Hylobius pine weevils adult host selection and antifeedants: feeding behaviour on host and non-host woody scandinavian plants

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Abstract

1 We searched for antifeedant activity in predomonantly non-host woody plants to find new compounds for seedling protection of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) against feeding by pine weevil *Hylobius abietis*. In total, 38 species from 25 families were compared in choice and no-choice tests.

2 In choice tests with *Empetrum*, *Juniperus*, *Ledum*, *Populus*, *Betula*, *Evonymus*, *Sorbus*, *Salix*, *Myrica* and *Pinus*, the weevils preferred *Pinus* to all others. In no-choice tests with the same species, the insects removed a similar or even greater area of the bark in three of 10 species than *Pinus*. The results were clearly different between the test modes.

3 In experiment 4, the areas of outer and inner bark (phloem) removed were quantified separately. The weevils removed significantly less of both outer and inner bark in *Ilex*, *Evonymus*, *Populus*, *Syringa*, *Taxus*, *Tilia*, *Viburnum*, *Lonicera* and *Sorbus* than *Pinus*.

4 Large areas of outer bark were removed in *Juglans*, *Fraxinus*, *Sambucus*, *Aesculus*, *Quercus*, *Corylus*, *Fagus*, *Salix*, *Alnus* and *Acer*. However, in the latter cases the insects stopped when reaching the inner bark. Thus, certain plant species have the outer bark removed by the insects but possessed an inner bark with antifeedant qualities.

Keywords Antifeedant, Curculionidae, feeding deterrent, *Hylobius abietis*, non-host plant, outer bark, phloem, pine weevil, seedling damage.

Introduction

The large pine weevil *Hylobius abietis* (L.) (Coleoptera: Curculionidae) is a conifer-feeding insect found in taiga and mixed conifer forests. Their larval food is dying conifer roots, whereas adults feed on conifers and other plants close to where roots are present (e.g. Nordlander, 1991; Nordlander *et al.*, 1997). The adult insects migrate over long distances to find dying roots suitable for breeding. In modern forestry, felling areas provide a very good biotope for the insects. Dying stumps and roots release volatile compounds (Von Sydow & Birgersson, 1997), mainly α-pinene and ethanol, which attract the insects over several kilometres distance. Incoming weevils feed mostly from the crown of the trees in or near the clear cut (Örlander *et al.*, 2000). This will cause little or no harm to a fully grown tree as feeding in relation to the biomass of bark is relatively small. The adult *H. abietis* female uses the conifer stumps and roots as breeding sites. After mating, females lay their eggs on the underground part of, or close to, the stumps (Elton *et al.*, 1964; Nordlander *et al.*, 1997). Hatched larvae feed in solitary galleries in the phloem under the bark where they grow, to finally construct a pupal chamber where they spend the winter. In June the following year they pupate and in August the new adults start to emerge (Novák, 1965). Both the newly emerged insects and the breeding adults feed extensively on most conifers but prefer Scots pine (*Pinus sylvestris* L.) as host (Långström, 1982; Leather *et al.*, 1994) and will find newly planted seedlings close to the stumps. The young seedlings have a small stem diameter in relation to how much damage an adult pine weevil causes (Thorpe & Day, 2002) and are frequently girdled and killed.

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The adult pine weevil causes damage on a few economically important conifers. However, the adults have been observed feeding on both coniferous and angiosperm tree species (Scott & King, 1974) and appear to be a oligophagous species. The insects have been presented to a number of woody plant species where they showed a preference in the order: *Pinus sylvestris* >> *Betula pendula* >> *Picea abies* >> *Fraxinus excelsior* > *Acer pseudoplatanus* (Bejer-Petersen *et al.*, 1962; Manlove *et al.*, 1997). *Pinus* is preferred over *Picea* (Leather *et al.*, 1994) despite the fact that both species are common host plants (Ohnesorge, 1953; Långström, 1982). One explanation may be that *H. abietis* fed on *Picea* exclusively has been shown to have a slower development and lower fecundity rate (Guslits, 1970).

However, Scots pine and Norway spruce (*Picea abies* (L.) H. Karst.) are the economically most important species in Scandinavian forestry and consequently, the pine weevil is the most serious insect pest in Swedish forestry today and has been considered as a pest in conifer plantations since the early part of the last century (Trädgårdh, 1913). Costs from plant death, re-planting and loss of growth are estimated to be between US$ 50 million and US$ 200 million per year in Sweden (Weslien, 1998). Conifer seedlings are today usually protected with Permethrin, a pyrethroid that will be banned in 2004 and there is therefore an urgent need for environmentally safe control methods.

Our hypothesis is that bark of non-host plant species may contain secondary compounds, antifeedants, causing the insects to starve rather than feed. Antifeedants affect both olfactory and gustatory chemoreceptors on the antennae, mouthparts (Bland, 1983) and legs (Rees, 1969) of the insects and can be both volatile and non-volatile. Examples of antifeedants are: (1) *repellents*, affecting the insect's olfactory receptors (insects orientate away without contact with the plant material, Dethier *et al.*, 1960; Beck, 1965; Chapman, 1974); (2) *arrestants*, affecting olfactory receptors (insects stop moving towards plant material, without contact with it, Dethier *et al.*, 1960); (3) *suppressants*, affecting olfactory and gustatory receptors (insects are suppressed from biting once contact has been made with plant material, Beck, 1965; Chapman, 1974); or (4) *feeding deterrents*, affecting gustatory receptors (insects are deterred from feeding after they have already bitten plant material once or repeatedly, Dethier *et al.*, 1960; Beck, 1965; Chapman, 1974). Antifeedants may also have postingestive effects, but are here defined as 'Volatile and non-volatile pre-ingestive inhibitors'. Antifeedant activity will here accordingly be regarded as inhibition by olfactory and gustatory responses and not by inhibition of a later stage in insect feeding and metabolism' (Månsson, 2001). Screening of non-hosts to find environmentally safe substitutes for pyrethroid pesticides is a preferable method, as plant compounds may protect seedlings from feeding without being harmful to the environment. By presenting the non-hosts to the weevils in choice and no-choice tests one may also identify a number of toxic compounds in cases where insects die from feeding.

To test our hypothesis we have measured feeding activity in *H. abietis* on host and non-host woody plant species. We tested 38 species of plants from 36 genera in 25 families, mainly from the taiga biome and from Southern Scandinavia. One species was non-woody, *Lythrum salicaria*, but had a texture suitable for this type of test. Two test modes were used: choice tests and no-choice tests. Attention was paid to whether feeding/removal of bark continued all the way down to the xylem or if removal of bark ceased when reaching the phloem.

Methods

Collection of plant material

Branches and stem-parts (width: 5–30 mm) from Scandinavian and non-Scandinavian woody plants were collected in southern Sweden during spring–summer 1996–1998 and 2000 (Table 1). The samples comprised plant material from *Pinus sylvestris*, 33 woody Scandinavian plants, one non-woody plant, and three non-Scandinavian woody plant species. All material was put in a freezer ($-18\,°C$) immediately or not later than 2 h after collection.

Insect collection and culture

Adult *H. abietis* were collected in May–June as they flew in and landed on sawdust piles at a number of sawmills located in southern Sweden. The overall procedures were similar to those in Klepzig & Schlyter (1999). The insects were placed in ventilated buckets for transport to the laboratory. Groups of 150–300 pine weevils were placed in ventilated plastic buckets containing moistened paper towelling and Scots pine branches. To slow down the metabolism of the weevils the buckets were stored in the dark in an $8–10\,°C$ cold room awaiting the experiments. Before initiation of an assay, the buckets were moved into a growth chamber set to conditions similar to those found in the field at the time of weevil collection ($24\,°C$, 75% RH, and a photo period of LD 20 : 4 h). The insects were allowed to feed from Scots pine branches for a week before the assays but were starved for 24 h before the experiments. By preparing an excess of insects, it was possible to select weevils of similar size for use in all of the experiments. Only large insects were used.

Assays

We tested 38 species of plants, including *P. sylvestris*, from 36 genera in 25 families, mainly from the Scandinavian flora. Two types of bioassay were conducted: choice tests and no-choice tests. Twig sections, 12 mm long and of approximately equal diameter (width: 5–10 mm) from each woody species to be tested, were prepared and placed on a filter paper moistened with 5 mL distilled water in a Petri dish (width: 90 mm). One *Pinus* twig, one twig from each of five other species, and one weevil were placed in each Petri dish. Each dish was closed such that the twig was wedged vertically against the lid. In total, six or 12 similar dishes were prepared and placed in an environmental chamber ($24\,°C$, 75% RH, LD 20 : 4 h). The insect was allowed to

Table 1 Plant material tested 1996–1998 and 2000

Family	Species	Common name	Expt. No.	Origin
Scandinavian species				
Pinaceae:	*Pinus sylvestris* L.	Scots pine	1, 2, 3, 4	Alnarp
	Larix decidua Mill.	Larch	4	Alnarp
Cupressaceae:	*Juniperus communis* L.	Juniper	1, 4	Asa
Taxacae:	*Taxus baccata* L.	Yew	3, 4	Alnarp
Salicaceae:	*Salix caprea* L.	Sallow	2, 4	Asa
	Populus tremula L.	Aspen	2, 4	Asa
Myricaceae:	*Myrica gale* L.	Bog myrtle	1, 4	Alnarp
Betulaceae:	*Betula pendula* Ehrh.	Silver birch	2, 4	Sjöbo
	Alnus glutinosa (L.) Gaertner	Alder	4	Asa
Corylaceae:	*Corylus avellana* L.	Hazel	4	Alnarp
	Carpinus betulus L.	Hornbeam	4	Alnarp
Fagaceae:	*Fagus sylvatica* L.	Beech	3, 4	Alnarp
	Quercus rubra L.	Oak	2(B), 4	Alnarp
Ulmaceae:	*Ulmus glabra* Huds.	Elm	4	Alnarp
Rosaceae:	*Sorbus aucuparia* L.	Rowan	2, 4	Asa
	Prunus spinosa L.	Sloe	3	Alnarp
	Sorbus intermedia (Ehrh.) Pers.	Whitebeam	4	Asa
	Prunus padus L.	Bird cherry	4	Alnarp
Fabaceae:	*Laburnum alpinum* Mill.	Scottish Laburnum	3	Alnarp
Aceraceae:	*Acer platanoides* L.	Maple	4	Alnarp
Hippocastaneaceae:	*Aesculus hippocastanum* L.	Horse-chestnut	4	Asa
Celastraceae:	*Evonymus europaeus* L.	Spindle tree	2, 4	Alnarp
Tiliaceae:	*Tilia cordata* Mill.	Linden	4	Asa
Aquifoliaceae:	*Ilex aquifolium* L.	Holly	4	Alnarp
Thymelaeaceae:	*Daphne mezereum* L.	Mezeron	3	Alnarp
Elaeagnaceae:	*Hippophae rhamnoides* L.	Sea buckthorn	4	Alnarp
Lythraceae:	*Lythrum salicaria* L.	Purple loosestreef	4	Bosjö kloster
Ericaceae:	*Ledum palustre* L.	Labrador tea	1	Asa
	Empetrum nigrum L.	Crowberry	1	Asa
Oleaceae:	*Fraxinus excelsior* L.	Ash	4	Alnarp
	Syringa vulgaris L.	Lilac	4	Alnarp
Caprifoliaceae:	*Sambucus racemosa* L.	Red elder	4	Alnarp
	Viburnum opulus L.	Guelder rose	4	Asa
	Symphoricarpos rivularis (L.) S. F. Blake	Snowberry	4	Alnarp
	Lonicera xylosteum L.	Red honeysuckle	4	Alnarp
Non Scandinavian species				
Juglandaceae:	*Juglans regia* L.	Walnut	4	Alnarp
Buxaceae:	*Buxus sempervirens* L.	Boxwood	3	Alnarp
Magnoliaceae:	*Magnolia grandiflora* L.	Southern Magnolia	3	Alnarp

feed from the twigs in each dish for 48 h and accordingly, choose between them. The area of bark removed and phloem consumed down to the xylem on each twig was measured and compared between each plant species.

The no-choice assay was prepared and conducted as the choice assays, but with only one twig in each Petri dish. The test in no-choice mode was essentially the same as in the no-choice test in Klepzig & Schlyter (1999). The weevil could not choose between species but only between feeding or not feeding.

A choice test may not only indicate that the non-hosts are containing antifeedants, but feeding patterns may be caused by the host alone being the most attractive. A no-choice test singles out the cases where the weevils prefer to starve for 48 h rather than feed on the bark from the cases where they accept the plant in lack of their host. Thus, choice tests were only used twice, as the no-choice test was found to be the more applicable method in this experimental set-up. The area consumed or removed in outer cortex bark (bark)

and inner bark (phloem) was observed to differ qualitatively between species in Experiments 2 and 3. To further separate the effects of a negative signal from antifeedants from the lack of a positive signal, the area of bark removed was quantified separately from area of phloem consumed or removed in the last experiment (Experiment 4).

To measure the area of bark and phloem removed after 48 h of feeding, we used a flexible transparent grid (mm^2) placed around the twig. In most cases, bark and phloem differed in colour, texture and thickness and were easy to distinguish between. The results were compared in an antifeedant index (AFI) (Blaney *et al.*, 1984; Klepzig & Schlyter, 1999) where $AFI = (T - C)/(T + C)$ ($T =$ Treatment, area removed) ($C =$ Control, area removed in *Pinus*). $AFI = -1$ indicates the best possible feeding stimulant, $AFI = 0$ indicates no effect and $AFI = +1$ indicates the best possible antifeedant effect. *Pinus* was used as control but as bark areas removed (T and C) does not have a normal distribution, the ratios of T and C forming the mean AFI in
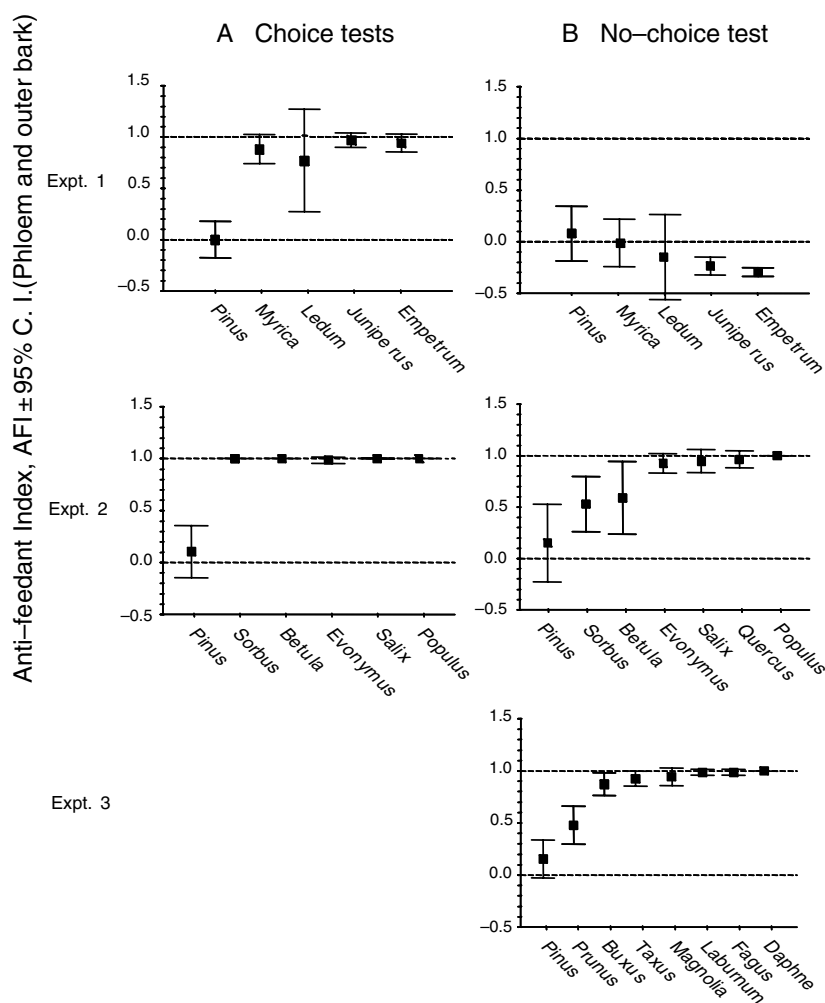
Figure 1 Choice and no-choice twig tests. Experiments 1 ($n = 6$) and 2 ($n = 12$) include Scandinavian taiga plants only. Experiment 3 ($n = 12$) includes taiga and non-Scandinavian plants. Area removed down to the xylem is recorded and compared by the Antifeedant Index $\pm$ 95% confidence interval to the host (*Pinus*) (see Methods).

no-choice experiments for *Pinus* may differ from 0. Removal of outer bark area and inner bark (phloem) area were quantified separately.

In Experiment 1, *P. sylvestris* L. was in one choice and one no-choice test compared with four taiga species. In Experiment 2, five other plant species were compared with *Pinus* in a choice test. In the no-choice test, *Quercus rubra* was added to the five. In Experiment 3, the test in choice mode was excluded. *Pinus* was compared with five Scandinavian and with two non-Scandinavian species in one no-choice test. Experiment 4 was conducted as a no-choice test. *Pinus* was compared with 28 Scandinavian woody plants, one Scandinavian non-woody plant (*Lythrium salicaria*), and one non-Scandinavian woody plant species (*Juglans regia*) (Table 1). The areas of bark and phloem were quantified separately.

Results

Experiment 1

The choice test gave a very clear preference for feeding on *Pinus*. All non-hosts were fed upon, but *Pinus* twigs signifi-

cantly more. The AFI shows close to the best possible antifeedant effect ($+ 1$) for three of four non-hosts, whereas *Ledum* twigs show a smaller antifeedant effect (> 0) (Fig. 1, A1).

The no-choice assay mode gave a feeding pattern dramatically different from the choice test of the same non-hosts. *Pinus* was compared with the same species as in the choice test but differed significantly (95% confidence intervals not overlapping) only from one of the non-hosts in this test mode: *Empetrum* twigs were significantly more fed upon than *Pinus* (Fig. 1, B1). *Juniperus, Ledum* and *Myrica* did not differ in feeding from *Pinus*, but *Empetrum* and *Juniperus* had a negative AFI value.

Experiment 2

Another batch of Scandinavian woody plants was compared with *Pinus* twigs in a choice test: *Salix, Populus, Betula, Sorbus* and *Evonymus*. *Pinus* was eaten, whereas four of five non-host twigs were left untouched. *Evonymus* was an exception, the only non-host fed upon to some degree, but the AFI confidence interval overlapped $+1$ (Fig. 1, A2). In contrast, all but one of the non-hosts were
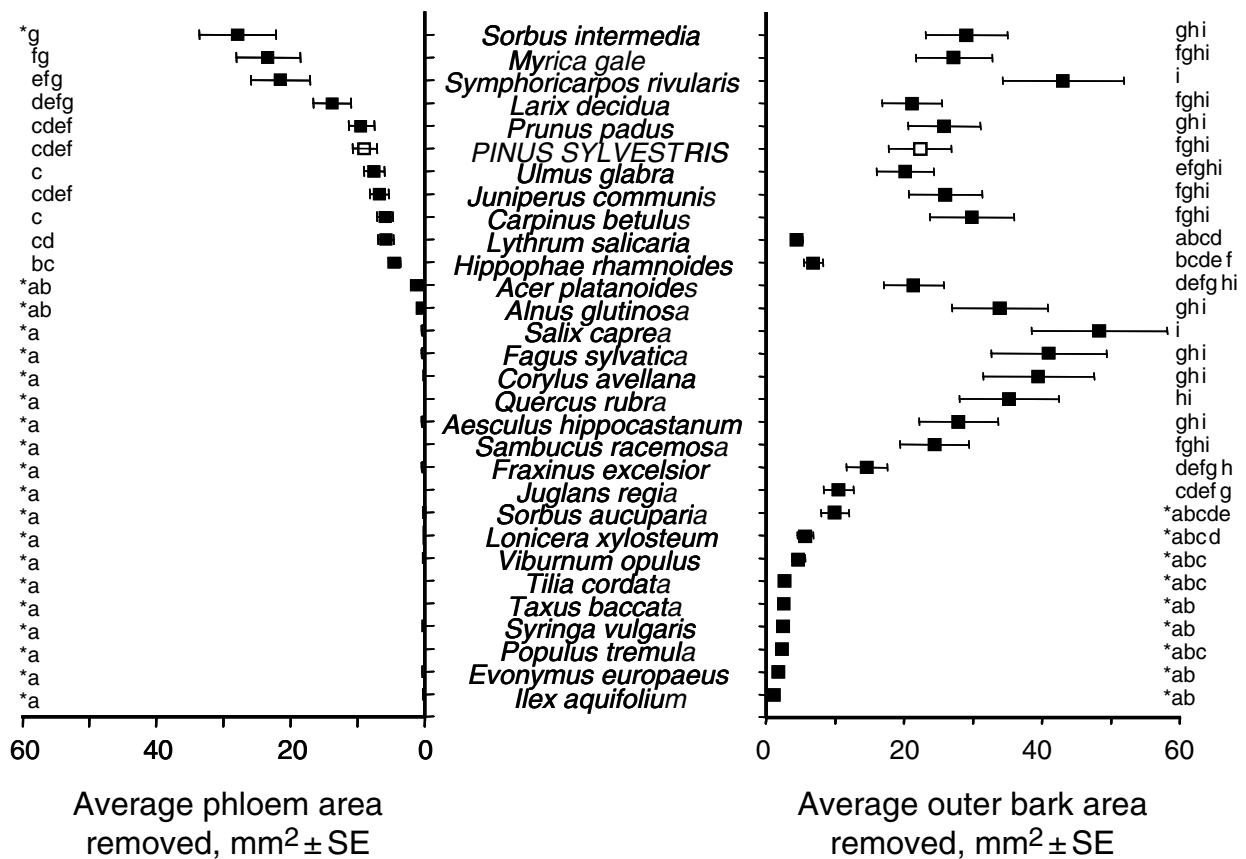
Figure 2 No-choice twig test, Experiment 4 ($n = 12$) includes *Pinus sylvestris*, 28 Scandinavian woody plants, one Scandinavian non-woody plant (*Lythrium salicaria*), and one non-Scandinavian woody plant species, *Juglans regia*. Removal of outer bark area and inner bark (phloem) areas were separately quantified. Bars show average area removed (mm²) ± SE. Lower case letters show the result from Tukey's multiple range test: rows with the same letter are not significantly different ($\alpha = 0.05$). Asterisks (*) indicate area removed significantly different from *Pinus*, $P < 0.05$. Species are ordered first by the area of outer bark consumed (when area of phloem consumed is 0) and then by the area of phloem consumed.

fed upon in the no-choice mode with the same non-hosts plus *Quercus*. None of them differed significantly from +1, whereas *Pinus* showed the same result as in the choice test with an AFI close to 0 (Fig. 1, B2). There was, as in the choice test, no feeding at all on *Populus*. *Betula* and *Sorbus* had a mean AFI between 0.2 and 0.9, but overlapped with *Pinus*. From Experiments 1 and 2 we concluded that the choice mode gave little information on the variation in antifeedant potential among the non-host species. In Experiments 3 and 4 only the no-choice mode was used.

Experiment 3

Prunus did show an antifeedant effect (AFI > 0) but was not significantly different from *Pinus*. The other six non-host species showed significant antifeedant qualities (mean AFI close to or overlapping +1). The strongest antifeedant effect (mean AFI = +1) was found in *Daphne*, where no feeding by the insects could be observed.

Experiment 4

Consumption of phloem from 19 of the 30 plants was significantly lower than in *Pinus* (Fig. 2). In most of these cases, the insects removed the outer bark but stopped feeding or only nibbled when reaching the phloem. Among these 19 cases, the phloem was penetrated only in *Acer* and in *Hippophae*. The outer bark area removed was smaller than in *Pinus* in seven cases: *Sorbus*, *Lonicera*, *Viburnum*, *Tilia*, *Taxus*, *Syringa*, *Populus*, *Evonymus* and *Ilex*. Only shallow nibbling on the bark was recorded in *Ilex*. The remaining 10 cases did not differ from *Pinus* in the removed area of either outer bark or phloem. *Sorbus intermedia* was an exception, where the area of phloem consumed was significantly larger than in *Pinus*. To get an overview of the results, the different plant species were divided into two groups based on Tukey's multiple range test (Table 2): species with both the outer bark and the phloem areas significantly less removed (group A), and a group with only the phloem areas less consumed than in *Pinus* (group B). Group A had nine species; except for *Tilia* they were all bushes or small trees. Group B had 10 species, mostly full-sized forest trees.

Table 2 Feeding patterns in *H. abietis*; discrimination between outer bark and phloem based on Tukey's multiple range test

Group A: Both outer bark and phloem less removed than in *Pinus*	
Sorbus aucuparia L.	Mountain ash
Lonicera xylosteum L.	Red honeysuckle
Viburnum opulus L.	Guelder rose
Tilia cordata Mill.	Linden
Taxus baccata L.	Yew
Syringa vulgaris L.	Lilac
Populus tremula L.	Aspen
Evonymus europaeus L.	Spindle tree
Ilex aquifolium L.	Holly
Group B: Phloem less removed than in *Pinus*	
Acer platanoides L.	Maple
Alnus glutinosa (L.) Gaertner	Alder
Salix caprea L.	Sallow
Fagus sylvatica L.	Beech
Corylus avellana L.	Hazel
Quercus rubra L.	Oak
Aesculus hippocastanum L.	Horse-chestnut
Sambucus racemosa L.	Red elder
Fraxinus excelsior L.	Ash
Juglans regia L.	Walnut

Discussion

Our Experiments 1 and 2 show that the results were strongly dependent on the test method used. When the weevils were allowed to choose between *Pinus* twigs and non-host twigs they always chose the *Pinus* twigs and did not feed from any non-host except *Evonymus*. However, when presented to the same species in the no-choice test, the insects fed from all non-hosts except from *Populus*. The results show that the pine weevil is able to choose another species than Scots pine or spruce when they are absent. The no-choice method gave the clearest results in our laboratory conditions. The method gives a good estimation of which plant species are suitable as food sources in a hierarchical structure, but does not give a clear picture of insect preference. The choice test gives a picture of preference under field conditions and can, by excluding the most preferred plant material stepwise, give a clear picture of the actual feeding preference in the field. However, the methods do not necessarily show what species is the best as a host for the insects: pine weevils feeding from *Betula pendula* have a higher mortality rate than those feeding from *Picea abies* even if *Betula* is preferred over *Picea* (Manlove *et al.*, 1997). Experiments 3 and 4 suggest that the taiga plants (normally encountered by beetles in their habitat) were relatively well accepted, whereas plants from non-conifer forests and more exotic plants were less accepted.

In Experiment 4 (Table 2), plants in group A may seem to contain the best species for further research on antifeedant content because the outer bark quality was less preferred than *Pinus*. These species probably have volatile compounds released from the bark, arrestants and/or repellents, which keep the weevils at a distance from the plant material, but the plants may also contain suppressants and deterrents. Suppressants may have kept the pine weevils from biting when in contact with the twigs. In some cases there

was shallow nibbling on the bark, but no continuous feeding. Sibul *et al.* (2001) showed that water extract from raw leaves from *Taxus baccata* decreased the feeding activity of pine weevils in a laboratory assay. In field conditions, the extracts showed antifeedant qualities. A similar effect can be seen in the bark from the same species in our experiments. However, it can not be excluded that the untouched twigs in group A (*Ilex*) were simply not regarded as food by the insects and may not contain any antifeedant compounds. The influence of bark texture and thickness is difficult to estimate but seems to have importance as the insects do not feed on the thicker bark of its common hosts *Pinus sylvestris* and *Picea abies* but prefer thinner stems and branches.

In contrast, in group B the outer bark was removed by the weevils but the phloem was not. The outer bark was probably peeled off to gain access to the phloem. Only further experiments on the phloem content can show if it contains antifeedants or if it simply has the wrong texture, but as the outer bark is generally harder than the phloem, this is probably not the case. The bark removed down to the phloem and the nibbling on the phloem suggests that the phloem in this group of plants contains less volatile feeding deterrents and, possibly, suppressants.

Ideally, one would like to find patterns of feeding preference related to the different plant families, related to similarities in secondary chemistry, but our study does not show that. Different insect feeding patterns on different plant families were not possible to discern here, probably due to the low sample sizes within each family.

In 10 non-hosts, both bark and phloem areas removed were as great as (phloem area in *S. intermedia* even greater than) in *Pinus* twigs. That may be due to their softer texture. The bark/phloem in these non-hosts can be even easier to remove than *Pinus* bark/phloem, even if not preferred under field conditions. The thickness of the material may be another property to be considered as thin bark/phloem may take shorter time to consume than thick. Nutrient content, e.g. N content, may also affect consumption.

Extensive work has been carried out on pine weevil olfactory responses (e.g. Mustaparta, 1975; review in Schlyter, 2004). A number of volatile allomone and kairomone compounds has been screened (e.g. Klepzig & Schlyter, 1999). Bratt *et al.* (2001) found that lodgepole pine (*Pinus contorta*) is less fed on than *Pinus sylvestris*. They isolated two compounds with antifeedant qualities against the pine weevil in *P. contorta*: ethyl *trans*-cinnamate and ethyl 2,3-dibromo-3-phenylpropanoate.

However, the less volatile compounds, affecting the gustatory receptors, need to be examined to understand the pine weevils' gustatory preferences. The results from our bioassay show that a number of plants may contain effective antifeedant signals against *H. abietis* pine weevils.

References

Beck, S.D. (1965) Resistance of plants to insects. *Annual Review of Entomology*, **10**, 207–233.

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 Entomologia Fennicae*, **17**, 1–17.

Bland, R.G. (1983) Sensilla on the antennae, mouthparts, and body of the larva of the Alfalfa weevil, *Hupera postica* (Gyllenhal) (Coleoptera: Curculionidae). *International Journal of Insect Morphology and Embryology*, **1**, 261–272.

Blaney, W.M., Simmonds, M.S.J., Evans, S.J. & Fellows, L.E. (1984) The role of secondary plant compound 2, 5-didroxymethyl 3,4 dihydroxypyrrolidine as a feeding inhibitor for insects. *Entomologia Experimentalis et Applicata*, **36**, 200–216.

Bratt, K., Sunnerheim, K., Nordenheim, H., Nordlander, G. & Långström, B. (2001) Pine weevil (*Hylobius abietis*) antifeedants from lodgepole pine (*Pinus contorta*). *Journal of Chemical Ecology*, **27**, 2253–2262.

Chapman, R.F. (1974) The chemical inhibition of feeding by phytophagous insects: a review. *Bulletin of the Entomological Research*, **64**, 339–363.

Dethier, V.G., Barton-Browne, L. & Smith, C.N. (1960) The designation of chemicals in terms of the responses they elicit from insects. *Journal of Economic Entomology*, **53**, 134–136.

Elton, T.G., Blankwaardt, H.F.H., Burger, H.C., Steemers, W.F. & Tichelman, L.C. (1964) Insect communities in barked and unbarked pine stumps with special reference to the large pine weevil (*Hylobius abietis* L.) (Coleoptera: Curculionidae). *Journal of Applied Entomology*, **55**, 1–54.

Guslits, I.S. (1970) Influence of the conditions of feeding upon fecundity and life activity in beetles *Hylobius abietis*. *Zoologisheskii Zhurnal*, **48**, 862–868 (in Russian).

Hori, M. (1999) Antifeeding, settling inhibitory and toxic activities of labiate essential oils against the green peach aphid, *Myzus persicae* (Sulzer) (Homoptera: Aphididae). *Applied Entomological Zoology*, **34**, 113–118.

Klepzig, K.D. & Schlyter, F. (1999) Laboratory evaluation of plant derived antifeedants against European Pine Weevil, *Hylobius abietis*. *Journal of Economic Entomology*, **92**, 644–650.

Långström, B. (1982) Abundance and seasonal activity of adult *Hylobius* weevils in reforestation areas during the first years following final felling. *Communicationes Instituti Forestalis Fenniae*, **106**, 1–23.

Leather, S.R., Ahmed, S.I. & Hogan, L. (1994) Adult feeding preferences of the large Pine Weevil, *Hylobius abietis* L. *European Journal of Entomology*, **91**, 385–389.

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**, 153–156.

Månsson, P. (2001) The role of antifeedants in host selection of herbivorous insects. *Introductory paper in chemical ecology: no. 5. Alnarp, September 2001.*

Mustaparta, H. (1975) Responses of single olfactory cells in the pine weevil *Hylobius abietis* L. (Coleoptera: Curculionidae). *Journal of Comparative Physiology*, **97**, 271–290.

Nordlander, G. (1991) Limonene inhibits attraction to α-pinene in the pine weevil *Hylobius abietis* and *H. pinastri*. *Journal of Chemical Ecology*, **16**, 1307–1320.

Nordlander, G., Nordenhem, H. & Bylund, H. (1997) Oviposition patterns of the pine weevil *Hylobius abietis*. *Entomologia Experimentalis et Applicata*, **85**, 1–9.

Novák, V. (1965) The pine weevil – *Hylobius abietis*. *Lesnicke Actuality*, **18**, 1–91 (abstract in English).

Ohnesorge, B. (1953) The influence of scent and flavour on the choice of food-plants by *Hylobius abietis*. *Beträge zür Entomologie*, **3**, 437–468.

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.

Rees, C.J.C. (1969) Chemoreceptor specificity associated with choice of feeding site by the beetle *Chrysolina brunsviciensis* on its food plant, *Hypericum hirsutum*. *Entomologia Experimentalis et Applicata*, **12**, 565–583.

Schlyter, F. (2004) Semiochemicals in the life of bark weevils. *Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis. Part II. Weevils* (ed. by F. Liutier *et al.*). Kluwer, Dordrecht.

Scott, T.M. & King, C.L. (1974) *The Large Pine Weevil and Black Scots Pine Weevil*. United Kingdom Forestry Leaflet No 58. HMSO, London.

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, Tartu, Estonia, January 24–25, 2001.*

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**, 187–194.

Trädgårdh, I. (1913) On the chemotropism of insects and its significance for economic entomology. *Bulletin of Entomological Research*, **4**, 113–117.

Von Sydow, F. & Birgersson, G. (1997) Conifer stump condition and pine weevil (*Hylobius abietis*) reproduction. *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière*, **27**, 1254–1262.

Weslien, J. (1998) How much are the Pine Weevil damages? *Kungl. Skogs- och Lantbrukakademiens Tidskrift*, **15**, 19–22 (in Swedish).