

# Olfactory and visual stimuli used in orientation to conifer seedlings by the pine weevil, *Hylobius abietis*

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**Abstract.** The influence of noncontact plant cues is investigated on the likelihood that individual conifer seedlings will be found by walking adults of the pine weevil, *Hylobius abietis*, in the field. Traps with solely odour or solely visual stimuli catch significantly more weevils than stimulus-free traps, and traps with the combination of odour and visual stimuli catch more weevils than traps with odour or visual stimuli alone. There is essentially an additive effect between odour and visual stimuli. The reactions to odour and visual stimuli are similar for three phases of the pine weevil's life cycle associated with three ages of clear-cuttings (i.e. sites where all trees have been harvested). Visual stimuli appear to be at least as important as odour for the pine weevil in finding an undamaged conifer seedling.

**Key words.** Curculionidae, host finding, host odour, *Hylobius abietis*, large pine weevil, olfactory stimuli, orientation, pitfall trap, stimulus interaction, visual stimuli.

## Introduction

The behavioural events leading a phytophagous insect to feed on a host plant can be divided into three sequential steps: (i) finding food; (ii) examining food; and (iii) consuming food (Miller & Strickler, 1984). Finding food can be further subdivided into levels (e.g. finding the habitat and finding the resource item itself) for which the importance of olfactory and visual stimuli may differ (Prokopy, 1986). The present study investigates the influence of noncontact plant cues on the likelihood that individual conifer seedlings will be found by walking adults of the pine weevil *Hylobius abietis* (L.) (Coleoptera, Curculionidae).

Many phytophagous insects orientate towards the odours from host plants (Bernays & Chapman, 1994), but most of the evidence for this is based on laboratory experiments and may not be relevant under natural conditions with many competing stimuli (Jermy *et al.*, 1988). Traps emitting high concentrations of host odours often catch large numbers of walking adult insects, but this does not prove the signifi-

cance of host odour in plant finding. Evidence is scarce for the hypothesis that the orientation of walking adult insects towards plants in the field is solely dependent on odours released by the plants. It has been proposed that distant olfactory attraction to host plants in nature may be much less common than was previously thought (Jermy *et al.*, 1988). The use of visual stimuli in detecting plants, although much less widely investigated, has also been shown for several species (Prokopy & Owens, 1983). As is the case with odours, many studies related to visual stimuli have been carried out in the laboratory, one of which showed that walking *Pissodes strobi* (Curculionidae) adults orientate preferentially towards silhouettes that are: (i) vertical rather than oblique; (ii) 3 cm in width rather than other diameters; and (iii) taller rather than shorter (VanderSar & Borden, 1977). These findings are consistent with the characteristics of spruce twigs attacked by *P. strobi* in the field. However, there are also examples of laboratory studies in which a visual stimulus alone did not elicit a response. For example, the adult plum curculio *Conotrachelus nenuphar* (Curculionidae) walking on tree twigs did not respond to visual fruit characteristics (Butkewich & Prokopy, 1993). In the field, attraction towards solely visual stimuli has been shown for the desert locust, which walks towards conspicuous vegetation from distances of at least 1.5 m (Kennedy, 1939).

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Multiple sensory modalities are often used before an insect arrives at a resource (Miller & Strickler, 1984; Prokopy, 1986). It is often claimed that an 'interaction' exists between odour and visual stimuli, but the interpretation of this term differs. For example, if the response to a combination of the stimuli is as large as the sum of the individual responses, it could be claimed that there is an interaction. However, using statistical terms, others would claim that there is no interaction in this case and refer to it as an additive response (Slinker, 1998). In the present study, the latter statistical definition of interaction is used. It is, however, important to test the stimuli both individually and together, as has been carried out in several studies. For example, the cabbage moth lands more frequently when an artificial leaf with added plant odour is presented than when an artificial leaf or plant odour are presented separately (Rojas & Wyatt, 1999). Similarly, the mean number of captured adult cabbage root flies tends to be higher when olfactory and visual stimuli are combined than when presented separately (Tuttle *et al.*, 1988).

If a control treatment with none of the stimuli is included, it is possible to determine the 'true response' of the other treatments (i.e. the part of the response above the control level that they induce). A control is also necessary to test if the stimuli act synergistically (i.e. if the total effect is greater than the sum of individual effects) (Slinker, 1998). Odour and colour have been reported to act synergistically on alighting for a species of leafhopper in an observation chamber (Todd *et al.*, 1990) and for the onion fly on three-dimensional traps in onion fields (Judd & Borden, 1991). Olfactory and visual (yellow vs. transparent) stimuli appear to act synergistically on the number of aphids landing on traps in the field (Chapman *et al.*, 1981). An example where the effect of odour and visual stimuli appears to be additive rather than synergistic is the response to tree models shown by adult plum curculio (Butkewich & Prokopy, 1997). Much less is known for walking adult insects but, in a laboratory experiment, the grasshopper *Melanoplus sanguinipes* approaches olfactory and visual stimuli from plant sources more frequently than a control, and the response to olfactory and visual stimuli combined is even stronger (Szentesi *et al.*, 1996). However, to the authors' knowledge, the present study is the first to investigate whether olfactory and visual noncontact stimuli act synergistically during resource finding for a walking insect in the field.

The physiological state of an insect may influence its resource-orientated behaviour (for a review, see Barton Browne, 1993). For various species, responses to noncontact odour and visual stimuli from resources have been shown to be influenced by the age and reproductive status of the insect and the season (e.g. Hoffman *et al.*, 1997). Similarly, in *H. abietis*, there is some evidence to suggest that the reaction to odour among weevils caught in clear-cuttings (i.e. where all trees has been removed from stands of timber) may be dependent on the phase in the adult life cycle the pine weevils have reached, which in turn is associated with the age of the clear-cutting (Nordlander, 1990; Nordenhem & Eidmann, 1991). Therefore, the present experiment is

performed on clear-cuttings of different ages, with weevils in different phases of their life cycle, to evaluate if the responses to olfactory and visual stimuli differ.

Large numbers of pine weevils, *H. abietis*, fly during late spring to fresh clear-cuttings, which provide abundant breeding material. After arrival, their flight muscles regress and they remain on the ground for the rest of the season (Nordenhem, 1989). The pine weevil is most active at twilight (Sibul *et al.*, 1999) and feeds on several tree species (Löf *et al.*, 2004). It is a serious pest in areas where clear-cutting with subsequent replanting is practiced because the adults feed on the stem bark of newly planted conifer seedlings (Långström & Day, 2004), but feeding also occurs in the crowns and roots of mature conifer trees (Örlander *et al.*, 2000).

In other pest systems, increased knowledge of the basic processes of resource finding has facilitated the development of more effective protection methods (Foster & Harris, 1997), and this general principle should also be valid for the pine weevil system. The present study has three main aims. First, to determine whether the number of pine weevils arriving at an individual conifer seedling is influenced solely by olfactory or visual stimuli. Second, to determine whether there is a synergistic effect between olfactory and visual stimuli, which requires the following test treatments: (i) only olfactory stimuli; (ii) only visual stimuli; (iii) olfactory and visual stimuli together; and (iv) a control (Slinker, 1998). Third, to investigate whether these reactions differ among the three phases of the pine weevil's life cycle (which are associated with three distinct ages of clear-cuttings). To answer these questions, it is necessary to ensure that the response to the stimuli used is of the same magnitude as the response to those found in nature.

## Materials and methods

In a field experiment, adult pine weevils of both sexes were caught in traps with different combinations of olfactory and visual stimuli and their numbers were recorded. The experiment was conducted near Uppsala in central Sweden during three periods of time, numbered according to the age of the weevils. The first period comprised 6 weeks in August and September 2000 on a 1-year-old clear-cutting (newly emerged, pre-reproductive weevils, before hibernation). The second comprised 6 weeks in May and June 2001 on a 2-year-old clear-cutting (pre-reproductive, premigratory, maturation feeding weevils) and the third comprised 4 weeks in June and July 2000 on a fresh clear-cutting (reproductive, immigrant weevils). The life-cycle phases mentioned are according to Nordenhem & Eidmann (1991). Before clear felling, the stands consisted of mixtures of Scots pine *Pinus sylvestris* (L.) and Norway spruce *Picea abies* (L.) Karst. A randomized block-design was used with 12 blocks on each clear-cutting and six traps with different treatments within each block. Each week, the traps were emptied, the numbers of trapped pine weevils recorded, stimuli renewed and the treatments randomly replaced

within blocks. Within each block, trap positions were chosen to ensure that the surrounding vegetation and other factors were as similar as possible. The traps were placed in undisturbed humus (i.e. no soil scarification was performed). There was at least 3 m between traps and at least 60 m between a trap and the edge of the clear-cutting. Slash was removed within a 1-m radius of the traps.

Pitfall traps, described by Björklund *et al.* (2003), caught approaching pine weevils at a 2.5-cm radius from the treatment (Fig. 1). A slippery surface was created on the sloping fall rim and on the inner side of the trap by applying Fluon® (ICI, U.K.). The traps were made of polyethylene terephthalate bottles, constructed without glue to avoid odour influence, and filled with water plus a small amount (one drop per 25 L) of odourless detergent (Brillo handdisk, Johnson Wax Professional, Kista, Sweden) to drown trapped weevils and to supply the conifer seedlings with water.

The following treatments were included: (i) control; (ii) spruce odour; (iii) dummy-seedling; (iv) dummy-seedling + spruce odour; (v) seedling; and (vi) seedling + spruce odour. Dummy-seedlings were used to provide an odourless visual stimulus. Treatments (v) and (vi) were included as positive controls to evaluate whether the responses to the surrogate stimuli used in the other treatments corresponded to the responses to the stimuli naturally emitted by seedlings. The seedlings used were 2-year-old containerized Norway spruce seedlings (provenance Rezekne). The spruce odour stimulus was created by burying three 5-cm long freshly-cut stem pieces, from the same batch of seedlings, in soil in the centre



Fig. 1. Dummy-seedling in the pitfall trap used in the experiments.

of the trap ensuring that their upper ends were level with the soil surface. The dummies were composed of a green metal wire (3 mm in diameter) mimicking the stem and 6-cm long thin metal wires covered with green plastic (CLIP'N'TWIST; Buyrite, Guangdong) twisted around the stem as twigs (Fig. 1). The dummies reached 25 cm above ground, and were of approximately the same size as the seedlings.

### Statistical analysis

The positive controls, treatments (v) and (vi), were not included in the subsequent analyses because the influence of olfactory and visual stimuli could not be separated in these treatments. The pine weevil catch was calculated as the total catch, summarized for each period, per treatment and block. The homogeneity among blocks of the responses to the different treatments was tested with Fisher's exact test (periods 1 and 2) or a  $\chi^2$ -test (when the calculations for Fisher's exact test were too cumbersome, period 3) for separate two-way contingency tables (12 blocks  $\times$  four treatments) (proc. FREQ; SAS Institute, 1999). The homogeneity among periods of the responses to the treatments was tested by a  $\chi^2$ -test for a two-way contingency table (three periods  $\times$  four treatments) (proc. FREQ; SAS Institute), which requires homogeneity among blocks of each period. A confidence interval for the response of treatment  $k$ ,  $k = 1, 2, 3, 4$ , was calculated as:

$$\hat{p}_k \pm 1.96 \times SE(\hat{p}_k)$$

where

$$\hat{p}_k = x_k/x.$$

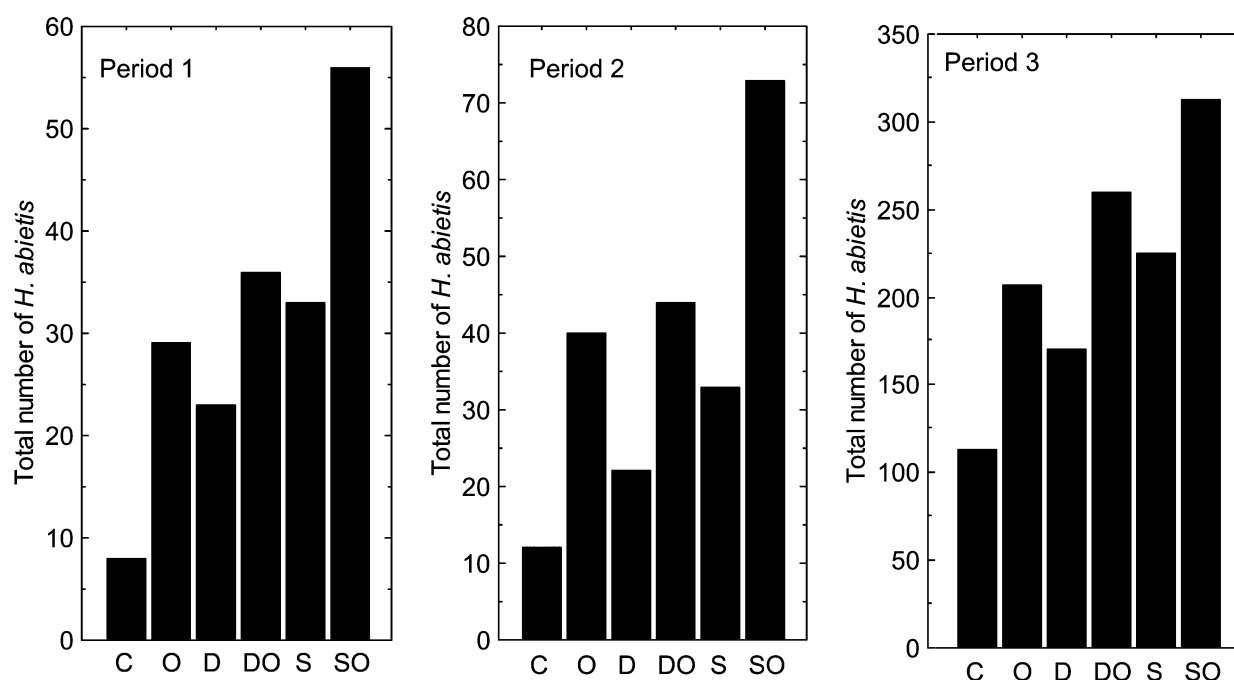
with  $x_k$  equal to the number of weevils caught at treatment  $k$  and  $x$ , equal to the total number of weevils. The standard error was calculated as:

$$SE(\hat{p}_k) = [\hat{p}_k(1 - \hat{p}_k)/x.]^{1/2}$$

To determine whether there was any interaction between olfactory and visual stimuli, a  $\chi^2$ -test was used for a two-way contingency table (combinations of absence and presence of odour and visual stimuli) (proc. FREQ; SAS Institute).

### Results

In total, 185 pine weevils were caught on the 1-year-old clear-cutting, 224 on the 2-year-old clear-cutting and 1288 on the fresh clear-cutting. The distributions of catches amongst the different treatments were similar during the three time periods (Fig. 2). The responses to the positive controls (spruce seedling and spruce seedling + spruce odour) were of the same magnitude as the responses to their artificial counterparts (dummy-seedling and dummy-seedling + spruce odour) and the relationships between the positive controls were similar to that between their artificial



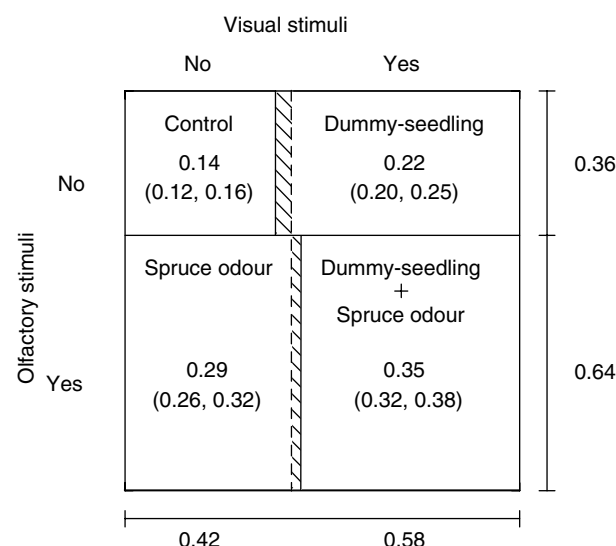
**Fig. 2.** Total numbers of *Hylobius abietis* caught in the pitfall traps. Period 1 = 1-year-old clear-cutting (newly emerged, pre-reproductive weevils, before hibernation). Period 2 = 2-year-old clear-cutting (pre-reproductive, premigratory, maturation feeding weevils). Period 3 = fresh clear-cutting (reproductive, immigrant weevils). Treatments: C = control; O = spruce odour; D = dummy-seedling; DO = dummy-seedling + spruce odour; S = seedling; SO = seedling + spruce odour.

counterparts (Fig. 2). More than twice as many weevils were caught in the traps around seedlings compared with that in stimulus-free traps. The positive controls were not included in the subsequent analysis. There were no differences in responses to the different treatments among blocks for period 1 (Fisher's exact test,  $P = 0.18$ ), period 2 (Fisher's exact test,  $P = 0.65$ ) or period 3 ( $\chi^2 = 30.92$ ,  $P = 0.57$ ). Therefore, it was appropriate to test for differences in responses to the different treatments among periods but, again, no differences were found ( $\chi^2 = 6.8$ ,  $P = 0.34$ ). In the subsequent analysis, the data from the three periods of time were pooled. Traps with solely odour and solely visual stimuli caught significantly more weevils than the stimulus-free traps, and the combination of odour and visual stimuli caught more weevils than olfactory or visual stimuli alone (Fig. 3). There was an interaction between olfactory and visual stimuli ( $\chi^2 = 3.95$ ,  $P = 0.049$ ) that was slightly antagonistic (i.e. a less than additive response) rather than synergistic. The size of the interaction effect is visualized in Figure 3.

## Discussion

The results obtained with the positive controls (i.e. spruce seedling and spruce seedling + spruce odour) confirm that the responses to the stimuli used are of the same magnitude as the responses to those emitted by seedlings. However, it

should be noted that the added spruce odour from cut stems of seedlings is likely to differ qualitatively from the odour of undamaged spruce seedlings. Furthermore, the effect of adding spruce odour to the artificial visual stimuli



**Fig. 3.** Mean proportion ( $\pm 95\%$  confidence interval) of *Hylobius abietis* caught in traps with the following treatments: control; spruce odour; dummy-seedling; and dummy-seedling + spruce odour. The shaded area represents the size of the interaction effect.

(dummy-seedlings) is similar to the effect of adding spruce odour to a spruce seedling. The stimulus-free treatment is assumed to measure the probability that insects are caught by chance. In support of this rationale, it has already been shown that the water with detergent present in this type of trap does not increase the catches (Björklund *et al.*, 2003). The catches in stimulus-free traps suggest that pine weevils would encounter conifer seedlings rather frequently, even in the absence of response to visual and olfactory stimuli. The response to seedlings demonstrated in this study is not in accordance with studies on the closely related *Hylobius pales*, in which similar numbers of weevils were caught in traps enclosing seedlings and in control traps (Hertel, 1970; Thomas & Hertel, 1979). However, with the type of trap used in these previous studies (0.6-m squares made from gutter pipe placed around seedlings), it is possible that the captured weevils were mainly outside the area in which stimuli from the seedlings could have induced a response.

Spruce odour alone increases the catches of walking pine weevils significantly. Several insect species have been shown to walk towards odours in laboratory experiments (Bernays & Chapman, 1994; Szentesi *et al.*, 1996). However, field studies with odour levels of the same magnitude as those emitted from natural plants are necessary to evaluate the significance of odours for finding food. For flying insects, some field experiments have shown that odour alone increases the number of caught insects (Chapman *et al.*, 1981; Butkewich & Prokopy, 1997). For many insects, olfactory and visual stimuli from the resource always occur in combination but, for others, olfactory stimuli are sometimes present without any visual stimuli. For example, *H. abietis* is able to locate roots when walking on the ground and burrow down to them for ovipositing or feeding (Nordlander *et al.*, 1986).

The visual stimulus of a dummy-seedling alone significantly increases the number of pine weevils caught. This is noteworthy because '... visual responses often occur only in the presence of an appropriate olfactory signal.', according to Bernays (2002). However, orientation towards solely visual stimuli has been shown for several species, both in the field and the laboratory (Prokopy & Owens, 1983). In the field, the desert locust *Schistocerca gregaria* walks towards solely visual stimuli of vegetation (Kennedy, 1939). Because it has been suggested that monophagous insects should be greater visual specialists than polyphagous insects (Prokopy & Owens, 1978), it is interesting that the polyphagous pine weevil shows such a strong reaction to visual stimuli.

When both olfactory and visual stimuli are provided, more pine weevils are caught than when olfactory and visual stimuli are provided separately. There is an interaction between olfactory and visual stimuli in the direction of a less than additive response rather than a synergistic response. However, the effect of the interaction is small compared with the responses to the separate stimuli and, essentially, the response to the combination of olfactory and visual stimuli can be regarded as additive. An additive response to noncontact olfactory and visual stimuli has been reported in several studies. Butkewich & Prokopy

(1997) demonstrated that the responses of walking and flying adult plum curculios to olfactory and visual stimuli from tree models in the field appeared to be additive. Similarly, the effects of odour and colour of paper strips on the number of flies caught were shown to be additive in a laboratory study by Harris *et al.* (1993). However, several examples of synergism have also been reported. For example, olfactory and visual stimuli from traps in the field act synergistically on the number of aphids landing on traps (Chapman *et al.*, 1981). Synergistic reactions to odour and colour affecting the number of alighting were demonstrated in the laboratory for a leafhopper (Todd *et al.*, 1990) and in the field for the onion fly (Judd & Borden, 1991). Whether the responses are additive or synergistic may depend on the strength of the stimuli involved. This hypothesis is supported by studies of the relative influence of different stimuli. For example, the relative influence of odour on the apple maggot fly increased as the visual stimulus weakened (Aluja & Prokopy, 1993) and, for a grasshopper, when the olfactory stimulus increased, the relative influence of visual stimuli decreased (Szentesi *et al.*, 1996). These relationships between stimuli indicate that the use of unnaturally strong olfactory stimuli may have led to an underestimation of the significance of visual stimuli in resource finding.

It is not possible to determine the exact relative influence of olfactory and visual stimuli with the experimental setup used in this study. Furthermore, Harris & Miller (1988) questioned whether it is possible at all. However, the odour-less dummy-seedling increases the number of weevils caught by approximately half as much as an undamaged conifer seedling, which suggests that the visual stimulus is at least as important as odour for finding an undamaged conifer seedling. The basis for this assertion is the essentially additive nature of the response to olfactory and visual stimuli.

The reaction to olfactory and visual stimuli is similar for each of the different time periods, indicating that none of the variables (i.e. reproductive status, age of the weevils, age of the clear-cutting or season) influences the responses to noncontact olfactory and visual stimuli from conifer seedlings. The finding that there is no interaction between odour orientation and period is in agreement with a study in which the proportion of attacks on wounded seedlings compared with intact seedlings remained similar during the same periods as those investigated in the present study (Nordlander, 1991). However, period-related responses to odours (limonene,  $\alpha$ -pinene and  $\alpha$ -pinene + ethanol) have been observed in studies where odour-releasing pitfall traps were used (Nordlander, 1990; Nordenhem & Eidmann, 1991). This may be because such traps mainly catch weevils searching for breeding material, which is not relevant for pre-reproductive weevils (present during periods 1 and 2 but not 3). The selectivity of these types of traps for reproductively mature individuals has been shown also for other *Hylobius* species (Hoffman *et al.*, 1997).

The number of insects arriving at a resource is not necessarily related to the probability that the resource will be utilized. For example, more pine weevils arrive at conifer seedlings planted in mineral soil than in humus,

but fewer seedlings are damaged on mineral soil (Björklund *et al.*, 2003). It was suggested that this is due to the humus providing sheltering and burrowing places. Similarly, more onion flies alight on cylinders larger than onion stems than on cylinders of the same size as onion stems, but the larger cylinders receive a lower percentage of the eggs (Harris & Miller, 1984). However, increases in the number of insects arriving at a *suitable* resource in a *suitable* environment are likely to be associated with increases in the probability that the resource is utilized. In support of this hypothesis, it has been shown that increases in spruce odour emissions increase both the number of pine weevils arriving at a spruce seedling and the number of attacks (Björklund *et al.*, 2003). Similarly, larger numbers of onion flies have been found to alight on yellow stems compared with blue or grey stems, and more eggs were laid on the yellow stems (Harris & Miller, 1983). In the present study, investigating catches in traps associated with a suitable resource (spruce seedlings) in a suitable environment (humus), both olfactory and visual stimuli from conifer seedlings increase the number of captured weevils.

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