

Adult large pine weevils *Hylobius abietis* feed on silver birch *Betula pendula* even in the presence of conifer seedlings

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- Abstract**
- 1 The feeding preference of the adult pine weevil *Hylobius abietis* (L.) (Coleoptera: Curculionidae) for *Betula pendula* Roth was studied in no-choice and paired-choice feeding experiments.
 - 2 In the first no-choice test, large quantities of silver birch bark in Petri dishes were consumed; on average, the daily consumption of each weevil was 67 mm².
 - 3 In the second no-choice test, the weevils were offered 1-year-old silver birch seedlings for 6 days. Initially, the weevils fed mostly on the stem bases; later, they moved upward to feed on other parts of the stems. In addition to the main shoots, scars caused by gnawing were also found on leaf bases, blades, veins and petioles. Feeding resulted in the death of the main stems in 15% of the seedlings.
 - 4 In the paired-choice tests, the conifers were preferred to silver birch, even though a large amount of silver birch was also consumed in the presence of conifers.
 - 5 In the paired-choice tests, equal amounts of Scots pine and Norway spruce were always consumed. When hybrid aspen was offered, only small amounts were gnawed.

Keywords Curculionidae, feeding, feeding preferences, *Hylobius abietis*.

Introduction

In Europe, the large pine weevil *Hylobius abietis* L. (Coleoptera: Curculionidae) is the most harmful pest in forest regeneration (Day & Leather, 1997; Grégoire & Evans, 2004). This species is distributed throughout the whole of Europe and most parts of northern Asia. The number of suitable breeding sites, and thus the population size of weevils, increases rapidly in clear-cut areas. Volatile compounds (e.g. several monoterpenes and ethanol) emitted from fresh wood, stumps and logging residues attract weevils to reforestation areas for several years after clear-cutting (Nordlander, 1987; Brattli *et al.*, 1998). In addition, feeding scars release increased amounts of host volatiles, which are essential for aggregation of pine weevils in the field (Selander & Kalo, 1979; Tilles *et al.*, 1986; Nordlander, 1991; Brattli *et al.*, 1998). Even though weevils also use sight to locate suitable food, seedlings that have not previously been attacked are mainly chosen randomly (Nordlander, 1987; Björklund *et al.*, 2003).

Pine weevils are polyphagous and cause economic losses to forestry feeding on the bark and phloem of 1- to 5-year-old pine *Pinus* sp. and spruce *Picea* sp. seedlings. Although a large part of the pine weevil's diet is composed of conifers, they also feed on shrubs and broadleaved trees (e.g. bilberry, *Vaccinium myrtillus*; birches, *Betula* spp.; willows, *Salix* spp.; bird cherry, *Prunus padus* L.; English oak, *Quercus robur* L.; European alder, *Alnus glutinosa* L. Gaertn.; European beech, *Fagus sylvatica* L.; common ash, *Fraxinus excelsior* L.) (Sylvén, 1927; Löf, 2000; Örlander *et al.*, 2001; Samuelsson, 2001). Bylund & Nordlander (2001) have estimated that conifer seedlings make up approximately 9% of the nourishment needs of adult pine weevils in clear-cut areas. If young seedlings are planted on such areas, they may be seriously damaged and extensive feeding may lead to death of the seedlings.

In Finland during the 1990s, an average of every tenth seedling delivered for planting by forest nurseries was silver birch *Betula pendula* Roth and, in the year 2001, the proportion was 6% (Finnish Forest Research Institute, 2002). In addition to Finland, substantial numbers of broadleaved seedlings are produced e.g. in Denmark, where up to 50% of the planted seedlings are deciduous (Olsson, 1999). Broadleaved species are commonly planted also in southern

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Europe, but the damage caused by pine weevils to deciduous trees has not been studied extensively there. On birch, pine weevil feeding scars change colour quickly and are more difficult to recognize than scars on conifers. Thus, these feeding scars may previously have been neglected or they may have been mistaken for damage caused e.g. by voles or fungal infections that have been able to infect seedlings through mechanical injuries. Earlier studies have also yielded controversial results regarding the palatability of birch to pine weevil (Manlove *et al.*, 1997; Månsson & Schlyter, 2004). This might be explained by the different origin, size and physiological age of the plant material.

The present study aimed to investigate feeding of the adult large pine weevil on silver birch. In the no-choice tests, the experimental weevils were allowed to feed on either pieces of silver birch stem or on living seedlings. Attention was also paid to which parts of the seedlings the weevils prefer and how the seedlings cope with the resulting damage. Furthermore, the weevils' feeding preferences were studied in paired-choice tests by offering the weevils pieces of stems of silver birch, Scots pine, Norway spruce and hybrid aspen *Populus tremula* × *tremuloides* Michx.

Materials and methods

Experimental insects

All experiments were conducted with adult pine weevils that had been collected between May and June 2002 and in June 2003 at the Iisvesi sawmill in Suonenjoki, Finland (62°39'N, 27°0'E). After collection, the weevils were kept in groups of ten in glass jars with sawdust at 6.5 °C. Water and fresh pine twigs were added to the jars as needed. Only healthy, medium-sized individuals were accepted as experimental insects. Before each experiment, at least twice the number of weevils needed were weighed, after which the selected individuals were placed singly in Petri dishes (Ø 14 cm) for 24 h with no food. After this fasting, the weevils were weighed and placed randomly either in Petri dishes, where they were allowed to feed on pieces of stem cut from seedlings, or in cages where they fed on living seedlings. The weevils were also weighed at the end of each experiment, left without food for another 24-h fast and weighed again.

Seedlings

All the seedlings used in the feeding experiments had been produced according to normal nursery practices. One-year-old silver birch seedlings (originating from seed-orchard seeds used in central Finland) had been grown in Plantek PL-25 trays (25 cavities per tray, 380 cm³ per cavity, 156 cavities/m²; Lännen Plant Systems, Finland). One-year-old hybrid aspen plants (clone 17 in 2002 and clone 14 in 2003) had been produced from root-cuttings that had been placed in a mixture of peat and sand. Rooted cuttings had been transplanted into PL-64 trays (64 cavities per tray, 115 cm³ per cavity, 434 cavities/m²). Two-year-old Scots pine and Norway spruce seedlings (originating from seed-orchard seeds used

in central Finland) had been grown in PL-81 trays (81 cavities per tray, 85 cm³ per cavity, 549 cavities/m²).

In Experiments I, III and IV, 10 cm long pieces of stem were cut from the bases of the seedlings and placed on moistened filter paper in Petri dishes. The filter papers were moistened every day with 1 mL of water. Branches were removed from the pieces, but the needles were left intact. The total bark area was calculated for each piece after its mean diameter and length had been measured with a digital pocket slide gauge (Table 1).

The feeding scars were copied with an overhead pen (OHPen Universal; Stabilo, Germany) on strips of soft PVC-foil (thickness 0.3 mm; Renolit-Werke GmbH, Germany) in Experiment II and on strips cut from plastic foils in the other experiments. The strips were then photographed with a digital camera (Nikon N90S; Nikon, Japan) attached with Kodak DCS460 digital part (Kodak, Rochester, New York) and the images were stored in a computer for further processing. The images of the feeding scars were edited as black using Adobe Photoshop 5.5 (Adobe Systems Inc., San Jose, California), after which the total gnawed bark areas were calculated with ColAn™ 1.6 (Colorsoft, Keminmaa, Finland) software.

Experiment I

In each of 50 Petri dishes, one randomly chosen silver birch piece of stem was offered to one pine weevil. This 5-day non-choice feeding experiment was conducted in a cooled incubator (RUMED, Rubarth Apparate GmbH, Model 3401, Germany) with long day conditions (LD 16 : 8 h photoperiod), 55% relative humidity (RH) and at a temperature of 20 °C.

Experiment II

Each of the 20 seedlings was planted into a 3.5-L plastic pot, which was then placed in a cage (Fig. 1). The growth medium consisted of 61% peat, 36% humus and 3% manure (Biolan Ltd, Finland). The lower part of each cage was a ring (height 13 cm, Ø 31 cm) made from a perforated stainless steel sheet. A 5-cm high plastic (PE-HD) ring had been screwed tightly on top of the ring. Mosquito net, which had been stapled to the rim of each seedling pot, reached over the plastic ring. The upper part of each cage was a clear plastic tube (Ø 31 cm; polymethylmeta-acrylate, Gammacril, Italy), the top of which had been covered with mosquito net. The tube was placed on the plastic ring in such way that the mosquito net encircling the pot remained clamped tightly between them. The total height of each cage was 68 cm. The cages were located in the research nursery at Suonenjoki Research Station, and the seedlings were irrigated when necessary. The no-choice experiment on living silver birch seedlings was conducted from 26 July to 1 August 2002.

Seedling heights and stem base diameters were measured at the beginning of the experiment. Each seedling was also marked into base, middle and top sections in relation to their length. There was one weevil per seedling in 15 of the cages and three individuals per seedling in five of them. During the experiment, the weevils were inspected intensively; special attention was paid to which parts of the seedlings the insects

Table 1 Characteristics of the pieces of stems used in pine weevil feeding Experiments I, III and IV

	No-choice Expt. I (mean \pm SD)	Paired-choice Expt. III (mean \pm SD)	Paired-choice Expt. IV (mean \pm SD)
Diameter of feeding piece (mm)			
<i>Betula pendula</i>	4.1 \pm 0.5	5.0 \pm 0.5 ^a	5.8 \pm 0.5 ^a
<i>Picea abies</i>	—	4.1 \pm 0.4 ^b	3.4 \pm 0.2 ^b
<i>Pinus sylvestris</i>	—	3.9 \pm 0.5 ^b	3.8 \pm 0.5 ^c
<i>Populus tremula</i> \times <i>tremuloides</i>	—	3.0 \pm 0.3 ^c	5.8 \pm 0.4 ^a
Total area of feeding piece (mm ²)			
<i>Betula pendula</i>	1285 \pm 146	1587 \pm 155 ^a	1829 \pm 151 ^a
<i>Picea abies</i>	—	1296 \pm 131 ^b	1058 \pm 73 ^b
<i>Pinus sylvestris</i>	—	1234 \pm 150 ^b	1195 \pm 153 ^c
<i>Populus tremula</i> \times <i>tremuloides</i>	—	956 \pm 111 ^c	1818 \pm 140 ^a
Mean area of gnawing scars (mm ²)			
<i>Betula pendula</i>	336 \pm 191	479 \pm 412 ^a	414 \pm 304 ^a
<i>Picea abies</i>	—	422 \pm 212 ^a	275 \pm 181 ^b
<i>Pinus sylvestris</i>	—	422 \pm 196 ^a	292 \pm 185 ^{a,b}
<i>Populus tremula</i> \times <i>tremuloides</i>	—	61 \pm 89 ^b	56 \pm 81 ^c

Differences between species are according to Dunnett's *C*-test. Significant differences between species at the 5% level are indicated by different superscript letters.

fed on. Feeding scars were counted twice a day during the first two days and once a day on the third, fourth and sixth day. The scars were also copied on plastic foils every other day.

After six days of feeding, the weevils and the cages were removed. The health of each seedling was then monitored weekly and rated on a scale from 1 to 4 (1 = healthy seedling, 2 = majority of leaves yellow or fallen, terminal bud alive or wilted, 3 = terminal shoot dead or broken, main stem alive, 4 = main stem dead). After two months, the remaining feeding scars were copied, and the height and stem base diameter of each seedling were measured.

The air temperature was monitored during both the feeding experiment and the 2-month inspection period. During feeding, the mean temperature inside the cages was 23.2 °C; the minimum was 10.6 °C and the maximum was 36.6 °C. Outside the cages, the temperatures in the shade were 21.7, 10.5 and 35.0 °C, respectively. During the inspection period, the mean temperature was 17.9 °C; the minimum was 1.1 °C and the maximum was 34.8 °C.

Experiment III

In the paired-choice test, 100 pine weevils were allowed to feed singly in Petri dishes for 7 days. Each Petri dish contained a pair of stem pieces: birch + birch, birch + spruce, birch + pine, birch + hybrid aspen, spruce + spruce, spruce + pine, spruce + hybrid aspen, pine + pine, pine + hybrid aspen or hybrid aspen + hybrid aspen. Individuals of stem pieces were chosen randomly. There were ten replications of each pair; hence 200 pieces in total. The experiment was conducted in a laboratory at 25.6 \pm 1.2 °C and at 40.2 \pm 6.8% RH.

Experiment IV

This paired-choice experiment corresponded to Experiment III. Furthermore, the sex of each weevil was determined before the experiment. A total of 50 females and 50 males

were used as experimental insects. There were ten replications of each pair of stem pieces; five of them were offered to females and the other five to males. During the experiment, the temperature in the laboratory was 24.9 \pm 1.5 °C and the relative humidity was 35.7 \pm 6.1%.

Statistical analysis

One-way analysis of variance (ANOVA) was used to compare the changes in weight of the weevils during the experiments and the fasts. The influence of weevil weight on the area of gnawed bark was tested with Pearson's correlation coefficient. In addition, the feeding characteristics and weevil weights after the fasts were also analysed with univariate variance analyses, with sex and tree species as fixed factors and total bark areas as covariates. Spearman's rho was used as the correlation coefficient to examine the relationship between the total area of gnawed bark and the state of health of the seedlings. In the paired choice experiments, the gnawed bark areas of different tree species were compared using one-way ANOVA. This analysis was also used to determine whether the presence of certain tree species affected the feeding pressure when the weevils were offered other tree species. The tests were performed with SPSS® 12.0.1 for Windows (SPSS Inc., Chicago, Illinois).

Results

No-choice feeding Experiment I

During the 5-day no-choice feeding experiment, each weevil consumed, on average, 336 mm² (i.e. 67 mm²/day) silver birch bark, which was 27% of the total bark area. The daily amount of bark consumed varied between 1 and 168 mm², but there was no significant correlation between the weevil initial weight after the first fast and the area of consumed bark ($r = 0.275$, $P = 0.053$, $n = 50$). The weevil weight

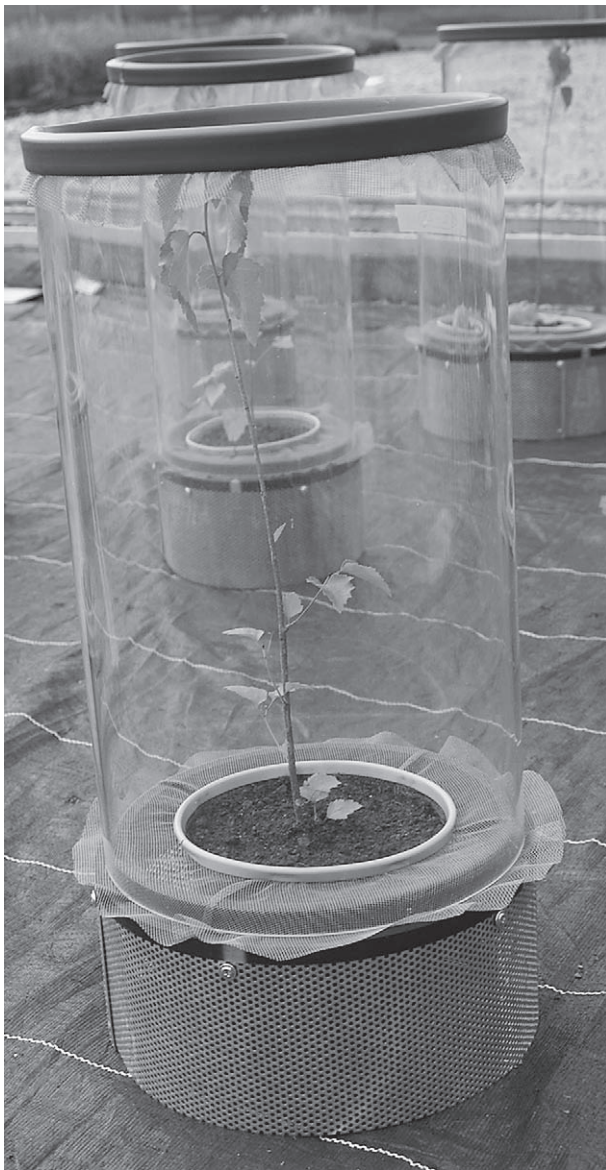


Figure 1 Polymethylmeta-acrylate cage used in a pine weevil (*Hylobius abietis*) no-choice feeding experiment (Experiment II) conducted on silver birch. (Photograph: Pekka Voipio)

after the final fast correlated positively with the area of consumed bark ($r = 0.379$, $P = 0.007$, $n = 50$). The mean weight of the weevils decreased during the experiment, first by 6% during the first fast ($F = 4.94$, $P = 0.029$), then by 3% during feeding and, finally, by 2% during the second fast (data not shown).

Feeding Experiment II in cages

The pine weevils consumed large amounts of silver birch bark outdoors on living seedlings. One weevil consumed an average of 45 mm²/day (minimum 3 mm²/day, maximum 128 mm²/day). Despite the extensive feeding, the weevils' mean weight decreased by 6% during the experiment (data not

shown). However, this was not a significant change, nor was the 3% reduction in weight during the fast at the beginning of the experiment.

After the first 24 h of feeding, 58% of the feeding scars were located at the base of the seedlings, after which the relative proportion of scars in the middle and top sections increased (Fig. 2). If the actual area of gnawed bark is considered instead of the number of the feeding scars, during the whole experiment, the weevils fed most at the base of the seedlings (Fig. 3). The seedlings that had three weevils feeding on them had an approximately three-fold greater amount of gnawed bark area compared with those with only one weevil (Fig. 3). The size of the insect did not affect the area of gnawed bark ($r = -0.369$, $P = 0.176$, $n = 15$) if only the seedlings that had one weevil feeding on them were taken into account. Feeding scars were also found on leaves, especially on leaf bases and petioles but, to some extent, also on leaf veins and blades.

The gnawed bark area correlated significantly ($r_s = 0.456$, $P = 0.043$, $n = 20$) with the state of health of the seedlings measured after the experiment (i.e. the more the bark had been gnawed the poorer was the condition of the seedling). Feeding at the top of the seedlings resulted in death of some terminal shoots. In addition, the whole main stems died in 15% of the seedlings, but sprouting from the stem bases was later observed. The majority (65%) of the seedlings coped well with the feeding injuries because they had feeding scars only on stems and almost all of them healed during the 2-month inspection period. At the end of this time, only a few unhealed scars remained; together, they covered an area of 61 mm², which was only 0.8% of the original total gnawed area.

The experimental seedlings increased in height despite the feeding damage. On average, the seedlings that had not lost their main stems were 16.5 ± 11.1 cm taller after the feeding experiment and the inspection period than before. On average, the bases of the seedlings had grown 4.0 ± 1.8 mm, which approximately doubled the diameters of the stem bases.

Paired-choice feeding experiments

Feeding preferences. The size of the gnawed bark area depended on the tree species. The most gnawing (on average,

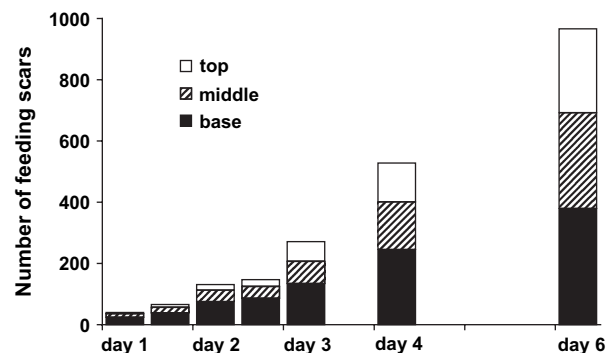


Figure 2 Total number of pine weevil (*Hylobius abietis*) feeding scars and their location on silver birch seedling stems during a 6-day feeding experiment (Experiment II) ($n = 20$ seedlings).

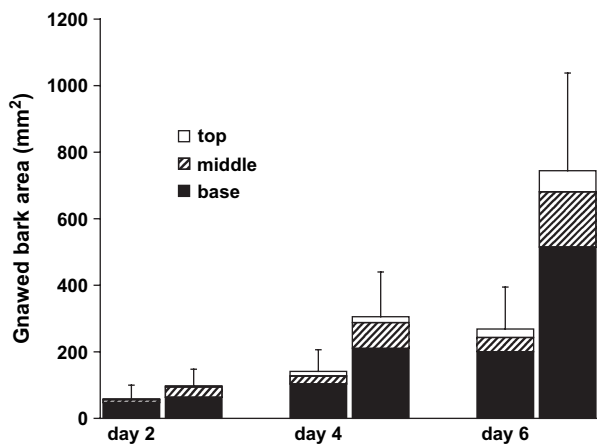


Figure 3 Areas (mean \pm SD) of silver birch bark consumed by pine weevils (*Hylobius abietis*) during a 6-day feeding experiment (Experiment II). The locations of the debarked areas on seedling stems are also indicated. Bars on the left represent seedlings with one weevil and the bars on the right seedlings with three weevils feeding on them ($n = 20$ seedlings).

68 mm² per day in Experiment III and 59 mm² per day in Experiment IV) occurred on silver birch. If only those silver birch pieces that were offered simultaneously with other silver birch pieces are considered, the means were 79 mm²/day and 60 mm²/day, respectively. Damage was also substantial on Norway spruce (on average, 60 mm²/day in Experiment III and 39 mm²/day in Experiment IV) and Scots pine (60 mm²/day and 42 mm²/day, respectively). Hybrid aspen was consumed in only small amounts (9 mm²/day and 8 mm²/day, respectively). The consumed bark area also depended on the species of the other piece of stem that was offered simultaneously (Fig. 4A,B). In these cases, conifers and silver birch were clearly preferred to hybrid aspen. In Experiment III, Norway spruce and Scots pine were also preferred to silver birch but, in Experiment IV, the differences were not significant. The conifers were preferred equally, and the areas of gnawed bark did not differ significantly between the two conifer species. In total, the differences in areas of gnawed bark were significant in the combinations: (i) Experiment III, birch + spruce, birch + pine, birch + hybrid aspen, spruce + hybrid aspen and pine + hybrid aspen and (ii) Experiment IV, birch + hybrid aspen, spruce + hybrid aspen and pine + hybrid aspen.

The differences in areas of gnawed bark in different tree species were also compared when only one tree species was available for the weevils. The differences were significant in all cases except between Norway spruce and Scots pine, which were again consumed in equal amounts. Furthermore, when offered simultaneously, the presence of hybrid aspen had no effect on the palatability of other species. The weevils consumed similar amounts of Norway spruce, Scots pine and silver birch bark regardless of whether there were two pieces of stem of these species present or one piece of these and one of hybrid aspen.

Weevil weight. The mean weight of the weevils decreased during the fasts before and after the experiments and

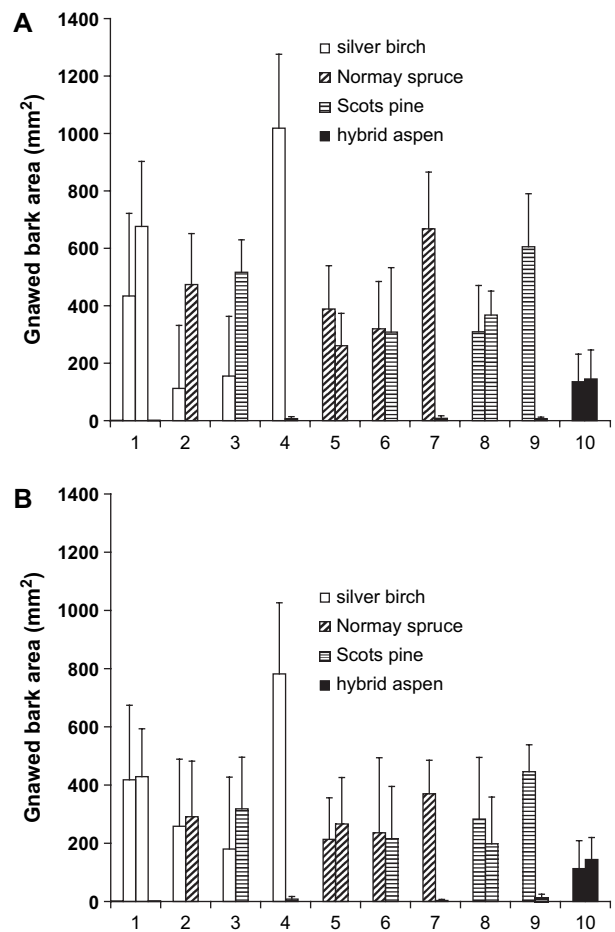


Figure 4 (A,B) Bark areas (mean \pm SD) consumed by pine weevils in two paired-choice laboratory feeding experiments; Experiment III in (A) and Experiment IV in (B). Different tree species were offered to pine weevils for seven days in the combinations: 1 = birch + birch, 2 = birch + spruce, 3 = birch + pine, 4 = birch + hybrid aspen, 5 = spruce + spruce, 6 = spruce + pine, 7 = spruce + hybrid aspen, 8 = pine + pine, 9 = pine + hybrid aspen, 10 = hybrid aspen + hybrid aspen ($n = 10$ replications of each combination).

increased by 3% during feeding (data not shown). The most weight was gained by those individuals that fed only on Norway spruce and the least by those that fed only on hybrid aspen, although none of the weight changes were significant. The weight of the weevils after the first fast ($F = 0.551$, $P = 0.647$) and after the second fast ($F = 0.795$, $P = 0.497$) did not differ significantly between individuals feeding on different tree species. However, the weevil weight after the first fast ($F = 24.035$, $P < 0.001$) and after the second fast ($F = 10.652$, $P < 0.001$) did differ between the sexes, with the males being lighter than the females.

Influence of sex on feeding behaviour. On average, females consumed more bark than males did ($F = 7.492$, $P = 0.001$; Table 2). Males gnawed larger feeding scars than females on silver birch, Scots pine and hybrid aspen but not on Norway spruce. On Scots pine, a male weevil gnawed, on average, 85-mm² feeding scar, which was approximately

Table 2 Means \pm SD of the bark consumption by *Hylobius abietis* in a 7-day laboratory experiment with paired-choice feeding (Experiment IV)

	Total gnawed area (mm ² /day)		No. of gnawing scars (day)		Average size of gnawed scar (mm ²)	
	Male	Female	Male	Female	Male	Female
<i>Betula pendula</i>	58 \pm 42	61 \pm 45	1.6 \pm 1.1	2.0 \pm 1.0	47 \pm 58	40 \pm 72
<i>Picea abies</i>	34 \pm 22	45 \pm 29	0.8 \pm 0.7	1.0 \pm 0.8	57 \pm 45	64 \pm 86
<i>Pinus sylvestris</i>	41 \pm 25	42 \pm 28	0.8 \pm 0.6	1.1 \pm 0.7	85 \pm 96	41 \pm 31
<i>Populus tremula</i> \times <i>tremuloides</i>	10 \pm 14	6 \pm 9	2.7 \pm 3.3	2.1 \pm 2.2	3 \pm 2	2 \pm 1

double the size of the feeding scar made by a female in a day (41 mm²). On hybrid aspen, there were no differences between sexes in feeding behaviour. Furthermore, there was no tree species \times sex interaction for feeding patterns (Table 3).

Discussion

Feeding preferences

If the total areas of gnawed bark are considered, silver birch was consumed the most, then Scots pine and Norway spruce. Thus, the results suggest that the large pine weevil is a potential damaging agent on seedlings of silver birch. The weevils that were feeding on silver birch gained less weight than did those individuals that fed on Norway spruce. Silver birch has thinner bark and phloem than conifers; hence, it requires more gnawing to offer the same amount of nutrition. It is also possible that silver birch is not a suitable source of nutrition for the pine weevil, and therefore feeding on it does not lead to quick weight gain. According to Manlove *et al.* (1997), because pine weevils feed well on silver birch, it may contain stimulating compounds. In our paired-choice tests, the presence of silver birch did not increase the total area of gnawed bark; it only enlarged the proportion of conifers of

the total gnawed area. When different tree species were offered to the weevils simultaneously, feeding on both conifers was more prominent than on silver birch (Fig. 4A,B). Despite this preference, silver birch was always consumed even in the presence of conifers. This finding clearly differs from that of Månsson and Schlyter (2004), in whose study the weevils did not feed on silver birch twigs at all if Scots pine twigs were also present.

In the present study, the amounts of gnawed bark on Norway spruce and Scots pine were similar in all cases. In previous laboratory experiments, pine weevils have preferred different tree species in the order: Scots pine, silver birch, Norway spruce, common ash and Sycamore maple *Acer pseudoplatanus* L. (Leather *et al.*, 1994; Manlove *et al.*, 1997). For example, Leather *et al.* (1994) reported that adult pine weevils prefer Scots pine to Norway spruce as a food source. In their experiment, the feeding material was, however, relatively thick (\varnothing 10 mm) and originated from older seedlings, which might have influenced their palatability. However, Scots pine has often also been considered to be the favourite source of nutrition of the pine weevil in field conditions (Sylvén, 1927; Långström, 1982; Leather *et al.*, 1994; Manlove *et al.*, 1997; Örlander *et al.*, 2000). This may be due to Norway spruce having traditionally been planted as bare-rooted and otherwise thicker seedlings than Scots pine, and in field conditions, seedling size is an essential damage-regulating factor. In addition, many compounds produced by plants, such as limonene and α -pinene, may cover up the effects of attractive compounds (Nordlander, 1990, 1991; Lindgren *et al.*, 1996). One reason for the differences in preferences between the two conifers may be that there is more (–)-limonene in Norway spruce than in Scots pine (Wibe *et al.*, 1998).

According to Sylvén (1927), aspen *Populus tremula* L. may also be part of the weevil's diet. By contrast, in a study by Månsson & Schlyter (2004), aspen was not consumed at all, neither when it was the only species offered to the weevils, nor in the presence of Scots pine. Furthermore, in the present study, hybrid aspen was not consumed when alternative nutrition was available. Even those weevils that fed solely on hybrid aspen, fed only lightly.

Silver birch contains phenolic glycoside compounds, which reduce palatability to many animals (Bratt, 2000). The differences in the quality and quantity of secondary metabolites depend, in addition to the species itself, on the age of the individual plant because seedlings have less

Table 3 Results of univariate analyses of variance of the feeding patterns of *Hylobius abietis* in a 7-day laboratory feeding experiment (Experiment IV)

Source	d.f.	F	P
Gnawed area (mm ² /day)			
Sex	1	0.1	0.741
Tree SP. \times Sex	3	0.5	0.708
Error	177		
Relative gnawed area (% day)			
Sex	1	0.1	0.746
Tree SP. \times Sex	3	0.5	0.709
Error	177		
No of feeding scars (day)			
Sex	1	1.5	0.216
Tree SP. \times Sex	3	0.4	0.729
Error	169		
Area per feeding scar (mm ²)			
Sex	1	2.3	0.133
Tree SP. \times Sex	3	0.7	0.579
Error	169		

Variables were ln-transformed.

chemical compounds than young trees (Julkunen-Tiitto *et al.*, 1996). Several monoterpenes attract weevils; conifers are known to emit feeding stimulants e.g. monoterpene hydrocarbons and ethanol (Selander & Kalo, 1979; Tilles *et al.*, 1986; Nordlander, 1990, 1991; Brattli *et al.*, 1998; Sjödin *et al.*, 2000). It is possible that volatile compounds emitted from conifers in the paired-choice experiments stimulated feeding.

In long-term feeding experiments, it should be possible to discover whether pine weevils can actually survive on a diet based solely on silver birch or hybrid aspen. Even though pine weevils can feed on deciduous trees, it has been suggested that the presence of a nonconiferous species may act as a feeding depressant for pine weevil *H. abietis* (Leather *et al.*, 1994). However, in our paired-choice experiments, the weevils fed on silver birch also in the presence of conifers.

Experimental conditions and insects

The feeding behaviour clearly differed between the sexes. Males tended to make more feeding scars, even though no significant interaction was found between tree species and sex. In total, the females consumed more bark. This might be due to the fact that the weevils were in the reproductive phase when they were collected. The cool storage of the weevils probably interrupted their reproduction, which was continued when they were transferred to laboratory conditions. Because the females were preparing themselves for oviposition, they fed more during the experiment, which in agreement with previous studies (Bylund *et al.*, 2004; Wainhouse *et al.*, 2004).

In Experiment I, which was conducted in an incubator, the temperature was set at 20 °C because weevils are expected to feed well at this temperature (Christiansen & Bakke, 1968; Leather *et al.*, 1994). The fairly strong ventilation may have dried weevils and caused feeding to decrease. On the other hand, in Experiment II with living seedlings, there was a lack of ventilation in the cages due to calm weather. This resulted in higher temperatures inside the cages (+1.5 °C), so the conditions for the weevils were not optimal. Temperature differences were especially great a few hours before and after noon, when, on average, it was +5.8 °C warmer inside the cages. Experiments III and IV had the most suitable feeding conditions.

Although the aim of the study had been to select seedlings of as equal size as possible, the experimental pieces of stems did differ significantly between species in their diameters and the total surface areas (Table 1). This is because there is some variation in the growth rates of different tree species and, in addition, the seedlings were of different ages.

Effect on growth

Several seedlings lost all of their leaves because of feeding damage at the leaf bases and petioles. When a silver birch sapling suffers from intense defoliation, it reduces height growth and number of current branches and decreases the width of the growth ring (Anttonen *et al.*, 2002). Defoliation causes chemical changes in seedlings, and silver birch has been found to react more severely to leaf damage caused by insects than to mechanical wounding (Hartley & Firn, 1989).

Because leaves make up a greater proportion of the biomass in seedlings than in adult trees, seedlings are especially vulnerable to defoliation, and also its consequences in the subsequent years (Haukioja & Koricheva, 2000).

According to the results of the present study, the more bark that was gnawed, the poorer was the health of the seedling after the experiment. In a field experiment by Samuelsson (2001), 57% of silver birch seedlings were attacked by pine weevil during the first season, but only 23% were badly damaged and a mere 4% of the seedlings died. In our study, 15% of the seedlings lost their whole main stems. In addition, apical dominance was destroyed in 20% of the experimental seedlings, which probably caused permanent changes in stem form. The older the seedling, the slower is the healing process, and also the more severe is the actual malformation (i.e. crookedness of the stem) (Lilja & Heikkilä, 1995). If bark has been damaged, microbes and fungi can easily infect the birch tree (Henttonen *et al.*, 1994; Lilja & Heikkilä, 1995). Stem lesions were apparently the reason why at least one of our experimental seedlings lost its main stem. Small feeding scars often heal over during the same growing season in which they appear but, for more extensive wounds, the healing process takes longer and may thus predispose the seedlings to infections.

Damage on silver birch due to pine weevil feeding may result in growth losses, deterioration of stem form or even death of seedlings. Feeding scars can also predispose seedlings to fungal infections. When silver birch seedlings are planted on fresh logging areas that have previously been dominated by conifers, damage can be considerable. For example, in Great Britain, if seedlings are planted on such areas, broadleaved seedlings are also treated with pesticides against the pine weevil (Heritage & Johnson, 1997). In Scandinavian nurseries, only conifer seedlings are currently treated with pesticides against the pine weevil, even though spraying of silver birch seedlings might be useful, especially when they are planted on areas where pine weevil feeding pressure is high.

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References

- Anttonen, S., Piispanen, R., Ovaska, J., Mutikainen, P., Saranpää, P. & Vapaavuori, E. (2002) Effects of defoliation on growth, biomass allocation, and wood properties of *Betula pendula* clones grown at different nutrient levels. *Canadian Journal of Forest Research*, **32**, 498–508.

- Björklund, N., Nordlander, G. & Bylund, H. (2003) Host-plant acceptance on mineral soil and humus by the pine weevil *Hylobius abietis* (L.). *Agricultural and Forest Entomology*, **5**, 61–65.
- Bratt, K. (2000) Secondary plant metabolites as defence against herbivores and oxidative stress: synthesis, isolation and biological evaluation. *Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology*, **567**, 1–45.
- Brattli, J.G., Andersen, J. & Nilssen, A.C. (1998) Primary attraction and host tree selection in deciduous and conifer living Coleoptera: Scolytidae, Curculionidae, Cerambycidae and Lymexylidae. *Journal of Applied Entomology*, **122**, 345–352.
- Bylund, H. & Nordlander, G. (2001) Snytbaggarna äter mycket mer än plantor [In Swedish]. *Plantaktuell*, **1**, 4–5.
- Bylund, H., Nordlander, G. & Nordenhem, H. (2004) Feeding and oviposition rates in the pine weevil *Hylobius abietis* (Coleoptera: Curculionidae). *Bulletin of Entomological Research*, **94**, 307–317.
- Christiansen, E. & Bakke, A. (1968) Temperature preference in adults of *Hylobius abietis* L. (Coleoptera: Curculionidae) during feeding and oviposition. *Zeitschrift für Angewandte Entomologie*, **62**, 83–89.
- Day, K.R. & Leather, S.R. (1997) Threats to forestry by insect pests in Europe. *Forests and Insects* (ed. by A.D. Watt, N.E. Stork and M.D. Hunter), pp. 177–205. Chapman & Hall, U.K.
- Finnish Forest Research Institute (2002) *Statistical Yearbook 2002*. Finnish Forest Research Institute, Vantaa Research Centre, Finland.
- Grégoire, J.-C. & Evans, H. (2004) Damage and control of BAW-BILT organisms, an overview. *Bark and Wood Boring Insects in Living Trees in Europe, A Synthesis* (ed. by F. Lieutier, K.R. Day, A. Battisti, J.-C. Grégoire and H.F. Evans), pp. 19–37. Kluwer Academic Publishers, The Netherlands.
- Hartley, S.E. & Firn, R.D. (1989) Phenolic biosynthesis, leaf damage, and insect herbivory in birch (*Betula pendula*). *Journal of Chemical Ecology*, **15**, 275–283.
- Haukioja, E. & Koricheva, J. (2000) Tolerance to herbivory in woody vs. herbaceous plants. *Evolutionary Ecology*, **14**, 551–562.
- Henttonen, H., Lilja, A. & Niemimäa, J. (1994) Myyrien ja hyönteisten aiheuttamat sieni-infektioit koivun taimien uhkana [In Finnish]. *The Finnish Forest Research Institute, Research Papers*, **496**, 125–129.
- Heritage, S. & Johnson, D. (1997) The use of post-planting sprays to improve the protection of plants from damage by *Hylobius abietis*. *Forestry Commission Research Information Note*, **272**, 1–5.
- Julkunen-Tiitto, R., Rousi, M., Bryant, J., Sorsa, S., Keinänen, M. & Sikanen, H. (1996) Chemical diversity of several Betulaceae species: comparison of phenolics and terpenoids in northern birch stems. *Trees*, **11**, 16–22.
- Långström, B. (1982) Abundance and seasonal activity of adult *Hylobius*-weevils in reforestation areas during first years following final felling. *Communicationes Instituti Forestalis Fenniae*, **106**, 1–23.
- Leather, S.R., Ahmed, S.I. & Hogan, L. (1994) Adult feeding preferences of the large pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae). *European Journal of Entomology*, **91**, 385–389.
- Lilja, A. & Heikkilä, R. (1995) Discoloration of birch trees after wounding or breakage. *Aktuellt Fra Skogforsk*, **4/95**, 30–32.
- Lindgren, B.S., Nordlander, G. & Birgersson, G. (1996) Feeding deterrence of verbenone to the pine weevil, *Hylobius abietis* (L.) (Col., Curculionidae). *Journal of Applied Entomology*, **120**, 397–403.
- Löf, M. (2000) Influence of patch scarification and insect herbivory on growth and survival in *Fagus sylvatica* L., *Picea abies* L. Karst. & *Quercus robur* L. seedlings following a Norway spruce forest. *Forest Ecology and Management*, **134**, 111–123.
- 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.E. & Schlyter, F. (2004) *Hylobius* pine weevils adult host selection and antifeedants: feeding behaviour on host and non-host woody scandinavian plants. *Agricultural and Forest Entomology*, **6**, 165–171.
- Nordlander, G. (1987) A method for trapping *Hylobius abietis* (L.) with a standardized bait and its potential for forecasting seedling damage. *Scandinavian Journal of Forest Research*, **2**, 199–213.
- Nordlander, G. (1990) Limonene inhibits attraction to α -pinene in the pine weevils *Hylobius abietis* and *H. pinastri*. *Journal of Chemical Ecology*, **16**, 1307–1320.
- 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.
- Olsson, C. (1999) Från frö till planta – en sammanställning av undersökningar och forskningsresultat mellan 1993 och 1998 som behandlar produktion av skogsplantor [In Swedish]. *Skogforsk arbetsrapport*, **438**, 1–42.
- 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.
- Örlander, G., Nordlander, G. & Wallertz, K. (2001) Extra food supply decreases damage by the pine weevil *Hylobius abietis*. *Scandinavian Journal of Forest Research*, **16**, 450–454.
- Samuelsson, F. (2001) Damage caused by the pine weevil to deciduous seedlings [In Swedish with English summary]. Master Thesis, Sveriges Lantbruksuniversitet: Institutionen för sydsvensk skogsvetenskap, Sweden.
- Selander, J. & Kalo, P. (1979) Evaluation of resistance of Scots pine seedlings against the large pine weevil, *Hylobius abietis* L. (Coleoptera, Curculionidae) in relation to their monoterpene composition [In Finnish with English summary]. *Silva Fennica*, **13**, 115–130.
- Sjödin, K., Persson, M., Fäldt, J., Ekberg, I. & Borg-Karlson, A.-K. (2000) Occurrence and correlations of monoterpene hydrocarbon enantiomers in *Pinus sylvestris* and *Picea abies*. *Journal of Chemical Ecology*, **26**, 1701–1720.
- Sylvén, H. (1927) Snytbaggarna: studier och fångstförsök [In Swedish with German summary]. *Svensk Skogsvårdsföreningens Tidskrift*, **25**, 521–551.
- Tilles, D.A., Nordlander, G., Nordenhem, H., Eidmann, H.H., Wassgren, A.-B. & Bergström, G. (1986) Increased release of host volatiles from feeding scars: a major cause of field aggregation in the pine weevil *Hylobius abietis* (Coleoptera: Curculionidae). *Environmental Entomology*, **15**, 1050–1054.
- Wainhouse, D., Boswell, R. & Ashburner, R. (2004) Maturation feeding and reproductive development in adult pine weevil *Hylobius abietis* (Coleoptera: Curculionidae). *Bulletin of Entomological Research*, **94**, 81–87.
- Wibe, A., Borg-Karlson, A.-K., Persson, M., Norin, T. & Mustaparta, H. (1998) Enantiomeric composition of monoterpene hydrocarbons in some conifers and receptor neuron discrimination of α -pinene and limonene enantiomers in the pine weevil, *Hylobius abietis*. *Journal of Chemical Ecology*, **24**, 273–287.

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