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The effect of chrysanthemum leaf trichome density and prey spatial distribution on predation of *Tetranychus urticae* (Acari: Tetranychidae) by *Phytoseiulus persimilis* (Acari: Phytoseiidae)

M.C. Stavrinides and D.J. Skirvin*

Horticulture Research International, Wellesbourne,
Warwick, CV35 9EF, UK

Abstract

The effect of plant architecture, in terms of leaf hairiness, and prey spatial arrangement, on predation rate of eggs of the spider mite, *Tetranychus urticae* Koch, by the predatory mite *Phytoseiulus persimilis* Athias-Henriot was examined on cut stems of chrysanthemums. Three levels of leaf hairiness (trichome density) were obtained using two different chrysanthemum cultivars and two ages within one of the cultivars. The number of prey consumed by *P. persimilis* was inversely related to trichome density. At low prey densities (less than ten eggs per stem), prey consumption did not differ in a biologically meaningful way between treatments.The effect of prey spatial arrangement on the predation rate of *P. persimilis* was also examined. Predation rates were higher in prey patches on leaves adjacent to the release point of *P. persimilis*, but significantly greater numbers of prey were consumed in higher density prey patches compared to low density patches. The predators exhibited non-random searching behaviour, spending more time on leaves closest to the release point. The implications of these findings for biological control and predator–prey dynamics are discussed.

Introduction

In the UK, consumer and government pressure to reduce pesticide inputs, insecticide resistance, and phytotoxicity problems make the development of robust biological control solutions in ornamental crops of crucial importance to the future of the horticultural industry (Hussey & Huffaker, 1976; Cranham & Helle, 1985; Devine *et al*., 2001).

Due to the great diversity of crops grown, natural enemies have to cope with a wide range of growth forms, and morphological features, such as different flower types, fruiting structures, and different levels of leaf hairiness (Skirvin & de Courcy Williams, 1999). In order to develop sustainable biological control strategies it is necessary to understand how habitat structure influences the ability of natural enemies to locate and eliminate sparsely distributed prey patches. Plant leaf trichomes are a common component of plant architecture, found on many ornamental crops, particularly chrysanthemums. They have been shown to have negative effects on the movement and searching behaviour of natural enemies (Treacy *et al*., 1984; Hua *et al*., 1987; Keller, 1987; Heinz & Parella, 1994; Sütterlin & van Lenteren, 1997; Koveos & Broufas, 2000). Hence, the development of robust biological control strategies relies on having a sound understanding of how the density of plant trichomes affects searching behaviour and predatory capacity of natural enemies.

Due to the low tolerance to pest damage in ornamental

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*Author for correspondence
Fax: +44 1789 470552
E-mail: david.skirvin@hri.ac.uk

crops, it is likely that a preventative approach to biological control will be necessary (Skirvin *et al.*, 2002). This requires natural enemies to eliminate sparsely distributed patches of prey, so that prey spatial distribution is very relevant to the success of biological control. Previous work (Eveleigh & Chant, 1982a,b) has shown that adult female *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) spend more time in patches with higher prey densities. The predators responded quickly to the density of prey within a patch, with greater numbers of predators being found in the patch with the highest prey density within 5 h of the start of the experiment. Therefore the predatory ability of any natural enemy must be evaluated not only in terms of prey density per unit area, but also in terms of the relative distribution of prey in that area.

This study examined the impact of chrysanthemum trichome density on the predatory ability of *P. persimilis*, a major predator of spider mites, *Tetranychus urticae* Koch (Acari: Tetranychidae), a key pest in ornamental crops, and how this predatory ability is affected by the distribution of prey at a set prey density. The implications of the results of this study for biological control in ornamental crops are discussed.

Materials and methods

Mites and plants

The spider mites (*T. urticae*) used in all experiments were obtained from a culture maintained at Horticulture Research International (HRI) on dwarf french beans, *Phaseolus vulgaris* L. (Fabaceae), in a controlled environment room at 19–21°C, 50–90% rh, with a 16:8 light:dark photoperiod.

Predatory mites (*P. persimilis*) were obtained from a commercial biological control company (Biological Crop Protection, UK) and maintained on standard culture platforms (Overmeer, 1985). The predators were supplied with an abundant supply of prey on bean leaves, and left on the platforms at room temperature and humidity for a minimum of 24 h and a maximum of 48 h before use in any experiment. Fresh batches were used for each experiment.

Chrysanthemum (*Chrysanthemum* × *grandiflora* Ramat. (Compositae)) cultivars Reagan and Swingtime were used in all experiments. The plants were maintained in an unheated glasshouse at Horticulture Research International.

Measurement of chrysanthemum trichome density

The mean density of non-glandular trichomes was determined per unit area (cm^2) for old and young leaves of cv. Reagan and for old leaves of cv. Swingtime, using scanning electron microscopy. Old leaves were defined as those from the basal area (lower third) of chrysanthemum plants, whilst young leaves were the first four fully expanded leaves near the growing tip.

Sixteen 22 mm^2 square sections were cut from a total of six leaves, with each leaf taken from a separate plant, for each cultivar and leaf age. These were then mounted, abaxial side uppermost, and frozen before being placed in the scanning electron microscope. Photographs of each sample were scanned into a computer and imported into SigmaScan^{TM} image analysis software for counting of the trichomes.

The trichomes were counted by sub-sampling two 4 mm^2 squares from each section. In the case of young leaves of cv. Reagan, the density of trichomes required a higher magnification and a sampling area of 1 mm^2 was used. The trichome density from all 32 sub-samples was converted to a standard trichome density per cm^2, to determine the mean.

Effect of trichome density on P. persimilis *predation rate*

The effect of trichome density on the functional response of *P. persimilis* was studied using three levels of trichome density: low (old cv. Reagan leaves), medium (old cv. Swingtime leaves) and high (young cv. Reagan leaves). All experiments were done on cut stems of chrysanthemum plants, which were prepared using the methods described by Skirvin & de Courcy Williams (1999) to ensure that all stems were covered with spider mite webbing. Stems had an approximate leaf area of 108 cm^2, comprising four leaves for cv. Swingtime and cv. Reagan (old), but eight leaves for cv. Reagan (young), based on measurement of scanned leaves using SigmaScan^{TM} image analysis software.

Five, 10, 20 or 80 *T. urticae* eggs were placed, using a fine paintbrush, on each stem, on the underside of a single leaf chosen at random. A single *P. persimilis* adult female was then released on a randomly chosen leaf. The cut stems were then inserted, individually, into 22 cm × 16 cm × 17 cm plastic cages, which were kept in an incubator at 25 ± 1°C and ambient humidity for 24 h.

After 24 h, stems were removed from the incubator and the number of eggs remaining counted. The status of *P. persimilis* was also noted, and only those stems where *P. persimilis* had survived were used in subsequent analysis. Control treatments, with no *P. persimilis*, were used to determine egg loss in the absence of predators.

The experiments were repeated 20 times for the different egg densities, and ten times for the controls, for each trichome density.

The different trichome densities were tested separately over time due to limited glasshouse space for the rearing of the chrysanthemum plants, limitations on incubator space for the experiments, and also because the aim was to fit a response curve to the data on predation for which it was necessary to have consistent data for all prey densities at a single trichome density. However, the sequence of trichome densities was randomized. Although this ordering of treatments constitutes a form of ‘pseudo-replication’ (Hurlbert, 1984) as trichome density is confounded with time, there was no evidence of temporal drift in the losses at the individual prey densities between replicates at a single trichome density or between trichome densities.

Effect of prey spatial distribution on P. persimilis *predation rate*

This experiment was done only at a medium trichome density (cv. Swingtime). Cut stems were prepared as for the previous experiment, and trimmed to four leaves to ensure a leaf area of approximately 108 cm^2, based on measurement of scanned leaves using SigmaScan^{TM} image analysis software.

Eighty *T. urticae* eggs were placed on each stem in four different arrangements: (i) all 80 eggs placed on the underside of a single leaf (1 × 80); (ii) 40 eggs placed on the underside of each of two leaves (2 × 40); (iii) 20 eggs placed on the underside of each of the four leaves (4 × 20); (iv) five, 10, 25 and 40 eggs placed on the underside of the four leaves (mix).

A single *P. persimilis* was released onto the top of each stem, and the stems placed in plastic cages and incubated for 24 h as in the previous experiment. After 24 h the stems were removed and the same protocol followed for counting as described above.

A single run of the experiment consisted of one set of the four treatments. Twenty-four runs were done to enable all combinations of prey density and leaf position in treatments (i), (ii) and (iv) to be included in the experiment. The control treatments were replicated 12 times, which enabled all possible prey density and leaf combinations from treatments (i) and (ii) to be carried out. The prey density and leaf position combinations for the controls from treatment (iv) were chosen to ensure that there was a control for each prey density in each leaf position. Any replicates where *P. persimilis* was not observed on the cut stem were omitted from the final analysis.

A subsidiary experiment was done to examine the distribution of *P. persimilis* on the stems with mixed prey densities. The stems were prepared as described above, and infested with prey as for the mixed prey density treatment (iv) previously described. A single adult female *P. persimilis* was released at the top of each cut stem, and left at room temperature and humidity (20–23°C, 25–35% rh) for 6 h. The leaf position of the predator was recorded hourly.

The experiment was repeated 24 times As with the main experiment described above, 24 runs of this experiment were done to ensure that all 24 possible prey density and leaf position combinations were investigated. Any replicates where *P. persimilis* was not observed on the cut stem were omitted from the final analysis.

Data analysis and models

Trichome density

The trichome densities on the different *Chrysanthemum* × *grandiflora* cultivars and leaf ages were analysed using analysis of variance on the log transformed counts of trichome density.

Effect of trichome density on P. persimilis *predation rate*

Due to the inclusion of controls in the functional response experiments, fitting the Holling (Holling, 1959) model to the data is not straightforward, and as the Holling models do not always provide the best fit for a simulation model as they do not allow for stochastic variation in the data, nor can their mechanistic concept be validated (Skirvin & Fenlon, 2001). Model 4 of Skirvin & Fenlon (2001) was fitted to the functional response data. This equation is based on a logistic function that describes the changing probability of predation with increasing prey availability, and uses a correction similar to Abbott's formula (Abbott, 1925) to correct for losses of prey in control treatments. The equation for the response is:

$$E(r) = n\left\{\lambda + k(1-\lambda)\frac{ac}{c+n}\right\} \tag{1}$$

where *E(r)* is the expected number of prey consumed or lost ('total predation'), λ is the proportion of prey lost, *k* is a parameter which is set to 0 if control data are being modelled and 1 when predation data is being modelled, *n* is the total number of prey available, and *a* and *c* are parameters whose product *ac* describes the asymptote of the hyperbolic response. The effective number of prey consumed (correcting for natural losses of prey (λ)) is therefore given by the following equation:

$$E(r') = n\left\{\frac{ac}{c+n}\right\} \tag{2}$$

where *E(r')* is the expected number of prey consumed after eliminating losses.

Effect of prey spatial distribution on P. persimilis *predation rate*

The data from this experiment were analysed using generalized linear model for binomial data in Genstat 5 for Windows, to examine differential predation on leaves. For arrangements (i) and (iv) leaf number and leaf order are totally confounded and therefore equivalent; for arrangement (ii) leaf order is partially distinct from leaf number, and for arrangement (iv) prey density also has some impact on predation. So for arrangements (i) and (iii) leaf number is the only factor fitted, whereas for arrangements (ii) and (iv) leaf order and prey number are fitted as co-variates prior to the fitting of leaf number, i.e. the effect of leaf number is adjusted for interfering factors. Also, except for (i) the individual plant (or assay) effect is removed and tests of significance occur at the within plant (or leaf) level. To account for the large levels of over-dispersion, F-tests were done of deviance ratios of the fitted models. Means and standard errors were corrected for imbalance using a standard algorithm (Lane & Nelder, 1982)

Results

Measurement of chrysanthemum trichome density

The lowest trichome density (± s. e.) was observed on old leaves of cv. Reagan (776 ± 36 trichomes per cm^2), whilst the highest density was on young leaves of cv. Reagan (3213 ± 92 trichomes per cm^2). The old leaves of cv. Swingtime had a trichome density (1684 ± 67 trichomes per cm^2) intermediate between those of old and young leaves of cv. Reagan. These trichome densities will be referred to as low, high and medium respectively in the remainder of this paper.

An analysis of variance showed that differences in trichome densities between the different cultivars and leaf ages were highly significant ($F = 344.52$, d.f. = 2,86, $P < 0.01$). The 95% confidence intervals for the means (mean ± 2 × s.e.) are distinct, indicating that the mean trichome densities were different between cultivar and leaf age. The shape of the trichomes was found to be the same in both cultivars. All trichomes were multicellular, two-armed, with both arms of equal length, as shown in fig. 1.

Effect of trichome density on P. persimilis *predation rate*

Analysis of variance indicated hugely significant differences ($P < 0.01$) in the response to trichome density (i.e. cultivar and leaf age), despite large inter-predator variances. Data were analysed using the FITNONLINEAR module of Genstat 5 for Windows, with the binomial likelihood function as argument. The fitted equations, for 'total predation', the sum of the prey consumed and natural prey losses, together with the data are shown in fig. 2. The predicted prey consumption in response to prey availability, derived from equation 2 is shown in fig. 3 for each of the

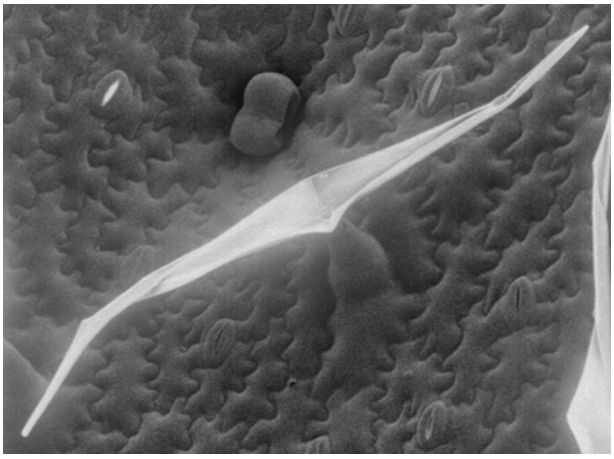

Fig. 1. Electron micrograph showing the shape of the trichomes of *Chrysanthemum* × *grandiflora*.

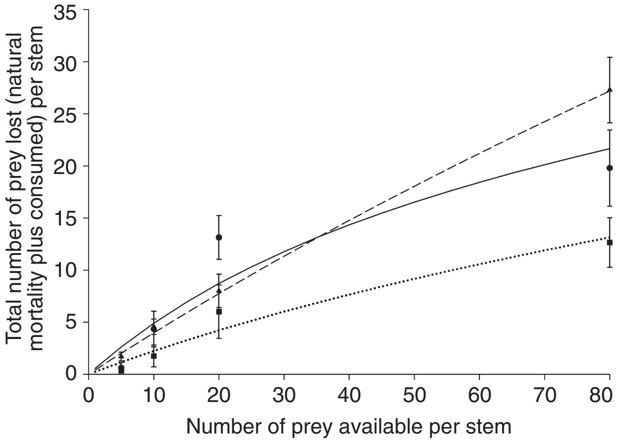

Fig. 2. The mean 'total predation' of an adult female *Phytoseiulus persimilis* on *Tetranychus urticae* eggs on cut stems of *Chrysanthemum* × *grandiflora* at three trichome densities (low: •, data; ——, fitted equation), (medium: ▲, data; – – –, fitted equation), (high: ■, data; ······, fitted equation). Error bars show ± 1 s.e. and relate to the 'total' observed prey losses, rather than the mean predicted by the model. See text for explanation of the term 'total predation'.

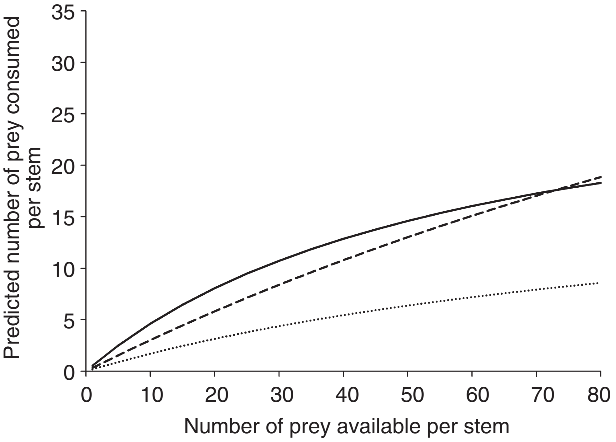

Fig. 3. Predicted number of *Tetranychus urticae* eggs eaten by an adult female *Phytoseiulus persimilis* at three trichome densities, after correction for natural losses of prey in the experiments. (low: ——, (medium: – – –), (high: ······).

trichome densities. The parameters of the fitted equations for each of the different trichome densities are shown in table 1.

The results indicated that there was a difference in predation of *T. urticae* eggs by *P. persimilis* between the three different trichome densities, as indicated by the markedly different parameter estimates for the fitted equations (table 1), with lowest predation at all prey densities occurring at the high trichome density. However the presence of pseudoreplication means that this cannot be formally tested. For the prey range 1–70, the fitted models predict a higher predation rate at low trichome density compared to medium trichome density. However, at the highest prey density used (80 eggs per stem), predation is predicted to be greater at a medium trichome density than at a low trichome density. At this highest prey density, there was a greater loss of prey in control treatments at the medium trichome density, which, when corrected for by equation 1, leads to an increased predicted predation rate.

Effect of prey spatial distribution on P. persimilis *predation rate*

Predation rates were calculated by dividing the number of prey missing from each leaf by the total number of prey originally placed on the leaf. The predation and natural mortality rates on each leaf for each treatment are shown in table 2. In all treatments, there was no significant difference in natural mortality rates between leaves, which means that any significant differences in predation rates on different leaves can be attributed primarily to the predator.

When all prey eggs were placed on a single leaf, there was no significant difference between predation rates on different leaves. This was also the case when prey were equally split between two leaves. In this latter case, predation on the nearer leaf to the *P. persimilis* release point was almost twice that on the further leaf, though this was not formally significant ($F_{1,13} = 3.63$, $P = 0.079$)

Comparisons of mean predation on each of the four leaves was not significant when eggs were equally split between the four leaves (table 2). However, examination of the contrast for position (essentially a regression on leaf order) showed a significant effect ($F_{1,48} = 5.08$, $P = 0.029$), with leaves closest to the release point showing a greater predation. Similarly, in the experiment using a mixture of prey densities, the formal significance for the overall comparison was not quite significant (table 2), but the regression on order was highly significant ($F_{1,36} = 7.47$, $P = 0.010$).

The results from the subsidiary observation experiment are shown in table 3. Analysis of the results using a Chi-squared test, with a null hypothesis that all leaves and prey densities would be equally visited, showed that leaf position was highly significant ($\chi^2 = 32.38$, d.f. = 3, $P < 0.01$) to the distribution of predators, with predators being observed more often on leaves closest to the release point. Predators also spent more time on leaves with a higher prey density

Table 1. Parameter estimates for the functional response model (Model 4 of Skirvin & Fenlon (2001) fitted to the predation of *Phytoseiulus persimilis* on *Tetranychus urticae* eggs on leaves of cultivars of *Chrysanthemum* × *grandiflora* with different trichome densities.

Parameter	Low trichome density cv. Reagan (old leaves)	Medium trichome density cv. Swingtime	High trichome density cv. Reagan (young leaves)
λ	0.0542 (0.0073)	0.136 (0.012)	0.0638 (0.0080)
a	0.540 (0.054)	0.315 (0.044)	0.186 (0.038)
c	58.8 (13.3)	238.0 (160.0)	108.8 (62.7)

The parameter λ represents the losses of prey not due to predation, and the product ac describes the asymptote of the hyperbolic response. Standard errors of parameter estimates are given in brackets.

Table 2. The effect of pest spatial distribution on the gross predation rate of *Tetranychus urticae* eggs (proportion of eggs lost due to both predation by *Phytoseiulus persimilis* and natural losses) and natural loss rate (proportion of eggs lost in control experiments without predators) of on each leaf of *Chrysanthemum* × *grandiflora* cv. Swingtime (standard errors are given in parentheses).

Treatment	Leaf number				F-value
	1	2	3	4	
1 × 80	0.250 (0.080)	0.113 (0.116)	0.246 (0.091)	0.396 (0.104)	$F_{3,7}$ = 0.96, P = 0.464
2 × 40	0.375 (0.263)	0.284 (0.134)	0.188 (0.097)	0.350 (0.207)	$F_{3,13}$ = 0.49, P = 0.698
4 × 20	0.144 (0.056)	0.235 (0.063)	0.362 (0.073)	0.332 (0.072)	$F_{3,48}$ = 2.14, P = 0.107
Mixed	0.135 (0.043)	0.229 (0.060)	0.336 (0.064)	0.348 (0.067)	$F_{3,36}$ = 2.77, P = 0.055
1 × 80 control	0.056 (0.026)	0.038 (0.043)	0.056 (0.021)	0.000 –	$F_{3,8}$ = 0.76, P = 0.547
2 × 40 control	0.095 (0.047)	0.029 (0.025)	0.030 (0.034)	0.085 (0.048)	$F_{3,9}$ = 0.42, P = 0.742
4 × 20 control	0.056 (0.022)	0.050 (0.021)	0.113 (0.030)	0.062 (0.023)	$F_{3,21}$ = 1.29, P = 0.303
Mixed control	0.054 (0.020)	0.109 (0.038)	0.071 (0.022)	0.058 (0.023)	$F_{3,30}$ = 0.71, P = 0.551

Leaf number indicates the position of the leaf from the base of the stem (leaf number 4 was closest to the predator release point). The F values for the effect of leaf number, within a treatment, are presented in the final column – for treatment (ii) (2 × 40) the effect of leaf number is fitted after that of leaf order (see text for details).

Table 3. The effect of leaf position and prey density on the total number of hourly observations of the location of *Phytoseiulus persimilis* on leaves of *Chrysanthemum* × *grandiflora* in the subsidiary experiment. Leaves are numbered with respect to their position from the base of the stem, with leaf 4 being closest to the predator release point.

Prey density (number per plant)	Leaf position			
	Leaf 1	Leaf 2	Leaf 3	Leaf 4
5	0	13	1	12
10	5	5	8	18
25	4	4	4	11
40	5	3	17	18

(χ^2 = 7.90, d.f. = 3, $P < 0.05$), and there was a highly significant interaction between leaf position and prey density (χ^2 = 31,86, d.f. = 3, $P < 0.01$).

Discussion

Effect of trichome density on P. persimilis *predation rate*

Trichome density had a substantial effect on the ability of *P. persimilis* to locate and consume eggs of *T. urticae* as measured by the functional response, suggesting that high trichome densities are likely to impede the searching efficiency of *P. persimilis*. These results are consistent with previous work showing that trichomes and leaf hairs impede movement of, and adversely affect the searching behaviour of natural enemies (Treacy *et al.*, 1984; Hua *et al.*, 1987; Keller, 1987; Heinz & Parella, 1994; Sütterlin & van Lenteren, 1997; Koveos & Broufas, 2000). Skirvin & Fenlon (2001) found that fewer *T. urticae* eggs were consumed by *P. persimilis* on *Ceanothus thyrsiflorus* Eschw. cv. 'Autumnal Blue', a plant with hairy leaves, than on smooth-leaved *Choisya ternata* HBK., which concurs with the results of this study. In addition, Krips *et al.* (1999) showed that the predation rate of *T. urticae* was inversely related to trichome density on cultivars of *Gerbera jamesonii* Adlam., particularly at prey densities below 2.5 *T. urticae* eggs per cm^2. The prey densities experienced by *P. persimilis* in this study ranged from 0.05 to 0.074 eggs per cm^2, which represent levels of prey likely to occur in the early stages of a pest infestation. However, the trichome densities used in this experiment are much higher than those used by Krips *et al*. (1999). Also, all the experiments in this study were done on cut stems, as opposed to small leaf discs, therefore providing a more realistic arena for predation studies.

The prediction of greater predation, at the highest prey density, for plants with a medium trichome density compared to plants with a low trichome density is surprising. It is likely to be due to low prey consumption at the high prey density, thereby biasing the mean number of prey consumed. The low consumption at this high prey density on the plants with low trichome density is caused by some outlying data in the number of prey eaten, where the predator survived the 24 h but consumed few if any prey. The consequence of a reduced mean number of prey consumed was to lower the fitted curve for the low trichome density functional response.

The most likely explanation for the lower predation rates on high trichome density chrysanthemums is that the trichomes impede the movement of *P. persimilis*, and therefore reduce the encounter rate between the predator and prey. It is also possible that at the higher trichome densities, the eggs of *T. urticae* can become hidden between the trichomes, making them less accessible to predation by *P. persimilis*. In addition, the small leaf size used for the high trichome density could have led to a decrease in predation due to a greater proportion of time lost by the predators in moving between eight leaves, as opposed to four. However, given the high mobility of the predators, it is unlikely that this is the case; it has been shown (Skirvin & Fenlon, 2003) that *P. persimilis* are able to cross up to ten stems of *Choisya ternata* within a 24 h period.

Although the experimental design includes pseudoreplication, this was due to limited resources for the experimental work, and the need to have consistent data for all prey densities within a single trichome density to allow the fitting of response curves to the data. However the degree of difference in the functional responses of the predatory mites on the three different trichome densities suggests that this is a real effect and not an artefact of the experimental design. In addition, the culture of predatory mites was enhanced with mites from commercial sources on a regular basis to prevent any inbreeding effects altering the responses of the predatory mites.

Effect of prey spatial distribution on P. persimilis *predation rate*

The results of the experiments on prey spatial distribution suggest that when prey are distributed in more than one patch on a single cut stem, the predators exhibit a non-random searching behaviour, spending more time on leaves situated closer to the release point and in patches with a higher density of prey. However, prey spatial arrangement did not influence the total number of prey consumed by *P. persimilis* in a 24 h period, suggesting that the 24 h time period used in these experiments allows sufficient searching time for the predator to locate most of the prey patches. This is in accordance with the work of Eveleigh & Chant (1982b) who also found no differences in predation rates between different prey spatial arrangements.

In the experiment where the patches on the four leaves differed in prey density the results suggest that *P. persimilis* may be able to discriminate between different levels of prey on the patches. Greater predation was experienced in patches with higher prey densities, irrespective of the position of these patches in relation to the release point, although there was still an effect of leaf position. However, as the release point for the *P. persimilis* was always at the top of the stems, it is unclear whether *P. persimilis* spend more time close to the release point because they are not searching far, or because they prefer to be at the apex of the plant. The data from the predation on individual leaves do show that the *P. persimilis* find the majority of leaves, suggesting that although most predation occurs close to the release point, they are searching over the whole cut stem. Nevertheless, further experimental work is necessary to ascertain the full effect of release point on predation rates. Such experiments should examine the effect of different release points vertically stratified through the cut stem on the predation rates in different prey patches.

It is known that *P. persimilis* responds to volatile kairomones produced by its prey, particularly eggs, as used here (Sabelis & Van de Baan, 1983; Sabelis *et al*., 1984a,b), and so it is possible that *P. persimilis* could use these to discriminate between the profitability of prey patches. However, the kairomones also act as an arrestant for *P. persimilis* (Sabelis *et al*., 1984b), and it may be that once a high density prey patch is found, the abundance of prey and kairomones serve to retain the predator longer in these patches. However, the minimum prey density required to retain *P. persimilis* in a patch is not known. Further experiments will be necessary, where the searching of *P. persimilis* is monitored continuously over a period of time rather than making spot observations at set time intervals, as was done in the subsidiary experiment.

Implications for biological control

The results of the experiments in this study have important implications for biological control of ornamental crops. Many ornamental crops have trichomes on their leaves, and the success of biological control will depend on the relative impact of these trichomes on predators compared with prey. If predation rate is reduced, due to the presence of a high trichome density, predators may still be effective if the trichomes have a greater effect on the prey. Skirvin & de Courcy Williams (1999) showed that plant species has a major influence on fecundity and movement of *T. urticae*, with the greatest reduction in both of these on a trichome rich leaf. Kondo *et al*. (1998) showed that *T. urticae* development and population increase differed markedly between varieties of chrysanthemums, which is likely to be explained by trichome density. Therefore, as long as the high trichome density plants reduce development, fecundity and movement of the prey sufficiently, it will still be possible for predators to maintain control, even with a reduced predatory efficiency. This conclusion is supported by modelling studies of the control of *T. urticae* by *P. persimilis* on tomato plants (Skirvin, unpublished). Despite reduced predation rates, the predator was still able to exert control over *T. urticae* on tomato plants with a high trichome density, due to a greater impact of the trichomes on the pest. However, Roda *et al*. (2001) showed that the predatory phytoseiids *P. persimilis* and *Typhlodromus pyri* Scheuten (Acari: Phytoseiidae) preferred to inhabit and oviposit in more pubescent apple leaves or arenas enhanced with cotton fibres. In this case the trichomes were suggested as having been acting more as domatia (Walter & O'Dowd, 1992) rather than being a defence mechanism of the plant. Therefore, it will be essential to understand which role any leaf trichomes are fulfilling (shelter for predators or plant defence) to determine how they will influence biological control on crops.

The lack of meaningful biological differences in the predation rates at low prey densities at the three trichome densities suggest that trichome density has little effect on the searching behaviour of *P. persimilis* at low prey density. This is encouraging for biological control in ornamentals, where prevention of pest establishment is important, due to the extremely low tolerance to pest presence on ornamental crops. Repeated, prophylactic releases of the predator may well provide a robust strategy for the biological control of *T. urticae* in ornamental crops. However, it would be useful to know whether trichome density has an impact on the walking speed of the predators, for, if the movement of the predators is too slow, they may die of starvation before locating a prey patch.

Previous work has shown that trichome–rich plants can lead to lower mobility of *T. urticae* (Skirvin & de Courcy Williams, 1999). Coll & Bottrell (1994) suggested that vegetation texture (plant density, species diversity and structural complexity) may influence the abundance of a herbivore by affecting its movement. Hence, the use of crop species in rows, on which the pest shows a decreased movement, as 'barrier' crops between more susceptible crops may well decrease the rate at which an infestation spreads. If this was combined with frequent releases of predators on the 'barrier' crop, then it could prevent infestations from spreading rapidly.

The results from the pest spatial distribution experiments also support the use of prophylactic releases of natural enemies. Even at the low pest densities used in this experiment, predators are able to locate prey patches and attack the prey with similar predation rates, irrespective of the relative location of the patch on the plant. The ability of the predator to locate and eradicate sparsely distributed prey patches is the cornerstone of preventative biological control. The only problem that may occur arises from the observation that predators spend most of their time on prey patches close to the release point. Therefore, if there were several patches on a single plant, the predator may only locate those closest to its release point. However, this should be overcome by release of many predators, as opposed to the single predator used in this study, and further experiments using multiple predators would determine whether this was the case. Also, the results showed that some predators did visit most of the leaves of the cut stems, and so even if the predators were concentrated on those leaves closest to the release point, it is likely that some predators would find their way to patches further away. In commercial nurseries, *P. persimilis* are usually released by sprinkling them over the crop, which should give a good coverage across the plants and would hence ameliorate any problems due to *P. persimilis* remaining close to the release point. However, there are currently no data on the extent of coverage of plants provided by this release method, and experiments are required to determine whether this release method does give good coverage of the plants.

The results from this study underline the complexity of the multitrophic interactions taking place within plant-pest–natural enemy systems, and highlight the need for further work to elucidate the impact of both plant architecture and prey spatial distribution on these systems.

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