Host location by adult and larval codling moth and the potential for its disruption by the application of kairomones

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Abstract

Many fruit boring insect pests are difficult to control because of the short time span during which the damaging stage can be targeted before it becomes protected by the host fruit. We investigated the host location behaviour of the codling moth *Cydia pomonella* (L.) (Lepidoptera: Totricidae) to its apple host (*Malus domestica* Mill.) in the laboratory, with a view to the potential for extending the susceptible time span by disrupting the host location behaviour of the insects. We found that apple extract arrested neonate larvae. It also both attracted adult female moths and stimulated oviposition. α-farnesene did not result in these effects to the same degree, suggesting that other components of apple odour are also important in the host location behaviour of this insect. By presenting a source of apple extract alongside an apple host, we examined whether the location of the apple host by larval and adult moths could be disrupted. We found that the application of apple extract could significantly increase the time taken for neonate larvae to locate an apple source. The source of apple extract also competed with the apple host, resulting in fewer eggs being oviposited near the apples. The results suggest that it may be possible to disrupt the host location behaviour of both the neonate larval and adult stage by the application of host kairomones.

Introduction

Many fruit boring insect pests are difficult to control because of the short time span the damaging larval stage is exposed on the surface of their host. Larvae may spend only a few hours locating the host fruit, often using semiochemicals produced by the host to locate it. Such chemicals are termed kairomones (Brown et al., 1970; Nordlund & Lewis, 1976). The larvae then complete their development inside the fruit where they are largely protected from the environment and most control agents. The host location phase is therefore the period when the larvae are most vulnerable and is a critical stage in the lifecycle of these insects.

Codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), is the most important insect pest of apples (*Malus domestica* Mill.) world-wide (Chapman, 1973; Barnes, 1991). It is also a serious pest of many other fruit crops, such as pear and walnut (Barnes, 1991). Adult moths lay eggs singly on foliage close to fruit (Geier, 1963) and so the neonate larvae have to locate and penetrate into the fruit. Larvae typically do this within 2 h of hatching (Geier, 1963) providing only a very short window for control of the damaging stage. Current control is based upon the use of organophosphate insecticides. However, increasing levels of resistance in codling moth (Varela et al., 1993; Knight et al., 1994; Sauphanor et al., 1998) and growing consumer concern about the use of insecticides means that efforts are focusing on ways of reducing dependence on conventional insecticides. The main alternative method is mating disruption, but this can fail to provide adequate control in many situations (Vickers & Rothschild, 1991; Trimble, 1995; Minks, 1996). The development of biopesticides, such as granulosus virus and *Bacillus thuringiensis*, has been hindered by the relatively

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long exposure time that these require and the short time that the larva is susceptible (Cross et al., 1999). If it was possible to extend the larval host location phase this would not only increase the exposure of the larvae to conventional insecticides, but would also make biopesticides more feasible as a control method.

Both the adult and neonate larvae codling moth use kairomones to locate fruit. The main component implicated is (*E, E*)-α-farnesene. This is produced primarily in the peel and wax of apple fruit (Murray et al., 1964; Huelin & Murray, 1966; Boeve et al., 1996). It has been found to act as an attractant to neonate larvae (Sutherland & Hutchins, 1972, 1973; Sutherland et al., 1974; Suski & Sokolowski, 1985; Bradley & Suckling, 1995) and as an attractant and oviposition stimulant to the adult female moths (Wearing & Hutchins, 1973; Sutherland et al., 1974; Hern & Dorn, 1999). In this study, we use simple laboratory bioassays to examine the host location behaviour of the codling moth, with a view to the possibility of disrupting it to control codling moth. We carried out two preliminary experiments to confirm if (*E, E*)-α-farnesene was the compound responsible for host location and thus the best candidate compound for use in disruption. We then investigated whether the number of adult moth or neonate larvae successfully locating a host could be reduced by the application of apple kairomones.

Materials and methods

General methodology

Codling moth larvae were obtained from a laboratory culture at the Horticultural Research International, Wellesbourne, and used to establish a stock culture at University of Southampton. Insects were kept at 24 ± 2 °C under L12:D12 and reared through the larval stage on artificial diet. For the larval experiments, neonate larvae were used within 4 h of hatching and only vigorous larvae were chosen. Prior to the adult experiments, newly emerged females were isolated with two males under L16:D8 for 48 h to allow mating to occur. It was previously established that the time of peak oviposition was between 18:30 h and 22:30 h (D. Gailey, unpubl.), 2 h before and after the onset of the scotophase, and all adult bioassays were carried out during this period using the mated females. The moths were isolated for 24 h following the experiment to confirm that they were ovipositing. Any replicates in which moths were not confirmed to be ovipositing were discarded.

The apples used in these experiments were free of pesticides, were approximately 5 cm in diameter and were of the Granny Smith variety. Apple extracts were prepared by placing 2 × 1 × 0.2 cm pieces of apple peel and flesh in dichloromethane (Sigma) for 48 h. The extract was then filtered and stored at −20 °C until use. (*E, E*)-α-farnesene was synthesized by the Institute of Arable crops Research, Rothamsted. The quantity of (*E, E*)-α-farnesene in the apple extract was estimated by gas chromatography and the synthetic (*E, E*)-α-farnesene diluted to give the same final concentration as in the apple extract ($0.2\ \mu g\ \mu l^{-1}$).

Experiment 1. Arrestment of neonate larvae

Glass Petri dishes 9 cm in diameter were used as bioassay arenas to compare the arrestment effect of apple extract and (*E, E*)-α-farnesene, in order to confirm that (*E, E*)-α-farnesene was the compound responsible for host location by neonate larvae. Dichloromethane solvent was used as the control. Fifty microlitres of the treatment chemical was applied over a 2-cm diameter circle at the centre of the Petri dish. The dish was left for 90 s to allow the solvent to evaporate and five neonate larvae were then placed in the centre of the circle using a fine paintbrush. The number of larvae remaining in the circle was recorded at 0, 0.25, 0.5, 1, 1.5, 2, 3, 4, and 5 min after application. The experiment was replicated 10 times.

Experiment 2. Oviposition and attraction of adult moths

This experiment confirmed the response of mated female moths to five sources: apple, apple, extract (*E, E*)-α-farnesene, pseudoapple, and control solvent. The sources were tested individually in order to establish if either apple extract or (*E, E*)-α-farnesene would result in the same response from the moths as that stimulated by whole apples. The chemical sources were applied in quantities of 50 μl on a rubber septa. The pseudoapple was a plastic sphere approximately the same size (5 cm diameter) as the apples used, and designed also to be of similar colour and texture to the apples. Each source was replicated eight times. Simple bioassay arenas, 45 cm diameter and 11 cm height, were prepared using clear plastic sheets. The walls of the arenas were lined with rough felt to discourage moths from ovipositing there. The arena floor was left smooth and underlaid with nine increasing concentric circles, each 5 cm greater in diameter than the previous one. Sources were placed at the centre of these circles and five mated female moths released into the arena. The number of eggs laid within each circle was recorded 4 h later. Moths were provided with a source of 10% honey water throughout this time.

Experiment 3. Disruption of host location by neonate larvae

The same basic methodology was used as in Experiment 1, but with a 2 × 1 × 0.2 cm piece of apple, with peel, being simultaneously presented for the larvae to locate. The experiment therefore tested if the host location behaviour of neonate larvae was adversely affected by a competitive source of apple kairomones being present. Apple pieces of a similar size have been used in Petri dishes to realistically stimulate host location behaviour by neonate codling moth larvae in many previous studies (Sutherland & Hutchins, 1972, 1973; Sutherland et al., 1974). The apple pieces were placed upright at the edge of the Petri dish and were therefore 3.5 cm from the centres of the application circles. Only apple extract and control solvent were tested because of the poor response elicited by (*E, E*)-α-farnesene in Experiment 1, with each being replicated 10 times. The number of larvae remaining within the circle and the number contacting the apple piece was recorded at 0, 0.25, 0.5, 1, 1.5, 2, and then at 1 min intervals for the remainder of a 10-min period.

Experiment 4. Disruption of host location by adult moths

To examine if apple extract or (*E, E*)-α-farnesene could disrupt the host location behaviour of adult moths, Experiment 2 was repeated but this time exposing the moths to a choice of two sources. This thus examined whether successful host location by the adult moths was reduced when a competitive source of apple kairomones was present. An apple was placed in one half of the arena and a source of either apple extract, (*E, E*)-α-farnesene or a pseudoapple control was placed in the opposite half. The sources were each placed 12.5 cm from the centre of the arena. The number of eggs laid in each half was then recorded after 4 h. Each source combination was replicated six times.

Statistical analysis

All the data were log or log $(x + 1)$ transformed prior to analysis. The effects of treatment on the numbers of larvae remaining in the application circles or in contact with the apple pieces were analysed using a repeated measures analysis of variance (ANOVA). The numbers of eggs laid in the second experiment and the distances that they were laid from the source were compared using a two-way ANOVA. In the fourth experiment, the total numbers of eggs laid in the apple halves of the arenas were examined with a one-way ANOVA and the oviposition in each pair of treatments was also compared with paired-sample *t*-tests.

Results

Experiment 1. Arrestment of neonate larvae

Larvae took significantly longer to leave the application circles treated with apple extract or (*E, E*)-α-farnesene when compared to solvent controls ($F_{16,216} = 5.99$, $P < 0.001$) (Figure 1). Almost all larvae left the control circles within the first minute of the experiment while an average of 2.5 ± 0.6 larvae still remained in the apple extract circles 5 min after application. Many of these larvae were seen to bite the base of the dish as though attempting to burrow into it. Although (*E, E*)-α-farnesene did increase the length of time for larvae to leave the circles the effect was minimal and much weaker than that caused by apple extract (Figure 1).

Experiment 2. Oviposition and attraction of adult moths

There was a significant effect of treatment both on the total number of eggs laid ($F_{4,35} = 51.1$, $P < 0.001$) and the position they were laid ($F_{32,315} = 4.70$, $P < 0.001$). The greatest numbers of eggs were laid when apples or apple extract were present (Figure 2). The number of eggs laid in the (*E, E*)-α-farnesene treatment was much lower, although still higher than when pseudoapples or controls were tested. In both the apple and apple extract treatments, a large majority of eggs were laid within 5 cm of the source

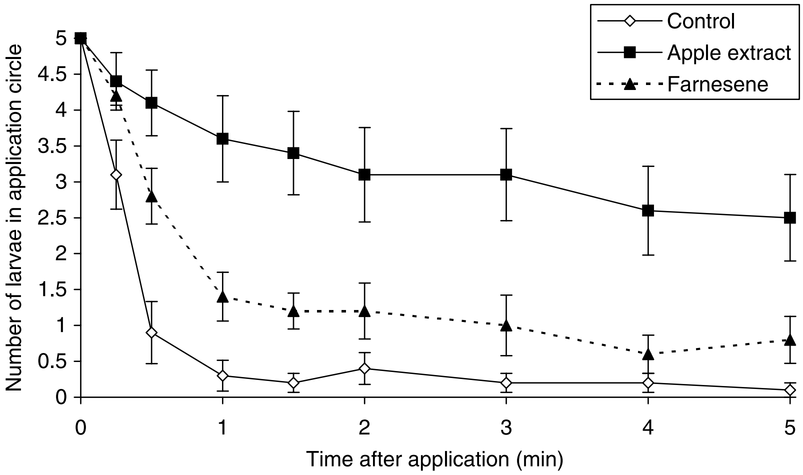


Figure 1 Mean (± SE) arrestment of neonate codling moth larvae placed in 2-cm diameter application circles in Experiment 1. Application circles were treated with either (*E, E*)-α-farnesene, apple extract, or dichloromethane control (n = 10). Larvae were applied in groups of five individuals.

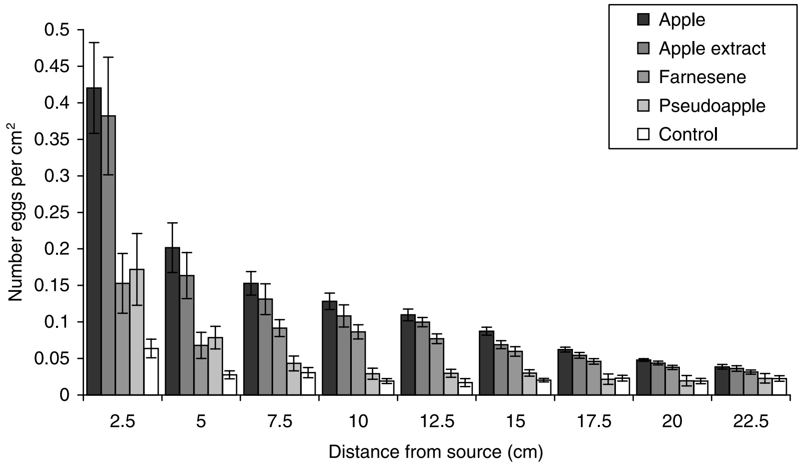


Figure 2 Mean (± SE) number of eggs laid by adult, mated female codling moths at various distances from attractant sources in Experiment 2. Sources were either an apple, a pseudoapple (plastic sphere) (*E, E*)-α-farnesene, apple extract or dichlormethane solvent (control) (n = 8). Moths were released into arenas in groups of five individuals.

while in the (*E, E*)-α-farnesene treatment and the controls this trend was less evident (Figure 2).

Experiment 3. Disruption of host location by neonate larvae

As in Experiment 1, larvae were significantly slower to leave the apple extract treated circles ($F_{13,234} = 11.7$, $P < 0.001$) (Figure 3). As a consequence, significantly fewer larvae located the apple piece within the 10-min experimental period when apple extract had been applied in the Petri dish than when the solvent control was applied ($F_{13,34} = 8.60$, $P < 0.001$).

Experiment 4. Disruption of host location by adult moths

Treatment significantly affected the number of eggs laid in the half of the arena containing the apple ($F_{2,25} = 28.3$, $P < 0.001$). Far fewer eggs were laid near the apples when a source of apple extract or (*E, E*)-α-farnesene was present in the arena than in the controls when no competitive source of apple kairomones was present (Figure 4). In the controls the majority of eggs laid were in the apple half (t = 11.2, d.f. = 5, $P < 0.001$). The proportion of total eggs laid that were in the apple half of the arena was lower in the (*E, E*)-α-farnesene replicates but still significantly greater than in the (*E, E*)-α-farnesene half of the arena (t = 4.55, d.f. = 5, P = 0.006). In the apple extract treatment, however, oviposition took place approximately equally in each half of the arena (t = 0.894, d.f. = 5, P = 0.412) with the moths appearing less able to successfully locate the apple host than in the other combinations.

Discussion

Both the larvae and adults of codling moth are well known to use kairomones in host location. Neonate larvae are attracted to apples from 1.5 cm in still air (Sutherland, 1972) and greater distances with airflow (Landolt et al., 1998, 2000). Mated adult female moths are stimulated to oviposit and also attracted by volatile components

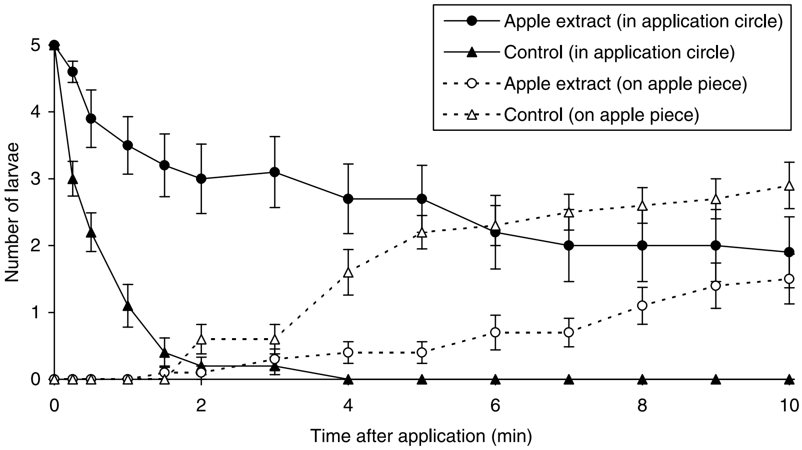
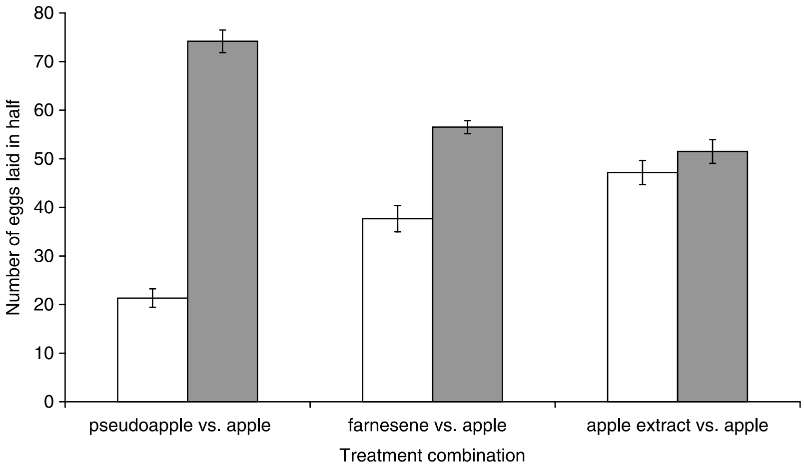


Figure 3 Disruption of host location by neonate codling moth larvae in Experiment 3. Larvae were placed in application circles treated with either apple extract or dichloromethane solvent (control) (n = 10), as in Experiment 1, but were simultaneously presented with an apple piece 3.5 cm outside the application circle to locate. Solid lines show the mean (± SE) number of larvae remaining in the application circles and dashed lines show the mean (± SE) number of larvae that had left the application circles and were in contact with the apple piece. Larvae were applied in groups of five individuals.

Figure 4 Disruption of host location by adult, mated female codling moths in Experiment 4. Moths were simultaneously presented with an apple host and a competitive source of either apple extract, (*E, E*)-α-farnesene, or a pseudoapple control (n = 6). Mean (± SE) numbers of eggs laid in either the apple half or the half containing the competitive source. Moths were released into the arenas in groups of five individuals.



produced by apples (Wearing et al., 1973; Yan et al., 1999). Here we found that apple extracts accurately reproduced these effects. Larvae placed on a source of apple extract were slow to leave it and in fact were often seen to attempt to burrow into the substrate. Mated female moths laid more eggs when presented with a source of apple extract. They also appeared to be attracted by apple extract, with the majority of eggs being laid within 5 cm of the source. This is a similar distance to that observed under natural conditions (Geier, 1963).

It has been found that a single hydrocarbon component of apple odour (*E, E*)-α-farnesene, can produce the same level of attraction from neonate larvae as apple pieces (Sutherland & Hutchins, 1972; Sutherland et al., 1974; Suski & Sokolowski, 1985; Bradley & Suckling, 1995). The results of Experiment 1, however, suggest that (*E, E*)-α-farnesene is not the only behaviourally active component. While larvae were strongly arrested by apple extract, (*E, E*)-α-farnesene produced only a slight effect. Most previous studies have involved larvae being attracted to the source from a distance (Sutherland & Hutchins, 1972; Sutherland et al., 1974; Suski & Sokolowski, 1985; Bradley & Suckling, 1995). It may therefore be the case that while (*E, E*)-α-farnesene acts as an attractant to neonate larvae, other compounds present in apple extracts are necessary to cause arrestment or to stimulate biting.

(*E, E*)-α-farnesene has also been found to stimulate oviposition and attraction in mated adult female moths (Wearing & Hutchins, 1973; Sutherland et al., 1974; Hern & Dorn, 1999). While it did result in more eggs being laid than in the controls in Experiment 2, the number laid was substantially lower than that associated with whole apples or apple extracts. The attractant effect also appeared to be lower. It appears that other apple kairomones may also be involved in host location and oviposition by adult moths. Our results suggest that the chemical ecology of host location by both adult and larval codling moths is more complex than was previously thought and that a re-examination may be warranted. This is further supported by several recent studies in which the apple volatiles hexyl hexanoate (Hern & Dorn, 2001) and methyl (2*E*, 4*Z*)-2,4-decadienoate (Knight & Light, 2001) were found to be highly attractive to neonate codling moth larvae, while ethyl (2*E*, 4*Z*)-2,4-decadienoate was highly attractive to both larvae and adult moths (Light et al., 2001).

The results have important implications for the control of codling moth. We found that the presentation of apple extract together with an apple host resulted in fewer eggs being oviposited near the apple than when the apple was presented alone. It appears that the apple extract volatiles either confused the female moths, making it harder for them to locate the apple, or caused them to treat the source of apple extract as an actual apple host. A similar effect results from the presentation of host volatiles to female moths of the navel orangeworm and has been found to reduce oviposition on the almond host of this pest in the field (Foster & Harris, 1997). The presentation of apple extract has the potential to achieve the same effect on codling moth. In addition, we found that the presence of apple extract significantly increased the time taken for neonate larvae to locate an apple piece. This may provide a second mechanism by which the application of apple kairomones can act as an effective control method. The survival of neonate larvae decreases rapidly with time exposed to normal environmental conditions (Jackson & Harwood, 1980). Larvae move slower as they age (W. O. H. Hughes, unpublished data) and so are decreasingly likely to locate a host fruit as posthatching time increases. In addition, mortality due to both biopesticides such as codling moth granulosus virus (Ballard et al., 2000) and conventional insecticides increases with time spent on the treated surface.

Much further work is needed to establish if these effects can be replicated under more realistic conditions and to identify the mixture of compounds that can best produce the effects. It seems certain from the results of previous work that (*E, E*)-α-farnesene plays a significant role. The data presented here, however, together with that in other recent studies (Hern & Dorn, 2001; Knight & Light, 2001; Light et al., 2001), suggests that other components may also be important. If the questions of formulation and application can be resolved, then an effective mixture has the potential to provide a useful and environmentally friendly method of codling moth control, either in itself or as an adjuvant to conventional insecticides or biopesticides. The technique of host location disruption through the application of host kairomones may also prove to be useful in the control of many other economically important insect pests.

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