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Influence of larval frass extracts on the oviposition behaviour of *Monochamus alternatus* (Col., Cerambycidae)

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Abstract: The oviposition behaviour and response of adult females of *Monochamus alternatus* to short lengths (bolts) of *Pinus massoniana* trunks treated with hexane extracts of larval frass of *M. alternatus* was investigated in the laboratory. Females gnawed significantly fewer oviposition scars, and deposited significantly fewer eggs, on extract-treated bolts than on control bolts. These results suggest the presence of a possible oviposition deterrent in larval frass of *M. alternatus*. Hexane extracts of larval frass were analysed by gas chromatography–mass spectrometry, and α-pinene, β-pinene, 3-carene, limonene, longifolene and butylated hydroxytoluene were identified. Experiments with synthetic mixtures indicated that a mixture of monoterpenes and butylated hydroxytoluene exhibited oviposition-deterring activity.

Key words: *Monochamus alternatus* Hope, *Pinus massoniana* Lamb, larval frass, oviposition behaviour

1 Introduction

The oviposition behaviour of phytophagous insects is often modified by the presence of conspecific eggs and larvae. Typically, females avoid depositing eggs on previously exploited hosts, a behavioural strategy to reduce the competition suffered by their offspring. The stimuli permitting females to distinguish between the occupied and unoccupied hosts act as signals (Dempster 1992; Mudd et al. 1997; Seeley 1998; Li et al. 2001), which may come from conspecific eggs (Anbutsu and Togashi 1996, 1997), larvae (Williams et al. 1986; Anbutsu and Togashi 1996) or larval frass (Dittrick et al. 1983; Anderson et al. 1993). In several species of Lepidoptera, larva-associated oviposition deterrents have been reported. For example, in *Spodoptera littoralis*, frass of larvae feeding upon cotton plant leaves (*Gossypium barbadense*) acts as a strong oviposition deterrent to conspecific females. Benzaldehyde and five terpenes, namely carvacrol, eugenol, nerolidol, phytol and thymol, identified from the larval frass, were shown to be oviposition-deterring components in naturally occurring concentrations. Moreover, the chemicals have a synergistic effect because removal of any one from the mixture results in a loss of the activity. These bioactive terpenes are likely derived from the diet and not synthesized by the larvae (Anderson et al. 1993). Methanol extracts of larval frass of *Ostrinia nubilalis* deterred conspecific females from oviposition (Dittrick et al. 1983). Li and Ishikawa (2004) identified volatile oviposition-deterring chemicals, namely palmitic, stearic, oleic, linoleic and linolenic acids, in the larval frass of *Ostrinia zealis*, *O. furnacalis*, *O. scapulalis* and *O. latipennis*. In Coleoptera, hexane extracts of larval frass of *Hylotrupes bajulus* influenced the behaviour of both sexes in a wind tunnel bioassay (Fettköther et al. 2000). Ipsenol, ipsdienol and *cis*-verbenol were isolated from male-produced frass of the bark beetle, *Ips confuses*, and attracted males and females in a laboratory olfactometer (Birch et al. 1977).

The pine sawyer, *Monochamus alternatus* Hope, transmits the pinewood nematode, *Bursaphelenchus xylophilus* (Steiner et Buhrer) Nickle, which causes a wilt disease of *Pinus densiflora* Sieb. et Zucc. and *P. thunbergii* Parl. in Japan (Kiyohara and Tokushige 1971; Mamiya and Enda 1972; Morimoto and Iwasaki 1972). In a pine forest infested with pine wilt disease, *M. alternatus* females deposit their eggs on pine trees killed recently by the disease. The next year, adult beetles infective with nematodes emerge from the dead trees, disperse, and transmit the nematodes to healthy trees (Anbutsu and Togashi 2001), and the intrusion cycle is completed. The destructive pinewood nematode was introduced into China in 1982 (Hu et al. 1997). Now, this nematode is distributed widely in Anhui Province, Guangdong Province, Jiangsu Province, Zhejiang Province and Shandong Province and causes considerable mortality of *P. massoniana*. *Monochamus alternatus* is a primary vector of the nematode. Thus, the management of this beetle may be the most effective way to control the

nematode. There are many studies on integrated pest management of *M. alternatus*, including biological control (Shimazu 1994; Shimazu and Sato 2003), insecticide application (Togashi 1990) and attractants control (Ikeda et al. 1980).

Anbutsu and Togashi (2002) demonstrated that larval frass and methanol extract of larval frass of *M. alternatus* deterred females from oviposition. But, the chemical identification of oviposition deterrents was not reported. This paper reports our work on the oviposition-deterring activity of larval frass and identification of the active compounds.

2 Materials and Methods

2.1 Insect source

An experimental colony of *M. alternatus* was established from insects collected on Jingting Mountain, Xuancheng, Anhui Province, China. According to gender, newly emerged adults were reared individually in iron-screened cages (50 cm length × 40 cm width × 30 cm high) on 1–2-year-old *P. massoniana* twigs at 25°C and under a 12L : 12D photoregime. Two weeks later, females and males were paired. Based on our observation, the females oviposited regularly 18 days after emergence. So, we chose females aged 18–25 days in the oviposition tests. To keep normal physiological condition as in pine forest, the adult females were allowed to oviposit before being used in oviposition tests (Anbutsu and Togashi 2001, 2002).

2.2 Larval frass

Larval frass of *M. alternatus* was collected from dead, infested *P. massoniana* on Jingting Mountain, Xuancheng, Anhui Province. After removing as much wooden fibre as possible, the larval frass was dipped in hexane for 48 h and then filtrated. The extract was concentrated to an equivalent of 1 g of larval frass per 1 ml of extract and stored at −20°C until used in the bioassay. In Gas chromatography–mass spectrometry (GC–MS) analysis, one millilitre of extract of larval frass was slowly concentrated to 100 μl under a constant stream of N_2, containing 1 ng/μl dodecane as internal standard (dodecane, 98%; Shanghai Chemical Reagent Co. Ltd, Shanghai, China).

2.3 Choice oviposition tests

The trunks of 10 healthy specimens of 8–10-year-old *P. massoniana* were cut into 15-cm lengths, hereafter termed pine bolts, without nodes on 12 May, 2004. The cut ends of the pine bolts were then sealed with liquid paraffin (melting point: 56–58°C) and stored in sealed black plastic bags at room temperature until used in oviposition tests. The bolts were 3.8–4.7 cm in diameter (mean ± SE = 4.2 ± 0.1 cm) and had a bark thickness of 1.2–2.3 mm (mean ± SE = 1.7 ± 0.1 mm).

For each test, two pine bolts similar in diameter and bark thickness were selected. One millilitre hexane extract of larval frass was applied to the bark surface of one of the two bolts using the tip of a calligraphy brush. The second bolt was treated with 1 ml hexane as a control. The treated and control bolts were then placed vertically in an iron-screened cage (20 cm length × 20 cm width × 20 cm high), each about 3.0 cm from the inner wall of the container and about 14.0 cm apart. Two 1–2-year-old *P. massoniana* twigs were then placed in the centre of each cage as food. One gravid female *M. alternatus* was then placed on the *P. massoniana* twigs at the onset of dusk. The beetle was removed 48 h later and the number of oviposition scars and eggs were counted. This test was replicated 20 times, each time using a different gravid female aged 18–25 days. The choice oviposition tests were designed to find out if gravid females had oviposition preferences between frass-treated and control bolts.

2.4 No-choice oviposition tests

No-choice oviposition tests were carried out to ascertain if gravid females oviposited when offered only treated bolts. Another reason for designing these tests was that the results of no-choice oviposition tests were even more in accord with the field results when oviposition deterrent was applied in a forest. The length of the pine bolts in these tests was the same as in the choice oviposition tests and they were 2.1–3.6 cm (mean ± SE = 2.9 ± 0.1 cm) in diameter and had a bark thickness of 1.0–1.5 mm (mean ± SE = 1.3 ± 0.1 mm). This experiment was conducted in the same manner as the choice experiment except that one treated or one control bolt was placed in the centre of the cage.

2.5 GC/MS analysis of extract of larval frass

Gas chromatography–mass spectrometry was conducted on a Hewlett-Packard (HP) 6890 GC interfaced with a HP 5793 mass selective detector (Hewlett-Packard, Little Falls, USA). A DB-5 ms capillary column (60 m × 0.25 mm i.d.; J&W Scientific, Palo Alto, CA, USA) was maintained at 50°C for 2 min after injection and then programmed to 200°C at 5°C/min, and held for 5 min. Nitrogen was used as carrier gas at 1 ml/min linear velocity. The injector was operated in the split mode (split ratio 50.0 : 1) and the injector temperature was 250°C. Compounds were identified by matching their mass spectra with those in the NIST Library and further verified by comparison of the diagnostic ions and the GC retention time with those of the respective authentic standard. The quantity of each compound was calculated on the basis of the peak area and calibrated by comparing it with that of dodecane.

2.6 Determination of the deterrent activity of the identified compounds

To confirm the deterrent effect of the compounds identified in larval frass, synthetic chemicals (listed in Table 1) were mixed in a similar ratio to that in larval frass, dissolved in analytical pure hexane and then applied to pine bolts in choice oviposition tests. The bolts were 15.0-cm long, 2.9–4.2 cm in diameter (mean ± SE = 3.6 ± 0.1 cm) and had a bark thickness of 1.0–2.0 mm (mean ± SE = 1.6 ± 0.1 mm). In each of 20 tests, two pine bolts, one treated with 1 ml of synthetic mixture and the other with 1 ml of analytical pure hexane as a control, were placed vertically in an iron-screened cage as in the choice oviposition tests. Each test lasted 48 h, and the numbers of oviposition scars and eggs were then recorded.

2.7 Data analysis

Data from tests were subjected to statistical analysis using the SPSS 11.0 for Windows software. Scheffe's test of the analysis of variance (ANOVA) was used to compare the mean numbers of eggs and scars between treatments and controls.

Table 1. *Oviposition response of* Monochamus alternatus *females to the tested synthetic mixtures. The amount used (μg/20 ml hexane) of each compound in each mixture is listed after the compound*

Compound[1]	Synthetic mixture no. SM1	SM2	SM3
Terpenes			
α-Pinene (27.6)	+	+	
β-Pinene (10.4)	+	+	
3-Carene (2.6)	+	+	
Limonene (3.5)	+	+	
Longifolene (4.4)	+	+	
Hydroxybenzene			
Butylated hydroxytoluene (43.2)	+		+
Deterrent activity			
Test (% of scar number)	39.76	46.55	46.20
Control (% of scar number)	60.24	53.45	53.80
n = total number of scars	166	174	171
Significance	*	NS	NS
Test (% of egg number)	37.76	47.56	47.47
Control (% of egg number)	62.24	52.44	52.53
n = total number of eggs	143	164	158
Significance	*	NS	NS

[1]Source and purity of compounds. α-pinene (98%), limonene (92%), butylated hydroxytoluene (≥99.8%), NJ, USA; β-pinene (>95%), 3-carene (>90%), Tokyo Kasei Kogyo Co. Ltd, Toshima, Japan; longifolene (≥99%), Sigma-Aldrich Chemie, Steinheim, Product of Switzerland. *Significant difference at $P < 0.05$. NS: not significant difference.

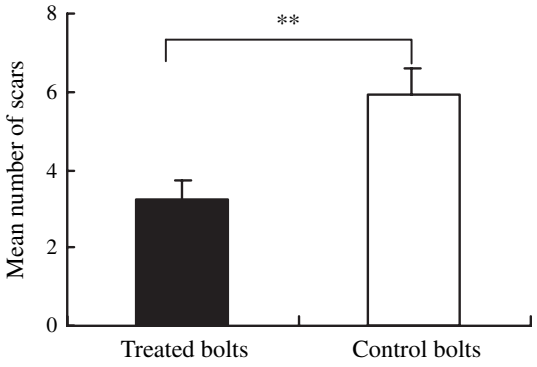

Fig. 1. *Number of scars in choice oviposition tests. Column shows mean number of excavated oviposition scars*

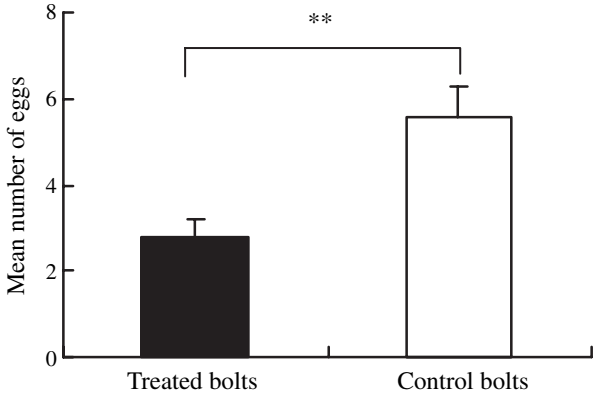

Fig. 2. *Number of eggs in choice oviposition tests. Column shows mean number of eggs*

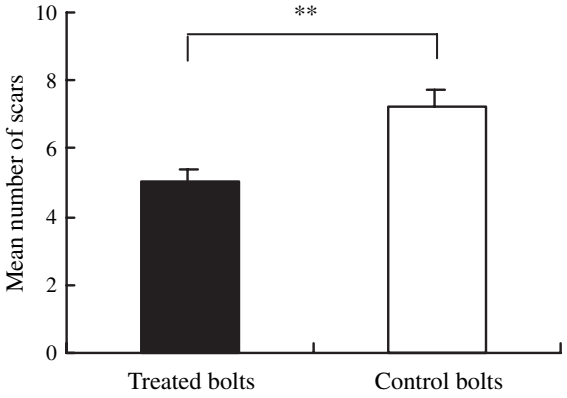

Fig. 3. *Number of scars in no-choice oviposition tests. Column shows mean number of excavated oviposition scars*

3 Results

3.1 Influence of hexane extracts of larval frass on the oviposition behaviour of female adults

During the 48 h choice oviposition tests, the females excavated fewer scars on the treated bolts than on control bolts, showing a significant difference ($F = 9.974$, $P = 0.003$) (fig. 1). The number of eggs deposited on treated bolts was also significantly less than on untreated bolts ($F = 12.013$, $P = 0.001$) (fig. 2). The results suggest the *M. alternatus* females preferred the untreated control bolts to the extract-treated bolts for oviposition.

The number of scars excavated by *M. alternatus* females on the bolts treated with hexane extracts of larval frass was also significantly less than on control bolts ($F = 10.833$, $P = 0.002$) in the no-choice oviposition test (fig. 3). The mean number of eggs deposited by each female was significantly less on the treated bolts than on the control bolts ($F = 13.667$, $P = 0.001$) (fig. 4).

The results of the choice and no-choice oviposition tests indicate the existence of a hexane-soluble oviposition deterrent in the larval frass of *M. alternatus*.

3.2 Chemical identification of oviposition deterrent chemicals in larval frass

The GC profile of the volatile from hexane extracts of larval frass included six major peaks (fig. 5). These peaks appeared, respectively, at 12.94, 14.44, 15.39, 16.05, 27.65 and 29.65 min. These compounds were analysed with the GC–MS system and were found to be α-pinene, β-pinene, 3-carene, limonene, longifolene and butylated hydroxytoluene. The relative percentage of each of these compounds identified in larval frass were 23.59%, 9.30%, 2.09%, 2.79%, 5.73% and 56.51%. The amount of each of these compounds in 1 g larval frass was 1.38, 0.52, 0.13, 0.18, 0.22 and 2.16 μg/g, respectively.

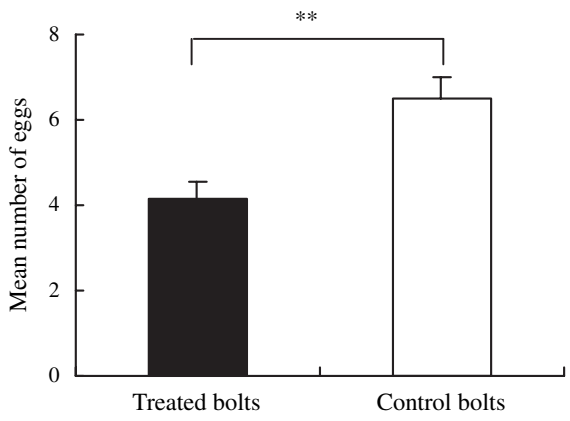

Fig. 4. *Number of eggs in no-choice oviposition tests. Column shows mean number of eggs*

3.3 Oviposition-deterring activity of identified compounds

A mixture of synthetic compounds identified in larval frass (synthetic mixture SM1) was tested and exhibited significant deterrent activity to oviposition. Gravid females excavated 60.2% fewer scars and deposited 62.2% fewer eggs on mixture-treated bolts than on untreated bolts. Two other mixtures, 5 monoterpenes (SM2) and butylated hydroxytoluene (SM3) did not show the oviposition-deterring activity (Table 1).

4 Discussion

When resource competition or cannibalism is likely, spacing mechanisms whereby females can recognize the unsuitability of potential oviposition sites may evolve to avoid conspecific overloads of eggs or larvae on a host. Avoidance of occupied hosts is typically mediated by cues and/or signals associated with eggs and larvae (Nufio and Papaj 2001). Females of a variety of species detect the presence of conspecific brood on the basis of visual or tactile stimuli associated with eggs and adjust allocation of eggs accordingly (Williams and Gilbert 1981; Li et al. 2001). Several examples are known where the insects themselves deposit a pheromone with their eggs, whose action is to reduce the likelihood of other females of that species laying eggs nearby (Averill and Prokopy 1987; Messina et al. 1987). For some phytophagous insects, larval frass deters oviposition on infested hosts. The deterrent effects of larval frass have been verified in some species of insects, including pineapple borer *Thecla basilides* (Rhainds et al. 1996), Egyptian cotton leaf worm *S. littoralis* (Anderson et al. 1993) and yellow cutworm *Agrotis segetum* (Anderson and Lofqvist 1996). These deterrent compounds in larval frass are either unaltered plant constituents or actively produced by larvae (Mitchell and Heath 1985; Hilker and Klein 1989).

Shibata (1984) reported that the spatial distribution patterns of oviposition scars, eggs, larvae, larval mines and emergence holes of *M. alternatus* were uniform. Therefore, this mechanism may have its biological significance in maximizing reproductive success. *Monochamus alternatus* females prefer dead pine trees or pine trees felled by man or inoculated with the pinewood nematode for oviposition (Ikeda et al. 1980). For oviposition, an adult female searches for a suitable site on the bark. After finding such a site, the female gnaws at the bark surface with her mandibles to make a wound and then inserts her ovipositor into the bark to deposit eggs. The female then plugs the hole of the oviposition scar with a jelly-like secretion and rubs the scar with the abdominal tip as soon as it withdraws its ovipositor. The jelly-like secretion, which contains deterrent chemical(s), originates from the spermathecal gland. Methanol extracts of the jelly-like secretion and of the female reproductive organ deter adult females from oviposition (Anbutsu and Togashi 2001). Larval frass and methanol extracts of larval frass also deter adult females from oviposition (Anbutsu and Togashi 2002).

In our study, *M. alternatus* females were deterred from oviposition by a hexane extract of larval frass in choice and no-choice oviposition tests. These results indicate the existence of a hexane-soluble oviposition deterrent in larval frass of *M. alternatus*. We have identified α-pinene, β-pinene, 3-carene, limonene, longifolene and butylated hydroxytoluene in larval frass by GC–MS. The results of experiments with synthetic mixtures showed that oviposition deterrence was elicited by a mixture of 5 monoterpenes and butylated hydroxytoluene in a similar ratio to that found in larval frass. It is possible that other mixtures of the six compounds in SM1 would elicit stronger oviposition

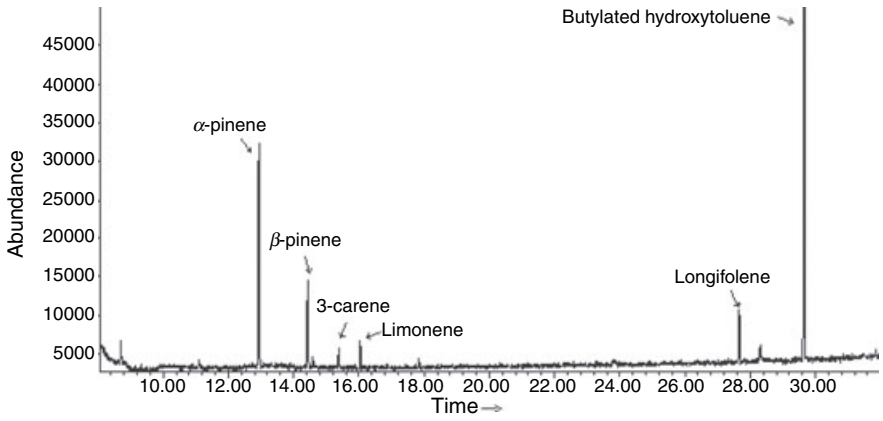

Fig. 5. *Gas chromatogram of hexane extract of larval frass*

deterrence, as only a limited number of the possible combinations of the compounds were tested. The origin of the oviposition-deterring compounds in larval frass is unclear. Possibly the 5 monoterpenes originate from the release of plant compounds associated with damage caused by oviposition or by tissue destruction when larvae feed (Landolt 1993), and are then adsorbed by larval frass. Butylated hydroxytoluene may come from the host plant and may be concentrated by larvae as semiochemical. Mitchell and Heath (1985) reported that a few deterrent compounds were unaltered plant constituents, and not metabolic by-products.

Oviposition deterrents are important in pest control. Katsoyannos and Boller (1976) reported their successful application of oviposition deterrent in the field to prevent infestation of tephritid flies on its host. The application of oviposition deterrents of *M. alternatus* to pine trees killed recently by pine wilt disease may deter *M. alternatus* females from ovipositing on such trees, resulting in a decrease in the beetle population and a reduced spread of the destructive nematodes.

Further studies, especially in the field of application of these chemicals, may elucidate the chemical and behavioural mechanisms underlying the egg distribution of *M. alternatus*, and may also contribute to better management of field populations.

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