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Physiological Entomology.

Citation for the published paper:

Björklund, N., Nordlander, G., Bylund, H. (2005) Olfactory and visual
stimuli used in orientation to conifer seedlings by the pine weevil,
Hylobius abietis. *Physiological Entomology*.

Volume: 30 Number: 3, pp 225-231.

<http://dx.doi.org/10.1111/j.1365-3032.2005.00451.x>

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1 Author's Pre-print: The definitive version is available at www3.interscience.wiley.com 1
2 Björklund, N., Nordlander, G. & Bylund, H. (2005) Olfactory and visual stimuli used in orientation to conifer 2
3 seedlings by the pine weevil *Hylobius abietis*. *Physiological Entomology* 30, 225-231 doi: 10.1111/j.1365-3
4 3032.2005.00451.x

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

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Abstract

A field experiment was conducted to determine the influence of non-contact plant cues on the likelihood that individual conifer seedlings will be found by walking adults of the pine weevil *Hylobius abietis* (L.) (Coleoptera, Curculionidae). Pine weevils were caught in traps when approaching different combinations of olfactory and visual stimuli and their numbers recorded. Treatments with solely odour or solely visual stimuli caught significantly more weevils than a non-stimuli treatment, and the combination of odour and visual stimuli caught more weevils than odour and visual stimuli alone. There was a slight interaction between odour and visual stimuli, in the direction of competition rather than synergism. However, the effect was small compared to the response to the separate stimuli and principally the response can be regarded as additive. The reaction to odour and visual stimuli was similar for three phases of the pine weevil's life cycle associated with three ages of clear-cuttings. Visual stimulus was at least as important as odour for the pine weevil in finding an undamaged conifer seedling. We suggest that the significance of visual stimuli in resource finding may be generally underestimated because of the use of unnaturally strong odour stimuli in many studies.

1 Introduction

2 The behavioural events leading a phytophagous insect to feed on a host plant can be divided
3 into three sequential steps: finding food, examining food, and consuming food (Miller &
4 Strickler, 1984). Finding food can be further subdivided into levels, e.g. finding the habitat
5 and finding the resource item itself, where the influence of olfactory and visual stimuli may
6 differ (Prokopy, 1986). This study concerns the influence of non-contact plant cues on the
7 likelihood that individual conifer seedlings will be found by walking adults of the pine weevil
8 *Hylobius abietis* (L.) (Coleoptera, Curculionidae).

9
10 Many phytophagous insects orient towards odours from host plants (Bell, 1984; Bernays &
11 Chapman, 1994; Visser, 1986), but most of the evidence for this is based on laboratory
12 experiments and may not be relevant under natural conditions with many competing stimuli
13 (Jermy *et al.*, 1988; Morris & Kareiva, 1991; Schoonhoven *et al.*, 1998). Baited traps emitting
14 very high concentrations of host odour often catch large numbers of walking adult insects but
15 this does not prove the significance of host odour in plant finding. The evidence is scarce for
16 the orientation solely towards odour released from a plant in the field by walking adult
17 insects. It has been proposed that distant olfactory attraction to host plants in nature may be
18 much rarer than has been thought (Jermy *et al.*, 1988). The use of visual stimuli in detecting
19 plants, although much less investigated, has also been shown for several species (Prokopy &
20 Owens, 1983). As is the case with odours, many studies have been carried out in the
21 laboratory, e.g. walking *Pissodes strobi* Peck (Curculionidae) adults orient preferentially
22 towards silhouettes that are: vertical rather than oblique, 3 cm in width rather than other
23 diameters, taller rather than shorter (VanderSar & Borden, 1977). These results are in good
24 agreement with the characteristics of spruce twigs attacked by *P. strobi* in the field. There are
25 also examples from the laboratory where a visual stimulus alone does not elicit a response,

1 e.g. the adult plum curculio *Conotrachelus nenuphar* (Herbst) (Curculionidae) walking on
2 tree twigs does not respond to visual fruit characteristics (Butkewich & Prokopy, 1993). In the
3 field, attraction towards solely visual stimuli has been shown for the desert locust, which
4 walks towards conspicuous vegetation from at least 1.5 m (Kennedy, 1939).

5

6 Multiple sensory modalities are often used before an insect arrives to a resource (reviewed in
7 (Miller & Strickler, 1984; Prokopy, 1986)). Authors often claim that they have found an
8 “interaction” between odour and visual stimuli, but the interpretation of this term differs. If,
9 for instance, the response to a combination of the stimuli is as large as the sum of the
10 individual responses some would claim that there is an interaction. Others, using statistical
11 terms, would claim that there is no interaction in this case but refer to it as an additive
12 response. In this study the statistical definition of interaction will be used (Slinker, 1998).

13

14 Several studies have shown that insects respond stronger when, for example, a visual stimulus
15 is added to an odour stimulus. It is tempting to conclude that the odour and visual stimuli
16 together are stronger than the odour by itself, but the visual stimulus may alone be as strong
17 as the combination. It is therefore important that the stimuli are tested both individually and
18 together. This has been done in several studies. For example, it has been shown that the
19 cabbage moth landed more often when an artificial leaf with added plant odour were
20 presented than when an artificial leaf or plant odour were presented separately (Rojas &
21 Wyatt, 1999). Similarly, the mean number of captured adult cabbage root flies tended to be
22 higher when odour and visual stimuli were combined than when presented separately (Tuttle
23 *et al.*, 1988).

24

1 If a treatment with none of the stimuli is included it is possible to determine the “true
2 response” of the other treatments, that is the fraction above the control level. A control is also
3 necessary to test if the stimuli acts synergistically, i.e. if the total effect is greater than the sum
4 of effects taken independently (Slinker, 1998). Odour and colour have been reported to act
5 synergistically on alighting for a species of leafhopper in an observation chamber (Todd *et al.*,
6 1990) and for the onion fly on three-dimensional traps in onion fields (Judd & Borden, 1991).
7 Odour and visual stimuli, i.e. yellow vs. transparent, appears to act synergistically on the
8 number of aphids landing on traps in the field (Chapman *et al.*, 1981). An example of where
9 the effect of odour and visual stimuli appears to be additive rather than synergistic is the
10 response to tree models by adult plum curculio (Butkewich & Prokopy, 1996). For walking
11 adult insects much less has been done, but in a laboratory experiment the grasshopper
12 *Melanoplus sanguinipes* (F.) approached odour and visual stimuli from plant sources more
13 frequently than the control, and the response to odour and visual stimuli combined was even
14 larger. The present study is, to our knowledge, the first that in the field has investigated if
15 odour and visual non-contact stimuli act synergistically during resource finding for a walking
16 insect.

17
18 The physiological state of an insect could influence resource-oriented behaviours (reviewed in
19 (Barton Browne, 1993). Responses to non-contact odour and visual stimuli from a resource
20 have been shown to be influenced by age and reproductive status of the insect and the season
21 (Barata & Araújo, 2001; Borden *et al.*, 1986; Brevault & Quilici, 1999; Hoffman *et al.*, 1997;
22 Landon *et al.*, 1997; Mathieu *et al.*, 2001; Prokopy, 1977). Also in *H. abietis* there is some
23 evidence for that the reaction to odour may be dependent on in which phase in the adult life
24 cycle the pine weevils are, which in turn is related to the age of the clear-cutting (Nordenhem
25 & Eidmann, 1991; Nordlander, 1990). The present experiment was therefore performed on

1 clear-cuttings of different ages, with weevils in different phases of their life cycle, to evaluate
2 if the response to odour and visual stimuli differ.

3
4 Large numbers of pine weevils *H. abietis* fly during late spring to fresh clear-cuttings, which
5 provides plenty of breeding material. After arrival their flight muscles regress and they remain
6 on the ground for the rest of the season (Långström, 1982; Nordenhem, 1989; Örlander *et al.*,
7 1997; Örlander *et al.*, 2000). The pine weevil is most active at twilight (Sibul *et al.*, 1999) and
8 feeds on several tree species (Leather *et al.*, 1994; Manlove *et al.*, 1997). It is a serious pest in
9 areas where clear-cutting with subsequent replanting is practised, since the adults feed on the
10 stem bark of newly planted conifer seedlings (Day *et al.*, 2004; Day & Leather, 1997;
11 Långström & Day, 2004) but feeding also occurs in the crowns and roots of mature conifer
12 trees (Örlander *et al.*, 2000).

13
14 It has been shown in other pest systems that an increased knowledge of the basic processes of
15 resource finding could bring about more effective protection methods (Duan & Prokopy,
16 1995; Foster & Harris, 1997), which should be valid also for the pine weevil system. The aim
17 of this study was to determine: 1) if the number of pine weevils arriving to an individual
18 conifer seedling is influenced by odour and visual stimuli presented separately 2) if there is a
19 synergistic effect between odour and visual stimuli (which requires the following treatments:
20 *only* odour stimuli, *only* visual stimuli, odour and visual stimuli, and control (Slinker, 1998)),
21 and 3) if these reactions differ among the three phases of the pine weevil's life cycle
22 associated with three ages of clear-cuttings. To answer these questions it was necessary that
23 the stimuli used were of the same magnitude as those found in nature.

24

1 Materials and methods

2 In a field experiment, adult pine weevils were caught in traps when approaching different
3 combinations of olfactory and visual stimuli and their numbers recorded. The experiment was
4 conducted near Uppsala in central Sweden during three periods of time: 1) during six weeks
5 in August and September 2000 on a 1-year-old clear-cutting (newly emerged pre-reproductive
6 weevils, prior to hibernation) 2) during six weeks in May and June 2001 on a 2-year-old
7 clear-cutting (pre-reproductive, pre-migratory, maturation feeding weevils), and 3) during
8 four weeks in June and July 2000 on a fresh clear-cutting (reproductive, immigrant weevils)
9 (Nordenhem & Eidmann, 1991). Before clear felling the stands consisted of mixed Scots pine
10 *Pinus sylvestris* (L.) and Norway spruce *Picea abies* (L.) Karst.. A randomised block-design
11 was used with 12 blocks on each clear-cutting and six traps with different treatments within
12 each block. Each week the traps were emptied, the numbers of trapped pine weevils recorded,
13 baits renewed, and the treatments randomly replaced within blocks. Within each block, trap
14 positions were chosen so that the surrounding vegetation and other factors were as similar as
15 possible. There was at least 3 m between traps and at least 60 m between a trap and the edge
16 of the clear-cutting. Slash was removed within a 1-m radius of the traps.

17
18 Pitfall traps, described by Björklund et al. (2003), caught approaching pine weevils at a 2.5-
19 cm radius from the treatment (Fig. 1). A slippery surface was created on the sloping fall rim
20 and on the inner side of the trap by applying Fluon® (ICI, Herts, U.K.). The traps were made
21 of polyethylene terephthalate (PETP) bottles, constructed without glue to avoid odour
22 influence, and filled with water with a few drops of detergent added to drown responding
23 weevils and to supply the conifer seedlings with water.

24

1 The following treatments were included: 1) control 2) pine odour 3) dummy-seedling 4)
 2 dummy-seedling + pine odour 5) seedling 6) seedling + pine odour. Dummy-seedlings were
 3 used to obtain an odourless visual stimulus, treatment 5 and 6 were used as positive controls.
 4 The seedlings used were two-year-old containerized Norway spruce seedlings (provenance
 5 Rezekne). Pine odour was achieved by burying three 5-cm long freshly cut stem pieces, from
 6 the same lot of seedlings, in soil in the centre of the trap with their upper end at level with the
 7 soil surface. The dummies was composed of a green metal wire (3 mm in diameter) as stem
 8 and 6-cm long thin metal wires covered with green plastic (CLIP'N'TWIST (Buryrite))
 9 twisted around the stem as twigs (Fig. 1). The dummies reached 25 cm above ground, which
 10 was approximately the same height as the seedlings.

11

12 **Statistics**

13 The positive controls, treatment 5 and 6, were not included in the following analyses. The
 14 pine weevil catch was calculated as the total catch, summarised for each period, per treatment
 15 and block. The homogeneity among blocks of the responses to the different treatments were
 16 tested with Fisher's exact test (period 1 and 2) or a χ^2 -test (period 3) for separate two-way
 17 contingency tables (12 blocks \times 4 treatments) (procedure FREQ, SAS Institute 1999). The
 18 homogeneity among periods of the responses to the treatments among the periods were tested
 19 by a χ^2 -test for a two-way contingency table (3 periods \times 4 treatments) (proc. FREQ, SAS
 20 Inst.), which requires homogeneity among blocks of each period. A confidence interval for
 21 the response of treatment k, k=1,2,3,4, was calculated as $\hat{p}_k \pm 1.96 \times SE(\hat{p}_k)$, when
 22 $\hat{p}_k = x_k/x$. with x_k equal to the number of weevils caught at treatment k and x. equal to the
 23 total number of weevils. By using facts about the binomial distribution the standard error was
 24 calculated as $SE(\hat{p}_k) = [\hat{p}_k(1 - \hat{p}_k)/x]^{1/2}$. To determine if there was any interaction between

1 odour and visual stimuli a χ^2 -test was used for a two-way contingency table (combinations of
2 absence and presence of odour and visual stimuli) (proc. FREQ, SAS Inst.).

3

4 Results

5

6 In total, 118 pine weevils were caught on the 2-year-old clear-cutting, 750 on the fresh clear-
7 cutting, and 96 on the 1-year-old clear-cutting. The distributions of catches on the different
8 treatments were similar during the three time periods (Fig. 2). The response to the positive
9 controls (conifer seedling and conifer seedling + pine odour) were similar although stronger
10 than the response to their experimental counterparts (dummy-seedling and dummy-seedling +
11 pine odour). The positive controls were not included in the following analysis. There was no
12 difference in responses to the different treatments among blocks for period 1 (Fisher's exact
13 test $P=0.18$), period 2 (Fisher's exact test $P=0.65$) or period 3 ($\chi^2=30.92$, $P=0.57$). It was
14 therefore appropriate to test for differences in responses to the different treatments among
15 periods, however no differences were found ($\chi^2=6.8$, $P=0.34$). In the following analysis the
16 data from the three periods were pooled. Treatments with solely odour and solely visual
17 stimuli caught significantly more weevils than the non-stimuli treatment, and the combination
18 of odour and visual stimuli caught more weevils than odour and visual stimuli alone (Fig. 3).
19 There was a weak interaction between odour and visual stimuli ($\chi^2=3.95$, $P=0.049$) in the
20 direction of competition rather than synergism (Fig. 3).

21

1 Discussion

2 The positive controls, i.e. conifer seedling and conifer seedling + pine odour, confirmed that
3 the stimuli used were of the same magnitude as those emitted by seedlings. Further, the effect
4 of adding pine odour to the artificial visual stimuli (dummy-seedling) was similar to the effect
5 of adding pine odour to a spruce seedling. The non-stimuli treatment is considered to measure
6 the probability that a spot is passed by chance. In support of this it has earlier been shown that
7 the water present in this type of traps does not increase trap catches (Björklund *et al.*, 2003).

8 The rather high catches in traps without any stimuli suggest that pine weevils should
9 frequently encounter conifer seedlings even in the absence of visual and olfactory stimuli. The
10 high catches in traps without stimuli emphasises the importance of having a non-stimuli
11 treatment since even a slightly deterrent stimuli could have caught a significant amount of
12 insects but still less than a non-stimuli treatment. Without a non-stimuli treatment results may
13 therefore be misinterpreted. Both odour and visual stimuli may act as deterrents (Strom *et al.*,
14 1999). The relationship between non-stimuli, seedling and seedling + pine odour was very
15 similar to those found in a previous study (Björklund *et al.*, 2003).

16
17 Pine odour alone increased the number of approaching walking pine weevils significantly.
18 Several species have been shown to walk towards odours in the laboratory (Bell, 1984;
19 Bernays & Chapman, 1994; Szentesi *et al.*, 1996). However, field studies with odours emitted
20 in similar amounts as emitted from natural plants are necessary to evaluate the significance of
21 odours for finding food. For flying insects, some field experiments have shown that solely
22 odour increase the number of approaching insects (e.g. (Butkewich & Prokopy, 1996;
23 Chapman *et al.*, 1981). For many insects odour and visual stimuli from the resource are
24 always provided together but for others it is sometimes necessary to use solely odour stimuli.
25 *Hylobius abietis* is able to locate roots when walking on the ground and burrow down to them

1 for ovipositing or feeding (Nordlander *et al.*, 1986; Nordlander *et al.*, 2000; Örlander *et al.*,
2 2000).

3
4 Solely the visual stimuli of a dummy-seedling increased the number of approaching pine
5 weevils significantly. This is noteworthy since "..., visual responses often occur only in the
6 presence of an appropriate olfactory signal." (p.531 Bernays, 2002). However, orientation
7 towards solely visual stimuli has been shown for several species, both in the field and in the
8 laboratory (Prokopy & Owens, 1983; Prokopy & Roitberg, 1984). In some cases rather
9 unspecific visual stimuli have elicited a positive response in the laboratory (Meyer, 1975;
10 Meyer & Raffensperger, 1974; Szentesi *et al.*, 1996). The sometimes observed lack of
11 response in the field may be due to that the resource provides a too unspecific stimulus to be
12 useful for the insect or that the tested visual stimuli do not sufficiently resemble the natural
13 resource. It has, however, been shown in the field that the desert locust *S. gregaria* walks
14 towards solely the visual stimuli of vegetation (Kennedy, 1939). Considering that it has been
15 suggested that monophagous insects should be greater visual specialists than polyphagous
16 insects (Prokopy & Owens, 1978), it is interesting that the polyphagous pine weevil shows
17 such a strong reaction to visual stimuli.

18
19 When both odour and visual stimuli were provided, more pine weevils approached than when
20 odour and visual stimuli were provided separately. There was a slight interaction between
21 odour and visual stimuli, in the direction of competition rather than synergism. However, the
22 effect was small compared to the response to the separate stimuli and principally the response
23 can be regarded as additive. An additive response to non-contact odour and visual stimuli has
24 been reported in several studies. The response of walking and flying adult plum curculio to
25 odour and visual stimuli from tree models in the field appears to be additive (Butkewich &

1 Prokopy, 1996). Similarly, the effect of odour and colour of paper strips on the number of
2 approaching flying flies were additive in a laboratory study (Harris *et al.*, 1993). Several
3 examples of synergism also exist. Odour and visual stimuli from traps in the field act
4 synergistically on the number of aphids landing on traps (Chapman *et al.*, 1981). A
5 synergistic reaction to odour and colour on the number of alighting has been shown in the
6 laboratory for a leafhopper (Todd *et al.*, 1990) and in the field for the onion fly (Judd &
7 Borden, 1991). Whether responses are additive or synergistic may depend on the strength of
8 the involved stimulus. This is supported by studies of the relative influence of different
9 stimuli. When the visual stimulus became weaker the relative influence of odour increased for
10 the apple maggot fly (Aluja & Prokopy, 1993), and for a grasshopper it has been shown that
11 when the olfactory stimulus increased the relative influence of visual stimuli decreased
12 (Szentesi *et al.*, 1996). These relationships between stimuli in many studies have probably
13 lead to an underestimation of the significance of visual stimuli in resource finding.

14

15 It is not possible to determine the exact relative influence of odour and visual stimuli with the
16 experimental setup used in this study, and it has been questioned if it is possible at all (Harris
17 & Miller, 1988). However, the odour-less dummy-seedling increased the number of
18 approaching weevils with approximately half as much as an undamaged conifer seedling,
19 which suggest that the visual stimulus is at least as important as odour for finding an
20 undamaged conifer seedling. This reasoning is possible since the response to odour and visual
21 stimuli was principally additive. The relative influence of odour for a damaged seedling is of
22 course larger since it emits a higher concentration of odour, and an increased odour emission
23 also increase the number of approaching weevils (this study; Björklund *et al.*, 2003) and the
24 number of attacks (Björklund *et al.*, 2003; Nordlander, 1991).

25

1 For *H. abietis* and closely related species, several studies have been conducted using traps
2 resembling small stumps. However, the trap type used precluded the possibility to have a
3 treatment with no visual stimulus at all, thus a true response to the visual stimulus could not
4 be determined. Further the results differed, i.e. *H. abietis* was caught in unbaited traps made
5 of tubes, with 4 cm of the tube above ground (Nordlander, 1987) whereas the closely related
6 *Pachylobius picivorus* (Germar) was not caught in similar unbaited traps (Hunt & Raffa,
7 1989). With another type of trap *P. picivorus* and *Hylobius pales* (Herbst) were caught in
8 unbaited traps, again no control without visual stimuli was used (Mizell & Tedders, 1999). In
9 studies where it has been tested if additional visual stimuli can increase catches in baited traps
10 the results are again hard to interpret. When an additional visual cue resembling a 20 cm high
11 stump was provided to baited traps, the catches of *H. abietis* did not increase (Nordlander,
12 1987). Similar baited traps painted white caught larger numbers of *P. picivorus* and *H. pales*
13 than those painted black (Hunt & Raffa, 1991), whereas the opposite results were shown with
14 two other types of traps (Fatzinger, 1985; Mizell & Tedders, 1999). In conclusion, the
15 discrepancy among the results of all the studies presented above suggests that responses to
16 visual stimuli need to be investigated in further detail. The results of the present study suggest
17 that it should be possible to increase trap catches with a combination of plant odour and an
18 appropriate visual stimulus.

19
20 The reaction to odour and visual stimuli was similar for the different time periods which
21 indicates that neither reproductive status, age of the weevils, age of the clear-cutting or season
22 influenced the response to non-contact odour and visual stimuli from conifer seedlings. The
23 result that there was no interaction between odour orientation and period is in agreement with
24 a study in which the proportion of attacks on wounded seedlings compared to intact seedlings
25 was similar during the same periods as investigated in the present study (Nordlander, 1991).

1 However, different responses to odours (limonene, α -pinene and α -pinene + ethanol) have
2 been observed in studies where baited pitfall traps (Nordlander, 1987) have been used
3 (Nordenhem & Eidmann, 1991; Nordlander, 1990). This may be due to that these traps
4 mainly catch weevils searching for breeding material which is not relevant for pre-
5 reproductive weevils. A lower proportion of pre-reproductive individuals in similar types of
6 traps has been shown also for some related *Hylobius* species (Hoffman *et al.*, 1997).

7
8 An increased number of insects arriving to a resource is not necessarily related to the
9 probability that the resource will be utilised. For example more pine weevils approached
10 conifer seedlings planted in mineral soil than in humus but fewer seedlings were attacked on
11 mineral soil in a study by Björklund *et al.* (2003). It was proposed that this was due to that the
12 humus provided hiding and burrowing places. It has also been shown that more onion flies
13 alighted on cylinders larger than onion stems than on cylinders of the same size as onion
14 stems, but the larger cylinders received a lower percentage of the eggs (Harris & Miller,
15 1984). However, an increased number of insects arriving to a *suitable* resource in a *suitable*
16 environment should increase the probability that the resource is utilised. In support of this it
17 has been shown that an increased pine odour emission increase both the number of pine
18 weevils approaching a conifer seedling and the number of attacks (Björklund *et al.*, 2003).
19 Similarly, it has been shown that yellow stems, compared to blue or grey, increased the
20 number of alighting and also the number of eggs laid by the onion fly (Harris & Miller, 1983).
21 In the present study it was shown that both odour and visual stimuli are used by pine weevils
22 for locating conifer seedlings.

23

1 References

- 2 Aluja, M. & Prokopy, R. J. (1993) Host odor and visual stimulus interaction during intratree host finding
3 behavior of *Rhagoletis pomonella* flies, *Journal of Chemical Ecology*, **19**, 2671-2696.
- 4 Barata, E. N. & Araújo, J. (2001) Olfactory orientation responses of the eucalyptus woodborer, *Phoracantha*
5 *semipunctata*, to host plant in a wind tunnel, *Physiological Entomology*, **26**, 26-37.
- 6 Barton Browne, L. (1993) Physiologically induced changes in resource-oriented behavior, *Annual Review of*
7 *Entomology*, **38**, 1-25.
- 8 Bell, W. J. (1984) Chemo-orientation in walking insects. In: *Chemical ecology of insects* (Eds, Bell, W. J. and
9 Cardé, R. T.) Chapman and Hall, London and New-York, pp. 93-109.
- 10 Bernays, E. A. (2002) Host seeking, for plants. In: *Encyclopedia of insects* (Eds, Resh, V. H. and Cardé, R. T.)
11 Academic Press, London, pp. 529-532.
- 12 Bernays, E. A. & Chapman, R. F. (1994) *Host-plant selection by phytophagous insects* Chapman & Hall, New
13 York.
- 14 Björklund, N., Nordlander, G. & Bylund, H. (2003) Host-plant acceptance on mineral soil and humus by the pine
15 weevil *Hylobius abietis* (L.), *Agricultural and Forest Entomology*, **5**, 61-65.
- 16 Borden, J. H., Hunt, D. W. A., Miller, D. R. & Slessor, K. N. (1986) Orientation in forest Coleoptera: an
17 uncertain outcome of responses by individual beetles to variable stimuli. In: *Mechanisms in*
18 *insect olfaction* (Eds, Payne, T. L., Birch, M. C. and Kennedy, C. E. J.) Clarendon Press, Oxford,
19 pp. 97-109.
- 20 Brevault, T. & Quilici, S. (1999) Factors affecting behavioural responses to visual stimuli in the tomato fruit fly,
21 *Neoceratitis cyanescens*, *Physiological Entomology*, **24**, 333-338.
- 22 Butkewich, S. L. & Prokopy, R. J. (1993) The effect of short-range host odor stimuli on host fruit finding and
23 feeding behavior of plum curculio adults (Coleoptera: Curculionidae), *Journal of Chemical*
24 *Ecology*, **19**, 825-835.
- 25 Butkewich, S. L. & Prokopy, R. J. (1996) Attraction of adult plum curculios (Coleoptera: Curculionidae) to host-
26 tree odor and visual stimuli in the field, *Journal of entomological science*, **32**, 1-6.
- 27 Chapman, R. F., Bernays, E. A. & Simpson, S. J. (1981) Attraction and repulsion of the aphid, *Cavariella*
28 *aegopodii*, by plant odours, *Journal of Chemical Ecology*, **7**, 881-888.
- 29 Day, K., Nordlander, G., Kenis, M. & Halldórsson, G. 2004. General biology and life cycles of bark weevils. In:
30 *Bark and wood boring insects in living trees in Europe: a synthesis* (Eds, Lieutier, F., Day, K.

- 1 R., Battisti, A. Gregoire, J.-P. & Evans, H. F.) Kluwer Academic Publishers, Dordrecht.
2 (Accepted).
- 3 Day, K. R. & Leather, S. R. (1997) Threats to forestry by insect pests in Europe. In: *Forests and Insects* (Eds,
4 Watt, A. D., Stork, N. E. and Hunter, M. D.) Chapman & Hall, London, pp. 177-205.
- 5 Duan, J. J. & Prokopy, R. J. (1995) Control of apple maggot flies (Diptera: tephritidae) with pesticide-treated red
6 spheres, *Journal of Economic Entomology*, **88**, 700-707.
- 7 Fatzinger, C. W. (1985) Attraction of the black turpentine beetle (Coleoptera: Scolytidae) and other forest
8 Coleoptera to turpentine-baited traps, *Environmental Entomology*, **14**, 768-775.
- 9 Foster, S. P. & Harris, M. O. (1997) Behavioral manipulation methods for insect pest-management, *Annual*
10 *Review of Entomology*, **42**, 123-146.
- 11 Harris, M. O. & Miller, J. r. (1983) Color stimuli and oviposition behavior of the onion fly, *Delis antiqua*
12 (Meigen) (Diptera: Anthomyiidae), *Annals of the Entomological Society of America*, **76**, 766-
13 771.
- 14 Harris, M. O. & Miller, J. R. (1984) Foliar form influences ovipositional behaviour of the onion fly,
15 *Physiological Entomology*, **9**, 145-155.
- 16 Harris, M. O. & Miller, J. R. (1988) Host-acceptance behaviour in an herbivorous fly, *Delia antiqua*, *Journal of*
17 *Insect Physiology*, **34**, 179-190.
- 18 Harris, M. O., Rose, S. & Malsch, P. (1993) The role of vision in the host plant-finding behaviour of the Hessian
19 fly, *Physiological Entomology*, **18**, 31-42.
- 20 Hoffman, G. D., Hunt, D. W. A., Salom, S. M. & Raffa, K. F. (1997) Reproductive readiness and niche
21 differences affect responses of conifer root weevils (Coleoptera: Curculionidae) to simulated
22 host odors, *Environmental Entomology*, **26**, 91-100.
- 23 Hunt, D. W. A. & Raffa, K. F. (1989) Attraction of *Hylobius radicus* and *Pachylobius picivorus* (Coleoptera:
24 Curculionidae) to ethanol and turpentine in pitfall traps, *Environmental Entomology*, **18**, 351-
25 355.
- 26 Hunt, D. W. A. & Raffa, K. F. (1991) Orientation of *Hylobius pales* and *Pachylobius picivorus* (Coleoptera:
27 Curculionidae) to visual cues, *Great Lakes Entomologist*, **24**, 225-230.
- 28 Jermy, T., Szentesi, A. & Horváth, J. (1988) Host plant finding in phytophagous insects: the case of the
29 Colorado potato beetle, *Entomologia Experimentalis et Applicata*, **49**, 83-98.

- 1 Judd, R. J. R. & Borden, J. H. (1991) Sensory interaction during trap-finding by female onion flies: implications
2 for ovipositional host-plant finding, *Entomologia Experimentalis et Applicata*, **58**, 239-249.
- 3 Kennedy, J. S. (1939) The behaviour of the desert locust (*Schistocerca gregaria*) (Forsk.) (Orthopt.) in an
4 outbreak centre, *The Transactions of the Royal entomological Society of London*, **189**, 385-542.
- 5 Landon, F., Ferary, S., Pierre, D., Auger, J., Biemont, J. C., Levieux, J. & Pouzat, J. (1997) *Sitona lineatus* host-
6 plant odours and their components: effects on locomotor behavior and peripheral sensitivity
7 variations, *Journal of Chemical Ecology*, **23**, 2161-2173.
- 8 Leather, S. R., Ahmed, S. I. & Hogan, L. (1994) Adult feeding preferences of the large pine weevil, *Hylobius*
9 *abietis* (Coleoptera: Curculionidae), *European Journal of Entomology*, **91**, 385-389.
- 10 Långström, B. (1982) Abundance and seasonal activity of adult *Hylobius*-weevils in reforestation areas during
11 first years following final felling, *Communicationes instituti Forestalis Fenniae*, **106**, 1-23.
- 12 Långström, B. & Day, K. 2004. Damage, control and management of weevil pests, especially *Hylobius abietis*.
13 In: *Bark and wood boring insects in living trees in Europe: a synthesis* (Eds, Lieutier, F., Day,
14 K. R., Battisti, A. Gregoire, J.-P. & Evans, H. F.) Kluwer Academic Publishers, Dordrecht.
15 (Accepted).
- 16 Manlove, J. D., Styles, J. & Leather, S. R. (1997) Feeding of the adults of the large pine weevil, *Hylobius abietis*
17 (Coleoptera: Curculionidae), *European Journal of Entomology*, **94**, 153-156.
- 18 Mathieu, F., Gaudichon, V., Brun, L. O. & Frerot, B. (2001) Effect of physiological status on olfactory and
19 visual responses of female *Hypothenemus hampei* during host plant colonization, *Physiological*
20 *Entomology*, **26**, 189-193.
- 21 Meyer, J. R. (1975) Effective range and species specificity of host recognition in adult alfalfa weevils, *Hyperia*
22 *postica*, *Annals of the Entomological Society of America*, **68**, 1-3.
- 23 Meyer, J. R. & Raffensperger, E. M. (1974) Kinetic orientation experiments on adult alfalfa weevils, *Annals of*
24 *the Entomological Society of America*, **67**, 143-144.
- 25 Miller, J. R. & Strickler, K. L. (1984) Finding and accepting host plants. In: *Chemical ecology of insects* (Eds,
26 Bell, W. J. and Cardé, R. T.) Chapman and Hall, London; New York, pp. 127-157.
- 27 Mizell, R. F. & Tedders, W. L. (1999) Evaluation of trap type and color for monitoring *Hylobius pales* and
28 *Pachylobius picivorus* in Florida, *Florida Entomologist*, **82**, 615-624.

- 1 Morris, W. F. & Kareiva, P. M. (1991) How insect herbivores find suitable host plants: the interplay between
2 random and nonrandom movement. In: *Insect-plant interactions*, Vol. 3 (Ed. by Bernays, E.)
3 CRC Press, Boca Raton, pp. 175-208.
- 4 Nordenhem, H. (1989) Age, sexual development, and seasonal occurrence of the pine weevil *Hylobius abietis*
5 (L.), *Journal of Applied Entomology*, **108**, 260-270.
- 6 Nordenhem, H. & Eidmann, H. H. (1991) Response of the pine weevil *Hylobius abietis* L. (Col., Curculionidae)
7 to host volatiles in different phases of its adult life cycle, *Journal of Applied Entomology*, **112**,
8 353-358.
- 9 Nordlander, G. (1987) A method for trapping *Hylobius abietis* (L.) with a standardized bait and its potential for
10 forecasting seedling damage, *Scandinavian Journal of Forest Research*, **2**, 199-213.
- 11 Nordlander, G. (1990) Limonene inhibits attraction to α -pinene in the pine weevils *Hylobius abietis* and *H.*
12 *pinastris*, *Journal of Chemical Ecology*, **16**, 1307-1320.
- 13 Nordlander, G. (1991) Host finding in the pine weevil *Hylobius abietis*: effects of conifer volatiles and added
14 limonene, *Entomologia Experimentalis et Applicata*, **59**, 229-237.
- 15 Nordlander, G., Eidmann, H. H., Jacobsson, U., Nordenhem, H. & Sjödin, K. (1986) Orientation of the pine
16 weevil *Hylobius abietis* to underground sources of host volatiles, *Entomologia Experimentalis et*
17 *Applicata*, **41**, 91-100.
- 18 Nordlander, G., Örlander, G., Petersson, M., Bylund, H., Wallertz, K., Nordenhem, H. & Långström, B. (2000)
19 *Pine Weevil Control Without Insecticides – Final Report of a Research Program, Report 1-*
20 *2000*. Asa försökspark, Sveriges lantbruksuniversitet, pp. 1-77 (In Swedish with English
21 summary).
- 22 Örlander, G., Nilsson, U. & Nordlander, G. (1997) Pine weevil abundance on clear-cuttings of different ages: a
23 6-year study using pitfall traps, *Scandinavian Journal of Forest Research*, **12**, 225-240.
- 24 Örlander, G., Nordlander, G., Wallertz, K. & Nordenhem, H. (2000) Feeding in the crowns of Scots pine trees by
25 the pine weevil *Hylobius abietis*, *Scandinavian Journal of Forest Research*, **15**, 194-201.
- 26 Prokopy, R. J. (1977) Attraction of *Rhagoletis* flies (Diptera: Tephritidae) to red spheres of different sizes, *The*
27 *Canadian Entomologist*, **109**, 593-596.
- 28 Prokopy, R. J. (1986) Visual and olfactory stimulus interaction in resource finding by insects. In: *Mechanisms in*
29 *insect olfaction* (Eds, Payne, T. L., Birch, M. C. and Kennedy, C. E. J.) Clarendon Press, Oxford,
30 pp. 81-89.

- 1 Prokopy, R. J. & Owens, E. D. (1978) Visual generalist with visual specialist phytophagous insects: host
2 selection behaviour and application to management, *Entomologia Experimentalis et Applicata*,
3 **24**, 609-620.
- 4 Prokopy, R. J. & Owens, E. D. (1983) Visual detection of plants by herbivorous insects, *Annual Review of*
5 *Entomology*, **28**, 337-364.
- 6 Prokopy, R. J. & Roitberg, B. D. (1984) Foraging behavior of true fruit flies, *American Scientist*, **72**, 41-49.
- 7 Rojas, J. C. & Wyatt, T. D. (1999) Role of visual cues and interaction with host odour during the host-finding
8 behaviour of the cabbage moth, *Entomologia Experimentalis et Applicata*, **91**, 59-65.
- 9 SAS Institute Inc., *SAS/STAT[®] User's Guide, Version 8*, Cary, NC: SAS Institute Inc., 1999.
- 10 Schoonhoven, L. M., Jermy, T. & van Loon, J. J. A. (1998) *Insect-plant biology* Chapman & Hall, London.
- 11 Sibul, I., Merivee, E. & Luik, A. (1999) On diurnal locomotor activity of *Hylobius abietis* L. (Coleoptera,
12 Curculionidae), *XXIV Nordic Congress of Entomology*, 163-166.
- 13 Slinker, B. K. (1998) The statistics of synergism, *Journal of molecular and cellular cardiology*, **30**, 723-731.
- 14 Strom, B. L., Roton, L. M., Goyer, R. A. & Meeker, J. R. (1999) Visual and semiochemical disruption of host
15 finding in the southern pine beetle, *Ecological Applications*, **9**, 1028-1038.
- 16 Szentesi, Á., Hopkins, T. L. & Collins, R. D. (1996) Orientation responses of the grasshopper, *Melanoplus*
17 *sanguinipes*, to visual, olfactory and wind stimuli and their combinations, *Entomologia*
18 *Experimentalis et Applicata*, **80**, 539-549.
- 19 Todd, J. L., Phelan, P. L. & Nault, L. R. (1990) Interaction between visual and olfactory stimuli during host-
20 finding by leafhopper, *Dalbulus maidis* (Homoptera: Cicadellidae), *Journal of Chemical*
21 *Ecology*, **16**, 2121-2133.
- 22 Tuttle, A. F., Ferro, D. N. & Idoine, K. (1988) Role of visual and olfactory stimuli in host finding of adult
23 cabbage root flies, *Delia radicum*, *Entomologia Experimentalis et Applicata*, **47**, 37-44.
- 24 VanderSar, T. J. D. & Borden, J. H. (1977) Visual orientation of *Pissodes strobi* Peck (Coleoptera:
25 Curculionidae) in relation to host selection behavior, *Canadian Journal of Zoology*, **55**, 2042-
26 2049.
- 27 Visser, J. H. (1986) Host odor perception in phytophagous insects, *Annual Review of Entomology*, **31**, 121-144.
28

1 **Legends to figures**

2

3 Fig. 1

4 Dummy-seedling in the pitfall trap used for the experiments.

5

6 Fig. 2

7 Total number of *H. abietis* caught in pitfall traps. Period 1=1-year-old clear-cutting (newly

8 emerged pre-reproductive weevils, prior to hibernation). Period 2=2-year-old clear-cutting

9 (pre-reproductive, pre-migratory, maturation feeding weevils). Period 3=Fresh clear-cutting

10 (reproductive, immigrant weevils). Treatments: C=control, P=pine odour, D=dummy-

11 seedling, DP=dummy-seedling + pine odour, S=seedling, SP=seedling + pine odour.

12

13 Fig. 3

14 Mean proportion (\pm 95% confidence interval) of *H. abietis* caught in traps with the following

15 treatments: control, pine odour, dummy-seedling, and dummy-seedling + pine odour. The

16 shaded area represents the size of the interaction effect.

17

1 Fig. 1
2

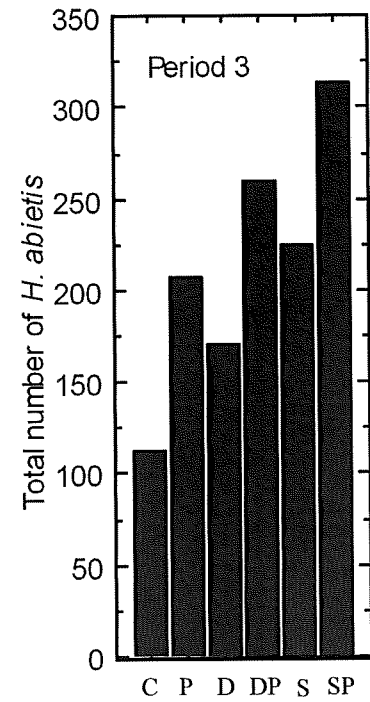
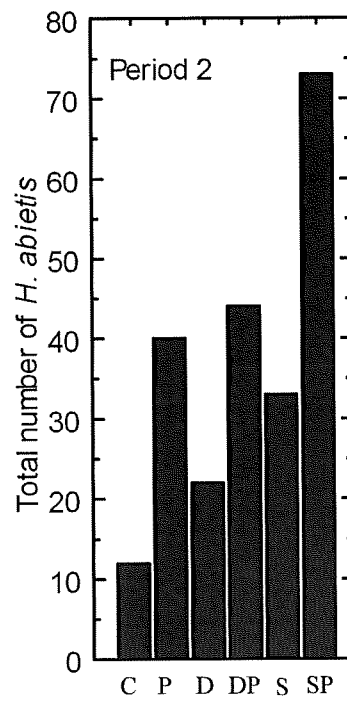
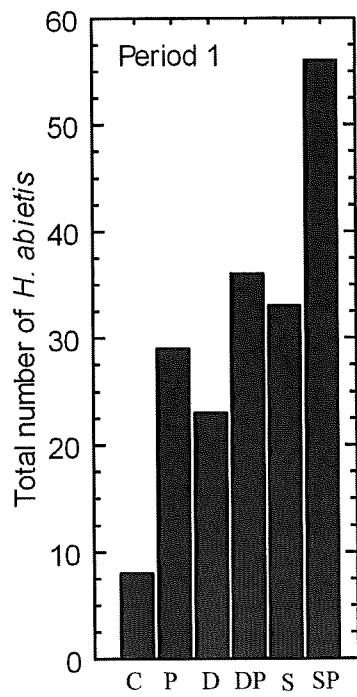


3

4

1 Fig. 2

2

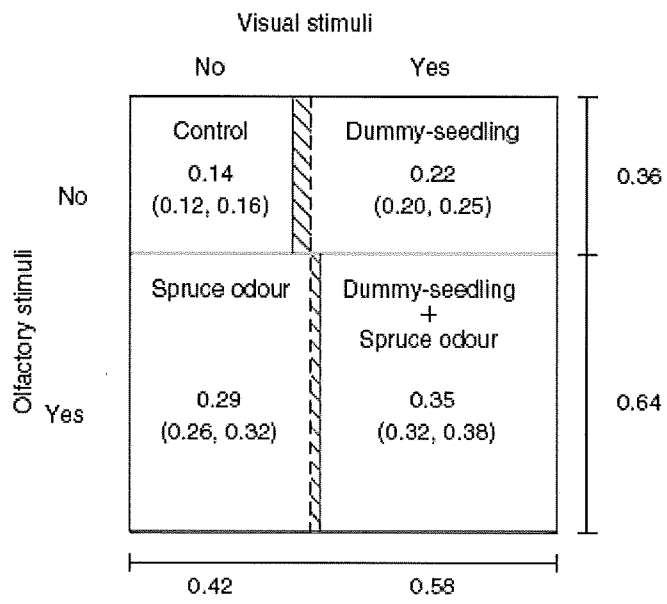


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1 Fig. 3

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