Host finding in the pine weevil *Hylobius abietis*: effects of conifer volatiles and added limonene

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Abstract

The attraction of *Hylobius abietis* (L.) (Coleoptera: Curculionidae) to α-pinene was recently shown to be inhibited by limonene. This study shows that added limonene also affects the response of *H. abietis* to odours from natural host material. The experiments included both pieces of Scots pine suspended in pitfall traps and planted pine seedlings that had either been manually wounded or left intact. By adding a limonene dispenser, the catch of pine weevils in pine-baited traps was reduced by about 80–90% in spring and autumn and by about 40–50% in summer. Limonene substantially reduced the rate at which manually wounded seedlings were attacked by weevils in spring and autumn. For intact seedlings, a limonene-induced reduction in attack rate was found only in autumn. In the absence of limonene, a small wound made on the stem of a seedling increased its probability of being attacked by about fivefold. This figure was estimated by comparing data from all experimental periods with a model assuming a constant ratio of attack rates for the two kinds of seedlings.

Introduction

The pine weevil *Hylobius abietis* (L.) uses phloem tissue of conifers as a substrate for both feeding and brood development. Females oviposit in roots of fresh stumps and recently killed trees, also utilizing stems and branches of such trees in close contact with the soil. About equal proportions of males and females are attracted to the breeding material, in the vicinity of which mate-finding is enhanced (Nordlander *et al.*, 1986). Adults of both sexes also feed on conifers before, during, and after the breeding period. Feeding is confined mainly to the tender bark of stems, twigs and roots of either living or freshly killed trees.

Inner bark from the stems of conifer seedlings is readily eaten, and seedlings are frequently girdled and killed by the weevils. Consequently *H. abietis* is an important economic forest insect pest in many parts of Europe and Asia where clear-cutting and reforestation by planting is practiced.

Pine weevils rely heavily on olfaction when searching for their coniferous hosts. Migrating weevils land *en masse* in areas where large amounts of host volatiles are released (Eidmann, 1974; Solbreck, 1986). Walking on the ground, weevils can locate potential breeding material present underground by responding to α-pinene and other monoterpenes (Nordlander *et al.*, 1986). Attraction to α-pinene and monoterpene

blends has also been found to be synergized by ethanol (Tilles *et al.*, 1986b; Nordlander, 1987). The role of olfactory orientation when weevils are searching for food is less well documented. It has been suggested, however, that volatiles emanating from wounds on living conifer seedlings greatly increase their likelihood of discovery by food-seeking weevils (Nordlander, 1987). Moreover, aggregations of *H. abietis* on coniferous hosts are apparently formed in response to volatiles released from feeding scars, rather than to any pheromone (Tilles *et al.*, 1986a).

The attraction of the pine weevil species *H. abietis* and *H. pinastri* to α-pinene alone and in combination with ethanol has recently been shown to be completely or partially inhibited by the addition of limonene, another monoterpene usually present in the coniferous hosts of these weevils (Nordlander, 1990). This effect of limonene appeared to be stronger on old than on fresh clear-cuttings.

The present study had four main objectives: 1) To evaluate the influence of added limonene on the response of *H. abietis* to natural host material of two kinds, viz, living seedlings, which serve as food for the adults, and pieces of pine stem, which can be perceived as either food or potential breeding material. 2) To determine how volatiles released from wounds on living seedlings influence the ability of pine weevils to locate seedlings. 3) To ascertain whether the weevil responses referred to under 1) and 2) vary during the season or between clear-cuttings of different age. 4) To confirm results from Nordlander (1990) that chirality and impurities in the limonene used do not influence its inhibitory effect.

Materials and methods

Field experiments with baited pitfall traps and planted pine seedlings were made during three periods in 1989, i.e. 26 April to 23 May, 5 June to 5 July, and 23 August to 13 September, on 2-year-old, fresh, and 1-year-old clear-cuttings respectively. The clear-cuttings encompassed areas of 0.2, 0.7, and 0.2 km² respectively, and were situ-

ated near Uppsala in central Sweden. The timing of the experiments and the ages of clear-cuttings were chosen so that the age structure and sexual development of the weevil populations could be expected to differ between the three periods, but with little change occurring during each period. Age and sexual development were estimated for all weevils trapped in May and August–September according to the methods described by Nordenhem (1989). Weevils observed on seedlings in August–September were also classified in one of two age groups based on the condition of their elytral scales.

Experiments with traps. Three different experiments were conducted using baited pitfall traps. Two of these (I and II) compared the effect of different limonene preparations by using α-pinene and ethanol as a highly attractive standard bait. The third experiment (III) was made to determine the effect of added limonene on the attractiveness of natural host material during each of the three main periods. In each individual test, traps were set out on the clear-cutting in 21 blocks containing one representative of each treatment. The distance between traps within a block was ca. 2 m, and the distance between blocks was ca. 20 m. In experiments I and II, analysis of treatment effects was carried out using Friedman's test followed by a multiple range test analogous to the Student-Newman-Keuls procedure (Zar, 1984). In experiment III, a two-tailed Wilcoxon paired-sample test was used.

The pitfall traps used in experiments I–III were of the type illustrated and described in Nordlander (1987). It was constructed from a capped, one-litre polypropylene jar with eight 1-cm-diam. holes equally spaced around the circumference, ca. 2 cm below the rim. The traps were filled with 0.15 l of water and buried with their holes just above ground level to allow walking weevils to enter.

The dispensers for volatile substances consisted of 3-ml test tubes supplied with a filter-paper wick extending up to the opening of the tube (see Nordlander, 1987; 1990). They were suspended vertically with their openings ca. 2 cm

below the trap lid. The treatments tested included various combinations of dispensers, each containing either limonene (1 ml), α-pinene (1.5 ml) or 70% ethanol (2.5 ml) (see Table 1 and 2). During the seven-day periods that the baits were in the field, ca. 0.4 ml of limonene, 0.8 ml of α-pinene and 1.9 ml of 70% ethanol were released (see Table 2 in Nordlander, 1990). The following monoterpene preparations, supplied by Fluka AG, CH-9470 Buchs, were used: (±)-limonene (techn., = 'dipentene') (I and III), (R)-(+)-limonene ($\sim 98\%$, $[\alpha]_D^{20} + 115 \pm 5°$), (S)-(−)-limonene ($\sim 97\%$, $[\alpha]_D^{20} - 90 \pm 5°$), and (1S)-(−)-α-pinene ($>97\%$, $[\alpha]_D^{20} - 42 \pm 3°$) (I and II). In experiment II a 1:1 mixture of the (+)- and (−)-limonene was also used.

In experiment III, stem sections (length 7 cm, diam. 3–5 cm) from one Scots pine (*Pinus sylvestris* L.) tree were split into two similar pieces and were placed within the two traps in each set. A limonene dispenser was attached to one of them at random. The pieces of pine were suspended with a wire in the middle of the trap, close to the lid and without reaching the water at the bottom of the trap. In all of the tests run for more than one week, baits and water were renewed every 7th day, at which time the trap catches were recorded.

The seedling experiment. For three weeks during each of the three experimental periods a test concerning pine weevil location of planted seedlings was conducted. The seedlings were either wounded prior to planting or left intact, and half of them were supplied with a limonene dispenser; thus, four treatments were included. The seedlings were set out in 50 blocks, containing one representative of each treatment, with ca. 2 m between seedlings within a block and ca. 20 m between blocks. The extent of pine weevil feeding on each seedling was rated on a scale from 0 (no feeding) to 3 at 7-day intervals. For the main analysis, however, the dichotomous nominal scale variables 'feeding scars present' (= located and attacked) and 'feeding scars absent' (= not attacked) were used. Differences between treatments at each inspection were tested statistically with Cochran's Q-test followed by a multiple comparison for dichotomous randomized block data (Zar, 1984). Because the Cochran Q-test was performed for each of the three recordings within a test, α was set to 0.05/3 = 0.0166 to achieve an overall error rate less than 0.05. Estimates of relative attack rates on differently treated seedlings were made with the aid of a model (see below).

Containerized Scots pine seedlings were obtained from a nursery just before outplanting on 26 April and 23 August. The seedlings planted on 5 June were from the same lot as those planted on 26 April and were stored outdoors protected from injurious insects until planting. The seedlings planted in August were considerably larger (height ca. 25 cm) than those used in May and June (height ca. 15 cm). To wound seedlings a cut was made with a surgical blade in the bark between the base of the stem and the lowest branches just before planting. The cut was ca. 2 cm long, 2 mm wide, and reached down to the xylem.

In two of the four treatments a dispenser releasing about 0.8 ml limonene per 7-day period was mounted on a thin bamboo stick ca. 1 cm from the stem of each seedling, with the opening ca. 1 cm above ground. Empty dispensers were similarly placed beside the seedlings in the other two treatments. The dispenser was of a novel type constructed by Dr. M. Lindström at the Royal Institute of Technology, Stockholm. It consisted of a 2.5-ml threaded glass vial with a permeable septum fitted inside a screwcap into which a 9-mm-diam. hole had been drilled. The septa were cut from a 0.4-mm-thick sheet of a polyether-polyamid copolymer (Pebax Nr. 3533). The dispensers were placed with the screwcap and septum downwards. In this position, with the permeant and the septum kept in continuous contact, the release rate should not depend on the amount of substance left (M. Lindström, pers. comm.). However, it was found that limonene affected the durability of the septa in the field. Therefore, the dispensers had to be changed once during every 3-week test period. Each dispenser was filled with 1.5 ml of limonene (techn.).

Estimating relative attack rates

Relative attack rates on differently treated seedlings were estimated by the following method, here presented in generalized form in view of its potential applicability in various analogous situations.

Let us assume that two kinds of food items of unequal attraction are available in limited supplies to foraging individuals. As soon as a food item is fed upon or consumed by a forager it is considered to have changed its state from 'unattacked' to 'attacked'. If attack rates on the two kinds of items are compared in an experiment, the likelihood of detecting differences will be highest after a certain period of time when an intermediate number of items of both kinds have been attacked.

In field experiments one is often faced with strong temporal variation in attack rates, e.g. due to weather conditions or to changes of populations. It is therefore difficult to determine the optimal time for making recordings. Although this uncertainty can be compensated for by increasing the number of recordings, it will nevertheless be difficult to make comparisons between experiments. This problem can, however, be circumvented under the following conditions.

The forager is assumed to attack food items of the two kinds (M and N) at rates of r_M and r_N. These attack rates are allowed to change over time; however their ratio is not allowed to change, viz

$$r_N/r_M = c$$

The forager is thus assumed *not* to change its behaviour in any frequency-dependent way, but the rates may vary as long as they are both equally affected.

Given the above assumptions, the number of *unattacked* food items of the two kinds after time t (M_t and N_t) will decrease exponentially, viz

$$M_t = M_o \, e^{-r_M t} \text{ and}$$

$$N_t = N_o \, e^{-r_N t}$$

if $M_o = N_o = 1$ and $r_N = c \, r_M$ then

$$M_t = e^{-r_M t} \text{ and}$$

$$N_t = e^{-c r_M t}$$

if $r_M t = v$ then

$$M_t = e^{-v} \text{ and}$$

$$N_t = e^{-vc}$$

If the numbers of *attacked* food items are denoted M_t^* and N_t^* then

$$M_t^* = 1 - e^{-v} \text{ and}$$

$$N_t^* = 1 - e^{-vc}$$

The trajectories of M_t^* versus N_t^* for different values of c are plotted in Figure 2B. These curves represent null hypotheses (for each c value) of the relationship expected between M_t^* and N_t^* under the assumption that no frequency-dependent changes occur in the attractivity of the two kinds of food.

Table 1. Influences of purity and chirality of limonene (L) on its effect on pine weevil catches in pitfall traps baited with α-pinene and ethanol (A & E)

Expt.[a]	Baits	Catch *H. abietis*		
		Week 1	Week 2	Total[b]
I	A & E	166	150	316 a
	A & E & ($\pm$)L	68	99	167 b
	A & E & ($\pm$)L (techn.)	86	86	172 b
	Empty control	8	12	20 c
II	A & E	119	95	214 a
	A & E & ($\pm$)L	53	38	91 b
	A & E & (+)L	44	29	73 b
	A & E & (−)L	45	49	94 b

[a] Expt. I: week 1 = 19-26 June, week 2 = 26 June-3 July. Expt. II: week 1 = 21-28 June, week 2 = 28 June-5 July; both tests made on a fresh clear-cutting.

[b] Column figures followed by the same letter are not significantly different at the 5% level (Friedman's test followed by a multiple range test).

Results

Experiments with traps. In experiments I and II, the addition of a limonene dispenser reduced the catch of *H. abietis* in pitfall traps baited with α-pinene and ethanol by one half to two thirds, and this reduction was significant in all instances (Table 1). Technical and the *purum* grades of limonene had similar effects and no significant difference was found between the effect of (±), (+), and (-)-limonene. No differences were found between the sexes in response to the various treatments (4 × 2 contingency tables, $\chi^2 = 3.89$ and 2.73).

In experiment III weevil catch was generally reduced when limonene was present in the pine-baited traps (Table 2). The effect was more pronounced on the 2-year-old clear-cutting in May than on the fresh one in June. On the 1-year-old clear-cutting the effect of limonene during the last week of August was about as weak as it had been in the June tests, whereas this effect was significantly stronger during the first two weeks of September (2 × 2 table, $\chi_c^2 = 6.16$, P < 0.05).

There was no difference between the three weeks of trapping in August–September with regard to the proportions of newly emerged prereproductive weevils (mean 66%) and postreproductive weevils captured (3 × 2 table, $\chi^2 = 1.33$). Nor was any difference found between the pro-

portional distribution of these two phases in traps with and without limonene (2 × 2 table, $\chi_c^2 = 0.84$).

Males and females did not differ significantly in their responses to the two treatments in experiment III during May, June, or August–September (2 × 2 tables, $\chi_c^2 = 0.06, 0.11$, and 0.39). The percentage of females in May (60%) and June (62%) differed significantly from that in August–September (40%) (2 × 2 table [May and June data pooled], $\chi_c^2 = 16.3$, P < 0.001).

The seedling experiment (Fig. 1) showed that wounding prior to planting increased the rate at which seedlings were attacked by pine weevils. The effect of adding limonene differed between experimental periods. In May and August–September, but not in June, limonene substantially reduced the attack rate among seedlings that were already wounded. For intact seedlings, a limonene-induced reduction in attack rate occurred only in August–September.

In May (Fig. 1A) the rates of attack on both wounded and intact seedlings provided with a limonene dispenser (WL and 0L) were similar to that on intact seedlings without limonene (00). The percentage attacked seedlings was significantly higher for wounded seedlings without limonene (W0) than for the other three treatments throughout the three-week test period. In

Table 2. Effects of limonene (L) on pine weevil catches in pitfall traps baited with pieces of pine (P) during different phases of the adult life cycle (Expt. III)

Phase[a]	Age of clear-cutting	Trapping period	Catch *H. abietis*		Level of significance[b]	Catch ratio: P/P & L
			P	P & L		
2	2-year	16-23 May	43	7	***	6.1
3	fresh	7-14 June	66	33	*	2.0
		14-21 June	84	54	NS	1.6
1 & 4	1-year	23-30 August	52	25	*	2.1
		30 Aug.-13 Sept.	41	5	**	8.2

[a] 1 = Newly emerged prereproductive weevils before hibernation; 2 = premigratory maturation-feeding weevils (42% prereproductive, 58% reproductive); 3 = reproductive weevils; 4 = postreproductive weevils.
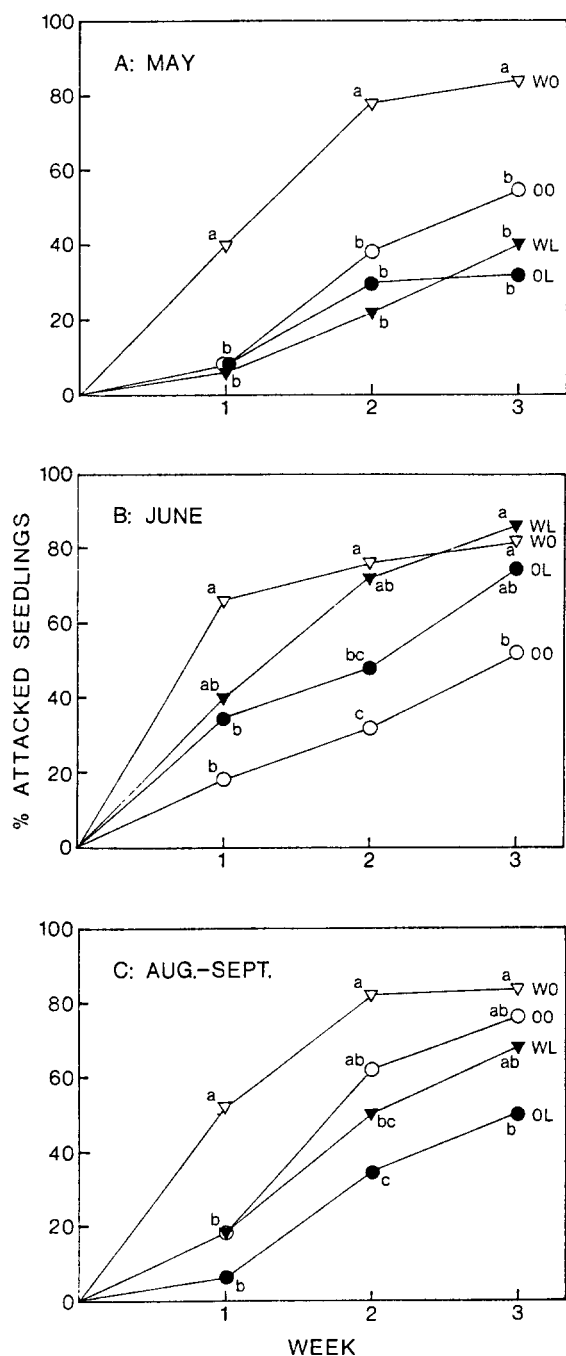[b] Two-tailed Wilcoxon paired sample tests (* = P < 0.05, ** = P < 0.01, *** = P < 0.001).

Fig. 1. Cumulative percentage of seedlings that were located and attacked by pine weevils in the field (n = 50 per treatment). W = seedlings wounded prior to planting; L = seedlings supplied with a limonene dispenser; 0/0 = not wounded/without limonene. Recordings from each occasion accompanied by the same letter are not significantly different at the 5% level (Cochran's Q-test [α = 0.05/3] followed by a multiple comparison). A. 26 April–16 May. B. 5–26 June. C. 23 August–13 September.

August–September (Fig. 1C) the pattern of attack was initially similar to that in May, but towards the end of the test only the W0 and 0L treatments differed significantly. However, a week earlier most accessible W0 seedlings had already been found by the weevils. It is notable that in the August–September test the percentage of attacks was consistently lower on the 0L treatment than on the 00 treatment, and this difference was significant at the end of week 2. In June (Fig. 1B), on the fresh clear-cutting, the W0 and 00 treatments differed significantly during the entire test period. The percentage of seedlings attacked in the treatments with limonene largely ranked in between values for W0 and 00, and there was no significant difference between WL and W0 or 0L and 00. However, after one week the difference between WL and W0 was nearly significant, while at the following two recordings most accessible seedlings had already been found.

The proportions of wounded (W0) and intact (00) seedlings attacked by pine weevils at various points of time show a curvilinear relationship, plateauing at 84% of attacked W0 seedlings (Fig. 2A). Field observations indicated that the remaining 16 percent of the seedlings may have been planted on sites which were largely inaccessible to weevils. The percentages of attacked seedlings were hence recalculated using a 16% lower n (n = 42 instead of 50) for both W0 and 00 (Fig. 2B). These corrected data follow the trajectory that would be expected if wounded seedlings are discovered at a rate five times that of intact ones (data largely in-between the trajectories for c = 3 and 7) (see Materials and methods). It is evident from Figure 2 that some recordings were made so late that differences in the numbers of attacked seedlings between treatments were apt to disappear. Hence, the last recording in each test as well as the second recording in June are of little value for decisive comparisons between wounded and intact seedlings without limonene.

In a comparison of the type presented in Figure 2B for W0 vs. WL seedlings (not shown), the estimated W0/WL attack ratio was 5–8 in May, 3–5 in August–September, and 1–2 in June.
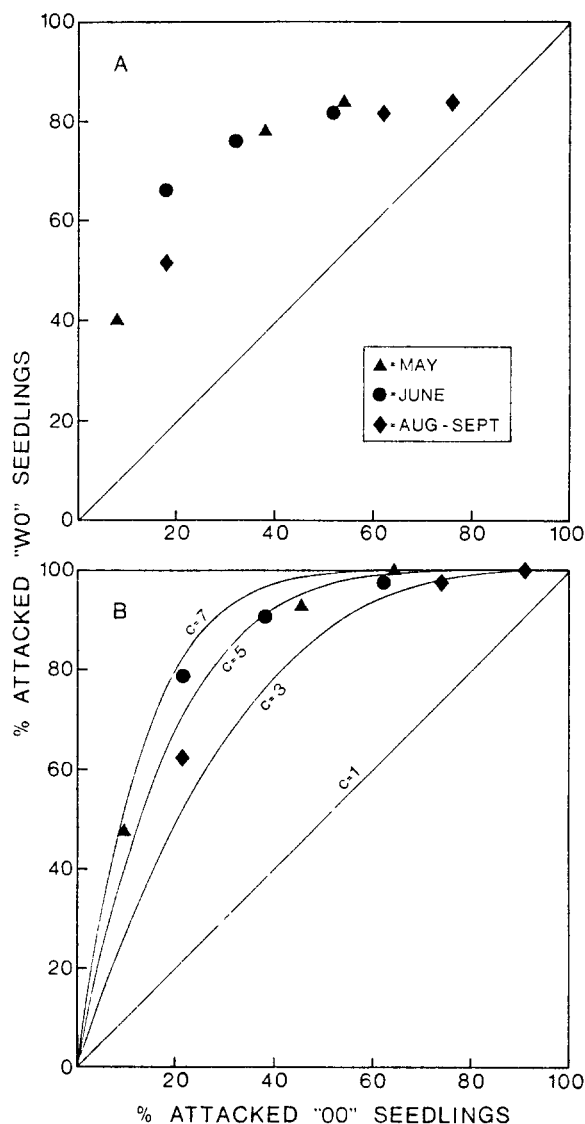
Fig. 2. Relationship between the proportions of wounded (W0) and intact (00) seedlings that had been attacked by pine weevils at various points of time (seedlings with a limonene dispenser not included). A. Original data (n = 50 seedlings per treatment). B. Recalculated data: 16°₀ of the seedlings assumed to be inaccessible to weevils (n = 42). The trajectories are based on two functions describing the relationship in question (see Materials and methods), where the relative attack rate for wounded seedlings is set at 1, 3, 5, or 7 times that of intact seedlings.

However, these results should be interpreted with care because there were only three recordings made during each period. Moreover, the release rate of limonene cannot be assumed to have been constant during the experiments.

Usually the seedlings became extensively damaged within a week after they had first been fed upon by a pine weevil. No difference between seedlings with a limonene dispenser and those without a dispenser was discerned in this respect. The degree of feeding on the stem of each attacked seedling was rated as follows: $1 = <10$ mm^2, $2 = 10$–50 mm^2, and $3 = >50$ mm^2. In all three tests, regardless of whether seedlings were supplied with limonene, damage class 2 had the highest relative frequency after one week, while class 3 had the highest relative frequency at the end of weeks two and three. Contingency table analyses of the data from week two in each of the three tests showed no significant differences in the frequency distributions of the three damage classes between seedlings with and without limonene.

Weevils observed on the seedlings while recording seedling damage in the August–September test were placed in one of two age-groups, based on their elytral-scale colour. Of 124 specimens 73% were newly emerged prereproductive weevils and 27% were older weevils, which should have been postreproductive at this time of the year (see expt. III above). The proportions of newly emerged and older weevils did not differ significantly from those recorded during the same period from traps (63/37%) baited with pine and pine plus limonene (2 × 2 table, $\chi_c^2 = 2.40$). Furthermore, there was no significant difference between newly emerged weevils and older ones in terms of their distribution among seedlings with and without a limonene dispenser (2 × 2 table, $\chi_c^2 = 0.04$).

Discussion

Pine weevils searching for food or breeding material probably walk in random directions until they perceive attractive host volatiles, which elicit responses leading to arrestment in the vicinity of the odour source (Nordlander, 1987). The present study showed that wounded seedlings are more likely to be found by pine weevils than uninjured ones, probably because host odours can be per-

ceived over a larger area around wounded seedlings. Assuming that the weevils behave according to the model employed in Figure 2B it can be concluded that the probability of being found was about fivefold higher for the seedlings with a small artificially made wound than for those without a wound. It is assumed in the functions that a constant relationship exists between relative attack rates of the two types of seedlings. However, a decrease in the relative attractivity of wounded seedlings, owing to wound healing processes, should be expected towards the end of the 3-week period. It is difficult to determine whether this was the case because few wounded seedlings remained unattacked after the second week.

The level of attractiveness of host volatiles emanating from wounded seedlings was apparently similar during each of the three experimental periods, as indicated by the fact that all nine recordings of relative attack rates follow the same curve (i.e., c = 5; Fig. 2B). This implies that the ability of weevils to locate a wounded seedling compared with their ability to locate an uninjured one is not decreased by the abundance of background odours from stumps and slash present on a fresh clear-cutting. However, the risk of seedling attack, measured in absolute terms, may still be affected by the amount and quality of other host material present in the area.

Added limonene has previously been demonstrated to inhibit the attraction of pine weevils to α-pinene or α-pinene and ethanol (Nordlander, 1990). A similar effect was found in the present study when limonene was placed together with natural host material, i.e. pieces of cut pine stems or living pine seedlings. On fresh clear-cuttings in June the inhibitory effect of limonene was previously found to be weak or absent (Nordlander, 1990). However, under similar conditions in the present study the addition of limonene reduced the number of captured weevils to about the half, regardless of whether the attractive odour source in the traps consisted of an α-pinene-ethanol bait or a piece of pine. In May and September the effect of limonene was even stronger, with the catch in traps baited with pieces of pine being

reduced by 80–90%. Generally, the effect of limonene on the attraction to (1) α-pinene-ethanol baits (Nordlander, 1990; present study), (2) pieces of pine, and (3) pine seedlings appears to be strongest on old clear-cuttings in May and August–September while it is considerably weaker on fresh clear-cuttings in June. Results from the 1-year-old clear-cutting were somewhat confusing. During the last week of August the number of captured weevils was reduced by only about 50%, whereas a 90% reduction resulted during the two following weeks. No other changes were observed during that time, e.g. in age structure or sex ratio. These results suggest that factors other than the presence of odours from fresh host material and the reproductive phase of the weevils may also influence the effect of limonene.

The inhibitory effect of limonene on the attraction of pine weevils to conifer volatiles was discussed by Nordlander (1990). However, no specific biological explanation for this behaviour could be offered. More knowledge about the quantitative changes in levels of limonene and other monoterpenes that occur when conifer trees are wounded or killed might provide clues as to why the weevils react the way they do. Furthermore, we need more information about how various parts of the tree differ in terms of monoterpene composition. For example, in *Pinus elliottii* Engelm., oleoresin from cortical tissues of branch tips contains a considerably higher proportion of limonene than stem xylem oleoresin (Squillace, 1977). Thus the relatively high limonene content (3–20%) in cortical oleoresin from branch tips of Scots pines in Sweden, reported by Yazdani *et al.* (1985) and Yazdani and Nilsson (1986), need not imply that similarly high proportions of limonene are released from wounded stems of Scots pine seedlings or from stumps of cut Scots pine trees, as assumed by Nordlander (1990). In fact, Strömvall and Petersson (1991) reported that limonene constituted only 1.7% of the monoterpenes in air samples taking during Scots pine harvesting.

This study has shown that added limonene decreases the risk of attack by pine weevils for wounded seedlings in spring and autumn and for

intact seedlings in autumn. Limonene might therefore be useful in reducing seedling damage in areas with moderate pine weevil populations. Such a technique, applied in an integrated pest management programme, should help reduce the need for insecticides.

Acknowledgements

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