

The effects of refuge size and number on acarine predator–prey dynamics in a pesticide-disturbed apple orchard

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Summary

1. In apple orchards, the use of pesticides such as pyrethroids for the control of lepidopteran and dipteran pests can severely disturb natural equilibria by killing or repelling acarine predators. After spraying, phytophagous mite populations will often subsequently increase to densities which are above economic thresholds. To conserve predator populations we manipulated the size and number of predator refuges. Refuges were made with various sizes of polyethylene sheeting placed over 0, 10, 30, 60 or 100% of the leaves on trees before spraying with the pyrethroid permethrin.

2. At the time of spraying the phytoseiid predator *Typhlodromus caudiglans* and the stigmatid predator *Zetzellia mali* were present in similar densities. The main phytophagous mites present were the tetranychid mites *Panonychus ulmi* and *Tetranychus urticae*. After spraying, *Typhlodromus caudiglans* was virtually eliminated from sprayed leaves, but not from refuge leaves. Recolonization of sprayed leaves by *T. caudiglans* was slow, probably due to toxic or repellent effects of the pyrethroid residue. Densities of *Z. mali* were only slightly affected by the pyrethroid, but this species was unable to control tetranychid densities on sprayed leaves in the absence of *T. caudiglans*. After spraying, *P. ulmi* and *Tetranychus urticae* increased on sprayed leaves to densities well in excess of crop economic thresholds, while densities remained low on refuge leaves.

3. The major effect of refuge size was a high positive correlation between entire-tree densities of *T. caudiglans* and refuge size, and a high negative correlation with *P. ulmi* densities. The refuge size necessary to control *P. ulmi* to below economically damaging densities was predicted to be in excess of 60% of each tree. Thus, only 40% of each tree would receive a pyrethroid spray. This is not practical for management purposes as the reduced spray coverage is unlikely to control target lepidopteran and dipteran pests. No significant effects of refuge number were observed.

4. The application of a pyrethroid spray resulted in a major disturbance to natural acarine population dynamics in this orchard for up to 11 weeks after spraying. While refuges were useful in conserving a population of the predator *Typhlodromus caudiglans* and reducing entire-tree densities of phytophagous mites, the use of refuges may be more valuable when using pesticides with a lower residual effect.

Key-words: biological control, dispersal, pyrethroid, spider mites, *Typhlodromus caudiglans*.

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Introduction

For many years, ecologists have recognized the importance of refuges in maintaining predator and prey equilibria. The importance of refuges in agri-

cultural systems has been highlighted by the destruction of hedgerows and the correlated reduction in predaceous and parasitic insects in England earlier this century (van Emden 1965). Huffaker (1958) was one of the first researchers to demonstrate that refuges could maintain predator–prey equilibria, and since that time others have correlated the presence of refuges with population persistence and biological con-

trol (Murdoch *et al.* 1989; Lampo 1994; Begon, Sait & Thompson 1995).

In undisturbed orchard systems, phytophagous mites are generally controlled to below economic thresholds by acarine predation (Hardman *et al.* 1985; Thistlewood 1991). However, pyrethroid sprays applied to kill lepidopteran and dipteran pests have been shown to kill mite predators, but not their comparatively resistant phytophagous mite prey (for a review see Gerson & Cohen 1989). After spraying, residues can also alter predator distributions by sublethal repellency effects, but may not repel phytophagous prey (Penman, Chapman & Jesson 1981; Hermans 1996). Out of equilibrium with their predators, phytophagous mites such as *Panonychus ulmi* Koch and *Tetranychus urticae* Koch (Acari: Tetranychidae) can increase to abundances resulting in economic loss (e.g. Hardman, Rogers & MacLellan 1988). Thus, the use of pesticides in these orchards can be considered a serious disturbance to the predator-prey equilibrium.

In stream systems, refugia from flow disturbance are one of the most important factors influencing the recolonization rate of disturbed areas by stream insects (Lancaster & Hildrew 1993). Refuge patches need to be large enough to maintain sufficient prey to allow a viable predator population, and spatially distributed sufficiently widely for recolonization of predators to remote areas (Brokaw 1985). Similarly, in an orchard acarine community, for refuges to be successful for biocontrol purposes they must allow for the maintenance of a predator population in sufficient numbers for successful recolonization of the sprayed parts of the orchard, and consequent control of phytophagous mites after the effects of pesticide have subsided. The number of refuges may also be significant by aiding the spatial dispersal of predators to otherwise remote prey, as the probability of parasitoid dispersion has been suggested to decrease with increasing distance from the refuge (Corbett & Rosenheim 1996).

In acarine systems, Hoyt (1969) noted that selectively spraying trees with the fruit thinner/insecticide carbaryl to only the upper and peripheral areas of apple trees conserved a population of the mite predator *Typhlodromus occidentalis* Nesbitt (Acari: Phytoseiidae), indicating the potential of refuges in terms of biological control. The aim of the present experiment was to examine the effects of refugia on acarine communities within individual apple trees. We manipulated a population of acarine predators in an attempt to determine both the refuge size and number necessary for control of phytophagous mites after pyrethroid spray disturbance.

Materials and methods

STUDY SITE

An orchard consisting of 7-year-old 'Empire' variety apple trees at Jordan Station, Ontario, Canada, was

used for this study. Trees were spaced in seven rows with 4.8 m between rows and 3.0 m between trees. The trees were pruned annually and the grass between the trees mown regularly. Within the orchard a block of 45 trees was initially sampled. After 10 weeks, 33 trees were chosen from the 45 for further experimentation on the basis of similarity of the number of leaves, absence of disease, and similarity of the mite fauna. The number of leaves on each tree was then counted, and trees then pruned to standardize the number of leaves on each tree to ≈ 4000 .

TREATMENTS AND PYRETHROID SPRAY

Trees were randomly assigned to each treatment. There were two control treatments, one where trees were completely sprayed and the other with completely unsprayed trees, achieved by making large plastic bags to fit entire trees. The remaining 27 experimental trees were randomly assigned, nine to each of one of three tree refuge sizes; 10% (≈ 400 leaves), 30% (≈ 1200 leaves) or 60% (≈ 2400 leaves). Within each refuge size treatment there were three refuge number treatments consisting of 1, 3 or 6 refuges. This gave a total of nine treatments, with three replicate trees randomly assigned to each treatment. Where there was more than one refuge number within each refuge size, refuges were equally spaced around the tree. Where it was impossible to make a single large refuge from one branch, branches next to each other were used. Refuges were made by forming bags from polyethylene 'Vapor Barrier' plastic [150 μm thickness; W. Ralston (Canada) Inc., Brampton, Ontario, Canada] and gently placed over the leaves and branches. For example, the '30% refuge size and 3 refuge number' treatment was achieved by placing three bags over 400 leaves each.

The treatment day was chosen *a priori* as the time when the predator number had risen to ≈ 0.1 leaf⁻¹. The pyrethroid 'permethrin' was applied at a rate of 150 g (active ingredient) per hectare (75% of the recommended rate) with the field application undertaken using the tree-row-volume method (Sutton 1988). Treatment took place early in the morning under near windless conditions. Bags were placed on the trees, the spraying undertaken and the bags removed within 1 hour after spraying had finished in order to limit the temperature fluctuations within the bags. The temperature within two of the largest and smallest refuges was monitored using maximum-minimum thermometers.

SAMPLING AND ANALYSIS

Mites were sampled once every 2 weeks from June to October 1996, giving a total of 11 samples; five prior to spraying and six afterwards. Each sample consisted of 30 leaves, collected at random. Prior to spraying, one sample was taken from each tree. After spraying,

two samples were taken from each tree, one of leaves picked randomly within the refuges, and one from the sprayed areas. In the laboratory, mites were brushed from the leaves onto a glass plate using a Henderson–McBurnie mite brushing machine, and examined using a binocular microscope. Both eggs and motile stages were counted and for the purpose of analysis were combined to give one density estimate per species. Phytoseiid mites were mounted on slides in Hoyer's medium, cleared for 1 week on a slide-warmer at $\approx 45^{\circ}\text{C}$ and identified. The phytophagous mite *Aculus schlechtendali* (Nalepa) (Acari: Eriophyidae) was sampled from 3 weeks prior to spraying onwards and only adult stages were counted (due to the small egg size).

For each treatment, the 'entire-tree' density of mite genera was obtained by multiplying the densities in refuges by the proportion of the tree that was refuge (either 0.1, 0.3 or 0.6), multiplying the densities out of refuges by the proportion of the tree that was out of the refuge (either 0.9, 0.7 or 0.4, respectively), and adding the two estimates together. This 'entire-tree' estimate was used because the analysis of the economic effects of the mites are based on the average number of mites leaf⁻¹ for the entire trees. Differences in mite entire-tree densities between treatments were analysed using repeated measures analysis of variance with refuge size as a between factor, and refuge number and date of samples as within factors. Mean densities were considered statistically significant if $P < 0.05$. All numerical data were square root transformed and the residuals from each ANOVA were examined for normality and homogeneity of variance.

The distribution of the dependent variable was examined for fit to a normal distribution using Chi-square and Kolmogorov–Smirnov tests. All results are given as mean \pm standard error leaf⁻¹.

Results

PRIOR TO SPRAYING

The acarine predator population consisted primarily of the phytoseiid *Typhlodromus caudiglans* (Schuster) and the stigmatid *Zetzellia mali* (Ewing). Throughout the study, these two predators together made up over 95% of the acarine predators sampled from the orchard. There were also a few occasional specimens of the phytoseiids *Amblyseius fallacis* (Garman) and *Typhlodromus pyri* (Scheuten). *Zetzellia mali* was the first predator observed and was present from the first sampling date onwards, initially in higher densities than the tetranychid species (Fig. 1).

One week before spraying, the mean orchard density of *T. caudiglans* was 0.117 ± 0.018 (Table 1), and for *Z. mali* 0.141 ± 0.018 leaf⁻¹, with no significant differences among samples (Table 1). Thus, we estimated at the time of spraying that an average tree with ≈ 4000 leaves would have ≈ 468 specimens of *T. caudiglans* and 564 of *Z. mali*. In refuges of 400, 1200 and 2400 leaves we estimated ≈ 47 , 140 and 280 specimens of *T. caudiglans*, and 56, 169 and 338 of *Z. mali*, respectively.

The dominant phytophagous acarine species observed were *P. ulmi*, *Tetranychus urticae* and *A. schlechtendali*.

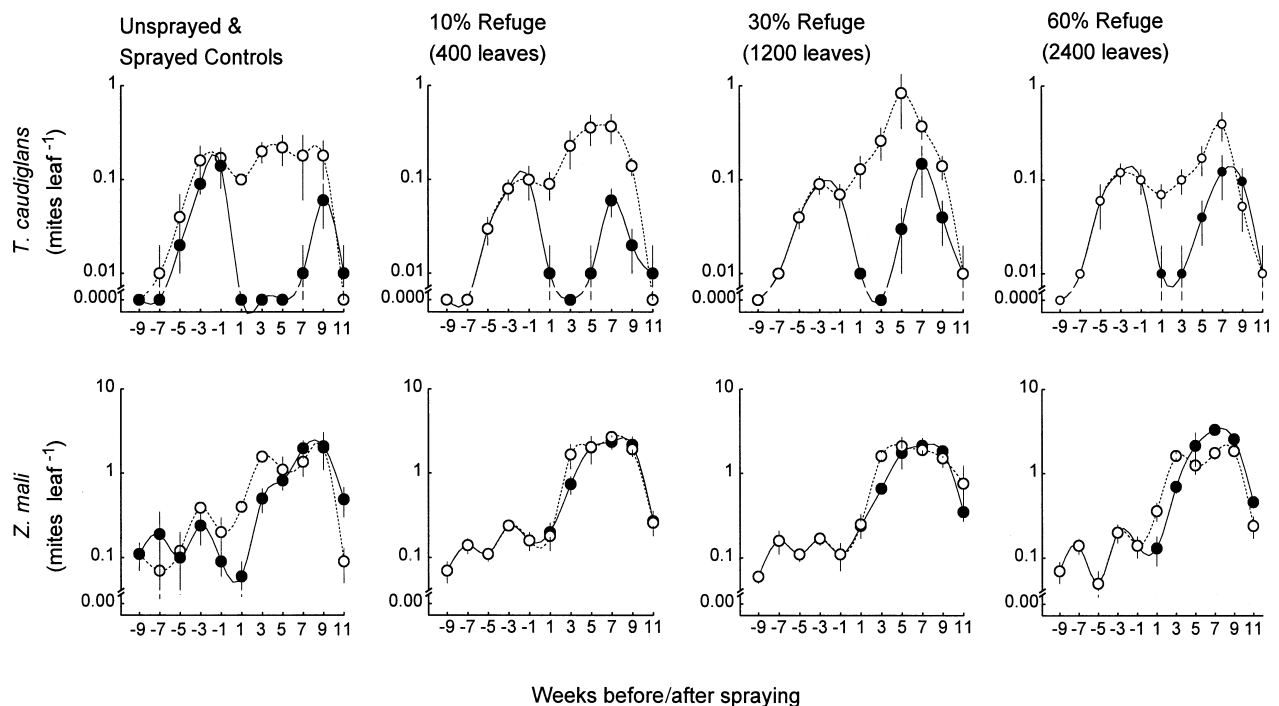


Fig. 1. Mean predatory mite (± 1 SE; $n = 9$) density of leaf⁻¹ in control, 10, 30 and 60% refuge treatments. Data points are for samples within refuges (○), and outside of refuges (●) after spraying. For controls; ○, unsprayed; ●, completely sprayed treatments.

Table 1. Entire-tree mean density (mites leaf⁻¹) of species in refuge size treatments

Species	Week	Refuge size					
		0%	10%	30%	60%	100%	
<i>P. ulmi</i>	-1	1.40	2.00	3.07	1.86	2.833	
	+1	2.18	6.25	7.77	6.25	5.078	
	+3	14.3	37.0	39.7	19.5	6.22	
	+5	67.9	77.4	58.2	30.1	9.6	
	+7	28.7	40.3	28.2	12.4	5.01	
	+9	7.47	7.87	5.82	3.66	1.89	
	+11	1.09	1.09	1.08	0.535	0.522	
	<i>T. urticae</i>	-1	0.122	0.267	0.278	0.278	0.578
		+1	0.155	0.282	0.290	0.269	0.700
		+3	0.589	1.73	1.74	0.797	0.544
		+5	2.17	4.01	4.73	1.89	2.81
+7		3.58	7.84	10.6	3.54	2.96	
+9		1.31	4.38	2.07	1.70	0.744	
<i>A. schlectendali</i>	+11	0.800	1.07	0.469	0.433	0.278	
	-1	1.43	3.85	0.566	0.515	1.85	
	+1	1.38	2.90	2.42	2.22	0.784	
	+3	12.4	17.7	12.2	9.67	12.5	
	+5	1.61	10.8	8.69	4.90	1.66	
	+7	7.01	11.5	6.02	2.32	1.09	
<i>T. caudiglans</i>	+9	14.0	9.02	5.04	3.43	0.845	
	+11	3.82	8.13	3.66	2.82	0.378	
	-1	0.144	0.103	0.070	0.100	0.167	
	+1	0.000	0.023	0.049	0.054	0.100	
	+3	0.00	0.042	0.085	0.069	0.200	
	+5	0.000	0.046	0.298	0.131	0.222	
<i>Z. mali</i>	+7	0.011	0.087	0.222	0.302	0.178	
	+9	0.056	0.031	0.074	0.067	0.178	
	+11	0.011	0.014	0.010	0.012	0	
	-1	0.089	0.159	0.115	0.141	0.200	
	+1	0.056	0.195	0.245	0.284	0.400	
	+3	0.500	0.824	0.973	1.310	1.567	
	+5	0.82	2.02	1.87	1.54	1.10	
	+7	1.97	2.40	2.06	2.27	1.36	
	+9	2.07	2.15	1.72	2.08	2.01	
	+11	0.489	0.273	0.485	0.314	0.089	

The latter was sampled from 3 weeks prior to spraying onwards. Throughout the sampling period we occasionally found tydeid and tarsonemid mites present in samples, but they were not identified beyond family.

The entire-tree mite analysis from all samples prior

to spraying indicated no significant differences for any mite species among trees with different intended refuge number or size treatments (Table 2). Only the time factor was significant, for all species except for *A. schlechtendali* ($F = 4.68$, $P = 0.074$).

Table 2. *F*-values from ANOVA on entire-tree refuge size (S), number (N) and time (T) effects, with interaction terms, for each mite species. * $P < 0.05$; *** $P < 0.001$

Species	Time	Effect						
		S	N	T	S × N	S × T	N × T	S × N × T
<i>P. ulmi</i>	Prior	0.238	0.327	55.0***	1.278	0.531	0.933	0.754
	After	5.99*	2.206	37.7***	0.558	0.773	0.618	1.077
<i>T. urticae</i>	Prior	0.220	0.592	26.2***	0.805	0.870	1.628	0.873
	After	1.910	0.567	15.0***	0.403	0.408	0.666	0.877
<i>A. schlechtendali</i>	Prior	1.013	0.363	4.670	0.988	0.827	1.558	0.933
	After	4.83*	0.429	14.5***	0.949	1.113	0.469	0.875
<i>T. caudiglans</i>	Prior	2.821	0.104	32.3***	0.783	0.441	1.008	1.022
	After	3.729	0.352	8.02***	2.289	1.822	0.280	1.040
<i>Z. mali</i>	Prior	0.412	2.422	9.12***	1.485	1.008	0.764	1.404
	After	0.947	1.112	38.2***	2.202	1.027	0.206	1.228

Spraying was undertaken with the pyrethroid permethrin on the 25th July 1996. Branches and leaves were bagged for a maximum of 95 min, while spraying was undertaken and until the leaves had dried. During this time, the maximum temperatures within the plastic bags ranged from 32°C in the smallest refuge, to 38°C in the largest refuge. While these temperatures were above that of ambient (range 21–23°C), they were not atypical for this orchard at this time of the year.

POST-SPRAYING

After spraying, no specimens of *Typhlodromus caudiglans* were found in sprayed trees for 5 weeks (Fig. 1). By contrast, their density in the refuges increased; in one tree up to 4.13 leaf⁻¹. Five weeks after spraying the average density of *T. caudiglans* in refuges throughout the orchard was 0.460 ± 0.199 leaf⁻¹, compared to 0.027 ± 0.009 on sprayed leaves. In weeks 0–7, the entire-tree *T. caudiglans* density was dependent on the presence of refuges. At week 7, a high proportion of the variation in densities could be

explained by the size of the refuges, though considerable variation was observed between replicates (Fig. 3). The highest entire-tree *T. caudiglans* density was found seven weeks after sampling, at 0.302 ± 0.098 leaf⁻¹ in the 60% refuge treatment (Fig. 3, Table 1). This probably resulted from higher prey availability in this treatment compared to that on unsprayed trees, from prey dispersing into refuges from adjacent sprayed leaves, and from a larger initial number of predators compared to that on completely sprayed trees.

The recolonization rate of *T. caudiglans* onto sprayed leaves was similar for trees in the sprayed control (0% refuge), and 10 and 30% refuge treatments (Fig. 1). In these treatments, the density of *T. caudiglans* was similar on sprayed and refuge leaves 11 weeks after spraying. For the 60% refuge treatment the density of *T. caudiglans* was similar on sprayed and refuge leaves 9 weeks after spraying. At no sampling date was *T. caudiglans* completely eliminated from the sprayed leaves of the 60% refuge treatment, although they were from the other refuge treatments (Fig. 1).

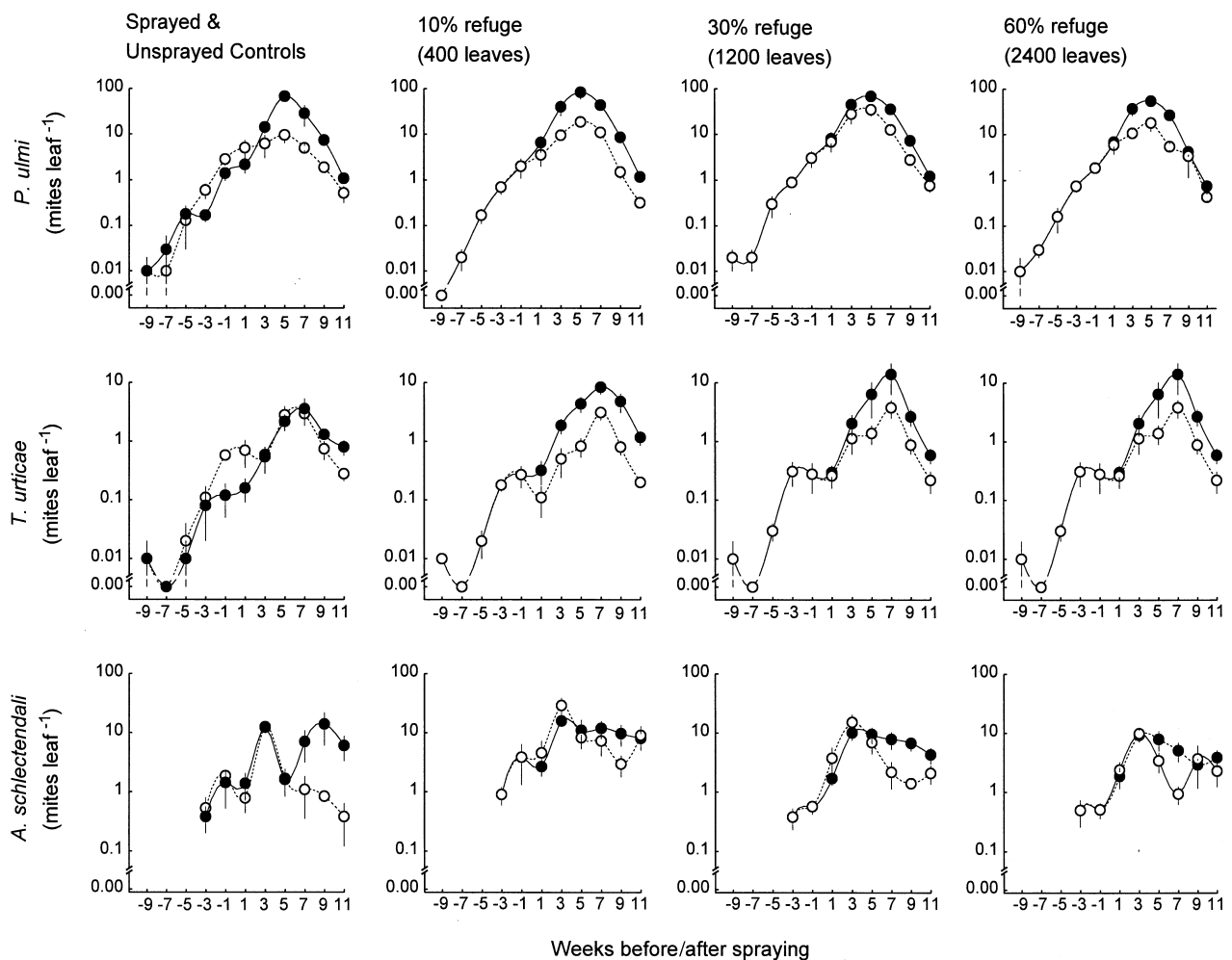


Fig. 2. Mean phytophagous mite (leaf⁻¹ ± 1 SE; n = 9) density in control, 10, 30 and 60% refuge treatments. Data points are for samples within refuges (○), and outside of refuges (●) after spraying. For controls; ○, unsprayed; ●, completely sprayed treatments.

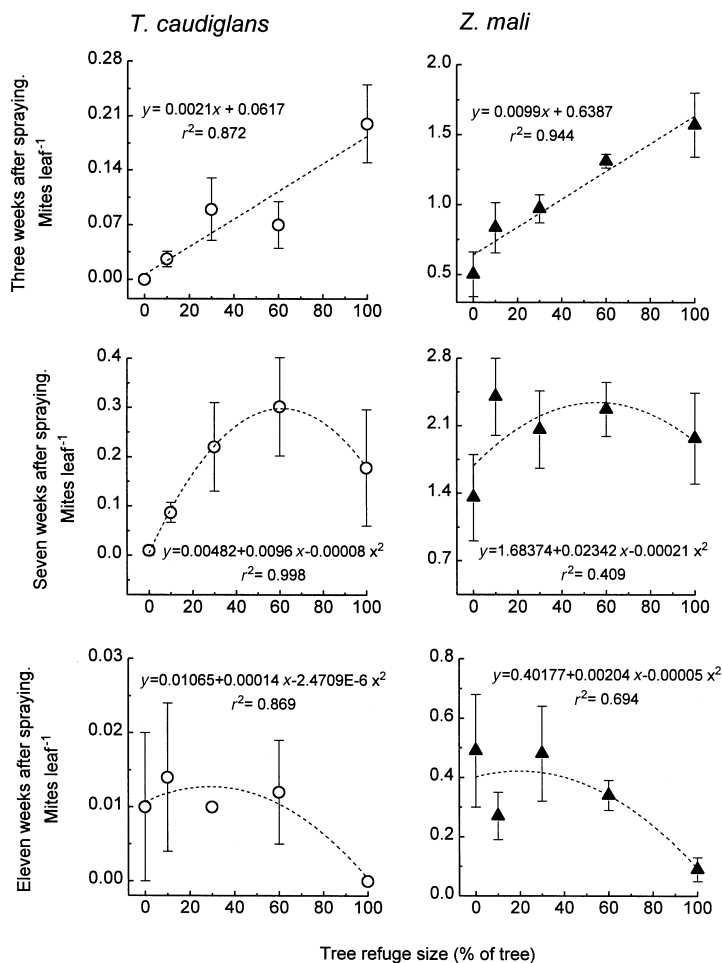


Fig. 3. The effect of refuges on predator densities, on a entire-tree basis (combining density estimates from both refuges and non-refuge leaves).

Prior to spraying, only the time factor was significant in our ANOVA model. For *T. caudiglans* after spraying, no significant differences in densities for entire-trees were found as a result of refuge size ($F = 3.729$, $P = 0.074$) or number ($F = 0.352$, $P = 0.710$), nor was any significance observed between interactions (Table 2). High variation within treatments may have clouded the observation of significant results. However, one of the drawbacks in using the repeated measures analysis was that it may have obscured significant results noted after the first few weeks after spraying. For example, 4 weeks after spraying the analysis resulted in both significant size ($F = 4.610$, $P = 0.048$) and time ($F = 8.351$, $P = 0.011$) effects.

The average density of the predator *Z. mali* in all refuges 5 weeks after spraying (1.971 ± 0.114 leaf⁻¹) was similar to that on sprayed leaves (1.786 ± 0.271). This is in contrast to the 3-week sample, when densities in refuges (1.633 ± 0.020) were higher than those on sprayed leaves (0.699 ± 0.024) (Table 1). Over 90% of the variation in entire-tree *Z. mali* densities is explained by the size of the refuges (Fig. 3). Seven weeks after spraying, the average densities in the

sprayed control, 10, 30 and 60% treatment were similar (combined mean of 2.21 ± 0.188 leaf⁻¹). This density was higher than that of the unsprayed control (1.335 ± 0.446), perhaps an effect of higher prey availability on sprayed leaves. Thus, *Z. mali* did not appear to be as affected by the pyrethroid spray as was *T. caudiglans*. Accordingly, no difference was observed between entire-tree refuge number or size treatments, or interactions thereof, and time was the only significant factor in the ANOVA ($F = 9.12$, $P = 0$; Table 2).

Densities of *P. ulmi* and *Tetranychus urticae* on sprayed leaves peaked on average at 69.0 ± 6.03 and 4.08 ± 0.89 leaf⁻¹, respectively, 5 weeks after spraying (Fig. 2). By contrast, mean densities on refuge leaves were 20.37 ± 5.36 and 1.55 ± 0.44 leaf⁻¹, respectively (Fig. 2). Similar differences in tetranychid densities between refuges and treated leaves continued for the remainder of the sampling period. Thus, spraying the pyrethroid in some way(s) increased the abundances of these mites. Densities of *P. ulmi* in refuges were slightly higher than those in unsprayed controls (Fig. 2), possibly an effect of mites dispersing from high (sprayed) to low (refuge) density areas.

A major effect of refuge size was to decrease the average entire-tree density of mites. For example, at 3, 7 and 11 weeks after spraying, between 83 and 92% of the variation in the *P. ulmi* density between treatments was explained by differences in refuge size (Fig. 4, Table 1). This trend was true for all samples taken three to nine weeks after spraying (Table 1). Significant effects of refuge size were found in the entire-tree analysis of *P. ulmi* densities ($F = 5.99$, $P = 0.027$), as well as a significant time factor ($F = 32.7$, $P = 0$) (Table 2). At no time did we observe a significant effect of refuge number or interaction effect on entire-tree tetranychid mite densities.

Densities of *P. ulmi* on sprayed control trees did not increase immediately as they did on sprayed leaves of other treatments. One week after spraying, densities on completely sprayed control trees were lower than densities of unsprayed controls, unlike densities on any of the other sprayed leaves (Fig. 2). To determine if this result was an outlier, we sampled three other completely sprayed trees (chosen at random within the orchard), and found densities which approximated

predicted values from the linear model fitted to data from the other treatments (Fig. 4). Densities of *P. ulmi* on sprayed control trees did reach similar densities as those on other sprayed leaves 5 weeks after spraying (Fig. 2). However, this effect typified the high variation in the response of the tetranychid mites to spraying. While densities of these mites increased on all treated leaves subsequent to spraying, some replicates of treatment populations peaked in density 3, 5 or 7 weeks after spraying.

Densities of *A. schlechtendali* in treatment trees initially appeared to show little response to spraying. However, after week 5, densities increased on sprayed leaves relative to those in refuges. This trend continued until week 9 when densities on sprayed leaves peaked at 9.98 ± 0.199 leaf⁻¹, compared to 1.73 ± 0.630 on unsprayed leaves, with the exception of the 60% refuge treatment. This result could in part be due to a decreased number of predators on the sprayed leaves.

The increased density of *A. schlechtendali* on sprayed leaves resulted in a significant effect of refuge size in the entire-tree analysis ($F = 4.83$, $P = 0.044$) (Table 2). The highest *A. schlechtendali* entire-tree density was observed nine weeks after spraying in the completely sprayed (0% refuge) treatment at 14.0 leaf⁻¹, which decreased in a linear fashion with percentage refuge, to 0.845 leaf⁻¹ on the unsprayed treatment (Table 1).

Discussion

After spraying the orchard with the pyrethroid permethrin, the predatory mite abundance decreased sharply, which is in agreement with other studies (reviewed by Gerson & Cohen 1989). Correlated with the decrease in predatory mites, the densities of the tetranychid mites *P. ulmi* and *Tetranychus urticae* increased on sprayed leaves relative to their densities on unsprayed leaves in refuges. For example, the mean orchard density of *P. ulmi* on sprayed leaves reached 69.0 leaf⁻¹, compared to 20.4 leaf⁻¹ on unsprayed leaves in refuges. This sprayed leaf peak density is over four times the estimated economic threshold (Croft & McGroarty 1977). The predator *Typhlodromus caudiglans* was virtually eliminated from sprayed leaves for 5 weeks after spraying, but populations were maintained on refuge leaves. However, the reduced predation may not have been the only factor in the increased tetranychid densities on sprayed leaves, as pyrethroids can increase factors such as the fecundity and dispersal behaviour of tetranychid mites (reviewed by Gerson & Cohen 1989).

The efficacy of a predatory mite for biological control depends on its predation rate, population growth rate, and its ability to disperse and spatially couple with prey populations (Sabelis 1992; Lesna, Sabelis & Conijn 1996). Our initial aim in this study was to manipulate the size of the refuge and, hence, the pred-

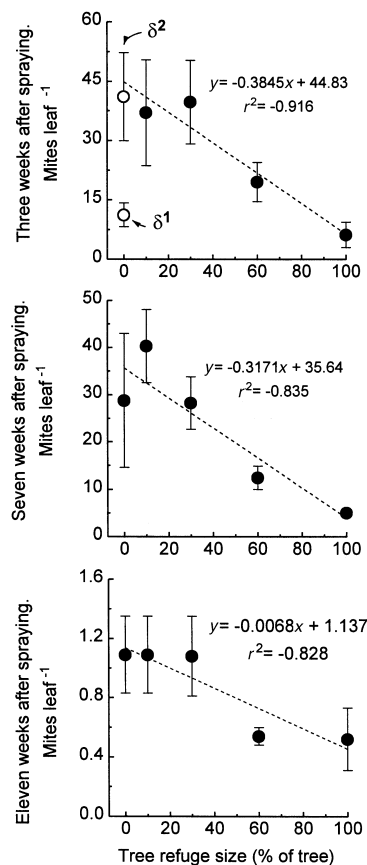


Fig. 4. The effect of refuges on *P. ulmi* densities, on a entire-tree basis (combining density estimates from both refuges and non-refuge leaves). δ_1 is the actual data value for the completely sprayed control treatment. As this point did not fit the model further samples were taken (δ_2), and δ_1 thus considered an outlier. Neither point was used in the regression analysis.

ator population in each treatment at the time of disturbance. These predators could then have acted as a founder population for each tree subsequent to spraying. However, densities of *T. caudiglans* on sprayed leaves remained low and uncoupled with those of *P. ulmi* for at least 5 weeks after spraying. This effect was probably due to residual effects of the pyrethroid, killing or repelling *T. caudiglans* (Penman, Chapman & Jesson 1981; Bostanian, Belanger & Rivard 1985). We may have observed a different effect if we used a pesticide with a low residual effect. However, significant effects were noted between entire-tree densities of the phytophagous mites *P. ulmi* and *A. schlechtendali*, indicating increased biological control in trees with larger refuge sizes.

For the phytophagous mites, sprayed leaves became a partial refuge from *T. caudiglans* predation, in that the predation rate was not completely eliminated, but rather the probability of predation was much reduced. During this time the major effect of the refuges was to decrease the entire-tree *P. ulmi* density, and maintain a predator population. Only after 7 weeks, when permethrin residues have usually dissipated significantly (Bostanian, Belanger & Rivard 1985), did *T. caudiglans* begin to appear in similar numbers on sprayed leaves to those on refuge leaves. For the completely sprayed, 10 and 30% treatments the *T. caudiglans* recolonization occurred at a similar time, suggesting that aerial dispersal from other trees was at least as important as recolonization from refugia within a tree. Aerial dispersal is also the method for recolonization of pesticide-disturbed habitat for other arthropod predators such as spiders, local populations of which may become extinct without refuges (Halley, Thomas & Jepson 1996).

A high aerial dispersal rate may have resulted in the observed lack of significant effects of refuge number. We hypothesized initially that the number of refuges within a tree could be important in aiding dispersion of the predator to otherwise remote prey populations, reducing the dispersal distance necessary to find the prey population. Even though *T. caudiglans* is supposedly a poor disperser relative to other phytoseiid mites (Johnson & Wellington 1984), refuge number effects were not significant. Consequently, for management practices, it appears that a single large refuge may be as effective as numerous small refuges.

The role of refuges in decreasing the amplitude of predator-prey oscillations has been noted elsewhere (Huffaker 1958; Murdoch *et al.* 1989; Hawkins, Thomas & Hochberg 1993), though not in the context of pesticide treatments. Earlier work has concentrated on providing prey species with a refuge in order to avoid over-exploitation of the prey by predators. In our study the effect was to provide a refuge for predators to avoid an extrinsic mortality factor (the pyrethroid spray), which would have destabilized the prey-predator system by the near complete elimination of predators leading to rapid population

expansion of the prey species. Predator populations in refuges acted by decreasing the mean entire-tree density of phytophagous mites, rather than the refuges providing a population of predators for dispersion to sprayed leaves. A high percentage of the variation in entire-tree predator and prey densities could be explained simply by the size of refuges. The predators *T. caudiglans* and *Z. mali* appeared to limit *P. ulmi*, *A. schlechtendali* and, to a lesser extent, *Tetranychus urticae* densities in unsprayed trees or refuges.

Densities of *Z. mali* were initially only slightly reduced on sprayed leaves and, subsequently, populations of this predator equalled or exceeded those on refuge leaves. However, *Z. mali* alone was unable to control the *P. ulmi* outbreak on sprayed leaves. This result is similar to that of Santos & Laing (1985) who showed that *Z. mali* is much less voracious than are phytoseiids, and is unable to control *P. ulmi* outbreaks. In fact, the presence of *Z. mali* in North American orchards has been shown in some cases to inhibit biological control of *P. ulmi* and *T. urticae* through intra-guild predation or competition (Clements & Harmsen 1990; MacRae & Croft 1996). This effect was highlighted in simulations which consistently showed decreased *Typhlodromus caudiglans* populations and increased *P. ulmi* populations, as densities of *Z. mali* increased (Woolhouse & Harmsen 1987). In the present study, *Z. mali* may have thus inhibited *T. caudiglans* recolonization and consequent biological control of *P. ulmi* onto sprayed leaves.

The creation of large refuges throughout time may serve to encourage predator diversity within managed orchards, as Hochberg & Hawkins (1992) postulated. In our study we commonly observed only two major predators, *T. caudiglans* and *Z. mali*. Compared to unsprayed orchards in this area, this is a much reduced predator diversity (Thistlewood 1991). The use of refuges may aid in increasing predator diversity, which has been correlated with an increased probability of biological control (Hawkins & Gross 1992), and there is some evidence for this effect in acarine systems of apple orchards (Croft & Slone 1997).

With the predator and prey densities observed in this study, we demonstrated that it was necessary to have a refuge of at least 60% of the tree to restrict *P. ulmi* densities to below economic thresholds, which appears impractical for pest control. However, in some crops refuges from pesticide disturbance do approximate this size. For example, sprays are applied to every alternative row of apples in Pennsylvania, maintaining mite predator populations within the orchard (Hull, Hickey & Kanour 1983). There is increasing evidence that refuges consisting of plants other than the crop (e.g. Corbett & Rosenheim 1996), or as part of the crop (e.g. Thomas, Wratten & Sotherton 1991), can maintain a source of predators for biological control. Further work is needed on the effects of refuge size on other orchard pest species, with their associated predators and parasitoids. The maintenance of predator popu-

lations for control of the pest when undisturbed, and their subsequent dispersal onto pesticide-disturbed leaves and trees, are two key factors for controlling phytophagous mite outbreaks that are themselves induced by agricultural practices.

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