

---

## REVIEW ARTICLE

---

# The biology and ecology of the large pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae): a problem of dispersal?

S.R. Leather<sup>1\*</sup>, K.R. Day<sup>2</sup> and A.N. Salisbury<sup>1</sup>

<sup>1</sup>Silwood Centre for Pest Management, Department of Biology, Imperial College, Silwood Park, Ascot, SL5 7PY, UK:

<sup>2</sup>Applied Ecology Research Group, School of Environmental Sciences, University of Ulster, Coleraine, Northern Ireland, BT52 1SA, UK

### Abstract

The biology and pest status of *Hylobius abietis* Linnaeus in Europe are critically reviewed. New data are presented and the relationships between the weevil and its host plants considered. In Europe, *H. abietis* is the major pest of establishment forestry causing millions of ECUs of damage annually and perpetuating the addition of insecticide residues to sensitive habitats. Predator and parasitoid complexes in Britain and Europe are compared and contrasted. The lack of knowledge of the processes involved in adult dispersal and longevity are highlighted as major areas of concern. The biology and behaviour of the adult and larval stages are reviewed and new data presented. The feeding preferences of the adult weevils are considered and the possibility of using deterrents as a pest management strategy discussed. The development of risk assessment and forecasting tools aimed at more effective deployment of pest-management options are discussed. Risk criteria have their origins in important ecological relationships which require new understanding, but the prospects for determining high-risk forest sites are promising. The options for biological control are evaluated, in particular the use of mycopesticides and increased larval predation. It is concluded that much more research into the biology and ecology of *H. abietis* is required before a successful Integrated Pest Management (IPM) programme can be initiated.

### Introduction

The large pine weevil *Hylobius abietis* Linnaeus (Coleoptera: Curculionidae) is a widely distributed pest of plantation forestry occurring throughout Europe and Asia

(Scott & King, 1974). It has been regarded as a pest of conifer plantations since the early part of the last century (Trägårdh, 1913). Congeneric species, *H. congener* Dalla Torre (Martin, 1964) and *H. pales* Herbst (Coleoptera: Curculionidae) (Lynch, 1984), fill similar niches in North America. In Britain, it is currently estimated that *H. abietis* costs the Forestry Commission (which holds about 50% of the British forest estate) approximately £2M per annum solely on control

---

\*Fax: 01344 294308  
E-mail: s.leather@ic.ac.uk

measures. This does not take into account the fact that where control fails and plants are destroyed, a further cost due to replanting is incurred. Private forestry estates suffer similar damage levels so the estimated cost to the forest industry in Britain is approximately £4M annually. In the absence of control measures at least 30% and up to 100% of all trees planted in restocking sites will die (Heritage *et al.*, 1989). It is thus a serious threat to British and European forestry. Current control measures are by the use of insecticides (Stoakley & Heritage, 1990a,b). This has serious implications, as the use of chemicals however carefully formulated, in this case the synthetic pyrethroids deltamethrin and cypermethrin, is objected to by the conservation and environmental bodies. In addition, forest workers find the protective measures tedious and many complain of allergies. Chemical control measures are applied widely throughout the forest industry as a prophylactic measure. There is no evidence that the levels of damage currently experienced will decrease unless a suitable alternative control strategy is sought and discovered.

### Life cycle

*Hylobius abietis* develops in the stumps and roots of dying and dead conifer trees. Eggs are laid in small notches on the bark of roots excavated by the adult weevils in late spring (Scott & King, 1974; Nordenhem & Nordlander, 1994) and pass through four larval moults before pupation. Some workers in Scandinavia report that the eggs are laid in the bark of roots or stumps just below the surface of the soil and that the larvae migrate further down into the roots on hatching (Pye & Claesson, 1981).

Depending on the microclimate and the host-quality of the stumps, pupation and emergence can take place within one year of egg laying or conversely pupation and adult emergence can be postponed until the late summer of the following year (fig. 1). In colder climates larval development habitually takes two years and can be as long as five years, although 75% of individuals in Europe develop within one year (Bejer-Petersen *et al.*, 1962). Adults emerge from hibernation in spring when temperatures reach 8–9°C (Munro, 1928; Nordenhem, 1989), but emergence in January and February during periods of mild weather is not unknown (Munro, 1928). The adult weevils, which feed on the bark of conifers and other woody plants, have a period of maturation feeding before ovipositing in the spring. After oviposition, the adult weevils remain on the site for the rest of the summer (Nordenhem, 1989). Some adults emerge from pupal cells at the end of the summer (July to September), although a large proportion overwinter within the pupal chamber (Nordenhem, 1989). Overwintering can thus take place at the third and fourth instar larval phases, and at the adult stage. The average supercooling point for larvae is –12.6°C (Luik & Voolma, 1989) which is not particularly low for a temperate insect species (Leather *et al.*, 1993) and is perhaps an indication of its adaptation to its sheltered living site. The adults can live for up to four years (Eidmann, 1979; S.R. Leather, unpublished). The sex ratio appears to be approximately 50:50, although the ratio caught by billet traps can range from 20% to 70% female depending on the time of year (Långström, 1982; Djeddour, 1996). Newly emerged females in their first breeding season take two to three weeks to reach reproductive maturity, whereas females in their second or third breeding seasons are ready

to mate almost immediately (Bejer-Petersen *et al.*, 1962; Nordenhem, 1989). After mating, females oviposit in fresh conifer stumps, laying one to five eggs in holes gnawed in the bark (Salisbury, 1996). The oviposition period lasts from May to September, but peaks in mid-May to early June (Bejer-Petersen *et al.*, 1962; Lekander *et al.*, 1985). Stumps can remain suitable as oviposition sites for up to three years (Nordenhem, 1989). As the temperature decreases (below 8°C), usually October in the UK, the adult weevils move below ground to hibernate (Munro, 1928) often being found in the soil/litter interface of mature forest stands (S.R. Leather, personal observation).

### Pest status and damage

*Hylobius abietis* is a pest of young conifers such as *Pinus sylvestris*, and is the only forest pest for which prophylactic treatment is routine in British forests (Stoakley & Heritage, 1990a). Transplanted seedlings are vulnerable because the absolute population densities of weevils on a site are often large relative to the availability of conifer stem material, and of course seedlings are easily accessed by weevils from the ground. Patches of gnawed stem bark can coalesce causing considerable losses of bark surface area and the damage can be aggregated as a result of weevil attraction to feeding scars (Tilles *et al.*, 1986a). The results of damage are often only clear where stem-girdling is followed by seedling mortality. The ability of seedlings to 'grow-away' from moderate damage may be an important factor in the regulation of the pest problem, but there is some evidence that plant growth may be inhibited in moderately damaged transplants some years after the damage was sustained (G. Lempérière, personal communication).

Although much is known concerning the damage effects of *H. abietis* to young transplants in restocking sites, the damage levels vary unpredictably from site to site (Heritage *et al.*, 1989). Damage surveys show little correlation with population levels of *H. abietis*, and it has been surmised that immigration into felled sites and restocking areas accounts for a great deal of the variability (Wilson & Day, 1994), but is the subject of a range of attempts to forecast areas of high damage risk (see later). This variability in immigration may be due to the result of enhanced release of volatile chemical attractants at some sites relative to others (Nordlander, 1991) but no work has been reported in this area. In addition, *H. abietis* can also be a vector of phytopathogenic fungi such as *Heterobasidion annosum* (Fries) Brefeld (Kadlec *et al.*, 1992; Levieux *et al.*, 1994).

*Hylobius abietis* adults will also feed on fallen tops and branches of conifers lying on the ground and will feed on the side branches and leaders of standing pines, larches and spruce (Munro, 1928). Munro (1928) reports that such feeding by *H. abietis* can result in a similar malformation of *P. sylvestris* as that caused by the pine shoot beetle *Tomicus piniperda* Linnaeus (Coleoptera: Scolytidae), the characteristic shepherd's crook syndrome.

An additional damage factor that has only been recently noticed is that *H. abietis* may act as a vector of the fungus *Leptographium procerum* (Kendrick) (Piou, 1993). It is possible that the fungus is picked up by emerging adults who then inoculate pine seedlings whilst feeding. There is thus a real possibility that the mortality rate of seedlings that would otherwise recover from minor feeding damage could be increased.

The influence of silvicultural practices on population levels of *H. abietis* is complex and poorly understood. Eidmann (1985) considered size and temporal patterns of clear cuts, methods of reforestation, time of planting, species planted and age and vigour of transplants as likely factors affecting economic losses by the weevil. It is, however, obvious that the pest status of this insect is a direct consequence of the activities of foresters. It is generally agreed that a silvicultural system based on clear-cutting seems to provide near ideal conditions for pine weevils (Örlander *et al.*, 1997), consequently only a few European countries such as Germany, Austria and Switzerland regard *H. abietis* as having only moderate pest status.

Before the advent of large scale forestry, *H. abietis* was dependent for breeding sites on the accidental death of trees, from either windblow or lightning strike, which allowed a stump to become colonizable by the adult weevils. Suitable breeding sites were thus a limiting resource on their population levels (fig. 1a) and active dispersal and recognition of breeding sites were thus highly important for the survival of this species. It is unlikely that there would have been a food shortage for adult beetles as they are capable of feeding on the bark of the young branches in the canopy of conifer

forests and are also able to feed on many species of woody stemmed plants. With the advent of large scale felling and reafforestation programmes, breeding sites were no longer such a limiting resource as many attractive stumps thus become available for breeding (fig. 1b). Although stumps only remain suitable as breeding sites for as long as the cambium remains in good condition, this can be for up to two or even three years (Henry, 1995). Even with a fallow period, large numbers of larvae will continue to develop and many adults are produced which either disperse to other sites or feed on surrounding woody vegetation or uncleared brash and lay eggs within the still viable stumps (fig. 1c). When the site is replanted there is obviously the potential for the devastating attacks that are commonly seen in restocking sites as the emerging adults have an easily available food supply in the form of the newly planted trees (fig. 1d).

## Control methods

### Chemical control

Plants may be protected against *H. abietis* by pre-planting and/or post-planting application of insecticides, e.g.

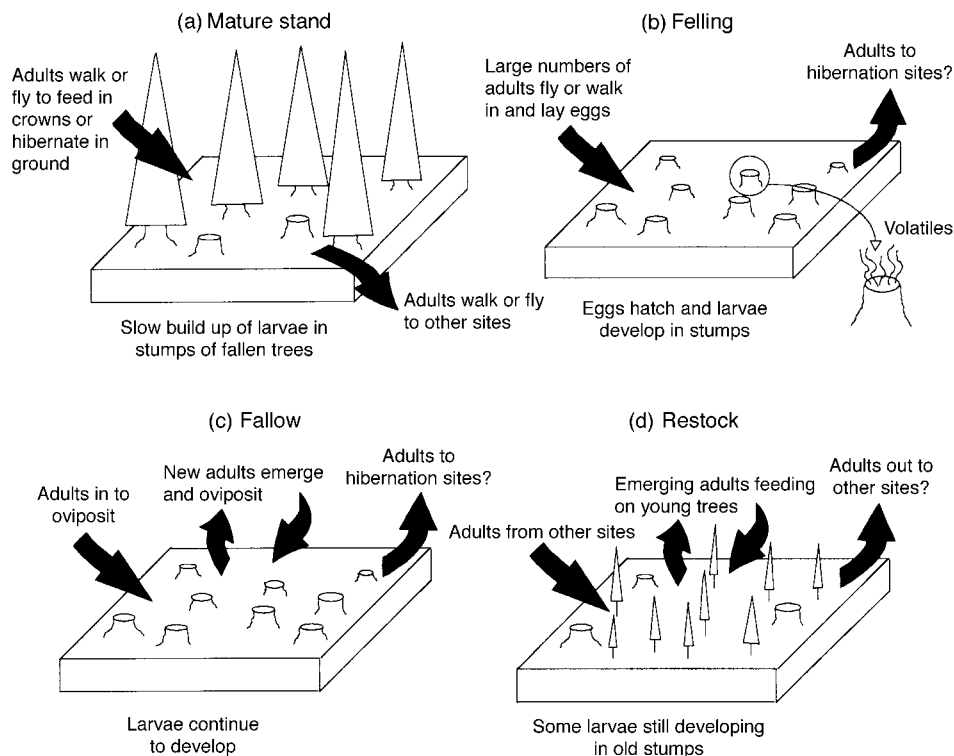


Fig. 1(a). Hypothetical mature conifer stand. *Hylobius abietis* adults feed in the canopy on thin barked branches and there is a slow build up of larvae in fallen trunks and old stumps in the generally cool and sheltered environment. Population levels generally low and adults are presumed to overwinter in the litter layer.

(b) The stand has been felled with the consequent release of volatiles. Adult weevils have been attracted in to the site and have laid eggs in the newly exposed stumps. Adults are likely to feed on the brash left on the site. Development rates of the larvae will tend to be high due to open aspect. Adults probably overwinter in nearby stands of mature trees as these are more sheltered from frosts.

(c) The site has been left fallow. The stumps are still attractive to ovipositing females from other sites and more eggs are laid. The stumps are still able to sustain larval development and the population continues to grow up. Newly emerging adults will probably mate and oviposit on the site, obtaining nutrition from the woody vegetation that has grown up on the site.

(d) The site has now been restocked with a conifer crop. These produce volatiles that attract in new adults and stimulate those adults and those emerging from the stumps to feed. Severe damage and tree death will result unless the trees have been treated.

pyrethroids such as permethrin and deltamethrin, although in the past organochlorines and organophosphates have been used (Stoakley, 1968). Pre-planting treatments involve the dipping of bare-rooted stock in a high concentration of insecticide or if the plants have been raised in Japanese paperpots, spraying at similar concentration (Stoakley & Heritage, 1989, 1990a,b). Insecticide may also be applied using an electrodyne spray system (Salisbury, 1996). Post-planting spraying at slightly lower concentrations may be carried out on trees planted in the forest. This is however, a less effective alternative.

A widely-used but more expensive long-term option for plant protection is based on the use of a slow-release systemic carbamate insecticide (carbosulfan) formulated as a granule based on a polymer matrix incorporating the active substance (Lempérière & Julien, 1989). The treatment can give good protection for 20 months, but is incomplete because it takes a week or so for the active substance to become incorporated into above-ground tissues of the seedling and weevils will sample bark tissue before being deterred (Mrlina *et al.*, 1994). If weevils are abundant, this low level of feeding can amount to significant plant damage. Nevertheless, this is a frequently used treatment in several European countries. An ideal insecticide for use against *H. abietis* would be one that was systemic and at the same time masked or modified the host plants volatiles that are attractive to the adult weevils. No such formulation is on the market at the present.

#### Cultural control methods

In the days before widespread availability of insecticides, mass trapping using sawdust piles was employed (Munro, 1929). However, Munro (1929) felt that the methods employed then and to a certain extent now, e.g. leaving a fallow period, protective sprays and the uprooting and burying of stumps to be useless. Despite this, the delaying of restocking sites by two or three years is still recommended to allow exhaustion of *H. abietis* breeding material (Scott & King, 1974; Doom & Frentzen, 1980). This method only has the desired effect when there are no fellings nearby, otherwise weevils will migrate in from these sites. Ploughing, ripping and stump removal are thought to reduce the numbers of *H. abietis* although the effects are not fully understood (Scott & King, 1974).

#### Alternative control methods

Protective collars (Lindstrom *et al.*, 1986), protective stockings (Eidmann & von Sydow, 1989) and the provision of shelterwood (von Sydow & Örlander, 1994) have all been advocated without great success. More recently, the use of entomopathogenic nematodes (Collins, 1993), parasitic wasps (Henry, 1995) and other natural enemies (Styles, 1994) have been suggested as a possible control option, although as yet there is little evidence for their success.

The use of wood-colonizing fungi, *Phlebiopsis gigantea*, to reduce weevil colonization of stumps seems a successful option and larval production has apparently been halved on clear-fells in Poland, but the approach needs greater study under different environmental conditions. The development of the fungal mycelium also reduced that attractiveness of branch material to adult weevils in olfactometer experiments (Skrecz & Moore, 1997).

### Natural enemies

#### Parasitoids

Relatively few parasitoids of *H. abietis* have been described and of those found, little is known of their effects on *H. abietis* populations. Two species of braconid wasps (Hymenoptera: Braconidae), *Perilitus areolaris* Gerdin & Hedqvist and *Perilitus rutilus* Nees are known to parasitize adult weevils in Scandinavia (Gerdin & Hedqvist, 1985) and *P. areolaris* is also known to parasitize the adults in Britain (Henry, 1995). The larval ectoparasitoid, *Bracon hylobii* Ratzenberg (Hymenoptera: Braconidae) is an important larval parasitoid of *H. abietis* in Britain and has been reported to cause up to 50% larval mortality (Munro, 1915, 1929; Henry, 1995). *Bracon hylobii* appears to have a non-uniform distribution within sites in Britain (Henry, 1995) and elsewhere (Elton *et al.*, 1964). This may be due to the cues used by the adult parasitoid wasps to locate suitable tree stumps. The cues used are unknown but it is likely that they are host plant volatiles as is seen in other parasitoids (Vet & Opzeeland, 1984). If these can be determined then it may be possible to augment natural enemy numbers within forest restocking sites although as the production of large numbers of parasitoids is very expensive (C.J. Henry, personal communication) it may be some time before biological control using these insects is possible. In addition, the distribution of the parasitoids and larvae of *H. abietis* within stumps seems to indicate that a substantial proportion of the larvae are inaccessible to the parasitoids (Henry, 1995). Munro (1929) also reports finding another species of parasitoid, *Dolichomitus tuberculatus* (Geoffroy) (Hymenoptera: Ichneumonidae) associated with *H. abietis*, but little is known regarding this association, although it is likely that this parasitoid may be able to parasitize larvae in the thicker barked part of the stump that *B. hylobii* is unable to reach (Hanson, 1943).

#### Predators

Surprisingly little research has been conducted on the predators of *H. abietis* and the little information known is, at best, incomplete. Elton *et al.* (1964) and Munro (1929), have suggested that several species of predatory Coleoptera (larvae and adults) found in and around pine stumps are possible predators of *H. abietis* larvae (table 1). Their lists include true predators such as wireworm (Elateridae) and ground beetles (Carabidae), as well as those insects that will possibly eat any *H. abietis* larvae they encounter. However, neither study observed any of the candidate species eating *H. abietis* at any stage. More recently, Styles (1994) presented larvae and adults of *H. abietis* to four species of carabid beetle, but only the larvae were eaten. One flaw of the work is that the larvae were presented to the predators in a thin layer of peat rather than within a feeding source and thus lacks realism. Vertebrate predation is considered to be unimportant (Munro, 1929; Scott & King, 1974) although no quantitative studies have been undertaken and the jay (*Sitta europaea affinis*) and starling (*Sturnus vulgaris*) have both been cited as taking *H. abietis* in Britain (Ossowski, 1941).

#### Microorganisms

Fungi are known to infect both the larval and adult stages of *H. abietis*. The pathogen *Beauveria bassiana* (Fungi:



Table 1. Suggested predators of the large pine weevil, *Hylobius abietis*.

Species/family	Authority	Country
<b>Diptera</b>		
Asilidae		
<i>Laphria gilva</i> (Linnaeus)	Elton <i>et al.</i> (1964)	The Netherlands
Dolichopodidae		
<i>Medetera</i> sp.	Elton <i>et al.</i> (1964)	The Netherlands
<i>Medetera (signaticornis) striata</i> Parent	Trägårdh (1929)	Sweden
<b>Coleoptera</b>		
Carabidae		
<i>Abax parallelipipedus</i> (Piller & Mitterpacher)	Salisbury (1996)	Britain
<i>Agonum assimile</i> (Paykull)	Salisbury (1996)	Britain
<i>Nebria brevicollis</i> (Fabricius)	Salisbury (1996)	Britain
<i>Pterostichus madidus</i> Fabricius	Salisbury (1996)	Britain
Cleridae		
<i>Thanasimus formicarius</i> (Linnaeus)	Munro (1929)	Britain
Elateridae		
<i>Melanotus (rufipes) villosus</i> (Geoffrey)	Elton <i>et al.</i> (1964)	The Netherlands
Nitulidae		
<i>Glischrochilus</i> spp.	Elton <i>et al.</i> (1964)	The Netherlands
<i>Pityophagous ferrugineus</i> Linnaeus	Elton <i>et al.</i> (1964)	The Netherlands
<i>Rhizophagus ferrugineus</i> Paykull	Elton <i>et al.</i> (1964)	The Netherlands
<i>Atheta</i> sp.	Elton <i>et al.</i> (1964)	The Netherlands
<i>Phloeonomus</i> sp.	Elton <i>et al.</i> (1964)	The Netherlands
Tenebrionidae		
	Elton <i>et al.</i> (1964)	The Netherlands
Staphylinidae		
	Elton <i>et al.</i> (1964)	The Netherlands

Imperfecti) has been shown to kill adults and larvae in the field (Gerdin, 1977) although only 4% of adults were found to be infected. Dorr (1996) has shown that doses of  $10^5$  conidia  $\mu\text{l}^{-1}$  were effective in causing substantial adult mortality. *Beauveria* infected adults are commonly found in field collections in Britain (S.R. Leather, personal observation), but infections are relatively slow to develop in laboratory cultures (S.R. Leather, unpublished). *Metarrhizium anisopliae* (Fungi: Imperfecti) has also been shown to kill adults and larvae of *H. abietis* in the laboratory but no infected individuals were found in the field (Gerdin, 1977). In field conditions, trapping bark (an attractant trap formed of fresh conifer bark) treated with *B. bassiana*, although effective at attracting *H. abietis* adults caused only slight immediate mortality (Wegensteiner & Fuhrer, 1988).

Under laboratory conditions the nematode *Neoaplectana carpocapsae* (Rhabditidae) has been shown to be pathogenic to both adults and larvae of *H. abietis* with 100% larval mortality occurring at a dose of less than 206 infective nematodes per host (Pye & Burman, 1977). Field trials have shown that the spraying of a clearfell site reduces numbers of adults and larvae and in some cases reduced damage to trees by 89% (Pye & Pye, 1985). However, Collins (1993), working in the United Kingdom, found that such results were only obtainable under certain environmental conditions and concluded that the use of this nematode would not replace chemicals but might have a use in an integrated control programme against *H. abietis*.

#### Competitors for breeding and development resources

Many insects utilize dead wood as a food source in the

larval stage, e.g. the longhorn beetles (Cerambycidae) (Hanson, 1943). These insects are therefore potentially competitors of *H. abietis*. Little is known concerning the degree of overlap between wood feeding insects although Munro (1929) considered the cerambycid *Rhagium inquisitor* (Gyllenberg) to be the only serious competitor of *H. abietis* as it frequently uses the upper regions of stumps and thus has the potential to exclude *H. abietis* larvae. However, it is possible that this exclusion may be the result of cerambycid larvae actually eating *H. abietis* larvae when they encounter them (Elton *et al.*, 1964). It is also possible that the beetles *T. piniperda* and *Hylurgops palliatus* Gyllenhal (Coleoptera: Scolytidae) may compete for larval resources (Hanson, 1943).

Fungi may also render the stump unsuitable for *H. abietis*, and are thus potential competitors. However, there appears to be little published work on this subject although Crooke & Kirkland (1956) found that stumps infected with *Heterobasidion annosum* and *Armillaria mellea* appeared to exclude *H. abietis* larvae from the infected part of the stump. Where larvae were already present when the fungal mycelium overtook them, there appeared to be very high larval mortality. The drawback of using these two agents as biological control agents is the fact that they are both serious root diseases of forest trees.

There is however, a possibility of introducing saprophytic fungi to freshly cut stumps as a control option against *H. abietis* (Skrecz & Moore, 1997). It may be possible, should a suitable formulation be developed, to introduce spores of saprophytic fungi at the same time as prophylactic treatment against *H. annosus* is conducted (D. Redfern, personal communication).

## Weevil–plant interactions

### Behaviour

How an insect behaves is dependent to a large extent on its physiological state. Evidence suggests that *H. abietis* may behave differently in response to various attractants depending on the time of year and state of its reproductive development (Nordenhem & Eidmann, 1991). Earlier work has shown that both sexes of *H. abietis* undergo developmental changes throughout the year and that this is not always related to the chronological age of the beetle (Munro, 1928; Nordenhem, 1989). For example, the orientation of adult weevils involves responses to light and humidity and their responses vary in different stages of their life cycle; older reproductive weevils are strongly photonegative (Havukkala & Selander, 1976; Havukkala, 1979). Adult weevils also respond to acoustic signals (Selander & Jansson, 1977), pheromones (Selander, 1978) and host volatiles (Nordenhem & Eidmann, 1991). It is important to know at what stage of physiological development the majority of the population is at any one time, in order to develop models that will describe dispersal accurately.

### Mating

Male/female recognition in *H. abietis* has been shown to be based on pheromones, and involves both contact and distant cues (Selander & Jansson, 1977; Tilles *et al.*, 1988). The volatiles extracted from different age classes of adult evoke different responses (Selander *et al.*, 1976) and newly emerged adults of both sexes do not respond to mating stimuli for several weeks (Selander, 1978). There appear to be two pheromones involved in the mating process, one produced by males to encourage aggregation and another produced by females to stimulate mating (Selander, 1978). Both of these pheromones may only be effective over short distances. Long distance orientation appears to be based on the release of host plant volatiles from suitable breeding material, e.g. felled trees (Selander *et al.*, 1974). On arrival at the site, the aggregation pheromone brings the weevils together, the sex pheromone attracts the males to the females (Tilles *et al.*, 1988) and then the males court the females by stridulating which causes the females to remain stationary and allow mounting (Selander & Jansson, 1977).

Further study into the mating behaviour, especially the identification of the aggregation and mating pheromones could lead to the development of a powerful tool for the monitoring, forecasting and control of *H. abietis*.

### Host plant location

Host plant volatiles are known to attract adult and larval *H. abietis* to suitable food sources and, although baited pitfall traps using a mixture of ethanol and pines have been used with some success (Nordlander, 1987; Raffa & Hunt, 1988; Lindelöw *et al.*, 1993; Örlander *et al.*, 1997), the exact combination of chemicals and their mode of action is unknown, although the site of action of several of the chemicals found in conifer species has been described (Mustaparta, 1975a,b). Once the feeding material is reached, the response to ethanol is reduced (Selander *et al.*, 1976).

Adult weevils of all ages respond positively to the monoterpenes, 3-carene and  $\alpha$ -terpineol, although the

degree of the response is modified by the physiological state of the weevil (Selander *et al.*, 1976). At very high concentrations, 3-carene and  $\alpha$ -terpineol elicit negative responses from pre-reproductive swarming weevils, whereas the newly emerged and reproductively mature weevils are much less sensitive. Similar results are found in the reactions of adult *H. abietis* to light and humidity, with newly emerged adults and reproductive older adults being photonegative, but the swarming weevils photopositive (Havukkala & Selander, 1976). All three classes of adult are hygronegative although the response is strongest in the females and weakest in swarming males (Havukkala & Selander, 1976). Thus, during the spring swarming period, *H. abietis* is photopositive and finds a mate and food by its olfactory orientation mechanisms. Once mated, the photonegative response and olfactory response to host volatiles means that the weevils feed nocturnally on young bark tissue. Other species of *Hylobius* show similar responses (Martin, 1964; Wilson, 1968). Larvae of *H. abietis* have also been shown to respond positively to ethanol and  $\alpha$ -pinene (Nordenhem & Nordlander, 1994).

There is some evidence that the monoterpene limonene may have an inhibitory effect on the efficiency of  $\alpha$ -pinene, one of the chemicals known to attract *H. abietis* (Nordlander, 1990, 1991). It may thus be possible to use limonene as an alternative to insecticide application or to use limonene-emitting material at restocking sites in some way to reduce weevil attack and damage.

In summary, *H. abietis* adults are attracted to host material by host volatiles emitted such as  $\alpha$ -pinene, but responses may vary according to specific volatiles released (Tilles *et al.*, 1986a,b) and the physiological state of the individual (Zagatti *et al.*, 1997). It is apparent that different host volatiles have differing effects on *H. abietis* and that there is a strong possibility that the olfactory responses of the adult weevils may depend and co-act with other responses such as the hygronegative responses reported by Havukkala (1979). These interactions require further study.

### Dispersal

Adult *H. abietis* are capable of long distance dispersal (Munro, 1925; Solbreck, 1980; Nilssen, 1984) but little is known of their movement patterns within a particular site once they have emerged from their overwintering site or have migrated into a particular area. Swarming and/or flying in response to host odours occurs as temperatures approach 13–16°C, usually over a seven week period during May and June (Munro, 1928; Solbreck & Gyldberg, 1979) and it has been estimated that some weevils can travel many kilometres (Solbreck & Gyldberg, 1979). It is known that individual weevils will remain at a particular clear-fell site for a number of months (Munro, 1925; Leather *et al.*, 1995) but movement patterns and residence times have not been well documented, although preliminary work suggests that some weevils will only move a few metres during the course of the summer (Swaine, 1951; Eidmann, 1968; S.R. Leather, personal observation) and perhaps a few hundred metres from adjacent stands (Munro, 1928; Zurr & Stary, 1994). This is in accordance with the closely related North American species *H. radialis* Buchanan (Coleoptera: Curculionidae) which is thought to be an infrequent flier (Rieske & Raffa, 1990b). Weevils released into clear fell sites on hot summer days tend to crawl away from the release site

and seek shelter under the soil or ground vegetation, whereas weevils released in mature stands tend to fly upwards towards the canopy (S.R. Leather, personal observation). The role that host plant volatiles play in this scenario is largely unknown.

Clearly habitat structure has some effect on the movement of weevils. In a field study involving the comparison of fresh, one-year-old and two-year-old clear-cuttings, Örländer *et al.*, (1997) found that the catches of weevils (baited traps) were higher on the parts of clear-cuttings where slash (pruned branches) had been removed, whereas the amount of damage to seedlings in areas with and without slash were similar. Örländer *et al.* (1997) suggest that higher trap catches were attributable to enhanced weevil mobility where there was no slash.

A much greater understanding of the factors governing the dispersal behaviour of adult weevils must be obtained before effective control strategies can be devised. Detailed studies on the migration of adult weevils in and between breeding sites and hibernation sites is urgently required.

It has recently been shown that larvae of *H. abietis* will move from one piece of buried pine stem to another (Nordenhem & Nordlander, 1994; Salisbury & Leather, 1998) and this may be related to both ethanol and  $\alpha$ -pinene (Nordenhem & Nordlander, 1994). The larvae can successfully move distances of up to 350 mm and, although they are vulnerable to predators such as carabid beetles, it is postulated that the risk of predation is lower than that of failing to complete development in a rapidly deteriorating food source (Salisbury, 1996; Salisbury & Leather, 1998). This has implications for possible biological control strategies.

#### Oviposition and fecundity

Oviposition rates and fecundity in insects are affected by a number of factors, e.g. size, longevity, adult and larval nutrition and plant stimulants (Leather, 1987, 1988; Leather *et al.*, 1995). The effect that adult nutrition and host plant volatiles have on the fecundity and longevity of *H. abietis* is unknown. Larval nutrition may be important in determining the adult size attained, but as *H. abietis* is a relatively long-lived insect, it is likely that adult nutrition and the factors affecting this will have the most marked effect on fecundity. However, adults arising from larvae that develop in spruce stumps are smaller and less fecund than those arising from pine stumps (Guslits, 1970).

Oviposition most often occurs in the top 100 mm of stumps, although eggs have been found at depths greater than 400 mm (Pye & Claesson, 1981). Under field conditions with a hard packed substrate, oviposition occurs in the top 50 mm. The larvae then tunnel downwards to more suitable feeding sites (Pye & Claesson, 1981). It is possible that as the regions of the stump closer to the soil surface are warmer than the those further below ground that egg and larval development will be more rapid. Rapid development increases the chance of survival from both sibling cannibalism (Henry, 1995) and natural enemies (Pye & Claesson, 1981).

Adult weevils can lay at least 25 eggs during the year, and these take approximately 12–14 days to hatch at 15°C (Salisbury, 1998). There is a positive correlation between size of female as measured by elytron length and the number of eggs contained within the reproductive tract (potential fecundity) (Christiansen, 1971a), but all eggs are resorbed by

the end of the reproductive season and the oocytes decrease in size (Christiansen, 1971a). In Norway, the mean number of eggs found in the oviducts of reproducing females ranges from 2.4 to 3.6, although the greatest number of eggs recorded in the oviducts was 13 (Christiansen, 1971a).

#### Larval development

Larval development is very dependent on temperature and climate. The generation time (egg to egg) can vary from as little as one year in western Europe (Scott & King, 1974) to as long as four years in the north of Finland (Bejer-Petersen *et al.*, 1962), although in southern Sweden development can take as little as one year (Bakke & Lekander, 1965).

The position of the larvae within the stump and the exposure of the stump to the sun also affect larval development. Larvae closer to the soil surface develop faster than those further down in the stump (Fraser, 1952; Bakke & Lekander, 1965) and also in stumps that are exposed to sunshine for longer periods (Bakke & Lekander, 1965).

Eidmann (1963) examined the effect of temperature in the laboratory on larvae of *H. abietis* and found that higher temperatures up to 25°C hastened development and also affected the onset and duration of the diapause period, being from 60 to 220 days at temperatures between 10° and 20°C but only 17 days at 25°C. Christiansen (1971b) also examined the effect of temperature on larval development and found that at 23°C larval development took only 40 days when cultured in *Pinus sylvestris* logs. He also found a significant negative correlation between larval population density and adult weight.

#### Feeding

*Hylobius abietis* is reputed to be better adapted to pine species as larvae (Munro, 1928) but as an adult is known to feed on the tender bark of a variety of woody stemmed hosts, e.g. hazel (*Corylus avellana*), oak (*Quercus* spp.) and even heather (*Calluna vulgaris*) (Munro, 1928; Djeddour, 1996), although there is some evidence to suggest that some woody plants commonly found on restocking sites, e.g. ash (*Fraxinus excelsior*), birch (*Betula pendula*) and sycamore (*Acer pseudoplatanus*), may have deterrent and perhaps even toxic effects on *H. abietis* adults (Leather *et al.*, 1994; Manlove *et al.*, 1997). Verbenone, a semiochemical associated with microbial breakdown of plant tissue has been shown to deter feeding in *H. abietis* and may be used as a cue to determine host quality (Lindgren *et al.*, 1996).

In field trials with different types of billet traps, results are fairly consistent from different parts of Europe and show that *P. sylvestris* billets are much more attractive than billets of *P. abies* (Långström, 1982), although if pine billets are absent then billets of *P. sitchensis* are more attractive than those of other conifer species (Wilson & Day, 1995).

Simple choice tests in the laboratory show that adult weevils prefer coniferous trees to deciduous tree species such as birch or sycamore. In all reported trials, *P. sylvestris* has been found to be the most preferred food plant with *P. abies* being a close second (Leather *et al.*, 1994; Djeddour, 1996; Manlove *et al.*, 1997). Although adult females are significantly heavier than the males, the amount of damage caused and the feeding choices shown do not differ significantly between the sexes (Djeddour, 1996). Preferences for food material may bear a direct relationship to larval

development times. Larvae of *H. abietis* are reported to develop more rapidly in stumps of *Pinus* spp. than in those of *Picea* spp. (Bejer-Petersen *et al.*, 1962). Despite the large amount of work carried out on the olfactory responses of *H. abietis* to host volatiles (e.g. Selander *et al.*, 1973, 1974, 1976; Nordlander, 1990, 1991; Nordenhem & Eidmann, 1991), relatively little work has been aimed at the effects of host plant on adult survival, fecundity and site selection. A greater emphasis on this aspect of the biology and behaviour of *H. abietis* may make it possible to plant forests that are less suitable for the weevil and thus reduce the levels of damage currently seen.

The apparent toxicity of non-host trees such as *F. excelsior* also requires investigation. Associated with such defence mechanisms there are likely to be semiochemicals that would allow the insects to avoid initial attack on these trees.

### Forecasting and risk assessment

A damage forecast or risk assessment of a forest site will be a useful management tool where damage between sites is quite variable and prior knowledge would enable better (more cost-effective) targeting of control measures. Risk rating systems arise from a desire to predict the likelihood of damage and are at a very early stage of development for *H. abietis*. For other forest pests, the terminology has applied to a scale of resolution ranging from an individual tree (hazard) to whole forest stands (risk), but a more meaningful use of the terms 'hazard' and 'risk' is suggested by Waters *et al.* (1985). Hazard is determined by factors (drought, age, etc.) which dispose a tree or stand to attack. Trees with even high hazard ratings may not be attacked if the pest is absent or rare, so risk is said to be a function of the presence and abundance of the pest. In the forest management systems where *H. abietis* has become a major pest, risk will be a function of immigration and the potential for breeding on a site, whereas hazard will be determined by the access and responses of weevils to planted seedlings, and to the health and welfare

of the seedling stock at the time of impact. With enough understanding, it may be possible in future to develop both risk and hazard ratings for *H. abietis* damage at forest sites, but at present it is hard to distinguish their separate relationships with the range of silvicultural and other conditions apparently linked to the amount of damage to plants.

### Risk factors potentially linked with pine weevil damage

A great many 'risk factors' could be considered. Four categories of risk are outlined in table 2 which summarizes relationships between damage and factors which are reported in the literature. Carefully documented information on such factors may ultimately lead to greater precision in seedling damage prediction.

Firstly, opportunities for breeding in clear-felled sites are focused on the stumps of the previous crop, and their species, quality, longevity and relationship with soil conditions will influence the population density of new adult weevils present in subsequent years.

Secondly, the rate of development of weevils and life-history traits will be affected by climate and therefore local conditions such as shading and, above all, latitude, will influence the dynamics of appearance of new generations capable of inflicting damage on seedlings. Thirdly, there is ample evidence that site factors and treatments will influence seedling susceptibility by reducing the probability of weevil-seedling contact. Such factors include the design and size of clear-fell, the rate of development and type of secondary vegetation, and pre-planting treatments designed to improve seedling competitive capability or initial growth potential.

Finally, the outcome of contacts between the insects and seedlings will include the genetic origin and physiological status of both the interactants. Depending upon whether realized damage or actual mortality rate of trees is the desired end-point of the risk rating system, it may be useful also to include site or plant-related assessment of the capability of seedlings to recover from damage events.

Table 2. Potential damage risk factors in four categories related to pine weevil biology.

Factor	Effect	Literature source
<b>Suitability of breeding site</b>		
Age of clear-fell	Greatest damage in spring following clear-fell	Christiansen (1971a), Miessner (1970)
Drainage	More generations on drained soils	Ozols <i>et al.</i> (1989)
Stump character	Tissue condition important for breeding	Tarasova & Sukhovol'skii (1986)
<b>Weevil development rate</b>		
Latitude	Climate influences life-history	Långstrom (1982)
Shading	Shade prolongs life-history and reduces available weevils	Bejer-Petersen (1975), Kudela (1983), Kuziemska-Grzeczka (1984)
<b>Planting site factors</b>		
Edge effect	More damage at the edge of a clear-fell	Eidmann (1968), Korczynski (1988 a,b)
Vegetation cover	Lower vegetation height corresponds with more damage	Stadnitskii (1978)
Scarification	Scarified or cultivated soils correspond to less damage	Christiansen & Sandvik (1974), Huser (1979), Osterstrom & Andersson (1975), Soderstrom (1976), Soderstrom <i>et al.</i> (1978), Turchinskaya (1983)
Mounding	Trees planted on mounds experience less damage	Soderstrom (1977), Soderstrom <i>et al.</i> (1978)
<b>Weevil-seedling interactions</b>		
Natural regeneration	Naturally regenerated plants are less susceptible to attack	Selander & Immonen (1991), Selander <i>et al.</i> (1990)
Fertilization	Nitrogen increases attack frequency	Selander & Immonen (1991)
Resistant chemotypes	Evidence unclear	Selander & Kalo (1979)



### Qualitative and quantitative studies

Most attempts to forecast damage by *H. abietis* have been based on qualitative analyses. Simple relationships between the time at which felling took place and the need for subsequent weevil control measures have been suggested (Miessner, 1970), and there have been short-term forecasts of risk by Korczynski (1984, 1985) who exposed sections of pine branch and indexed the prediction of damage to seedlings from the number of branches weakly and heavily attacked. Working from measures of stump size and condition, Tarasova & Sukhovol'skii (1986) calculated the number of weevils present on a felled area, and by implication, the subsequent levels of damage.

Interception of adult weevils either in traps (Nordlander, 1989) or with billets (Trauboth, 1987) have been used to indicate probable high-risk areas (Wilson & Day, 1996) or as one of several variables in risk models (Wilson *et al.*, 1997). The problem with billets is that their attractiveness is inherently variable (Örlander *et al.*, 1997) and that they cannot prevent attracted weevils from leaving. Chemically baited traps may provide a good index of reproductive females in some forest environments (Örlander *et al.*, 1997) but trap relatively low numbers in others (Wilson & Day, 1994). Baited traps do not estimate pre-reproductive weevils reliably (Malphettes *et al.*, 1994). Consequently, trapped weevil numbers are only weakly correlated with measures of damage in most studies (Nordlander, 1987; Szmidt & Korczynski, 1983).

One of the primary difficulties with pine weevil risk assessment is to obtain a reliable estimation of the damage to seedlings with which to compare locally measured risk variables. Detailed damage and mortality data obtained from plants systematically sampled may be preferred, whereas damage indices giving only a general reflection of the local situation and perhaps obtained from local forest managers, may be inherently unreliable for building a forecasting system. Nevertheless, the latter may give some broad clues to high risk factors when little alternative information is available.

One of the more structured analyses of risk has been attempted by Nef & Minet (1992) in 34 forest departments in Belgium. They derived an index of risk from three components: damage frequency, an estimation of the importance of damage, and the proportion of forests treated with weevil control measures. Potential risk factors were drawn from information on the annual area of forest planted, two factors relating to the ecological zones where forests were planted, and five further climatological or phenological factors. The data submitted for stepwise correlation revealed that 65% of the variability in the risk index could be explained by a temperature factor and the area of forest planted. The model provides a useful regional tool, but the level of resolution of the risk assessment could not be expected to assist in decision-making at a forest stand scale. Unusually, the index of risk in Belgium had a clear geographical component, with highest risk zones occurring further to the east. Elsewhere such systematic spatial zoning in damage is unlikely to be apparent.

### Different types of risk model

The simplest system, a Classification Model, has been used for a similar species in Canada, *H. congener* (Pendrel,

1990) but such an approach involves considerable subjectivity and lacks precision or statistical reliability (Berryman, 1986). Discriminant Analysis may best distinguish high from low risk sites and has been effectively used for the southern pine beetle *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae) on loblolly pine (Belanger *et al.*, 1981). Its drawback is that the method requires data segregated into discrete damage classes, whereas pine weevil damage data is normally based on field estimation of damage in specified plots and is a more or less continuous variable (Wilson & Day, 1994). Linear Regression is a more appropriate approach for such data (Stage & Hamilton, 1981). Ultimately there may be much to recommend a modified Logistic Function to describe levels of damage, since it can also allow the concept of a varying threshold to be incorporated, i.e. the number of weevils and the damage which is necessary to kill a tree may vary according to its physiological condition (Paine *et al.*, 1984).

This approach to the analysis of a large data set from more than 80 forests in Northern Ireland was used by Wilson *et al.* (1997). For each site, weevil damage was recorded systematically from 41 Sitka spruce seedlings selected in two groups by initially locating points randomly within each forest site. Damage to each seedling was recorded in one of four categories (Långström, 1982), but by amalgamation these were reduced to two for the analysis. The independent variable for modelling was the number of trees bearing moderate to heavy damage. Dependent or risk variables were derived on-site or from maps and other sources of information. One hundred and four variables, some inter-related, were recorded originally. This number was reduced by omission or amalgamation to a list of some 48 variables for initial exploration of the data. A summary of the main variables is given in table 3.

Table 3. General categories of risk variables for Northern Ireland forests (from Wilson *et al.*, 1997).

Category	Variable type
Relating to forest location	District New or re-planted Altitude Rainfall
Felling and planting	Area Species Year
Adjacent forest	Natural regeneration Species Felling data Windthrow Perimeter
Soil	Type Water content Litter depth
Stumps	Quality Spatial density Diameter
Weevils	Numbers Timing of sample Sample distance from plot edge
Vegetation	Height Community type
Treatments	Brushings Burning Fertilization

The damage variable was logit transformed and submitted to multivariate regression using GLIM (Aitken *et al.*, 1989). The model employed was a linear response model with a logistic link function. A stepdown procedure was adopted in which each variable was omitted in turn, the maximum likelihood model recalculated and the statistical significance of the change in scaled deviance was tested to determine the exclusion or inclusion of the variable. By repeatedly modelling sub-routines of variables, the number of explanatory variables was reduced progressively until the most acceptable model comprised four terms and explained 53% of the variation in damage (Wilson *et al.*, 1997).

#### *Explanatory variables from the Northern Ireland study*

None of the important variables were different in character from those outlined in table 2. For example, less damage was evident at forest sites where the majority of trees forming the sample were naturally regenerated rather than planted. There is some experimental evidence that naturally regenerated Scots pine plants are more resistant to *H. abietis* (Selander *et al.*, 1990) but the model suggests there is a need to understand the difference in susceptibility of plants more fully.

Unsurprisingly, sites which had no legacy of clear-felling were also those where damage levels were the lowest. Since the scale of Northern Ireland forests is generally small, there is always the possibility of weevils immigrating from suitable breeding sites nearby or even at some distance, but this does not seem to have been the case for the sampled afforested sites in this study.

Trees on two- or three-year-old clear fells experienced more (recent) damage than trees on one-year-old clear fells. The most likely explanation is that pre-planting pesticide treatments were more effective in the year of plantation than subsequently. However, there were correlated factors such as the effects of cultivation and the extent of vegetation re-growth, which may have played a part in this result and demonstrate the frequent difficulty of interpreting surveys of this nature.

The relationship between site area and damage suggested a diminishing proportional reduction in damage with increasing plantation area. Areas around 4 ha seem particularly prone to weevil attack while the change in damage level beyond 15 ha is barely perceptible. Higher levels of plot-perimeter damage known from other studies early in the season (Korzynski, 1988b) could imply a general phenomenon related to weevil mobility.

Although suitability of breeding site, weevil development rate, planting site factors and weevil-seedling interactions are capable of explaining more than half of the variation in damage, there were small additional contributions made by the spring estimates of weevils, stump quality (assessed in terms of deterioration, bark adherence and wood cracking), litter depth adjacent to stumps (less damage where deeper litter), and the volume of conifer timber felled within 500 m of a study site.

#### *Forecasting potential*

The model (Wilson *et al.*, 1997) has substantial predictive capacity and provides clear guidance on high-risk site conditions. However, the study also highlights the need to

determine in advance the precision required in estimating 'risk' since damage to transplanted seedlings can vary quite considerably within a forest plantation compartment and not every tree attacked will be killed. Where low-resolution estimates of risk are required, damage variability can be described satisfactorily by very simple models (Nef & Minet, 1992). High-resolution estimates of risk (plants within 30 m of each other and damage recorded as percentage of trees in each of four categories of feeding scar extent) inevitably appear to 'perform' less satisfactorily (Wilson *et al.*, 1997). Developing a risk-assessment system to a desired level of predictive capacity is frequently a problem. None of the four recommended hazard/risk systems applied to mountain pine beetle damage in more than 100 forest sites, for example, proved adequate (Bentz *et al.*, 1993).

Forecasting potential of a risk model can only be demonstrated with independent data. With this in mind, the model based on Northern Ireland (Wilson, *et al.*, 1997) was evaluated against damage assessments from 85 different forest plantations in a different year (Wilson, Day and Power, in preparation). Using four discrete damage categories, it was found that the model correctly placed 52 of the 85 sites (61%), but the model accurately determined 8 out of 10 high-risk sites where 15% mortality of trees resulted in replanting the whole site, in local terms an economic threshold for damage.

The results of pine weevil risk assessment suggest that a great deal more remains to be learned about the interactions of the weevil with its host plants, and of the integrated variables which might strengthen a model's performance. It has been noted elsewhere that the forest conditions experienced by *H. abietis* vary enormously throughout its range. A shortcoming of empirical models is their failure to predict beyond the range of data on which the models are built. For this reason, comparable data extending the range of critical conditions will be necessary to tune a risk model for the pine weevil throughout Europe. The full effectiveness of hazard/risk-rating for *H. abietis* will ultimately be realized when combined with an economic analysis of predicted losses and the costs of newly emerging, environmentally sensitive control measures.

#### **Conclusions**

Although, as a consequence of its pest status, *H. abietis* is a well studied beetle, surprisingly little information is confirmed. The life cycle and behaviour, although well known, is not completely understood and what is known appears to vary between countries. This may be due to the wide distribution of *H. abietis* and it could be concluded that *H. abietis* is plastic in its behaviour and life cycle. A full comparison of its life cycle and behaviour throughout its range may confirm this. The responses to host volatiles and to its own semiochemicals is also still far from resolved. A detailed understanding of dispersal behaviour and overwintering site selection is urgently required. The relationships between *H. abietis* and its natural enemies have only been briefly considered. Control of this serious pest still relies on prophylactic chemical treatment. In these days of burgeoning concern for the environment this is a far from satisfactory position. Further investigation into all the above factors should provide a more effective and environmentally sensitive way of managing this insect's damage.

### Acknowledgements

We appreciate the assistance of the Department of Agriculture, Forest Service (N.I.) and support from COFORD (Eire). We thank Fern Leather for drawing the pictures.

### References

- Aitken, M., Anderson, D., Francis, B. & Hinde, J. (1989) *Statistical modelling in GLIM*. Oxford, Clarendon Press.
- 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. *Meddeleser fra det Norske Skogsforsøksvesen* **20**, 117–135.
- Bejer-Petersen, B. (1975) Length of development and survival of *Hylobius abietis* as influenced by silvicultural exposure to sunlight. *Arsskrift, Kongelige Veterinaer og Landbohøjskole, København* **1975**, 111–120.
- Bejer-Petersen, B., Juutinen, P., Kangas, E., Bakke, A., Butovitsch, V., Eidmann, H., Heqvist, K.J. & Lekander, B. (1962) Studies on *Hylobius abietis* L. I. Development and life cycles in the Nordic countries. *Acta Entomologica Fennica* **17**, 1–107.
- Belanger, R.P., Porterfield, R.L. & Rowell, C.E. (1981) Development and validation of systems for rating the susceptibility on natural stands in the Piedmont of Georgia to attack by the Southern pine beetle. pp. 79–86 in R.L. Hedden, S.J. Barras, and J.E. Coster (Eds) *Hazard-rating systems in forest insect pest management*. Symposium proceedings, USDA Forest Service General Technical Report WO-27: 79–86, USDA.
- Bentz, B.J., Amman, G.D. & Logan, J.A. (1993) A critical assessment of risk assessment systems for the mountain pine beetle. *Forest Ecology and Management*, **61**, 349–366.
- Berryman, A.A. (1986) *Forest insects: principles and practice of population management*. 279 pp. New York, Plenum.
- 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. *Meddeleser fra det Norske Skogsforsøksvesen* **28**, 393–415.
- Christiansen, E. (1971b) Laboratory study on factors influencing pre-imaginal development in *Hylobius abietis* L. (Col., Curculionidae). *Norske Entomologisk Tidsskrift* **18**, 1–8.
- Christiansen, E. & Sandvik, M. (1974) Damage by *Hylobius abietis* to Scots pine on scarified patches. *Norsk Skogbruk* **20**, 8–9.
- Collins, S.A. (1993) *The potential of entomopathogenic nematodes to reduce damage by Hylobius abietis L.* PhD thesis, Imperial College, University of London.
- Crooke, M. & Kirkland, R.C. (1956) The gale of 1953: an appraisal of its influence on forest pest populations in pine areas. *Scottish Forestry* **10**, 135–145.
- Djedbour, D. (1996) *An investigation into adult feeding preferences of the large pine weevil, Hylobius abietis (Coleoptera: Curculionidae) with particular reference to the potential of broad leaf species mixtures to act as feeding depressants*. MSc thesis, Imperial College, University of London.
- Doom, D. & Frentzen, G.W.P. (1980) Postponement of planting as a silvicultural method to prevent damage by the large pine weevil *Curculio (Hylobius) abietis*. *Nederlands Bosbouw Tijdschrift* **52**, 217–227.
- Dorr, J. (1996) *Evaluation of the biocontrol potential of four isolates of the fungal pathogen Beauveria bassiana for the large pine weevil Hylobius abietis L. (Coleoptera: Curculionidae)*. MSc thesis, Imperial College, University of London.
- Eidmann, H.H. (1963) Zur Diapause einiger Forstinsekten. *Zeitschrift für Angewandte Entomologie* **52**, 362–367.
- Eidmann, H.H. (1968) Invasion of conifer plantations by radioactively labelled *Hylobius abietis*. pp. 75–84 in *Isotopes and radiation*. Proceedings of a Symposium, Vienna, 4–8 December 1967 jointly organized by the IAEA and FAO, Vienna, IAEA.
- Eidmann, H.H. (1979) Integrated management of pine weevil (*Hylobius abietis* L.) populations in Sweden. pp. 103–109 in *Current topics in forest entomology*. Forest Service General Technical Report WO-8. USDA.
- Eidmann, H.H. (1985) Silviculture and insect problems. *Zeitschrift für Angewandte Entomologie* **99**, 105–112.
- Eidmann, H.H. & von Sydow, F. (1989) Stockings for protection of containerised conifer seedlings against pine weevil (*Hylobius abietis* L.) damage. *Scandinavian Journal of Forest Research* **4**, 537–547.
- 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 the large pine weevil (*Hylobius abietis* L., Col., Curculionidae). *Zeitschrift für Angewandte Entomologie* **55**, 1–53.
- Fraser, N.R. (1952) *Certain aspects of the morphology and bionomics of the pine weevil, Hylobius abietis L.* Thesis for the Diploma of Imperial College.
- Gerdin, S. (1977) Observations on pathogens and parasites of *Hylobius abietis* (Coleoptera: Curculionidae) in Sweden. *Journal of Invertebrate Pathology* **30**, 263–264.
- Gerdin, S. & Hedqvist, K. (1985) *Perilitus areolaris* sp. n. (Hymenoptera: Braconidae), an imago parasitoid of the large pine weevil, (Linnaeus), and its reproductive behaviour. *Entomologica Scandinavica* **15**, 363–369.
- Guslits, I.S. (1970) Vlijanie uslovij pitaniya plodovitost' I ziznedejatel'nost' zukov bol'sogo osnovnogo dolgonosika – *Hylobius abietis* L. *Zoologicheskii Zhurnal* **49**, 862–868.
- Hanson, H.S. (1943) The control of bark beetles and weevils in coniferous forests in Britain. *Scottish Forestry Journal* **57**, 19–45.
- 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. & Selander, J. (1976) Reactions of the large pine weevil, *Hylobius abietis* L. (Coleoptera: 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 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.
- Heritage, S.G., Collins, S. & Evans, H.F. (1989) A survey of damage by *Hylobius abietis* and *Hylastes* spp. in Britain. pp. 28–33 in Alfaro, R.I. & Glover, S.G. (Eds) *Insects affecting reforestation: biology and damage*. Victoria, Canada, Pacific and Yukon Region, Forestry Canada.
- Huser, R. (1979) Height growth of a Scots pine plantation in the Upper Palatinate, with and without deep ploughing. *Forstwissenschaftliches Centralblatt* **98**, 258–263.



- Kadlec, Z., Stary, P. & Zúmr, V. (1992) Field evidence for the large pine weevil, *Hylobius abietis* as a vector of *Heterobasidion annosum*. *European Journal of Forest Pathology* **22**, 316–318.
- Korczynski, I. (1984) Possibilities for predicting damage to Scots pine stands by *Hylobius abietis*. *Sylvan*, **128**, 51–56.
- Korczynski, I. (1985) Trials of a new field method for measuring feeding intensity of *Hylobius abietis*. *Sylvan*, **129**, 59–64.
- Korczynski, I. (1988a) Effect of width and area of Scots pine plantations on the intensity of damage by the pine weevil *Hylobius abietis*. *Sylvan* **132**, 49–52.
- Korczynski, I. (1988b) Seasonal changes in the spatial distribution of feeding by the pine weevil *Hylobius abietis* in Scots pine plantations. *Sylvan* **132**, 49–53.
- Kudela, M. (1983) Influence of site temperature conditions on large pine weevil (*Hylobius abietis* L.) population density. *Sbornik Ustavu Aplikovane Ekologie a Ekotechniky Vysoke Skoly Zemedelskev Praha* **1**, 129–148.
- Kuziemska-Grzeczka, G. (1984) Potential for and rate of development of *Hylobius abietis* (Col., Curculionidae) on various tree species in sunny and shaded areas. *Folia Forestalia Polonica A Lesnictwo*, **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**, 2–22.
- Leather, S.R. (1987) Pine monoterpenes stimulate oviposition in the pine beauty moth, *Panolis flammea*. *Entomologia Experimentalis et Applicata* **43**, 295–297.
- Leather, S.R. (1988) Size, reproductive potential and fecundity in insects: things aren't as simple as they seem. *Oikos* **51**, 386–389.
- Leather, S.R., Walters, K.F.A. & Bale, J.S. (1993) *The ecology of insect overwintering*. Cambridge, Cambridge University Press.
- Leather, S.R., Ahmed, S.I. & Hogan, L.M. (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. & Bøgh, S. (1995) Seasonal variation in local abundance of adults of the large pine weevil, *Hylobius abietis* (Col., Curculionidae). *Journal of Applied Entomology* **119**, 511–513.
- 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). *Journal of Applied Entomology* **100**, 417–421.
- Lempérière, G. & Julien, J. (1989) Premiers résultats de tests pour l'évaluation de l'efficacité d'un insecticide systématique contre l'Hylobe (*Hylobius abietis* L., Col., Curc.). *Revue Forestière Française* **5**, 411–422.
- Levieux, J., Piou, D., Cassier, P., Andre, M. & Guillaumin, D. (1994) Associations of phytopathogenic fungi for the Scots pine (*Pinus sylvestris* L.) with the European pine weevil *Hylobius abietis* (L.) (Col., Curculionidae). *Canadian Entomologist* **126**, 929–936.
- Lindelöw, 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**, 1393–1404.
- 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.
- Lindstrom, 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.
- Luik, A. & Voolma, K. (1989) Some aspects of the occurrence, biology and cold-hardiness of *Hylobius* weevils. pp. 28–33 in Alfaro, R.I. and Glover, S.G. (Eds) *Insects affecting reforestation: biology and damage*. 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.
- Malphettes, C.B., Fougères, D. & Saintonge, F.X. (1994) Untersuchung über der Sexualentwicklung der mit Kairomonenfallen gefangenen Weibchen des grossen braunen Rüsselkäfers (*Hylobius abietis* L.) (Coleoptera: Curculionidae). *Anzeiger für Schädlingskunde und Umweltschutz*.
- Manlove, J.D., Styles, J.S. & Leather, S.R. (1997) Feeding of the large pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae). *European Journal of Entomology* **94**, 153–156.
- Martin, J.L. (1964) The insect ecology of red pine plantations in central Ontario. II. Life history and control of Curculionidae. *Canadian Entomologist* **96**, 1408–1417.
- Miessner, K.H. (1970) Are all afforestation and planting sites liable to weevil attack? New findings on the biology and ecology of *Hylobius abietis*. *Sozialistische Forstwirtschaft*, **20**, 45–47.
- Mrlina, G., Lempérière, G. & Calmon, J.P. (1994) Determination and uptake of carbosulfan and carbofuran in young Douglas firs *Pseudotsuga menziesii* Mirb. *Journal of Agricultural and Food Chemistry* **42**, 1569–1571.
- Munro, J.W. (1915) The structure and life history of *Bracon* sp.: a study in parasitism. *Proceedings of the Royal Society of Edinburgh* **36**, 313–333.
- Munro, J.W. (1925) *Hylobius abietis* attracted by light. *Entomologist's Monthly Magazine* **61**, 161–162.
- Munro, J.W. (1928) The biology and control of *Hylobius abietis* L. *Forestry* **2**, 31–39.
- Munro, J.W. (1929) The biology and control of *Hylobius abietis* L. Part II. *Forestry* **3**, 61–65.
- Mustaparta, H. (1975a) Response of single olfactory cells on the pine weevil *Hylobius abietis* L. (Col., Curculionidae). *Journal of Comparative Physiology* **97**, 271–290.
- 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.
- Nef, L. & Minet, G. (1992) Evaluation des risques de dégâts d'*Hylobius abietis* L. dans les jeunes plantations de conifères. *Silva Belgica* **99**, 15–20.
- 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. & Nordlander, G. (1994) Olfactory oriented migration through soil by root-living *Hylobius abietis* (L.) larvae (Col., Curculionidae). *Journal of Applied Entomology* **117**, 457–462.
- Nordenhem, H. (1989) Age, sexual development, and seasonal occurrence of the pine weevil *Hylobius abietis* (L.). *Journal of Applied Entomology* **108**, 260–270.



- 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**, 353–358.
- Nordenhem, H. & Nordlander, G. (1994) Olfactory orientated migration through soil by root-living *Hylobius abietis* (L.) (Col., Curculionidae) larvae. *Journal of Applied Entomology* **117**, 457–462.
- 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. (1989) The use of artificial baits to forecast seedling damage caused by *Hylobius abietis* (Coleoptera: Curculionidae). pp. 34–35 in Alfaro, R.I. & Glover, S.G. (Eds) *Insects affecting reforestation: biology and damage*. Victoria, Canada, Pacific and Yukon Region, Forestry Canada.
- Nordlander, G. (1990) Limonene inhibits attraction to  $\alpha$ -pinene in the weevils *Hylobius abietis* and *H. pinastri*. *Journal of Chemical Ecology* **16**, 1307–1320.
- Nordlander, G. (1991) Host finding in the pine weevil *Hylobius abietis*: effects of conifer volatiles and added limonene. *Entomologia Experimentalis et Applicata* **59**, 229–237.
- Örlander, G., Nilsson, U. & Nordlander, G. (1997) Pine weevil abundance on clear-cuttings of different ages: a six-year study using pitfall traps. *Scandinavian Journal of Forest Research* **12**, 225–240.
- Ossowski, L. (1941) The large pine weevil and methods of defence against it (with special reference to the methods adopted in the state forests of Poland. *Scottish Forestry Journal* **55**, 24–31.
- Osterstrom, L.O. & Andersson, B. (1975) Site preparation checks *Hylobius abietis*. *Skogsagaren* **51**, 30–31.
- Ozols, G.E., Menniks, E.A. & Bichevskis, M.Y. (1989) Dynamics of the abundance of weevils of the genus *Hylobius* (Col. Curculionidae) in clearings of drained forests. pp. 53–63 in Salvin'sh, Z.P. (Ed.) *Zashchita sosny i eli v Latviiskoi SSR*. Riga, USSR.
- Paine, T.D., Stephen, F.M. & Taha, H.A. (1984) Conceptual model of infestation probability based on bark beetle abundance and host tree susceptibility. *Environmental Entomology* **13**, 619–624.
- Pendrel, B. (1990) *Hazard from the seedling debarking weevil: a revised key to predicting damage on sites to be planted*. Maritimes Region, Technical Note 236, 4pp. Forestry Canada.
- Piou, D. (1993) Rôle d'*Hylobius abietis* (L.) (Col. Curculionidae) dans le transport de *Leptographium procerum* (Kendr) Wingf et son inoculation au pin sylvestre. *Annales de Sciences Forestière* **50**, 297–308.
- Pye, A.E. & Burman, M. (1977) Pathogenicity of the nematode *Neoalectana carpocapsae* (Rhabditida, Steinernematidae) and certain microorganisms towards the large pine weevil, *Hylobius abietis* (Coleoptera, Curculionidae). *Annales Entomologici Fennici* **43**, 115–119.
- 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.
- Pye, A.E. & Pye, N.L. (1985) Different applications of the insect parasitic nematode *Neoalectana carpocapsae* to control the large pine weevil, *Hylobius abietis*. *Nematologica* **31**, 109–116.
- Raffa, K.F. & Hunt, D.W.A. (1988) Use of baited pitfall traps for monitoring Pales weevil, *Hylobius pales* (Coleoptera: Curculionidae). *Great Lakes Entomologist* **21**, 123–125.
- Riseke, L.K. & Raffa, K.F. (1990a) Use of a monitoring system to evaluate pesticide efficacy and residual activity against two pine root weevils, *Hylobius pales* and *Pachylobius picivorus* (Coleoptera: Curculionidae), in Christmas tree farms. *Great Lakes Entomologist* **23**, 189–193.
- Rieseke, L.K. & Raffa, K.F. (1990b) Dispersal patterns and mark-and-recapture estimates of two pine root weevil species, *Hylobius pales* and *Pachylobius picivorus* (Coleoptera: Curculionidae), in Christmas tree plantations. *Environmental Entomology* **19**, 1829–1836.
- Salisbury, A.N. (1996) *Predation and migration of Hylobius abietis (L.) (Col. Curculionidae) larvae*. MSc thesis, Imperial College, University of London.
- Salisbury, A.N. (1998) Some observations on the large pine weevil *Hylobius abietis* (L.), (Coleoptera: Curculionidae). *Entomologist's Monthly Magazine* (in press).
- 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* (in press).
- Scott, T.M. & King, C.J. (1974) *The large pine weevil and black pine beetles*. Forestry Commission Leaflet 58, London, HMSO.
- Selander, J. (1978) Evidence of pheromone-mediated behaviour in the large pine weevil, *Hylobius abietis* (Coleoptera, Curculionidae). *Annales Entomologici Fennici* **44**, 105–112.
- Selander, J. & Immonen, A. (1991) Effect of fertilization on the susceptibility of Scots pine seedlings to the large pine weevil *Hylobius abietis*. *Folia Forestalia* **771**, 1–21.
- 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.
- Selander, J. & Kalo, P. (1979) Evaluation of resistance of Scots pine seedlings to *Hylobius abietis* L. (Coleoptera, Curculionidae) in relation to their monoterpenes composition. *Silva Fennica* **13**, 115–130.
- 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* **38**, 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* **39**, 40–45.
- Selander, J., Havukkala, I. & Kalo, P. (1976) Olfactory behaviour of *Hylobius abietis* L. (Col., Curculionidae). II. Response to 3-carene and  $\alpha$ -pinene during three stages of its life cycle. *Annales Entomologici Fennici* **42**, 63–66.
- Selander, J., Immonen, A. & Raukko, P. (1990) Resistance of naturally regenerated and nursery-raised Scots pine seedlings to the large pine weevil. *Folia Forestalia* **766**, 1–199.
- Skreecz, I. & Moore, R. (1997) The attractiveness of pine branches infected with selected wood-colonising fungi to the large pine weevil (*Hylobius abietis*). in Gregoire, J.C., Liebhold, A.M., Stephen, F.M., Day, K.R. and Salom, S.M. (Eds) *Integrating cultural tactics into the management of bark beetle and reforestation pests*. General Technical Report NE. US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. Radnor, Pennsylvania, USDA Forest Service.

- Soderstrom, V. (1976) The effects of scarification before planting conifers on newly clear-felled areas. *Sveriges Skogsvårdsförbunds Tidskrift* **74**, 59–333.
- Soderstrom, V. (1977) Problems and methods in forest regeneration IV. Trials with methods of soil preparation. *Kungl Skogs och Lantbruksakademiens Tidskrift* **116**, 43–52.
- Soderstrom, V., Backe, J., Byfalk, R. & Jonsson, C. (1978) A comparison of mineral soil mounds with other soil treatments for planting. *Rapporter och Uppsatser Institutionen för Skogsskotsel* **11**, 1–177.
- Solbreck, C. (1980) Dispersal distances of migrating pine weevils, *Hylobius abietis* (Coleoptera, Curculionidae). *Entomologia Experimentalis et Applicata* **28**, 123–131.
- Solbreck, C. & Gyldberg, B. (1979) Temporal flight pattern of the large pine weevil, *Hylobius abietis* L. (Col., Curculionidae), with special reference to the influence of weather. *Zeitschrift für Angewandte Entomologie* **88**, 532–536.
- Stadnitskii, G.V. (1978) Effect of the living ground vegetation on damage to Scots pine plantations by *Hylobius abietis*. *Lesnoi Zhurnal*, **6**, 26–29.
- Stage, A.R. & Hamilton, D.A. (1981) Sampling and analytical methods for developing risk-rating systems for forest pests. pp. 87–92 in Hedden, R.L., Barras, S.J. and Coster, J.E. (Eds) *Hazard-rating systems in forest insect pest management*. Symposium proceedings, USDA Forest Service General Technical Report WO-27: USDA.
- Stoakley, J.T. (1968) Control of the pine weevil, *Hylobius abietis* L. and of *Hylastes* species. *Forestry* **41**, 182–188.
- Stoakley, J.T. & Heritage, S.G. (1989) Application leaflet on the use of 'Gamma-Col' and 'Lindane flowable' for pre-planting treatment of young trees against *Hylobius abietis* and *Hylastes* spp. *Research Information Note* **147**, 1–6.
- Stoakley, J.T. & Heritage, S.G. (1990a) *Application leaflet on the use of 'Permit' and 'Permasect 25 EC' for pre-planting treatment of young trees against Hylobius abietis and Hylastes spp.* Research Information Note 177, Farnham, Forestry Commission Research Division.
- Stoakley, J.T. & Heritage, S.G. (1990b) *Approved methods for insecticidal protection of young trees against Hylobius abietis and Hylastes spp.* Research Information Note 185, Farnham, Forestry Commission Research Division.
- Styles, J.S. (1994) *Observations of Hylobius abietis and its possible control using natural enemies*. MSc thesis, Imperial College, University of London.
- Swaine, G. (1951) Population studies on *Hylobius abietis* L. (Coleoptera, Curculionidae). *Annals of Applied Biology* **38**, 606–614.
- Szmidt, A. & Korczynski, I. (1983) Population density of the pine weevil *Hylobius abietis* L., and its feeding activity, as indices for forecasting damage. *Prace Komisji Nauk Rolniczych i Komisji Nauk Lesnych* **54**, 137–144.
- Tarasova, O.V. & Sukhovolskii, V.G. (1986) Development of the pine weevil *Hylobius abietis* on felled areas, and assessing the danger of the pest for the stands. *Lesnoi Zhurnal* **2**, 24–27.
- Tilles, D.A., Nordlander, G., Nordenhem, H., Eidmann, H.H., Wassgren, A. & Bergstrom, G. (1986a) Increased release of volatiles from feeding scars: a major cause of field aggregation in the pine weevil *Hylobius abietis* (Coleoptera: Curculionidae). *Environmental Entomology* **15**, 1050–1054.
- Tilles, D.A., Sjödin, K., Nordlander, G. & Eidmann, H.H. (1986b) Synergism between ethanol and conifer host volatiles as attractants for the pine weevil, *Hylobius abietis* L. (Coleoptera: Curculionidae). *Journal of Economic Entomology* **79**, 970–973.
- Tilles, D.A., Eidmann, H.H. & Solbreck, B. (1988) Mating stimulant of the pine weevil *Hylobius abietis* (L.). *Journal of Chemical Ecology* **14**, 1495–1503.
- Trägårdh, I. (1913) On the chemotropism of insects and its significance for economic entomology. *Bulletin of Entomological Research* **4**, 113–117.
- Trägårdh, I. (1929) Undersökningar över den större snytbaggen och dess bekämpande. *Meddelanden från Statens Skogsforskningsinstitut* **25**, 29–92.
- Trauboth, V. (1987) Results of trapping with trap-billets in an outbreak of *Hylobius abietis* in Bad Salzungen State Forest Enterprise. *Sozialistische Forstwirtschaft* **37**, 283.
- Turchinskaya, I. A. (1983) The silvicultural and biological basis of prophylactic measures against the pine weevil. *Lesnoe Khozaystvo* **7**, 50–51.
- Vet, L.E.M. & van Opzeeland, K. (1984) The influence of conditioning on olfactory microhabitat and host location in *Asobara tabida* (Nees) and *A. rufescens* (Foerster) (Braconidae: Alysiinae) larval parasitoids of Drosophilidae. *Oecologia* **63**, 171–177.
- von Sydow, F. & Örlander, G. (1994) The influence of shelterwood density on *Hylobius abietis* occurrence and feeding on planted conifers. *Scandinavian Journal of Forest Research* **9**, 367–375.
- Waters, W.E., Stark, R.W. & Wood, D.L. (1985) *Integrated pest management in pine-bark beetle ecosystems*. New York, Wiley (Interscience).
- Wegensteiner, R. & Fuhrer, E. (1988) Zur Wirksamkeit von *Beauveria bassiana* (Bals.) Vuill. gegen *Hylobius abietis* L. (Col.: Curculionidae). *Entomophaga* **33**, 339–348.
- Wilson, L.F. (1968) Habits and movements of the adult pine root collar weevil in young red pine plantations. *Annals of the Entomological Society of America* **61**, 1365–1369.
- 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 estimation of pine weevil (*Hylobius abietis* L.) (Col., Curculionidae) density indices. *Journal of Applied Entomology* **119**, 157–160.
- Wilson, W.L. & Day, K.R. (1996) Variation in the relative abundance of the large pine weevil among Sitka spruce plantation sites. *Forestry* **69**, 177–179.
- Wilson, W.L., Day, K.R. & Hart, E. (1997) 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**, 203–222.
- Zagatti, P., Lempèriere, 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. (1994) Monitoring of seasonal occurrence of *Hylobius abietis* (L.) (Col., Curculionidae) in different forest environments of a model area. *Journal of Applied Entomology* **118**, 361–364.

(Accepted 3 August 1998)

© CAB INTERNATIONAL, 1999