Influence of ground cover on spider populations in a table grape vineyard

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Abstract. 1. Cover crops and/or resident ground vegetation have been used in California vineyards to increase the number of predators and decrease the number of pestiferous herbivores. The most common resident predators in vineyards are spiders (Araneae). Several observational studies suggest that the addition of cover crops results in an increase in spider density and a decrease in insect pest densities.

2. To test experimentally the effects of cover crops and/or resident ground vegetation (hereafter collectively referred to as *ground cover*) on spider populations, a 3-year study was undertaken in a commercial vineyard. Large, replicated plots were established with and without ground cover during the growing season. Spider species diversity was analysed on the vines and on the ground cover.

3. On the vines, there was no significant difference in spider species richness or the total number of spiders in plots with and without ground cover. There were differences in the relative abundance of two spiders between treatments, with one species (*Trachelas pacificus* [Chamberlin & Ivie]) more abundant in plots with ground cover and another (*Hololena nedra* Chamberlin & Ivie) more common on vines in plots with no ground cover. Annual variation in spider abundance was greater than variation due to ground cover treatment.

4. On the ground cover, the spider species diversity was considerably different from that found on the vines above, suggesting that there is little movement of spiders between the ground cover and the vines. Enhancement of *T. pacificus* populations on vines with ground covers may be a result of prey species movement between the ground cover and the vines. Spider abundance was sparse on the bare ground.

5. The maintenance of ground cover increased spider species diversity in the vineyard as a whole (vine and ground cover). However, the relatively small changes in spider abundance on the vines indicate there are limitations in the use of ground covers for pest management with respect to generalist predators.

Key words. Cover crops, crop diversity, grapes, natural enemies, spiders, *Trachelas*.

Introduction

A diverse plant community can influence arthropod natural enemy populations by providing critical food or habitat resources that might not be found in a simple plant community (Perrin, 1980; Andow, 1991; Bugg & Waddington, 1994). In agroecosystems, the plant community can be manipulated through the addition of cover crops or by allowing resident (weedy) vegetation to grow (Altieri, 1991). This increased diversity in the plant community sometimes results in an increase in the numbers of entomophagous insects and a decrease in the numbers of herbivores (reviewed by Altieri & Letourneau, 1982; Risch *et al*., 1983; Russell, 1989; Andow, 1991). However, the apparent negative correlation between natural enemy and herbivore abundance may not consistently or solely explain how vegetational diversity results in lowered herbivore density. In fact, the exact ecological mechanisms through which crop diversification changes arthropod populations are poorly known for most agricultural systems (Sheehan, 1986; Letourneau, 1990). For example, the addition of cover crops to any agroecosystem can change the herbivore's host plant characteristics and the agroecosystem's microclimate, both of which can result in a change in herbivore abundance (e.g. Grüber & Dixon, 1988; English-Loeb, 1989; Silvanima & Strong, 1991; Castañé & Savé, 1993; Willmer *et al*., 1996) that might otherwise be attributed to an increase in natural enemy numbers.

In order for pest management decisions to be consistently effective, it is vital that the ecological processes that govern pest population dynamics are understood. In Californian vineyards, the management of ground cover, either in the form of planted cover crops and/or resident vegetation, has become a popular component of integrated pest management (Ingels & Klonsky, in press). The primary insect pests in the vineyard ecosystem are leafhoppers (*Erythroneura elegantula* Osborn and *E. variabilis* Beamer), moths (*Desmia funeralis* [Hübner], *Harrisina brillians* Barns & McDunnough, and *Platynota stultana* Walshingham), spider mites (*Tetranychus pacificus* McGregor and *Eotetranychus willametti* [McGregor]) and mealybugs (*Pseudococcus maritimus* [Ehrhorn] or *P. affinis* Maskell). Each of these pests is attacked by variety of specialist and/or generalist natural enemies. A survey of generalist predators on grapevines found a whirligig mite (*Anystis agilis* [Banks]), the convergent lady beetle (*Hippodamia convergens* Guérin-Méneville), a damselbug (*Nabis americoferus* Carayon), green lacewings (*Chrysoperla* spp. and *Chrysopa* spp.), and a diverse complex of spider species (Cate, 1975). The objective of this study was to assess experimentally the effect of ground cover on natural enemies that are found in the vineyard. It was decided to focus efforts on spiders for three reasons. First, spiders comprise $>$ 90% of predators (excluding predators of mites) collected on the vines (M. J. Costello & K. M. Daane, unpublished data) and are thus the best indicator in assessing the relative differences in the generalist predator populations between cover cropped and clean cultivated vineyards. Secondly, spiders (as a group) can probably affect the population density of most of the primary insect pest species listed previously. Thirdly, it has been suggested that ground cover can increase spider density, resulting in a decrease in the density of leafhoppers (Settle *et al*., 1986; Wilson *et al*., 1992).

Materials and methods

Study site

The experiment took place in a table grape vineyard (cv. Ruby Seedless) near Reedley, Fresno County, California. The grapevines were trained to a bilateral cordon, and trellised on a 0.9 m cross-arm with two catch wires. Rows were spaced 3.6 m wide and vines were spaced 2.4 m within the row. The two treatments tested were: (1) maintenance of cover crop and/or resident vegetation during the growing season (hereafter referred to as the *ground cover* treatment), and (2) no ground cover within or between rows during the growing season (hereafter referred to as the *no cover* treatment). Establishment of the *ground cover* plots took place in the autumn prior to the study season; in November 1992 and 1993, the entire site was seeded to a 4:1 cover crop mixture of purple vetch (*Vicia benghalensis*) and barley (*Hordeum vulgare*) at a rate of 11 kg seed ha^{-1}. In November 1994, the site was seeded to a 1:1:1 cover crop mix of fava beans (*Vicia fava*), Austrian winter peas (*Pisum sativum*) and common vetch (*Vicia sativa*) at a rate of 23 kg seed ha^{-1}. In March of each season (1993, 1994 and 1995) the cover crop was mowed, then allowed to regrow, mature and set seed. By late May, the seeded cover crop was replaced by a mixture of resident grasses that included cupgrass (*Echinochloa* spp.), large crabgrass (*Digitaria sanguinalis* [L.] Scopoli), yellow foxtail (*Setaria gracilis* Kunth), and Bermuda grass (*Cynodon dactylon* [L.] Pers.). In 1995, all vegetation in the ground cover treatment was removed in mid-July with a treatment of glyphosate. Establishment of the *no cover* plots took place by tilling under the cover crop in late March of each year. Afterwards, the *no cover* plots were kept free of resident vegetation until mid-August, using multiple applications of glyphosate (1993) or by cultivating between the vine rows and French ploughing within vine rows (1994 and 1995). The experimental design was a randomized complete block, with five replicates of each block. Each plot (experimental unit) was 1.4 ha (eight rows wide $\times$ eighty vines long).

Pesticides used during the 3-year period were sulphur, applied weekly beginning just after budbreak (early April) and continuing until harvest (September), to control powdery mildew (*Uncinula necator* Burrill), and cryolite (sodium fluoaluminate) (Cryocide, Elf Atochem North America, Philadelphia, Pennsylvania), applied in May to control two lepidopteran pests (*H. brillians* and *P. stultana*). These materials were applied equally to all plots.

Arthropod sampling

Spiders and other predators were sampled using methods described by Costello & Daane (1995). In brief, to sample spiders on the vines, a 9 $\times$ 3 m muslin drop cloth was laid on the ground directly underneath the area covered by the trunk, canes, and foliage of two adjacent vines. For $\mp$ 15 s the vine foliage was shaken by hand and the vine trunks were beaten with mallets to dislodge predators onto the muslin sheet. With the exception of spider mite predators, all dislodged ambulatory predators were collected with small battery-powered vacuums. In 1993 and 1994, one drop cloth sample plot^{-1} was taken in the morning (between 07.00 and 11.00 hours) and again in the evening (between 19.00 and 23.00 hours). The morning and evening samples were taken to account for sampling error that might result from nocturnal movements of spiders from the ground cover to the vines. Because there was no significant difference in the species composition or abundance between diurnal and nocturnal samples (M. J. Costello & K. M. Daane, unpublished data), in 1995 all samples were taken between 07.00 and 11.00 hours. To sample spiders on the ground cover, a 1.0 $\times$ 1.5 m frame was placed in two randomly selected sections of ground cover in each plot. All spiders on the vegetation within the frame were collected using a D-vac, in this case a gasoline powered blower-vacuum (Echo Inc., Lake Zurich, Illinois) that had an intake rate of 10.8 m^3 min^{-1} when fitted with a 10-cm diameter orifice. Spiders were collected in an organdy net placed inside the intake port. For each plot, the two D-vac samples collected on each sampling date were combined. Observations indicated that spider density on the ground in the *no cover* treatment was very low, so no attempt was made to sample with the D-vac. Spiders from vine and ground cover samples were stored in 70% alcohol and later identified in the laboratory to genus or species. Samples were taken each month from May to September.

Statistical analysis

It has been shown that data sets consisting of multiple species of spiders do not meet the ANOVA assumption of independence of mean density and variance (Costello & Daane, 1997a). Therefore, for the total spider density analysis, monthly means of all spider species combined were ranked (PROC RANK, SAS Institute, 1995) and an ANOVA was performed on the ranks (equivalent to the Kruskal–Wallis one-way test, PROC GLM, SAS Institute, 1995). For individual spider species, an attempt was made to stabilize the variance by log or square root transformation of the data (Southwood, 1978). Four spider data sets did not meet the assumption of independence: *Metaphidippus vitis* (Cockerell), *Oxyopes* spp. (*Oxyopes scalaris* Hentz and *Oxyopes salticus* Hentz), *Hololena nedra* Chamberlin & Ivie, and *Neoscona oaxacensis* (Keyserling). Mean densities for these species were ranked (PROC RANK, SAS Institute, 1995) and an ANOVA was performed on the ranks (equivalent to the Kruskal–Wallis one-way test, PROC GLM, SAS Institute, 1995). For all Kruskal–Wallis analyses, a split-plot design was used, with ground cover management as the main plot factor, study year as the subplot factor, and monthly samples as replications. Thus, the main plot error was ground cover × replicate interaction (d.f. = 4) and the subplot error was the floor management × replicate × year interaction (d.f. = 8).

Two spider species data sets (*Trachelas pacificus* [Chamberlin & Ivie] and *Cheiracanthium inclusum* [Hentz]) were square root transformed, and were subsequently analysed by repeated measures ANOVA (PROC GLM, SAS Institute, 1995).

Because there was no ground cover × year interaction for total spider population density or for any spider group ($P > 0.05$), analyses were performed for the entire 3-year period. Numbers of adult and immature spiders were combined for these analyses.

Spider species similarity between the vine canopy and the ground cover was estimated by the Bray-Curtis measure of dissimilarity (Bray & Curtis, 1957; Krebs, 1989):

$$B = \frac{\Sigma|X_{ij} - X_{ik}|}{\Sigma(X_{ij} - X_{ik})}$$

where X_{ij}, X_{ik} = percentage of species i in each sample.

This index is presented as a measure of similarity by using the complement of B, (1 – B), as suggested by Wolda (1981). Values of 1 – B range from 0 (dissimilar) to 1 (similar).

Results

On the vines, there were no major differences in spider species richness or total abundance between treatments with and without ground cover (Table 1). Six spider species comprised 93.1 and 92.0% of the collected spiders on vines in treatments with and without ground cover, respectively. These were: *T. pacificus*, *C. inclusum*, *Oxyopes* spp., *M. vitis*, *H. nedra*, and *N. oaxacensis* (Table 1). Total spider abundance (all species combined) tended to be higher in the *no cover* treatment early in the season, and higher in the *ground cover* treatment thereafter (Fig. 1). Overall, spider density on the vines did not differ significantly between treatments ($F_{1,4} = 0.35$, $P = 0.4533$) (Table 2).

On an individual species basis, there were some differences in relative abundance of spiders between treatments. *Trachelas pacificus*, which was the dominant spider at this site, had a season-wide abundance that was 53.2% higher in the *ground cover* treatment than in the *no cover* treatment ($F_{1,90} = 5.15$, $P = 0.026$) (Table 2). This corresponds to an average of 2.5 more *T. pacificus* per vine with cover crop than without. However, the seasonal pattern of *T. pacificus* shows a greater difference between treatments late in the season (Fig. 2), which corresponds to peak densities of pests such as leafhoppers. In August and September, average *T. pacificus* abundance was consistently higher in the *ground cover* treatment and was 59.6% higher over the 3-year period ($F_{1,30} = 26.20$, $P<0.0001$) (Fig. 2). This corresponds to an average of 7.0 more *T. pacificus* per vine in *ground cover* plots than in *no cover* plots during August and September.

Of the other species, only *H. nedra* abundance was significantly different between treatments. Overall, numbers of *H. nedra* were 52% higher in the *no cover* treatment than in the *ground cover* treatment ($F_{1,4} = 64.85$, $P = 0.001$) (Table 2). Because *H. nedra* does not constitute a very high proportion of spiders in this vineyard, this amounted to an average increase of only 0.6 *H. nedra* per vine in *no cover* plots compared with *ground cover* plots. This difference was not consistent among sample years and appears to be largely a result of 1995 data, when numbers of *H. nedra* were twice as high with ground cover as without (Table 2).

On the ground, there were considerable differences in spider diversity with or without ground cover. However, no statistical analysis was made to compare spiders on the ground cover with spiders where there was no cover. Throughout the experiment, however, ground dwelling spiders were observed in the *no cover* treatment and only one species, *Pardosa ramulosa* (McCook), was commonly found. In contrast, the ground cover supported a diverse assemblage of spider species (Table 1).

Spider diversity in the vine canopy was slightly different between treatments, with a similarity index of 0.851 (Table 3). Spider diversity between spiders collected on the vine and on the ground cover was very different, the similarity index between spiders on the ground cover and on vines with ground cover was 0.279, and on vines with no cover was 0.360 (Table 3). This is reflected in the differences seen in relative abundance for each of the spider taxa. For example, *T. pacificus*, *C. inclusum* and *M. vitis* were common on the vine but accounted for only 2.0, 2.6 and 0%, respectively, of species on the ground cover (Table 1). There were some spider taxa with closely matched relative abundances, e.g. *Oxyopes* spp. (O. *scalaris* and *O. salticus*), the most common spiders

Table 1. Total number and percentage spider composition of spiders (adults and immatures combined) collected on grapevines in plots with and without ground cover and in the ground cover itself. Data are combined from samples taken in 1993, 1994 and 1995.

		Vines					
		Ground cover treatment		No cover treatment		Ground cover	
Family	Species	*n*	%	*n*	%	*n*	%
Corinnidae	*Trachelas pacificus*	2131	47.4	1382	34.4	7	2.0
Clubionidae	*Cheiracanthium inclusum*	660	14.7	683	17.0	9	2.6
Clubionidae	Unidentified clubionids	0	0	0	0	4	1.2
Oxyopidae	*Oxyopes* spp.	516	11.5	719	17.9	100	28.9
Salticidae	*Metaphidippus vitis*	447	9.9	354	8.8	0	0
	Metacyrba taeniola	19	0.4	20	0.5	0	0
	Phidippus clarus	5	0.1	4	0.1	0	0
	Thiodina spp.	3	<0.1	1	<0.1	6	1.7
	Phidippus johnsoni	2	<0.1	2	<0.1	0	0
	Habronattus spp.	0	0	1	<0.1	2	0.6
	Platycryptus californicus	3	<0.1	2	<0.1	0	0
Salticidae	Unidentified salticids	10	0.9	14	0.3	14	6.1
Agelinidae	*Hololena nedra*	239	5.3	362	9.0	9	2.6
Araneidae	*Neoscona oaxacensis*	193	4.3	198	4.9	19	5.5
	Unidentified araneids	4	<0.1	6	0.1	0	0
Theridiidae	*Theridion* spp.	68	1.5	98	2.4	0	0
	Latrodectus hesperus	0	0	1	<0.1	0	0
Linyphiidae	*Erigone dentosa*	55	1.2	80	2.0	38	11.0
Lycosidae	*Pardosa ramulosa*	25	0.6	15	0.4	84	24.3
	Schizocosa mccooki	1	<0.1	1	<0.1	0	0
Gnaphosidae	*Nodocion voluntarius*	32	0.7	21	0.5	0	0
Thomisidae	Unidentified thomisids	21	0.4	19	0.5	8	2.3
Anyphaenidae	*Anyphaena pacifica*	6	0.1	0	0	4	1.1
	Aysha incursa	6	0.1	8	0.2	5	1.4
Dictynidae	*Dictyna calcarata*	0	0	1	<0.1	6	1.7
Mimetidae	*Mimetus hesperus*	4	<0.1	3	<0.1	0	0
Unidentified	Miscellaneous species	32	0.7	21	0.5	19	5.5
Total		4495	100	4018	100	345	100

on the ground cover and also common on the vines in both treatments. However, *P. ramulosa* and *Erigone dentosa* (O.P.-Cambridge) accounted for 24.3 and 11.0% of spider species on the ground cover, respectively, but only 0.5 and 1.6% of the species on the vines (both treatments combined). Spider species richness was greater on the vines (twenty-four species or genera) than the ground cover (thirteen species or genera), although a greater percentage of spiders on the ground cover were unidentifiable.

Discussion

In central Californian vineyards, spiders are the most abundant predators of insects, regardless of the presence or absence of ground cover (M. J. Costello & K. M. Daane, unpublished data). Roltsch *et al*. (in press) showed that there were higher numbers of spiders in vineyards with ground cover than in clean cultivated vineyards. In other perennial systems, Altieri & Schmidt (1985) and Wyss *et al*. (1995) found higher densities of spiders in apple orchards with ground cover and concluded that increased predators in the apple canopy helped to decrease pest densities. With one exception (Wyss *et al*., 1995), these results are not from replicated studies.

These studies and work conducted in other agroecosystems suggest that increased plant diversity can result in an increase in the abundance and diversity of entomophagous predators (reviewed by Altieri & Letourneau, 1982; Sheehan, 1986; Russell, 1989; Andow, 1991). However, there have been relatively few studies that directly correlate ground cover to the increase of a particular entomophagous predator or predators and the subsequent decrease in herbivores. Fewer still can separate the biotic from the abiotic effects that ground cover might have on herbivore populations (Sheehan, 1986).

This study sought to determine whether the continuous presence of ground cover leads to changes in the spider community that could reduce herbivore densities. Several observations have been made on the decrease in the number of leafhoppers (*E. elegantula* and *E. variabilis*) after the addition of ground cover to vineyards (Settle *et al*., 1986; Roltsch *et al*., in press). However, the results of this study showed relatively few differences in spider species diversity or density on grapevines with or without continuously managed ground cover. Therefore, this research casts doubt on the hypothesis that observed decreases in leafhopper abundance in vineyards with ground cover are solely the result of changes in the spider community on the vines. Nevertheless, the results do not rule out a relationship among ground cover, spiders, and herbivores, for although there was no difference in total spider abundance, there was a small, but significant, seasonal increase in the abundance of the dominant spider at this site, *T. pacificus*. In laboratory studies, *T. pacificus*, a nocturnal hunting spider, was one of the better leafhopper predators (M. J. Costello & K. M. Daane, unpublished data). The greatest increases in *T. pacificus* density on vines with ground cover occurred during August and September of each study year, corresponding to decreases found in third generation leafhopper abundance (Daane & Costello, in press). This suggests that increases in populations of *T. pacificus* might contribute additionally to leafhopper control. However, *T. pacificus* does not comprise a significant proportion of the spider community in every vineyard (Costello & Daane, 1995), and the presence of ground cover has been shown to decrease leafhopper nymphs even where *T. pacificus* populations are low or non-existent (Costello & Daane, in press).

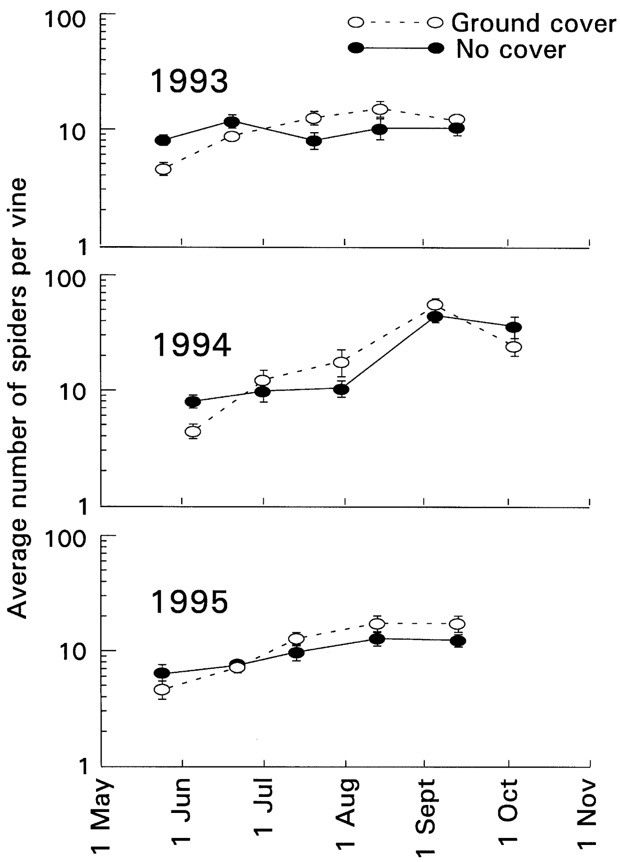

Fig. 1. Monthly mean spider density (± SEM) in the grapevine in plots with and without ground cover for 1993, 1994 and 1995. Across sampling dates and years, spider density did not differ between treatments (P = NS).

There are three possible explanations for the increased abundance of *T. pacificus* on vines in the ground cover treatment. First, that *T. pacificus* utilizes the ground cover as an alternate source of prey or protective habitat. This implies that *T. pacificus* moves between the vines and the ground cover. This is an unlikely scenario because very few *T. pacificus* were collected on the ground cover. In fact, when comparing the spider species diversity of the vines and ground cover, it appears that the ground cover is not significantly utilized by any vine dwelling spiders, with the possible exception of the *Oxyopes* spp. A second possibility is that the ground cover altered the microclimate (temperature and/or humidity) such that the development or reproduction of *T. pacificus* was favoured. This is also an unlikely explanation. Temperatures were monitored throughout the study and only in 1994 were there significant differences in vine canopy temperature between treatments (Costello & Daane, 1997b). Furthermore, these temperature differences were not large, with the mean daily temperature ⊤ 2 °C lower in vines in the *ground cover* treatment in the warmest months of the season (July and August). These temperature differences would not appear to

Table 2. Mean spiders per vine (± SEM) collected on grapevines in treatments with and without cover crops.

	Year							
	1993		1994		1995		Overall	
Species	Cover	No cover	Cover	No cover	Cover	No cover	Cover	No cover
T. pacificus	5.15 (0.59)	4.46 (0.39)	10.48 (1.52)	6.42 (0.69)	5.88 (0.79)	3.19 (0.42)	7.15 (0.63)	4.66 (0.31)*
C. inclusum	0.93 (0.14)	0.69 (0.11)	5.33 (0.94)	5.92 (1.00)	0.44 (0.08)	0.45 (0.09)	2.21 (0.36)	2.30 (0.38)
Oxyopes spp.	0.77 (0.13)	0.75 (0.15)	3.00 (0.55)	5.46 (1.48)	1.48 (0.29)	1.19 (0.27)	1.73 (0.22)	2.42 (0.52)
M. vitis	1.95 (0.25)	1.46 (0.21)	1.71 (0.33)	1.30 (0.14)	0.84 (0.15)	0.83 (0.11)	1.50 (0.15)	1.19 (0.10)
H. nedra	0.38 (0.08)	0.45 (0.08)	0.81 (0.18)	0.72 (0.15)	1.22 (0.16)	2.48 (0.33)	0.80 (0.09)	1.22 (0.15)**
N. oaxacensis	0.41 (0.08)	0.76 (0.22)	0.71 (0.12)	0.79 (0.13)	0.82 (0.11)	0.46 (0.07)	0.64 (0.06)	0.66 (0.08)
All spiders	10.39 (0.81)	9.49 (0.66)	23.08 (3.17)	21.79 (2.94)	11.94 (1.14)	9.77 (0.70)	15.08 (1.22)	13.57 (1.10)

Trachelas pacificus and *C. inclusum* density for all years combined was analysed by repeated measures ANOVA. For all other spider species and the total spider density, ANOVA was not used to separate treatment means because a necessary assumption of ANOVA (independence of mean density and variance) was not met. For these treatment mean separations, monthly were combined and ranked (PROC RANK, SAS Institute, 1995) and an ANOVA was performed on the ranks (equivalent to the Kruskal–Wallis one-way test, PROC GLM, SAS Institute, 1995). Significance between treatments was found for *T. pacificus* (* all years combined, $P = 0.02$) and *H. nedra* (** all years combined, $P < 0.0001$).

influence *T. pacificus* fecundity, development or survivorship (M. J. Costello & K. M. Daane, unpublished data). There was no consistent effect on relative humidity due to ground cover (Costello & Daane, 1997b). A third possibility is that the ground cover harbours alternative prey species that migrate from the ground cover to vine canopy, where they are used as food by *T. pacificus*. Although not enumerated, several prey types were found commonly on the ground cover, consisting primarily of Diptera (muscids and chironomids) and Homoptera (delphacids and aphids**).** These prey items were commonly observed flying around the vineyards. Of the three possibilities discussed, this is the most likely. Similarly, Wyss *et al*. (1995) found a higher number of orbweaver (*Araniella* spp.) spiders on apple trees that were undersown with a weedy cover. They concluded that the beneficial effect of the ground cover was not in providing extra habitat for spiders, but in providing a greater number of alternative prey for spiders dwelling in the apple canopy.

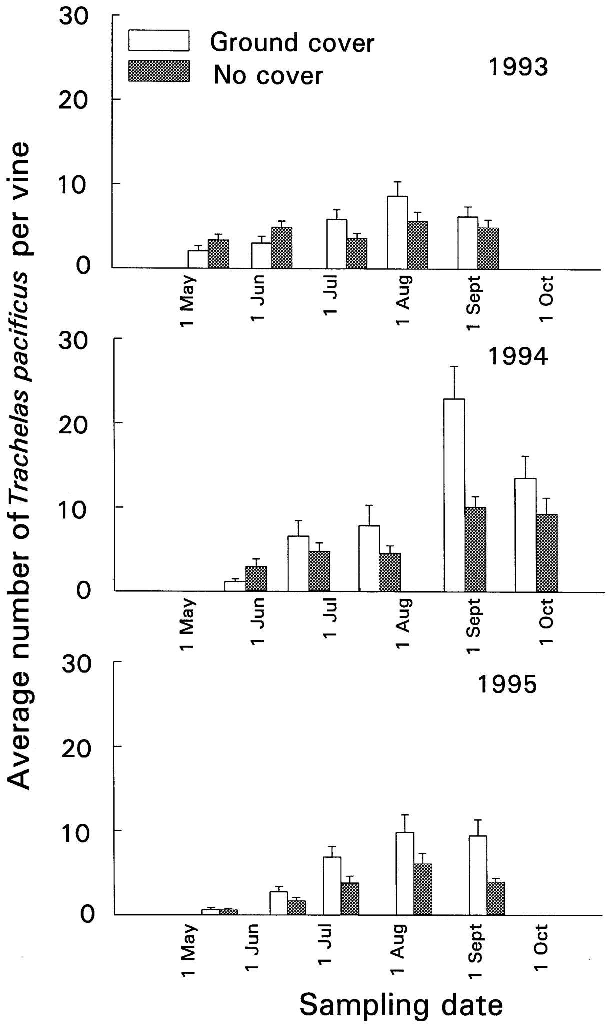

Fig. 2. Monthly mean *T. pacificus* density (± SEM) in the grapevine in plots with and without ground cover for sampling years 1993–95. Over all years, *T. pacificus* density was higher in the *ground cover* treatment than the *no cover* treatment ($P = 0.02$).

If this scenario is accurate, many other questions are raised. For example, why is there such a distinct difference between spider species composition on the vines and on the ground cover? On the vines, the most commonly collected spiders were in the families Corinnidae, Clubionidae, and Salticidae, whereas on the ground cover the most common spider families were the Linyphiidae and Lycosidae. Only spiders in the Oxyopidae were common on both vines and ground cover. Other studies have found similar distinctions between spider species found on a perennial crop and those on the ground cover, often following similar differences in vertical distribution. For example, Mansour & Whitcomb (1986) found that spiders in the families Clubionidae and Theridiidae accounted for 86% of the spiders collected on citrus trees, whereas spiders in the families Lycosidae and Gnaphosidae accounted for 78% of the spiders found on ground cover. Even in annual cropping systems there are vertical differences in spider species diversity. Ferguson *et al*. (1984) found that spiders associated with soybean foliage were dominated by Oxyopidae, Thomisidae and Salticidae, whereas ground-dwelling spiders consisted primarily of Lycosidae and Linyphiidae.

One explanation may be differences in colonization and competition. *Trachelas pacificus*, *C. inclusum*, *Oxyopes* spp. and *M. vitis*, which are common on central Californian grapevines, overwinter as half-grown juveniles to adults under the bark of the vine trunk (M. J. Costello & K. M. Daane, unpublished data). These species are long-lived and have overlapping age structure (Costello & Daane, 1995), and begin the season established in the vineyard and in late developmental stages, placing them at a competitive advantage over many of the non-established species that balloon in throughout the season. Mowing the ground cover presents a continuous disruption of the ground cover habitat, and consequently there are always openings for new immigrants. The relative equality with which *Oxyopes* spp. are distributed between ground cover and vines may also be explained by colonization. The drop in *Oxyopes* spp. adult abundance to very low levels by mid-season is followed by a steady increase in number of juveniles (Costello

Table 3. Measures of spider species similarity (Bray–Curtis method) among vine canopy in the ground cover treatment, vine canopy in the no cover treatment and ground cover. The index (1 – B) ranges from 0 (dissimilar) to 1 (similar).

	Vines (ground cover)	Vines (no cover)	Ground cover
Vine canopy (ground cover)	–		
Vine canopy (no cover)	0.851	–	
Ground cover	0.279	0.360	–

& Daane, 1995). Without large adult populations, this steady increase in *Oxyopes* is most likely to be explained by immigration, although the lag time between egg sac production and hatch may also contribute to this phenomenon. *Oxyopes salticus* has been found to be a good colonizer in other field studies (Agnew & Smith, 1989) and inhabits both soil and plant zones (LeSar & Unzicker, 1978). Therefore, because *Oxyopes* spp. overwinter on the vines, they can compete well in that relatively stable habitat, and because they are good colonizers, they can compete well in the ephemeral ground cover habitat. Another possibility for *Oxyopes* is that the two species partition themselves according to vine or ground cover habitat, with *O. salticus* favouring the ground cover and *O. scalaris* favouring the vines, although this has yet to be shown.

Another important question is, if indeed the ground cover was a source of alternative prey, why did only *T. pacificus* take advantage of the greater numbers of prey available? And why was the apparent enhancement of *T. pacificus* not offset by a greater decline in other spider species? Perhaps *T. pacificus*, by virtue of its dominance at this site prior to the ground cover experiment, was in a stronger competitive position. However, there was never a response to *ground cover* treatment by *C. inclusum*, even in 1995 when it reached population levels equivalent to *T. pacificus* in 1993 or 1994. There was no response of *C. inclusum* to *ground cover* treatment at other sites, even where it was the dominant spider species (Costello & Daane, in press). The explanation for the very different response by these two species may lie in the timing of reproduction and longevity of adults. *Cheiracanthium inclusum* is semelparous, the mother dying shortly after the spiderlings have hatched, whereas *T. pacificus* is iteroparous, producing up to three egg sacs, and longevity of mothers is considerably greater than for *C. inclusum* (Costello & Daane, 1995). Therefore, the reproductive capacity of *C. inclusum* can be expanded only by increasing the number of eggs per sac (because only one sac is produced), whereas *T. pacificus* can increase the number of eggs per sac as well as the number of sacs. Therefore, compared to *C. inclusum*, there may be a higher rate of prey transformation into *T. pacificus* offspring, which may explain its late-season population enhancement. As for spiders that may offset this increase in *T. pacificus*, *H. nedra* was the only species that showed statistically significant lower densities on vines without ground cover. However, the absolute numbers of spiders collected (Table 1) suggest that there are additional species that are favoured by the lack of ground cover (*Oxyopes* spp., *E. dentosa*, *Theridion* spp.) and perhaps one more that is favoured by the presence of ground cover (*M. vitis*). The lack of statistically significant treatment effects by these species may be explained by the inconsistency of response (Table 2), or the relatively low density of their populations.

In evaluating the benefits of ground cover as a management practice to enhance spider density and improve pest management, it should be noted that the differences in spider population density due to annual variation were in general greater than those due to *ground cover* treatment effects. During the course of this study, 1994 was a relatively high density spider year. The most dramatic increase was seen with *C. inclusum*, whose population in 1994 was 5.9-fold more dense than in 1993, and 11.8-fold more dense than in 1995 (Table 2). In addition, in 1994 *T. pacificus* abundance was 76 and 86% higher, and *Oxyopes* spp. 4.5- and 2.2-fold higher than in 1993 and 1995, respectively (Table 2).

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