below.

4.4 Silvicultural countermeasures

4.4.1 Choice of reforestation method

As was mentioned above, the pine weevil problem is very much related to the practice of clear-felling and planting. There is clear evidence showing that pine weevil problems are smaller in natural regeneration than in plantations (Juutinen 1962). The main reason for this is probably the timing in seedling development as compared to weevil occurrence, i.e. most weevils have disappeared from the site when the self-sown seedlings grow up. The number of natural seedlings is also often high enough to allow for a substantial mortality without open patches in the seedling stand. One can, however, often find heavily attacked natural seedlings with healed feeding scars all along the stem that still are alive and growing well, while similar sized newly planted seedlings suffer heavy mortality. Hence, naturally regenerated seedlings display a higher resistance to weevil damage than planted ones. Consequently, natural regeneration is often a good strategy to avoid *Hylobius*-damage at sites where it can be practiced, but old spruce stands are often unstable and natural regeneration hence risky. In Norway, for example, nearly all Scots pine is naturally regenerated, and hence pine weevil damage is mainly a spruce problem there (E. Christiansen pers. comm.).

Seeding is not used anywhere on a larger scale, but is more similar to natural regeneration than planting when it comes to pine weevil problems (Juutinen 1962). In central Europe, many countries follow the practice used in Switzerland, and nowadays also Germany and the Netherlands, which is a form of forestry based on dimensional cutting and natural gap regeneration that creates no large clear-fellings and hence no weevil problems. This kind of forestry, however, requires a certain type of site, and cannot be practised everywhere.

4.4.2 Fallow period

The use of a fallow period is based on the fact that pine weevil damage is highest during the first years after the final felling (see eg Christiansen 1971; Doom and Frenken 1980; Långström 1982; Örländer *et al.* 1997). Hence, by waiting until the weevils have disappeared from the site, i.e. 2-4 years depending on the length of the development period, pine weevil damage can be avoided. This time lag is the most likely reason that self-sown seedlings suffer little *Hylobius*-caused mortality. In northern parts of Europe, where the generation period is more than 2 years, there is also a 1-2 year gap between the occurrence of the parent and young beetles (Långström 1982), that can be exploited by the forester for planting in the second year after the final felling. During the years between the ban of DDT and the registration of permethrin, Swedish forestry relied mainly on the fallow period for minimizing *Hylobius*-damage (Eidmann 1979). It has also been used to some extent elsewhere in Europe (at least in Austria, Finland, Norway and Poland), but has never been popular for two reasons: weed problems and increased rotation length. Nowadays, it seems to be more or less abandoned in most countries, except in northern Sweden where a 1-year delay in planting is still common practice.

4.4.3 Soil scarification

Soil scarification is beneficial for newly planted seedlings in several ways, but it was observed many years ago that weevil damage was less frequent on seedlings

standing openly in mineral soil (Ormerod 1890; Lekander and Söderström 1969; Christiansen and Sandvik 1974). The observation was originally interpreted as a case of "agoraphobia" (i.e. fear of open space), and more recent studies indicate that weevils do not avoid the mineral soil but walk faster and straighter than in humus (Kindvall *et al.* 2000). This may reduce risks of predation or desiccation. It is clear that the decision to feed on a seedling is taken in the very close vicinity of a plant (Björklund *et al.* 2003). Soil scarification has been adopted as a standard procedure in Scandinavian forestry, and much work has been done to create the optimal technique both for seedling establishment as such, and as a countermeasure against weevil damage. None of the other BAWBILT countries, however, mentions this as an option against the large pine weevil. In western Ireland, the re-growth of vegetation is so rapid on clear-cuts that there is a very real possibility of scarified patches losing their protective effect before seedlings outgrow their vulnerability (KR Day, pers.comm.).

4.4.4 Shelter trees and alternative food

The large pine weevil is highly polyphagous and known to feed on most woody plants, although thin conifer bark is preferred food (Escherich 1923; Leather *et al.* 1994). On fresh clear-cuttings, the logging waste provides alternative food for a while but it soon dries out, and then there remains little else than the newly planted seedlings for the weevils to feed upon. Fairly recently, von Sydow and Örländer (1994) reported that seedlings were less damaged under shelter woods than in clear-fellings despite the fact that trap catches were similar. Obviously, weevil activity was either lower in the shade of the shelter trees, or there were other food sources. It was further found that weevils feed in tree crowns during the main flight period in early summer but not thereafter (Örländer *et al.* 2000). Seedlings also suffered less damage if extra food (i.e. fresh branches) was experimentally added to the plots (Örländer *et al.* 2001). In addition, it has recently been found that weevil damage was twice as high in clear-fellings than in shelterwoods at the same population density (Nordlander *et al.* 2003a), and that seedlings growing close to stand edges were less damaged than those further out on the open site (Nordlander *et al.* 2003b). When feeding budgets were calculated for the pine weevil it became obvious that seedlings constitute a minor proportion of the total food consumption (Bylund and Nordlander 2001). In the shelterwoods, the main food supply has been suggested be the living roots of the shelter trees (Nordlander *et al.* 2003a, b), and thereby the "shelter-tree-effect" was clarified. This may in turn at least partly explain why weevil damage is minimal in the gap-regeneration forestry practised in central Europe.

4.4.5 Seedling properties

It is common knowledge that large seedlings resist/tolerate more pine weevil damage than small ones. It is also well known that healthy seedlings in good physiological condition stand more damage than newly planted seedlings suffering a planting shock. The choice of appropriate planting stock and the timing of the

planting operation are common practice among foresters, but as will be shown below, there is much more to learn and to implement here.

4.5 Biological control

Biological control is not used against the large pine weevil in any BAWBILT country, except for Poland where stump treatment with a fungus is becoming part of the control strategy (see below under biocontrol). In the UK, there is also a great interest in using nematodes for stump treatment, and hitherto more than 100 ha have been treated on a semi-commercial scale as will be discussed below (Stuart Heritage, pers. comm.)

4.6 Integrated control

Only Poland and Sweden are implementing some kind of an IPM strategy against the large pine weevil. Elements of that can, however, be traced in other countries as well although the "tool box" used is basically limited to the choice of a reforestation option and/or use of chemical seedling protection. In 2002, Denmark took a large step towards IPM of *Hylobius* by accepting a policy implying that insecticides should not be used on state lands. The Danish policy is much influenced by Swedish work on silvicultural countermeasures to prevent weevil damage (H.P Ravn, pers. comm.) Use of shelter trees and soil scarification are main components in this strategy (see below). In the UK, an ambitious pest management program is under development, where the Forestry Commission is planning to replace insecticides with an IPM program where risk assessment, population suppression using nematodes and increased seedling resistance are key elements (Wainhouse *et al.* 2002).

The Polish strategy seems to be based on including the whole tool-box. According to Skrzecz (1997), chemical seedling protection is supplemented with providing alternative food (traps, trap barks or twig bundles), use of more resistant seedlings (i.e. large and containerized seedlings), and lately stump treatment using *Phlebiopsis gigantea* to prevent root rot and to reduce weevil production. Traps are also used for monitoring weevil populations, and presumably the control options are chosen based on the critical levels of trap catches. Fallow period and trap ditches were used earlier, but are now abandoned.

The current Swedish strategy for integrated pest management of the large pine weevil is based on combining physical seedling protection with silvicultural countermeasures. The viability of this concept was tested in a large scale field experiment where four plots (soil scarification, shelter trees, both treatments, and neither treatment) were compared at 10 sites (Petersson and Ölander 2003). In order to maximise the weevil pressure, no fallow period was used. At each plot, spruce seedlings from the same seed lot were planted with one of the following treatments: no seedling protection, waxy stem coating ("Bugstop"), Fluon®-coated cylinders ("Hylostop"), and permethrin twice (prior to planting and next year at the site). After three field seasons, ca 90 % of the control seedlings were dead, whereas shelter trees and soil scarification alone reduced the mortality to 60 and 25 %, and in combina-



Figure 1. Two typical reforestation sites in northern Europe: above, a sitka spruce plantation in Northern Ireland (photo: Keith Day), and below a reforestation site with few seed trees in central Sweden (Photo: Claes Hellqvist)

tion to ca 15%. The use of physical barriers alone reduced mortality to ca 50%, i.e. better than shelter trees but worse than soil scarification). Combining "Bugstop" with both silvicultural measures resulted in a mortality of a few percent, that was fully comparable with that obtained from insecticide treatment alone. Although this experiment does not fully represent field practise, it shows that pine weevil damage can be handled without insecticides, but probably at a high cost.

5. SEARCH FOR ALTERNATIVES IN SEEDLING PROTECTION

5.1. New insecticides

There is little work reported on replacement of the currently dominating synthetic pyrethroids for seedling protection with new insecticides. The main reason for this is that few believe that possible new insecticides may be environmentally safer or politically more acceptable than the pyrethroids. Rather recently, Bancol (bensultap) which is derived from marine organisms (annelids), has been tested in Denmark and Norway, and found to be fairly efficient against the pine weevil. It has been used for seedling protection to some extent in Norway (Kohmann 2000), but its use will come to an end in 2003 (E. Christiansen pers. comm.). Currently, two other insecticides (Fipronil and Imidacloprid) are being tested in Denmark and Sweden (P. Christensen, pers. comm.). The latter was recently registered in Sweden for a two-year-period (2004-05). Bensultap and fipronil are also being tested in Hungary (F. Lakatos pers. comm.).

In the UK, novel application techniques based on the electrodyn sprayer conveyor have been developed (Heritage *et al.* 1997). A drive plant feeder (conveyer sprayer system) has led to better deposition of lambda-cyhalothrin, decreased volume used, improved economy of use and better safety (Rose 2002).

Recent studies indicate that pyrethroids also seem to repel weevils (Heritage and Johnson 1997). Weevils can clearly detect pyrethroids, the effect of which is to depress feeding rates while the mortality suffered by weevils exposed to normal doses with which plants are pre-treated, is low (Rose 2002).

In Estonia, neem and some other plant extracts have been tested for seedling protection against the pine weevil, but most of these are antifeedants rather than toxic substances and the results have generally been poor (Luik *et al.* 2000).

5.2 Physical protection

The idea of preventing the walking pine weevil from reaching the seedling dates back to the beginning of the previous century when Berger (1904, see Escherich 1923) reported a collar made of metal with hinges, that was applied around a seedling and moved to a new plantation after a few years. This idea was later turned into the TENO-collar that was used in the late 1970s (ca 9 million altogether) in Sweden (Lindström *et al.* 1986). The collar was soon followed by the plant stocking (Eidmann and von Sydow 1989), and a cylindrical barrier called "Hylostop" coated with fluon® i.e. polytetrafluoroethylene (Eidmann *et al.* 1996) that is still being tested and improved. There are a number of other candidates that have been or are being tested (Fig. 2), but none of them is close to practical application yet (Hagner and Jonsson 1995; Örlander 1998; Nordlander *et al.* 2001, Petersson *et al.* 2004).

The other idea for physical barriers is based on applying a protective coating to the lower stem of the seedling prior to planting. This has also been tried before (Escherich 1923), but new materials have provided new opportunities. A latex-based coating was tried fairly early in the Czech Republic (Zumr and Stary 1995), and was also found to give good seedling protection in Sweden but technical application



Figure 2: Four different types of physical barriers for seedling protection against pine weevil damage, that have shown promising results in field tests in Sweden: upper left, "KANT-skyddet" a plastic collar with a brim preventing access to the seedling; upper right "Hylostop" a paper cylinder with a slippery coating of Fluon® at the upper end preventing weevils from climbing the shelter; lower left "Bugstop" a mineral wax sprayed on the lower stem to protect it against weevil feeding; and lower right, "Conniflex" consisting of mineral particles of defined size in a flexible carrier sprayed on the lower stem (all pictures taken by Claes Hellqvist).

problems have halted the further development of this idea (Örlander and Peterson 1998) Large experiments have been carried out in Sweden with waxy coatings of "Bugstop" that give good protection against weevil damage but application without phytotoxic effects seems difficult to achieve, and these problems that have not yet been fully resolved (Örlander 1998; Hellqvist 2001). For the time being, the most promising approach is a coating called "Conniflex" that contains small hard mineral particles of a given size in a water-soluble and flexible carrier (Nordlander *et al.* in prep.) This concept is based on a similar principle as the Austrian Hylobex-coating which has been available on the market for some time (Rudolf Wegensteiner pers. comm.). Conniflex is now commercially available and half a million of seedling have hitherto been treated in Sweden. Altogether, physical barriers are, as such, more expensive than a traditional insecticide treatment and the mass application involves different technical problems that need to be solved. Despite massive investments in Sweden in some of the ideas mentioned above, none of the concepts is yet ready for practical use on a large scale. Hence, physical barriers cannot fully replace insecticides for seedling protection against pine weevil damage yet.

5.3 Antifeedants

Feeding deterrent substances have been tried against the pine weevil long before insecticides were available (Escherich 1923). Pine oil and garlic are among those substances that have had a documented seedling-protecting effect against the pine weevil (Eidmann 1987; Luik *et al.* 2000). Another is carvone that among others is tested in a large research program aiming at finding antifeedants against *H.abietis* (Schlyter and Löfqvist 1998; Klepzig and Schlyter 1999). There are also some natural seedling substances with repellent or antifeedant activity but these are discussed under the resistance heading.

It was recently observed that the weevil female covers the oviposition site with faeces containing a chemical compound with extremely strong antifeedant activity (Nordlander 2001). The substance is identified and has been tested in large scale field trials with good seedling-protecting results. Difficulties with finding a suitable carrier in combination with phytotoxic effects indicate, however, that this is not the ultimate seedling protection as it seemed. Hence, with all efforts made in Sweden in this field during the last decade, antifeedants are far from offering a worthy substitute for insecticides for protection of conifer seedlings against the large pine weevil.

As was mentioned above, the pine weevil problem is very much related to the practice of clear-felling and planting, and some countries have solved their weevil problems by abandoning this practice. In other countries, this is not possible for ecological or economic reasons, and there other measures like using a fallow period, soil scarification and or shelter trees offer some help, but the main strategy is still to protect the seedlings with insecticides. There seems to be little, if any, work on developing new or improved silvicultural countermeasures against weevil damage in Europe, except for Sweden. Even there, the focus is mainly on creating the optimal mineral soil patch around the seedling (Petersson and Örlander 2001). Current work

indicates that the quality of the patch is more important than the size, i.e. a few cm of fresh mineral soil around the seedling is enough, and the protective effects deteriorate after the first field season (Örlander & Nordlander 2003). One concept being pursued is artificial mounding where a "cow dung heap" consisting of a cup of a sandy slurry is placed on the soil together with the seedling (Göran Örlander pers. comm.).

As the newly planted seedlings are not the main food resource for the weevils (Bylund and Nordlander 2001, Bylund *et al.* in press), all measures providing alternative food sources for the weevils can release the weevil pressure on the seedlings (Örlander *et al.* 2001). The positive effect of shelter trees should most likely be ascribed to the fact that their living roots may constitute an important food source for the adult weevils (Nordlander *et al.* 2003a, b).

In northern Scandinavia, there may also be something to gain from the timing of the planting operation if the main emergence period of the new generation is known (cf. Långström 1982). In southern Sweden, however, weevil pressure is high throughout the first 3-4 years, and hence there is no "window" for planting there (Örlander *et al.* 1997; Örlander and Wallertz 1999).

Seedling properties are also part of the silvicultural concepts but these are discussed separately below. Altogether, we need to know much more about the feeding behaviour of the weevils before we can start to further modify silvicultural countermeasures. At present, we can see that they are important components in future insecticide-free management plans against *H. abietis*.

7. SEEDLING PROPERTIES - HOST RESISTANCE

Hylobius abietis (and presumably *H. pinastri* as well) is a highly polyphagous species (Escherich 1923; Leather *et al.* 1994), and adult feeding may take place on most woody plants in its environment. Thin conifer bark on seedlings or larger trees is, however, preferred food. Host recognition and utilization are discussed in chapters 15 and 16, so here we focus on physical and physiological host properties.

It is common knowledge that large seedlings resist/tolerate more pine weevil damage than small ones. In a comparative study, Eidmann (1969), however, concluded that large seedlings were more resistant, but they were also clearly more attacked than smaller ones. In Swedish forestry practice, large 4-yr old spruce seedlings are commonly used for planting in areas with high weevil abundance. Spruce seedlings with a stem base diameter exceeding 10 mm suffered low and acceptable losses, but producing and planting such large seedlings becomes prohibitively expensive, and hence other means are needed to control the weevil problem (Thorsen *et al.* 2001). Pine seedlings are not kept that long in nursery, and are hence smaller when planted, and consequently often suffer heavy losses from weevil damage unless properly protected.

Earlier it was noted that pine weevil problems are smaller in natural regeneration than in plantations. The main reason for this is probably the timing in seedling development as compared to weevil occurrence, i.e. most weevils have disappeared from the site when the self-sown seedlings grow up. The number of natural

seedlings is also often high enough to allow for a substantial mortality without open patches in the seedling stand. One can, however, often find heavily attacked natural seedlings with healed feeding scars all along the stem that are still alive and growing well, while similar sized newly planted seedlings suffer heavy mortality. In a series of Finnish experiments, Selander *et al.* (1990) demonstrated that self-sown seedlings of pine were less attacked and tolerated more damage than comparable planted seedlings. It has also been shown that watering and fertilization affect the feeding preference of the pine weevil (Selander and Immonen 1992), and furthermore that levels of nitrogen and phosphorus in the phloem affected seedling susceptibility to weevil damage. Other studies point in the same direction to the importance of physiological status of the seedling for its chances of surviving an insect attack (Wainhouse *et al.* 1998, 2000, 2004). This relates to the possibility of the plant repairing feeding scars by wound healing, but also to its ability to defend itself by deterring the weevils. It is obvious that that a well-established seedling with all physiological processes functioning has a larger potential for defense and wound healing than a newly planted seedling in physiological imbalance due to the planting shock.

The conventional wisdom that large and vigorous seedlings should be used to reduce weevil damage is still true, but there is some interesting input coming from different directions. One promising trait under development in Sweden is the use of very small (< 5cm) seedlings for planting. Compared to conventional seedlings, these small seedlings suffer much less mortality altogether and especially due to pine weevils (Lindström and Hellqvist 2001). There are probably two mechanisms involved: first, these small seedlings may, to a larger extent escape detection by the weevils, and second, their establishment is fast with an amazing root and shoot development in their first field season. This opens up interesting perspectives for timing of planting with respect to weevil abundance.

Another contribution to the importance of seedling vigour comes from Iceland, where larch seedlings with established mycorrhiza at the time of planting were less vulnerable to feeding damage by *Otiorrhynchus*-larvae (Halldorsson *et al.* 2000). This again emphasizes the role of seedling vigour, in this case a functioning water and nutrient uptake, for the resistance properties of seedlings. In the case of the white pine weevil, *P. strobi*, a systematic program to screen progeny in resistance is well advanced, with resistant seedlings commercially available (Alfaro *et al.* 2002).

Vegetatively propagated cuttings constitute another possible trait for improved plant survival, as the physical bark properties (texture, and presence of needles etc.) seem to encourage less weevil feeding than on comparable seedlings (Hannerz *et al.* 2002). Almost nothing is known about the role of the genetic make up of the seedlings or cuttings for their susceptibility to weevil damage, but observed morphological differences between different genetic origins are alone interesting enough for further studies. In addition, Alfaro *et al.* 2002 have indicated that the presence of high numbers of thick-walled sclerid cells in the phloem, prevents weevils attack on spruce shoots.

During recent decades, bark beetle researchers have made major advances in understanding resistance mechanisms of conifers against bark beetles (Lieutier 2002) and the terminal weevil (Alfaro *et al.* 2002), as detailed elsewhere (Lieutier,

chapter 9). The emerging pattern is a complex network of interacting physiological and chemical processes that are under genetic control. Basically, tree defences operate on three levels where preformed or primary defences (resin duct resin, polyphenolic parenchyma cells, lignin-containing stone cells) seem to aim at halting the intruder while the second line of defence consisting of an induced reaction (lesion formation, traumatic resin ducts) is mobilized and if successful enclosing the intruder in necrotic tissue isolated from the living tissue by a wound periderm. The third defence level occurs in trees surviving an attack and consists of an acquired resistance (that may or may not be systemic) that results in an elevated resistance against later stem attacks during the same or next season (Krokene *et al.* 1999, 2000). Some of this knowledge should be applicable to conifer seedlings fending off stem attacking insects like the pine weevils as well, and a few approaches in this direction have been made.

The pine weevils seem to feed differently on seedlings growing more or less to their full potential. On self-sown seedlings weevil damage often occurs as many small feeding scars, whereas large and coalescing feeding areas mainly occur on less vital i.e. newly planted seedlings. It is tempting to interpret these observations as an expression of a behavioural response of the weevils to a different strength in the primary resin flow. Furthermore, it has been observed that weevils avoid feeding on wound tissue, resulting from previous feeding scars (Selander and Kalo 1979; Ericsson *et al.* 1988), which represents some kind of an induced defence reaction. Even more interesting is the fact that seedlings responded to a topical application of methyl-jasmonate by forming traumatic resin ducts not only locally but in a systemic way (Franceschi *et al.* 2002). When exposed to pine weevil attack these seedling did better than untreated ones but at a high cost, as height growth was retarded by the methyl-jasmonate treatment (E. Christiansen pers.comm.)

The chemical basis of conifer resistance to stem-attacking insects seems to be very complex and is far from understood. The role of terpenes and polyphenols in this context is reviewed in chapter 9 with regards to bark beetles, and much less is known for seedlings fending off e.g. pine weevils. Terpenes are important in the host finding of the pine weevils (Tilles *et al.* 1986; Nordlander 1991), and *H.abietis* has chemoreceptors for these on their antennae (Wibe *et al.* 1996). Limonene has been shown to inhibit the attraction of pine weevils to α -pinene (Nordlander 1990). Terpenes are also known to be toxic to the weevils, but it has been difficult to relate resistance to the monoterpene composition of the seedlings (Selander and Kalo 1979). Thorpe (1999) found great variation in concentrations of resin, polyphenols, carbohydrates and nitrogen when comparing different host materials for the pine weevil in the UK. She also observed that both larval development and adult feeding correlated positively with concentrations of carbohydrates and resin, whereas correlations were negative for nitrogen and polyphenols in clonal seedlings of Sitka spruce (*Picea sitchensis*). In Scots pine, wound tissue with elevated resin acid content has been found to deter *H. abietis* from feeding (Ericsson *et al.* 1988). Some phloem phenolics may also be involved in pine defenses against pine weevils (Lieutier *et al.* 1997). Recently, Bratt *et al.* (2001) isolated a bromine compound with antifeedant properties from bark of lodgepole pine (*Pinus contorta*) that does

not occur in Scots pine. Verbenone, which is known as a component in bark beetle pheromones that normally are synthesized from host material, has also been demonstrated to have a feeding deterrent action on the pine weevil (Lindgren *et al.* 1996). These scattered observations indicate that there is much more to explore in host chemistry of conifer seedlings that could also relate to host resistance properties against generalist feeders like the pine weevils.



Figure 3. Left: Feeding scars at the base of a pine seedling caused by the large pine weevil ; note absence of resin exudation indicating low seedling vigour (photo: Niklas Björklund); right: healed feeding scar at the base of pine seedling showing successful recovery from weevil damage (Photo: Bo Långström).

The roles of the genetic make up, physiological condition, morphological properties and defense chemistry of seedlings in avoiding and/or sustaining attack by pine weevils should hence be studied in a more systematic way, as seedling properties will probably be important components in future pest management systems.

8. NATURAL ENEMIES AND BIOLOGICAL CONTROL OF *HYLOBIUS*

Due to their concealed way of life, larvae of the pine weevils are not much exposed to predators or other natural enemies. As discussed in chapter 18, a few species of insects, fungi or other microorganisms coexist with the weevil larvae in the dying roots of conifer stumps. Some of these may cause larval mortality by competing for food, others may use *Hylobius*-larvae as their food source. In the former group we

find some root-colonizing fungi and insects, in the latter group we have at least one braconid, *Bracon hylobii* (Hedqvist 1958; Henry and Day 2001), and some nematodes parasitizing weevil larvae as well as entomopathogenic fungi (Wegensteiner and Führer 1988) and microsporidia (Purrini 1981; Purrini and Ormieres 1982).

Adult pine weevils are long-lived and seem to have few natural enemies during their adult lifetime. One braconid (*Perilitus areolaris*) seems to be specialized on *H. abietis* (Gerdin and Hedqvist 1985), and this species may be an important mortality factor in the adult stage as it seemed to be abundant in adult weevils one year after clear-cutting in Sweden (Bylund in prep.). The species is also reported from the Czech Republic (Stary *et al.* 1988), but from Poland as *Perilitus rutilus* (Slizynski 1969; Korczynski 1984). In Finland, a braconid, *Pygostolus sp.* was regularly found together with larvae of the genus *Tomicobia* sp. (Hym., Pteromalidae) in the abdomen of adults of *H. abietis* (Långström 1972). *Pygostolus falcatus* is reported from *Otiorrhynchus ovatus* in Finland and from other curculionids elsewhere in Europe (Suomalainen 1942; Schindler 1964), but the species found in pine weevils is so far unidentified. As only larvae were found, it cannot be excluded that Långström's (1972) findings may as well have been *P. areolatus*. The parasitism by *Tomicobia* and *Pygostolus* was observed at several sites but seldom exceeded 10 % (but only large larvae were noted).

None of these bio-control agents has so far been used in forestry practice, but several ongoing projects, aiming at finding alternatives for insecticides in weevil control, explore possibilities of including biological control in IPM-systems for pine weevils. In most cases, the concept is to suppress weevil populations at least locally and thereby to reduce seedling damage. Regardless of the technique used, there is no evidence so far that suppression of *Hylobius*-populations is a really viable approach, at least not on the landscape level.

Pine weevil larvae are sensitive to the quality of their food (root phloem), and hence manipulation of this resource may be a possible way to reduce weevil populations. Early efforts to debark the stumps down to ground level have been abandoned as inefficient and laborious (Elton *et al.* 1964). Treatment of fresh stumps in order to retard or accelerate microbial colonization had little effect on weevil production (von Sydow and Birgersson 1997). In a Polish study, Skrzecz (1996) found a negative correlation between the presence of *P. gigantea* and the number of *Hylobius*-larvae in Scots pine roots. Laboratory experiments also showed that *Hylobius*-females were repelled from sticks inoculated with *P. gigantea* (Skrzecz and Moore 1997). As this fungus is common in pine and spruce stumps (von Sydow 1993), and is nowadays commercially used (Rotstop®), at least in Scandinavia, for stump treatment against the root rot (*Heterobasidion annosum*), the study was repeated in Sweden using Rotstop and another root-colonizing fungus, *Resinicium bicolor*. Unfortunately, no effects were seen on *Hylobius* performance in the field and contradictory results were obtained in the laboratory (Rothpfleffer 2000). As colonized roots produced few weevils, the main problem was slow dispersal and growth of the fungi into the roots from the stump surface. Similar

negative results are reported from Scotland (Skrzecz and Moore 1997), and hence this option may not work in a colder climate (see also Creevey 1999).

Entomopathogenic nematodes represent another approach for suppressing weevil populations that is currently intensively studied in the UK and Ireland (Armendariz *et al.* 2002, and references therein). Already in the 1970s, Pye and Burman (1977) had tested the pathogenicity of the nematode *Neoaplectana carpocapsae* against larvae of *H. abietis*, and demonstrated substantial weevil mortality in stumps treated with a nematode suspension (Pye and Pye 1985). The practical interest for this method has, however, been low in Sweden, and hence no further development has taken place. In contrast, good results against seedling damage by *Hylobius congener* have been reported from Canada when seedling roots were treated with nematodes prior to planting (Eidt *et al.* 1995).

9. MONITORING, RISK ASSESSMENT AND SUPPRESSION OF WEEVIL POPULATIONS

Prophylactic use of pesticides or routine employment of silvicultural and other measures to protect seedlings, is likely to be wasteful if the challenge from *Hylobius* is sporadic and patchy, with many areas experiencing low damage levels without treatment. While this might rarely be the case for clear cut plantation forestry in northern Europe (Örlander and Nilsson 1999), it remains possible that the correct identification of lower risk sites might enable focusing of the most cost-effective preventative measures on sites with the highest risk from weevil attack.

Ever since the large pine weevil became a reforestation problem, different trap devices have been designed and used to suppress weevil populations, but generally with poor results. Escherich (1923) reports a number of approaches based on trap logs, trap ditches, bark pieces that all may attract large numbers of weevils. In Sweden, Sylven (1927) caught ca 100 weevils per trap in a season, and concluded that 100-200 traps per ha were needed for trapping out the population. This implies a population size of tens of thousands of weevils per ha. The few existing estimates range from a few thousand (Eidmann 1997) to 40 000 weevils per ha (Ozols 1967). Even higher larval populations are reported from Sweden (Anon. 1978) and Russia (Charitonova 1965). Currently, a mark-recapture study in Sweden reported similar population levels (ca 14000 adult weevils per ha) on a clear-cut and a shelter tree site (Nordlander *et al.* 2003b.) Similar studies in UK (Moore unpublished) are being evaluated and hence better population estimates will shortly be available for that region as well. Judging from studies based on relative trap catches, large differences can be expected between sites and regions (Ozols 1967; Långström 1982; Voolma 2000, 2001).

Knowing the abundance and mobility of the weevils, population suppression is a difficult task, as the efforts have to be coordinated over large areas to have a chance to be successful. The probability for success is small in a forested landscape like the Nordic where clear cuts are more or less evenly distributed in time and space. Hence, suppression of the weevil population has never really been considered an option in this part of Europe. It may, however, work in a less forested landscape

where clear cuts are relatively small and far apart like in the UK, where weevil suppression using nematodes is currently given serious consideration (Brixey 1997). The Polish approach with stump treatment using a fungus (Skrzecz 1996), that was mentioned above is also aiming at population suppression, but no results on the population level have been reported yet.

One interesting question in this context is whether the current large scale use of insecticides for seedling protection is having an effect on the local weevil populations. Nowadays, we know that the weevils locate most, if not all, planted seedlings at the site (Björklund *et al.* 2003), and hence get in contact with the insecticide. In Finland, on average, one dead pine weevil per seedling was found in the humus below lindane-treated seedlings (Långström 1972), but more than 10 weevils were found around the most attacked seedlings (Långström, unpubl. data). Considering that population estimates indicate that the ovipositing *Hylobius* population is below, rather than above, 20 000 weevils per hectare (Eidmann 1997; Nordlander *et al.* 2003b), and that ca 2000 insecticide-treated seedlings normally are planted per hectare, many weevils are likely to encounter the insecticide, and there should hence be a substantial reduction in the parent weevil population at treated sites. It is unclear and probably not very likely that a reduction in parent beetle numbers really affects the size of the next generation, but the possibility cannot be excluded and should be studied. The situation may, however, be different with the pyrethroids, as they do not always seem to kill the long-lived weevils (Rose 2002). Nowadays, weevil traps or trap billets are mainly used for monitoring purposes. eg in Poland, 10 weevils per trap is considered a critical number in a monitoring procedure using 5-10 traps per ha (Skrzecz 2003). In Romania, however, trap barks treated with insecticides are deployed at 100-400 pieces per ha at high-damage sites (Olenici, pers comm.). The use of weevil traps (or billets) for monitoring purposes is, however, also complicated by the fact that catches do not always match with seedling damage (Szmidt and Korczynski 1983; Nordlander 1987; von Sydow 1997; Örländer *et al.* 1997). The reason for this is still unclear, but is probably linked to weevil behaviour.

Hence, risk assessments based on trap catches are poor estimators of the actual hazard for seedling damage. In Northern Ireland, Wilson *et al.* (1996) developed a model based on site characteristics that gave clear guidance for identifying high-risk sites (Day and Leather 1997). The key variables were simple (size and age of planted area, previously planted or not, and planted or self-seeded) and apparently relevant for those conditions, but probably irrelevant for Scandinavian conditions. In an unpublished M.Sc. thesis, Pullinen (1989) built a logistic model for predicting the hazard for an individual seedling to become attacked by pine weevils, and found that the planting spot (i.e. mineral soil or humus), distance to humus, micro-topography and surrounding vegetation had the best explanatory power in south-western Finland. Selander (1993) applied a proportional hazard model to a data set of seedlings followed over 5 years, and found that the girdling damage had the greatest effect on survival, whereas logging slash, seedling type and diameter also influenced the rate of survival. In Denmark, high-risk areas have been roughly identified based on site (light soils) and forestry (much conifer plantation and high cutting activity)

variables (Fjelstad-Pedersen and Ravn 2000), and in Sweden such work is in progress (Johansson and Långström in prep.).

10. CONCLUSIONS

Despite substantial research efforts in different parts of Europe during more than 100 years, much more work is needed before the current routine use of insecticides for seedling protection can be replaced by integrated pest management strategies that do not rely on chemical seedling protection. Recent Swedish work indicates that it is possible to achieve adequate seedling protection by combining silvicultural methods with physical barriers, albeit at a higher cost than with insecticides. Major break-throughs in bark beetle and shoot weevil research open up interesting avenues of work towards increasing seedling resistance against weevil damage. Recent and current work on natural enemies point to several different approaches for population suppression. Although this is not an easy way to go, stump treatment with fungi or nematodes as well as exploitation of adult parasitoids deserve further attention. Recent work has uncovered astonishing facts about weevil behaviour (such as oviposition and larval migration in the soil), and there is little doubt that we need to know much more about weevil behaviour and dispersal in order to develop new pest management strategies, and even more so if we attempt to suppress weevil populations. As weevil control without insecticides will be more costly and more site-specific, there is a large need for risk rating systems that at least can identify high- and low-risk areas with reasonable accuracy.

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12. REFERENCES

- Alfaro, R.I., Borden, J.H., Fraser R.G. & Yanchuk, A. 1995. The white pine weevil in British Columbia: basis for an integrated pest management system. *Forest Chronicle*, 71, 61-73.
- Alfaro, R.I., Borden, J.H., King, J.N., Tomlin E.S., McIntosh R.L., Bohlmann, J. 2002. Mechanisms of resistance in conifers against shoot infesting insects, In: *Mechanisms and deployment of resistance in trees to insects*. Wagner, M.R., Clancy, K.M., Lieutier, F., T.D. Paine, (Eds), Kluwer Academic Publishers Dordrecht-Boston-London.
- Anonymous 1978. Snytbaggeutredningen. Om skydd mot insektsskador på plantor. Skogsstyrelsen, 1-161.
- Armendariz, I., Downes, M. J., & Griffin, C. T., 2002. Effect of timber condition on parasitisation of pine weevil (*Hylobius abietis* L.) larvae by entomopathogenic nematodes under laboratory conditions. *Biocontrol Science and Technology*
- Beitzen-Heineke, I., & Kolbe, H. 1987. Der "Teno Kragen" und die Abwehr von *Hylobius abietis*. Versuche und Praxiserfahrungen in Niedersachsen. *Forst und Holzwirt* 42, 40 pp.
- Björklund, N. & Nordlander, G. 2001. Snytbaggen hittar *alla* plantor! *Plantaktuellt*, 2001, 5.

- Björklund, N., Nordlander, G. & Bylund, H. 2003. Host-plant acceptance on mineral soil and humus by the pine weevil *Hylobius abietis* (L.). Agricultural and Forest Entomology, 5, 61-65.
- Blomqvist, A.G. 1883. Finlands trädslag i förstligt hänseende beskrifna. I. Tallen. Finska forstför. medd. 3, 1-196.
- Bratt, K., Sunnerheim, K., Nordenhem, H., Nordlander, G. & Långström, B. 2001. Pine weevil (*Hylobius abietis*) antifeedants from lodgepole pine (*Pinus contorta*). Journal of Chemical Ecology, 27, 2253-62.
- Brixey J., 1997. The potential for biological control to reduce *Hylobius abietis* damage. Forestry Commission Research Information Note, 273.
- Bylund, H., Nordlander, G. & Nordenhem, H. 2004. Feeding and oviposition rates in the pine weevil *Hylobius abietis* (Col., Curculionidae). Bull Ent Res 94, (in press).
- Charitonova, N.S. 1965. Bolschoj sosnovij dolgonosik i borja s nim. Moskva, 1-88.
- Christiansen, E. 1971. Time of attack by the pine weevil (*Hylobius abietis* L.) in young reforestation areas. Medd. Norske skogsundersøksv. 28, 421-27.
- Christiansen, E. & Sandvik, M. 1974. Skade av gransnutebille på furuplantor i markberedningsflekker. (Damage by pine weevils to Scots pine seedlings in scarified patches of varying size). Norsk skogbruk 20:8-9. In Norwegian with English abstract.
- Creevey, C.J., 1999. Fungal colonisers of coniferous stumps as deterrents of the large european pine weevil (*Hylobius abietis* L.). M.Sc. Thesis, National University of Ireland Maynooth. 1999.
- Day, K.R. & Leather, S.R., 1997. Threats to forestry by insect pests in Europe (Chapter 11). In A.D. Watt, N.E. Stork, M.D. Hunter (Eds.) Forests and Insects, Chapman & Hall.
- Doom, D., Frenken, G. W. P., 1980. Het uitstellen van herbeplantingen als maatregel tegen schade door de grote dennenruitkever, *Curculio abietis* [Postponement of replanting as a silvicultural method to prevent damage by the large pine weevil *Curculio [Hylobius] abietis*. [Dutch]]. Nederlands Bosbouw Tijdschrift, 52, 217-27.
- Eidmann, H.H. 1969. Rüsselkäferschäden an verschiedenen Nahrungspflanzen. Anz. Schädlingsk. Pflanzenschutz, 42, 22-26.
- Eidmann, H.H. 1974. *Hylobius* Schönh. In. *Die Forstsäädlinge Europas. 2 Käfer*, :W. Schwenke, Hamburg.
- Eidmann, H.H. 1979. Integrated management of pine weevil (*Hylobius abietis* L.) populations in Sweden. in *Current topics in forest entomology*. Forest Service General Technical Report WO-8, USDA.
- Eidmann, H.H. 1987. Attractants and deterrents of natural origin for the suppression of bark beetle attacks. Proceedings, European seminar on wood production and harvesting, Vol 3, Bologna 1987 , 56-62.
- Eidmann, H.H. 1997. Assessment of pine weevil numbers on clear-cut and forest sites with shelter boards and pitfall traps. Anz. Schädlingskunde, Pflanzenschutz, Umweltschutz 70, 68-72.
- Eidmann, H.H. & von Sydow F., 1989. Stockings for protection of containerized conifer seedlings against pine weevil (*Hylobius abietis* L.) damage. Scandinavian Journal of Forest Research 4, 537-47.
- Eidmann, H. H., Nordenhem, H. & Weslien, J. 1996. Physical protection of conifer seedlings against pine weevil feeding. Scandinavian Journal of Forest Research 11, 68-75.
- Eidt, D.C., Zervos, S., Pye, A.E., & Finney-Crawley, J.R. 1995. Control of *Hylobius* congener Dalla Torre, Schenkling and Marshall (Coleoptera:Curculionidae) using entomopathogenic nematodes. Canadian Entomologist 127, 431-38.
- Elton, E.T.G., Blankwaardt, H.F.H., Burger, H.C., Steemers, W.F. & Tichelman, L.G. 1964. Insect communities in barked and unbarked pine stumps, with special reference to large pine weevil (*Hylobius abietis* L., Col., Scolytidae). Zeitschrift für angewandte Entomologie, 55, 1-54.
- Ericsson, A., Gref, R., Hellqvist, C., & Långström, B. 1988. Wound response of living bark of Scots pine and its influence on subsequent feeding by *Hylobius abietis*. In: *Mechanisms of woody plant defenses against insects*, W.J. Mattson, J. Levieux, C. Bernard-Dagan (Eds). Springer Verlag. New York, Berlin, Heidelberg.
- Escherich, K. 1923. *Die Forstinsekten Mitteleuropas II*. Verlag Paul Parey, Berlin.
- Fjelstad-Pedersen, A., & Ravn, H.P. 2000. Stor näletraesnudebille - biologi, modforholdsregler og strateg. Skov&landskab, Skovbruksserien 26, 1-49.
- Franceschi, V.R., Krekling, T., & Christiansen, E. 2002. Application of methyl jasmonate on *Picea abies* (Pinaceae) stems induces defense-related responses in phloem and xylem. American Journal of Botany, 89, 578-86.

- Gerdin, S., & Hedqvist, K.J. 1984. *Perilitus areolaris* sp. n. (Hymenoptera: Braconidae), an imago-parasitoid of the large pine weevil, *Hylobius abietis* (Linnaeus), and its reproductive behaviour. *Entomologica Scandinavica* 15, 363-69.
- Hagner, M. & Jonsson, C. 1995. Survival after planting without soil preparation for pine and spruce seedlings protected from *Hylobius abietis* by physical and chemical shelters. *Scandinavian Journal of Forest Research*, 10, 225-34.
- Halldorsson, G., Sverrisson, H., Eyjolfsdottir, G.G. & Oddsdottir, E.S. 2000. Ectomycorrhizae reduce damage to Russian larch by *Otiorrhynchus* larvae. *Scandinavian Journal of Forest Research*, 15, 354-58.
- Hannerz, M., Thorsen, Å., Mattsson, S., & Weslien, J. 2002. Pine weevil (*Hylobius abietis*) damage to cuttings and seedlings of Norway spruce. *Forest Ecology and Management* 160, 11-17.
- Harding, S., Annila, E., Ehnström, B., Halldorsson, G., & Kvamme, T. 1998. Insect pests in forests of the Nordic countries 1987-1990. *Rapport fra Skogforskningen - Supplement 3*, 1-22.
- Hedqvist, K.-J. 1958. Notes on *Bracon hylobii* Ratsb. (Hym. Braconidae), a parasite of the Pine weevil, (*Hylobius abietis*). *Annales Entomologici Fennici*, 24, No 2.
- Hellqvist, C. 2001. Bugstop:skador på planter i humus. *Plantaktuellt* 1, 7.
- Henry, C.J. & Day, K.R., 2001. Biocontrol of the large pine weevil: structure of host (*Hylobius abietis* [L.]) and parasitoid (*Bracon hylobii* Ratz.) populations in felled stumps of Sitka spruce. In *Protection of World Forests from Insect Pests: Advances in Research*. R.I. Alfaro, K. Day, S. Salom, K.S.S. Nair, H. Evans, A. Liebhold, F. Lieutier, M. Wagner, K. Futai, K. Suzuki (Eds), IUFRO World Series, Vol. 11 , IUFRO Secretariat, Vienna.
- Heritage, S., Collins, S., & Evans, H.F. 1989. A survey of damage by *Hylobius abietis* and *Hylastes* spp. in Britain. In: *Insects affecting reforestation: biology and damage*. Alfaro RI & Glover SG (Eds). Proceed. Vancouver, Victoria, Canada. Forestry Canada.
- Heritage, S., Jennings, T., Johnson, D., 1997. The use of Marshal/Suscon granules to protect plants from *Hylobius* damage.. Research Information Note - Forestry Commission. Forestry Commission, Forest Research Station, Farnham, UK. 269.
- Heritage, S., Jennings, T., Johnson, D., 1997. The use of permethrin 12ED through the electrodyn sprayer conveyor to protect forest plants from *Hylobius* damage.. Research Information Note - Forestry Commission. Forestry Commission, Forest Research Station, Farnham, UK. 271.
- Holmgren, E.A. 1867. De för träd och buskar nyttiga och skadliga insekterna jemte utrotningsmedel för de sednare. Stockholm , 1-362.
- Juutinen, P. 1962. Tutkimuksia metsätuhojen esiintymisestä männyn ja kuusen viljelytaimistoissa Etelä-Suomessa. Referat: Untersuchungen ueber das Auftreten von Waldschäden in den Kiefern- und Fichtenkulturen Sudfinnland. Comm. Inst. For. Fenn. 54, 1-80.
- Kindvall, O., Nordlander, G. and Nordenhem, H. 2000 Movement behaviour of pine weevil *Hylobius abietis* in relation to soil type: an arena experiment. *Entomologia Experimentalis et Applicata*, 95, 53-61.
- Klepzig, K.D. & Schlyter, F. 1999. Laboratory evaluation of plant-derived antifeedants against the pine weevil *Hylobius abietis* (Coleoptera: Curculionidae). *Journal of Economic Entomology*, 92, 644-50.
- Kohmann, K. 2000. Voksbehandling av rothalsen på skogplanter som alternativ til insekticider som brukes mot insektgnag etter utplanting. *Rapport fra Skogforskningen* 5, 1-15.
- Korczynski, I. 1984. Population density of the large pine weevil (*Hylobius abietis* L) and the extent of damage done by it in Scotch pine (*Pinus silvestris* L) plantation in dependence on the time of cutting (In Polish). *Sylwan* 128, 53-58.
- Korczynski, J., 1984. Nowe dane o wystepowaniu w Polsce *Perilitus rutilus* Nees (Hymenoptera, Braconidae), jako pasozyta szeliniaka sosnowca - *Hylobius abietis* L. (Coleoptera, Curculionidae) [New data on the occurrence in Poland of *Perilitus rutilus* Nees (Hymenoptera, Braconidae) as a parasite of the pine weevil - *Hylobius abietis* L. (Coleoptera, Curculionidae). [Polish]]. *Polskie Pismo Entomologiczne*. 54, 2, 403-06.
- Krokene P, Christiansen E, Solheim H, Berryman AA, Franceschi VR (1999) Induced resistance to pathogenic fungi in Norway spruce. *Plant Physiol.ogy*, 121, 565-70
- Krokene, P., Solheim, H., & Långström, B. 2000. Fungal infection and mechanical wounding induce disease resistance in Scots pine. *European Journal of Plant Pathology*, 106, 537-41.
- KSLA 1998. Klarar vi snytbaggen utan insekticider? *Kungliga Skogs –och Lantbruksakademiens Tidskrift*, 137, 15.

- Långström; B. 1972. Snytbaggarnas (*Hylobius* spp., Col., Curculionidae) uppträdande på hyggen av varierande ålder och skogstyp i Finland 1970-1971. Licentiate-thesis at the Faculty of Forestry at the University of Helsinki, 1-100 (In Swedish only but partly summarized in Långström 1982, see below)
- Långström, B. 1982. Abundance and seasonal activity of adult *Hylobius*-weevils in reforestation areas during first years following final felling. Comm Inst For fenn 106, 1-23.
- Långström, B. 1998. Varför är snytbaggen fortfarande ett problem?. KSLA Tidskrift 137, 23-33.
- Leather, S.R., Ahmed, S.I. & Hogan, L. 1994. Adult feeding preferences of the large pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae). European Journal of Entomology, 91, 385-89.
- Leather, S. R., Day, K. R. & Salisbury, A. N., 1999. The biology and ecology of the large pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae): a problem of dispersal. Bulletin of Entomological Research, 89, 1, 3-16.
- Lekander, B., & Söderström, V. 1969. Studier över snytbagge-angrepp på barrträdsplantor. Sveriges skogsv.förb. Tidskr. 4, 351-83.
- Lekander, B. & Lindelöw, Å. 1977. Helträdsutnyttjande och insekterna. Proj. Helträdsutnyttjande, PHU 52, 1-25.
- Lieutier, F., Garcia, J., Yart, A., Laetitia, G., Malphettes, C.-B., & Romary, P. 1997. Preliminary investigation on the relationships between phloem phenolic content of Scots pine and maturation feeding of the pine weevil *Hylobius abietis*, In: *Integrating cultural tactics into the management of bark beetles and reforestation pests*. J.C. Gregoire, F.M. Liebhold, F.M. Stephen, K.R. Day, & S. Salom (Eds), USDA Forest Service, General Technical Report NE-236.
- Lieutier, F. 2002. Mechanisms of resistance in conifers and bark beetle attack strategies. In: *Mechanisms and deployment of resistance in trees to insects*. M.R. Wagner, K.M. Clancy, F. Lieutier, F., T.D. Paine, T.D. (Eds), Kluwer Academic Publishers Dordrecht-Boston-London.
- Lindgren, B. S., Nordlander, G. & Birgersson, G. 1996. Feeding deterrence of verbenone to the pine weevil, *Hylobius abietis* (L.) (Col., Curculionidae). Journal of Applied Entomology 120, 397-403.
- Lindström, A. & Hellqvist, C. 2001. Miniplantor lutar snytbaggen? Plantaktuellt 1, 14.
- Lindström, A., Hellqvist, C., Gyldberg, B., Långström, B., & Mattsson, A. 1986. Field performance of a protective collar against damage by *Hylobius abietis*. Scandinavian Journal of Forest Research 1, 3-15.
- Linnaeus, C. 1767. Systema naturae. Tom I. Pars II. Editio duodecima reformata. Holmiae.
- Luik, A., Sibul, I. & Voolma, K. 2000. Influence of some plant water extracts and neem preparations on the maturation feeding of the large pine weevil, *Hylobius abietis* L. Baltic Forestry 6, 53-58.
- Moore, R. 2001. Emergence trap developed to capture adult large pine weevil *Hylobius abietis* L. (Coleoptera: Curculionidae) and its parasite *Bracon hylobii* (Hymenoptera: Braconidae). Bulletin of Entomological Research, 91, 109-15.
- Nordlander, G. 1987 A method for trapping *Hylobius abietis* (L.) with a standardised bait and its potential for forecasting seedling damage. Scandinavian Journal of Forest Research, 2, 199-213.
- Nordlander, G. 1990. Limonene inhibits attraction to alpha-pinene in the pine weevils *Hylobius abietis* and *H. pinastri*. Journal of Chemical Ecology 16, 1307-20.
- Nordlander, G. 1991. Host finding in the pine weevil *Hylobius abietis* - Effects of conifer volatiles and added limonene. Entomologia Experimentalis et Applicata 59, 229-37.
- Nordlander, G. 2001. Gnagavskräckande ämne kan bli framtidens plantskydd. Plantaktuellt 2001, 16.
- Nordlander, G. 2001. Forskningsprogrammet Snytbagge 2005. Plantaktuellt 2001, 3.
- Nordlander, G., Petersson, M., von Hofsten, H. & Lindström, A. 2001. Plantskydd mot snytbagge – principerna och verkligheten. SkogForsk Resultat 12, 1-4.
- Nordlander, G., Örländer, G. & Langvall, O. 2003a. Feeding by the pine weevil *Hylobius abietis* in relation to sun exposure and distance to forest edge. Agricultural and Forest Entomology 5: 191-98.
- Nordlander, G., Bylund, H., Örländer, G., & Wallertz, K. 2003b. Pine weevil population density and damage to coniferous seedlings in regeneration areas with and without shelterwood. Scandinavian Journal of Forest Research 18, 438-48.
- Örländer, G. & Nordlander, G. 1998. Skärmars, markberedning och andra skogsskötselåtgärder - kan de minska snytbaggeskador? Kungl. Skogs- och Lantbr.Akad. Tidskrift 137, 57-67.
- Örländer, G. & Petersson. M. 1998. Mekaniska snytbaggeskydd. Kungl. Skogs- och Lantbr.Akad. Tidskrift 137, 43-50.
- Örländer, G. & Nilsson, U. 1999. Effects of reforestation methods on pine weevil (*Hylobius abietis*) damage and seedling survival. Scandinavian Journal of Forest Research 14, 314-54.

- Örlander, G. & Wallertz, K. 1999. Sommaravverkning gav mer snytbaggeskador. Skogseko 1, 14-15.
- Örlander, G. & Nordlander, G. 2003. Effects of field vegetation control on pine weevil (*Hylobius abietis*) damage to newly planted Norway spruce seedlings.. Annals of Forest Science 60, 667-71.
- Örlander, G., Nilsson, U., & Nordlander, G. 1997. Pine weevil abundance on clear-cuttings of different ages: A 6-year study using pitfall traps. Scandinavian Journal of Forest Research 12, 225-40.
- Örlander, G., Nordlander, G., Wallerz, K. & Nordenhem, H. 2000. Feeding in the crowns of Scots pine trees by the pine weevil *Hylobius abietis*. Scandinavian Journal of Forest Research, 15, 194-201.
- Örlander, G., Nordlander, G. and Wallerz, K. 2001 Extra food supply decreases damage by the pine weevil *Hylobius abietis*. Scandinavian Journal of Forest Research, 16, 450-54.
- Ormerod, E.A. 1890. A manual of injurious insects. Second edition, London: Simpkin, Marshall, Hamilton, Kent & Co; Ltd, p 260-64
- Ozols, G. 1967. Biologie der Rüsselkäfer der Gattung *Hylobius* und ihr Einfluss auf die Waldverjüngung in der Lettischen SSR. Les i sredaRiga, 136-163. (In Russian with German summary).
- Pettersson, M. & Örlander, G. 2003. Effectiveness of combinations of shelterwood, scarification and feeding barriers to reduce pine weevil damage. Canadian Journal of Forest Research, 33, 64-73.
- Pettersson, M., Örlander, G., & Nilsson, U. 2004. Feeding barriers to reduce damage by pine weevils (*Hylobius abietis*). Scand J For Res 19, 48-59.
- Pullinen, J. 1989. Mahdollisuksista ennakkoidaan uudistusalan kasvupaikkatekiöiden perusteella tukkimiehentäin tuhoja mäännyn taimilla. Helsingfors universitet, pro gradu-arbete, 1-94.
- Purrini, K. 1981. *Nosema hylobii* n. sp., (Nosematidae: Microsporidia), a new microsporidian parasite of *Hylobius abietis* L. (Curculionidae: Coleoptera). Zeitschrift für Angewandte Entomologie 92, 1-8.
- Purrini, K., & Ormieres, R., 1982. *Gregarina hylobii* and *Ophryocystis hylobii* n.sp. (Ophryocystidae, Neogregarinida) parasitizing *Hylobius abietis* (Curculionidae, Coleoptera).. Journal of Invertebrate Pathology. 39, 164-73.
- Pye, A.E., & Burman, M. 1977. Pathogenicity of the nematode *Neoaplectana carpocapsae* (Rhabditida: Steinernematidae) and certain microorganisms towards the large pine weevil *Hylobius abietis* (Coleoptera: Curculionidae). Annales Entomologici Fennici 43, 115-19.
- Pye A, E., & Pye N, L. 1985. Different applications of the insect parasitic nematode *Neoaplectana carpocapsae* to control the large pine weevil, *Hylobius abietis*. Nematologica 31, 109-16.
- Ratzeburg, J.T.C. 1839. *Die Forst-Insekten, Erster Teil, Die Käfer*. Berlin, 247 pp.
- Rose, D. 2002. Control of the large pine weevil, *Hylobius abietis* L. unpublished Ph.D Thesis, University of London (Imperial College).
- Rothpfeffer, C. 2000. Fält- och laboratoriestudier av pergamentsvampens (*Phlebia gigantea*) och *Resinicium bicolor*'s effekt på snytbaggens (*Hylobius abietis*) föryngring i tallstubbar. Examensarbete i entomologi 1/2000. Handledare: Bo Långström, Jan Weslien och Jan Stenlid.
- Schindler, U. 1964. Zur Imaginalparasitierung forstlicher Curculionidae. Zeitschrift fur angewandte Entomologie 51, 501-07.
- Schltyter, F. & Löfqvist, J. 1998. Kan insekticider mot snytbaggen ersättas med naturliga eller syntetiska "antifeedants"? Kungliga Skogs- och Lantbruksakademiens Tidskrift 137, 51-58.
- Selander, J. 1993. Survival model for *Pinus sylvestris* seedlings at risk from *Hylobius abietis*. Scandinavian Journal of Forest Research 8, 66-72.
- Selander, J. & Kalo, P. 1979. Evaluation of resistance of Scots pine seedlings against the large pine weevil, *Hylobius abietis* L. (Coleoptera, Curculionidae) in relation to their monoterpane composition. Silva Fenn. 13:115-30. (In Finnish with English summary).
- Selander, J., & Immonen, A. 1992. Effect of fertilization and watering of Scots pine seedlings on the feeding preference of the pine weevil, *Hylobius abietis* L. Silva Fennica 26, 75-84.
- Selander, J., Immonen, A., & Raukko, P. 1990. Resistance of naturally regenerated and nursery-raised Scots pine seedlings to the large pine weevil, *Hylobius abietis* (Coleoptera, Curculionidae). Folia Forestalia 776, 1-19.
- Sibul, I., 2000. Abundance and sex ratio of pine weevils, *Hylobius abietis* and *H. pinastri* (Coleoptera: Curculionidae) in pine clear-cuttings of different ages. In: *Development of environmentally friendly plant protection in the Baltic region*, L. Metspalu, S. Mitt. (Eds), International Conference, Tartu, Estonia, 28-29 September 2000. Transactions of the Estonian Agricultural University.
- Skrzecz, I. 1996. Impact of *Phlebia gigantea* (Fr.:Fr.) Donk on the colonization of Scots pine (*Pinus sylvestris* L.) stumps by the large pine weevil (*Hylobius abietis* L.). Folia Forestalia Polonica 38, 89-101.

- Skrzecz, I. 1997. Mechanical and biological methods of the protection of forest plantation and thickets against pest insects. Proceedings of the Symposium on Effectiveness and practical application of biological control in plant protection, Skiermiewice, Poland, 18-19 March, 1997, 21-24.
- Skrzecz, I. 2003. Non-target insects in the pine weevil (*Hylobius abietis* L.) traps with Hylodor dispenser. *Folia Forestalia Polonica*, 45, in press.
- Skrzecz, I., & Moore, R. 1997. The attractiveness of pine branches infected with selected wood-colonizing fungi to the large pine weevil (*Hylobius abietis*). In: Gregoire *et al.* (Eds), 146-52.
- Slizynski, K. 1969. *Perilitus rutilus* Nees (Hym., Braconidae)- the parasite of the imago of *Hylobius abietis* L. (Col., Curculionidae) new for the Polish fauna e. *Polskie Pismo Ent* 39, 406-16.
- Stary, P., Sterba, J., & Soldan, T. 1988. *Perilitus areolaris* G. & H. (Hymenoptera, Braconidae), a parasitoid of the pine weevil *Hylobius abietis* (L.) in Czechoslovakia. *Acta Entomologica Bohemoslovaca* 85, 428-33.
- Suomalainen, E. 1942. Parasitenwespen aus *Oriorrhynchus ovatus*. *Annales entomologici Fennici* 8, 258.
- Szmidt, A., & Korczynski, I. 1983. Summary: Population density of *Hylobius abietis* L. beetles and their feeding intensity as the prognosis index. *Prace Komisji Nauk Rolniczych I Komisji Nauk Lesnych* 5;137-44.
- Sydow, F. von 1997. Abundance of Pine Weevils (*Hylobius abietis*) and Damage to Conifer Seedlings in Relation to Silvicultural Practices. *Scandinavian Journal of Forest Research* 12, 157-67.
- Sydow, F. von, & Örländer, G. 1994. The influence of shelterwood density on *Hylobius abietis* (L.) occurrence and feeding on planted conifers. *Scandinavian Journal of Forest Research*, 9, 367-75.
- Sydow, F.von & Birgersson, G. 1997. Conifer stump condition and pine weevil (*Hylobius abietis*) reproduction. *Canadian Journal of Forest Research*, 27, 1254-62.
- Sylven, H. 1927. Snytbagarna - studier och fångstförsök. Zusammenfassung: Die Russelkäfer - Studien und Fangversuche. Sv. Skogsårdsfören. Tidskrift 25, 521-51.
- Thorpe, K.V. 1999. The feeding ecology of the large pine weevil (*Hylobius abietis* L.) in relation to host plant resistance. University of Ulster, School of Environmental Studies, PhD thesis.
- Thorsén, Å., Mattsson, S. & Weslien, J. 2001. Influence of stem diameter on the survival and growth of containerized Norway spruce seedlings attacked by pine weevils (*Hylobius* spp.). *Scandinavian Journal of Forest Research* 16: 54-66.
- Thuresson, T., Samuelsson, H., & Claesson, S. 2003. Konsekvenser av ett förbud mot permetrinbehandling av skogsplantor. *Skogsstyrelsen, meddelande* 2, 1-65.
- Tilles, D.A., Sjodin, K., Nordlander, G., & Eidmann, H.H. 1986. Synergism between ethanol and conifer host volatiles as attractants for the pine weevil *Hylobius abietis* (L.) (Coleoptera: Curculionidae). *Journal of Economic Entomology* 79, 970-73.
- Voolma, K. 1994. Atraktantpüüniste kasutamine männikärsakate ja juureüraskite arvukuse hindamiseks. (Use of baited ground traps for monitoring pine weevil, *Hylobius abietis*, and root-colonizing bark beetles). *Metsanduslikud Uurimused* 26, 96-109.
- Voolma, K. 2000. Comparison of two traps used for monitoring large pine weevil populations, *Hylobius abietis* L. (Coleoptera: Curculionidae), In: *Development of environmentally friendly plant protection in the Baltic region*, L. Metspalu S. Mitt (Eds), International Conference Tartu, Estonia, 28-29 September 2000, (Transactions of the Estonian Agricultural University, 209).
- Voolma, K. 2001. Harilik männikärsakas (*Hylobius abietis* L.) Räpina metskonna raiestikel: uurimus atraktantpüünistega. (The large pine weevil, *Hylobius abietis* L., in the felling areas of the Räpina forest district: a case study with baited ground traps). *Metsanduslikud Uurimused* 35, 172-78.
- Wainhouse, D., Ashburner, R., Ward, E., & Rose, J. 1998. The effect of variation in light and nitrogen on growth and defence in young Sitka spruce. *Functional Ecology* 12, 561-72.
- Wainhouse, D., Ashburner, R., Forrest, I., & Boswell, R. 2000. The effect of variation in light and nitrogen on the composition of resin in young Sitka spruce. *Silvae genetica* 49, 45-49.
- Wainhouse, D., Cross, D.J., & Howell, R.S. 1990. The role of lignin as a defence against the spruce bark beetle *Dendroctonus micans* - Effect on larvae and adults. *Oecologia* 85, 257-65.
- Wainhouse, D., Evans, H., Moore, R., Webber, J., Thorpe, K., & Staley, J. 2002. The integrated forest management programme. *Forest Research Annual Report and Accounts 2000-2001*, 43-47.
- Wainhouse, D., Staley, J., Johnston, J., & Boswell, R. 2004. The effect of environmentally induced changes in young conifers on feeding behaviour and reproductive development of adult *Hylobius abietis*. *Ecological Entomology*, in press.
- Ward, D. 1988. The large pine weevil: an inevitable forest pest. *Res. Note, Forest Service, Research Branch Bray, Ireland* 2.

- Wegensteiner, R., & Führer, R. 1988. Zur Wirksamkeit von *Beauveria bassiana* (Bals.) Vuill. gegen *Hylobius abietis* L (Col: Curculionidae). Entomophaga 33, 339-48.
- Weslien, J. 1998. Vad kostar snytbaggeskadorna? Kungliga Skogs- och Lantbruksakademiens Tidskrift 137, 19-22.
- Wibe, A., Borg-Karlsson, A. K., Norin, T., & Mustaparta, H., 1996. Identification of plant volatiles activating the same receptor neurons in the pine weevil, *Hylobius abietis*. Entomologia Experimentalis et Applicata. Ninth International Symposium on Insect-Plant Relationships held on 24-30 June 1995 in Gwatt, Switzerland. 80, 39-42.
- Wilson, W.L. & Day, K.R. 1994. Spatial variation in damage dispersion, and the relationship between damage intensity and abundance of the pine weevil (*Hylobius abietis* L.). International Journal of Pest Management 40, 46-49.
- Wilson, W.L. & Day, K.R. 1995. The comparative effectiveness of chemical traps, and fir, spruce and larch billets, for the estimations of pine weevil (*Hylobius abietis* L.) density indices. Journal of Applied Entomology, 119, 157-60.
- Wilson, W.L. & Day, K.R. 1996. Variation in the relative abundance of the large pine weevil among Sitka spruce plantation sites. Forestry, 69, 169-71.
- Wilson, W.L., Day, K.R. & Hart, E.A. 1996. Predicting the extent of damage to conifer seedlings by the pine weevil (*Hylobius abietis* L.): a preliminary risk model by multiple logistic regression. New Forests, 12, 203-22.
- Zumr, V. & Stary, P. 1993. Baited pitfall and flight traps in monitoring *Hylobius abietis* (L.) (Col. Curculionidae). Journal of Applied Entomology, 115, 454-61.
- Zumr, V. & Stary, P. 1994. Seasonal occurrence of *Hylobius abietis* (L.) (Col., Curculionidae) in different forest environments of a model area. Journal of Applied Entomology, 118, 361-64.
- Zumr, V. & Stary, P. 1995. LATEX paint as an antifeedant against *Hylobius abietis* (L) (Col, Curculionidae) on conifer seedlings. Anz Schadlingsk Pflanz Umwelt 68, 42-43.

Part 3

Buprestids & Longhorns

Chapter 20

BIOLOGY, ECOLOGY AND ECONOMIC IMPORTANCE OF BUPRESTIDAE AND CERAMBYCIDAE

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1. INTRODUCTION

Most jewel beetles (Coleoptera: Buprestidae) and Longhorn beetles (Coleoptera: Cerambycidae) are xylophagous species, although a few buprestids mine leaves and some cerambycids live on the roots of herbs. Some species are phloem feeders and reside entirely within the bark, while others are xylem feeders and feed both in the phloem and within the wood. Most of the species attack dying or dead trees, and are ecologically important components in the insect community that utilises and contributes to degradation of dead wood. Many species have also declined and become endangered due to the lack of breeding material in parts of Europe. However, some species are able to invade healthy or weakened trees, eventually killing them due to girdling of the phloem system as a result of extensive larval feeding under the bark. Therefore some of the Buprestidae and Cerambycidae are considered to be damaging to living trees. Even if they are not lethal to standing trees, the secondary economic effects on naturally damaged or felled timber can be considerable.

2. BUPRESTIDAE

This family includes about 15,000 species that are mainly distributed in the warm parts of the globe and are easily recognised by their often bright metallic colour which gives rise to the common name *jewel beetles*. The family comprises about 200 species in Europe, of which 48 species reach northern Europe. The buprestids have

an enormous range in size, shape and coloration. Some species are narrow and elongate while others are quite flat and roundish. The variability in coloration is very wide, from entirely black species to species bearing all the colours of the spectrum, often brightly metallic (Bilý, 1982).

2.1. Morphology and biology

2.1.1. Morphology of adult Buprestidae

The head is short and vertical with biting mouthparts. The eyes are oval, elliptical or reniform, sometimes projecting beyond the outline of the head. The antennae are moderately long. In most species, the abdomen is completely covered by the elytra which have longitudinal grooves, or rows of punctures, or longitudinal keels. Minor morphological differences between the two sexes occur frequently, and may exceptionally be very pronounced. More detailed information can be found in Bilý, 1982 and Schönherr, 1974.

2.1.2. Morphology of Buprestidae larvae

The larvae of buprestids are dorso-ventrally flattened, segmented, almost hairless, usually with the thoracic part of the body very enlarged. It is possible to distinguish several morpho-ecological types of larvae (Bilý, 1982; Schönherr, 1974).



Figure 1: The larva of *Agrilus biguttatus* makes zigzagging galleries in living oak trees; the last abdominal segment terminates in a pair of minute black-brown horns. (Photo: Alterra / A. van Frankenhuyzen).

2.1.3. Biology and ecology of the Buprestidae

Adult buprestids are diurnal, sun-loving beetles. The majority of the beetles are oligophagous, developing only in a single tree genus or in several related genera. The females place their eggs singly or in small groups into ridges of bark or wood. The eggs are covered with a secretion which hardens.

2.1.4. Host selection and life cycle

Most buprestids are tree specialists. They are dependent on living, but weakened, trees. When the trees are growing vigorously, the larvae tend to be destroyed by plant defence mechanisms such as formation of callus. However, the phloem and xylem only remain suitable for larval development for a relatively short time once the trees are dead. This restricts the period of vulnerability of a given tree to a relatively narrow window when the trees are in a suitably weak condition to support colonisation and larval development. Apparently the females are able to detect suitable trees, weakened by water stress (drought or flooding), root damage by biotic (e.g. voles, fungal infection, etc.) or abiotic (physical damage during soil cultivation, wind movement of the stem and roots, excess application of fertilisers, etc.) or defoliation leading to general stress, including loss of photosynthetic and transpiration capacity. Some species such as *Agrilus viridis* are even able to detect parts of trees which are not healthy; such as bark zones with heat cancer (sun damage) of beech trees.



Figure 2: Dead tree with old larval galleries of *Agrilus biguttatus* (Photo: Alterra / Leen Moraal)

The typical life cycle of buprestids will span one or, exceptionally two years. Adult emergence takes place in the spring (usually May or June in temperate, northern hemisphere regions) and is characterised by D-shaped emergence holes in the bark of trunk and/or branches. Adults feed on foliage, pollen or nectar initially then females lay eggs on the bark surface or within cracks and crevices. After egg hatch, the neonate larvae move to the phloem and commence feeding and pass through several instars (usually four) before the winter. Pupation takes place in the spring just prior to adult emergence.

In experiments on the interaction of *Agrilus suvorovi* (*A. populneus*) and poplars, Arru (1962) found that trees with lower moisture content (MC) in the bark were

more selected for egg deposition. Even differences of 4% lower MC were detected by the female. No egg deposition occurred in more desiccated bark. However apart from the moisture content of the bark, other factors, such as chemical substances, could be involved in detecting suitable hosts (Arru, 1962). *Phaenops cyanea* is able to determine the suitability of host trees in a stand with variable crown densities and tends to attack trees with thinner crowns (Apel *et al.*, 2000). The needles of these trees had significantly lower dry weights and water contents and increased proline contents compared with more resistant trees. The latter had higher concentrations of condensed tannins such as procyanidins and vanillin. Other species of buprestid show extreme sensitivity to infrared, which enables them to detect and colonise fire-damaged trees. In *Melanophila acuminata* this is achieved by infrared-sensitive sensillae in the antennae (Gronenberg & Schmitz, 1999).

2.1.5. Host plant resistance

In the USA, the buprestid *Agrilus bilineatus* attacks oak trees that have been weakened by prior environmental or biotic stress. Oaks that attracted large numbers of individuals or that were successfully colonized by the pest produced significantly less callus than did non-attacked trees when experimentally wounded. It is suggested that callus formation may limit the establishment of small larvae that feed slowly in the cambial region. The results indicate that current theory regarding relationships between increased tree stress and decreased allocation of energy reserves to radial growth and defence against phloem borers may be an oversimplification. It is suggested that tree growth and the defensive response of phloem tissues may be limited more by the rate of carbohydrate utilization or by changes in source-sink relationships than by storage levels. Callus formation and the synthesis of allelochemicals in wounded phloem may be under the same control as cambial activation, which is mediated by plant growth regulators and can be influenced by environmental conditions (Dunn *et al.*, 1990).

The glycoside rhododendrin was found in the inner bark of a large number of *Betula* spp. in the USA. Rhododendrin was naturally hydrolysed to rhododendrol when trees or branches were under drought stress. Rhododendrol may act as a stimulant to oviposition by the bronze birch borer, *Agrilus anxius*, in white-barked species. Selection and breeding, of borer-resistant trees should emphasize those species or individuals found to produce little or no rhododendrin (Santamour & Lundgren, 1997).

2.2. Economic importance of the Buprestidae

North European buprestids have not been regarded as economically important (Bilý, 1982), whereas in the central and southern parts of Europe these beetles can be very destructive. However, it is expected that global warming will increase the vulnerability of forests to insect attack. There is evidence for this in warm-loving *Agrilus* spp. and *Phaenops cyanea* in Germany (Wulf, 1995).

A summary of records from BAWBILT database on damage and control includes a range of buprestids pests (Table 1).

Table 1. Buprestidae considered to be damaging to trees.

Insect species	Tree species	Pest area
<i>Agrilus angustulus</i>	<i>Quercus</i>	Hu
<i>Agrilus ater</i> (<i>A. sexguttatus</i>)	<i>Salix, Populus</i>	
<i>Agrilus elongatus</i>	<i>Quercus</i>	
<i>Agrilus biguttatus</i> (<i>A. pannonicus</i>)	<i>Quercus</i>	Cz, Fr, Ge, It, NL, Pl, Sl,
<i>Agrilus sinuatus</i>	Broadleaves	
<i>Agrilus sulcicollis</i>	<i>Quercus, Fagus, Castanea</i>	
<i>Agrilus suvorovi</i>	<i>Populus</i>	Hu, Sl
<i>Agrilus viridis</i>	Broadleaves	It, NL, Ro
<i>Chrysobothris affinis</i>	<i>Quercus</i>	
<i>Coroebus florentinus</i> (<i>C. bifasciatus</i>)	<i>Quercus, Castanea</i>	It, Pr, Sp
<i>Coroebus undatus</i>	<i>Quercus, Fagus</i>	Pr, Sp
<i>Lampra rutilans</i>	<i>Tilia</i>	
<i>Melanophila picta</i>	<i>Populus, Salix</i>	Pr, Sp
<i>Palmar festiva</i> (<i>Lampra f.</i>)	Cupressaceae	
<i>Phaenops cyanea</i> (<i>Melanophila cyanea</i>)	<i>Pinus</i>	Cz, Ge, Hu, Pl, Ro, Sl, Sw

Cz: Czech Republic; Et: Estonia; Fr: France; Ge: Germany; Hu: Hungary ; It: Italy; NL: the Netherlands; Pl: Poland; Pr: Portugal; Ro: Romania; Sl: Slovakia; Sp: Spain; Sw: Switzerland

2.3. Case studies

2.3.1. *Coroebus florentinus* (*C. bifasciatus*)

Coroebus florentinus affects oak trees in the Mediterranean region. *C. florentinus* is considered a primary pest attacking old trees, causing wounding and death of branches and shoots but not killing the trees; damage by growth losses and by affecting tree shape is rated of medium importance. Considered of low aggressivity and having a low to medium distribution, control measures seem to be practised only in Spain, where visual surveys indicate affected branches which can be pruned before adult emergence.

Figure 3: Adult of *Coroebus florentinus*. Photo: Juan A Pajares.



Specific biology: Females lays eggs in June-July in the bark of young healthy branches of various species of oak, often near the tips of the current year's growth of twigs. The larvae feed at first on the acorns, later boring downwards into the branches, first in the cambium layer and later by boring a gallery that may reach a length of 1.5 m, towards to the base of the branch. When it is fully grown, the larva bores an almost complete ring under the bark. This cuts the flow of sap and leads to desiccation and death of the whole distal part of the branch. Larvae live between 20 months and four years. Deterioration of cork oak and evergreen oak may be considerable, particularly on young trees under the canopies of older trees. This damage is serious on young trees, which may be almost completely affected, but mature healthy trees recover after the infested branch drops off and, sometimes, when the larval galleries are occluded by scar tissue (Dajoz, 2000; Solinas, 1974).

2.3.2. *Coroebus undatus* (in cork oaks)

C. undatus is a primary pest attacking cork oaks of all ages in the Iberian Peninsula. Although it does not usually kill the trees, it causes significant wounding, particularly in the cork producing tissues, leading to important economic losses in the amount and quality of the cork harvested. Rated as of low aggressivity and low to medium distribution, no control measures against this pest are taken currently.

Specific biology: Soon after adult emergence in May and June, *C. undatus* females lay their eggs, individually or in small groups, in bark crevices on the lower part of the stem, but also in the bases of the main branches. Egg hatch occurs in two or three weeks and young larvae penetrate the cork reaching the cork generating layer, where they bore long S-shaped galleries, up to 2 m. long and 3-4 mm. wide, filled with dark, packed frass. After five larval instars, mature larvae bore into the cork layer and excavate pupal cells where later they become adults that leave the trunk through elliptical emergence holes and move to the crowns to feed on the leaves. Generation development usually takes two years, but a sizeable proportion of the individuals may complete their life cycle in one year (Romaník and Cadahía, 1992).

Economic damage in cork oaks arises from larval galleries affecting the new cork layer and the "mother layer" of cork generating tissues; also pupation cells within the cork greatly decrease its quality and value. Repeated attacks result in the weakening of the tree and may lead to its death. Increasing attacks by *Coroebus* species in the Iberian Peninsula are associated with holm and cork oak decline occurring during the last decade. Although in many areas of Spain oak decline has been primarily linked to infection by the soil pathogen *Phytophthora cinnamomi* (Brasier *et al.*, 1993), this decline is assumed to be the result of the combined actions of several factors, especially unusual prolonged drought periods. *Coroebus* species are among the main insect pests involved in the decline syndrome. Mortality of oaks weakened by oak decline and infested by *C. undatus* has been observed also in Germany, where increasing abundance of this formerly rare species of buprestid has been related to favourable climatic conditions (Kontzog, 2001). Attack intensity by this species is also dependent on site and stand characteristics. For example, damage was found to be higher at lower altitudes and on south facing slopes in France

(Merle and Attié, 1992) and in denser stands with thicker understories in Spain (Soria *et al.*, 1992).

2.3.3. *Agrilus* species

Agrilus spp infesting broadleaves, especially *A. biguttatus* and *A. viridis* on *Quercus* and *Fagus*, are generally considered secondary species which may attack all ages but prefer older trees. In a few cases, however, *Agrilus* beetles are rated as primary pests. It seems that situations or criteria for the type of impact are different among countries. In central and western Europe these insects can kill the trees directly, while in the Mediterranean area damage is confined to wounding and death of branches and shoots. *Agrilus* spp have been implicated as important agents in the decline of oak trees in Europe (Moraal and Hilszczanski, 2000) and North America (Muzika *et al.*, 2000). In some cases, they may also contribute to the spreading of oak diseases in stem and branches (Vannini *et al.*, 1996); in Hungary, death of oaks is reported to be caused by a fungus associated with *A. angustulus*.

The type of damage resulting from these pests is also variable among European countries. Even when tree death is caused directly by the insect, economic damage is rated mainly at a medium level, which also applies to damage leading to timber degradation and growth losses. It has been also observed that attacks by the most damaging species follow weakening of the trees by insect defoliation or by the raising of the water table and poor drainage in the soil. Even though some of the *Agrilus* species are considered responsible for tree death on weakened trees, control strategies are applied rarely. Occasional preventive burning and insecticide application to felled trees are indicated in a few cases, but silvicultural management is the most common strategy. Selective thinning is carried out as an occasional control measure in many countries, whereas forest sanitation is either a main or an occasional practice in some. Clear felling and/or pruning are applied only occasionally in some countries. Silvicultural choice as a main tactic is applied in Poland against *A. biguttatus*, where it is considered to be a primary pest causing tree death. Prevention by control of preceding defoliation is also practised in Germany against this pest. No other control tactics are so far applied in Europe, except very few instances of occasional trapping out of the beetles in trap trees or logs. Most of the countries monitor these insects through visual surveys/sampling carried out occasionally in the forest. Several countries also employ questionnaires, but only in one case were these used routinely. No monitoring at all is performed in the countries where these insects are considered of minor impact. Risk rating and decision support systems are absent from management practices, although a local risk model for *A. biguttatus* is used in Germany.

Agrilus viridis: Outbreaks sometimes occur on beech, especially following hot and dry years. Galleries of this species are found mainly under those parts of the bark exposed to the sun at the southern edges of woodlands. It is therefore difficult to make a distinction between damage done by the beetle and that caused by drought and insolation (Dajoz, 2000). In the past this beetle has destroyed large areas of young beech one year after planting (Schönherr, 1974).

Agrilus biguttatus (*A. pannonicus*). In Europe, oak decline is in general associated with a complex of biotic and abiotic stress factors, such as repeated insect defoliation, fungi, late winter frost and drought (Moraal & Hilszczanski, 2000). Some of these primary stress factors are reversible and oaks may recover. However, stressed oaks may be attacked by this species of buprestid beetle such that the trees may be killed before they are able to recover from the original stress factors. *A. biguttatus* has caused losses from a few thousand m³ in Slovakia to hundreds of thousands m³ in France during the 1990s. In Poland, timber losses by all pests in broadleaves, including *A. biguttatus*, amounted to more than 2 m m³ in the same period. *A. biguttatus* is also considered the more aggressive and extended species within the genus, particularly in western and central Europe.

Specific biology: The larvae excavate galleries under the bark of weakened trees, which are killed through girdling. The beetle deposits groups of eggs, mainly on the south-side of the bark of living trees and show a preference for larger trees with thick bark. The larvae excavate long, zigzagging galleries under the bark. Relatively vigorous trees can ward off early larval feeding by wound reactions, which show as dark cracks with slime flux. Warm summers in combination with a large supply of weakened trees are assumed to favour this thermophilic insect (Hartmann & Blank, 1992, 1993).

Agrilus sulcicollis and *A. angustulus*. In several countries these species also play a role in oak decline. To reduce the population of the beetle, a feasible countermeasure might be the removal of those stems which are heavily infested with larvae. Non-infested trees, which are already dead for more than one year, or dead trees with evidence of the beetles' exit holes, may be left in the stands for their contribution in the development of dead wood fauna. Long-term measures include increasing age structure, and developing the shrub and under-storey layers to provide shady conditions that decrease the susceptibility of the trees for infestation (several authors in: Moraal & Hilszczanski, 2000).

Specific biology: These species prefer to infest upper parts of the stems, branches and smaller sized host trees.

2.3.4. *Phaenops cyanea* (*Melanophila cyanea*)

Among buprestids attacking conifers, *Phaenops cyanea* is a pest causing damage to Scots pine pole stands in several European countries. Whether considered primary or secondary, it does cause tree death directly in most cases. Aggressivity of this pest is rated high in western-central countries, where it is widely distributed, whereas in Eastern Europe it appears less aggressive and scarcer. It is one of the most serious pests of pine in Poland, mainly in older stands weakened by biotic agents (insects and root fungi) and abiotic agents (industrial pollution, fluctuation of the level of groundwater, fires) (Sowinska *et al.*, 2000). In the Nordic countries, seed trees that are exposed after cutting are colonised in hot, dry summers. *P. cyanea* was the main insect pest involved in a massive dieback of *Pinus sylvestris* in Germany in 1969-1971, for which the primary cause was root rot as a result of abnormally high water-table during 1965-69. This was the first occurrence of *P. cyanea* in pest proportions

in the region. Freshly felled stems (with or without crowns), when laid on sunny places, were found to be very attractive as trap logs and more so than girdled trap trees (Dengler, 1975). In Sweden, this buprestid can kill draught-stressed trees on shallow soils during hot summers, but it has also been occasionally observed to attack sun-exposed seed trees (Ehnström & Axelsson 2002).

Specific biology: This species attacks the lower stem of Scots pine logs or standing weakened trees. At least in northern Europe, it prefers sun exposed sites, and was not uncommon in fire-damaged trees (Ehnström *et al.* 1995). In southern France, trap logs of *Pinus halepensis*, were preferred over Scots, black and maritime pine (Lieutier *et al.* 1997).

Economic damage by this insect is important, ranking from medium to high levels, particularly due to timber degradation but also to growth losses or even tree mortality, though estimates of it are provided just in one case. Preventative strategies based on physical treatments, including debarking, burning or processing, are occasionally implemented in half of the countries where it is considered a pest. As with other buprestids, silvicultural management is the control option applied most frequently, particularly by selective thinning, clear felling and forest sanitation. Pruning and silvicultural choice are also practised sometimes. Occasional spraying of felled trees and trapping out beetles in trees or logs are complementary measures observed in some cases. Most countries involved do carry out occasional monitoring of this species, mainly through visual surveys, but also using trap trees and questionnaires. In Poland, a forecast method has been proposed using a risk index of threat to stands based on glued belt trap catches (Sowiska, 2000), but in Germany only a risk rating model is used locally; also in this country a pest prediction model for simulating *P. cyanea* population dynamics has been developed (Groll *et al.*, 1993).

Poplars are affected by two buprestid species. *Agrilus suvorovi* (*A. populneus*) is a primary pest of pole trees in Hungary, quite aggressive and distributed, causing a moderate degree of tree death and growth losses, but only occasional surveys and selective thinning are applied as control measures; low damage to poplar transplants by this species is also reported from Slovakia. *Melanophila picta* is a pest of poplar transplants in the Iberian Peninsula associated to low vigour trees growing in unsuitable sites, where it may cause their death. Sanitation, chemically spraying of standing trees and planting in proper sites are practices occasionally used.

2.4. Conclusions on Buprestidae

Buprestids are considered mostly secondary species that may attack trees of all ages, but more commonly at pole and older stages. Their type of impact may vary from wounding trees and causing death of shoots and branches to directly killing the trees. In many species attacks are associated with previous weakening of trees due to drought, repeated defoliation, infection by pathogens, unsuitable sites for healthy growth or a combination of these. Economic damage caused by buprestids is generally rated to be moderate but reaches high levels in some cases, arising from

tree death, growth losses or timber/cork degradation. However, quantitative data are rarely offered and damage estimations appear to be based more on qualitative assessment. Consistent with being classed as secondary, buprestids are usually classed as of low aggressivity, even though in some countries *A. biguttatus* and *P. cyanea* are considered fairly aggressive. Geographic distribution is quite variable, depending on the particular pest and country, appearing frequently of local importance, with some having larger distributions.

Regardless of the damage caused, strategies for controlling these beetles seem to be scarce or non-existent. No preventative measures are carried out in the majority of cases, but silvicultural management is by far the main option employed in Europe, especially by means of selective thinning and sanitation, but only in a few instances are these applied more than occasionally. Chemical spraying to standing or felled trees and trapping out in trees and logs are used sporadically, and no biological control tactics appeared mentioned in any case. Occasional monitoring of buprestids seems to be carried out in most countries, mainly through visual surveys/sampling and, to a lesser extent, questionnaires. Risk rating models and decision support systems seem far from being integrated in buprestid pest management in Europe. By contrast, many buprestid species have received considerable interest from conservation biologists. Many species are red-listed in several countries, and buprestids are good indicators of biodiversity in the communities of saproxylic insects. Hence, buprestids are currently attaining more significance as biodiversity components than as forest pests. In contrast with longhorn beetles (see below), a few buprestid species are rated as pests in one part and red-listed in another part of Europe, indicating that great care must be taken in classifying the pest status and in carrying out any control measures against this family of BAWBILT organisms.

3. CERAMBYCIDAE

The longhorn beetles, with about 25,000 species, are one of the largest groups of Coleoptera. Most of the species can be found in tropical and subtropical regions. European longhorn beetles are divided in the two families Cerambycidae and Vesperidae and include about 550 species, although there is a distinct decrease from South to North in the number of species (Bense, 1995). In northern Germany 26% of the species are associated with broadleaved trees and 50% with coniferous trees (Dajoz, 2000). Cerambycid beetles, together with representatives of other saproxylic families are good biological indicators of woodland biodiversity. Only a few species are damaging to living trees, although they may also be technical pests causing cosmetic damage by boring into the wood, thus reducing its value as premium timber. As with the buprestids, many species of longhorn beetles have declined due to changes in forest practice that tend to leave less dead wood in the woods, and are hence red-listed in many countries. A few species are rare or even protected in some countries, and considered as pests in other parts of Europe. For example, *Cerambyx cerdo* is protected in the whole of Europe and is a "strictly protected species" in the Bern Convention and in the Nature 2000 directive. However, it is not always

infrequent and its status may vary from rare (e.g. in Sweden (Ehnström & Axelsson 2002) and in the Netherlands (Huijbregts 2003)), to common (e.g. France (Dajoz 2000)) and it is, therefore, listed as occasionally attacking living trees in Table 2. However, it is not listed as a pest in the BAWBILT database. Another example, is *Monochamus urussovi*, which is rare in northern Sweden (Ehnström & Axelsson 2002), but one of the most important pests in Siberia (Isaev 1995, Vetrova *et al.* 1999).

3.1. Morphology and biology

3.1.1. Morphology of adult Cerambycidae

These beetles are called longhorns because of their often long antennae, especially in males. Cerambycidae mostly have elongate and almost cylindrical bodies. They vary greatly in length: from a few mm up to 55 mm for *Cerambyx cerdo*. For more detailed information see Bense, 1995; Bilý, 1982 and Hellrigl, 1974.

3.1.2. Morphology of Cerambycidae larvae

The larvae have a soft and depigmented integument; the legs are reduced or lacking. Cerambycid larvae that live in the phloem are compressed like those of buprestids; those that bore their galleries in xylem have cylindrical bodies. For more detailed information see Bense, 1995; Bilý, 1982 and Hellrigl, 1974.

3.1.3. Biology and ecology of the Cerambycidae

Most of the species usually infest only particular areas of the plants such as roots, stems (wood, cambial zone, bark), branches or twigs. The conditions of the substratum (nutrient content, humidity, temperature) are of great importance. These factors are decisive for infestation. Some species are monophagous (*Tetropium gabrieli* in *Larix*), some are oligophagous (*Saperda* spp. in *Populus* and *Salix*) while other (*Leiopus nebulosus*) are polyphagous in many different tree-species. An adaptation towards either conifers or broadleaf trees exists in most cases (Bense, 1995).

The adults of many species visit flowers where they feed on nectar and pollen, while others carry out feeding on bark in the crowns of trees. The mating can take place on the flowers or on the host plants. The eggs (one egg or a group of eggs) are usually deposited under bark or in cracks in the wood with the help of the ovipositor. Some species (*Saperda* and *Monochamus* spp.) gnaw excavations into the wood and deposit a single egg in this hollow. During larval development, which mostly lasts 1-3 years, several larval stages (for example, up to 14 in laboratory rearing of *Anoplophora glabripennis*) are passed through, ending with pupation within characteristic pupal cells in the host tree (Bense, 1995).

3.1.4. Host finding in the Cerambycidae

Cerambycid adults are well adapted to locate suitable host trees, particularly if they respond to volatiles produced by dying or recently dead trees, especially in those attacking conifers. For example, in common with other wood borers, *Monochamus* adults are attracted to pine monoterpenes (Erbilgin and Raffa, 2000), and this has led to some commercial wood borer baits being developed to simulate the odours of a stressed or dying tree which release host monoterpenes, usually α -pinene, and ethanol. Recently, addition to host volatiles of ipsenol and ipsdienol or of blends containing several bark beetle pheromone components resulted in increased attraction of several North American *Monochamus* to traps (Allison *et al.*, 2001, 2003). Other species, such as *Anoplophora glabripennis*, are attracted to living and stressed trees by host volatiles but also use visual and tactile clues to determine the suitability of the host tree. Bark texture, leaf characteristics and other factors, such as the density of the trees, all contribute to host selection in this genus of beetles (Wang *et al.*, 2000).

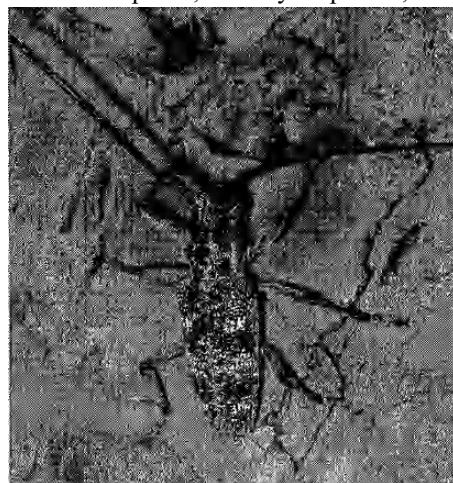


Figure 4: *Monochamus galloprovincialis* adult on pine bark. Photo: Fernando Ibeas

3.1.5. Host plant resistance

There is evidence that certain tree species are more resistant than others for the same wood boring insect. One of the key components is the indirect effect of drought stress that changes the chemical and physical nature of the tree, thus making it more attractive and, after colonisation, more susceptible to beetle attack. Key among the defence strategies employed by trees is sap or resin flow and its chemical composition.

In the case of *Saperda populnea* there are significant differences in population sizes on different poplar strains. This finding was positively correlated with dissolvable total sugar and water content in branches, but no significant correlation was found with total nitrogen and protein nitrogen content. Amino acid content differed significantly between poplar strains but was not correlated with *S. populnea* population size (Gao *et al.*, 2001).

There are several studies on host resistance in relation to the larvae of the cerambycid *Phoracantha semipunctata* on *Eucalyptus*. Larvae achieved a larger size in fresh logs, which may offer a fitness advantage because of higher resource quality. However, greater infestation of that material also increases the probability of mortality from competition among larvae. The results suggest that there are potential ecological interactions among food quality, host resistance, natural enemies, and competition that must be considered in evaluating the population dynamics of this species in native and novel environments (Paine *et al.*, 2001).

Another study investigated the relative susceptibilities to *P. semipunctata* of 12 *Eucalyptus* species in two plantations in California (Hanks *et al.*, 1995). The trees in these plantations were stressed by water deficit resulting from a prolonged drought. Some tree species appeared to be resistant to the borer. Survival of trees was influenced by fine scale moisture variation resulting from slope and irrigation effects. Resistance characteristics of these *Eucalyptus* species did not correlate with taxonomic relatedness or bark characteristics but were those that are most tolerant of drought in Australia. Larvae were unable to colonize the bark of logs that were maintained at high moisture content, but were able to colonize the bark of dry logs and artificially water-stressed trees that had reduced bark moisture content. It is proposed that bark moisture content plays a critical role in the resistance of *Eucalyptus* trees against colonization by larvae of *P. semipunctata* (Hanks *et al.*, 1991).

For the Asian Longhorn Beetle, *Anoplophora glabripennis*, it has been shown that glycoside and phenolic acid contents of the bark were related to insect resistance in Poplar trees. In particular, *Populus tomentosa* was more resistant than *P. alba* (Wang *et al.*, 1995).

3.2. Economic importance of the Cerambycidae

About 20% of the European longhorn beetles are of forestry importance or are of interest, as technical pests, for the timber industry. Within this range of species, there is a difference between those attacking living trees (*Saperda*, *Cerambyx*, *Monochamus*, *Tetropium*, *Anoplophora* and *Phoracantha*), species attacking dying wood with bark still attached and species attacking dry wood. The last two genera are introduced pests in Europe, and are potentially invasive species requiring special attention. The same applies to the genus *Monochamus* as potential vector of the pine wood nematode that was recently found in Portugal. Most species are secondary and exploit either sick or recently felled trees, but some secondary species may occasionally kill weakened trees as well. For example, *Arhopalus rusticus* was often regarded as the cause of mortality of fire-damaged Scots pine trees in Sweden (Ehnström *et al.* 1995). Cerambycids that live on decayed wood are more polyphagous than those that feed on recently dead trees. For more detailed information see Hellrigl (1974). In judging pest status, regional differences occur. Some cerambycids are pests in one region but are very rare or even protected by law elsewhere.

In the BAWBILT questionnaires, a number of more or less damaging species of Cerambycidae on trees throughout Europe is mentioned in table 2:

3.3. Case studies

3.3.1. *Anoplophora glabripennis*.

This species, called the Asian longhorn beetle in Europe and North America, is part of a complex of species in the genus *Anoplophora*, many of which cause damage to living trees. They are widely distributed in China and SE Asia but have also attacked

Table 2. Cerambycidae considered to be damaging to trees.

Insect species	Trees species	Pest area
<i>Acanthocinus aedilis</i>	<i>Pinus</i>	
<i>Arhopalus rusticus</i>	<i>Pinus</i>	It, Pr
<i>Arhopalus tristis</i>	<i>Pinus, Picea</i>	
<i>Aromia moschata</i>	<i>Salix, Acer</i>	
<i>Callidium violaceum</i>	<i>Picea</i>	
<i>Cerambyx cerdo</i>	Broadleaves	
<i>Cerambyx scopolii</i>	<i>Quercus</i>	
<i>Cerambyx welensis (C.velutinus)</i>	<i>Quercus</i>	Pr, Sp
<i>Ergates faber</i>	<i>Pinus, Picea, Abies, Cedrus</i>	
<i>Isarthron castaneum</i>	<i>Picea</i>	
<i>Isarthron gabrielis</i>	<i>Larix</i>	
<i>Lamia textor</i>	<i>Salix, Populus</i>	Hu, Ro
<i>Leiopus nebulosus</i>	Broadleaves	
<i>Molorchus minor</i>	<i>Pinus, Picea</i>	
<i>Monochamus galloprovincialis</i>	<i>Pinus, Picea</i>	It, Pr, Ro
<i>Monochamus sartor</i>	<i>Pinus, Picea, Abies</i>	Hu, Ro, Sl
<i>Monochamus sutor</i>	<i>Pinus, Picea</i>	Hu, Ro, Sl
<i>Oberea linearis</i>	<i>Carpinus, Juglans</i>	
<i>Oberea oculata</i>	<i>Salix</i>	
<i>Phoracantha semipunctata</i>	<i>Eucalyptus, Angophora, Cupressus</i>	It, Pr, Sp
<i>Phymatodes testaceus</i>	Broadleaves	
<i>Plagionotus arcuatus</i>	<i>Quercus</i>	
<i>Pogonochaeerus fasciculatus</i>	<i>Pinus, Picea, Abies, Larix</i>	
<i>Prinobius scutellaris</i>	Broadleaves	
<i>Prionus coriarius</i>	<i>Quercus</i>	
<i>Pyrrhidium sanguineum (Callidium s.)</i>	<i>Quercus</i>	
<i>Rhagium bifasciatum</i>	<i>Quercus</i>	
<i>Rhagium inquisitor</i>	<i>Pinus, Picea, Abies</i>	
<i>Rhagium mordax</i>	Broadleaves	
<i>Saperda carcharias</i>	<i>Populus, Salix</i>	Et, Fr, Hu, It, NL, Ro, Sl, Sp
<i>Saperda populnea</i>	<i>Populus, Salix</i>	Fr, Hu, NL, Ro, Sl, Sp
<i>Semanotus laurasi</i>	<i>Thuja</i>	
<i>Tetropium castaneum</i>	<i>Picea</i>	Cz, Et, It, Ro, Sl, Sw
<i>Tetropium fuscum</i>	<i>Picea</i>	Et, Ro
<i>Tetropium gabrieli</i>	<i>Larix</i>	Cz, Ge, Hu, Sl, Sw
<i>Toxotus cursor</i>	Conifers	

Cz: Czech Republic; Et: Estonia, Fr: France; Ge: Germany; Hu: Hungary ; It: Italy; NL: the Netherlands; Pl: Poland; Pr: Portugal; Ro: Romania; Sl: Slovakia; Sp: Spain; Sw: Switzerland

trees in the USA (Haack *et al.*, 2002) and in Austria (Tomiczek *et al.*, 2002). Those species known to be damaging include *A. glabripennis*, *A. chinensis* (=*A. malasiaca*) (recorded in Italy) and *A. macularia*. The latter two species are fairly polyphagous but are most damaging on citrus and various fruit trees, as well as ornamental trees, whereas *A. glabripennis* is more a problem on forest and shelterbelt trees, including

the genera *Populus*, *Acer* and *Salix* (Lingafelter & Hoebeke, 2002). A recent taxonomic revision by Lingafelter & Hoebeke (2002) has clarified the synonymy of several species within the genus. The experience with *A. glabripennis* has illustrated the risks of movement of pests in international trade; there have been many examples of interception of members of this genus in packing wood associated with goods imported from China. Most European countries as well as Canada, USA, Australia, New Zealand and South Africa, have reported interceptions and the cases of USA and Austria, where there have been infestations on living trees in the receiving countries. Eggs are laid in egg slits arising from female feeding on the bark; there is usually one egg per slit. Larvae go through several instars feeding on the phloem and it is the girdling of the branches and, sometimes, the stems that lead to damage and mortality. The mature larvae bore into the wood and form a U-shaped gallery, culminating in a pronounced pupal chamber, accompanied by production of copious wood shavings. Exit holes made by the adults are completely round. CLIMEX® analysis of the ecoclimatic suitability of Europe for *A. glabripennis* indicates that the climate of most of southern and central parts of Western Europe is suitable for establishment and, therefore, damage by this species (MacLeod *et al.*, 2002, 2003).

Several measures for controlling this insect have been studied in China, where it is an important pest of poplar plantations. In field tests, planting the highly resistant *Melia azedarach* together with the highly attractive *Acer negundo* within poplar plantations greatly reduced damage to poplars (Sun *et al.*, 1990). Biological control trials using the entomopathogenic fungi *Beauveria bassiana* and *B. brongniartii*, cultured in non-woven fabric strips, gave moderate population reduction in poplar stands (Zhang *et al.*, 1999). Chemical control has been also applied against this pest, resulting in good control by directly injection of insecticide into larval galleries or by spraying it in contact-breaking microcapsules (Pan Hua, 2001).

The recent introduction of this pest has caused great concern in the United States. Estimates of the proportions of urban tree populations at risk range from 12 to 61%, and national maximum potential impact has been set at 1.2 billion trees killed and monetary losses amounting to \$669 billion (Nowak *et al.*, 2001). Eradication campaigns have been attempted by the felling of thousands of infested trees and further chipping and incineration, although chipping alone has been demonstrated to be sufficiently effective (Wang *et al.*, 2000). Studies of adult dispersal in their native range have indicated that effective surveys for adult beetles and infested trees should cover a minimum distance of 1,500 m from previously attacked trees (Smith *et al.*, 2001). Rearing protocols and predictive models of invasion are also being developed in North America as part of the eradication and management strategies for this pest, (Dubois *et al.*, 2002). There has been little progress in developing biological control methods and current strategies for eradication in the USA rely on survey, tree felling and destruction or use of the insecticide imidacloprid to kill the larval stages in standing, living trees (Haack, 2003).

3.3.2. *Phoracantha semipunctata*.

The *Eucalyptus* longhorned borer *P. semipunctata* is native to Australia and has become established in most of the regions of the world where its *Eucalyptus* host trees have been introduced. It was first detected in Europe in 1969 (Sardinia, Italy) later being found on the Italian peninsula (1975), Portugal (1980) and south of Spain (1981).

P. semipunctata is a primary insect infesting water stressed eucalyptus stands at the pole and older stages in southern Europe. In general, attacks result in significant economic damage from tree mortality, timber degradation and from aesthetic/recreational impacts, although no quantitative evaluation is available. Ranked as having low aggressivity, its distribution is restricted to eucalyptus plantations in the Mediterranean area. Physical debarking of colonised trees is the main preventative measure practised in Spain, and a range of silvicultural tactics, such as selective thinning, clear felling, forest sanitation and silvicultural choice are occasionally applied in the affected countries. In addition, biological control by parasitoids has been employed occasionally in Portugal and is soon to be implemented in Spain. Visual surveys or trapping are commonly employed to monitor this pest, and local or regional risk rating models are utilised sometimes.

General biology: Adults are active during the hours of darkness, resting under litter, loose bark or bark crevices during the day. They feed on flowers of vigorous trees but reproduce on stressed, weakened trees. Both sexes congregate on stressed trees or cut logs where males locate and identify females by antennal contact, which results in larger males having greater reproductive success due to their greater antennal spread and to their dominance in fighting off other males (Hanks *et al.*, 1996). Mated females lay some 300 eggs each, in batches of 10 to 110, under loose bark, bark crevices or in the undersides of logs. After a few days, eggs hatch and neonate larvae penetrate the bark and bore feeding galleries along the cambium layer, consuming phloem and primary xylem. Mature larvae leave the frass filled galleries in the bark, entering into the sapwood to burrow pupal cells isolated from the outside by a plug of packed frass. After some 10 to 15 days, new adults chew their way out of the tree, leaving typical elliptic emergence holes (Romanyk and Cadahía, 1992).

The number of generations is depending on climate, but one complete (spring-summer) and a partial second (autumn-winter) generation are typical in the Iberian Peninsula. In warm areas, development time from egg to adult emergence is quite short, averaging 3 moths, with a range of 2 to 15 months (Gonzalez, 1992). In southern Europe, adults are continuously present from early spring to late autumn; emergence and dispersal is extended for several months and require periods of mean air temperatures above 15°C (Gonzalez, 1992), with dispersal distance increasing with temperature (Hanks *et al.*, 1998). In the laboratory, cold treatments to larvae delayed adult emergence and resulted in a more synchronised flight, but had no effect on survivorship or longevity, suggesting that cold tolerance of larvae would allow spreading of this species into most areas occupied by eucalyptus (Hanks *et al.*, 1991).

Host location: Several studies have been carried out to elucidate the role of host volatiles in host location by this species. In field tests, logs and leaves of *Eucalyptus globulus* attracted males and females to traps (Barata *et al.*, 1992) and in other laboratory and field experiments, logs originating from damaged trees attracted more adults and received more eggs by females than those from vigorous trees; significant differences were also found between odour bouquets released by damaged and undamaged trees. It was hypothesised that long range attraction might be mediated by terpene compounds, whereas host selection and oviposition would be affected by odours indicating host tissue damage (Paiva *et al.*, 1993).

In wind tunnel trials, host odours emanating from a log of *E. globulus* affected walking and flight behaviour of adults in both sexes, inducing a more directed upwind movement leading to the insects landing on the target, whereas no attractive responses were observed when the adults were presented with a visual stimulus in the absence of host odours (Barata and Araujo, 2001). Further studies have suggested that both sexes are able to detect a large number of plant volatiles, including terpenoids and non-terpenoids, from host and non-host trees, employing them to discriminate between plant species through narrowly tuned olfactory receptor cells (Barata *et al.*, 2000). Responses from single receptor neurones to host (*E. globulus*) and non-host (*Pinus pinaster*, *Olea europaea*) odours, obtained by GC-SCR, showed that olfactory neurones seemed specialised for detection of one or two related compounds. Although most of them responded to host and non-host compounds, a few neurones fired specifically when exposed to volatiles from just one species, suggesting that plant odour information could be conveyed to the brain in *P. semipunctata* by two parallel routes, single channels for specific odorants and multiple channels for other compounds (Barata *et al.*, 2002; Lopes *et al.*, 2002).

Host resistance: Environmental stresses, particularly water deficits, predispose eucalyptus trees to infestation by *P. semipunctata*. During drought years this insect colonises and kills standing trees at a higher rate than in its native habitat. When the relative susceptibilities to attack were examined in drought stressed eucalyptus trees of different species, resistant species were not taxonomically related but they did correspond to the most drought tolerant species in their native range (Hanks *et al.*, 1995).

Resistance of trees to attack by the eucalyptus woodborer has been attributed to several factors. Recently hatched larvae failed to survive when introduced in vigorous standing eucalyptus trees or in watered logs, whereas many were able to colonise dry logs and root-pruned trees. Bark moisture content was correlated with such differences (Hanks *et al.*, 1991). In artificially infested, water stressed potted trees, reduced water potentials were associated with susceptibility to colonisation by neonate larvae; in trees and logs with high bark moisture, larvae were unable to bore into the cambium and were restricted to feeding on poorer quality tissues beneath the bark surface (Hanks *et al.*, 1999). Field tests with groups of water stressed, rain-fed or irrigated trees, found that larval mortality was lower in the former group and appeared to be related to bark moisture content; higher concentration of soluble sugars in the bark of stressed trees was also found, accounting for the higher weight

gains of larvae growing in these trees. However, water stress effects on insect performance were non linear, indicating the existence of a bark moisture threshold above which larvae survival decreased (Caldeira *et al.*, 2002).

“Kino” exudate, a dark gummy polyphenolic flow emanating from parenchyma tissues after mechanical or insect injuries to bark, has been also implicated in eucalyptus resistance. Although dead larvae covered by kino might be seen in tree galleries, several studies could not conclude that it was a main defensive mechanism against borer attack (Hanks *et al.*, 1991; 1995; Caldeira *et al.*, 2002), but it may serve as a barrier zone against micro-organisms (Tippet *et al.*, 1983).

Damage and control: *P. semipunctata* can colonise trees from very young, 4-5 cm diameter, to mature. Larval activity in the phloem and cambium layers often leads to complete girdling of the stem, resulting in tree death, although older and larger trees may survive a first attack. Besides tree mortality, economic damage by timber losses in harvested trees might be considerable and impact on eucalyptus recreational and aesthetic values in urban landscapes are also important in some areas.

Monitoring of *P. semipunctata* populations in eucalyptus plantations can be carried out by regular sampling of eggs in trap logs with bark incisions (Gonzalez, 1984) or pinned loose bark pieces (Cillié and Tribe, 1991) to induce oviposition on them. A model for predicting adult emergence based on accumulated heat units has been developed for southern Spain (Gonzalez, 1992). The risk of tree mortality can be reduced by selection of more resistant eucalyptus species, although this would be dependent also on the specific adaptation of the species to particular environment conditions. In Morocco, a list of 99 eucalyptus species classed by their relative resistance to attack within three different climatic regions was provided as a guide in the silvicultural choice for plantations (El-Yousfi, 1992).

Silvicultural management has been the main control strategy applied against this pest. The planting and management of plantations to reduce tree stress and to promote vigorous growth is the main measure employed. Debarking of recently felled trees, selective thinning and sanitation of attacked trees are also among the tactics used commonly. Attracting large numbers of beetles to insecticide treated trap logs has occasionally been successfully used in Spain and Portugal.

Although some early attempts at parasitoid introduction were made, integration of this approach in the management of this pest has only recently been introduced. Since the discovery of the encyrtid *Avetianella longoi* (Siscaro, 1992), this egg parasitoid has been the subject of promising biological control programmes against *P. semipunctata*, being implemented in several countries (Paine *et al.*, 1995; Hanks *et al.*, 2001). This species has also been tested on eggs of the other eucalyptus woodborer, *P. recurva*, but oviposition and development on this host was lower than in *P. semipunctata* (Luhring *et al.*, 2000). Several studies have been conducted in Australia to select larval parasitoids for biological control; the braconids *Syngaster lepidus* and *Callibracon limbatus* were found to be dominant, host specific on eucalyptus woodborers and broadly distributed and are being introduced as biological control agents in California (Paine *et al.*, 2000; Hanks *et al.*, 2001). Recently, protocols for mass rearing of *S. lepidus* and of the gregarious *Jarra phoracantha* has been developed there for

continuous production and release against *P. semipunctata* and *P. recurva* (Millar *et al.*, 2002).

3.3.3. *Monochamus* spp.

This genus is notable because of its role as the vector for the pine wood nematode, *Bursaphelenchus xylophilus*, which is the causal organism of pine wilt disease, a major tree killer in the Far East. The transmission of the nematodes to susceptible dying or dead trees occurs during female oviposition. Extensive tree mortality in Japan and China is associated with the presence of highly susceptible tree species, suitable vector species and a high summer temperature. Pest risk assessments have been carried out to determine the risks to Europe, and it is concluded that the nematode would undoubtedly survive in Europe, but that tree mortality is likely only in the warmer southern countries, such as in Portugal where an outbreak has been observed. Methods to prevent transfer of nematodes to Europe are discussed in relation to European Union legislation (Fielding & Evans, 1996).

In south and eastern Europe, three species of *Monochamus* are classed as secondary pests attacking pole and older tree ages of pines, spruces or firs, generally not killing their hosts but causing wounding and timber losses. Economic damage from these insects is mainly through timber degradation (technical damage) and is rated mainly as medium, although in Romania it reaches much higher levels, with 120,000 m³ of timber and 90,000 ha affected by *M. sutor* and *M. sartor* in the 1990's. Social impact arising from damage and reduction of the recreational/aesthetic value of timber due to *M. galloprovincialis*, is also of medium importance in Portugal. Apart from their known effects in Europe, the potential roles of *Monochamus* species as vectors of the pine wood nematode (*Bursaphelenchus xylophilus*) in Europe are of enormous relevance. Transmission of the nematode by *M. galloprovincialis* between trees has already been demonstrated in Portugal, where the nematode was first discovered in 1999 (Mota *et al.*, 1999; Sousa *et al.*, 2001).

In general *Monochamus* species are considered of low aggressivity with a restricted geographical distribution, except for *M. sartor* in Romania, where it seems to be highly aggressive and quite extensively distributed, attacking weakened standing trees or fallen trees previously infested by bark beetles. Prevention of attack by physical debarking of trees, forest sanitation, chemical spraying on felled trees and trapping out beetles are the main measures carried out in that country against *Monochamus* pests. Monitoring by questionnaires and selective thinning are the only measures occasionally implemented in other European countries.

In contrast to the situation in Europe, where *Monochamus urussovi* is rare, this species alone and together with the Siberian silk moth (*Dendrolimus sibiricus*) have caused disastrous tree mortality in Siberian spruce and fir forests (Isaev 1995, Vetrova *et al.*, 1999). Hundreds of thousands of hectares have been devastated, and the maturation feeding of the adult beetles on the twigs alone has rendered the trees susceptible to stem attack in a self-perpetuating vicious circle. As far as known, the pine wood nematode is not involved in this process.

Monochamus spp. are among the most destructive technical pests causing timber degradation in North America log yards. Annual losses attributable to large wood borers have been estimated to be \$CAN43.6 m in British Columbia alone (Allison *et al.*, 2001). Recent work on attractive baits, based on host volatiles and bark beetle pheromones (Allison *et al.*, 2001, 2003), together with an improved trap design (Groot and Nott, 2001; Morewood *et al.*, 2002) could lead to an efficient device for monitoring and mass-trapping of these pests.

In Japan, the Japanese pine sawyer *M. alternatus* is the main vector of the pine wood nematode, responsible for the spreading of the nematode which, combined with highly susceptible tree species and high temperatures, has resulted in massive tree mortality from pine wilt disease (Mamiya, 1988). Several studies have been conducted to integrate efficient biological control tactics with classical sanitation and removal of infested trees, using the predator *Trogossita japonica* (Ogura and Hasada, 1995), the nematode *Steinernema carpocapsae* (Yamanaka, 1994) and the fungi *Beauveria bassiana* and *B. brogniartii* (Shimazu, 1994) as control agents. Diverse delivery methods for *B. bassiana* have been tested, including wheat-bran pellets (Shimazu *et al.*, 1992), mass-release of *Cryphalus fulvus* (Coleoptera: Scolytidae) beetles as vectors (Kiuura *et al.*, 1999) and non-woven fabric strips; the latter technique applied to trees and logs obtained a high larval mortality (Shimazu *et al.*, 1995) and reduced longevity and oviposition of emerged adults (Okitsu *et al.*, 2000), proving that it could be suitable for practical use.

The discovery of pinewood nematode in Portugal in 1999 has resulted in considerable activity in that country to determine both the extent of the infestation and also to introduce an eradication programme. Measures to identify, fell and destroy trees showing wilt symptoms have been in place since 1999 and are included in a national eradication programme under the acronym PROLUNP (<http://www.dgf.min-agricultura.pt/prolunp/html/home-final.htm>). An affected zone, surrounded by a buffer zone has been delineated and all trees showing symptoms of wilt are felled and some (affected zone) or all (buffer zone) are assessed for the presence of the nematode. Research into the vector relationships in Portugal have revealed that *M. galloprovincialis*, which is the representative of the genus in the southern part of Portugal, has taken on the role of vector for the nematode (Sousa *et al.*, 2001).

3.3.4. *Tetropium* spp

Three species of *Tetropium* longhorns affect spruce and larch stands in north and central Europe. Rated as secondary pests attacking pole and older stages, their impacts range from wounding to directly causing tree death, depending on the species and country considered. The larch longhorn, *T. gabrieli* will attack dying or severely stressed standing trees such as those affected by the root rot fungi *Armillaria* spp. or *Fomes* spp. Eggs are laid in the bark during the summer and the larvae initially tunnel beneath the bark but penetrate into the wood later in the year (Speight & Wainhouse, 1989). *T. gabrieli* lives on larch, but females can be induced to lay their eggs on pine and spruce, on both of which larvae grow normally (Dajoz, 2000). *T. gabrieli* wounds and generally kills its hosts in north and central Europe,

causing economic damage arising from tree death and timber degradation. In Switzerland, it also has considerable impacts by reducing the roles of trees in protection from avalanches and from erosion; even though its economic impact is of medium importance; however, no quantitative estimates are provided. Although less widely distributed than *T. castaneum*, it seems more aggressive, even highly aggressive in Germany, where during dry and hot summers, population build-ups occur on felled trees, leading to attacks on living neighbouring stands.

T. castaneum causes significant economic damage attributable to tree death, growth losses and timber degradation in Switzerland and Romania; in the latter it affected 180,000 ha and 225,000 m³ of spruce in the 1990s, where attacks by this species were related to bark beetle and weevil attacks and an associated fungus. Although regarded as aggressive in Romania, *T. castaneum* is generally ranked as minor in the other countries, although it is widely distributed. A third species, *T. fuscum* is reported as a pest of lesser importance in a few BAWBILT countries. In Finland, *T. fuscum* and *T. castaneum* were earlier considered major mortality factors of senescent Norway spruce trees (Juutinen 1955), but with intensified forestry their importance in Nordic forestry has decreased. The recent finding of *T. fuscum* in Canada (Halifax, Nova Scotia) where it appears to be killing weakened trees indicates that, given suitable conditions, it can be damaging (Smith & Humble, 2000). Preventative strategies against *Tetropium* pests are quite widespread among the more affected countries. The strategies include, as the main measure, debarking although covering felled timber, processing and burning are also employed on occasion. Silvicultural management, whether it is clear felling, selective thinning or forest sanitation, is also applied in these countries, but not as a main practice. A few cases of insecticide application to felled trees and direct trapping out in trees or logs are also reported. Population monitoring and forecasting of these longhorns is not common practice in Europe, but several countries carry out occasional surveys/sampling or distribute questionnaires. Even less frequently a simple risk-rating model, based on percentage of attacked trees, may be applied.

3.3.5. *Saperda carcharias* and *S. populnea*

These are wood-boring beetles on poplar and willow in many parts of Europe. *S. carcharias* produces galleries in the wood in an upward direction with a length of about 25 cm. It acts either as a primary or a secondary pest, affecting poplar plantations mainly in the pole and older stages. Generally it does not kill the trees, but causes wounding of trunks. Economic damage arising from timber degradation or even growth losses is regarded as moderate, with figures averaging 2-3,000 ha or 4,000 m³ affected during the last decade in some countries. In Finland, hybrid aspen was found to be particularly sensitive to attack by *Saperda* (Löyttyniemi 1972). Other types of damage, such as recreational or aesthetic impact, death of transplants and risk of trees falling during rainstorms in roadside plantations where tree structure has been weakened by high larval activity, may be of particular relevance in certain countries. The degree of aggressive attack and extension of the range of this pest is quite variable among countries, generally being ranked from low to medium.

Common in amenity areas, *S. populnea* produces galls on the branches. *Populus tremula* and *P. alba* are especially affected. *S. populnea* is a primary pest in many areas, causing wounding and death of branches and shoots to poplar transplants or even complete mortality. Distortion of tree shape, which is of medium importance, is the main economic damage resulting from this insect, but growth losses and, to a lesser extent, tree death and timber degradation are also noted occasionally. Quantitative estimates are scarce, but it may have affected 2-4,000 ha of plantations in some east European countries during the 1990s. Although poorly documented, massive attacks of *S. populnea* in plantations of hybrid aspen in southern Sweden in the 1950s (Brammanis 1963), in fact terminated the plans to grow hybrid aspen for the match industry in Sweden. Considered to have variable aggressivity, from low to high, its presence also ranges from local to widely distributed.

Quarantine or preventative measures are not applied for controlling these species of *Saperda*, except for very few instances of movement restriction and burning. Again, silvicultural management seems to be the main control strategy used in Europe, mostly through selective thinning and forest sanitation applied regularly through the life of the forest crop. Other measures such as clear felling, site preparation or even pruning are less widespread and only used occasionally. Chemical insecticide spraying on standing trees against adults is also employed infrequently in several countries. In Italy, good results in preventing adult movement and oviposition were obtained using stem barriers made of an aqueous dispersion of teflon applied to the basal meter of trees (Allegro, 1990). Occasional monitoring by visual surveys/sampling is carried out in the majority of countries, but a local risk model is used only in Romania.

3.3.6. *Cerambyx welensii*

In the Iberian peninsula, *Cerambyx welensii* is a secondary pest causing wounding in holm and cork oak stands, particularly those stressed or weakened by drought, or suffering decline for unknown reasons. Significant effects on tree shape, protective and recreational values, or even tree death are assigned to this insect, which has affected more than 20,000 ha during the last decade in Spain. Of low aggressivity but widely distributed, this pest is mainly managed through selective thinning, pruning and sanitation of oak stands, whereas visual surveys and occasional deployment of light traps are used for population monitoring.

3.4. Conclusions on Cerambycidae

In summary, bark and wood boring cerambycids in Europe form a group of species considered mainly to be secondary pests, although some are classed as primary. They are generally of low aggressivity and have restricted geographical ranges. The majority would be included in the stressed host species category (*sensu* Hanks, 1999), attacking woody plants that are severely stressed, often near to death, by drought or by the actions of other organisms. However, a few such as *A. glabripennis* and *Saperda* spp, could be classed as damaging to healthy hosts or weakened hosts, ovipositing only in growing trees that are fully vigorous or

weakened in some way, but not to a significant extent that could lead to tree mortality. Impacts produced by longhorn larvae on pole and older trees are mainly wounding and death of branches, but in some cases, tree mortality may directly result from beetle attack. Main economic damage is derived from their impacts on timber quality, frequently considered as of medium significance, but a lack of quantitative estimates makes it difficult to provide specific information on this aspect. Although of lesser overall importance, impact by tree death is also a serious threat in certain species. Other types of economic impact of decreasing relevance produced by these longhorn beetles are loss of volume increment, impacts on tree shape and reduction of recreational, aesthetic and protective values.

Among control strategies, preventative measures are rarely applied against these insects, though occasional physical treatments, generally by debarking or even burning, are used for the most damaging species. In many cases, when damage is regarded as low or even medium significance, no management is practised against these pests. However, basic silvicultural management through selective thinning and/or forest sanitation is generally applied in the most affected countries, even though only in half of the cases are these measures regularly conducted. Insecticide spraying on felled or standing trees and, to a lesser extent, trapping out of insects in trees and logs, are tactics complementary to sanitary felling that may be used occasionally in some countries. Many of them do carry out non-routine surveys for monitoring of cerambycid pests, but there are very few examples of simple, local risk models utilised in their management. The arrival of pinewood nematode, *B. xylophilus*, in Portugal has increased the interest in *Monochamus* spp. and has resulted in improvements to the monitoring and management of *M. galloprovincialis* in the Iberian Peninsula.

4. OVERALL CONCLUSIONS

- Most of the European Buprestidae and Cerambycidae are of secondary importance, because many of them only infest trees which are weakened by severe drought or defoliation, etc. Many of these species have declined in numbers and are rare, red-listed or even protected in parts of Europe.
- Some tree species are more resistant than others to boring insects, but often this is related to environmental factors, such as the incidence of drought, rather than intrinsic genetic resistance. Some insect species are attracted by secondary plant metabolites but the quantities of these may be linked to the state of health of the tree, especially when extrinsic factors such as drought, wind damage, etc. are involved.
- The maintenance of healthy, vigorous trees is always the best defence against insect attack. This can involve irrigation where possible and necessary, possible use of fertilizers and the removal of infested trees and, particularly, the growing of tree species and seed origins appropriate to the particular site and climate of the area.
- Sustainable forestry practices should diminish the factors which cause poor physiological condition of the trees. On dry sites certain broadleaved trees could be replaced by more adapted trees e.g. pine. Long-term measures should also include broadening the age structure by encouraging natural regeneration, formation of

mixed forests and developing the shrub and underwood layers. This underwood produces organic material, and by this, improving the formation of good organic soil. Furthermore, underwood provides shade on the tree trunks which can decrease the susceptibility of the trees for infestation by sun loving borers, especially the Buprestidae. Care should be taken in carrying out thinning and harvesting because of changes to microclimate and potential mechanical damage to the remaining standing trees.

- For the majority of buprestid and longhorn species conservation issues are important elements of sustainable forestry with the aim of maintaining a high biodiversity. Thus, a crucial question in forest management is how to provide suitable brood material for rare species without risking increased population levels of pest species. This is a major challenge for research in forest protection and conservation.

5. REFERENCES

- Allegro, G., 1990. Lotta meccanica contro i principali insetti xilofagi del pioppo mediante impiego di sbarramenti sui tronchi. *Informatore Agrario*, 46, 91-95.
- Allison, J. D., Borden, J. H., McIntosh, R.L., Grott, P. & Gries, R., 2001. Kairomonal responses by four *Monochamus* species (Coleoptera: Cerambycidae) to bark beetle pheromones. *Journal of Chemical Ecology*, 27, 633-46.
- Allison, J. D., Morewood, W.D., Borden, J. H., Hein, K.E. & Wilson, I.M., 2003. Differential bio-activity of *Ips* and *Dendroctonus* (Coleoptera: Scolytidae) pheromone components for *Monochamus clamator* and *M. scutellatus* (Coleoptera: Cerambycidae). *Environmental Entomology*, 32, 23-30.
- Apel, K. H., Katzel, R., Luttschwager, D., Schmitz, H. & Schutz, S. (2000). Investigations on possible mechanisms of the host finding by *Phaenops cyanea* F. (Col., Buprestidae). *Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie* 12, 23-27.
- Arru, G.M., 1962. Agrius suvorovi populneus Schaefer (Coleoptera: Buprestidae) dannoso ai Pioppi nell' Italia settentrionale. *Boll. Zool. Agr. Bachic.*, (Ser. 2) 4, 159-287.
- Barata, E.N., Fonseca, P., Mateus, E. & Araujo, J., 1992. Host-finding by *Phoracantha semipunctata* (Coleoptera: Cerambycidae): host volatiles, electroantennogram recordings and baited field traps. In : Menken S.B.J., Visser J.H., Harrewijn (Eds). *Proceedings of the 8th International Symposium on Insect-Plant Relationships*. Kluwer Academic, Dordrecht.
- Barata, E. N., Pickett, J. A., Wadhams, L.J., Woodcock, C. M. & Mustaparta, H., 2000. Identification of host and non-host semiochemicals of the eucalyptus woodborer *Phoracantha semipunctata* Fabricius (Coleoptera: Cerambycidae), by gas chromatography couples electroantennography. *Journal of Chemical Ecology*, 26: 1877 – 95.
- Barata, E. N. & Araujo, J., 2001. Olfactory orientation responses of the eucalyptus woodborer, *Phoracantha semipunctata*, to host plant in a wind tunnel. *Physiological Entomology*, 2, 26-37.
- Barata, EE. N., Mustaparta, H., Pickett, J. A., Wadhams, L. J. & Araujo, J., 2002. Encoding of host and non-host plant odours by receptor neurones in the eucalyptus woodborer, *Phoracantha semipunctata* (Coleoptera: Cerambycidae). *J. Comp. Physiology A*, 188, 121 – 33.
- Bense, A. 1995. *Longhorn beetles: illustrated key to the Cerambycidae and Vesperidae of Europe*. Margraf Verlag, Eikersheim.
- Bily, S. 1982. *The Buprestidae (Coleoptera) of Fennoscandia and Denmark*. Scandinavian Science Press, Klampenborg.
- Brammanis, L. 1963. Zum Vorkommen und zur Bekämpfung des Kleinen Aspenbockes *Saperda populnea* L. in Schweden. *Z ang Entomol* 51, 122-29.
- Brasier, C.M., Robredo, F. & Ferraz, J.F., 1993. Evidence for *Phytophthora cinnamomi* involvement in Iberia oak decline. *Plant Pathology*, 42, 140-45.
- Caldeira, M. C., Fernández, V. & Pereira, J. T. J., 2002. Positive effect of drought on longicorn borer larval survival and growth on eucalyptus trunks. *Annals of Forest Science*, 59, 99-106.

- Cillié, J. J. & Tribe, G. D., 1991. A method for monitoring egg production by the *Eucalyptus* borers *Phoracantha* spp. (Cerambycidae). South African Forestry Journal, 157, 24-26.
- Dajoz, R. 2000. *Insects and forests: the role and diversity of insects in the forest environment*. Intercept Ltd, Paris.
- Dengler, K. 1975. Control of *Phaenops cyanea* (Col., Buprestidae). Zeitschrift für Angewandte Entomologie 78, 5-9.
- Dubois, T., Hajek, A. E. & Smith, S., 2002. Methods for rearing the Asian longhorned beetle (Coleoptera: Cerambycidae) on artificial diet. Annals of the Entomological Society of America, 95, 223-30.
- Dunn, J.P., Potter, D.A. & Kimmerer, T.W.. 1990. Carbohydrate reserves, radial growth, and mechanisms of resistance of oak trees to phloem-boring insects. Oecologia 83, 458-68.
- Ehnström, B. & Axelsson, R. 2002. *Insektsnag i bark och ved. Artdatabanken* SLU Uppsala. (In Swedish only)
- Ehnström, B., Långström, B. & Hellqvist, C. 1995. Insects in burned forests - forest protection and faunal conservation (preliminary results). Entomologica Fennica 6, 109-17.
- El-Yousfi, M., 1992. Possibilités de lutte préventive contre *Phoracantha semipunctata* (F.) par la sélection d'espèces d'*Eucalyptus*. Boletín de Sanidad Vegetal, Plagas, 18, 735-43.
- Erbilgin, N. & Raffa, K. F., 2000. Opposing effects of host monoterpenes on responses by two sympatric species of bark beetles to their aggregation pheromone. Journal of Chemical Ecology, 26, 2527-48.
- Fielding, N.J. & Evans, H.F. 1996. The pine wood nematode *Bursaphelenchus xylophilus* (Steiner and Buhrer) Nickle (= *B. lignicolus* Mamiya and Kiyoohara): an assessment of the current position. Forestry 69, 35-46.
- Gao, C.Q., Sun, S.H., Ren, X.G., Song, L.W., Zhang, X.J., Dai, W.Z., Xiao, H., Zhuang, C.Y., Yi, D.G., Zhu & Z.Y. & Ren, H.B.. 2001. Relationship between trophic component of different poplar strains and occurrence of *Saperda populnea*. Journal of Forestry Research 12, 263-65.
- Gonzalez Tirado, L., 1984. Lucha contra *Phoracantha semipunctata* Fab. En el suroeste español. Boletín del Servicio de Defensa contra Plagas, 10, 185-204.
- Gonzalez Tirado, L., 1992. Estudio sobre integrales térmicas de *Phoracantha semipunctata* Fab. (Col: Cerambycidae), insecto perforador del género *Eucalyptus*, en Huelva (España). Boletín de Sanidad Vegetal, Plagas, 18, 529-45.
- Groll, E., Schultz, A., Häussler, D. & Apel, K. H., 1993. Die Modellierung von forstwirtschaftlichen Schaderregern mit dem Simulationssystem SCHAPRO Beiträge für Forstwirtschaft und Landschaftsökologie, 27, 112-16.
- Gronenberg, W. & Schmitz, H. (1999). Afferent projections of infrared-sensitive sensilla in the beetle *Melanophila acuminata* (Coleoptera: Buprestidae). Cell and Tissue Research 297, 311-18.
- Groot, P. de, & Nott, R., 2001. Evaluation of traps of six different designs to capture pine sawyer beetles (Coleoptera: Cerambycidae). Agricultural and Forest Entomology, 3, 107-11.
- Haack, R. A. (2003). Research on *Anoplophora glabripennis* in the United States. Nachrichtenbl.Deut, Pflanzenschutzd. 55, 68-70.
- Hanks, L. M., 1999. Influence of the larval host plant on reproductive strategies of cerambycid beetles. Annual Review of Entomology, 44, 483-505.
- Hanks, L. M., Paine, T.D. & Millar, J. C., 1991. Mechanisms of resistance in *Eucalyptus* against larvae of the eucalyptus longicorn borer (Coleoptera: Cerambycidae). Environmental Entomology, 20, 1583-88.
- Hanks, L. M., Millar, J. G. & Paine, T. D., 1991. Evaluation of cold temperatures and density as mortality factors of the eucalyptus longhorned borer (Coleoptera: Cerambycidae) in California. Environmental Entomology, 20, 1653-58.
- Hanks, L. M., Paine, T. D., Millar, J. G. & Hom, J. L., 1995. Variation among *Eucalyptus* species in resistance to eucalyptus longhorned borer in Southern California. Entomologia Experimentalis et Applicata, 74, 185-94.
- Hanks, L. M., Millar, J. G. & Paine, T. D., 1996. Body size influences mating success of the *Eucalyptus* longhorned borer (Coleoptera: Cerambycidae). Journal of Insect Behavior, 9, 369-82.
- Hanks, L. M., Millar, J. G. & Paine, T. D., 1998. Dispersal of the eucalyptus longhorned borer (Coleoptera: Cerambycidae) in urban landscapes. Environmental Entomology, 27, 1418-24.
- Hanks, L. M., Paine, T. D., Millar, J. G., Campbell, C. D. & Schuch, U. K., 1999. Water relations of host trees and resistance to the phloem-boring beetle *Phoracantha semipunctata* F. (Coleoptera: Cerambycidae). Oecologia, 119, 400-07.

- Hanks, L. M., Millar, J. G., Paine, T. D., Wang Qiao & Paine, E. O., 2001. Patterns of host utilization by two parasitoids (Hymenoptera : Braconidae) of the eucalyptus longhorned borer (Coleoptera : Cerambycidae). *Biological Control*, 21, 152-159.
- Hartmann, G. & Blank, R. 1992. Winterfrost, Kahlfrass und Prachtkäferbefall als Faktoren im Ursachenkomplex des Eichensterbens in Norddeutschland. *Forst und Holz* 47, 443-452.
- Hartmann, G. & Blank, R. 1993. Etiology of oak decline in Northern Germany: History, symptoms, biotic and climatic predisposition, pathology. In: *Recent advances in studies on oak decline*. N. Luisi *et al.* (Eds). Dipartimento di Patologia Vegetale, Università Degli Studi, Bari, Italy.
- Hellrigl, K. 1974. Cerambycidae. In: *Die Forstsäädlinge Europas, 2 Band. Käfer*, W. Schwenke, W. Parey, Hamburg.
- Hellrigl, K.G. 1978. Ökologie und Brutpflanzen Europäischer Prachtkäfer (Col., Buprestidae). Teil 2. *Zeitschrift für Angewandte Entomologie* 85, 253-275.
- Huijbregts, H., 2003. Beschermd kevers in Nederland (Coleoptera). Nederlandse Faunistische Mededelingen 19, 1-33.
- Isaev, A.S. 1995. The principles and methods of integrated protection of Siberian forests from destructive insect, p. 628-634. In: *Behavior, population dynamics and control of forest insects*. Hain, F.P., Salom, S.M., Ravlin, W.F., Raffa, K.F., & Payne, T.L. (Eds) Proceedings of the joint IUFRO conference for Working Parties S2.07-05 and S2.07-06, Maui, Hawaii, 6-11 February 1994.
- Juutinen, P. 1955. Zur Biologie und forstlichen Bedeutung der Fichtenböcke (*Tetropium Kirby*) in Finnland. *Acta Entomologica Fennica* 11, 1-112.
- Kinuura, H., Ohya, E., Makihara, H., Nagaki, A. & Fujioka, H., 1999. Infection rate of *Monochamus alternatus* Hope (Coleoptera: Cerambycidae) by an entomogenous fungus through mass-release of vector beetles *Cryphalus fulvus* Niijima (Coleoptera: Scolytidae) using an improved application device. *Journal of the Japanese Forestry Society*, 81, 17-21.
- Kontzog, H. G., 2001. Der Wellenbindige Eichenprachtkäfer (*Coraebus undatus* F.) in Eichenbeständen Sachsen-Anhalts. Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie, 13, 481-84.
- Lieutier, F., Vouland, G. & Pettinetti, M. 1997. Testing the preference of Scolytidae and other xylophagous insects for various Mediterranean pine species under natural conditions. Test de choix de pins méditerranéens par les Scolytides et autres insectes xylophages en conditions naturelles. *Revue Forestière-Française*, 49, 3, 215-24.
- Lingafelter, S. W. & Hoebeke, E. R. 2002. *Revision of Anoplophora (Coleoptera: Cerambycidae)*, Entomological Society of Washington, Washington DC, USA.
- Lopes, O., Barata, E. N., Mustaparta, H. & Araujo, J., 2002. Fine structure of antennal sensilla basiconica and their detection of plant volatiles in the eucalyptus woodborer, *Phoracantha semipunctata* fabricius (Coleoptera: Cerambycidae). Arthropod Structure and Development, (in press).
- Luhring, K. A., Paine, T. D., Millar, J.G. & Hanks, L. M., 2000. Suitability of the eggs of two species of eucalyptus longhorned borers (*Phoracantha recurva* y *P. semipunctata*) as host for the encyrtid parasitoid *Avetianella longoi*. *Biological Control*, 19, 95-104.
- Löyttyniemi, K. 1972. Hybridihaavikoiden hyönteistuhoista (Insect damages in hybrid aspen stands). *Silva Fennica* 6, 187-92.
- Macleod, A., Evans, H. F. & Baker, R. H. A. 2002. An analysis of pest risk from an Asian longhorn beetle (*Anoplophora glabripennis*) to hardwood trees in the European community. *Crop Protection* 21, 635-45.
- Macleod, A., Evans, H. F. & Baker, R. H. A. 2003. The establishment potential of *Anoplophora glabripennis* in Europe. *Nachrichtenbl. Deut. Pflanzenschutzd.* 55, 83-84.
- Mamiya, Y. 1988. History of pine wilt disease in Japan. *Journal of Nematology* 20, 219-226.
- Merle, P. du & Attié, M., 1992. *Coraebus undatus* (Coleoptera: Buprestidae) sur chêne liège dans le Sud-Est de la France: estimation des dégâts, relations entre ceux-ci et certains facteurs du milieu. *Annales des Sciences Forestières*, 49 (6) : 571-588.
- Millar, J. G., Paine, T. D., Campbell, C. D. & Hanks, L. M., 2002. Methods for rearing *Syngaster lepidus* and *Jarra phoracantha* (Hymenoptera: Braconidae), larval parasitoids of the phloem-colonizing longhorned beetles *Phoracantha semipunctata* and *P. recurva* (Coleoptera: Cerambycidae). *Bulletin of Entomological Research*, 92, 141-146.
- Moraal, L.G. & Hilszczanski, J., 2000. The buprestid beetle, *Agrilus biguttattus* (F.) (Col., Buprestidae), a recent factor in oak decline in Europe. *Journal of Pest Science*, 73, 134-138.

- Morewood, W.D., Hein, K.E., Katinic, P.J. & Borden, J. H., 2002. An improved trap for large wood-boring insects, with special reference to *Monochamus scutellatus* (Coleoptera: Cerambycidae). Canadian Journal of Forest Research, 32, 519-525.
- Mota, M. M., Braasch, H., Bravo, M. A., Penas, A. C., Burgermeister, W., Metge, K. & Sousa, E. 1999. First report of *Bursaphelenchus xylophilus* in Portugal and in Europe. Nematology 1, 727-34.
- Muzika, R. M., Liebhold, A. M. & Twery, M. J., 2000. Dynamics of twolined chestnut borer *Agrius bilineatus* as influenced by defoliation and selection thinning. Agricultural and Forest Entomology, 2, 283-89.
- Nowak, D. J., Pasek, J. E., Sequeira, R. A., Crane, D. E. & Mastro, V. C., 2001. Potential effect of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on urban trees in the United States. Journal of Economic Entomology, 94, 116-22.
- Ogura, N. & Hosoda, R., 1995. Rearing a coleopterous predator, *Trogossita japonica* (Col., Trogossitidae), on artificial diets. Entomophaga, 40, 371-78.
- Okitsu, M., Kishi, Y. & Takagi, Y., 2000. Control of adults of *Monochamus alternatus* Hope (Coleoptera: Cerambycidae) by application of non-woven fabric strips containing *Beauveria bassiana* (Deuteromycotina: Hyphomycetes) on infested tree trunks. Journal of the Japanese Forestry Society, 82, 276-80.
- Paine, T. D., Millar, J. G. & Hanks, L. M., 1995. Integrated program protects trees from eucalyptus longhorned borer. California Agriculture, 49, 34-37.
- Paine, T.D., Millar, J.G., Paine, E.O. & Hanks, L.M.. 2001. Influence of host log age and refuge from natural enemies on colonization and survival of *Phoracantha semipunctata*. Entomologia Experimentalis et Applicata 98, 157-63.
- Paine, T. D., Paine, E. O., Hanks, L.M. & Millar, J.G., 2000. Resource partitioning among parasitoids (Hymenoptera: Braconidae) of *Phoracanta semipunctata* in their native range. Biological Control, 19, 223-31.
- Paiva, M. R., Mateus, E. & Farrall, M. H., 1993. Chemical ecology of *Phoracantha semipunctata* (Col., Cerambycidae): potential role in *Eucalyptus* pest management. Bulletin OILB/SROP, 16, 72-77.
- Pan Hua, P., 2001. Experiment on the application of microcapsules against *Anoplophora glabripennis* in poplars. Forest Pest and Disease, 20, 17-18.
- Romanyk, N. & Cadahía, D. 1992. *Plagas de insectos en las masas forestales españolas*. Ministerio de Medio Ambiente, Madrid.
- Santamour, F.S. & Lundgren, L.N.. 1997. Rhododendrin in *Betula*: a reappraisal. Biochemical Systematics and Ecology. 25, 335-41.
- Schönherr, J., 1974. Buprestidae. In: *Die Forstschädlinge Europas, 2 Band*. Käfer, W. Schwenke. Parey, Hamburg.
- Shimazu, M., 1994. Potential of the cerambycid-parasitic type of *Beauveria brongniartii* (Deuteromycotina: Hyphomycetes) for microbial control of *Monochamus alternatus* Hope (Coleoptera: Cerambycidae). Applied Entomology and Zoology, 29, 127-30.
- Shimazu, M., Kushida, T., Tsuchiya, D. & Mitsuhashi, W., 1992. Microbial control of *Monochamus alternatus* Hope (Coleoptera: Cerambycidae) by implanting wheat-bran pellets with *Beauveria bassiana* in infested tree trunks. Journal of the Japanese Forestry Society, 74, 325-30.
- Shimazu, M., Tsuchiya, D., Sato, H. & Kushida, T., 1995. Microbial control of *Monochamus alternatus* Hope (Coleoptera: Cerambycidae) by application of nonwoven fabric strips with *Beauveria bassiana* (Deuteromycotina: Hyphomycetes) on infested tree trunks. Applied Entomology and Zoology, 30, 207-13.
- Siscaro, G., 1992. *Avetianella longoi* sp. n. (Hymenoptera, Encyrtidae) egg parasitoid of *Phoracantha semipunctata* F. (Coleoptera, Cerambycidae). Bollettino di Zoologia Agraria e di Bachiocoltura, 24, 205-12.
- Smith, G. A. & Humble, L. M. (2000). The brown spruce longhorn beetle. *Exotic Forest Pest Advisory - Pacific Forestry Centre, Canadian Forest Service* 1-4.
- Smith, M. T., Bancroft, J., Li, G. H., Gao, R.T. & Teale, S., 2001. Dispersal of *Anoplophora glabripennis* (Cerambycidae). Environmental Entomology, 30, 1036-40.
- Solinas, M. 1974. *Coraebus florentinus* (Col., Buprestidae): biology, damage and control. Entomologica 10, 141-93.
- Soria, F. J., Villagrán, M. & Ocete, M. E., 1992. Estudios poblacionales sobre *Coroebus undatus* (Fabricius) (Coleóptera, Buprestidae) en alcornocales de Andalucía Occidental. I: Relación infestación-bosque. Boletín de Sanidad Vegetal, Plagas, 18, 377-83.

- Sousa, E., Bravo, M. A., Pires, J., Naves, P., Penas, A. C., Bonifacio, L. & Mota, M. M. 2001. *Bursaphelenchus xylophilus* (Nematoda; Aphelenchoididae) associated with *Monochamus galloprovincialis* (Coleoptera; Cerambycidae) in Portugal. *Nematology* 3, 89-91.
- Sowiska, A., Kolk, A. & Wolski, R., 2000. Study results on new methods of forecasting and controlling *Phaenops cyanea* (F.) (Coleoptera, Buprestidae). *Sylwan*, 144, 17-32.
- Speight, M. R. & Wainhouse, D. (1989). *Ecology and management of forest insects*, Oxford University Press, Oxford.
- Sun, J. Z., Zhao, Z. Y., Ru, T. Q., Qian, Z. G. & Song, X. J., 1990. Control of *Anoplophora glabripennis* by using cultural methods. *Forest Pest and Disease*, 2, 10-12.
- Tippett, J. T., Shea, S. R., Hill, T. C. & Shearer, B. I., 1983. Development of lesions caused by *Phytophthora cinnamomi* in the secondary phloem of *Eucalyptus marginata*. *Australian Journal of Botany*, 31, 197-210.
- Tomiczek, C., Krehan, H. & Menschhorn, P. (2002). Dangerous Asiatic longicorn beetle found in Austria: new danger for our trees? AFZ/Der Wald, Allgemeine Forst Zeitschrift für Waldwirtschaft und Umweltvorsorge 57, 52-54.
- Vannini, A., Biocca, M. & Paparatti, B., 1996. Contributo alla conoscenza del ciclo biologico di *Hypoxylon mediterraneum* su *Quercus cerris*. *Informatore Fitopatologico*, 46, 53-55.
- Vetrova, V.P., Stasova, V.V. & Pashenova, N.V. 1999. Effect of defoliation on resistance response of *Abies sibirica* Lebed. to inoculation with blue-stain fungi. In: *Physiology and genetics of tree-phytophage interactions*. Lieutier, F., Mattson, W.J., Wagner, M.R. (Eds), Les Colloques de INRA.
- Wang, B., Mastro, V. C. & McLane, W. H., 2000. Impacts of chipping on surrogates for the longhorned beetle *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in logs. *Journal of Economic Entomology*, 93, 1832-36.
- Wang, R., Ju, G., Qin, X., Wang, R. & Ju, G.S. 1995. Study on the chemicals in bark of *Populus tomentosa* Carr. resistant to *Anoplophora glabripennis* Motsh. *Scientia Silvae-Sinicae*, 31, 185-88.
- Wulf, A., 1995. Einfluss von Klimaänderungen auf die phytosanitäre Situation im Forst. Schriftenreihe des Bundesministeriums für Ernährung, Landwirtschaft und Forsten. *Angewandte Wissenschaft* 442, 71-79.
- Yamanaka, S., 1994. Field control of the Japanese pine sawyer, *Monochamus alternatus* (Coleoptera: Cerambycidae) larvae by *Steinernema carpocapsae* (Nematoda: Rhabditida). *Japanese Journal of Nematology*, 23, 71-78.
- Zhang, B., Bai, Y., Shimaza, M. & Jiro, I. 1999. Microbial control of *Anoplophora glabripennis* adults by application of non-woven fabric strips with *Beauveria bassiana* and *B. brongniartii*. *Journal of Northwest Forestry College*, 14, 68-72.

Chapter 21

NATURAL ENEMIES OF CERAMBYCIDAE AND BUPRESTIDAE INFESTING LIVING TREES

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1. INTRODUCTION

Several species of Cerambycidae are known to attack living trees in Europe. Conifers are attacked by *Tetropium castaneum* L., *T. fuscum* F., *T. gabrieli* Weise, *Arhopalus rusticus* (L.), *Monochamus galloprovincialis* (Olivier), *M. sartor* (F.) and *M. sutor* (L.). Broadleaved trees are damaged by *Saperda populnea* (L.), *S. carcharias* (L.), *Lamia textor* (L.), *Cerambyx cerdo* L. and *C. velutinus* Brullé. Among Buprestidae, the following European species are associated with living trees: *Agrilus angustulus* (Illiger), *A. biguttatus* (F.) (= *pannonicus* Piller and Mitterpacher), *A. populneus* Schaeffer (= *suvorovi* Obenberger), *A. viridis* (L.), *Coraebus florentinus* (Herbst), *Coraebus undatus* (F.), and *Melanophila picta* Pallas on broad-leave trees, and *Phaenops cyanea* (F.) on conifers.

Although many studies have investigated various aspects of the biology, ecology, damage and control of these insects, the information on their natural enemies is surprisingly limited. Hardly anything is known of their associated pathogens and nematodes, and knowledge of predators is usually limited to non-quantified observations. Parasitoids have received more attention, particularly in a few target host species, e.g. *Tetropium* spp., *Saperda* spp. and *A. viridis*. However, most of these studies are old, often incomplete, and confined to a limited geographic area. Other species (e.g. *Monochamus* spp., *L. textor*, *Cerambyx* spp., *C. undatus*, *M. picta*, *A. angustulus*), have never been the target of specific studies. In most cases, information on parasitoids is restricted to unreliable host-parasitoid records in catalogues or taxonomic books. Tables 1-3 list most species mentioned as parasitoids in the literature in Europe. A preliminary sorting has been made in the tables to separate dubious records from reliable data, but this list probably still contains numerous errors.

In addition, exotic cerambycid species have recently invaded Europe; these include the Australian *Phoracanta semipunctata* F, attacking eucalypt plantations in southern Europe, and *Anoplophora chinensis* (Forster) and *A. glabripennis* (Motchulsky), newly introduced Asian pests of broadleaves. These species have been also introduced elsewhere in the world and, as such, have been the target of biological control programmes including specific studies on their natural enemies.

2. CERAMBYCIDAE

2.1. Conifer feeding species

2.1.1. *Arhopalus rusticus*

There has been no specific study on the natural enemies of this pine and spruce-feeding beetle. A few records are found in the literature (Table 1), some more reliable than others. The most often cited parasitoid of *A. rusticus* is the ichneumonid *Odontocolon dentipes* (Gmelin) (e.g. Herting 1973; Aubert 1969; Slama 1998; Hilszczanski 2002). This species is commonly found on *A. rusticus* in old pine forests, with apparently two generations per year (Hilszczanski, unpublished). Another reliable record is the ichneumonid *Dolichomitus mesocentrus* (Gravenhorst) (Dominik 1958; Kinelski 1971), a common species found on different wood borers on conifers. The other records are less verifiable. Some are very doubtful, such as the ichneumonids *Poemenia notata* Holmgren, a parasitoid of sphecid wasps, and *Xorides fuligator* (Thunberg), a parasitoid usually reared from broadleaved trees.

Several Polish authors briefly mention predators of *A. rusticus*. Dominik (1958) suggested that the larvae of the asilid fly *Laphria gibbosa* (L.) was one of the main natural enemies of *A. rusticus*, attacking mainly larvae. He also mentioned woodpeckers, badgers and wild boars looking for larvae in decaying stumps. Wiackowski, (1957) and Slama (1998) cite elaterids of the genera *Athous*, *Melanotus* and *Elater*, and the histerids *Plegaderus saucius* Erichson and *Paromalus parallelepipedus* (Herbst) as potential predators of larvae and pupae.

2.1.2. *Monochamus galloprovincialis*

Very little is known of the natural enemies of this pine feeding species. Until recently, *M. galloprovincialis* was considered to be of secondary and minor importance because it attacks mainly dying or stressed trees. However, it is regarded as the main vector of the recently introduced pine wood nematode in Portugal (Sousa *et al.* 2001) and, as such, will probably attract more attention in the near future. Until now, there has been no specific study on the parasitoids of *M. galloprovincialis*. The braconids *Atanycolus genalis* (Thomson) and *Meteorus corax* Marschall are the most reliable record listed in Table 1. *A. genalis* is a very common and widespread species found on many cerambycid species feeding on conifers (Filippenkova 1971, as *A. initiator* F.; Tobias 1986). *M. corax* has been mentioned as a parasitoid of *M. galloprovincialis* by Tobias (1986) and Martikainen and

Koponen (2001), but little is known of its biology. Other recent records include undetermined species. Campadelli and Dindo (1994) mention a solitary, unidentified ichneumonid parasitoid on larvae in Italy, and Tomminen (1993) an undetermined tachinid on larvae in Finland. Apart from woodpeckers, predators and pathogens are not known (Slama 1998).

2.1.3. *Monochamus sartor* and *M. sutor*

These two closely related species are found mainly on spruce and, occasionally, on pine, over a large part of Europe. As is the case for their congeneric species *M. galloprovincialis*, predators and pathogens are not known, and the only records of parasitoids are found in host-parasitoid lists and in taxonomic books, which often contain many doubtful host-parasitoid associations. The list of parasitoids provided in Table 1 includes species that are well-known parasitoids of spruce *Tetropium* spp., such as the braconids *Helconidea dentator* (F.) and *Atanycolus genalis* (Schimitschek 1935, 1964; Capek 1985; Tobias 1997), which may attack *Monochamus* spp. in the same spruce logs. Other possible records include the braconid *Iphiaulax impostor* (Scopoli), often cited as parasitoid of both species (Herting 1973; Capek 1985; Tobias 1986), or *Dolichomitus tuberculatus* (Fourcroy) (Schimitschek, 1935, 1964), a polyphagous ichneumonid parasitoid of large xylophagous beetles in conifer logs. Three species of the genus *Rhyssa* are also mentioned (Schimitschek 1935; Aubert 1969). *Rhyssa* spp. are usually associated with siricid wood wasps but it seems that they may also attack cerambycids (Schimitschek 1929, who observed cocoons in galleries of *Tetropium gabrieli*), and, thus, their association with *Monochamus* spp. cannot be totally ruled out.

2.1.4. *Tetropium castaneum* and *T. fuscum*

These two species are closely related. They both attack spruce logs, co-occur in most parts of the distribution of spruce in Europe, have a very similar biology, and are very difficult to identify at the larval stage. Consequently, they tend to share the same parasitoid complex, and records attributed to one species might in fact concern the other species. *Tetropium* spp. are the only European conifer cerambycids of which the parasitoid complex is rather well known, thanks to specific studies. In particular, Juutinen (1955) published an extensive work on *T. castaneum* and *T. fuscum* in Finland, including a good description of their parasitoid and predator complexes. Similarly, Schimitschek (1929) described the natural enemy complex of *T. fuscum* (and *T. gabrieli*) in Moravia and Austria, and Wettstein (1951) provided some information on parasitism of *T. fuscum* in Austria. These studies contain reliable host-parasitoid records and some aspects of the impact and biology of parasitoids. However, since these are old publications, parasitoid identification is confusing. In Table 1, we mention the presently accepted taxonomic identities, but misidentifications in the original studies are possible.

The most important parasitoid of spruce *Tetropium* spp. is undoubtedly the braconid *Helconidea dentator*. In Schimitschek (1929), Wettstein (1951) and Juutinen (1955), it was by far the main parasitoid (e.g. 84% of all parasitoids in Finland). It is mainly known as a parasitoid of *Tetropium* spp. (including *T. gabrieli*

on larch), but host records also include other longhorn beetles in the genus *Monochamus* (Table 1).

Table 1. Parasitoids of European Cerambycidae living in fresh conifer wood. XX = mentioned as reared from the host in a study specifically focused on the host or parasitoid; (XX) = As XX, but parasitoid identification appears doubtful to the authors; X = Recorded in a catalogue, host-parasitoid list, taxonomic publication or from a non-specific study; (X) As X, but parasitoid identification or host-association appear doubtful to the authors.

	<i>Arhopalus rusticus</i>	<i>Monochamus Gallo-provincialis</i>	<i>Monochamus sartor</i>	<i>Tetropium castanum</i>	<i>Tetropium fuscum</i>	<i>Tetropium gabrieli</i>
Main host trees	<i>Pinus</i>	<i>Pinus</i>	<i>Picea</i>	<i>Picea</i>	<i>Picea</i>	<i>Larix</i>
Main references ¹	2,3,5, 7,11, 13,14 17,23	2,6,25 13,19	2,3 20,23 25	13,19 13,14 16,17 19,23 24,25	2,10,11 13,14 15,16,18 19,20,21 23,25,26 26	2,9,10 11,13,14 14,18,19 20,21,22 23,25 27
Ichneumonidae						
<i>Clistopyga sauberi</i> Brauns						(X)
<i>Coleocentrus caligatus</i> Gravenhorst				X		
<i>Deuteroxorides elevator</i> (Panzer)					(X)	
<i>Dolichomitus aciculatus</i> (Hellén)						X
<i>D. dux</i> (Tschech.)					XX	
<i>D. imperator</i> (Kriechbaumer)	X					XX
<i>D. mesocentrus</i> (Gravenhorst)	XX		X	X	XX	XX
<i>D. populneus</i> (Ratzeburg)						X
<i>D. sericeus</i> (Hartig)					XX	
<i>D. terebrans</i> (Ratzeburg)					X	
<i>D. tuberculatus</i> (Geoffroy)		X		X ¹	X ¹	
<i>Helcostizus restaurator</i> (F.)				X ¹	X ¹	X
<i>Ischnoceros caligatus</i> (Gravenhorst)	X					XX
<i>Lissonota buccator</i> (Thunberg)					(X)	
<i>Neoxorides collaris</i> (Gravenhorst)					XX	XX
<i>N. nitens</i> (Gravenhorst)					X	
<i>Odontocolon appendiculatum</i> Grav.	(X)					
<i>O. dentipes</i> (Gmelin)	XX				(X)	
(= <i>pinetorum</i> (Thomson))						
<i>O. quercinum</i> (Thomson)		(X)				
<i>O. spinipes</i> (Gravenhorst)					XX	
<i>Odontocolon</i> sp.						X
<i>Perithous divinator</i> (Rossi)		(X)				
<i>Podoschistus scutellaris</i> (Desv.)					(X)	
<i>Poemenia hectica</i> (Gravenhorst)					X ¹	X ¹
<i>P. notata</i> Holmgren		(X)			(X)	
<i>Rhimphoctona lucida</i> (Clément)						(X)
<i>R. megacephalus</i> (Gravenhorst)				(X)	X	XX
(= <i>austriacus</i> (Tschech.))						
<i>R. obscuripes</i> (Holmgren)						X
<i>R. pectoralis</i> Kriechbaumer					X	

Table 1. (cont.)

	<i>Arhopalus rusticus</i>	<i>Monochamus Gallo-provincialis</i>	<i>Monochamus sartor</i>	<i>Monochamus sutor</i>	<i>Tetropium castaneum</i>	<i>Tetropium fuscum</i>	<i>Tetropium gabrieli</i>
<i>R. teredo</i> (Hartig) (=xorioidea (Strobl))			X	X	XX		
<i>R. xoridiformis</i> (Holmgren)	X			X	XX	XX	
<i>Rhyssa amoena</i> Gravenhorst			(X)				
<i>R. persuasoria</i> (L.)			(X)	(X)			XX
<i>Townesia tenuiventris</i> (Holmgren) (=antefurcalis Thomson)					(X)		
<i>Xorides ater</i> (Gravenhorst)	(X)				(X)	(XX)	(X)
<i>X. brachylabis</i> (Kriechbaumer)	X				XX	XX	XX
<i>X. ephialtoides</i> (Kriechbaumer)				(X)			
<i>X. fuligator</i> (Thunberg)	(X)						
<i>X. irrigator</i> (F.)					XX	X	XX
<i>X. praecatorius</i> (F.)					X	XX	
<i>X. propinquus</i> (Tschech)					X		
<u>Braconidae</u>							
<i>Atanycolus denigrator</i> (L.)					X	X	XX
<i>A. genalis</i> (Thomson) (=initiator F.)	X		X	X	XX	XX	
<i>A. ivanowi</i> (Kokujev) (=sculpturatus Thomson))							X
<i>A. neesii</i> (Marschall)	X					X	XX
<i>Coeloides forsteri</i> Haeselbarth							X
<i>Doryctes leucogaster</i> (Nees)					X		
<i>D. mutillator</i> (Thunberg) (=obliteratus (Nees))					X	X	XX
<i>D. undulatus</i> (Ratzeburg)					X		
<i>Helcon angustator</i> Nees (=redactor (Thunberg))						X	X
<i>H. tardator</i> Nees							
<i>Helconidea dentator</i> (F.)	X	X		XX		XX	XX
<i>Iphiaulax impostor</i> (Scopoli)	X	X					
<i>Meteorus corax</i> Marshall	X						
<i>Ontsira antica</i> (Wollaston)					X	X	
<i>O. imperator</i> (Haliday)					X	X	
<u>Tachinidae</u>							
<i>Billaea adelpha</i> (Loew)						X	
<i>B. triangulifera</i> (Zetterstedt)					XX	XX	XX
Undetermined Tachinidae	X						

1 Recorded from *Tetropium* sp. on spruce

2 References: 1: Achterberg (1987); 2: Aubert (1969); 3: Capek (1985); 4: Chrystal and Skinner (1931); 5: Dominik (1958); 6: Filippenkova (1971); 7: Fitton *et al.* (1988); 8: Gorius (1955); 9: Hedqvist (1967); 10: Hedqvist (1998); 11: Hellrigl (1974); 12: Hellrigl (1985); 13: Herting (1973); 14: Hilszczanski (2002); 15: Hilszczanski (unpublished); 16: Juutinen (1955); 17: Kinelski (1971); 18: Schimitschek (1929); 19: Schimitschek (1935); 20: Schimitschek (1964); 21: Schimitschek (1967); 22: Skrzypczynska and Król (1974). 23: Slama (1998); 24: Thompson (1943); 25: Tobias (1986); 26: Wettstein (1951); 27: Wichmann (1955).

Among ichneumonids, *Rhimphoctona xoridiformis* (Holmgren) and *Xorides brachylabis* (Kriechbaumer) are also major parasitoid of *Tetropium* spp. (Schimitschek 1929; Juutinen 1955). *X. brachylabis* appears strongly associated with the genus *Tetropium* (Aubert 1969; Hilszczanski 2002) whereas very little information is available on the host range of *R. xoridiformis*. *Neoxorides collaris* (gravenhorst) is also abundant and often cited from both spruce *Tetropium* spp. in the whole Europe (Schimitschek 1929; Juutinen, 1955; Aubert 1969; Kinelski 1971; Herting 1973; Slama 1998; Hilszczanski, unpublished). Schimitschek (1929), and Juutinen (1955) also mention as frequent parasitoids the ichneumonids *Xorides praecatorius* (F.), *X. ater* (Gravenhorst) (although often confused with *X. brachylabis*), and *Odontocolon spinipes* (Gravenhorst), the braconid *Atanycolus genalis* (as *A. initiator*) and the tachinid *Billaea triangulifera* (Zetterstedt), which has also been observed by Wettstein (1951). Other reliable records are the ichneumonids *Rhimphoctona teredo* (Hartig) and *Xorides irrigator* (F.), reared by Hilszczanski (2002) in Poland, and mentioned by Schimitschek (1935) and Wichmann (1956) in Austria and Germany. Hedqvist (1998) reared the braconids *Ontsira antica* (Wollaston) and *O. imperator* (Haliday) from both species in Sweden, whereas *Doryctes mutillator* (Thunberg) and *D. leucogaster* (Nees) are mentioned by several authors (Herting 1973; Tobias 1997; Hedqvist 1998; Slama 1998). Finally, several *Dolichomitus* spp. are frequently mentioned in the literature (Table 1) (e.g. Schimitschek 1929, 1935, 1967; Slama 1998), but the taxonomy of this ichneumonid genus is confusing, and the list probably contains misidentifications. A certain record is *D. sericeus* (Hartig), reared from *T. fuscum* by Hilszczanski (unpublished) in Poland.

Although all parasitoids parasitising *Tetropium* spp. kill their hosts at the larval stage, they have different biologies, described by Schimitschek (1929) and Juutinen (1955). Some of the hymenopteran parasitoids oviposit into young larvae, overwinter inside them, then in spring kill their host and build a cocoon in the pupal gallery in the wood. This biology is encountered in *H. dentator*, and probably *Rhimphoctona* spp. In contrast, Ichneumonidae of the sub-families Xoridinae (*Xorides* spp., *Odontocolon* spp.), Pimplinae (*Dolichomitus* spp., *Neoxorides* spp.), and the braconids *Atanycolus* spp., oviposit on larvae in the inner bark, develop externally on paralysed larvae, and build a cocoon, in which they overwinter, between the bark and the wood. The tachinid *B. triangulifera* also lives endoparasitically and puparia are found in the pupal gallery in the wood (Juutinen 1955). Schimitschek (1929) also provides further information on the biology of the main parasitoids such as the period of adult emergence, and a detailed description of all developmental stages, including cocoons.

Parasitism rates are not negligible. Averages of 42.6% and 20.3% have been observed in southern Finland, for both spruce species. In Moravia/Austria, Schimitschek (1929) found, for *T. fuscum* and *T. gabrieli* together, about 20% parasitism in the first year, but the rate increased to 51 and 75 % in the second and third years, after he had left on site the logs with the highest parasitism rates. In the same two years, host population levels had dropped 20-fold. However, it is not clear whether this strategy of parasitoid conservation was responsible for the increase in

parasitism and the collapse of host population. Wettstein (1951) found only 6.5% parasitism in Austria, but this was on a single, heavily attacked log.

Predators, nematodes and fungi are mentioned in Schimitschek (1929) and Juutinen (1955) for *T. fuscum*, and Juutinen (1955) and Slama (1998) for *T. castaneum*. The three authors mention woodpeckers as the most important predators of *Tetropium* spp. In Finland, Juutinen observed that an average of 20% of the galleries were opened by woodpeckers. Schimitschek (1929) observed the black woodpecker (*Dryocopus martius* L.) feeding on *Tetropium* spp. in larval and pupal galleries, as well as on parasitoid larvae and cocoons. Among insect predators, the following species were found feeding on *Tetropium* spp. on spruce: *Thanasimus formicarius* (L.) (Col.: Cleridae) in Finland, Moravia/Austria and Poland, *Athous subfuscus* Müller (Col.: Elateridae) *Palloptera usta* (Meigen) (Dipt.: Pallopteridae) and *Raphidia xanthostigma* Schummel (Neur.: Raphidiidae) in Finland, *Raphidia notata* F., *Inocellia crassicornis* (Schummel) (Neur.: Raphidiidae), and *Forficula auricularia* L. (Derm.: Forficulidae) in Austria. Schimitschek (1929) gives a detailed description of the biology and morphology of the earwig and the Raphidiidae. All these insects are known as polyphagous predators of various bark and wood boring insects. Mites on adults and nematodes in larvae were mentioned by both Schimitschek (1929) and Juutinen (1955), but their exact role could not be assessed. Finally, Juutinen (1955) found about 1% of *Tetropium* larvae killed by unidentified fungi. However, it was not clear whether these fungi were really entomophagous or saprothitic. A higher mortality was caused by competition with *Armillaria mellea* (Vahl), whose mycelium was often found overwhelming *Tetropium* larvae and pupae.

2.1.5. *Tetropium gabrieli*

This species is taxonomically and biologically close to *T. castaneum* and *T. fuscum*, but it is found exclusively on larch. The most complete study on its natural enemy complex has been carried out by Schimitschek (1929) in Moravia and Austria, and additional information is found in Chrystal and Skinner (1931) in England, Gorius (1956) in Germany, Hellrigl (1985) in northern Italy, and Slama (1998) in former Czechoslovakia. Parasitism in Central Europe is rather similar to that observed in spruce *Tetropium* spp. Schimitschek (1929) observed, as main parasitoids, the braconid *H. dentator*, and the ichneumonids *N. collaris* and *X. brachylabis*, three parasitoids that also dominated in the same area on *T. fuscum*. Other important parasitoids were *X. irrigator*, *Atanycolus denigrator* (L.), *A. neesi* (Marschal), and *Rhyssa persuasoria* (L.). The latter is a parasitoid usually associated with siricid woodwasps. Schimitschek reared it from *T. gabrieli* larvae, but in England Chrystal and Skinner (1931) observed that *R. persuasoria* emerging from larch logs containing *T. gabrieli* larvae were in fact always associated to the woodwasp *Sirex cyaneus* F. In Germany, Gorius (1956) found *H. dentator*, *X. irrigator*, *R. xoridiformis* and the braconid *Doryctes mutillator* as main parasitoids. In Italy, Hellrigl (1985) also reared *H. dentator*, but it was dominated by *Rhimphoctona lucida* (Clément), an ichneumonid reared in low numbers in Austria by Schimitschek (1929), and by the tachinid *Billaea triangulifera*, which has also been

obtained from spruce *Tetropium* spp. in Finland by Juutinen (1955) and in Germany by Wettstein (1951). Other reliable records include the ichneumonids *Ischnoceros caligatus* (Gravenhorst), reared from *T. gabrieli* in Czechoslovakia and Poland (Slama 1998; Hilszczanski 2002), *Dolichomitus* spp. reared from larvae in Austria, Germany and Czechoslovakia, despite probable species misidentifications (Schimitschek 1929, 1935, 1967; Gorius 1956; Slama, 1998), and *A. genalis* (as *initiator*) (Gorius 1956; Slama 1998). *T. gabrieli* has been introduced into England in the early 20's century, where it is attacked by two parasitoids, *X. brachylabis* and *X. irrigator* (Chrystal and Skinner 1931). A eupelmid, *Calosota acron* (Walker) (as *C. anginalis* Ruschka) was found as hyperparasitoid in *X. brachylabis* cocoons.

The biology and morphology of most of these species is described in Schimitschek (1929) (see above in the paragraph on spruce *Tetropium* spp.). In addition, Chrystal and Skinner (1931) provide a detailed study on the biology of *X. brachylabis* and *X. irrigator*, including flight periods, mating and oviposition behaviour, description of developmental stages and host specificity. Both species lay their eggs through the bark on paralysed larvae in galleries. The parasitoid develops quickly on the host larva and the last instar larva builds a cocoon in the inner bark, in which it overwinters. Laboratory screening tests on other longhorn beetles suggest that *X. brachylabis* is specific to *Tetropium* but *X. irrigator* was reared from longhorns *Acanthocinus griseus* (F.), *Rhagium inquisitor* (L.) and *Obrium brunneum* (F.) (Hilszczanski 2002). Parasitism in England varied from 16 to 59.5%. In Italy parasitism at emergence was 41.5 and 68% at two sites (Hellrigl 1985). In Austria/Moravia, Schimitschek (1929) observed 20% parasitism in *T. gabrieli* and *T. fuscum*, but a parasitoid conservation programme increased parasitism rates to 51 and 75% in the following years.

Schimitchek (1929) observed the same polyphagous predators feeding on larvae of *T. gabrieli* as in *T. fuscum*: the black woodpecker, the earwig *Forficula auricularia*, the raphidiid *Inocelia crassicornis*, the beetles *Malachius bipustulatus* (L.) and *Thanasimus formicarius*, and underdetermined dipteran larvae. Gorius (1956) emphasises the role of woodpeckers as natural enemies and estimated that between 10 and 20% of the larvae and pupae were eaten by woodpeckers. In this study, the raphidiid *Raphidia notata* was the main insect predator, whereas the earwig *F. auricularia* and the flies *Palloptera usta* and *Lonchaea zetterstedti* Becker (Dipt.: Lonchaeidae) were also observed preying on larvae and pupae.

2.2. Broadleaf feeding species

2.2.1. *Saperda populnea* and *S. carcharias*.

The small poplar longhorn, *S. populnea* is probably the most damaging native cerambycid in Europe and, as such, it has been the target of many studies. However, information of its natural enemy complex is usually restricted to lists of parasitoids and predators reared as part of general studies. Table 2 lists the parasitoids of *S. populnea* cited in the literature. This list does not include old records which are particularly dubious, e.g. from Scheidter (1917). However, Table 2 still contains many errors, which result either from identification mistakes or wrong host-

parasitoid associations. Most studies on natural enemies of *S. populnea* in the last 40 years cite the same few parasitoid and predator species (Brammanis 1963, in Sweden; Kailidis 1964, in Greece; Schneiderowa 1968, in Poland; Strojny and Czaplicka 1975, in Poland; Pulkkinen and Yang 1984, in Finland; Tsankov and Georgiev 1991, in Bulgaria; Georgiev 2001, in Bulgaria; Smith *et al.* in press, in Europe), but only Pulkkinen and Yang (1984) provide details on the biology of parasitoids and predators. Postner (1954) studied *S. populnea* in Germany and listed many parasitoid species, but he did not mention which species were obtained from his own rearing.

Natural enemies of the large poplar longhorn, *S. carcharias*, have been less investigated. Among the few studies are Schneiderowa (1961, 1968) in Poland and Srot (1983) in Czechoslovakia. These studies tend to show that there is a large overlap between the natural enemy complexes of the two species.

Eggs and 1st instar larvae of *S. populnea* and *S. carcharias* are attacked by the euphorids *Euderus albitalis* (Zetterstedt.) and *E. caudatus* Thomson. Mature larvae of *E. albitalis* have been recovered by Pulkkinen and Yang (1984) in egg-chambers of *S. populnea* where they overwinter, but also in the mine of a first instar larva, suggesting that it may also attack young instars. Smith *et al.* (in press) also reared *E. albitalis* from 1st instars in Finland. It is a polyphagous parasitoid, also recorded from Scolytidae, Lepidoptera and other insects (Noyes 2001). *E. caudatus* is known only from eggs of *S. populnea* and *S. carcharias*, and is particularly abundant on the latter. Schneiderowa (1961) observed up to 17% egg parasitism in Poland and Srot (1983) an average parasitism of 6.5% in the Czechoslovakia. In Italy, a programme was developed to screen insecticides, used against 1st instar larvae of *S. carcharias*, for their harmfulness on *E. caudatus* (Arru, 1972).

The tachinid fly *Billaea irrorata* (Meigen) was found to be the main larval parasitoid of *S. populnea*, from northern to southern Europe (e.g. Postner 1954; Brammanis 1963; Strojny and Czaplicka 1975; Pulkkinen and Yang 1984; Tsankov and Georgiev 1991; Georgiev 2001). *B. irrorata* is an endoparasitoid killing its host in the prepupal stage. Larvae, emerging from the dead host larvae in the host pupal chamber prepare a way out for the adult before pupating (Pulkkinen and Yang 1984). Parasitism by *B. irrorata* was about 4% in Finland (Pulkkinen and Yang 1984) and 9-19% in Bulgaria (Tsankov and Georgiev 1991). Interestingly, *B. irrorata* has never been recorded from *S. carcharias*, suggesting that it is rather specific. In their monograph on European tachinids, Tschorasnig and Herting (1994) cite only the cerambycids *Oberea* spp. as other hosts.

Other important larval parasitoids of *S. populnea* include the braconids *Iphiaulax* spp., and the ichneumonids *Dolichomitus* spp. Species of these two genera are idiobiont ectoparasitoids, i.e. they oviposit through the bark on previously paralysed host larvae. *Iphiaulax* spp. parasitise mid-instar larvae in the first year, whereas *Dolichomitus* spp. seem to attack later instars in the second year (Pulkkinen and Yang 1984; Georgiev 2001; Smith *et al.* in press). *Iphiaulax impostor* was recorded from many regions in Europe, from Greece (Kailidis 1964) and Bulgaria (Tsankov and Georgiev 1991; Georgiev 2001) to Sweden (Brammanis 1963), with parasitism rates below 3%. However, another, unidentified *Iphiaulax* sp. has been reared in

Finland, with a parasitism rate of 1% (Pulkkinen and Yang 1984), and Postner (1954) mentions *I. multiarticulatus* (Ratzeburg). Many *Dolichomitus* spp. have been cited as parasitoids of *S. populnea* (Table 2), but the two most regular and reliable records are *D. populneus* (Ratzeburg) and *D. messor* (Gravenhorst). In particular, *D. populneus* has been reared from most studies, but parasitism was usually low (e.g. 2.3% in Finland (Pulkkinen and Yang 1984), 0.5-1.7% in Bulgaria (Tsankov and Georgiev 1991)), except in Germany where Funke (1957, in Pulkkinen and Yang 1984) observed up to 70% parasitism by *D. populneus* or closely-related species. Larvae of *S. carcharias* are also parasitised by *D. populneus* and *D. messor*, but not by *Iphiaulax* spp. In a study in Czechoslovakia, the main larval parasitoid of *S. carcharias* was the ichneumonid *Ischnoceros rusticus* (Geoffroy), but larval parasitism remained low (about 5.5%) (Srot 1983). Records of all other parasitoids of *Saperda* spp. listed in Table 2 have to be viewed with caution.

Among predators, the most investigated species is the Dipteron odiniid *Odinia xanthocera* Collin, a major mortality factor in Finland (Pulkkinen and Yang 1984; Yang, 1984). Eggs are laid at the entrance of the host tunnel. Hatching larvae enter the tunnel and feed first on larval frass of *S. populnea*, whereas older larvae feed on the cerambycid pupae. It also preys on the weevil *Cryptorhynchus lapathi* (L) in the same host tree. In Finland, *O. xanthocera* killed about 10.5% of the *S. populnea* population. Other insect predators mentioned in the literature include Staphilinidae (Coleoptera), Pentatomidae and Reduviidae (Heteroptera), Asilidae and Chloropidae, (Herting 1973; Smith *et al.* in press) but, in most cases, these insects have been found in the beetle galleries and their predatory behaviour has not been verified.

Woodpeckers (e.g. *Dendrocopos major* or *D. minor*) have been often observed feeding on *S. populnea* and *S. carcharias*. (e.g. Brammanis 1963; Strojny and Czaplicka 1975; Srot 1983; Pulkkinen and Yang 1984; Tsankov and Georgiev 1991). The level of predation varies from 9-10% in Finland and Czechoslovakia (Pulkkinen and Yang 1984; Srot 1983) to 54-71% in Bulgaria (Tsankov and Georgiev 1991). However, Pulkkinen and Yang (1984) rightly point out that the foraging behaviour of woodpeckers further weakens the main shoots attacked by *S. populnea*, causing them to break.

Diseases have been only occasionally mentioned as natural enemies of *Saperda* spp. Srot (1983) observed that about 13% of the larvae of *S. carcharias* in Czechoslovakia were killed by *Pseudomonas septica*. In Greece, up to 3% of *S. populnea* larvae died from a fungal disease (Tsankov and Georgiev 1991).

In general, mortality rates attributed to natural enemies of *Saperda* spp. do not exceed 20-30%. Other mortality factors are sometimes considered more important. For example, in Czechoslovakia, healing responses of the host tree to the oviposition wounds killed 56% of the eggs and 61% of the newly hatched larvae (Srot 1983). However, the additional mortality caused by natural enemies should not be neglected. Further studies are needed to better assess the proper impact of natural enemies in the population dynamics of *Saperda* spp.

2.2.2. *Lamia textor*

Natural enemies of this poplar-feeding beetle have never been the target of any particular study. The only records in the literature are the ichneumonid *Dolichomitus messor* (Herting 1973; Aubert 1969) and the tachinid fly *Billaea adelpha* (Loew) (Tschorasnig and Herting 1994) (Table 2). Nothing is known of their impact and biology.

2.2.3. *Cerambyx cerdo* and *C. velutinus*

To our knowledge, there is no information available in the literature on the natural enemies of *C. velutinus*, a minor pest of oak in southern Europe. *C. cerdo* is a rare and protected species in most of Europe. However, it attacks living trees and it is considered a pest in some regions, such as Romania and North Africa. The most often cited parasitoid of *C. cerdo* is the encyrtid egg parasitoid *Oobius rudnevi* (Novicki) (Noyes 2001). Other parasitoids include the ichneumonids *Dolichomitus imperator* (Slama 1998) and *D. tuberculatus* (Herting 1973). In his review, Hellrigl (1974) lists several other parasitoids, most of which are doubtful records.

2.3. Exotic species

2.3.1. *Phoracantha semipunctata*

The eucalyptus borer, *P. semipunctata* is an Australian species feeding on trunks of *Eucalyptus* spp. It was introduced in most parts of the world in which eucalypts have been planted, e.g. southern Africa, North Africa, North America, and southern Europe. In its region of origin, *P. semipunctata* is attacked by a large range of natural enemies, especially parasitoids (Austin *et al.* 1994). In Europe and North Africa, few natural enemies were observed. *Avetianella longoi* Siscaro (Hym.: Encyrtidae), an Australian egg parasitoid was found in Portugal, Italy and Spain (Siscaro 1992; Mansilla-Vazquez *et al.* 1999). *A. longoi* was introduced as a biological control agent in California (Hanks *et al.*, 1996) and South Africa (G. Tribe, personal communication). Another egg parasitoid, *Platystasius transversus* Thomson (Hym.: Platynostridae) was reared from *P. semipunctata* in Morocco (Fraval and Haddan 1988). Ants are considered as important natural enemies both in Morocco (Haddan *et al.* 1988) and Portugal (Way *et al.* 1992). A biological control programme against *P. semipunctata* is presently carried out in California using parasitoids from Australia (Millar *et al.* 2002).

2.3.2. *Anoplophora* spp.

Two Asian species of *Anoplophora*, both attacking a large range of broadleaved trees, have been recently introduced accidentally into Europe. *A. chinensis* (= *A. malasiaca* Thomson) was found recently in Italy, and is considered to be established (Colombo and Limonta 2001). *A. glabripennis* was observed attacking trees in Austria (Krehan 2002) and France (F. Lieutier, pers. comm.) and is presently the target of eradication programmes, but its establishment in Europe has not been confirmed. Both species have also been recently introduced in the USA. Until recently, very little was known on the natural enemies of these two pests in their region of origin. However, following the recent introduction of *A. glabripennis* to

North America, a biological control programme is being developed, and natural enemies are presently being evaluated in Asia, as well as in Europe on other cerambycids (Smith *et al.*, 2002). In China, the entomopathogenic nematodes

Table 2. Parasitoids of European Cerambycidae living in fresh broadleaf trees. XX = mentioned as reared from the host in a study specifically focused on the host or parasitoid; (XX) = As XX, but parasitoid identification appears doubtful to the authors; X = Recorded in a catalogue, host-parasitoid list, taxonomic publication or from a non-specific study; (X) As X, but parasitoid identification or host-association appear doubtful to the authors. The most doubtful host-parasitoid associations, including all associations with Saperda populnea originating from Scheidtter (1917) were not included in the table.

	Main host trees	Cerambyx cerdo	Lamia textor	Saperda carcharias	Saperda populnea
		<i>Quercus</i>	<i>Populus</i>	<i>Populus</i>	<i>Populus</i>
Main references ¹		1,5,6,7 12	1,6,18	1,3,6,7 10,11 13,14	1,2,3,4,6,7 8,9,11,13 15,16,17,18
Ichneumonidae					
<i>Absyrtus vicinator</i> (Thunberg) (= <i>luteus</i> Holmgren)				(X)	
<i>Apechthis capulifera</i> (Kriechbaumer)					(X)
<i>Coelichneumon impressor</i> (Zetterstedt)					(X)
<i>Deuteroxoides elevator</i> (Panzer) (= <i>albitarsus</i> (Gravenhorst))					X
<i>Dolichomitus agnoscendus</i> (Roman)					X
<i>D. cognator</i> (Thunberg)					X
<i>D. imperator</i> (Kriechbaumer)	X			X	X
<i>D. mesocentrus</i> (Gravenhorst)					X
<i>D. messor</i> (Gravenhorst)		X		X	XX
<i>D. populneus</i> (Ratzeburg)				X	XX
<i>D. terebrans</i> (Ratzeburg)					X
<i>D. tuberculatus</i> (Geoffroy)	X			X	
<i>Echthrus reluctator</i> (L.)			X		(X)
<i>Epiphantes manifestator</i> (L.)	X				X
<i>Ischnoceros caligatus</i> (Gravenhorst) (= <i>seticornis</i> (Kriechbaumer))				X	
<i>I. rusticus</i> (Geoffroy) (= <i>filicornis</i> (Kriechb.))				XX	
<i>Liotryphon crassisetus</i> (Thomson)					(X)
<i>L. punctulatus</i> (Ratzeburg)					(X)
<i>Mastrus rufobasalis</i> (Habermehl) (hyperpar.?)				(X)	
<i>Medophron afflictor</i> (Gravenhorst) (hyperpar.?)					(X)
<i>Megarhyssa perlata</i> (Christ) (= <i>clavata</i> (F.) = <i>gigas</i> (Laxmann))	(X)				
<i>M. superba</i> (Schrank)		X			
<i>Neoxorides nitens</i> (Gravenhorst)				X	
<i>Orthocentrus fulvipes</i> Gravenhost					(X)
<i>Podoschistus scutellaris</i> (Desvignes) (= <i>wahlbergi</i> (Holmgren))				X	
<i>Rhimphoctona grandis</i> (Fonscolombe) (= <i>Pyracmon fulvipes</i> (Holmgren))				X	
<i>Rhyssa amoena</i> Gravenhorst		(X)			
<i>R. persuasoria</i> (L.)		(X)			

Table 2. (cont.)

	<i>Ceranthyx cerdo</i>	<i>Lamia textor</i>	<i>Saperda carcharias</i>	<i>Saperda populnea</i>
<i>Stenomacrus pusillator</i> Aubert (= <i>pusillus</i> (Holmgren))				(X)
<i>Townesia tenuiventris</i> (Holmgren)				(X)
<i>Virgichneumon monostagon</i> (Gravenhorst)				(X)
<i>Xylophrurus augustus</i> (Dalman)				(X)
<i>X. lancifer</i> (Gravenhorst) (= <i>dispar</i> Thunberg)				(X)
Braconidae				
<i>Atanycolus denigrator</i> (L.)				X
<i>A. neesii</i> (Marschall)			X	
<i>Bracon discoideus</i> (Wesmael)				X
<i>Iphiaulax impostor</i> (Scopoli)				XX
<i>I. multiarticulatus</i> (Ratzeburg)				X
<i>Iphiaulax</i> sp.				XX
<i>Ontsira longicaudis</i> (Giraud)		X		
Encyrtidae				
<i>Oobius rudnevi</i> (Novicky)		XX		
Eulophidae				
<i>Euderus albitalis</i> (Zetterstedt)				XX
<i>E. caudatus</i> Thomson			XX	X
Tachinidae				
<i>Billaea adelpha</i> (Loew)		X		
<i>B. irrorata</i> (Meigen)				XX
<i>Pales pumicata</i> (Meigen)			(X)	
<i>Triarthria setipennis</i> (Fallén)				X
Calliphoridae				
<i>Rhinophora lepida</i> Meigen				(X)

¹ 1: Aubert (1969); 2: Brammanis (1963); 3: Delplanque (1998); 4: Georgiev (2001); 5: Hellrigl (1974); 6: Herting (1973); 7: Noyes (2001); 8: Postner (1954); 9: Pulkkinen and Yang (1984); 10: Schnaiderova (1961); 11: Schnaiderova (1968); 12: Slama (1998); 13: Smith *et al.* (2003); 14: Srot (1983); 15: Strojny and Czaplicka (1975); 16: Tobias (1986); 17: Tsankov and Georgiev (1991); 18: Tschorsnig and Herting (1994)

Steinernema spp. and *Heterorhabditis* spp. have been tested against *A. glabripennis*, with some success (e.g. Liu *et al.* 1992). Interestingly, an egg parasitoid, *Aprostocetus* sp. (Hym.: Eulophidae) has been found associated with *A. chinensis* in Italy, and is presently investigated for its biological control potential against *Anoplophora* spp. in North America (Smith *et al.* in press).

3. BUPRESTIDAE

3.1. Conifer feeding species

3.1.1. *Phaenops cyanea*

Parasitoid records for this important pest of pine trunks are rather numerous (Table 3), but only few of them are reliable. The ichneumonid *Xorides depressus*

(Holmgren) is often cited as parasitoid of *P. cyanea* (Aubert 1969; Hilszczanski 2002). It was found associated with mature larvae of *P. cyanea* and *Nothorhina punctata* (F.) (Col.: Cerambycidae) inhabiting Scots pine bark (Hilszczanski 2002). Adults are found on pine trunks infested by *P. cyanea* in September-October (Hilszczanski, unpublished). Filipenkova (1971) mentions three braconid parasitoids in Russia, *Coeloides sordidator* (Ratzeburg) (as *C. melanostigma* Strand), usually associated with weevils of the genus *Pissodes* (Kenis 1997), *Doryctes mutillator* and *Atanycolus genalis* (as *A. initiator*, see Tobias, 1986), the latter two being responsible for up to 80-90% parasitism in Russia, in a pine stand that had recently burned. All other records must be considered with great caution. Some of them are obvious errors, such as the ichneumonid *Poemenia notata*, a well-known parasitoid of sphecids (Hym. Sphecidae) nesting in empty beetle galleries, or the braconid *Ascogaster varipes* Wesmael, which belongs to a genus exclusively associated with Lepidoptera.

Predators have been reported in Russia by Kolomiec and Bogdanova (1980), who observed *Thanasimus formicarius*, *T. rufipes* Brahm. (Col.: Cleridae), *Xylophagus cinctus* (De Geer) (Dipt.: Xylophagidae), *Zabradia minutissima* (Zetterstedt) (Dipt.: Stratiomyidae) and *Lonchaea collini* Hackman (Dipt.: Lonchaeidae) on larvae and *Laphria gilva* (L.). (Dipt. Asilidae) on adults.

3.2. Broadleaf feeding species

3.2.1. *Coraebus undatus* and *C. florentinus*

Nothing is known of the natural enemies of *C. undatus*, whereas knowledge on natural enemies of *C. florentinus* is limited to a single study carried out in Italy by Solinas (1974) who investigated mortality factors at different developmental stages. About 25% of eggs were eaten by unknown predators and about 10% destroyed by an unidentified egg parasitoid. Second and third instar larvae were frequently parasitised by the braconid *Spathius radjabii* Fisher, which has one generation per year and overwinters in a cocoon in the host gallery. Fourth and fifth instar larvae were parasitised at lower intensities by two braconids, an unidentified species of the subfamily Braconinae, and a species tentatively determined as *Bracon maculiger* Wesmael (= *variator* Nees). Finally, last instar larvae were attacked by a large ichneumonid wasp, cited by Solinas (1974) as *Cryptus maculipennis* Dufour, but this name was not found in the most recent ichneumonid nomenclature. It attacks mature instars in early spring in pupal cells and builds a cocoon in which it overwinters. Up to 50% of the *C. florentinus* larvae were parasitised by this ichneumonid, which was considered by Solinas (1974) to be one of the factors causing the collapse of host populations. He mentioned that *C. maculipennis* has also been recorded as a parasitoid of *C. florentinus* in France by De La Perraudière (1902, in Solinas 1974). Solinas also mentions woodpeckers and the wasp *Cerceris bupresticida* Dufour (Hym.: Sphecidae) as predators of larvae and adults, respectively, as well as fungi, bacteria and viruses on larvae, but he does not provide any further details.

Other parasitoids recorded as parasitoids of *C. florentinus* in the literature are the ichneumonid wasp *Rhimphoctona megacephalus* (Gravenhorst), the braconid *Polystenus rugosus* Foester (as *Eucorystes aciculatus* (Reinhard)) (Herting 1973) and the eupelmid *Eusandalum ibericum* (Bolivar & Pieltrain) (Thompson, 1943).

Table 3. Parasitoids of European Buprestidae living in fresh wood. XX = mentioned as reared from the host in a study specifically focused on the host or parasitoid; (XX) = As XX, but parasitoid identification appear doubtful to the authors; X = Record in a catalogue, taxonomic book, host-parasitoid list or from a non-specific study ; (X) As X, but parasitoid identification or host-association appear doubtful to the authors.

	<i>Agrilus angustulus</i>	<i>Agrilus biguttatus</i>	<i>Agrilus populeus</i>	<i>Agrilus viridis</i>	<i>Coraebus florentinus</i>	<i>Melanophila picta</i>	<i>Phaenops cyanea</i>
Main host trees ²	Q	Q	Po	BL	Q, C	Po, S	Pi
Main references ¹	9,11 12	5,7,91 1,12 18,19 20,22	7,12 15	1,4,7,8 9,10 11,12 13,14	2,7,12 17	3,5,7 9,12 16	5,6,7 9,11 12,21 22 21,23
Ichneumonidae							
<i>Atractogaster semisculptus</i> Kriechbaumer						X	
<i>Bathyplectes</i> sp.							(X)
<i>Cryptus maculipennis</i> (Dufour) ³						XX	
<i>Deuterocorides elevator</i> (Panzer) (= <i>albitarsus</i> (Gravenhorst))				XX			
<i>Dolichomitus imperator</i> (Kriechbaumer)				(X)			XX
<i>Dolichomitus</i> sp.							XX
<i>Foersteria puber</i> (Haliday) (= <i>flavipes</i> Szépligeti)					(X)		
<i>Isadelphus gallicola</i> (Bridgman) (= <i>Cecidonomus nigriventris</i> (Thomson))						X	
<i>Poemenia notata</i> Holmgren							(X)
<i>Rhimphoctona megacephala</i> (Gravenhorst)						X	
<i>R. pectoralis</i> Kriechbaumer							(X)
<i>Xorides depressus</i> (Holmgren)							XX
<i>X. irrigator</i> F.							(X)
<i>X. praecatorius</i> (F.)					XX		
<i>Xylophrurus augustus</i> (Dalman) (= <i>dentatus</i> Taschenberg)					(X)		
Braconidae							
<i>Ascogaster varipes</i> Wesmael							(X)
<i>Atanycolus genalis</i> (Thomson) (= <i>initiator</i> F.)							XX
<i>A. ivanowi</i> (Kokujev)						X	
<i>A. neesii</i> (Marshall)		X			XX		X
<i>A. sculpturatus</i> (Thomson)		(X)					
<i>Bracon variator</i> Nees (= <i>maculiger</i> Wesmael)						(XX)	
<i>Coeloides abdominalis</i> (Zetterstedt)							X
<i>C. scolyticida</i> Wesmael					X		
<i>C. sordidator</i> (Ratzeburg) (= <i>melanostigma</i> Strand)							XX
<i>Dimeris</i> (= <i>Pambolus</i>) <i>mira</i> (Ruthe)							(X)

Table 3. (cont.)

	<i>Agrilus angustulus</i>	<i>Agrilus biguttatus</i>	<i>Agrilus populinus</i>	<i>Agrilus viridis</i>	<i>Coracbus florentinus</i>	<i>Melanophila picta</i>	<i>Phaenops cyanea</i>
<i>Doryctes leucogaster</i> (Nees)				(X)			
<i>D. mutillator</i> (Thunberg)		(X)				X	
<i>D. undulatus</i> (Ratzeburg)				(X)			(X)
(= <i>brachyurus</i> Marschall)							
<i>Helcon claviventris</i> Wesmael				(XX)			
<i>Iphiaulax impostor</i> (Scopoli)						XX	
<i>Microgaster globata</i> (L.)				(X)			
<i>Ontsira antica</i> (Wollaston)					X		
<i>O. longicaudis</i> (Giraud)							
<i>Pareucorystes varinervis</i> Tobias					X		
<i>Polystenus rugosus</i> Förster				XX		X	
(= <i>Eucorystes aciculatus</i> (Reinhard))							
<i>Spathius brevicaudis</i> Ratzeburg					XX		
<i>S. curvicaudis</i> Ratzeburg			XX				(XX)
<i>S. depressus</i> Hedqvist					X		
<i>S. lignarius</i> (Ratzeburg)			X				(X)
<i>S. melanophilae</i> Fisher						X	
<i>S. phymatodis</i> Fisher					X		
<i>S. polonicus</i> Niezabitowski				X			
<i>S. radjabii</i> Fisher						XX	
<i>S. radzayanus</i> Ratzeburg		X			(XX)		
<i>S. rubidus</i> (Rossi)		X					
Undetermined Braconinae						XX	
<u>Eulophidae</u>							
<i>Baryscapus agrilorum</i> (Ratzeburg)		X	XX		XX		
<i>B. hylesini</i> Graham			X				
<i>Entedon ergias</i> Walker					X		
<i>Euderus agrili</i> Boucek			XX		X		
<i>Quadrastichus misellus</i> (Delucchi)					XX		
<i>Tetrastichus heeringi</i> Delucchi					XX		
<i>T. murcia</i> (Walker)					X		
(= <i>trichops</i> Thomson)							
<u>Eupelmidae</u>							
<i>Calosota vernalis</i> Curtis					(XX)		
<i>C. aestivalis</i> Curtis					X		
<i>Eusandalum elongatum</i> (Ruschka)							(X)
<i>E. ibericum</i> Bolivar & Pieltrain						X	
<i>E. walkeri</i> (Curtis)	X						
<u>Pteromalidae</u>							
<i>Aggelma agrili</i> Boucek					X		
<i>Aggelma spiracularis</i> (Thomson)							(X)
<i>Agrilocida ferrierei</i> Steffan		X					
<i>Apelioma pteromalimum</i> (Thomson)							(X)
<i>Heydenia pretiosa</i> Förster							(X)
<i>Oodera formosa</i> (Giraud)			XX		X		
<i>Rhopalicus guttatus</i> (Ratzeburg)					(X)		
<i>Trichomalus</i> sp.					X		

Table 3. (cont.)

	<i>Agrilus angustulus</i>	<i>Agrilus biguttatus</i>	<i>Agrilus populi</i>	<i>Agrilus viridis</i>	<i>Coreobius florentinus</i>	<i>Melanophila picta</i>	<i>Phaenops cyanea</i>
<i>Trigonoderus cyanescens</i> Förster							(X)
<u>Encyrtidae</u>					X		
<i>Ooibius zahaikewitshi</i> Trjapitzin							
<u>Chalcididae</u>							
<i>Cratocentrus fastuosus</i> Masi						X	
<u>Tachinidae</u>							
<i>Freraea gagatea</i> Robineau-Desvoidy (= <i>Gymnophania nigripennis</i> B. & B.)				XX			

¹ References: 1: Schimitschek (1935); 2: Thompson (1943); 3: Fisher (1966); 4 Schimitschek (1967); 5: Aubert (1968); 6: Filippenkova (1971); 7: Herting (1973); 8: Kolomiec and Bogdanova; 9: Tobias, 1986; 10: Tschorsnig and Herting (1994); 11: Hedqvist (1998); 12: Noyes (2001); 13 Kamp (1952); 14: Heering (1957); 15: Arru (1962); 16 : Kailidis (1968); 17 : Solinas (1974); 18: Shaw (1988); 19: Moraal and Hilszczanski (2000); 20: Moraal and van Achterberg (2001); 21: Hilszczanski (2002); 22: Hilszczanski (unpublished); 23 : Schimitschek (1964).

²Q = *Quercus*; Po = *Populus*; BL = Broadleaves; C = *Castaneus*; S = *Salix*; Pi = *Pinus*

³Probably *Chirotica maculipennis* (Gravenhorst)

R. megacephala is a parasitoid usually associated with Cerambycidae in conifer trunks, and *E. aciculatus* is a well-known parasitoid of *Agrilus viridis* (see below).

3.2.2. *Melanophila picta*

Data on natural enemies of *M. picta* are restricted to a few parasitoid records (Table 3). In Greece, Kailidis (1968) reared three larval parasitoids, the ichneumonid *Dolichomitus* sp. and the braconids *Iphiaulax impostor* and *Spathius curvicaudis* Ratzeburg, with parasitism rates of 12, 13 and 25% respectively at one sample site, and no parasitism at a second site. But no details on their biology were provided. Another reliable record is the braconid *Spathius melanophilae* Fisher, which was first described from specimens emerged from *M. picta* in Spain (Fisher 1966). Other records include the ichneumonid *Atractogaster semisculptus* Kriechbaumer (Aubert 1969), which is probably a hyperparasitoid, the braconid *Atanycolus ivanowi* (Kokujev) in Russia (Tobias 1986), and the Chalcididae *Cratocentrus fastuosus* Masi, in Morocco (Herting 1973). The only mention of predators is in Kailidis (1968) who observed the green woodpecker *Picus viridis* feeding on larvae.

3.2.3. *Agrilus angustulus*

A. angustulus is the least studied species of the four *Agrilus* spp. treated in this review. However, it should be noted that misidentifications are frequent in *Agrilus* spp. in Europe, especially at the larval stage, and many records of *A. viridis* and *A. biguttatus*, the two most common species, may actually refer to other species.

Only three parasitoid records were found for *A. angustulus* (Table 3), without any information on biology or abundance. The braconid *Spathius rubidus* (Rossi)

(Tobias 1986; Hedqvist 1998) is a polyphagous species attacking mainly Anobiidae and Buprestidae larvae (Hedqvist 1998), sometimes also recorded from Curculionidae (Kenis and Mills 1994). The pteromalid *Agrilocida ferrierei* Steffan was described from one male emerged from a log containing *A. angustulus*. Since then, it has been reared from *Scolytus multistriatus* Marsham (Col.: Scolytidae) in Israël (Mendel 1986) and from *Anthaxia* sp. (Col.: Buprestidae) in Turkey (J. Hilszczanski, unpublished). Finally, the Eupelmid *Eusandalum walkeri* (Curtis) is known only from *A. angustulus* (Noyes 2001).

3.2.4. *Agrilus biguttatus*

The most frequently cited natural enemy of *A. biguttatus* is the braconid larval parasitoid *Spathius curvicaudis* (e.g. Shaw 1988; Hedqvist 1998; Moraal and Hilszczanski 2000; Moraal and van Achterberg 2001). *S. curvicaudis* is a gregarious parasitoid of mature larvae, with up to 14 cocoons developing on a host larva (Shaw 1988). Moraal and van Achterberg (2001) found a parasitised host larva in the overwintering cavity in the bark in the summer, whereas healthy larvae usually reach the bark only in autumn. They speculate that *S. curvicaudis* induces the larva to bore through the bark earlier, to allow easier emergence of the adult parasitoid.

Another reliable parasitoid record for *A. biguttatus* is *Deuterroxorides elevator* (Panzer) which has been reared from a larval gallery of *A. biguttatus* (J. Hilszczanski, unpublished), and is a parasitoid associated mainly with wood-boring beetles infesting oak logs. Other records listed in Table 3 are less reliable. However, some of them are also recorded from other *Agrilus* spp. and could equally attack *A. biguttatus*. *Spathius rubidus* is also mentioned as a parasitoid of *A. angustulus*. Another braconid, *Atanycolus neesi* is a well-known parasitoid of *A. viridis*, and the euplid *Baryscapus agrilorum* (Ratzeburg) is also known from *A. populneus*.

Predators of *A. biguttatus* have never been studied in detail. Moraal and Hilszczanski (2000) mention woodpeckers and Herting (1973) lists the clerid beetle *Thanasimus formicarius*.

3.2.5. *Agrilus populneus*

A single study (Arru 1962) on *A. populneus* includes data on natural enemies. He mentions four parasitoids of *A. populneus* in Italy. The braconid *Spathius polonicus* Niezabitowski, for which no other host is known, the pteromalid *Oodera formosa* (Giraud), and the two euplids *Euderus agrili* Boucek and *Baryscapus agrilorum*, three species known from other *Agrilus* spp. (Noyes 2001). *B. agrilorum*, a gregarious species with up to 16 individuals per brood, was by far the most abundant species. It had one generation per year and was well synchronized with its host. Arru (1962) considered that parasitism was not an important mortality factor, but he did not provide any level of parasitism. In addition, Noyes (2001) lists another euplid, *Baryscapus hylesini* Graham, as a parasitoid of *A. populneus*, and Arru (1962) mentions woodpeckers as predators on larvae and pupae.

3.2.6. *Agrilus viridis*

This species is by far the most studied buprestid in Europe. Several studies have focused on its life history, of which a few included investigations on its natural enemy complex. Consequently, a substantial number of parasitoid records have been found in the literature (Table 3). However, it is possible that some of these records refer to other *Agrilus* spp. because identifying *Agrilus* spp. is difficult and forest entomologists tend to use the name *A. viridis* when the identity is uncertain.

The two most complete studies on mortality factors in *A. viridis* populations have been carried out in Germany by Kamp (1952) and Heering (1957). Most details are provided for parasitoids, but predators are also mentioned. Kamp (1952) mentions substantial rates of larval parasitism (from 11 to 67%) whereas Heering (1957) observed lower rates (6.5% on average, but variations from 0 to 95% from site to site). In Heering (1957), about 95% of all parasitoids reared from *A. viridis* belonged to three eupelphid species, *Tetrastichus heeringi* Delucchi (50%), *Baryscapus* (as *Tetrastichus*) *agrilorum* (35%) and *Quadrastichus* (as *Tetrastichus*) *misellus* (Delucchi) (10%). Kamp (1952) found *B. agrilorum* and a *Tetrastichus* sp., which could be *T. heeringi*. These eupelphid wasps are gregarious ectoparasitoids of larvae in galleries, with up to 28 specimens per host larva (average 3 to 5), but Kamp (1952) also observed egg parasitism by *Tetrastichus* sp. Egg parasitism was about 3 to 4%. Other larval parasitoids reared from *A. viridis* in Germany include the braconids *Atanycolus neesi*, *Polystenus rugosus* (as *Eucorystes aciculatus*), *Spathius brevicaudis* Ratzeburg, *S. radzayanus* Ratzeburg (identity doubtful) and the ichneumonid *Xorides praecatorius*, also reared by J. Hilszczanski (2002) in Poland. *Doryctes undulatus* (Ratzeburg) has been reported as parasitoid of *A. viridis* in Russia (Kolomiec and Bogdanova 1980). Kamp (1952) and Heering (1957) also reared the eupelmid *Calosota vernalis* Curtis (likely a misidentification for *C. aestivalis* Curtis), probably a hyperparasitoid through braconid cocoons. In addition, Kamp (1952) reared the tachinid fly *Freraea gagatea* Robineau-Desvoidy (as *Gymnophania nigripennis* B. B.) in larval galleries of *A. viridis*. *F. gagatea* is known as a parasitoid of carabid beetles (Tschorasnig and Herting 1994). The other parasitoid records listed in Table 3 are less reliable, or undoubtedly wrong, such as *Microgaster globatus* (L.), a parasitoid belonging to the braconid sub-family Microgastrinae, which only includes parasitoids associated with Lepidoptera.

Kamp (1952) and Heering (1957) also mention observations of predators. Kamps (1952) cites birds (woodpeckers and nuthatch), *Lonchaea chorea* (F.) (Dipt.: Lonchaeidae), and *Lasius niger* (L.) (Hym.: Formicidae) feeding on larvae and pupae. He also found in larval galleries the clerid beetle *Thanasimus formicarius* and *Rhaphidia* sp. (Neur.: Rhaphididae). Heering (1957) observed woodpeckers feeding on larvae, and tits and nuthatches picking eggs. He also suggested slugs as egg predators. Among insects, Asilidae (Diptera) were observed preying on adults. Eggs were eaten by the ant *L. niger* and, to a lesser extend, by the clerid *T. formicarius* and *Tomoxia biguttata* Gyllenhal (Col.: Mordellidae).

4. CONCLUSIONS AND FUTURE RESEARCH

The knowledge of natural enemies of cerambycid and buprestid pests in Europe varies with species and regions. Some species such as *Saperda* spp., *Tetropium* spp. and *Agrilus viridis* have been relatively well covered whereas most other species have been very poorly studied. This discrepancy is only partly explained by the relative importance of the pest species in forestry. Traditionally, applied forest entomology was more developed in central and northern Europe than in southern Europe, and it is not surprising that very little is known of natural enemies of species occurring more typically in southern Europe, such as *Cerambyx velutinus*, *Monochamus galloprovincialis*, *Coraebus* spp., etc. Until recently, these pests were considered of minor importance in forestry. However, the importance of *M. galloprovincialis* is likely to increase because it is considered to be the main vector of the newly introduced pine wood nematode in Portugal, and new control methods will have to be developed, including those involving natural enemies.

Even the most complete studies on natural enemies of cerambycid and buprestid beetles in Europe are usually restricted to the description of larval parasitism. Egg and adult parasitism, as well as predators and pathogens, have been largely neglected. Obviously, forest management would benefit from a better knowledge of natural enemies. Firstly, a quantification of the impact of natural enemies is desirable, e.g. through life tables and population dynamics studies, to understand the absolute and relative importance of natural enemies, as well as their variation in time and space. Then, a better knowledge of the influence of environmental factors on natural enemies and parasitism should allow the development of cultural practices that would enhance their impacts. These studies should be made at ecosystem level rather than at pest level. For example, cerambycids and buprestids attacking living or freshly cut trees share part of their natural enemy complexes with other xylophagous beetles living in dead wood. Thus, it is likely that management methods related to logging waste and dead wood removal will have an influence on the population dynamics of the target pests.

Wood-boring beetles are particularly prone to introduction and establishment into new regions, as shown by the recent introductions of *Anoplophora* spp. and *Phoracantha semipunctata* in various parts of the world, of *T. fuscum* in Canada (Smith and Hurley 2000), and of the emerald ash borer, *Agrilus planipennis* Fairmaire, an Asian species, in the USA (McCullough and Roberts 2002). These examples also show that, in their new environment, insects often become more damaging than in their region of origin. Beetles enter new countries in logs, nursery stock and, especially, solid wood packing material, such as pallets, crating or packing blocks. Considering the continuous increase in world trade, Europe will probably face new introductions in the near future, and, at the same time, European beetles will become invasive elsewhere. Therefore, improved international collaboration is desirable, firstly to develop quarantine and containment methods and, secondly, to build up collaborative research programmes on sustainable control methods, including a better knowledge of natural enemies, for biological control purposes.

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6. REFERENCES

- Achterberg, C. van 1987. Revision of the European Helconini (hymenoptera : Braconidae : Helconidae). *Zoologische Mededelingen*, 61, 263-85.
- Arru, G.M. 1962. *Agrius sutorovi populneus* Schaefer (Coleoptera: Buprestidae) dannoso ai Pioppi nell'Italia settentrionale. *Bollettino di Zoologia Agraria e Bachicoltura*, Sr. II, 4, 159-287.
- Arru, G. M. 1972. Sopravvivenza di *Euderus caudatus* Thom. (Chalcidoidea Eulophidae), endoparassita oofago di *Saperda carcharias* L. (Coleoptera Cerambycidae), ai trattamenti contro le larve neonate della vittima. *Bollettino di Zoologia Agraria e Bachicoltura*, 11, 1-10,
- Aubert, J.F. 1969. *Les Ichneumonides Ouest-Palearctiques et leur Hôtes, I. Pimplinae, Xoridinae, Acaenitinae*. Alfortville, France: Quatres Feuilles Editeur.
- Austin, A.D., Quicke, D.L.J., & Marsh, P.M. 1994. The hymenopterous parasitoids of eucalypt longicorn beetles, *Phoracantha* spp. (Coleoptera : Cerambycidae) in Australia. *Bulletin of Entomological Research*, 84, 145-74.
- Brammanis, L. 1963. Zur Vorkommen und zur Bekämpfung des kleinen Aspenbockes *Saperda populnea* L. in Schweden. *Zeitschrift für Angewandte Entomologie*, 51, 122-29.
- Campadelli, G. & Dindo, M.L. 1994. *Monochamus galloprovincialis* (Oliv.) (Coleoptera Cerambycidae) nella Pineta di S. vitale. *Informatore Fitopatologico*, 44, 31-34.
- Capek, M. 1985. The braconids (Hymenoptera, Braconidae) as parasitoids of forest insect pests. *Lesnický Casopis*, 31, 199-212 (in Czech).
- Chrystal, R.N. & Skinner, E.R. 1931. Studies in the biology of *Xylonomus brachylabris* Kr. and *X. irrigator* F., parasites of the larch longhorn beetle, *Tetropium gabrieli* Weise. *Forestry*, 5, 21-33.
- Colombo, M. & Limonta, L. 2001. *Anoplophora malasiaca* Thomson (Coleoptera Cerambycidae Lamiinae Lamiini) in Europe. *Bollettino di Zoologia Agraria e di Bachicoltura*, 33, 65-68
- Dominik, J. 1958. *Criocephalus rusticus* biology, damage prevention and control. *Folia Forestalia Polonica* (Lesnictwo), 1, 45-127 (in Polish).
- Fan, M. Z., Guo, C. & Li, N. C. 1990. Application of *Metarrhizium anisopliae* against forest pests. In. *Proceedings and Abstracts, 7th International Colloquium on Invertebrate Pathology and Microbial Control*. Adelaide, Australia, 20-24 August 1990.
- Filippenkova, V.V. 1971. Parasites of stem pests of pine in forests of the Middle Volga. *Entomologicheskoe Obozrenie*, 50, 763-69 (in Russian).
- Fisher, M. 1966. Studien über Braconiden (Hymenoptera). *Zeitschrift für Angewandte Entomologie*, 53, 215-36.
- Fitton, M.G., Shaw, M.R. & and Gauld, I.D. 1988. Pimpline Ichneumon-Flies. Hymenoptera, Ichneumonidae (pimplinae). Handbooks for the Identification of British Insects, 7, 1-110.
- Fraval, A. & Haddan, M. 1988. *Platistasis transversus* (Hym.: Platygasteridae) parasitoïde oophage de *Phoracantha semipunctata* (Col.: Cerymbycidae) au Maroc. *Entomophaga*, 33, 381-82.
- Georgiev, G. 2001 Parasitoids of *Saperda populnea* (L.) (Coleoptera : Cerambycidae) on aspen (*Populus tremula* L.) in Bulgaria. *Anzeiger für Schädlingskunde*, 74, 155-58.
- Gorijs, U. 1956. Untersuchungen über den Lärchenbock, *Tetropium gabrieli* Weise, mit besonderer Berücksichtigung seines Massenwechsel. *Zeitschrift für Angewandte Entomologie*, 38, 157-205.
- Haddan, M., Fraval, A. & Thevenot, M. 1988. Ennemis naturels de *Phoracantha semipunctata* (F.) (Col., Cerambycidae), ravageur xyloophage des eucalyptus au Maroc. *Bulletin de l'Institut Scientifique, Université Mohammed V*, 12, 167-70.
- Hanks, L.M., Paine, T.D. & Millar, J.G. 1996. Tiny wasp helps protect eucalypts from eucalyptus longhorned borer. *California Agriculture*, 50, 14-16.
- Hedqvist, K.J. 1967. Note on Helconini (Ichneumonoidea, Braconidae, Helconidae). Part 1. *Entomologisk Tidskrift*, 88, 133-43.

- Hedqvist, K.J. 1998. Bark beetle enemies in Sweden 2. Braconidae (Hymenoptera). Entomologica Scandinavica, Supplement 52, 1-86.
- Heering, H. 1957. Zur Biologie, Ökologie und zum Massenwechsel des Buchenpracht-Käfers (*Agrilus viridis* L.) II. Teil. Zeitschrift für Angewandte Entomologie, 39, 76-114.
- Hellrigl, K. 1974. Cerambycidae, Bockkäfer. In. *Die Forstsäädlinge Europas, 2 Band*. W. Schwenke, (Ed.). Hamburg and Berlin: Paul Parey.
- Hellrigl, K. 1985. Über Parasitierung und Farbformen des Lärchenbockes *Tetropium gabrieli* Weise (Col., Cerambycidae) in Südtirol. Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz, 58, 88-90.
- Herting, B. 1973. *a Catalogue of parasites and predators of terrestrial arthropods, Section A, Volume III, Coleoptera to Strepsiptera*. Farnham Royal, UK: Commonwealth Agricultural Bureaux.
- Hilszczanski, J. 2002. Polish xoridines and their host associations (Hym., Ichneumonidae, Xoridinae). In. *Proceedings of the Conference "Parasitic wasps: Evolution, Systematics, Biodiversity and Biological Control"*. 17-17 May 2001. G. Melika and C. Thuroszy (Eds.) Köszeg, Hungary : Agroinform Kiado es Nyomda.
- Juutinen, P. 1955. Zur Biologie und forstlichen Bedeutung der Fichtenböcke (*Tetropium Kirby*) in Finnland. Acta Entomologica Fennica, 11, 1-112.
- Kailidis, D.S. 1964. Beobachtungen über Pappelschädlinge in Griechenland. Anzeiger für Schädlingskunde und Pflanzenschutz, 37, 66-68
- Kailidis, D.S. 1968. Beobachtungen über zwei Pappelschädlinge in Griechenland. Anzeiger für Schädlingskunde und Pflanzenschutz, 41, 38-41.
- Kamp, H.J. 1952. Zur Biologie, Epidemiologie und Bekämpfung des Buchenprachtkäfers (*Agrilus viridis* L.). Mitteilungen der Württembergischen Forstlichen Versuchsanstalt, 9, 1-42.
- Kenis, M. 1997. Biology of *Coeloides sordidator* (Hymenoptera : Braconidae), a possible candidate for introduction against *Pissodes strobi* (Coleoptera : Curculionidae) in North America. Biocontrol Science and Technology, 7, 157-64.
- Kenis, M. & Mills, N.J. 1994. Parasitoids of European species of the genus *Pissodes* (Coleoptera: Curculionidae) and their potential for biological control of *Pissodes strobi* (Peck) in Canada. Biological control, 4, 14-21.
- Kinelski, S. 1971. Parasites of Cerambycidae and Siricidae in the SGGW experimental forests at Rogow. Zeszyty Naukowe Szkoły Gospodarstwa Wiejskiego Warszawa (Lesnictwo), 16, 137-53 (in Polish).
- Kolomic, N.G. & Bogdanova, D.A. 1980. *Parasites and Predators of Wood Borers of Siberia*. Novosibirsk, USSR: Nauka. (in Russian).
- Krehan, H. 2002. Asian Longhorned beetle in Austria: Critical comments on phytosanitary measures and regulations. In. *Proceedings U.S. Department of Agriculture Interagency Research Forum on Gypsy Moth and other Invasive Species, 2002*. S.L.C. Fosbroke and K.W. Gottschalk (Eds.). USDA General Technical Report NE-300.
- Liu, S.R., Zhu, C.X. & Lu, X.P. 1992. Field trials of controlling several cerambycid larvae with entomopathogenic nematodes. Chinese Journal of Biological Control, 8, 176.
- Mansilla-Vazquez, P., Perez-Otero, R., Ruiz-Fernandez, F., & Salinero-Corral, C. 1999. *Avetianella longoi* Siscaro, parasito de huevos de *Phoracantha semipunctata* F.: primera cita de su presencia en Espana y bases para la puesta en practica del control biológico del xilofago. Boletín de Sanidad Vegetal, Plagas, 25, 515-22.
- McCullough, D.G. & Roberts, D.L. 2002. *Emerald Ash Borer*. USDA Forest Service Pest Alert NA-PR-07-02.
- Martikainen, P. & Koponen, M. 2001. *Meteorus corax* Marschall, 1898 (Hymenoptera : Braconidae), a new species to Finland and Russian Karelia, with an overview of Northern species of *Meteorus* parasitizing beetles. Entomologica Fennica, 12, 169-72.
- Mendel, Z. 1986. Hymenopterous parasitoids of bark beetles (Scolytidae) in Israël: host relation, host plant, abundance and seasonal history. Entomophaga, 31, 113-25.
- Millar, J.G., Paine, T.D., Campbell, C.D. & Hanks, L.M. 2002. Methods for rearing *Syngaster lepidus* and *Jarra phoracantha* (Hymenoptera: Braconidae), larval parasitoids of the phloem-colonizing longhorned beetles *Phoracantha semipunctata* and *P. recurva* (Coleoptera: Cerambycidae). Bulletin of Entomological Research, 92, 141-46.
- Moraal, L.G. & van Achterberg, C. 2001. *Spathius curvicaudis* (Hymenoptera: Braconidae) new for the Netherlands; a parasitoid of the oak buprestid beetle, *Agrilus biguttatus* (Coleoptera: Buprestidae). Entomologische Berichten (Amsterdam), 61, 165-68.

- Moraal, L.G. & Hilszczanski, J. 2000. The oak buprestid beetle, *Agrilus biguttatus* (F.) (Col., Buprestidae), a recent factor in oak decline in Europe. *Journal of Pest Science*, 73, 134-38.
- Noyes, J.S. 2001. *Interactice Catalogue of World Chalcidoidea 2001*. CD Rom. Taxapad, Vancouver, Canada.
- Postner, M. 1954. Zur Biologie und Bekämpfung des kleinen Pappelbockes *Saperda populnea* L. (Cerambycidae). *Zeitschrift für Angewandte Entomologie*, 36, 156-77.
- Pulkkinen, M. & Yang, Z.-Q. 1984. The parasitoids and Predators of *Saperda populnea* (Linnaeus) (Coleoptera, Cerambycidae) in Finland. *Annales Entomologici Fennici*, 50, 7-12.
- Scheidter, F. 1917. Über die Eiablage von *Saperda populnea* L. *Naturwissenschaftliche Zeitschrift für Land- und Forstwirtschaft*, 15, 113-38.
- Schimitschek, E. 1929. *Tetropium gabrieli* Weise und *Tetropium fuscum* L. Ein Beitrag zu ihrer Lebensgeschichte und Lebensgemeinschaft.. *Zeitschrift für Angewandte Entomologie*, 15, 231-334.
- Schimitschek, E. 1935. Ergebnisse von Parasitenzuchten. *Zeitschrift für Angewandte Entomologie*, 22, 558-64.
- Schimitschek, E. 1964. Liste der 1934-1936 und 1940-1953 gezogenen Parasiten und ihrer Wirte. *Zeitschrift für Angewandte Entomologie*, 53, 320-41.
- Schimitschek, E. 1967. Parasitenzuchtergebnisse 1961 bis 1965. *Zeitschrift für Angewandte Entomologie*, 59, 64-73.
- Schnaiderowa, J. 1961. Economic importance and control of *S. carcharias* L. (Cerambycidae, Coleoptera). Prace Instytutu Badawczego Lesnictwa, 234, 3-99 (in Polish).
- Schnaiderowa, J. 1968. Reasons for the outbreak of *Saperda carcharias* and *S. populnea* in Poland. Prace Instytutu Badawczego Lesnictwa, 355, 3-90 (in Polish).
- Shaw, M.R. 1988. *Spathius curvicaudis* Ratzeburg (Hym.: Braconidae) new to Britain and parasitising *Agrilus pannonicus* (Piller and Mitterpacher) (Col.: Buprestidae). *Entomological Records*, 100, 215-16.
- Siscaro, G. 1992. *Avetianella longoi* sp. n. (Hymenoptera Encyrtidae) egg parasitoid of *Phoracantha semipunctata* F. (Coleoptera Cerambycidae). *Bollettino di Zoologia Agraria e di Bachicoltura Sr. II*, 24, 205-12.
- Skrzypczynska, M. & Krol, A. 1974. Secondary insect pests of Eurasian Larches in the IUFRO plantation at Kolanow near Krakow. *Acta Agraria et Silvestria, Series Silvestris*, 14, 123-33.
- Slama, M. 1998. *Longhorn beetles Cerambycidae of Czech and Slovak Republics*. Czech Republic: Tercie (publ.) (in Czech).
- Smith, G. & Hurley, J. 2000. First North American record of the Palearctic species *Tetropium fuscum* (Fabricius) (Coleoptera: Cerambycidae). *Coleopterists Bulletin*, 54, 540.
- Smith, M. T., Yang, Z.Q., Hérard, F., Fuester, R., Bauer, L., Solter, L., Keena, M. & D'Amico, V. 2002. Biological control of *Anoplophora glabripennis* (Motsch.): A synthesis of current research programs. In: *Proceedings U.S. Department of Agriculture Interagency Research Forum on Gypsy Moth and other Invasive Species*, 2002. S.L.C. Fosbroke & K.W. Gottschalk (Eds.). USDA General Technical Report NE-300.
- Smith, M.T., Fuester, R., Hérard, F. and Hanks, L. in press. Prospects for inundative release of natural enemies for biological control of *Anoplophora glabripennis*. In: *Proceedings U.S. Department of Agriculture Interagency Research Forum on Gypsy Moth and other Invasive Species*, 2003. K.W. Gottschalk (Ed.). USDA General Technical Report.
- Solinas, M. 1974. *Coroebus florentinus* (Herbst) (Coleoptera, Buprestidae). *Biologia, danni, lotta Entomologica*, 10, 141-93.
- Sousa, E., Bravo, M.A., Pires, J., Naves, P., Penas, A.C., Bonifacio, L. & Mota, M.M. 2001. *Bursaphelenchus xylophilus* (Nematoda; Aphelenchoididae) associated with *Monochamus galloprovincialis* (Coleoptera; Cerambycidae) in Portugal. *Nematology*, 3, 89-91.
- Srot, M. 1983. Factors reducing the population density of the large poplar borer (*Saperda carcharias* L.). *Lesnictvi*, 29, 785-804 (in Czech).
- Strojny, W. & Czaplicka H. 1975. Niektóre problemy z biologii rzemlika osikowca, *Saperda populnea* (L.) (Coleoptera, Cerambycidae). *Przeglad Zoologiczny*, 19, 309-21.
- Thompson, W.R. 1943. *A catalogue of the parasites and predators of insect pests. Section 1 Parasite host catalogue. Part 1 Parasites of the Arachnida and Coleoptera*. Belleville, Canada: Imperial Parasite Service.
- Tobias, V.I. 1986. *Keys to the Fauna of the European USSR. Vol. III, Part V. Hymenoptera, Braconidae*. Leningrad: Nauka Publishers. Translation: 1997. New Dehli: Oxonian Press.

- Tomminen, J. 1993. Development of *Monochamus galloprovincialis* Olivier (Coleoptera, Cerambycidae) in cut trees of young pines (*Pinus sylvestris* L.) and log bolts in southern Finland. Entomologica Fennica, 4, 137-42.
- Tsankov, G. & Georgiev, G. 1991. Records on parasitoids of smaller poplar borer, *Saperda populnea* (Coleoptera, Cerambycidae) along the Danube in Bulgaria. Entomophaga, 36, 493-98.
- Tschorsnig, H.-P. & Herting, B. 1994. Die Raupenfliegen (Diptera: Tachinidae) Mitteleuropas: Bestimmungstabellen und Angaben zur Verbreitung und Ökologie der Einzelnen Arten. Stuttgarter Beiträge zur Naturkunde Serie A (Biologie), 506, 1-170.
- Way, M.J., Cammel, M.E. & Paiva, M.R. 1992. Studies on egg predation by ants (Hymenoptera: Formicidae) especially on the eucalyptus borer *Phoracantha semipunctata* (Coleoptera: Cerambycidae). Bulletin of Entomological Research, 82, 425-32.
- Wettstein, O. 1951. Über eine Zucht von *Tetropium fuscum*. Mitteilungen der Fortslichen Bundes-Versuchsanstalt, Mariabrunn, 47, 42-69.
- Wiackowski, S. 1957. Results of rearing parasites of forest insects. Part I. Polski Pismo Entomologiczne, 26, 311-20.
- Wichmann, H.E. 1956. Untersuchungen über *Ips typographus* L. und seine Umwelt. Asilidae, Raubfliegen. Zeitschrift für Angewandte Entomologie, 39, 58-62.

Part 4

“Non-Coleopteran”
BAWBILT organisms

Chapter 22

“NON-COLEOPTERAN INSECTS”

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1. INTRODUCTION

B. Långström

By definition the BAWBILT concept includes all insect species that attack and damage the main stem of living trees. Apart from beetles, which are dealt with in parts 1-3, there is a number of xylophagous species in other insect orders that are part of the BAWBILT community. Some of these are listed in the damage & control database, but as a result of their unclear or variable pest status, reporting to the database is inconsistent and incomplete (table 1). There are also some species related to the listed ones that could and perhaps should have been included, but since no country has done so they are not there.

Despite the few records in the database, it is easy to conclude that these "non-coleopteran pests" are of much less importance in Europe than e.g. bark beetles and pine weevils. Hence, these species do not deserve the same attention as the economically important ones, but totally ignoring them would result in an incomplete BAWBILT synthesis. Furthermore, a few of these species have become major pests in other parts of the world after accidental introduction to new

continents. Thus, a selected number of representatives of these very different pest categories are treated in this chapter.

Table 1. Aggressiveness and extention of non-coleopteran" BAWBILT pests according to the reported information in the damage & control database

Country	Rhy buo	Dio spl	Cos cos	Zeu pyr	Par tab	Ses api	Syn myo	Sir cya	Sir juv	Uro gig	Ara cin	Phy bet
Bel			*/*	*/*			*/*	*/*	*/*	*/*		
Est	**/**								*/*	*/*	*/*	
Fin											**/**	*
Fra		*/*		*/*								
		**		**								
Hun	***/*			**/	**/	**/	**/					
	**			**	**	**	**					
Ire	***/*			*/								*/*
	**			*/								
Ita		*/*	***/			***/	*/					
		*	**			**	*/					
Lit												*/*
Por		*/*	*/	*/	*/	*/	*/					*/*
Rom	***/*		***/		***	***/	**/					***/
					/*	*	*					*
Slov	*/**		*/			*/						
Spa		*/		*/		*/**	*/					
Net	**/**		**/**			*/						*/**
	*		*									*/**
UK	*/		*/	*/			*/					*/

* , ** or *** = low, medium or high aggressiveness/extention

Bel = Belgium, Est = Estonia, Fin = Finland, Fra = France, Hun = Hungary, Ire = Ireland, Ita = Italy, Lith = Lithuania, Por = Portugal, Rom = Romania, Slo = Slovakia, Spa = Spain, Net = The Netherlands, UK = The United Kingdom

Rhy buo = *Rhyacionia buoliana*, Dio spl = *Dioryctria splendidella*, Cos cos = *Cossus cossus*, Zeu pyr = *Zeuzera pyrina*, Par tab = *Paranthrene tabaniformis*, Ses api = *Sesia apiformis*, Syn myo = *Synanthedon myopaeformis*, Sir cya = *Sirex cyaneus*, Sir juv = *Sirex juvenscens*, Uro gig = *Urocerus gigas*, Ara cin = *Aradus cinnamomeus*, Phy bet = *Phytobia betulae*

From an economic point of view, we are dealing with basically two kinds of problems. Firstly, damage to the leader shoot(s) of growing young trees leads to growth losses and later to reduced timber quality due to stem crooks and internal defects. This kind of damage is mainly caused by larvae of microlepidoptera (see below), but the damage caused by the pine bark bug (*Aradus cinnamomeus*, see below) also belongs to this category. There are also a few sawfly species (like *Nematus ericsoni* on larch and different *Pristiphora* species on spruce and larch) which normally feed on the foliage, but which also may cause this kind of damage, but these are not included here as they were not listed in the database. Shoot damage is also caused by some beetles (*Tomicus* sp, *Saperda populnea* etc), which are treated elsewhere in this volume.

The second type of damage is technical damage to the lower stem of older trees leading to degraded timber value due to feeding tunnels in the wood. Typical examples here are goat moths and clearwings (see below), some longhorn beetles (see part 3) and the very special case with the dipteran *Phytobia betulae* (see below). The siricid wasps (horntails) form a special case of this group, as they are mainly timber pests that occasionally attack living trees (see below). Wood-dwelling ants like the genus *Camponotus* could also be included here, as well as termites in the Mediterranean area, but as they were not listed in the database they are also omitted here.

Among Hemiptera, we have a few species that can be considered BAWBILT insects, and of these *Aradus cinnamomeus* is reported as a pest in the damage & control database. Under certain circumstances the feeding damage of this species may lead to reduced growth and eventually to tree death. Several aphids and scale insects, like *Matsucoccus feytaudi* and *Pineus pini* on pine and *Cryptococcus fagisuga* on beech may cause substantial tree mortality, but none of these was included in the database, and they are hence omitted here.

Among Lepidoptera (moths) we have species belonging to different families causing shoot or stem damage in living trees. The largest and probably most diverse group of species is the one causing damage to terminal shoots and by so dying eventually reducing the timber value by causing external or internal defects. Nearly all conifer species are exposed to this kind of damage but problems of economic importance are reported from pine only. The pine shoot moth (*Rhyacionia buoliana*) is probably the most well known and economically important of the tortricids causing this kind of damage. The species has become established in North America as well, and is known there as the European pine shoot moth. Among related species causing shoot damage in pine that all used to be included in the genus *Evetria*, we have *Petrova resinella*, and *R. pinicolana*. At least in Scandinavia, similar damage can be done by pyralid moths like *Dioryctria mutatella* (and occasionally *D. abietella* in years when spruce cones are scarce). Of these species, only *R. buoliana* was listed in the damage & control database, and hence only this species is included below. There is another *Dioryctria* species, namely *D. sylvestrella*, which deserves attention in this context. This species is causing substantial stem damage to Maritime pine in south-western France by causing stem cancers at the base of the branches where the larva is developing. Similar damage is also done by the tortricid *Laspeyresia pactolana*, and related species, but this damage is presumably of low economic importance.

Among broad-leaved trees, shoot damage in poplars caused by clearwing moths of the family Sesiidae is probably the most common and important pest case. In this context, *Paranthrene tabaniformis* is the principal species although other clearwings may cause similar damage in other hosts. Another clearwing species *Sesia apiformis* causes damage to the lower stem of poplars by tunnelling and destroying the wood. Even better known are the larvae of the goat moth *Cossus cossus* and the leopard moth *Zeuzera pyrina* that commonly tunnel the wood of preferably senescent trees of different broad-leaved species.

Among Hymenoptera, we have the horntails (Siricidae) with the following species listed in the database: *Urocerus gigas*, *Sirex cyaneus* and *Sirex juvencus*. In Europe, they are mainly timber pests (and hence not really BAWBILT species) but they may also attack living trees via mechanical wounds. As the siricids convey pathogenic fungi into the wood, they may cause tree mortality as well. For unknown reasons the globally most important species, *Sirex noctilio*, is not listed in the database. This has been a big problem on radiata pine in Australia and New Zealand where it was accidentally introduced in the beginning of the last century.

Finally, among dipterans we have the peculiar damage caused by *Phytobia betulae* in living birch trees that later shows up as spectacular brown stripes in the veneer cut from birch logs. This is mainly a problem for the Finnish veneer industry.

In conclusion, the following species are selected as the most important organisms representing “non-coleopteran” BAWBILT species:

Hemiptera: *Aradus cinnamomeus*

Lepidoptera: *Rhyacionia buoliana*, *Dioryctria sylvestrella*, *Cossus cossus*, *Zeuzera pyrina*, *Paranthrene tabaniformis*, *Sesia apiformis*

Hymenoptera: Siricidae (*Urocerus gigas*, *Sirex noctilio*, *Paururus juvencus*)

Diptera: *Phytobia betulae*

2. ARADUS CINNAMOMEUS, THE PINE BARK BUG

K. Heliövaara

2.1 Taxonomy and systematics

The flat bugs of the family Aradidae (Heteroptera) constitute a well defined family of the Aradoidea (Gyllensvärd 1964) and contain eight closely related subfamilies. The only economically significant species belongs to the genus *Aradus*, whose members are usually called the bark bugs. Adult pine bark bugs are 3.5–4.5 mm long but only 0.75 mm thick. Adults are brown, but small nymphs are bright red. When disturbed, pine bark bugs secrete a characteristic smell of pear.

2.2 General biology

Aradus cinnamomeus has a two-year life span in most parts of Europe; in northern Europe close to the tree limit, the life span is three years (Brammanis 1975, Heliövaara and Väisänen 1987). Eggs are laid in May, nymphs hatch in June, and reach the fourth instar during the first summer. After hibernation at the base of the tree or in surrounding litter (Brammanis 1975), the bugs become adult in July–August, after which they hibernate. It is not until the following spring that the bugs mate and begin egg-laying (Tropin 1949, Brammanis 1975).

The two-year life span of the pine bark bug has led to periodicity and a unique biogeographical pattern of distribution. In most of Europe, there seem to be two major alternate-year populations that live in different geographical areas (Heliövaara

and Väisänen 1987). For instance, the bugs reproduce in even-numbered years in eastern Finland and eastern Sweden, and in odd-numbered years in western parts of these countries.

2.3 Host finding

Aradus cinnamomeus displays exceptional wing polymorphism. Most females (ca. 97 %) are brachypterous. The proportion of macropterous females is usually 3%, but it may increase as living conditions on the host tree worsen. Males are "stenopterous", i.e., their hemelytra reach almost the tip of the abdomen but are greatly narrowed in their apical three-quarters. Only the few macropterous females can fly. Migration takes place in August on warm, sunny days, just after the final molt.

2.4 Natural enemies

Generally, 25 % of the laid eggs are parasitized by a scelionid wasp, *Telenomus aradi* Kozlov (Heliövaara et al. 1982). Parasitoids of nymphs or adults are not known. Other invertebrate predators include *Raphidia* (Neuroptera) larvae, a bdellid mite *Bdella longicornis* (L.), and spiders such as *Philodromus fuscomarginatus* Degeer, *Clubiona subsultans* Thorell, *Drapetisca socialis* (Sundevall), *Micaria subopaca* Westring, *Salticus cingulatus* (Panzer) and *Moebilia penicillata* (Westring). However, spiders only rarely seem to eat pine bark bugs (Hokkanen et al. 1987).

2.5 Associated organisms

The fungal feeding of aradids has been confirmed repeatedly, with the possible exception of the only economically important species, the pine bark bug *Aradus cinnamomeus* Panzer. This species pushes its stylets into phloem, cambium and xylem tissues of living pine saplings, disturbing their growth. However, it is possible that even this species utilizes some fungi living on pine (Usinger and Matsuda 1959).

2.6 Damage and control

The pine bark bug is a pest of pines. In central and eastern Europe the pine bark bug has long been regarded as a harmful pest of pines. It has caused serious damage, especially in pine stands planted in nitrogen-poor sandy soils in the Ukraine, Byelorussia, Latvia, and Poland (Tropin 1949).

Pine bark bugs live in crevices in the bark of the trunk. Both adults and nymphs suck sap with their highly specialized piercing mouthparts from the young tissues surrounding the cambium, thus disturbing the conduction of fluids in the tree. Presence of the bugs in large numbers causes noticeable growth retardation, yellowing of needles, and withering of the pine (Tropin 1949, Brammanis 1975).

Several chemical and biological methods including systemic insecticides and fungal diseases have been used with variable results in the control of *Aradus cinnamomeus*. The bug seems to be a tenacious species with a high resistance to chemicals, and the results obtained with a wide range of chemicals have not been encouraging. Forest fertilization has been tested as a control method against the pine bark bug, but the results are contradictory. No real progress has yet been achieved in the biological control of the pine bark bug.

Because no single effective method of controlling *Aradus cinnamomeus* is yet available, the use of several prophylactic silvicultural practices probably gives the most favorable results. As the bugs thrive best in warm and light conditions, high stocking densities should be used in pine stands in potential damage areas. The structure of a resistant pine stand should be even and dense without gaps, and heavy early thinnings should be avoided (Brammanis 1975, Hokkanen et al. 1987).

2.7 References

- Brammanis, L. 1975. Die Kiefernrendenwanze, *Aradus cinnamomeus* Panz. (Hemiptera-Heteroptera). Ein Beitrag zur Kenntnis der Lebensweise und der forstlichen Bedeutung. *Studia Forestalia Suecica* 123: 1-81.
- Gyllensvärd N. 1964. A key to Swedish Aradidae (Hem. Het.) with figures of the male genitalia. *Opuscula Entomologica*. 29: 110-116.
- Heliövaara, K., E. Terho, and M. Koponen 1982. Parasitism in the eggs of the pine bark-bug, *Aradus cinnamomeus* (Heteroptera, Aradidae). *Annales Entomologici Fennici*. 48: 31-32.
- Heliövaara, K. & Väistönen, R. 1987. Geographic variation in the life-history of *Aradus cinnamomeus* and a breakdown mechanism of the reproductive isolation of allochronic bugs (Heteroptera, Aradidae). *Annales Zoologici Fennici*. 24: 1-17.
- Hokkanen, T., K. Heliövaara, and R. Väistönen 1987. Control of *Aradus cinnamomeus* (Heteroptera, Aradidae) with special reference to pine stand condition. *Communicationes Instituti Forestalis Fenniae* 142: 1-27.
- Tropin, I. V. 1949. The pine bark bug and its control. Goslesbumizdat, Moscow, 55 pp. (in Russian).
- Usinger, R. L., and R. Matsuda 1959. Classification of the Aradidae (Hemiptera-Heteroptera). British Museum (Natural History), London.

3. RHYACIONIA BUOLIANA, EUROPEAN PINE SHOOT MOTH

M. Turčáni

3.1 Taxonomy & systematics

The European pine shoot moth (*Rhyacionia buoliana* Denis & Schiffermüller, 1775) belongs to the family Tortricidae, subfamily Olethreutinae, genus *Rhyacionia* Hübner, 1813. The species was described as *Tortrix buoliana* by Denis & Schiffermüller in 1775. Other species of the genus are: *R. pinicolana* (Doubleday, 1849), *R. pinivorana* (Lienig & Zeller, 1846), *R. duplana* (Hübner, 1813) and *R. piniana* (Herrich-Schaffer, 1851) which all occur on pine in Europe.

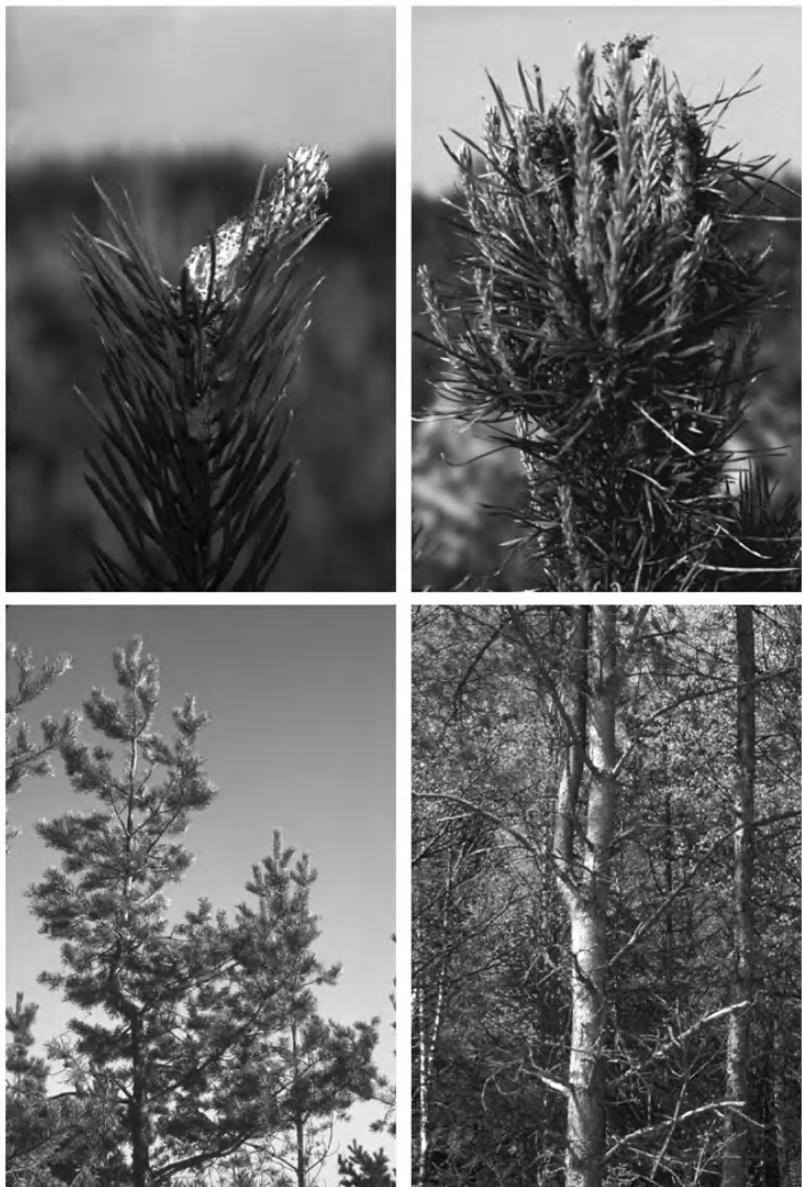


Figure 1. Upper left: current expanding pine shoot attacked by *Rhyacionia buoliana*; upper right: severely stunted pine sapling following several years of repeated attacks by *R. buoliana* in the uppermost shoots; lower left: young pine tree after several years of shoot attacks leading to a lasting bend on the stem; lower right: destroyed timber quality due to attack by *R. buoliana* decades ago (all pictures taken by Bo Långström).

3.2 General biology

The European pine shoot moth occurs throughout Europe and parts of Asia where it is a major pest of pine plantations. It has also been brought to North America in 1914 and later to South America (Chile), where it is a pest on *Pinus radiata* and *P. contorta*.

The damage is done by larvae, which bore in shoot and bud tissue. Adults emerge during June-July, and the moths are active around sunset but usually do not fly during cool or wet days. Air temperatures below 12 °C inhibit flight. Female moths lay eggs on host pines that may be scattered over a large area. Eggs hatch in one to two weeks, and the new larvae begin feeding by mining needles first, and then they move into the buds. The larvae spend the winter under a resin/silk shelter between the buds or in buds. The following spring the larvae continue feeding in the buds or move into the expanding shoots which become tunnelled, distorted and often killed. Attacks frequently occur in young trees (below 30 years of age). All pines are attacked, but *Pinus sylvestris* appears to be especially susceptible. Developing shoots are tunnelled and killed. Pupation occurs in shoots and lasts two to three weeks in late spring. There is only one generation per year.

3.3 Host finding

Little is known about the host finding of this species, but according to Tsankov & Kostov (1985), *R. buoliana* appeared in the third year after plantation establishment, and reached maximum numbers in plantations that were 5-6 years old. Smelyanets (1995) observed that the pest spread from weakened to more resistant groups amongst the pines.

3.4 Host resistance

Generally, pine species that have high resin yields are highly resistant to the *R. buoliana*. In the series *Laricinoes*, *Pinus nigra* is most likely to provide highly resistant material. *Pinus resinosa* has significantly lower resistance than the other pines in the series. According to Turčáni (1988), *Pinus nigra* was significantly more resistant in conditions of central Slovakia in areas influenced by strong air pollution. Infestation of *Pinus sylvestris* buds reached 18.5 to 24.3 %, whereas in *Pinus nigra* only 0.5 to 2.8 % of the buds were attacked. Growth of *P. nigra* was not much affected in spite of the fact, that chronological outbreak of *R. buoliana* occurred there, whereas the attacks caused bushy growth in *P. sylvestris* in these polluted areas.

Smelyanets (1977) considers that the essential oils of pine trees regulate their resistance to *R. buoliana* and act as a protective system warding off infestation. They act through the physiological processes of the insect in the larval stage. Investigations in the Ukraine showed differences in the constitution of the haemolymph of larvae that had fed on trees of different degrees of resistance, as evidenced by different contents of essential oils in the buds. The results of the same author showed that the parameters characterising the level of physiological condition

of the trees and consequently their resistance to insect attack differed widely, particularly the intensity of resin exudation from cut shoots, the resin pressure in the trunks, the content of beta -pinene, limonene and phellandrene in the needles, and the content of camphene and other terpenoids in the shoots (Smelyanets 1978).

A relationship between damage caused by *R. buoliana* and *Blastesthia turionana* and genetic forms of Scots pine with seeds of different colours has also been found (Rostovtsev, 1979). Only 22.9 % of plants of the black/brown seed form were damaged, whereas the corresponding figure was 94.9% for the brown/black seed form. In general, the dark-seeded forms are more resistant to tortricids attack. In field studies conducted in the Ukraine, infestation by *Rhyacionia buoliana* on Scots pine trees produced an immune response (an increase in the concentration of essential oils). However, not all trees in study plots produced high concentrations of essential oils, allowing small populations of *R. buoliana* to survive and act as reservoirs for future outbreaks (Smelyanets 1996).

The influence of the summer climate both on resin production and population increase is important both in Europe and in North America. In drought years the trees produce little resin and are thus unable to repel the shoot moth larvae. Consistently, *R. buoliana* populations are high in areas where the period May to July is dry. Summer temperatures also influence the duration of development from oviposition to the 3rd instar (5-14 weeks). Then in a warm summer, the third instar larvae attack the newly formed buds, whereas in a cool summer the larvae attack after the buds are protected by well-developed resin canals. According Tsankov et al. (1979) considerable differences were found between the provenances of *P. nigra* in their resistance to the insect. The least resistant provenances were of Corsican origin, but these also exhibited rapid rates of growth and may be used for afforestation in areas where wood volume production rather than stem quality is important.

3.5 Natural enemies

Natural enemies play an important role in *R. buoliana* population dynamics. Over 100 parasitoids and predators have been identified worldwide. Important parasitoids are braconids *Glypta resinanae* Htg. and *Scambus brevicornis* Grav. Other larval parasitoids are the braconid *Orgilus obscurator* (Nees), and the ichneumonids *Eulimneria rufifemur* (Thoms.) and *Temelucha interruptor* (Grav.). *T. interruptor* was disclaimed as a cleptoparasitoid detrimental to the potential impact of *O. obscurator* (Tarwacki 1998).

Orgilus obscurator is a specific larval parasitoid with a high fecundity and an efficient host finding ability that permits it to avoid both superparasitism and very low host density situations. In contrast, *T. interruptor* is a more general parasitoid of Microlepidoptera and while it also has a high fecundity it is inefficient at host finding and oviposits most successfully in host larvae previously attacked by *O. obscurator*. Both parasitoids attack young host larvae and only develop further when the host larvae approach maturity.

According to Zerova et al. (1989) there are also some other parasitoids: *Scambus calobatus* (Grav.), *Pimpla turionellae* L., *Lissonota dubia* Hgn. , *Lissonota folii* Thom., *Bracon stabilis* Wesmael, *Meteorus incertus* Nees, *Charmon extensor* L., *Microdus rufipes* Nees, *Apanteles lineipes* Wesmael, *Habrocytus semotus* Walker, *Trichogramma telengai* Sorokina. Tarwacki (1998) mentioned two species of ichneumonid parasitoids (*Pristomerus orbitalis* Hgn. and *Scambus sagax* Htg.) which were reared from larvae and pupae of two tortricids (*R. buoliana* and *Blastesthia turionella*) and one tineid (*Exoteleia dodecella*). The pupa was the most frequently attacked stage. Tsankov (1998) observed that the most common parasitoids of *R. buoliana* on *Pinus nigra* and *P. sylvestris* in Bulgaria were *Exeristes robator* F. and *Campoplex submarginatus* Cresson. Low winter temperatures, below -25 °C, negatively affect the abundance of *Rhyacionia buoliana*, and especially important are periods of low temperatures which follow warm periods, when resistance of overwintering larvae is small. The reduction of abundance is, however, not long-lasting as the abundance usually reaches normal levels in two years.

3.6 Damage and control

The larval feeding results in dead buds and shoots, but damaged terminal shoots often survive although they are badly bent. This leads to reduced growth, but even worse are the lasting stem crooks that destroy the timber value of the butt log. Abundant and repeated attacks lead to bushy trees with no main stem, and it may take years for these trees to eventually recover to normal height growth. Even so, log quality will remain low due to internal timber defects.

Damage is considerable in plantations of Christmas trees or nursery plants, when killed terminals cause bushy growth that may render nursery plants or Christmas trees unmarketable. Forest stands on poor soils, or areas influenced by air pollution are mainly damaged. The highest aggressiveness was recorded in central Europe (Hungary, Romania and Slovakia). Out of this centre, other spots with higher aggressiveness were recorded in Ireland and The Netherlands.

There are three points in the life cycle of *R. buoliana* when insecticides can be effective – migrating larvae (early spring), adults (early summer) and newly hatched larvae (early summer). Accurate timing of insecticide application is critical for satisfactory control. In recent years some success has been achieved with summer applications targeted at adult and young larvae. These applications can be timed with help of pheromone traps. Spraying is done one week after the 1st adults are detected in pheromone traps. Moth activity lasts about 4 weeks.

Ecological prevention has been studied by Rodziewicz & Kolk (1980), who found that intersowing with lupins reduced the numbers of pine buds and shoots damaged by *R. buoliana* by $\frac{2}{3}$. The ability of *Trichogramma dendrolimi*, *T. telengai* (both originating from Bulgaria) and *T. nerudai* (native Chilean species) to parasitize on ova of *Rhyacionia buoliana* (insect pest of *Pinus radiata*) was investigated by Cerdá & Gerding (1999).

Tiberi et al. (1988) investigated the effectiveness of the mating disruption technique for control of *Rhyacionia buoliana*. Based on the results of catches in pheromone traps and percentage infestation, the results from the first year indicated that this method was effective in reducing the population of the tortricid. It is suggested that possible immigration of mated females from neighbouring pine stands might have reduced the effectiveness of the treatment. In 1988, the population of the pest had increased by only 6% in the treated pine stand compared with 38% in the untreated one. In small isolated areas of pine stands surrounded by broadleaf trees mass trapping using pheromone traps (pheromone E9-12Ac + 12Ac 1:1 in dose 1000 µg) with 5-10 m spacing could also be used (Turčáni 1988).

3.7 References

- Cerda R., C. & Gerding P., M. 1999. Biological control of *Rhyacionia buoliana* Den et Schiff (Lepidoptera: Tortricidae) with *Trichogramma* spp. Agro-Ciencia, 15, 279-83.
- Rodziewicz, A. & Kolk, A. 1980. Effect of perennial lupins on the density of *Rhyacionia buoliana* and other insects in young Scots pine plantations. Sylwan, 124, 23-30.
- Rostovtsev, S. A. 1979. Damage by pine shoot moths to forms of Scots pine differing in seed colour. Lesnoe Khozyaistvo, 9, 63-64.
- Smelyanets, V. P. 1977. Mechanisms of plant resistance in pine trees, *Pinus sylvestris*. 1. Indicators of physiological state in interacting plant-insect populations. Zeitschrift fur Angewandte Entomologie, 83, 225-33.
- Smelyanets, V. 1995. Cascade form of process at arising of an aggressive biotype of the winter pine shoot moth (*Rhyacionia buoliana* Schiff., Lepid. Tortr.). 1. Heterogeneity of the main parameters in a pest population and in a protective system of the pine as a base of mechanism of forming of initial aggressive groups of the pest. Archives of Phytopathology and Plant Protection, 29, 317-25.
- Smelyanets, V. 1996. Dynamics of trophical niches of the winter pine shoot moth (*Rhyacionia buoliana* Schiff., Lepidoptera: Tortricidae) and response of the protective system of the Scots pine to the affection. 2. Response of the protective system of the Scots pine to affection by the winter pine shoot moth. Archives of Phytopathology and Plant Protection, 30, 421-28.
- Smelyanets, V. P., Lopatina, N. V. & Koveshnikova, I. V. 1978. Changes in the fat-body and haemolymph of larvae of the pine budworm overwintering after feeding on pine trees differing in resistance. Zakhist Roslin, 24, 95-102.
- Tarwacki, G. 1998. Pine tortricids (Tortricidae) and their parasitoids in the Forest Experimental Department (LZD) at Rogów. Sylwan, 142, 89-95.
- Tiberi, R.; Covassi, M. & Roversi, P. F. 1988. Use of the confusion method against *Rhyacionia buoliana* (Den. et Schiff.) in young pine stands in central Italy (Lepidoptera, Tortricidae). Redia, 71, 356-68.
- Tsankov, G. 1988. The ichneumonoid parasites of the European pine shoot moth caterpillars in Bulgaria (Hymenoptera: Ichneumonoidea). Advances in parasitic Hymenoptera research: Proceedings of the II Conference on the Taxonomy and Biology of Parasitic Hymenoptera, 391-94.
- Tsankov, G.; Kostov & K. D. 1985. Pest-resistance and growth of Scots pine provenances outside their natural range at Rabisha, Belogradchik forest. Gorskostopanska Nauka, 22, 23-30.
- Tsankov, G.; Buchvarov, D. & Kostov, K. D. 1979. The resistance to *Rhyacionia buoliana* of seedlings of *Pinus nigra* of different provenances in the trial plantation at Sirakovo village, Khaskovo region. Gorskostopanska Nauka, 16, 70-80.
- Turčáni, M. 1988: Survey of occurrence and harmless of *Rhyacionia buoliana* in polluted area close to Žiar nad Hronom. Diploma thesis, 1-46.
- Zerova M.D., Seregina L.Ya., Tolcanic V.I. & Kotenko A.G. 1989: The annotated list of entomophagous insect of the *Tortrix viridana* L. (Lepidoptera, Tortricidae) in the south-west of the European part of the USSR. Infomation journal of IOBC – east palaearctic section, p. 18-53.

4. DIORYCTRIA SYLVESTRELLA

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4.1 Taxonomy & systematics

Dioryctria sylvestrella (Ratzeburg 1840) belongs to family Pyralidae, subfamily Phycitinae, genus *Dioryctria* Zeller, 1846. The species was described as *Dioryctria sylvestrella* by Ratzeburg in 1840, but has also been known as *Dioryctria splendidella* (Herrich-Schäffer 1848) which is a junior synonym. Other species of the genus are: *D. abietella* (Dennis et Schiffermuller, 1775), *D. simpliciella* Heinemann, 1863 and *D. schuetzeella* Fuchs, 1899, which cause damage to cones.

4.2 General biology

D.sylvestrella occurs throughout Europe, northern Africa and large part of Asia. It is more common in southern part of the distribution area, where is one of the important pests of pine plantations. In Europe it occurs up to the arctic circle.

This species is feeding on pines (cones, shoots, buds and stems) and less frequently on spruce. It is one of the major pests of Maritime pine (*Pinus pinaster*). Female moths lay eggs on fast growing pine trees, and fertilised or highly productive stands experience severe damage. In central Europe, the species is often found at sites infested by *Endocronartium* (=*Peridermium*) *pini* and *E. strobi* (Szucejki 1995). The larvae also damage stems of young trees that have suffered previous mechanical damage. Within a stand of maritime pine, trees attacked by *D. sylvestrella* showed no spatial aggregation and clusters of 66 trees proved to be an optimum sampling unit for determining overall percentage infestation. The larva is pink or greenish in colour, and the larvae make galleries into floem and provoke resin production, which is mixed with frass. The activity of the larva slows down in the autumn and the larva overwinters in the gallery. The flight period is July and August, when the species can be taken at light. It is also a sporadic migrant.

4.3 Host finding

It appears that the most productive stands are most infected by *D. sylvestrella*. Trees with the best radial growth are attacked first. It is suggested that larval penetration in the inner bark is aided by any bare tree surface (linked wounds or cut branches) as well as the presence of a thin bark; and that the quality and quantity of inner bark affects larval growth (Carisey *et al.* 1994).

4.4 Host resistance

Maritime pine susceptibility to this insect is evidently related to the terpene composition (Jactel *et al.* 1994). The level of attack on pruned trees increased strongly with the intensity of pruning, showing a significant positive correlation with the number of pruning wounds. The removal of dead branches did not result in any

increase of infestation. The infestation of pruned trees had no contagious effect towards neighbouring unpruned trees. The majority of the attacks were located in the vicinity of the branch insertion, and in 2- to 3-year-old internodes. In the second year, the percentage of pruned re-attacked trees continued to show a significant positive correlation with the severity of pruning. Jactel et al. (1999) found that tree susceptibility was positively and genetically correlated with tree diameter. Infested trees contained significantly more terpinolene and the regression between percentage of attacked trees and mean proportion of terpinolene per family was significant.

The infestation dynamics of *D. sylvestrella* is also related to fertilisation of the Maritime pine. Fertilised trees exhibit significantly greater tree growth and higher infestation rates than control. The rate of infestation also showed a significant positive correlation with the mean percentage of terpinolene. The distribution of infested tree frequencies indicated, that both tree pruning, which creates bark wounds, and tree vigour, which increases bark cracking, could simultaneously increase wood resin flow, thus enhancing tree attractiveness.

4.5 Natural enemies

Mainly species of Braconidae and Ichneumonidae attack *D. sylvestrella*. The braconid *Itoplectis cristatae* Momoi was recorded as a parasitoid in Japan. Several other parasitoids of *D. sylvestrella* have been found, including the genus *Macrocentrus* (Colombo & Eördegh 1995). The ichneumonid *Macrocentrus resinellae* L. also often infests this pest. *Macrocentrus abdominalis* Fabr. is a major natural enemy of *D. sylvestrella* in China, and *M. watanabei* also plays an important role. Other species of genus *Macrocentrus* were also found to be parasitoids of this species: *M. linearis* Nees, *M. nitidus* Wesmael, *M. sylvestrella* van Achterberg. *Scambus capitator* Aubert and *Venturia robusta* (Hym., Ichneumonidae) are known as parasitoids of the *D. abietella* larvae. Among insect predators, the genus *Ancistrocerus* spp. (e.g. *Ancistrocerus ichneumonideus* Ratz. and *A. gazella* Panzer) was recognised as feeding on larvae. These small wasps collect paralysed larvae and bring them to rearing chambers into nest. There are also some indirect indications about the role of birds in predation of larvae and pupae.

4.7 Damage and control

The highest aggressiveness was recorded in the southern Europe (France and Italy). Lower extension of damage was found in Spain and Portugal. Jactel et al. (2002) described, that the percentage of trees infested was significantly lower in the pine stands bordered by broadleaved stands than in the pine stands surrounded by other pine stands, and in the former, *D. sylvestrella* infestation showed a significant logistic increase with distance from the stand edge. This could be due to effects of resource concentration or natural enemy attack. These results suggest that the conservation or restoration of non-productive mixed-species stands adjacent to intensively managed plantations is a useful preventive method for pest management in forest monocultures.

Application of insecticides against newly laid eggs or newly hatched larvae reduces damage from 66 –100% to 0-20%. Timely sanitation fellings of heavily infested tree is recommended.

Direct and indirect selection using terpinolene as a biochemical marker could be used for increased host resistance, but genetic gains for tree resistance have to be weighed against possible genetic losses in tree growth.

4.8 References

- Carisey, N.; Menassieu, P.; Baradat, P.; Lemoine, B. & Lévieux, J. 1994. Sensitivity of maritime pine (*Pinus pinaster*) to attack by the pine moth *Dioryctria sylvestrella* (Lepidoptera, Pyralidae) in a range of site conditions. Relationships to certain growth characteristics. Annales des Sciences Forestières, 51, 67-75.
- Colombo, M. & Eördogh, F. R. 1995. *Dioryctria sylvestrella* Rtz. (Lep., Pyralidae) in nursery of *Pinus cembra*. Informatore Fitopatologico, 45, 38-40.
- Hirose, Y. & Nozato, K. 1975. Habitat specificity in three sympatric species of pine shoot moths. Kontyu, 43, 40-48.
- Jactel, H.; Menassieu, P. & Raisé, G. 1994. Infestation dynamics of *Dioryctria sylvestrella* (Ratz.) (Lepidoptera: Pyralidae) in pruned maritime pine (*Pinus pinaster* Ait.). Forest Ecology and Management, 67, 11-22.
- Jactel, H.; Kleinhertz, M.; Raffin, A. & Menassieu, P. 1999. Comparison of different selection methods for the resistance to *Dioryctria sylvestrella* Ratz. (Lepidoptera: Pyralidae) in *Pinus pinaster* Ait. Physiology and genetics of tree-phytophage interactions. International Symposium, Gujan, France, 31 August-5 September, 1997, 137-49.
- Jactel, H.; Goulard, M.; Menassieu, P. & Goujon, G. 2002. Habitat diversity in forest plantations reduces infestations of the pine stem borer *Dioryctria sylvestrella*. Journal of Applied Ecology, 39, 618-28.
- Szujecki, A. 1995. *Forestry entomology*. Wydawnictwo SGGW Warszawa 1995, 2 Volumes.

5. COSSUS COSSUS, THE GOAT MOTH

M. Turčáni

5.1 Taxonomy & systematics

Cossus cossus, Linnaeus 1758 belongs to family Cossidae, subfamily Cossinae, genus *Cossus* Fabricius, 1793. This species was described by Linnaeus in 1758. All species of this family feed inside the stems or roots of woody plants.

5.2 General biology

Cossus cossus infests many fruit trees (apple, cherry, pear, plum, olive) and other deciduous trees such as sweet chestnut (*Castanea*), elm (*Ulmus*), oak (*Quercus*), poplar (*Populus*), chestnut (*Aesculus*), lime (*Tilia*), maple (*Acer*) and willows (*Salix* spp.).

The egg is elliptical 1.2 x 1.7 mm, reddish-brown with a black longitudinal stripe. They are laid in groups of 15-50 eggs in crevices in the trunks or in wounds in the bark. A female lays about 500-1200 eggs with a maximum of 2000. The larva takes 3-4 years to develop in the wood of the tree and then it hibernates in the wood

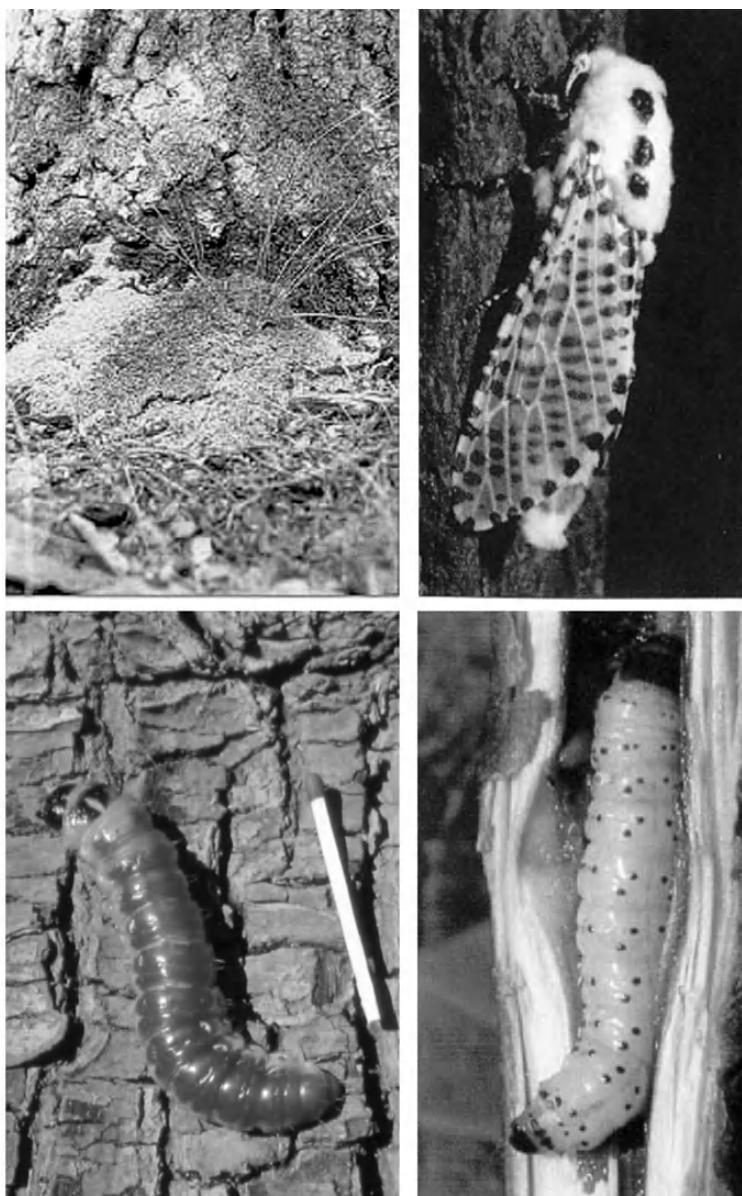


Figure 2. Upper left: large amounts of boring dust exuded from poplar tree under attack by *Cossus cossus* (photo: G. Csoka); upper right: resting adult of *Zeuzera pyrina* (photo: G. Csoka); lower left: fullgrown larva of *C. cossus* (photo: M. Zubrik; lower right: large larva of *Z. pyrina* (photo: G. Csoka)

or sometimes outside the trunk in the soil. A mature larva reaches a length of 90 to 100 mm. The young caterpillar is carmine pink; the colour is darker and more pronounced in older individuals. The ventral surface is light yellow, the head black with powerful mandibles. Larva changes colour prior the pupation. The young larvae feed jointly beneath bark, and after the 1st hibernation in the wood. Frass and faeces are ejected out of the larval galleries which are elliptical and often vertically oriented. Up to several tens of larvae could feed within one tree. The later instars are able to migrate from one to another tree. Glands joined to the mouthparts secrete a smelly substance, that resembles the smell of old leather, vinegar or poor quality wine. The pupa is 50 to 60 mm long, with groups of sharp spicules, which enable it to crawl towards the opening of the gallery just before emergence. Pupation occurs in spring, and the adults fly in early summer, laying eggs in deep cracks in the bark. Emergence of moth follows 3-4 weeks after pupation. The adult is a large moth of 70 to 80 mm wingspan, greyish coloured, with a massive body covered in hairs. The forewings have a dull appearance; the hind wings are grey and hairy on their basal part. Flight period is at June – July after sunset. During day-time specimens rest on trunks relying on their mimicry coloration.

5.3 Host finding

The female moth prefers older and bigger, often wounded trees. The eggs are deposited in the wounds in the bark this enables the young larvae to invade the tree easily. Damage by *C. cossus* is very common in roadside trees. This is partly attributed to the damage caused by mowing machines to the trunks.

5.4 Host resistance

Some resistance appeared by planting resistant and non-resistant tree species in an alternating pattern (interplanting). Thus, *Tilia* interplanted with *Picea* or *Pinus* suffers little from attack by *Zeuzera pyrina*, to which it is otherwise susceptible, and *Acer* interplanted with *Ailanthus* seems resistant to *C. cossus*.

5.5 Natural enemies

The tachinid *Xylotachina diluta* (Meigen) is a specific parasitoid of *C. cossus* larvae. Up to 15% of the larvae were found to be parasitized by this tachinid. The larvae are also parasitized by other tachinids species such as *Nilea lethifera* Pand. and *Phorocera assimilis* Fall. Other parasitoids are the ichneumonids *Dicaelotus pussilator* Grav., *Stenarella gladiator* Scop., *Lissonota setosa* Fourcr. and *Herpestomus arridens* Grav. The adults of *C. cossus* are frequently attacked by owls and bats (Szucejki 1995).

Larval diseases are caused by *Spicaria cossus* Petsch. Also *Bacillus thuringiensis* was isolated from larvae of *C. cossus* (Grassi & Deseö 1984). Several nematode species were found on *C. cossus* in the Tashkent region (Zemlyanskaya & Lysikova 1976). In Turkey, the larvae were found to be a host of *Verticillium lecanii*. Virus

infection by *Borrelinavirus cossi* and *Entomopoxvirus (Vagoiavirus) cossi*) is considered to be the main mortality factor in *C. Cossus* populations, sometimes more than 50% of the larvae are infested (Weiser 1996).

5.6 Damage and control

From the BAWBILT database it was derived that the highest aggressiveness of *C. cossus* was recorded in southern and south-eastern Europe (Italy and Romania). Lower aggressiveness was found in Hungary and The Netherlands – where poplar plantings are also common. The larval tunnels interfere with sap circulation, this makes the branches or trunks susceptible to breakage in the wind and sometimes the tree is killed; although the moth usually attacks trees, which are wounded by traffic and mowing activities. In situations with an overpopulation of too many larvae within one tree, some of the full-grown larvae may leave the tree and crawl to another tree. These full-grown larvae are able to invade into healthy, non-wounded trees.

Survey of pest abundance is done by assessment of damage to the trees. The number of males captured by pheromone traps can also be used. Control should be done by removal of the heavily infested trees from forest stands. It is necessary to burn or transport the felled trees out of the forest stands, because older larvae are able to finish development in the felled trees or they can migrate to surrounding living trees (Novotný & Zúbrik 2002).

Control measures should be preventive, owing to the difficulty of killing the larvae within their galleries. Chemical control consists of sprays of insecticides on the base of the tree and on the surrounding soil against ovipositing females and newly hatched larvae. However, in many countries, the use of insecticides in urban trees and forests is not sustained. The use of the fungus *Beauveria bassiana* causes mortality of *C. cossus* in lab conditions but an appropriate method of field application is not yet possible.

Ecological control using pheromone dispensers can be done with a pheromone blend Z3-C10Ac+Z5-C12Ac at a 4:1 ratio. The mating disruption method applied in apple orchards, showed an encouraging confirmation. In orchards, the percentage of infestation in the trunks decreased within the treated field year by year compared with the initial level and the level of infestation in the control fields. It thus seems possible to achieve sufficient control, and to keep the pest below a damaging threshold with a . Regarding the mass trapping method, any statistical difference between 5 and 10 traps/ha managed was relieved. The trap type used was the pyramidal funnel with wings in eyes height (Pasqualini & Natale 1999).

Several species and/or strains of *steinernematid* and *heterorhabditid* nematodes have been tested for efficacy against the larvae of the *C. cossus*, both in laboratory and field conditions. Some of the tested nematodes (*Steinernema glaseri*, *S. feltiae* "100" and "1192" strains) proved to be very effective in the bioassays, but they provided a poor control when applied locally in the larval galleries. *S. feltiae* strain (not tested previously in the laboratory) gave the best control, though still poor (25%) in the localized applications carried out (Rovesti 1989).

5.7 References

- Grassi, S. & Deseö, K. V. 1984. Distribution of *Bacillus thuringiensis* Berl. and prospects of using it in plant protection. Atti Giornate Fitopatologiche, 425-33.
- Novotný, J. & Zúbrík, M. 2002 *Biotic Pests of Slovakian forests*. Gerlach Slovakia, 1-206.
- Pasqualini, E.; Natale, D. 1999. *Zeuzera pyrina* and *Cossus cossus* (Lepidoptera, Cossidae) control by pheromones: four years advances in Italy. Bulletin OILB/SROP, 22:9, 115-24.
- Rovesti, L. 1989. Experiments with entomoparasitic nematodes against *Cossus cossus* L. (Lepidoptera: Cossidae). Difesa delle Piante, 12, 23-32.
- Szujecki, A. 1995. *Forestry entomology*. Wydawnictwo SGGW Warszawa, 2 Volumes.
- Weiser, J. 1996 *Insect diseases*. Academia, Nakladatelství československé akademie věd Praha.
- Zemlyanskaya, A. I. & Lysikova, E. A. 1976 The nematodes of insect pests of decorative plantations and of forests in the Tashkent area. Ekologiya i biologiya paraziticheskikh chervei zhivotnykh Uzbekistana., 48-54.

6. ZEUZERA PYRINA, THE LEOPARD MOTH

M. Turčáni

6.1 Taxonomy & systematics

Zeuzera pyrina belongs to family of Cossidae, subfamily Zeuzerinae, genus *Zeuzera* Latreille, 1804. The species was described by Linnaeus in 1761. All species of this family feed in stems or roots of woody or herb species.

6.2 General biology

Zeuzera pyrina infests a large number of shrubs and tree species such as apple, pear, plum, cherry, olive, pomegranate (*Punica granatum*), quince, black currant, currant, Citrus, vine, oak (*Quercus*), ash (*Fraxinus*), willow (*Salix*), lime (*Tilia*), plane (*Platanus*), beech (*Fagus*), poplar (*Populus*), maple (*Acer*), tamarisk (*Tamarix*), etc. The female adult has a 50 to 60 mm wing span, this is 35 to 40 mm for the male. The thorax is white and hairy with 6 blue spots. The abdomen is relatively long. The wings are white, sprinkled with small metallic blue spots. It does not feed and its lifespan is extremely short, from 8 to 10 days. The female mates soon after it has emerged. The female lays about 1,000 eggs deposited in clusters on the trees, preferably in places where the female can insert her ovipositor (crack, old larval gallery); it can occasionally lay eggs in the ground. The egg is oval-shaped, about 1 mm, with a light yellow to bright salmon colour. Its embryonic development lasts 7 to 23 days. The mature larva is 50 to 60 mm, bright yellow with numerous small black points on each segment. The head and the thoracic plates are shiny black. The caterpillars at first remain clustered in a silken cocoon from which they eventually disperse at dawn or at dusk. They bore into the tips of branches and shoots, and move downwards to attack the young parts of the tree (twigs, spurs, pouches, central veins and leaf peduncles on certain shrubby species).

The caterpillars generally move around, to penetrate lower in the twigs and branches. After several migrations, the larvae attack the larger branches and the

trunk, in which they form ascending galleries under the bark, later in the wood. The entry holes of the larvae are marked by small heaps of saw-dust and frass (in the shape of small cylinders) accompanied by sap outflows, particularly visible on the large branches, typically at a stage where the damage is already very advanced.

The life cycle is annual in the southern part of Europe; it lasts 2-3 years in the northern regions. The adults generally appear from the beginning of June to August. In the Mediterranean region, the flight takes place from April to October. The young caterpillars, attached to a silk thread, can be carried by the wind. This mode of dispersal is often found in young stands; it also occurs on trees situated close to hedges and thickets. In spring, the larva continues boring its gallery in the wood, often in the centre of the branch. Pupation occurs from April to July. According to Katlabi (1992) the flying period of *Zeuzera pyrina* is from late August to November in Syria.

6.3 Host finding

The female prefers older and bigger trees, often weakened, particularly in dry years and on dry soils. Damage by *Z. pyrina* is often found on roadside trees. This is partly attributed to the damage of the bark caused by mowing machines. Healthy trees resist attacks better (favourable influence of irrigation and of a balanced mineral supply).

6.4 Host resistance

There are some indications of resistance. According to Lagunov (1981) green ash (*Fraxinus pennsylvanica*) was damaged more frequently and severely (25% vs. 7%) than hybrid ash (*F. excelsior* x *F. pennsylvanica*). Survival of young larvae artificially applied to current-year shoots was 90-97% on green ash and 57-77% on hybrid ash. The shoots of green ash contained more starch and less Ca and Mg than those of the hybrid ash. This suggests that starch is responsible for the greater susceptibility of green ash. Preliminary observations with various walnut (*Juglans regia*) varieties show promising levels of tolerance to *Zeuzera pyrina* (Monastrá et al. 1997). Also interplanting with resistant and non-resistant species shows some relationships e.g.: *Tilia* interplanted with spruce or pine suffered little from attack by *Z. pyrina*, to which it is otherwise susceptible.

6.5 Natural enemies

Campadelli (1998) found as parasitoids several species e.g.: Ichneumonids: *Neoxorides nitens* (Grav.), *Dolichomitus messor* (Grav.), *Diadegma terebrans* (Panz.), *Pristomerus vulnerator* (Panz.), Braconids: *Dolichogenidea laevigata* (Ratz.), *Helcon* sp. Chalcidids: *Perilampus tristis* Mayr, Diptera: *Megaselia praeculta* (Schmith), *Odinia meijerei* Collin. Also braconids *Apanteles lacteipennis* Curt., *Apanteles albipennis* Nees., *Apanteles laevigatus* Ratz., ichneumonids *Ichneumon abeillei* Berth., *Schreineria zeuzerae* Ashm., *Horogenes punctoria*

Roman, chalcidids *Elasmus ciopkaloi* Nov., *Euderus* sp., *Copidosoma truncatellum* Dalm., *Elasmus albipennis* Thoms., *Elasmus schmidti* Ruschka, *Elachertus nigritulus* Zett., are known as parasitoids of *Z. pyrina*. Disney & Campadelli (1997) described *Megaselia zeuzerae* sp. nov. as a parasitoid of the larvae of *Zeuzera pyrina*.

Among the predators, mainly birds are known: *Dendrocopos major*, *D. minor*, *Picus viridis*, *Pediculoides ventricosus* Berl. Furthermore there are some fungi such as *Aspergillus parasiticus*, *Mucor hiemalis* and *Fusarium solani* known to be pathogenic to larvae of *Zeuzera pyrina*.

6.6 Associated organisms

Trees weakened by leopard moth attacks are frequently subject to other xylophagous pests such as hornet clearwing moth (*Synanthedon myopaeformis*), goat moth (*Cossus cossus*) and bark beetles. Furthermore, the old larval galleries serve as a refuge to the woolly aphid (*Eriosoma lanigerum*), which thus partially escapes from chemical treatments.

6.7 Damage and control

The highest aggressiveness was recorded in central and south-eastern Europe (Hungary and Romania) in Danube basin. This species seems to be less important than its bigger relative *Cossus cossus*. The seriousness of the attacks varies according to the age of the plantations on young trees: 1 caterpillar is enough to kill a tree; 3-year-old trees can lose part of their structure. The attacked trees become extremely vulnerable to wind damage and the central axis system is permanently affected. Therefore, results clearly indicate the mating disruption technique used is working very well and effectively should protect the heavily infested stands against *Z. pyrina* (Sarto 1999).

Current control practices include either manual killing of larvae inside their galleries by introducing a flexible wire into it, a time consuming, labour intensive and therefore costly procedure, or wide spectrum insecticide applications against adults. Due to the prolonged adult emergence period, however, and the short residual activity of the insecticide sprays, a large number of applications is required throughout the active period of the insect (about three to four months) for an effective control, resulting in undesired environmental side effects of such applications.

Guario *et al.* (2001) compared the effectiveness of insecticides, pruning and disposal of infested branches, and pheromone traps to control *Zeuzera pyrina* in olive groves in Italy. The insect was controlled by application of triflumuron, teflubenzuron, hexaflumuron and azinphos-methyl. Following 2 applications (at 20 and 25 days), the initial infestation of 75% of the trees was reduced to 3-6%. Hexaflumuron, azinphos-methyl and teflubenzuron were the most effective. In another study (Pasqualini *et al.* 1999), horticultural (pruning), mechanical (removal of larvae) and chemical (spraying) treatments were evaluated for their efficiency

against *Zeuzera pyrina*. The results showed 16-20, 64-69 and 60-81% reduction of infestation for the three treatments, respectively. When the treatments were applied for two successive years, the respective reduction increased to 32, 82 and 74-86%. Simon et al. (1999) describe control of *Zeuzera pyrina* by the use of *Bacillus thuringiensis*.

Some experiments with nematodes Saleh & Abbas (1998) e.g.: *Steinernema riobravae* [*S. riobrave*], *S. abbasi*, *S. carpocapsae* S2, *Heterorhabditis* sp. SAA1 and *S. feltiae*, were done in Egypt. Laboratory experiments showed that the larvae of *Z. pyrina* were highly susceptible to the nematode infection and produced more infective juveniles (IJ) within a shorter time than the pupae. The tested nematodes caused 87.5-100% larval mortality within 48 hours at a dose of at least 20 IJ/larva.

Bioassays were conducted to determine the susceptibility of *Zeuzera pyrina* to different spore conc. of *Metarrhizium anisopliae*. The fungus was highly virulent against the larval stage of *Z. pyrina*. The percentage mortalities were 49.4, 100 and 100 for 3rd-instar larvae and 35, 90 and 100 for 6th-instar larvae at 10^5 , 10^6 and 10^7 spores/ml conc. resp., 7 days after treatment. The results suggested the possibility of using *M. anisopliae* to control *Z. pyrina*.

6.7 References

- Campadelli, G. 1996. Some parasitoids of *Zeuzera pyrina* L. (Lep., Cossidae) in Emilia-Romagna. Bollettino dell'Istituto di Entomologia 'Guido Grandi' della Università degli Studi di Bologna, 50, 127-31.
- Disney, R. H. L. & Campadelli, G. 1997. A new species of *Megaselia* Rondani (Diptera: Phoridae) reared from a moth larva (Lepidoptera: Cossidae) in Italy. Bollettino dell'Istituto di Entomologia 'Guido Grandi' della Università degli Studi di Bologna, 51, 63-68.
- Guario, A., Marinuzzi, V., Milella, G., Alfarano, L. & Falco, R. 2001. Chemical control of *Zeuzera pyrina* in olives. Informatore Agrario, 57, 63-65.
- Katlabi, H. S. Y. 1992. Flying period of leopard moth adults (*Zeuzera pyrina* L.) in olive trees in Syria. Olivae, 41, 32-36.
- Lagunov, A. G. 1981. Effect of the chemical constituents of ash wood on the severity of damage by *Zeuzera pyrina* L. Biologicheskie Nauki, 12, 32-34.
- Monastrà, F., Limongelli, F. & Barba, M. 1997. European walnut germplasm from Caserta. Options Méditerranéennes. Série B, Études et Recherches, 16, 41-48.
- Pasqualini, E., Civolani, S., Vergnani, S. & Natale, D. 1999. IPM improvement on pome fruit orchards in Emilia-Romagna (Italy). Bulletin OILB/SROP, 22, 111-20.
- Saleh, M. M. E. & Abbas, M. S. T. 1998. Suitability of certain entomopathogenic nematodes for controlling *Zeuzera pyrina* L. International Journal of Nematology, 8, 126-30.
- Sarto i Monteys, V. 2001. Control of leopard moth, *Zeuzera pyrina* L., in apple orchards in NE Spain: mating disruption technique. Bulletin OILB/SROP, 24, 173-78.
- Simon, S., Corroyer, N., Getti, F. X., Girard, T., Combe, F., Faurel, J. & Bussi, C. 1999. Organic farming: optimization of techniques. Arboriculture Fruitière, 533, 27-32.

7. SESIIDAE, CLEARWING MOTHS

L.G. Moraal

7.1 Taxonomy & systematics

The family of Sesiidae (clearwing moths) are unusual wasp-like moths with partly clear (scale-less) wings and a distinct fan-like anal tuft of scales. The larvae are stem borers in shrubs and trees. In Europe, about 15 species can cause more or less damage on trees in orchards, cities and forests, and more information about the Sesiidae can be found in Lastuvka & Lastuvka (2001). The genera *Paranthrene* Hübner 1819 (*Scapteron* Staud.) and *Sesia* Fabr. 1775 are the most important ones. Both genera have only a few species; the most important are the Poplar clearwing moth, *Paranthrene tabaniformis* Rott. and the Hornet clearwing moth, *Sesia apiformis* (Clerck). In this chapter, information is given on these two species.

7.2 *Paranthrene tabaniformis* - Poplar clearwing moth

7.2.1 General biology

The poplar clearwing moth, *Paranthrene tabaniformis* Rott. (syn. *Scapteron tabaniformis*) is a common and destructive pest of young poplars. The insect is widely distributed in Europe, Asia, North America and northern Africa. The larvae bore tunnels in the wood and cause loss of vigour and structural weakness of the stems. Young trees may break, thus resulting in malformed, bushy or dead trees. In The Netherlands, seasonal flight pattern of *P. tabaniformis* shows considerable variation. Trapping studies in various parts of the Netherlands in 1984-86 with the pheromone (3E,13Z)-3,13-octadecadien-1-ol, showed considerable variation in seasonal occurrence. The flight period lasted from late May to mid-September (i.e. longer than usually stated). Positive correlations were found between catches and climatic factors such as maximum or mean daily temperatures. Flight activity of males occurred chiefly at mid-day (Moraal *et al.*, 1988). Eggs are laid on the stems near wounds or crevices in the bark. The neonate larvae quickly bore into the stems, producing galleries in the wood. The larvae hibernate in the trees for 1-2 times; Rearing on artificial media suggest that the number of hibernations is not genetically fixed in regional races, but that temperatures are important (Moraal, 1989c). More details on the bionomics can be found elsewhere (e.g. Moraal, 1988, 1989c; 1996; Moraal *et al.*, 1993; Schnaiderova, 1980; Schwenke, 1978; Srot, 1966).

7.2.2 Host finding

It is well known that adult females have a preference to deposit their eggs on poplars wounded by pruning, mowing, bark diseases such as *Dothichiza populea*, chafing of metal or plastic tree guards, and fraying by roe deer. These wounds possibly release volatile constituents that attract the females. Therefore, it is important to avoid any wounding of the trees. For instance, pruning of young trees should not be carried out prior to and during the flight period. The moths are very lively and are fast flyers over



Figure 3. Upper left: adult and chrysalis of *Sesia apiformis*; upper right: larval galleries of *S. apiformis*; lower left: adult and chrysalis of *Paranthrene tabaniformis*; lower right: broken shoot with gall of *P. tabaniformis* (all pictures taken by ALTERRA)

large distances; they can easily migrate from older forests into nurseries and young plantations where they can cause large problems (Moraal *et al.*, 1993).

7.2.3 Natural enemies

Not all infestations will result into severe damage. In The Netherlands it was found that, up to 55% of the *P. tabaniformis* larvae, can be parasitized by *Apanteles evonymellae* (Braconidae) (Moraal, 1987). In Bulgaria, the mortality of the larvae by *A. evonymellae* varied from 2.4 to 35.4%, while the average mortality of hibernating larvae caused by the parasitoid *Eriborus terebrans* was 4.7% (Georgiev, 2001a,b). During an experiment in the summer of 1986, fresh eggs of *P. tabaniformis*, oviposited on paper strips, were attached to one-year-old poplars in a nursery in the Netherlands. In September, 18 females of *Telenomus phalaenarum* (Hym.: Scelionidae) were reared from these eggs. This nursery was adjacent to a mixed forest: we have tried to detect any egg-parasitization in large monotonous poplar plantations, but we could not find parasitized eggs. This suggests that vegetation diversity could be favourable to the pest's natural enemies (Moraal, 1989b).

7.2.4 Damage and control

Serious damage caused by *P. tabaniformis* can occur in those situations where large areas are planted with young trees. This occurred in The Netherlands in the new polders, on formerly sea bottom, during the seventies and eighties. In China, it was reported that in the eighties, mega-areas of ten thousands hectares of land were afforested and that many trees were attacked (Miao *et al.*, 1987, 1989). For certain areas in Europe, it is foreseen that large areas of land will be withdrawn from agriculture. The planned utilization of this land will include reforestation and the planting of woody crops for biomass and timber production using fast growing species such as poplar. This could induce large-scale problems in the future.

Control by mass-trapping in the field. In China, mass trapping by using the sex attractant (3E,13Z)-3,13-octadecadien-1-ol, was evaluated in field studies during 3 years. The results indicate that the population densities reduced from about 0.3 to 0.01 larvae/tree. Here, 15 traps/ha were used for mass trapping in lightly to moderately damaged forests, 30 traps/ha were used in heavily damaged forests and 4-8 traps/ha were used for a suppressive measure throughout the year (Du *et al.*, 1985). Also in China, as a cheaper alternative by avoiding expensive installation of traps, smearing of tree stems with a sticky pheromone paste, was used to control *P. tabaniformis*. The area under control covered 267 000 ha, and the average percentage of infested trees decreased from 8.2% to <1% (Miao *et al.*, 1989). In The Netherlands, the sex attractant was applied during 3 years in 'lure and kill' and 'mass trapping' experiments to prevent infestations in young poplar plantations. However, although the number of males was reduced, there was no statistically significant decrease in infestations by comparison with untreated plots (Moraal *et al.*, 1993).

Chemical control in the nursery. It is recommended, to plant sound plant material without hibernating *P. tabaniformis* larvae inside the stems, from the nursery to a new plantation. Therefore, it is necessary to require an effective preventive chemical control in the nurseries. Flight period of *P. tabaniformis*, and thereby the period of egg depositing, can take place during the whole summer. This means that one-year-old poplars in the nursery can be infested with larvae of different ages. Small larvae can be overlooked very easily, and trees together with hibernating larvae, can be planted out in the field and thus create heavy infestations on this new location in the subsequent years. It is therefore necessary, to require an effective preventive chemical control in the nursery. The spraying of Permethrin was effective as fluid (250 g/litre) or 25% wettable powder at dosages of 50 cm³ or 50 g/100 litres carrier: 5 treatments from early June to August gave complete control (Wouters, 1979). Monitoring of the flight with sex-attractant baited traps is considered to be very useful for timing this control. Nevertheless, newly planted sound poplars, can be infested in their new plantations, by migrating moths from adjacent older poplar stands (Moraal et al., 1993).

Control with biological agents. In experiments, the nematode *Neoaplectana carpocapsae* was sprayed in aqueous suspensions, on young infested poplar stems, or injected into larval boreholes. Even at the lowest dosage (250 nematodes/ml) the larvae were killed in each gallery (Wouters, 1977). The fungus *Beauveria bassiana* was applied in suspensions in the larval boreholes; this resulted in a control up to 50% (Cavalcaselle, 1975). However, the methods as mentioned above are very labour-intensive and therefore very costly.

Resistance and tolerance of poplars. Certain secondary plant metabolites such as phenol glycosides could play a role in the chemical defence against herbivores, because they may have feeding deterrent or toxic properties (Augustin et al., 1993). However, the small neonate larvae of *P. tabaniformis* can crawl over distances up to 140 cm, to find a suitable place to invade the tree. They bore easily into the young stem, through wounds, lenticels or at the rough surface near the crotch of a twig. Within one hour, they have disappeared inside the stem (Moraal, 1994). We have no information if the neonates ingest some amount of the bark tissue, before reaching the xylem. If they do not, they probably bypass the plant's chemical defence system. In the literature, we could not find statistical reliable data to designate clones to be more or less resistant.

Tolerance is often confused with a low or moderate level of genetic resistance. However, tolerance does not affect the population dynamics of the pest but does raise the threshold level of the plant. For example: during experiments in 1988, the clone 'Florence Biondi' had relatively more infestations than 'Robusta'. However, in 1989 and 1990 it was almost the reverse. The recovery of 'Florence Biondi' may be attributable to this clone's ability to grow faster than 'Robusta' during the first years after planting. Rapid growth during the first years after planting has the advantage that larval galleries are overgrown more rapidly, and therefore the risks of stem snapping decreases strongly (Moraal, 1996; Moraal et al., 1993).

It has to be kept in mind that infestations may show interaction between clonal resistance or tolerance and local conditions such as climate, soil characteristics, quality of nursery material and distribution of the insect. Also Noh *et al.* (1994) found significant differences among 25 genotypes of poplar against borers, such as the Osier weevil, *Cryptorrhynchus lapathi*, but tolerance was more affected by environmental factors than by genotype.

Fewer problems in vigorous trees. Wounded trees may release volatile constituents, which attract the females. Therefore, it is important to avoid any wounding. For instance, pruning of trees should not be carried out prior to and during the flight period of the moth. Vegetation diversity could play an important role to suppress insect pests. It makes the environment less favourable to the pest and more favourable to the pest's natural enemies. In areas with a high infection pressure of *P. tabaniformis*, we recommend to stimulate a rapid growth of the poplars during the first years, because larval galleries are overgrown more rapidly. This can be achieved by planting on suitable locations and by using clones which are known as rapid starters. Also application of fertilizers can be an important preventive measurement to keep the trees vigorous.

7.3 *Sesia apiformis* - hornet clearwing moth

7.3.1 General biology

The Hornet clearwing moth, *Sesia apiformis* (Clerck) (*Aegeria apiformis*; *Trochilium apiformis*) (Lepidoptera: Sesiidae) is the largest member of the family of clearwing moths in Europe. The young larvae tunnel in the cambial layer and later in the wood of the trunk and major roots of mainly *Populus*. The larvae live beneath the bark for 2-3 years. The mature larva is 30-40 mm long; the body is yellowish-white with a large reddish-brown head. The last winter is spent in a cocoon of bark scrapings just under the bark or, less commonly, in the earth near the tree. The larva pupates in the cocoon in the following spring. Adults emerge from mid-June to mid-July, rarely in August, and leave an exit hole about 8 mm in diameter, near the base of the trunk. The 2-3 cm long empty pupal cases can be found around the base of the tree up to about 60 cm height (Schwenke, 1978; Arundell & Straw, 2001). The date of the adult emergence depends on temperature and occurs from May to June. The adults live for several weeks and pairing occurs after a few days in the crowns of the trees. During the daylight, the adults are not very active; the activity takes place during the night. The females lay their eggs (1400-1500 each) on the lower parts of the trunks near the soil (Kolomoets *et al.*, 1978). However, according to Schwenke (1978) the female is sitting on the basal part of the trunk or on low branches and let fall her small eggs on the ground or they glide into the crevices in the rough surface of the trunk.

The neonate larvae are very mobile and enter the trunks at or below soil level forming galleries 20-50 cm long. Development from egg to adult lasts 2 years. The larva hibernates twice in the lower parts of the trunk. For pupation, the larvae gnaw

their way to the surface of the trunk. Pupation takes place between late April and mid-May (Kolomoets et al., 1978; Schwenke, 1978).

7.3.2 Host finding

The moth does not seem to have a limitation in the preference on the age of the trees. The attacks can occur on 2-year-old trees, as well as on 30-year-old trees. There was no preference in the direction of the empty pupal cases, because many were facing to the north and others to the south. Attacks also occur in trees, surrounded by dense vegetation around the base of the tree, and even in trees, which bases covered on all sides by *Hedera helix*. In general, trees surrounded by dense vegetation showed more infestations than trees surrounded by mown grassland. There could be more predation of pupae when vegetation is very low. Therefore, egg-laying females may select trees surrounded by vegetation to reduce this threat (Coleman & Boyle, 2000).

7.3.3 Host plants

The moth is widely distributed in Europe; *Populus tremula* is attacked in the north and in the east, while a diversity of species is infested in the south (Schwenke, 1978). The insect is common on *Populus* (and occasionally on *Salix*, *Tilia*, *Betula* and *Fraxinus*) in amenity areas and forests. The physical damage caused by *S. apiformis* to the trunk has been described by several authors, but less information is available on the role of the moth in causing dieback in the crown, or its ability to attack and kill healthy trees. However, attacks have been described for a longer time without any fatal effects (Arundell & Straw, 2001). In the U.K. it was found that *Populus x euramericana* showed the highest rates of infestations while *P. alba*, *P. nigra* var. *Italica* and *P. canescens* showed less or no signs of infestations. However, despite the lack of *Sesia*-infestations, *P. canescens* had an average of 37% crown dieback. So, in certain cases the dieback is not caused by the attacks (Arundell & Straw, 2001).

Poplar trees showing severe dieback, defoliation or death within a growing season, have been reported during recent years from eastern England. Here, many of the trees were attacked by *S. apiformis*. Because of the larval activities, this might be the cause of the decline in tree health. A survey in 1999 of 801 poplar trees showed a correlation between the amount of dieback and the number of exit holes in the trunk. However, a significant number of trees showed severe dieback but no infestations. The data demonstrate that dieback in many trees cannot be attributed to *S. apiformis*. Up to 53% of trees with severe dieback occurred in shelterbelts, and many of these sites were situated on reclaimed land or other man-made substrates. The area where dieback has been most prevalent is one of the hottest and driest parts of the UK, and the reports of dieback in poplar and the apparent increase in *S. apiformis* activity, follow particular dry springs and early summers in 1995 and 1996. The available evidence suggests that the deterioration in the health of poplars in this region is not caused directly by *S. apiformis*, but by a combination of climate and human influences (Arundell & Straw, 2001).

7.3.4 Natural enemies

For *S. apiformis* only a few parasitoids have been described such as *Cryptus pseudonymus* Tschek. and *Meniscus setosus* Four (Ichneumonidae), but apparently they are not very important as natural enemies (Schwenke, 1978). *Leskia aurea* (Tachinidae) was reared from some mature larvae of *S. apiformis* infesting the trunks of *Populus* in Italy (Campadelli, G. 1986).

7.3.5 Damage and control

Extensive tunnelling by *S. apiformis* destroys the cambial layers and outer wood in the lower portion of the trunk. In small trees, less than 10-years old, the tunnels can permeate the whole cross-section. Trees with such extensive damage are susceptible to breakage at ground level. In larger trees, the larvae tunnel mainly around the periphery and the tunnels do not cut very deeply into the wood (Schwenke, 1978). The symptoms are presence of exit holes, sometimes with old pupal cases, remaining in the hole at the base of trunks, lines of sawdust at the foot of the tree and deep galleries with a circular section. Infestation is less likely to be the principal factor causing structural instability in larger trees. However, damage by the larvae facilitates the entry of fungi and other organisms that cause decay. The maintenance of healthy, vigorous trees is always the best defence against insect attack. This can be done by irrigation where necessary and the use of fertilizers. In case of heavy infestation one could fell the trees and remove the stumps and destroy the larvae. Control is difficult when the larvae are deep in their galleries. In extreme cases high value trees can be sprayed at the start of insect flight and repeated again every 2-3 weeks during the flight period. A possible confusion can occur with the Poplar clearwing moth, *Paranthrene tabaniformis* and the Osier weevil, *Cryptorhynchus lapathi* on young trees. On older trees the infestations could be confused with those from the Goat moth, *Cossus cossus* and the Large poplar longhorn beetle, *Saperda carcharias* (Arundell & Straw, 2001; Schwenke, 1978).

7.4 References

- Arundell, J.C. & N.A. Straw. 2001. Hornet clearwing moth (*Sesia apiformis* Clerck) and dieback of poplars in Eastern England. Arboriculture Journal 25, 235-53.
- Augustin, S., C. Courtin & A. Delplanque. 1993. Poplar clones effect on development, mortality and fecundity of *Chrysomela (Melasoma) populi* L. and *Chrysomela tremulae* F. (Col., Chrysomelidae). Journal of Applied Entomology 116,: 39-49.
- Campadelli, G. 1986. [Biological notes on little known Diptera Tachinidae]. Bolletin Società Entomologica Italia 118, 161-66.
- Cavalcaselle, B. 1975. Possibilité d'emploi de produits à base de *Beauveria bassiana* (Bals.) Vuill. contre les larves de quelques insectes xylophages. XXVII International Symposium on Phytopharmacy and Phytiistry. Mededelingen Faculteit Landbouw Rijksuniversiteit Gent. 437-42.
- Ceianu, I., D. Radoi and E. Constantinescu, 1967. [*Paranthrene tabaniformis*: studies on its biology and control]. Institutul de Cercetari Forestiere, Bucharest.
- Coleman, D.A. & M.K. Boyle. 2000. The status and ecology of the hornet moth, *Sesia apiformis* (Clerck) (Lepidoptera: Sesiidae), in suburban South London. British Journal of Entomology Natural History 13, 99-106.
- Du, J.W., S.F. Xu, X.J. Dai & X. Zhang. 1985. [Strategies for control of poplar clearwing moth *Paranthrene tabaniformis* Rott. by mass trapping]. Shanghai Institute Entomology Control 5, 19-24.

- Georgiev, G., 2001a. Notes on the biology and ecology of the parasitoids of the poplar clearwing moth, *Paranthrene tabaniformis* (Rott.) (Lep., Sesiidae) in Bulgaria. I. *Apanteles evonymellae* (Bouche, 1834) (Hym., Braconidae). Journal of Applied Entomology 125, 141-45.
- Georgiev, G., 2001b. Notes on the biology and ecology of the parasitoids of the poplar clearwing moth, *Paranthrene tabaniformis* (Rott.) (Lep., Sesiidae) in Bulgaria. II. *Eriborus terebrans* (Gravenhorst, 1826) (Hym., Ichneumonidae). Journal of Applied Entomology 125, 289-92.
- Kolomoets, T.P., A.M. Sinelnikova, V.M. Kovalenko & N.V. Danilkina. 1978. [The great poplar clearwing]. Zashchita-Rastenii 1: 36.
- Lastuvka, Z. & A. Lastuvka. 2001. *The Sesiidae of Europe*. Apollo Books, Stenstrup.
- Miao, J.C., G.Y. Li, W.F. Xia & X.L. Li. 1989. [A study on the control of *Paranthrene tabaniformis* by stem smearing with sticky pheromone paste]. Forest Science Techniques 8, 28-30.
- Moraal, L.G., 1987. [*Apanteles evonymellae* fauna n. sp., a new parasitoid of the poplar clearwing moth, *Paranthrene tabaniformis* (Hymenoptera: Braconidae; Lepidoptera: Sesiidae)]. Entomologische Berichten Amsterdam 47, 137-39.
- Moraal, L.G., 1988. [Monitoring of the poplar clearwing moth *Paranthrene tabaniformis* Rott.) with sex attractant baited traps]. Nederlands Bosbouwtijdschrift 60, 43-49.
- Moraal, L.G., 1989a. [Poplar clearwing moth, *Paranthrene tabaniformis* Rott., preventive control in the nursery with carbofuran]. Nederlands Bosbouwtijdschrift 61, 70-78.
- Moraal, L.G., 1989b. [*Telenomus phalaenarum* fauna nov. spec., as an egg parasitoid of the poplar clearwing moth, *Paranthrene tabaniformis* (Hymenoptera: Scionidae; Lepidoptera: Sesiidae)]. Entomologische Berichten Amsterdam 49, 65-68.
- Moraal, L.G., 1989c. Artificial rearing of the poplar clearwing moth, *Paranthrene tabaniformis*. Entomologia Experimentalis et Applicata 52, 173-78.
- Moraal, L.G., C. van der Kraan and H. van der Voet. 1993. Studies on the efficacy of the sex attractant of *Paranthrene tabaniformis* Rott. (Lep., Sesiidae). Journal of Applied Entomology 116, 364-70.
- Moraal, L.G., 1994. The effect of the game deterrent Wöbra on attacks by the poplar clearwing moth, *Paranthrene tabaniformis* Rott. (Lep., Sesiidae). Anzeiger für Schädlingskunde, Pflanzenschutz und Umweltschutz 67, 72-73.
- Moraal, L.G., 1996. Evaluation of infestations by the poplar clearwing moth, *Paranthrene tabaniformis* Rott. In: Proceedings 20th Session of the FAO International Poplar Commission, Budapest, October 1-4.
- Noh, E.R., S.K. Lee and H.S. Park. 1994. [Tolerance of *Populus davidiana* clones to poplar borers]. Forest Genetics Research Institute 30, 24-29.
- Schnaiderova, J., 1980. [*Kleiner Pappelglasschwärmer*, *Paranthrene tabaniformis* Rott.]. Prace Inst. Badawczego Lesnictwa, Warszawa nr.
- Schwenke, W., 1978. *Die Forstsäädlinge Europas. 3. Schmetterlinge*. Parey, Hamburg.
- Srot, M., 1966. [Einige Erkenntnisse aus der bionomie des kleinen Pappelschwärmers, *Paranthrene tabaniformis* Rott., in der CSSR und seine Bekämpfung]. Prace Vulhm 32.
- Wouters, L.J.A., 1977. [the use of parasitic nematodes on the control of larvae of the poplar clearwing moth]. Populier 14, 59-60.
- Wouters, L.J.A., 1979. [The control of larvae of the poplar clearwing moth on nurseries]. Populier 16, 39-40.

8. SIRICIDAE (HORNTAILS)

M. Viitasaari & K. Heliövaara

8.1 Taxonomy and systematics

The extant taxa of Siricoidea belong to one single family, the Siricidae, and those of Xiphydrioidea to the single family Xiphydriidae. Representatives of Siricidae are here called horntails, and those of the Xiphydriidae wood wasps, following Quicke (1997).

The extant taxa of the family are divided into the subfamilies Siricinae and Tremicinae. There are more than 100 living world species. Most species are native to the northern forests; southern extensions reach northern Africa (in central Africa there are two species), northern Central America, Cuba, New Guinea, Indonesia, and northern India. Introduced species are known in Australia, New Zealand, Brazil, Chile and South Africa. No living Siricidae are native to South America, but a siricid fossil is found in Paleocene shales in Patagonia, Argentina. This indicates that the Siricinae were once much more widespread than they are now (Fidalgo & Smith 1987). The southernmost occurrence of living, native Siricidae in the Western hemisphere is northern Central America which coincides with the southern extent of the northern lineages of Conifers.

In the northern parts of Europe are represented the genera *Urocerus* (by three species), *Sirex* (three species), *Xeris* (one species) and *Tremex* (one species) are represented in the northern parts of Europe. The three first genera are conifer-feeders, *Tremex* is associated with deciduous trees.

8.2 General biology

Horntails are in flight in late summer and autumn, and their copulation takes place in tree-crowns. Females lay eggs often before copulation, these eggs producing males.

Horntails oviposit in weakened trees, frequently also in newly felled logs. Females drill deep into tree trunks to oviposit and at the same time inject mucus and arthrospores of a symbiotic fungus. The injected mucus has phytotoxic effects; this is demonstrated especially in *Sirex noctilio* (e.g. Spradberry 1973). The number of eggs laid depends on the size of the female. In average the ovaria contain 250600 eggs, but as many as 1000 eggs are counted in a female of *Urocerus augur* (Scheidter 1923). However, all eggs will not be laid.

Siricids live in symbiosis with basidiomycete fungi, and females carry spores of the fungi and introduce the spores into host trees during oviposition. The insect-fungus associations often damage or kill trees. In the Xiphydriidae, the presence of reservoirs of symbiont fungi was confirmed by Kajimura (2000).

The round gallery of a horntail larva is filled with fine, packed powder. The drying patterns in the top and base of a tree affect the proportions of larvae, which tunnel either up or down the tree. For the same reasons, the larvae, which originated from eggs deposited in the same drill shaft can emerge as adults at the same time but be of very different sizes. Therefore the length and shape of the larval gallery is related more to the performance and degree of invasion of the fungus than to the larvae. Moulting may follow the attainment of a particular minimum size and be attained without obligatory turning, as claimed by Rafes (1960). However, moulting is accompanied by a change in direction if the larvae encounter resin pockets, dense branch nodes or other larval galleries (Madden 1981, on *Sirex noctilio*). Pupation takes place in the larval gallery, usually a few centimeters from the trunk surface. The pupation stage lasts a few weeks; the young adult gnaws its way out and often remains in the gallery at the exit for a long time before leaving. The round exit holes of various sizes remain visible in the bark. The development from egg to adult takes

15 years (Nuorteva 1969). According to Escherich (1942), the development may take even 6 or more years, because emerged horntails may appear in new buildings made of wood or containing processed timber, several years after the construction of the building. They are able to pierce solid obstacles, even lead plates (Pax 1921, Escherich 1942).

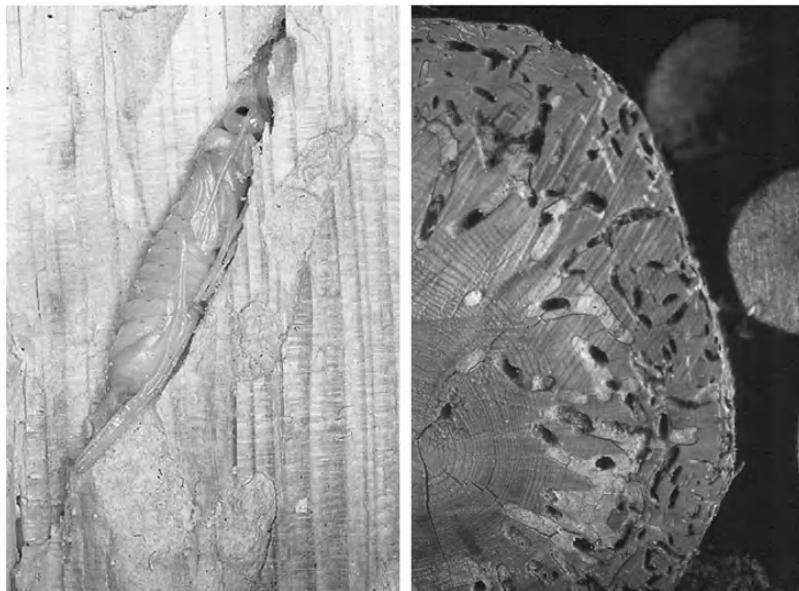


Figure 4. Left: pupa of female horntail (*Urocerus gigas*) in pupal chamber, note hardly visible frass-filled larval tunnels in the wood; right: log in cross section with abundant larval galleries of horntails (both pictures taken by Kari Heliövaara)

8.3 Associated organisms

Every horntail species carries only one symbiotic fungus species, but the same fungus can be symbiotic with other horntail species. The symbiont of many siricids is unidentified or uncertain. The fungus symbiosis is considered species specific in principal, but because of some conflicting information it needs a final verification. Wyniger (1974) used ordinary dried yeast for instant rearing of horntail larvae in cooked sawdust.

A few species of the wood-rottening basidiomycetes of the genus *Amylostereum* (Peniophoraceae) have been reported as symbionts of the conifer-feeding Siricinæ: *Amylostereum areolatum* (Fr.:Fr.) Boidin, *Amylostereum chailletii* (Persoon: Fries) Boidin, „*Amylostereum laevigatum*“ (Fries : Fries) Boidin.

Of these fungi, *A. areolatum* (Chaill.) Boid. is known only in connection with *Sirex*; *A. chailletii* (Pers.) Boid. occurs with *Sirex* and *Urocerus* (Gaut 1970, Talbot

1977), and *A. laevigatum* .with two species of *Urocerus* according to Tabata & Abe (1997, 1999a).

Two species of basidiomycetes (Polyporaceae) are proposed as symbionts in the genus *Tremex* (Francke-Grosmann 1938, 1939; Stillwell 1964, 1965); of those, *Cerrena unicolor* (Fr.) Murr. was isolated from the mycangia of *Tremex longicollis* in Japan (Tabata & Abe 1995).

In the Xiphydriidae the genus *Xiphydria* may have a shared symbiotic fungus, but its identification is not verified. Francke-Grosmann (1967) reported a fungus resembling the ascomycete *Daldinia concentrica* (Bolt.) Ces. and de Not., as the symbiont of some European species of *Xiphydria*. Kajimura (2000) discovered mycangia and mucus in adult female *Xiphydria ogasawarai* Matsumura woodwasps in Japan; the females examined carried a single unidentified fungal species in their mycangia. According to Sinadskij (1967), the imperfect fungus *Melanconium bicolor* Nees, was isolated from the tunnels of *Konowia betulae*, but perhaps it only contaminated the culture?

The mucus and the fungus together have a phytotoxic effect in the wood, causing resin flow (Spradbery 1973). This attracts more females to oviposit in the particular tree.

8.4 Natural enemies

There are several parasitoid species in the larvae of the horntails. Some insect parasitoids of horntails localize the eggs (Ibaliidae: *Ibalia*) or larvae (Ichneumonidae: *Rhyssa*) of the hosts by the smell of the symbiotic fungus, *Amylostereum areolatum* being more attractive to *Ibalia* than *A. chailletii* (Spradbery 1974). In addition, the parasitic nematode *Beddingia siricidicola* (Neotylenchidae) is of importance

8.5 Damage and control

Siricids are insects of economic importance in forestry. Most siricids attack only damaged or dying trees, and native species are secondary pests, which are not regarded dangerous. Because the larval tunnels are filled with tightly packed powder, the damage is often recognized only during further processing of sawn timber. Xiphydriids do not damage soft wood timber before the subsequent summer after the egg laying in Fennoscandian conditions (Löyttyniemi & Uusvaara 1977).

An introduced species can cause severe damage as seen in the case of *Sirex noctilio*. This species is rather harmless in Europe, but is able to kill relatively healthy trees in Australia, South America and South Africa, aided by its phytotoxic mucus and the symbiotic fungus (e.g. Spradbery 1973). The most destructive outbreak occurred between 1987 and 1989 in the states of South Australia and Victoria; more than 5 million *Pinus radiata* trees with a royalty value of A\$10-12 million were killed (Haugen *et al.* 1990).

S. noctilio is the only horntail known to be able to kill rather healthy trees, and in an outbreak of this species a high number of drills may remarkably weaken pine

trees. The flight period is in Europe in autumn, when the metabolism of trees is minimal. In Australia the flight period is in March-April, during the growing season of *Pinus radiata*. This may explain the importance of *S. noctilio* in the Australian region (Spradbery 1973). Another apparent factor is the stress of the introduced *Pinus radiata* in the hot and dry Australian climate. A National Sirex Fund was established in Australia in 1962 to finance survey, research, and eradication work in an attempt to prevent further spread. Control of *Sirex* populations established in a plantation is achieved by biological means using the parasitic nematode *Beddingia siricidicola* (by artificially inoculating nematode cultures into *Sirex*-attacked trees whence they sterilise, and are carried by the emerging *Sirex* adults), and parasitoid wasps (Elliott et al. 1998). *B. siricicola* was first used in the biological control of *Sirex noctilio* in Australia and New Zealand, by rearing and distributing the mycetophagous cycle (Bedding & Akhurst 1974, Zondag 1979). The nematodes inhibit the development of the ovaria and extensively diminish the number and size of eggs. Silvicultural treatment of *P. radiata* plantations by thinning to maintain or improve tree vigour is a key factor in preventing *Sirex* establishment or keeping damage within acceptable levels.

8.6 References

- Escherich, K. 1942. *Die Forstinsekten Mitteleuropas V*, Berlin.
- Fidalgo, P. & Smith, D.R. 1987. A fossil Siricidae (Hymenoptera) from Argentina, Entomological News 98, 63-66.
- Kajimura, H. 2000. Discovery of mycangia and mucus in adult female xiphydriid woodwasps (Hymenoptera: Xiphydriidae) in Japan.- Annals of the Entomological Society of America 93, 312-17.
- Madden, J.L. 1981: Egg and larval development in the woodwasp *Sirex noctilio* F, Australian Journal of Zoology 29: 493-506.
- Madden, J.L. & Coutts, M.P. 1979. The role of fungi in the biology and ecology of woodwasps (Hymenoptera: Siricidae). In: *Insect-fungus symbiosis. Nutrition, mutualism and commensalism*, Batra, L.R. (Ed.), New York.
- Madden, J.L. & Coutts, M.P. 1988. *Sirex* in Australasia. In: *Dynamics of forest insect populations*, A.A. Berryman (Ed.), Plenum Press, New York and London.
- Nuorteva, M. 1969. Beobachtungen über die Taxonomie und Bionomie von *Urocerus gigas* (L.) und *Sirex juvencus* (L.) (Hym., Siricidae), Annales Entomologici Fennici 35: 160-68.
- Pax, F. 1921. *Beobachtungen über Beschädigungen von Bleikämmern durch Holzwespen*, Jahresschrift des Vereins für Schlesische Insektenkunde zu Breslau.
- Quicke, D. 1997. Parasitic wasps, Chapman & Hall, London.
- Rafes, P.M. 1960. Type of galleries of siricids and regularities in the behaviour determining the form of its galleries in wood, Doklady Akad. Nauk SSSR 132: 478-480.
- Scheidter, F. 1923. Zur Lebensweise unserer Holzwespen, Z. Schädlingsbekämpfung, Berlin 1: 89-98.
- Spradbery, J.P. 1973. A comparative study of the phytotoxic effects of siricid woodwasps on conifers.- Annals of Applied Biology 75: 309-20.
- Spradbery, J.P. 1974. The responses of *Ibalia* species (Hymenoptera: Ibalidae) to the fungal symbionts of siricid wood wasp hosts, Journal of Entomology (A) 48: 217-22.
- Spradbery, J.P. 1977 The oviposition biology of siricid woodwasps in Europe, Ecological Entomology 2: 225-230.
- Spradbery, J.P. 1990. Predation of larval siricid woodwasps (Hymenoptera: Siricidae) by woodpeckers in Europe, The Entomologist 109: 67-71.
- Spradbery, J.P. & Kirk, A. 1978. Aspects of ecology of siricid woodwasps (Hymenoptera, Siricidae) in Europe, North Africa and Turkey with special reference to the biological control of *Sirex noctilio* F. in Australia, Bulletin of Entomological Research 68: 341-59.

- Spradberry, J.P. & Kirk, A. 1981. Experimental studies on the responses of European siricid woodwasps to host trees, *Annals of Applied Biology* 98: 179-185.
- Tabata, M. & Abe, Y. 1997. *Amylostereum laevigatum* associated with the Japanese horntail, *Urocerus japonicus*.- Mycoscience (Japan) 38, 421-27.
- Tabata, M. & Abe, Y. 1999. *Amylostereum laevigatum* associated with a horntail, *Urocerus antennatus*.- Mycoscience (Japan) 40, 535-39.
- Talbot, P.H.B. 1977. The *Sirex-Amylostereum-Pinus* association, *Annual Review of Phytopathology* 15: 41-54.
- Talman, P.N. 1948. O rogovhostah *Sirex gigas* L. I *Xanthosirex tardigradus* Ced. (Hymenoptera, Siricidae), Entomol. Obozr. 30, 82 -87.

9. PHYTOBIA BETULAE

Tiina Ylioja

9.1 Taxonomy & systematics

All extant species within the genus *Phytobia* Lioy (formerly *Dizygomyza* Hendel (subgen. *Dendromyza* Hendel)) within family Agromyzidae (Diptera) feed within the cambial cylinder of woody plants (Spencer 1976). *Phytobia* spp. in Europe feed e.g. on *Betula*, *Alnus*, *Salix*, *Populus*, *Corylus*, *Carpinus*, *Sorbus*, *Malus*, *Crataegus*, *Prunus* and *Quercus* (Spencer 1973, Barnes 1933, von Tscharnhaus 1992, 1993, Lee 1953). Over 50 *Phytobia* species have been described in the world and many tree species demonstrate typical larval galleries of *Phytobia* spp., but often the link between the insect and the host is unknown (Spencer 1973). Von Tscharnhaus (1992, 2000) synonymized *Phytobia betulae* Kang. with *P. cambii* Hendel, a species that feeds on *Salicaceae* and is reported from willow and poplar plantations (Barnes 1933, Moraal 1986). Allozyme studies in Finland, however, demonstrate the existence of a separate species that feeds in *Betula* sp. and *Alnus* sp. (Nyman *et al.* 2002) referred as *Phytobia betulae* according to Kangas (1935). *P. cambii* and *P. betulae* are similar both in their morphology and biology.

9.2 General biology

P. betulae is univoltine and adults emerge in early summer (Kangas 1935). Adults of *P. betulae* are black and ~ 4 – 5 mm long (Kangas 1935). Females oviposit into the new current year's shoots within the crowns of birch trees (*Betula pendula* Roth and *B. pubescens* Ehrh.). They position a single egg with their ovipositor under the soft bark. Eggs are white and oval. The duration of egg stage is ~ 1 week. After hatching, larvae mine towards the stem and downwards in the stem within the layer of differentiating xylem in the cambial cylinder (Ylioja *et al.* 1998). Larval tunnels are filled with brown parenchyma tissue and can be extremely long (17 m), typically reaching the base of the trees (Ylioja *et al.* 1998). The tunnels become up to 3-4 mm wide as larvae grow. Larvae are slender, cylindrical, white or transparent (early instar). Larval mandibles both have two teeth, the two on the left about half in length than those in the right. Last instar (3rd) measures 15 – 20 mm. Narrow larval tunnels are difficult to detect up in the canopy where they start from. Typical larval tunnels

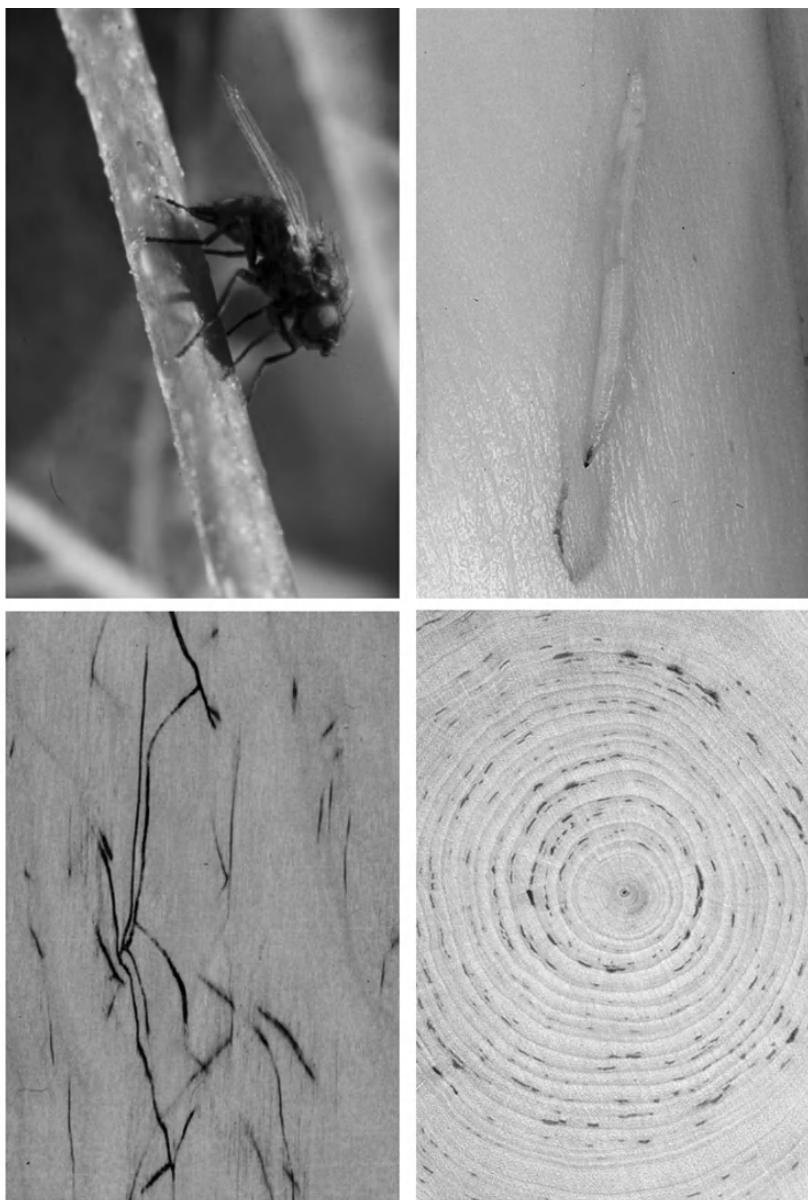


Figure 5. Upper left: ovipositing female of *Phytobia betulae* (photo: J. Lehto); adult (photo: J. Lehto); upper right: larval gallery with almost invisible larva of *P. betulae* (photo: J. Lehto); lower left: typical old and dark-brown longitudinal larval galleries in the veneercut from an infested log (photo: J. Lehto); lower right: cross section of birch tree with cut larval galleries in many annual rings indicating a long period of attacks (photo: M. Rousi).

contain short side-branches that are more frequent at the distal end of the tunnels (Ylioja *et al.* 1998). If trees are short, larvae reverse their direction and mine upwards and again downwards at the stem base and in the roots until they are ready to pupate. Larvae come out through the bark in late summer or early autumn, at the base of the stem or roots and pupate under the litter layer or deeper in the soil. Pupae overwinter. Barrel shaped puparium is light-yellow or whitish.

As the life cycle repeats itself year after year larval tunnels create a record within the annual rings of the host tree of the past abundance of larvae. Larval tunnels visible in stem cross-sections are referred to in the literature as 'pith flecks', 'parenchyma flecks' or 'medullary spots'.

9.3 Host finding

Phytobia betulae is common throughout Finland and elsewhere in Scandinavia. This may indicate that their dispersal is efficient. Host finding is not a well known process. Vision and olfaction and gustation likely play roles. After landing on a shoot, females test the shoot with their ovipositor, behaviour that has been described also for *P. cambii* (Coutin *et al.* 1990). Successful ovipositions (from which larvae hatch) are concentrated on fast growing shoots in the upper parts of crowns (Ylioja *et al.* 2002).

9.4 Host resistance

Trees of all ages can be attacked by *P. betulae*. No mechanisms for resistance against *P. betulae* are known. Fast growth of trees benefits *P. betulae*: fast growing birch genotypes are susceptible and environmental factors that enhance growth (e.g. silvicultural practices, site quality, fertilizers) increase susceptibility (Ylioja *et al.* 2001, 2002, Ylioja and Rousi 2001). Years with high radial growth are especially suitable for *P. betulae* larvae (Ylioja *et al.* 1999). Fast growing trees may provide more suitable feeding material than slow growing trees or the quality of plant tissue improves for the herbivore. Furthermore, if radial growth lasts longer in fast growing trees than in slow growing trees, it allows more time for larvae to finish their development. Absolute abundance of *P. betulae* in a tree increases until trees reach the age of ~30 years, and declines as trees grow older (Ylioja *et al.* 1999).

9.5 Associated organisms

Associated organisms for *P. betulae* are not known. Barnes (1933), however, described an inquiline gall midge *Profeltiella dizogymzae* sp. n. (Cecidomyidae) in larval tunnels of *P. cambii*. There has been some concern that *Phytobia* sp. could introduce plant pathogens (bacteria and fungi) either via oviposition or the resulting larval tunnels.

9.6 Natural enemies

Pupae of *P. betulae* have been parasitized by two species of Braconidae (Hymenoptera), *Sympyta hians* Nees. and *Sympyta ringens* Hal., and one species of Ichneumonidae, *Cremnoderes atricapillus* Grav. (Moraal, 1987). Parasitoids place their eggs probably into eggs or first instar of *P. betulae*. Predation on pupae has not been studied. Presumably pupae under the litter layer and within the soils are vulnerable to predation, e.g. by small mammals, predatory insects, and ground-feeding birds.

9.7 Damage and control

Brown coloured larval tunnels are an aesthetic defect in birch wood used for furnishings, interior design and carpentry, including furniture, floorings, doors, panels, plywood, veneer and wooden ornaments and objects. *P. betulae* is harmful in Scandinavian countries, especially in Finland, where 15% of the growing stock is birch and there is a long tradition in processing birch. Larval tunnels lower the quality and value of finished products and affect the efficient use of raw material. The economic significance of *P. betulae* is appreciable when otherwise superior raw material has to be downgraded due to larval tunnels. Special quality logs that are free of *P. betulae* have much higher value than ordinary birch logs. On the other hand, compared to the whole use of wood in Finnish Forest Industry the proportion affected by *P. betulae* is small. Of the annual use of birch in Finland, 2% is used as saw timber and 11% is used in plywood industry; in the latter, only a part of the products are aimed for furnishings.

P. betulae is a common species that occurs at relatively low numbers and without conspicuous outbreaks: e.g., 6 - 38 larvae tree⁻¹ year⁻¹ in a 47-year-old birch stand (Ylioja *et al.* 1999). The damage it causes cannot be recognized from the outside appearance of birch trees. *P. betulae* does not weaken trees for secondary pests. Larval tunnels do not affect the physical strength of wood, but may weaken very thin veneer. The latter has been mentioned with respect to *P. cambii* tunnels in poplar used for cheese boxes in France (Régnier 1952).

There are no known methods for control of *P. betulae*. Growing birch mixed with conifers has been suggested to decrease damage. Conifers could interfere with host finding, but the lower density of larval tunnels in birch grown in mixed stands appears to be related to decreased growth of the birch trees among conifers. Old birch trees have most of the outer rings free of larval tunnels especially in the lower stem, which increases the yield of veneer that is free of *P. betulae* tunnels.

9.8 References

- Barnes, H. F. 1933. A cambium miner of basket willows (Agromyzidae) and its inquiline gall midge (Cecidomyiidae). 1933. The Annals of Applied Biology 20, 498-519.
- Coutin, R., Martinez, M & Gumez, J.-L. 1990. Comportement de ponte sur Populus des femelles de *Phytobia cambii* (Hendel), (Diptera, Agromyzidae). 2. Conference Internationale sur les Ravageurs en Agriculture. 4-5-6 Decembre 1990, Versailles. Annales ANNP, Paris (France) 2, 651-54.
- Kangas, E. 1935. Die Braunfleckigkeit des Birkenholzes und Ihr Urheber Dendromyza (Dizygomyza) *betulae* n. sp. Vorläufige Mitteilung. Comm. Inst. For. Fenn. 22, 31 pp.
- Lee, N. R. 1953. Note on a plum cambium miner (Agromyzidae). in: Rep. E. Malling Res. Sta. for 1952.

- Martinez, M., Gumez, J.-L. & Munnier, P. 1985. Un ravageur mal connu: la mouche mineuse du cambium des peupliers. *Phytoma* 372, 51-53.
- Moraal, L.G., 1987. [*Cremnoderes atricapillus*, a new parasitoid of the cambium miner, *Phytobia cambii*, with notes on *Sympya* spp. (Hymenoptera: Ichneumonidae; Diptera: Agromyzidae)]. *Entomologische Berichten Amsterdam* 47, 5-8.
- Nyman, T., Ylioja, T. & Roininen, H. 2002. Host-associated allozyme variation in tree cambium miners, *Phytobia* spp. (Diptera: Agromyzidae). *Heredity* 89, 394-400.
- Régnier, R. 1952. Importance des dégâts de la mineuse du cambium du peuplier pour l'industrie du déroulage. in: *Transactions of the IXth International Congress of Entomology*, Amsterdam, August 17-24, 1951, Volume I.
- Spencer, K. A. 1973. *Agromyzidae (Diptera) of economic importance*. Series *Entomologica* vol. 9. Dr. W. Junk. B. V. Publishers, The Hague.
- Spencer, K. A. 1976. *The Agromyzidae (Diptera) of Fennoscandia and Denmark. Fauna Entomologica Scandinavica. Vol. 5*. Scandinavian Science Press Ltd. Klampenborg, Denmark.
- von Tschirnhaus, M. 1992. Minier- und Halmfliegen (Agromyzidae, Chloropidae) und 52 weitere Familien (Diptera) aus Malaise-fallen in Kiesgruben und einem Vorstadtgarten in Köln. *Decheniana-Beihefte* 31, 445-97.
- von Tschirnhaus, M. 1993. Minierfliegen (Diptera: Agromyzidae) as Malaise-Fallen in spezifischen Pflanzengesellschaften: Ein Weinberg der Ahr-Eifel in Entwicklung zu einem Felsenbirnen-Gebüsch (Cotoneastro-Amelanchieretum). *Beiträge Landespflege Rheinland-Pfalz* 16, 481-534.
- von Tschirnhaus, M. 2000. Agromyzidae. In: *Die historische Dipteren-Sammlung Carl Friedrich Ketel Revision einer zwischen 1884 und 1903 angelegten Sammlung von Zweiflüglern (Diptera) aus Mecklenburg-Vorpommern*. Ziegler, J. & Menzel F. (Eds.) Nova Suppl. Ent. Berlin.
- Ylioja, T., Hinkkanen, S., Roininen, H. & Rousi, M. 2002. Oviposition and mining by *Phytobia betulae* (Diptera: Agromyzidae) in genotypes of European white birch (*Betula pendula*). *Agricultural and Forest Entomology* 4, 11-20.
- Ylioja, T., Roininen, H., Ayres, M. P., Rousi, M. & Price, P. W. 1999. Host-driven population dynamics in an herbivorous insect. *Proc. Natl. Acad. Sci. USA* 96, 10735-40.
- Ylioja, T. & Rousi, M. 2001. Soil fertility alters susceptibility of young clonal plantlets of birch (*Betula pendula*) to a dipteran stem miner. *Écoscience* 8, 191-98.
- Ylioja, T., Saranpää, P., Roininen, H. & Rousi, M. 1998. Larval Tunnels of *Phytobia betulae* (Diptera: Agromyzidae) in Birch Wood. *J. Econ. Entomol.* 91, 175-81.

Research needs and priorities for Europe

Chapter 23

GENERAL CONCLUSIONS AND RESEARCH PRIORITIES FOR BAWBILT ORGANISMS IN EUROPE

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As surmised in the introductory chapter, studies of BAWBILT organisms has been for a long period characterized by scattered research effort in several languages all over Europe with few opportunities for interactions accompanied by duplications of research in some areas, and the persistence of gaps in others. Nevertheless, with presently more than 200 experts working in the BAWBILT fields, the research potentialities are high in Europe, although unequally distributed among the different countries as far as the forest area is concerned (Battisti and Faccoli, chapter 2). The present synthesis evidently reflects this diversity of approaches. Many advances have been made in all fields of BAWBILT research, but this has been uneven. We present below the weighing up of this synthesis and propose research priorities for Europe in the field of BAWBILT organisms. We will first discuss each group separately and will then conclude with proposals regarding research fields that deserve to be developed through European collaboration in the coming years.

1. BARK BEETLES

Because of their high economic impacts, a considerable research has been devoted to bark beetles in Europe during the last 30 years, which has resulted in very significant progress in the knowledge of bark beetle biology in general, their taxonomy and phylogeny, their communication systems, and their relations with the host tree, other living organisms (associated fungi and pathogens, parasitoids, predators, etc.) and abiotic factors. Synthetic theories have been developed regarding their population dynamics and the risk of damage. Practical applications

have been proposed from these different research fields and some have been tested in nature, but results are far from enabling the construction of general models and integrated methods to evaluate damage risks and control beetle population levels preventatively or curatively. Considerable work is needed in each of these fields, as well as their interrelations since all the above-mentioned factors interact with each other in bark beetle population dynamics. Moreover, investigations at the level of individual organisms are still necessary to understand the detailed mechanisms of the interactions, while the comprehension of population dynamics relies on studies at the population level.

European bark beetle species and their relative systematic position need to be defined in detail by sequencing specific regions of the DNA in phylogenetic studies, in relation to morphological characters. For phylogeography, fast evolving genetic markers, such as microsatellites, are needed to analyse questions related to recent past and quarantine aspects (Stauffer, chapter 6). Only a few have been (recently) isolated for bark beetles. Genetic studies will also be very useful to evaluate the possibilities of beetle adaptation to new hosts (climatic change, introductions) or to selected hosts (resistance). In taxonomy, the morphological characters of the immature stages of many species are still unknown (Knizek and Beaver, chapter 5).

Although the most damaging species have been intensively studied, progress in the understanding of their life cycles is needed. Indeed, as a consequence of scattered research teams, most life cycles have been described in relation to conditions in a particular region. This progress is needed especially in the field of the effects of environmental factors and their interactions on the life cycles (for example, temperature and photoperiod). It would allow the construction of models applicable in large areas of Europe. (Sauvard, chapter 7). The model of bark beetle population dynamics proposed for the aggregative species, built at the tree level, is difficult to use in forest management. The reasons refer to the facts that areas occupied by bark beetles are poorly known, due to difficulties in appreciating their spatial distribution at the forest scale, and that no good estimator of population levels is available (Sauvard, chapter 7). The only available estimate is the level of damage, which is not accurate and utilizable only at an epidemic level. Also, although the key factor (tree resistance, see Lieutier, chapter 9) has been the subject of many studies, several other parameters of the population dynamics are still poorly understood (mortality during dispersal, role of sister broods). The role of insect quality is completely unknown. Capacities for modelling population dynamics of European bark beetle species is much lower than for North American species, due to lack of models regarding the different parameters of the dynamics (Sauvard, chapter 7). Approaches managing space-time data, such as G.I.S., will be very useful to better understand bark beetle population dynamics, if they develop in parallel to bark beetle population modelling.

Chemical communication is an important aspect to consider in the scope of managing bark beetle populations and their damage to host trees. There is still a lot to do in nearly all fields of the chemical ecology of the insect-insect and insect-plant relationships (Byers, chapter 8). Promising new fields especially need to be developed with regard to practical applications. These include the roles of

semiochemicals in tri-trophic interactions, and the role of non host compounds in relation to beetle behaviour.

Knowledge of the mechanisms of conifer resistance to European bark beetles has increased considerably during the last 20 years, but still many aspects are not understood (Lieutier, chapter 9). The respective roles of the various defence systems are not very clear. Information on several points of the defence mechanisms themselves is needed, not only for the recently described systems (induced resin flow and induced resistance), but also for the preformed defences and the hypersensitive reaction (Lieutier, chapter 9). Sapwood defences are very poorly understood, although they certainly play a role in the establishment of the aggressors. Detailed mechanisms on elicitation and development of the induced defences are almost completely unknown. Effects of these defence systems on insects and fungi have been poorly investigated, especially for the European species. The role of tree genetic factors merits development by focusing on the utilization of resistance predictors at juvenile stages of the trees. Possible counter-adaptations by beetles and fungi should also be studied. Research in relation to environmental factors is particularly needed in relation to global change (Lieutier, chapter 9). Considerable gaps exist both in Europe and North America regarding the effects of these factors on the mechanisms involved in tree defence systems, be they attacks on trees by other organisms (defoliators, pathogens), water or nutrient stress, fire, pollution, or others. Very little information is available either regarding the relations between silviculture (thinning, tree biodiversity, etc) and tree resistance, although this represents a considerable component of modern forestry. Characterizing the physiological state of the stands in relation to their susceptibility is also a necessity prior to building risk prediction models. Almost nothing is known regarding defence systems to bark beetle attacks in deciduous trees.

Considerable progress has been made in the knowledge of fungi from the Ophiostomataceae family associated with bark beetles. However, the meaning of the association is still a matter of discussion, especially regarding the role of the fungi and the spore load carried by the beetles in exhausting tree defences, the relations between their pathogenicity and beetle aggressiveness, and their role in the tree killing process (Lieutier, chapter 9; Kirisits, chapter 10). Relatively few associations have already been studied and research is needed in a large array of models if we want to clarify the debate (Kirisits, chapter 10). Moreover, certainly a large number of *Ophiostoma* species are still to be discovered and further surveys will improve the knowledge on taxonomy, ecology and biogeography of these organisms. In this task, as for the bark beetles themselves, the use of molecular markers will help considerably. The species composition of the fungal flora associated with a given bark beetle species varies considerably between localities, even over short distances, and the factors driving these variations are still poorly known (Kirisits, chapter 10).

As in North America, research on parasitoids and predators of European bark beetles has been concentrated on a few beetle species, leaving the natural enemy complex of others almost completely unknown (Kenis *et al.*, chapter 11). This is a regrettable gap because most natural enemies are not host- or prey-specific and knowledge on enemies of secondary beetles would help in understanding the natural control of the economically important species. Moreover, research has been more

focused on parasitoids, whereas predators have been largely under-investigated, although they also have large potential for natural regulation of beetle populations (Kenis *et al.*, chapter 11). The available information differs largely between species in the same group. The role of natural enemies in bark beetle population dynamics needs to be better assessed. Except for the *D. micans* / *R. grandis* relationships, few attempts to use the natural enemies have been made in the field. Classical biological control must be considered, owing to the possibility of introductions of exotic bark beetle species to Europe. However, because presently all European bark beetle pests are indigenous, biological control by favouring indigenous natural enemies seems most promising. Taxonomy and identification studies for natural parasitoids and predators are also an important field that needs to be developed, since identification is a crucial step in any biological control program (Kenis *et al.*, chapter 11). Many species of pathogens have been described, but very little is known on their impacts on populations and effects on the hosts (Wegensteiner, chapter 12). This information is needed, in relation to the period of the year, host generation or environmental factors. Many pathogens (viruses, fungi, microsporidia) seem promising for the biological control of bark beetles, but methods for artificially contaminating beetles must be investigated, as well as infectivity of the pathogens for the non-target organisms, before envisaging practical control aspects.

2. WEEVILS

Among the twenty-two species of Curculionidae which are listed in this volume as bark and wood boring weevils of living trees in Europe, only three genera are likely to be considered pests of trees and only one species is genuinely a persistent problem in forestry. Species of the genus *Pissodes* are capable of killing trees although their role as primary or secondary pests requires further clarification. Species of *Otiorrhynchus* can seriously damage seedling crops, but such reports are rare and localised in Europe. Nevertheless, further investigation of *Otiorrhynchus articus* and *O. nodosus* would seem prudent since current understanding rests largely on the better known surrogate, *O. sulcatus*.

Hylobius abietis is arguably the single most economically important forest weevil pest in Europe, hence much of the existing literature and a significant part of this volume is devoted to it. How far has this research effort informed current forest management? The goal of successfully replacing the use of insecticides for seedling protection in all plantation forests and at no additional cost may seem a long way off. However, much progress has been made in suggesting measures which may improve seedling survival, as several chapters emphasise (Långström and Day, chapter 19; Day *et al.* chapter 14; Schlyter, chapter 15; Wainhouse, chapter 16; Kenis *et al.*, chapter 18). It is clearly already possible to achieve adequate seedling protection by combining silvicultural methods with physical barriers, but hitherto, the relatively high cost has not encouraged the universal implementation of this approach. Changes to the unit cost and effectiveness of physical barriers seems now to give cause for optimism. A new type of barrier consisting of a flexible coating containing mineral particles and applied to the lower part of the seedling stem can

provide good protection at low cost through mass use and machine production (G. Nordlander, pers. comm.). With rational application, low cost per plant and long-lasting protection, this approach could be successful.

The investigation of silvicultural management of pine weevil damage has paid dividends in recent years. The Swedish research effort, for example, has demonstrated through carefully designed field experiments to what extent seedling conifers can be protected, at what cost, and the mechanisms for this protection from an ecological perspective. Continued experimentation on weevil behaviour, physiology and performance are vital to understanding the processes which will eventually underpin an effective and flexible pest management system.

Important aspects of the biology of all BAWBILT weevils still require investigation. As well as *Hylobius*, adults of *Pissodes* spp. have been poorly studied, especially in the field. Very little is known about the chemical relationships between *Pissodes* species and their hosts. This has proved an important area of knowledge supporting the management of *Pissodes* pests in N America and should also be given attention in Europe (Day *et al.*, chapter 14). Should a sex pheromone be identified for *Hylobius*, it would be a useful route for testing a low-volatile compound for behavioural modification (Schlyter, chapter 15).

The plant-insect interface will continue to be a priority target of research. Dispersal and reproduction of *Hylobius* are both dependent on adult feeding, which in turn must be selective in order to acquire sufficient nitrogen. To some extent, the main bark defensive system – resin – mediates the pattern of feeding (Wainhouse, chapter 16). Bark feeding therefore has two important outcomes – one is the amount of short-term seedling mortality it generates and the other is the longer-term effect of adult nutrition on subsequent population growth (and the probability of exporting future weevil problems to other sites).

The relationships between consumption of bark, reproduction, and the development and resorption of flight muscles and migration are poorly understood. How does bark feeding relate to seedling damage and are there conditions at a site that mitigate feeding? Where do weevils occur in the forest environment and where do they feed? These are rather obvious but, as yet, unanswered questions. The ecology of larval and maturation feeding needs to be better understood so the outcomes of reproductive success and damage to seedlings can be modelled.

Seedling conifers seem very vulnerable to attack by pine weevils, but even small degrees of resistance may play a part in the future integrated management of this pest. The underlying mechanisms of resistance to feeding need further exploration; existing research indicates a role for both induced resistance and tolerance but field and laboratory investigations are needed to show how plant phenotype influences resistance expression (Wainhouse chapter 16). The effect of seedling size on the damage sustained from weevil attack is one of a number of phenotypic characteristics that are only partially understood (Wainhouse, chapter 16; Långström and Day, chapter 19). The structure and activity of antifeedants deserve more attention; adult feeding decisions are partly based on contact chemoreception , and may be redirected (Schlyter, chapter 15).

Conditions in the conifer stump which affect the number of weevils emerging from a site, have received some attention, but not enough. It is here that most of the

weevil life cycle is played out yet we know little about the range of factors which determine the performance of weevils in this environment. Field experiments are needed to verify the possibility of high larval mortality in the early stage of root-stump colonisation (Wainhouse, chapter 16).

Populations of *Hylobius abietis* are highly damaging to forest trees, but they are also elusive and difficult to track in time and space. Our knowledge of their population dynamics is still rudimentary, yet this knowledge is essential to predicting the potential impact of management and to fully understanding the relationship between silviculture and the impact of weevils on transplanted seedlings. As we have implied, larval development will require more intensive study and overall levels of larval mortality (including that attributable to natural enemies) must be investigated more holistically. Eventually, such knowledge will contribute to the estimation of site-related adult production and the subsequent risks to neighbouring and more distant sites.

Existing data and new experimental data should be harnessed to generate useful, thermally-dependent developmental models for larvae and adults so that the presence of weevils on a clear cut can be described by thermal data. Such models will require a stochastic approach, so that the ranges of temperature that might be dependent on larval position in the soil or site structural factors, can be readily incorporated and can help predict the outcome in terms of weevil phenology or performance. Risk rating systems should be based upon better, spatially-explicit population models which can express the results of new research on, for example, the population consequences of insect-plant interactions, the effect of thermal environment on insect development, or the influence of silvicultural interventions.

Work will continue on finding new and improved tools for suppressing weevil populations or limiting their access to forest seedlings. Many of these tools have commercial potential. Some, like natural enemies, could be sustainable solutions. The role of parasitoids and other natural enemies in regulating populations of their weevil hosts is unclear (Kenis *et al.*, chapter 18). While the overall impact of parasitoids on populations of *Pissodes* is likely to be considerable and on *Hylobius* or *Otiorrhynchus*, much less (Kenis *et al.*, chapter 18), there is scope for integrating small gains in host population reduction with other control strategies. In particular, design and implementation of strategies for enhancing parasitoid impact through silvicultural management should be a priority. On the subject of the use of biocides, there is further potential for the formulation of commercially competitive nematode products for application against *Hylobius*.

In conclusion, the literature on BAWBILT weevils, particularly *Hylobius*, is considerable but only in recent years has the pace of research accelerated in order meet the demands of forest protection and forest environmental policy. This research has created a platform in several novel and promising areas. It is from these that further research results will need to emerge in order to successfully tackle one of the major challenges to Europe's forest industry.

3. BUPRESTIDAE AND CERAMBYCIDAE

The two beetle families Buprestidae and Cerambycidae offer interesting contrasts in their biologies and, particularly, their pest statuses within the overall BAWBILT group of organisms. Although there are pest representatives in both families, either in their own rights or as vectors of damaging organisms (e.g. cerambycids in the genus *Monochamus* are vectors of the highly destructive pinewood nematode, *Bursaphelenchus xylophilus*), the majority of representatives are scarce and, often, of biodiversity significance.

Among the pest representatives in the Buprestidae, most attention has been paid in central and southern parts of Europe where they can be quite destructive and have been linked to climate change. With the exception of the genus *Phaenops*, all are pests of broadleaved trees. In relation to future studies of this group an important consideration should be the interface between pest status and biodiversity status. There is clearly a fine balance between these two extremes and there is too little information on the environmental and population dynamics characteristics that determines the final status of a given species. In addition, interaction with other groups of BAWBILT organisms, especially the Scolytidae, requires attention. The fact that some buprestids have moved internationally and are causing significant damage in new regions of the world (e.g. *Agrilus planipennis* is killing ash trees in north America after its introduction from China) is also a subject for future research.

Cerambycidae are ubiquitous components of natural and managed forests and are generally at relatively low levels, especially when there is relatively little weakened or freshly killed material present. In this sense they tend to be regarded as "technical pests" causing damage to the final wood product rather than killing trees in their own right. However, the switch to attacking living trees, albeit usually when they are weakened, is a characteristic that requires further study both in their native ranges and when they have established in new locations, e.g. *Tetropium fuscum* in Nova Scotia. Other species, exemplified by *Phorocantha semipunctata* and *Anoplophora glabripennis* have caused significant damage to living trees as they have moved around the world in international trade and have established in new locations. More studies are needed of the nature of the interactions that lead to successful establishment in a given area and, particularly, to the factors that lead to tree damage and mortality.

Although both families of beetle are regarded as being associated with stressed trees, the question of climate change and increased availability of exotic tree hosts may change this perception over time. Research into the future effects of differing climatic conditions, compounded with local site characteristics should be studied at a European scale, especially since the range of climatic and environmental conditions in this area is already quite large.

4. NON-COLEOPTERAN BAWBILT ORGANISMS

In comparison with bark beetles and pine weevils, the species treated under part 4 are clearly less important as pests on living trees. They seldom cause tree mortality and the growth losses resulting from attacks by some of the species are mostly modest and transient. The horntails constitute one exception to this statement, as

they - outside of Europe - have become serious pests in pine plantations in the southern hemisphere. The main damage caused by this diverse group of "other" BAWBILT-organisms is related to the wood formation of the growing trees where they may inflict severe and lasting disturbances that eventually will affect the quality of the end product, the harvestable timber. Thus, their damage is in fact comparable to that caused by "true" timber pests i.e. insects that degrade the timber quality after the trees have been felled. As for most timber pests, there are few, if any, control options available against current attacks by any of these other BAWBILT organisms. The main emphasis in research and practical forest protection should hence be on preventing damage from occurring rather than controlling ongoing attacks. Understanding the population dynamics of the pest species in question as well as the host resistance mechanisms are crucial for any forest protection strategy and especially those based mainly on damage prevention.

As has been shown in part 4, the general biology of these BAWBILT pests is fairly well known but their population dynamics are still poorly understood. In most of these species, population regulation seems to be more of the bottom-up-type. i.e. host factors may be more important than natural enemies in the population dynamics of these, and probably most of the species described in this book.

Typically, most BAWBILT species live in an intimate relationship with their host plants, as most of the life cycle is spent inside the living plants, mainly in the phloem but sometimes also in the xylem of the stem, branches, shoots or buds. Thus, the pest-host interaction becomes central in the understanding of the population dynamics of the BAWBILT pests. Although considerable knowledge has been gathered in recent decades about host defence strategies and systems, much remains to be discovered regarding the genetic, physiological and chemical basis for host resistance. Considering the powerful study tools that are becoming available via biotechnological research, it seems reasonable to assume that, given the research opportunities, we could elucidate much of the physiological and chemical properties relating to pest resistance in different host species, and that this could open up new avenues for selection or breeding of more resistant varieties, or even immunity to pests via genetic engineering.

On the other hand, processes involved in host and mate finding of the pest species, offer tools for monitoring and disturbing pest populations. Sexual pheromones have been identified for most of the lepidopteran species included here, and probably exist for all of them. The host finding and selection processes are still poorly understood in all these species, but deserve more attention.

At least in some of these species (*Aradus*, *Dioryctria* and *Phytobia*), cultural practice and stand composition seem to play important roles in damage occurrence. Mixed stands seem to suffer less damage, but the reasons for this are still unknown, although mixed stands are thought to support more natural enemies which in turn may stabilize pest populations. Site quality and stand treatment may play different roles for different pests, as the occurrence of *Aradus*-damage clearly decreases with increasing soil fertility, whereas the pattern is rather the opposite in *Dioryctria*. These examples show that there is a potential for preventive measures incorporating novel forest management schemes promoting biological control and increased tree vigour against BAWBILT pests.

5. RESEARCH PRIORITIES AT THE EUROPEAN LEVEL

Research prospects that we consider essential in the BAWBILT domain in relation to the present needs of society, and that should be developed in a cooperative approach at the European level, can be grouped into two main areas. The first concerns the further development of the most essential and promising fields which have been identified by consideration of accumulated research, including the need to fill important and fundamental gaps that impede our understanding of the mechanisms of population dynamics. The second is concerned with new situations, particularly in the socio-economic sphere, that characterize the beginning of the 21st century.

5.1. Promising fields to be developed and fundamental gaps to be filled, arising from previous research

5.1.1. Better understanding population dynamics of European BAWBILT

A good knowledge of its population dynamics will always be the key to open the door on damage risk evaluation and control methods of a pest. In none of the European BAWBILT species, is this knowledge sufficient. Factors appearing to play a key-role have been studied more thoroughly, such as tree resistance for most bark beetle pest species. However, rarely is one factor alone a sufficient explanation for observed insect population dynamics. Other factors suspected of playing at least an important secondary role have been largely underestimated for all BAWBILT. This is especially the case for natural enemies and diseases, which would be worthy of a joint research effort in order to take into account a wide range of natural situations. Similarly, the quality of both the host and the insect merits rapid and joint consideration by the community of European BAWBILT scientists. The nutritional quality of the host has almost never been considered in North America and research on this factor in Europe has just begun on *H. abietis* (Wainhouse, chapter 16), although certain aspects of the tree constitutive defences may be considered in this direction (Lieutier, chapter 9). Research on qualitative variations in beetle populations, especially by comparing endemic and epidemic populations, should give very useful information on the role of insect quality in population dynamics. This approach has started recently on bark beetles in both North America (*D. rufipennis*) and Europe (*I. typographus*) and has concerned the morphometry, the behaviour, the genetics and the associated fungi of the beetles (Wallin and Raffa, 2004; Sallé, 2004).

There are thus several parameters that deserve to be considered for a better understanding of population dynamics of European BAWBILT organisms. In such a situation, a holistic approach at a European scale, taking into account several factors which possibly interfere with population dynamics, is recommended. We suggest that one BAWBILT model be chosen for which all these factors will be studied simultaneously and at a wide scale. Considering the accumulated knowledge, the available methodologies, and the economic interest, *I. typographus* and *T. piniperda* seem the best candidates.

In relation to beetle population dynamics, a reliable and accurate method of rapidly estimating the beetle population level is urgently needed. Owing to the diversity of the natural situations, it can only result from a European cooperative program. Looking for indicators related to qualitative characteristics of the populations such as those cited above, might be a promising research track.

5.1.2. To define pan-European policies and develop control methods (genetic selection, silviculture, IPM).

Damaging BAWBILT pest organisms ignore boundaries, and damage often extends over areas spanning several different countries at the same time or consecutively. There is a crucial need for building common control procedures and defining pan-European policies. A first step towards this objective has been met within the BAWBILT EU project through a tentative approach to estimating damage on a common basis and to synthesize control methods (Grégoire and Evans, chapter 4). Future exchanges of information and integration of experiences from various European countries, parallel to improvements in knowledge of pest population dynamics, are needed to go further and to develop procedures of wide applicability. It is also essential, probably as the next step, to improve quantification of the cost and effectiveness of pest management. Intensive cooperation with socio-economists is evidently needed.

Regarding control itself, very few field assays have been made and only in some localities. In particular, IPM approaches on *Hylobius* control that have been developed in Sweden and UK should be extended to other parts of Europe (Långström and Day, chapter 19). Tree resistance offers several promising perspectives for applications in both genetic selection and silviculture (Lieutier, chapter 9). Chemical indicators of Norway spruce and Scots pine resistance to bark beetles should be thoroughly studied and the findings extended to several conifer species with research emphasis on their applicability at the juvenile stage of the tree. Resistance is known to be expressed both genetically and environmentally, the latter bring modifiable through silvicultural manipulation. The potential for research here justifies the development of cooperative projects aimed at defining the possibilities of manipulating tree resistance through silviculture. Basic research is, however needed in the field of the relationships between tree resistance and environmental factors (Lieutier, chapter 9 and see 5.2.1).

5.1.3 Filling gaps regarding BAWBILT species of secondary economic importance and species of broadleaves trees

The number of published papers on the different European BAWBILT species is related directly to the economic importance of the organisms. This situation is particularly evident for bark beetles for which one fifth of the research papers deals with *I. typographus* and half with 6 species only (Sauvard, chapter 7). It is even more striking for weevils where a very large majority of research papers is devoted to *H. abietis* (Day *et al.*, chapter 14). This seems logical because there is a crucial need to control dangerous species, and the consequent higher likelihood of obtaining funding to study these species. The consequences, however, are that only the

biology of these dangerous species is known in detail. Detailed information on less damaging species is often dramatically missing, although it would be very useful for comparisons and generalization, and would certainly also lead to a better understanding of the reasons for the aggressiveness of the dangerous species. There is therefore a wide and regrettable gap in our knowledge of secondary BAWBILT organisms, and this situation is the same everywhere in the world. Similarly, the role of BAWBILT organisms in deciduous stands has attracted little attention, due to their much lower pest status than in conifer stands. It is especially true that resistance mechanisms in these trees are completely unknown with regard to attacks by BAWBILT organisms.

5.2. New fields to explore in relation to the emergence of a new social context

5.2.1 The environmental dimension and global change

Placing BAWBILT research in the context of global change is essential, since relations between environment and society are global priorities at the beginning of the 21st century. In all fields considered in the different chapters of this synthesis, several aspects still need to be studied to understand BAWBILT basic biology, their relations with other organisms, and their population dynamics. However, almost all chapters have also emphasized that information regarding the effects of environmental factors represent a large gap. This gap is regrettable in the present context. The environmental dimension should be taken into account while improving knowledge on various topics, and all fields that have been presented should be re-considered under the scope of environmental changes. Present models of BAWBILT population dynamics, although taking some account of climatic conditions, do not generally consider a changing environment, particularly in prediction of future impacts and risks to forests. Taking into consideration this new dimension at a large geographic scale should lead to more dynamic models. However, a consideration of the environmental dimension in BAWBILT research supposes new basic research on the insects, their associated organisms, their natural enemies, their host trees, and the relations between these different biological components.

5.2.2. Forest sustainability, wood production, biodiversity and conservation

The assurance that wood production is compatible with the social functions of forests and the preservation of biodiversity in a sustainable forest environment is also one of the priorities of the 21st century. BAWBILT research is particularly concerned with this aspect. BAWBILT comprises comprise many insects that impede wood production or social functions of the forest (the “classical pests”). In this way, they can compromise forest sustainability and biodiversity, especially in forests that have been actively managed for a long time, which includes the major part of the European forest estates. Studies dealing with relations between outbreaks, damage, and forest sustainability should be initiated. The temporal and spatial scales considered in such studies certainly represent an important factor to consider, which justifies a pan-European project over several years. Biodiversity

aspects are also another dimension where BAWBILT organisms are considered as pests. There is already experimental evidence that plant (especially tree) biodiversity can affect damage by BAWBILT organisms. However, there is a large field of research that still remains unexplored. On the other hand, some species that are pests in one region of Europe can be a significant factor in forest sustainability or an important component of biodiversity and conservation in another region. Moreover, even in a similar location, classical pests have relationships with biodiversity as they open the succession leading to wood decomposition. In addition, an insect is a pest only when it reaches a certain population level. During its endemic phases, it can even play an important role in maintaining biodiversity. Even though they are often mentioned in the literature, the relations between these different situations have been rarely studied thoroughly.

5.2.3. Emerging pest problems

Another challenge for European forest research is the emergence of new pest problems, for which BAWBILT organisms are frequently responsible. Such problems can result from the rapid expansion of markets between continents, leading to accidentally introduced insects or to voluntarily introduced hosts. New pest problems can also emerge from climatic changes that modify the geographic distributions of the BAWBILT organisms and their associates. In the latter case, the problem overlaps that of climatic change presented above. Pests can be insects themselves, such as *Phoracantha* species that have followed their *Eucalyptus* hosts in Southern Europe, or the recently introduced species of *Anoplophora* that have established on many indigenous hardwood tree species in Central and southern Europe. Pests can also be other organisms that are vectored by BAWBILT organisms. In this situation, the BAWBILT vector can be introduced while carrying the pest, or can be an indigenous insect collecting an introduced pest, such as for the pinewood nematode *Bursaphelenchus xylophilus* recently introduced in Southern Portugal, probably with its original vector but which adapted to the local vector *Monochamus galloprovincialis*. All present or potential emerging pest problems must be considered very seriously when they represent high threats for European forests. Research on the BAWBILT pests that have recently been introduced in Europe is urgently needed. Preventative studies should also be developed for alien species likely to be introduced to determine the possible routes of introduction and extension, the possibilities for their establishment, the risks of damage, and the available control methods. In all cases, research must be conducted at the level of the whole of Europe, in collaboration with the countries of origin.

6. REFERENCES

- Sallé, A. 2004. Caractéristiques génétiques, morphométriques et flore fongique associée à *Ips typographus* (Coleoptera : Scolytinae), application à l'estimation des niveaux de population du ravageur. Thèse Université d'Orléans: Physiologie et biologie des organismes.
- Wallin, K.F. & Raffa, K.F. 2004. Feedback between individual host selection behavior and population dynamics in an eruptive herbivore. Ecological Monographs, 74, 1001-16.

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