

Dropping behaviour in *Aulacorthum solani* (Hemiptera: Aphididae) following attack by *Aphidius ervi* (Hymenoptera: Braconidae): are sticky stem bands a useful integrated pest management method?

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Abstract—We studied the dropping behaviour of the foxglove aphid, *Aulacorthum solani* (Kaltenbach) (Hemiptera: Aphididae), in response to disturbance by the parasitoid *Aphidius ervi* Haliday (Hymenoptera: Braconidae). We banded plant stems with sticky tape to prevent aphids from returning to the plants to determine if these would serve as an integrated pest management strategy for *A. solani*. Stem banding prevented *A. solani* that had dropped from returning to the plant; but the mortality associated with banding was not necessarily complementary to biological control by *A. ervi*. Up to 80% of aphids dropped in response to foraging by *A. ervi*, and thus could be killed on sticky stem bands. The fraction of aphids that dropped to the ground also contained as much as 90% of the parasitoid's offspring. Overall, mortality of aphids on sticky stem bands was not compatible with parasitoids. Although numbers of aphids declined more rapidly in the first 2 weeks of the trial in the presence of stem bands and parasitoids than in the presence of parasitoids alone, the numbers of aphids were identical in the two treatments from the 3rd week onward. Mortality on the stem bands replaced mortality from parasitoids, and reduced recruitment of parasitoids.

Résumé—Nous étudions le comportement par lequel le puceron de la digitale, *Aulacorthum solani* (Kaltenbach) (Hemiptera: Aphididae), se laisse choir au sol en réaction à la perturbation causée par le parasitoïde *Aphidius ervi* Haliday (Hymenoptera: Braconidae). Nous avons entouré des tiges de plantes d'une bande de ruban à dos adhésif pour empêcher les pucerons de retourner sur les plantes afin d'évaluer si cette méthode pouvait servir de stratégie de lutte intégrée (IPM) contre *A. solani*. Les bandes sur les tiges empêchent les *A. solani* qui se sont laissés tomber de retourner sur le plant; mais la mortalité associée à la pose des bandes n'est pas nécessairement complémentaire au contrôle démographique exercé par *Aphidius ervi*. Jusqu'à 80% des pucerons se laissent tomber au sol en réaction aux *A. ervi* en recherche de proies et peuvent ainsi être tués sur les bandes à dos adhésif sur les tiges. La fraction des pucerons qui tombent au sol contient aussi jusqu'à 90% des rejetons des parasitoïdes. En gros, la mortalité des pucerons sur les bandes à dos adhésif sur les tiges n'est pas compatible avec les parasitoïdes. Bien que le nombre de pucerons diminue plus rapidement durant les deux premières semaines de l'essai en la présence conjointe de bandes sur les tiges et de parasitoïdes qu'en présence des parasitoïdes seuls, les nombres de pucerons sont identiques dans les deux situations à partir de la troisième semaine. La mortalité sur les bandes à dos adhésif remplace la mortalité due aux parasitoïdes et réduit le recrutement des parasitoïdes.

Introduction

The foxglove aphid, *Aulacorthum solani* (Kaltenbach) (Hemiptera: Aphididae), is a damaging

pest of greenhouse pepper crops. A number of parasitoid and predator species are used for biological control of this pest (Rabasse and van Steenis 1999; Blümel 2004). The foxglove aphid

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is, however, still considered difficult to control by greenhouse growers. All stages of the foxglove aphid readily drop from plants and otherwise disperse when approached by parasitoids or predators. This provides opportunities for the aphid to escape predators and parasitoids, and leads to the spread of injury in crops (Henry *et al.* 2010).

Dropping behaviour in aphids has been widely studied as an antipredator response (Nault *et al.* 1976; Roitberg and Myers 1978; Dill *et al.* 1990; Stadler *et al.* 1994; Andrade and Roitberg 1995; Chau and Mackauer 1997; Losey and Denno 1998a, 1998b). Dropping from the leaf removes the aphid from the threat of predation on the plant but exposes the aphid to the risk of starvation, desiccation, and predation on the soil surface (Nault 1973; Roitberg and Myers 1978; Dill *et al.* 1990; Losey and Denno 1998a). In greenhouse horticulture, the natural enemies that are released against aphids forage on plant surfaces. No generalist predators that could prey on aphids are deliberately released on the floor of the greenhouse and our experience is that generalist predators such as ground beetles (Coleoptera: Carabidae) and larger rove beetles (Coleoptera: Staphylinidae) are generally not present in greenhouses. In the absence of mortality sources on the floor of the greenhouse, and assuming foxglove aphids can readily return to plants, dropping behaviour could disrupt biological control by providing the aphids with a refuge from predation and parasitism that takes place on the plant foliage. This refuge might be the basis of growers' difficulties with control of foxglove aphids. Adding a source of mortality on the floor of the greenhouse might complement the mortality from natural enemies foraging on the plant. If, however, the proportion of the parasitoid population is greater in aphids that drop from leaves than in aphids that remain, then the population dynamics of the aphid may benefit in the long term. Deliberately introducing large, generalist, ground-dwelling predators into greenhouse crops for aphid control is problematic. The floor of most commercial greenhouses is generally covered with plastic or concrete, and does not offer much shelter or alternative prey. Predator refuges such as "beetlebanks" (Collins *et al.* 2002) might provide the former, but alternative prey to maintain such predator populations

might be difficult and expensive to maintain, and polyphagy would likely interfere with the intended effect (Prasad and Snyder 2006). However, simply preventing aphids from returning to plants once they have dropped would have the same effect on population dynamics as predation, since these aphids will die either from desiccation or starvation. Devices that interfere with aphids climbing stems, such as sticky stem bands could therefore serve as a surrogate for predation in greenhouse environments, without the potential complications.

We studied the dropping behaviour of *A. solani* in response to disturbance by the parasitoid *Aphidius ervi* Haliday (Hymenoptera: Braconidae). We banded plant stems with sticky tape – which prevented aphids from returning to the plants – to simulate mortality from ground-dwelling predators. Our objectives were first to determine if adding a source of mortality on the floor of greenhouses would reduce reproduction and recruitment of foxglove aphids, second to determine if mortality from dropping has the potential to interfere with the impacts of the parasitoid on aphid populations, and third to test the efficacy of stem banding to prevent dropped aphids returning to the plant, as an integrated pest management (IPM) strategy for *A. solani*.

Materials and methods

Insect rearing

Pepper plants, cultivar Bell Boy (Stokes Seeds Inc., Thorold, Ontario, Canada) were grown from seed on greenhouse benches, isolated from aphid infestations. These plants were used for maintenance of aphid and parasitoid colonies, and for most experiments. Plants were grown at 20°C, in a soilless mixture (peat and perlite) and were watered daily, or more frequently with a 1% solution (W/V) of 20-20-20 water soluble fertiliser. Lighting was supplemented with 400 W HpS lamps to provide a 16-hour day in the greenhouse compartment.

Foxglove aphids were originally isolated from greenhouse pepper plants, *Capsicum annuum* Linnaeus (Solanaceae) in a commercial greenhouse. They were maintained in small cages on excised pepper leaves in an insectary room at ~23°C, with a 16-hour day provided by fluorescent lamps. Small leaf pieces with aphids were transferred to fresh excised leaves in small

cages, twice per week. Aphids from these stock cages were used to produce aphids for experiments, and to rear parasitoids. Aphids of uniform ages were produced by transferring 10 adult aphids onto an excised pepper leaf in a small cage, and allowing them to produce offspring for 24 hours. The adults were then removed and the offspring held in the small cages until they reached the desired age.

Parasitoids were maintained in small cages on excised leaves in an insectary room separate from aphids, at 21°C, with a 16-hour day. Adult females and males were released into small cages containing an abundance of aphids of mixed ages for 24 hours, and then transferred to new cages. As adults from these small cages emerged, individuals were transferred to holding cages for 24–48 hours, and provided with water and 5% sugar solution. These individuals were either used to continue colonies, or for experiments. Colonies of *A. ervi* were established from stock material provided by Koppert Canada (Leamington, Ontario, Canada).

Host location by foxglove aphid after dropping

We determined the ability of foxglove aphids of different ages, to relocate plants after they had dropped in response to disturbance from parasitoids. We used arenas consisting of trays (34 × 46 × 10 cm) filled with a bedding plant mix (peat and perlite), with a 6-week-old pepper plant (~17 cm high) planted in the centre. The lower leaves of plants were removed so that no leaf touched the arena surface. The experiment was conducted with 3-day-old, 5-day-old, and 7-day-old foxglove aphids. These aphids represented, at our rearing temperatures, roughly second-instar, fourth-instar, and adult aphids. Ten aphids of the same age were placed on the upper leaves of pepper plant and allowed to settle for 30 minutes. Experienced *A. ervi* females, 24–48 hours old and reared on foxglove aphids, were introduced onto pepper plants by allowing them to walk onto the plants from release vials. The foxglove aphids were observed continuously during the experiment, until they regained the plant, left the arena, or 60 minutes had passed. We only observed aphids that were attacked, and recorded whether these aphids dropped from, or walked off the plant in response to disturbance.

We also recorded either the distance that they fell from the base of the stem, or for aphids that walked from the plant, the maximum distance that they walked away from the stem. We determined if individual aphids relocated the host plant after dropping or leaving, and the time for dropped aphids and aphids that walked off plant to return to the stem of the plant. Data were analysed by either logistic regression (analysis of response to disturbance, and the likelihood of relocating the plant), least-squares analysis of variance (ANOVA) (distance travelled by aphid), or by survival analysis (non-parametric cumulative hazard function, time taken to return). All analyses were performed in Systat 9.0 (Systat Software Inc., Chicago, Illinois, United States of America).

Fate of parasitoid offspring following dropping of foxglove aphids

We investigated the effects of aphid population density and age on the fate of parasitoid offspring deposited in foxglove aphids following a foraging bout by female *A. ervi*, in cages on a greenhouse bench. We wanted to determine if the parasitism rate among aphids that dropped from plants was greater than among those that remained on leaves. Foxglove aphids aged 2, 5, and 8 days old, at densities of 20, 40, and 60 per leaf, were used. Aphids were placed on an excised pepper leaf, ~50 cm². The petiole of the leaf was immersed in water, through a 3 mm hole in the lid of a 16 dram vial. The vial was placed in the centre of a white, 22.9 cm Styrofoam plate in an insect cage (60 cm³). Both the vial and styrofoam plate were coated with aqueous polytetrafluoroethylene (Fluon[®] AD 1, ICI Fluoropolymers, Wilmington, Delaware, United States of America) to prevent fallen aphids from climbing back onto the leaf or walking off the Styrofoam plate.

Mated, inexperienced females, 24–48 hours old, were used for the experiment. A female parasitoid was introduced into each cage by allowing her to walk out of a collection vial onto the leaf surface. After 1 hour, aphids that had dropped, and those that remained on leaves, were counted and reared on separate leaves in a Styrofoam rearing cup at 22°C. Mummies formed from dropped aphids and aphids on leaves were counted. The experiment was repeated from 12 to 15 times for different combinations of age and density of aphids.

Our questions from this experiment were twofold. Firstly, what fractions of a female parasitoid's offspring fell from the plant and were therefore vulnerable to mortality, or remained on the plant? Secondly, what was the relative proportion of mortality from parasitism in the two fractions of the aphid population, and was this a function of aphid age and population density? We determined if age or density of aphids affected the proportion of aphids that dropped using a simple, one-way least-squares ANOVA on untransformed proportions that dropped. The purpose was not to perform a rigorous analysis of a well-known effect, but simply to check that the underlying theory (Dill *et al.* 1990; McAllister *et al.* 1990) was relevant in this system. We then determined if age of the aphid host affected the numbers of parasitoid offspring that dropped to the ground or remained on the plant. During preliminary analysis, we found that the number of available aphids (density) and the number of parasitoid offspring that dropped were weakly correlated (Pearson correlation coefficient = 0.16, $\chi^2 = 2.97$, $df = 2$, $P = 0.085$). We therefore investigated the effects of aphid age within each density class, using a repeated-measures multivariate analysis of variance (MANOVA). The dependent variables in this analysis were the proportion of the mummies formed on the leaf and proportion of mummies formed on the ground, within individual parasitoid mothers. We investigated the effects of aphid age and density on parasitism rates also using a repeated-measures MANOVA. Parasitism rates of the aphid populations on the leaf and on the ground were the dependent variables, within individual parasitoid mothers, and age and density effects and their interaction were the independent variables. We calculated parasitism rates as the proportion of parasitoid mummies formed in the total number of individuals (aphids and parasitoids), within each fraction of the population. Due to a significant interaction term in this last analysis, we further explored the effects of aphid density on the distribution of parasitism, within each age class, using repeated-measures MANOVA, as above. In all our analyses we included only those replications in which female attack produced one or more offspring, as measured by the formation of mummies. All analyses were performed in Systat 9.0.

Effect of dropping behaviour on population dynamics

a. Small cage study. Six-week-old pepper plants (cultivar Bell Boy) were transplanted into plastic pillow bags (28 × 40 cm) filled with sawdust. Before transplanting, pepper plants were dipped in insecticidal soap solution (Safer's Insecticidal Soap, Woodstream Canada, Scarborough, Ontario, Canada) at 10 mL concentrate per L, to kill all aphids, then dipped in water to rinse the soap from the leaves. All plants were inspected to make sure they were free of aphids, mummies, and adult parasitoids. Plants were placed singly, in 20 insect cages (Bugdorm 3, Bioquip, Rancho Dominguez, California, United States of America) on a bench in a greenhouse.

The base of 10 of the pepper plants was covered with carpet tape (48 mm wide) (Henkel Consumer Adhesives, Inc., Ohio, United States of America) to prevent dropped aphids from returning to pepper plants, and 10 plants were left without tape. Thirty foxglove aphids (15 four-day-old and 15 five-day-old) were placed on the plant and allowed to settle for 24 hours, after which a mated, inexperienced, *A. ervi* female (24–48 hours old) was introduced into each cage. The parasitoids were removed after 1 hour, and foxglove aphids that had dropped from the plants were counted. The *A. ervi* used in this experiment were obtained from Koppert Canada Ltd. (Scarborough, Ontario, Canada) and were not reared on foxglove aphids. Aphids, parasitoid mummies, and parasitoid adults were counted every 7 days thereafter for 21 days. Data were analysed by a repeated-measures MANOVA in Systat 9.0.

b. Large cage study. A study of the long-term effects of excluding aphids from returning to plants after dropping, was conducted in eight, 1.8 m wide × 3.2 m long × 1.8 m high field cages (Bioquip, Rancho Dominguez, California, United States of America), placed inside a greenhouse compartment. Two 400 W, high-pressure sodium lamps on a 16-hour daylength, mounted above and outside each cage to reduce the effects of shading on the plants inside the cages. Ten pepper plants (CV 4Ever, Enza Zaden, Enkhuizen, The Netherlands) were transplanted into plastic grow bags in sawdust, in two rows of five in each cage. Plants were supported on trellis strings that were tied to wires suspended on the cage frame. Plants were approximately 8 weeks old when planted, on

22 January 2008. In four of the cages, foxglove aphids were prevented from returning to the plants after dropping by wrapping the base of each of the plants with a band of carpet tape (Henkel Consumer Adhesives, Inc., Ohio, United States of America). We also placed a strip of tape around the perimeter of the cage to prevent aphids walking up the sides of the cages, and from moving from cage to cage on the floor of the greenhouse through any gaps that might have been present. Forty foxglove aphids divided among four age classes (10 two-day-old, 10 three-day-old, 10 five-day-old, and 10 seven-day-old aphids) were placed on each plant on 23 January 2008. These were dispersed on four leaves of each plant, and were placed as mixed age groups (*i.e.*, some of each age group was placed on each leaf). Parasitoids were released on 24 January 2008 at a rate of one female *A. ervi* per plant. Each parasitoid had emerged from a foxglove aphid host, and was 24–48 hours old, mated, and inexperienced with respect to foxglove aphids. Females were released singly at the base of plants, by allowing them to walk from a glass collecting tube onto the stem of the plant, above the trap tape where this was present. Sampling started on 28 January 2008, and was conducted weekly thereafter. We counted all aphids and mummies on each plant. To avoid pseudoreplication, all counts were summed for each cage to give a total per cage. In one cage, two plants became infested with *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) early in the experiment, and these were removed. The values for aphid numbers, parasitoid numbers, and parasitism rates in this cage were adjusted to 10 plants, based on samples

from the remaining eight plants. Data were analysed by repeated-measures MANOVA, in Systat 9.0.

Results

Host location by foxglove aphid after dropping

Aphid age affected the proportion of aphids disturbed by parasitoids (logistic regression, loglikelihood $\chi^2 = 13.21$, $df = 2$, $P = 0.0014$). In the different age classes, 0.47 ± 0.05 of 7-day-old, 0.69 ± 0.07 of 5-day-old, and 0.54 ± 0.09 of 3-day-old aphids were disturbed. More 5-day-old than 7-day-old aphids, but not 3-day-old than 7-day-old, were disturbed (odds ratio 5-day-old 2.54 ± 0.66 , $P = 0.0004$; odds ratio 3-day-old 1.32 ± 0.36 , $P = 0.29$). Foxglove aphids were much more likely to drop from the plant in response to disturbance than to walk down the plant (Table 1, logistic regression, loglikelihood $\chi^2 = 15.37$, $df = 2$, $P = 0.0005$). When disturbed, 7-day-old aphids were more likely to walk down the plant than 3-day-old or 5-day-old aphids (odds ratios, 3-day-old aphids 0.27 ± 0.16 , 5-day-old aphids 0.16 ± 0.09). There was a significant effect of age on the probability of relocating the plant among aphids that dropped (Table 1, logistic regression, loglikelihood $\chi^2 = 13.09$, $df = 2$, $P = 0.0014$). Three-day-old aphids were slightly less likely to return to the plant than 7-day-old aphids and 5-day-old aphids were much more likely to return to the plant than 7-day-old aphids (odds ratios: 3-day-old 0.84 ± 0.38 ; 5-day-old 4.2 ± 2.08). Aphid age had no effect on the probability of relocating the plant among aphids

Table 1. Effect of age on the percent of foxglove aphids exhibiting defence responses (walking or dropping in response to attack by adult *Aphidius ervi* females on pepper plants, and the percent of those returning to the plant).

Aphid age	Behaviour	% responding	Fate following disturbance	
			Relocated the plant (%)	Did not relocate the plant
3	Drop off	91	58	42
	Walk off	9	67	33
5	Drop off	94	87	13
	Walk off	6	67	33
7	Drop off	73	62	38
	Walk off	27	50	50

Table 2. Effect of aphid age on mean ± SE distance travelled during a return to the plant, and time required to relocate the plant among aphids that successfully returned to the plant after dropping.

Aphid age	Distance travelled (cm)	Return time (s)
3 (19)	4.1 ± 0.54a	825.1 ± 200.39a
5 (48)	6.3 ± 0.5b	864.9 ± 90.12a
7 (34)	6.5 ± 0.65b	286.9 ± 41.81b

The number for each age class is in brackets following the class. Numbers in columns followed by the same letter are not significantly different (Tukey's honestly significant difference, α = 0.05).

that walked off the plant (loglikelihood $\chi^2 = 1.51$, df = 2, $P = 0.47$). Among the aphids that dropped from the plant, aphid age affected the distance walked by those that successfully returned to the plant (ANOVA, $F_{1,98} = 3.5844$, $P = 0.0315$) and the time taken to return (survival analysis, proportional-hazards $\chi^2 = 35.41$, $P < 0.0001$). Three-day-old aphids that successfully returned to the plant walked a shorter distance than 5-day-old or 7-day-old aphids, and 7-day-old aphids took less time to return to the plant than 3-day-old or 5-day-old aphids (Table 2).

Fate of parasitoid offspring following dropping of foxglove aphids

The proportion of the aphid population that dropped from leaves during exposure to *A. ervi* (Table 3) was affected by age of the aphids (least-squares ANOVA, $F_{2,98} = 14.91$, $P < 0.0001$), but not by density of aphids in the patch or the interaction between age and density ($F_{2,98} = 1.42$, $P = 0.25$, and $F_{4,98} = 0.16$, $P = 0.97$). A lower proportion of 8-day-old aphids dropped than either 2-day-old and 5-day-old aphids, which were not different from one-another (Tukey's honestly significant difference, α = 0.05). Within density classes of aphids (20, 40, and 60 aphids per leaf), more of each female parasitoid's mummies were formed in the fraction on the ground (dropped) than in the fraction on the leaf (Table 3; repeated-measures MANOVA; 20 per leaf: $F_{1,32} = 10.60$, $P = 0.0027$; 40 per leaf: $F_{1,31} = 35.80$, $P < 0.0001$; and 60 per leaf: $F_{1,35} = 24.06$, $P < 0.0001$). The numbers of mummies in the leaf and ground fractions of

Table 3. The effects of parasitoid foraging on proportion of *A. solani* that dropped from leaves, the numbers of parasitoid offspring in the two fractions of the aphid population, and the respective parasitism rates.

Aphid age	Number per leaf	% of aphids dropping	Number of mummies in leaf fraction	Number of mummies in dropped fraction	Parasitism rate (%) in leaf fraction	Parasitism rate (%) in dropped fraction
2	20	74 ± 11.5 (7)	0.14 ± 0.143 (7)	4.00 ± 1.345 (7)	17 ± 16.7 (6)	25 ± 5.8 (7)
2	40	80 ± 5.9 (12)	0.33 ± 0.333 (12)	8.67 ± 1.772 (12)	4 ± 4.2 (12)	26 ± 4.8 (12)
2	60	74 ± 6.4 (12)	0.42 ± 0.260 (12)	7.83 ± 1.894 (12)	2 ± 1.1 (12)	16 ± 3.5 (12)
5	20	70 ± 8.1 (14)	0.57 ± 0.251 (14)	5.21 ± 1.017 (14)	17 ± 8.6 (13)	36 ± 5.8 (14)
5	40	83 ± 4.8 (12)	0.92 ± 0.398 (12)	7.42 ± 1.464 (12)	26 ± 11.7 (12)	22 ± 4.2 (12)
5	60	70 ± 6.7 (14)	1.64 ± 0.700 (14)	4.21 ± 1.100 (14)	0.18 ± 0.097 (14)	9 ± 2.0 (14)
8	20	39 ± 6.9 (14)	2.71 ± 0.873 (14)	1.57 ± 0.900 (14)	26 ± 7.2 (14)	15 ± 5.2 (14)
8	40	51 ± 9.8 (10)	2.30 ± 0.716 (10)	2.60 ± 0.806 (10)	13 ± 4.1 (10)	16 ± 5.3 (10)
8	60	46 ± 9.8 (12)	1.50 ± 0.793 (12)	5.17 ± 1.804 (12)	5 ± 2.3 (12)	25 ± 7.9 (12)

Numbers are arithmetic means ± SE of the mean (n).

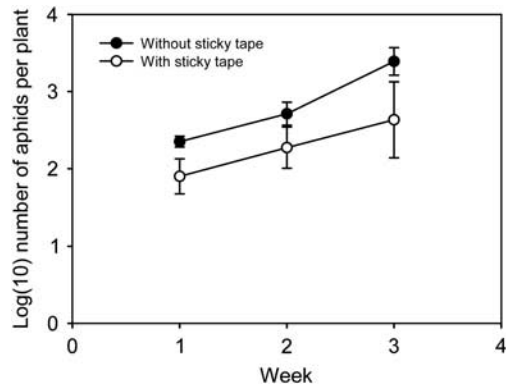
the aphid populations were affected by the age of the aphid population for densities of 20 and 40, but not 60 aphids per leaf (Table 3; repeated-measures MANOVA; 20 per leaf, $F_{2,32} = 7.25$, $P = 0.0025$; 40 per leaf $F_{2,31} = 7.87$, $P = 0.0018$; and 60 per leaf: $F_{2,25} = 2.49$, $P = 0.10$). A greater number of mummies dropped to the ground in 2-day-old and 5-day-old aphids than 8-day-old aphids within density classes 20 and 40 per leaf, but not within 60 per leaf (Hotelling's t -square, $\alpha = 0.05$).

The overall parasitism rates in the two fractions of the aphid populations within parasitoid mothers were different (Table 3; rate on leaf = 0.14, rate on ground = 0.21; repeated-measures MANOVA $F_{1,96} = 0.0145$). There was, however, a significant interaction between age and density within the dependent variable ($F_{4,96} = 4.93$, $P = 0.0012$), so further analysis was conducted within each age class to determine the source of the interaction term. Within 2-day-old aphids, the parasitism rate in the ground fraction was greater than the parasitism rate on the leaf ($F_{1,27} = 12.06$, $P = 0.0018$), but these rates were not affected by density of the aphids ($F_{2,27} = 1.64$, $P = 0.21$). Within 5-day-old aphids, the parasitism rates in the two fractions were not different, and were not affected by density ($F_{1,36} = 0.24$, $P = 0.62$ and $F_{2,36} = 2.76$, $P = 0.08$, respectively). Within 8-day-old aphids, parasitism rates in the two fractions were affected by density ($F_{2,33} = 6.13$, $P = 0.0054$). Parasitism rates in the leaf fraction were much lower than in the ground fraction at 60 aphids per leaf, but not at 20 or 40 per leaf (Table 3).

Effect of dropping behaviour on the population dynamics of foxglove aphid

a. Small cage study. In the small cage study, 30 aphids on a pepper plant were exposed to a single *A. ervi* for 24 hours only, either on plants that had sticky tape at the base to prevent aphids returning to the plant, or not. Within cages tape treatments had an effect on the increase of aphids over time (Fig. 1; repeated-measures MANOVA, $F_{2,26} = 1.80$, $P = 0.19$), although aphid numbers did increase over time (repeated-measures MANOVA, $F_{2,26} = 8.22$, $P = 0.0017$). Overall, fewer aphids were found on plants with the tape than without (Fig. 1; repeated-measures MANOVA $F_{1,13} = 4.69$, $P = 0.05$).

Fig. 1. Mean numbers of foxglove aphids, *Aulacorthum solani*, on pepper plants with and without sticky tape to prevent return of dropped aphids to the plant following a 1 hour exposure to one *A. ervi* female. Bars represent the standard error of the mean.



b. Large cage study. There was an interaction between time and tape treatment on the numbers of aphids on plants during the 7 weeks of observations (repeated-measures MANOVA, $F_{6,30} = 7.43$, $P < 0.0001$), which demonstrates that the populations developed in different ways. There was an overall effect of time ($F_{6,30} = 7.43$, $P < 0.0001$), but the effect of the tape treatment was not significant (repeated-measures MANOVA $F_{1,5} = 4.73$, $P = 0.0816$), suggesting that the overall numbers of aphids were not different between treatments (Fig. 2A). The numbers of aphids in the two treatments were different in the first 2 weeks of the experiment (repeated-measures MANOVA, between subjects, $F_{1,5} = 11.27$, $P = 0.02$) but not during the latter 5 weeks of the experiment (repeated-measures MANOVA, between subjects, $F_{1,5} = 0.05$, $P = 0.84$). For the numbers of non-emerged mummies, there was a significant interaction between time and tape treatment (repeated-measures MANOVA, $F_{6,30} = 3.65$, $P = 0.008$) and a significant effect of time (repeated-measures MANOVA $F_{6,30} = 8.75$, $P < 0.0001$). Although there was not a between-subjects effect of treatment on numbers of parasitoid mummies (Fig. 2B, repeated-measures MANOVA, $F_{1,5} = 4.76$, $P = 0.08$), analysis of data at week 3, where there was maximum separation of the means, suggests a difference between the mean numbers of parasitoid offspring at that time (t -test, pooled variance, $t = 3.55$,

Discussion

We posed three questions regarding the dropping behaviour of *A. solani*: would mortality on the floor of a pepper greenhouse complement mortality from natural enemies on the plant; would mortality on the floor interfere with the population dynamics of parasitoids such as *A. ervi*; and would stem banding with a sticky material, to prevent *A. solani* from returning to plants following dropping be an appropriate method for producing additional mortality in the aphid population? Our results demonstrate that stem banding prevented *A. solani* that had dropped from returning to the plant; but that the mortality associated with banding was not necessarily complementary to biological control by *A. ervi*. In fact, stem banding might have interfered with the population dynamics of the parasitoid. Thus, as in most pest management decisions relating to biological control, the value and application of sticky stem bands for management of *A. solani* would depend entirely on context, as we discuss below.

Sticky bands on stems of pepper plants prevented foxglove aphids from returning to the plants. Following a short (1 hour) bout of foraging by *A. ervi*, preventing the return of aphids that had dropped resulted in a large and persistent difference in numbers of aphids on plants (Fig. 1). Because of the short foraging bout, this effect stemmed primarily from a reduction in the initial number of aphids through dropping caused by the foraging parasitoid, and not from the effects of parasitism. In the longer-term experiment (Fig. 2), *A. ervi* were allowed continuous access to *A. solani* populations in the presence and absence of sticky bands, and passed through approximately three generations. The combined effects of sticky bands and parasitoid foraging resulted in the rapid decline in aphid numbers in cages in the first week of the experiment, relative to cages without bands. The sticky tape trapped and killed aphids that were dislodged by the parasitoids. However, after 3 weeks, as a result of parasitoid-induced mortality, the numbers of aphids were identical in cages with and without sticky tapes, and remained identical to the end of the experiment. Although the sticky bands caused a rapid reduction in aphid numbers, it is not clear if this reduction has a practical value in pest management.

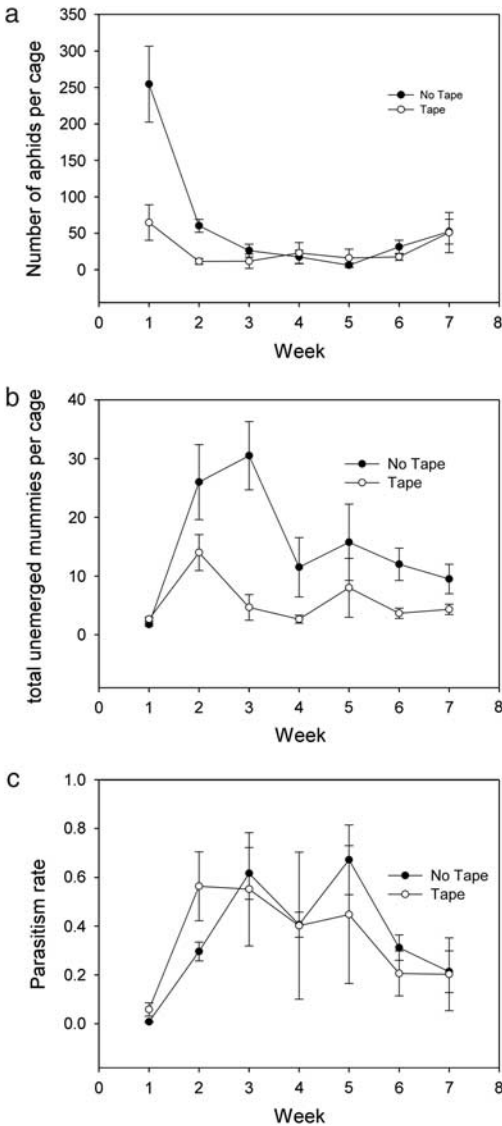


Fig. 2. Numbers of aphids (A), numbers of mummies (B), and percent parasitism (C) in large cages, where plants either had sticky tape to prevent return of dropped aphids to plants, and numbers of aphids on the tape in cages with sticky tape. For all figures, $n = 4$ and the error bars are standard error of the mean.

$df = 6$, $P = 0.01$). There was no effect of treatment on percent parasitism (Fig. 2C), either overall (repeated-measures MANOVA, between subjects, $F_{1,5} = 2.4$, $P = 0.64$) or across time (repeated-measures MANOVA, within subjects, time \times treatment, $F_{6,30} = 1.96$, $P = 0.10$), although parasitism did change through time (repeated-measures MANOVA, $F_{6,30} = 15.54$, $P < 0.0001$)

Injury to pepper plants by *A. solani* is caused by a relatively low number of aphids (Sanchez *et al.* 2007). Growth reductions and stem, leaf, and fruit abnormalities are caused by the aphid saliva (Sanchez *et al.* 2007). In addition, *A. solani* vectors a number of economically important viruses (Blackman and Eastop 2000). Henry *et al.* (2010) demonstrated that the dispersal of patches and aggregations of *A. solani* following parasitoid attack caused the aphid injury to spread to nearby plants. This resulted in greater total plant damage than when aphids remained undisturbed, because the majority of the population remained concentrated on a single plant or small group of nearby plants (Henry *et al.* 2010). Sticky bands on pepper stems could reduce the spread of aphid injury, and restrict the transmission of viruses, by intercepting the dispersing aphids.

We found that fewer 8-day-old *A. solani* dropped from leaves in response to foraging by *A. ervi* than younger age classes (Table 3). For pea aphids, *Acyrthosiphon pisum* Harris (Hemiptera: Aphididae), the response of individual aphids to attack by predators depends in part on the age of the aphid—aphid immatures that are near-adult are likely to produce some offspring before being killed by a parasitoid, and may therefore be less likely to drop in response to attack by *A. ervi* (McAllister *et al.* 1990). However, very few of the 8-day-old aphids remaining on the leaves were parasitised, and we do not know if recently parasitised 8-day-old *A. solani* were able to produce offspring before being killed by the parasitoid. The lower response could also have been due to differential foraging. The *A. ervi* used in our experiments were reared on *A. solani*, which likely biased the foraging and host acceptance to younger aphids. Henry *et al.* (2005, 2006) demonstrated that *A. ervi* reared on *A. solani* are more likely to attack younger, and more vulnerable individuals than wasps reared on larger hosts, such as *A. pisum*. This has implications for the complementarity of sticky stem bands and parasitoid wasps in an IPM system. Younger aphids, which are more likely to be parasitised, would drop to the ground and both the aphid and the parasitoid offspring would be killed on the sticky stem band while returning to the plant. In contrast, older and adult aphids, which may be less likely

to be parasitised, would remain on the plant, continue to reproduce, and would replenish the aphid population quite quickly. Mortality of *A. solani* on sticky stem bands would therefore not complement parasitoid mortality, because the mortality would be biased toward individual aphids that have already been “killed” by the parasitoid. This contrasts with the results of Losey and Denno (1998a), who found that *A. pisum* dropping in response to threat from a predator, *Coccinella septempunctata* (Linnaeus) (Coleoptera; Coccinellidae), increased the susceptibility of aphids to ground-dwelling predator, *Harpalus pennsylvanicus* (De Geer) (Coleoptera: Carabidae). Thus, sticky bands on stems of pepper plants in greenhouses might be used to good effect in the presence of predators such as coccinellid beetles, or could be combined with the application of alarm pheromone formulations and abiotic disturbance.

Our final question – “would sticky stem bands interfere with the long-term population dynamics of *A. ervi*?” – cannot be entirely answered from our results. The proportion of aphids that dropped from leaves contained a disproportionately large fraction of the female parasitoids’ reproduction. In the long-term cage experiment, this resulted in about half the number of parasitoid mummies in cages with sticky stem bands compared to cages without. Population dynamics of aphids and parasitoids at the crop and landscape level are influenced by metapopulation dynamics, *i.e.*, immigration and emigration processes (Weisser 2000). Since the reduction of recruitment of parasitoids would also reduce numbers available to immigrate into undiscovered patches of aphids, there might be a tendency for other patches in the habitat to remain undiscovered longer and therefore be larger on average when sticky stem bands are present.

Our results suggest that sticky stem bands on pepper plants have the potential to reduce injury from *A. solani* over the short term. However, the investment in sticky stem bands would simply replace mortality from parasitoid females, and would therefore not add value to the IPM system over the long term. Moreover, in an aphid IPM system dominated by braconid parasitoids, the long-term impacts of the sticky stem bands on parasitoid population dynamics might tend to produce greater numbers of aphids, by reducing

recruitment of parasitoids. However, in IPM systems that emphasise disruptive predators such as coccinellid beetles, sticky stem bands could provide an additional, complementary source of mortality that would have the added benefit of restricting the spread of injury to plants.

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