Relative impact of spider predation and cover crop on population dynamics of *Erythroneura variabilis* in a raisin grape vineyard

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Abstract

Experimental and correlative evidence has steadily mounted over the past 30 years implicating spiders in the suppression of insect herbivore pests in crop fields. A large body of evidence has also shown that increasing agroecosystem vegetation diversity often influences the abundance of herbivores and their natural enemies. In previous experiments, the abundance of several species of spiders on grapevines in a raisin grape vineyard was twofold enhanced in vineyard plots vegetationally diversified with a cover crop. A concomitant reduction in the abundance of the leafhopper pest *Erythroneura variabilis* Beamer was observed on grapevines in the diversified plots, but a causal relationship was not established. In the present study, we simultaneously manipulated spider densities (in open-vine spider exclusion and vine-shoot enclosures) and ground cover to determine their relative impact on *E. variabilis* population dynamics. Open-vine spider exclusion resulted in an average 35% increase in the density of *E. variabilis* the greatest effect with occurring during the first and second leafhopper generations. The negative impact of spiders on *E. variabilis* densities was corroborated with vine-shoot enclosure experiments. Under the conditions of the present study, the cover crop per se did not affect the dynamics of *E. variabilis* populations on grapevines, despite a 1.6-fold increase in spider densities on vines in cover crop plots, compared with vines in bare ground plots, probably due to insufficient spider enhancement and low overall *E. variabilis* abundance during the summer months. The cover crop had little effect on vine macronutrient status (and presumably vine water status). While this study provided further support for the hypothesis that vegetation diversity can enhance spider abundance, this enhancement does not always lead to lower pest densities, thus underscoring the complexity and variability that exists in interactions involving cover crop, spiders, and crop plants and their herbivore pests.

Introduction

Spiders are among the most common generalist arthropod predators in natural and managed agroecosystems (Young & Edwards, 1990). While numerous studies have implicated spiders in suppression of pest populations (see reviews by Riechert & Lockley, 1984; Nyffeler & Benz, 1987; Wise, 1993; Sunderland & Samu, 2000), the extent of their role in biological control remains controversial. Evidence collected over last decade from field experiments has clearly suggested, however, that spiders as assemblages (after Riechert & Bishop, 1990) of various spider taxa may be able to provide a satisfactory control of pest populations if conditions are not conducive to severe pest outbreaks, and if habitat quality is improved in order to enhance the size of spider populations (Riechert & Bishop,

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1990, and see for reviews Rypstra et al., 1999 and Sunderland & Samu, 2000).

A large body of evidence has also accumulated over the past 30 years in support of the hypothesis that increasing agroecosystem vegetation diversity can exert a substantial, albeit variable, impact on populations of herbivore pests and their natural enemies including spiders (reviewed by Risch et al., 1983; Russell, 1989; Andow, 1991; Wise, 1993; Riechert, 1999). In a recent review of the literature by Sunderland & Samu (2000) on the effect of agricultural diversification on spider populations, 63% of reviewed studies reported an increase in spider abundance by agricultural habitat diversification, but the ecological mechanisms underlying the increase in spider abundance remained poorly understood in most agroecosystems. It has been argued that a diversified agroecosystem that increases spiders' prey diversity and abundance, and improves the environmental quality of the spiders' habitat, may enhance their abundance and their ability to limit prey densities (Provencher & Vickery, 1988). Few studies, however, have simultaneously manipulated spider abundance and vegetation diversity in a crop field in order to determine the relative impact of the two factors on pest densities, and the mechanisms by which diversified systems affect pest and spider abundance (see recent reviews by Rypstra et al., 1999 and Sunderland & Samu, 2000). Here we report on a field experiment in which we simultaneously manipulated spider densities and vegetation diversity (by cover cropping) in a farmer's vineyard, in order to determine the relative impact of the two factors on the abundance of the leafhopper *Erythroneura variabilis* Beamer (Homoptera, Cicadellidae), an important pest of grapes in central and southern California.

Two leafhopper species, *Erythroneura elegantula* Osborn and *E. variabilis*, infest grapevines in California. Historically, *E. elegantula* has been the dominant species in central and northern California. However, *E. variabilis*, which was first reported in southern California in 1929 and in the central San Joaquin Valley in 1980, has largely replaced *E. elegantula* in vineyards located in the inland valleys of southern California and in the central and southern San Joaquin Valley (Wilson et al., 1992a). While *E. elegantula* populations can be kept under satisfactory biological control by *Anagrus* spp. (Hymenoptera: Mymaridae) in vineyards where these parasitoids are abundant (Wilson et al., 1992b), *E. variabilis* populations are not generally regulated by *Anagrus* spp. (Settle & Wilson, 1990; Wilson et al., 1992a). Several species of spiders are the only other natural enemies present in sufficient abundance to have a potentially negative impact on *E. variabilis* (and *E. elegantula*) populations in California vineyards (Wilson et al., 1992a; Roltsch et al., 1998; Costello & Daane, 1999).

Grapevine canopies in San Joaquin Valley vineyards harbor numerous species of spiders belonging to several families (Njokom, 1991; Costello & Daane, 1995; Roltsch et al., 1998). Although species composition and abundance varies widely between vineyards, six species *Hololena nedra* Chamberlin and Ivie, *Theridion dilutum* Levi, *Theridion melanurum* Hahn, *Cheiracanthium inclusum* (Hentz), *Trachelas pacificus* (Chamberlin and Ivie), and *Metaphidippus vitis* (Cockerell) are the most common spiders on grapevines (Roltsch et al., 1998; Costello & Daane, 1999). All these spiders, except *M. vitis*, have been observed feeding on leafhoppers in San Joaquin Valley grape vineyards (R. Hanna, pers. obs.). Field evidence to date linking spiders to leafhopper abundance in vineyards remains correlative and ambiguous, as none of the previous studies attempted to experimentally manipulate spider abundance to determine their impact on leafhoppers.

In a non-replicated experiment, Settle et al. (1986) observed elevated spider abundance and lower *E. variabilis* densities in the presence of a 'weedy' summer ground cover (periodically mowed resident summer vegetation). More recently, we demonstrated in two replicated field experiments in a raisin grape vineyard, that planting a ground cover of specific vegetation type (hereafter referred to as a cover crop) composed of a mixture of 'Cayuse' oat (*Avena sativa* L.), common vetch (*Vicia sativa* L.), and purple vetch (*Vicia benghalensis* L.) resulted in elevated levels of vine canopy-dwelling spiders and lower *E. variabilis* abundance compared with vines in bare ground plots (Roltsch et al., 1998). These abundance patterns, however, were only suggestive of a causal relationship between elevated spider levels and lower leafhopper abundance. Other factors associated with the cover crop (e.g., differences in vine nutrient and water status, leafhopper movement patterns, or differences in other biotic and abiotic factors) could also have contributed to lower *E. variabilis* abundance in cover crop plots. Here we report on two field experiments conducted in the same vineyard we used previously (Roltsch et al., 1998), and designed to answer the following questions:

- Does a cover crop with specific plant species composition and cultural management affect spider populations on grapevines?
- Can the spider assemblage found in San Joaquin Valley raisin vineyards suppress leafhopper populations on grapevines?
- What are the relative effects of cover crop and spiders on leafhopper populations in vineyards?
- How does this cover crop system affect vine nutrient status, and how might that affect leafhopper populations?

Materials and methods

The study site

The field experiments were conducted in a 39-year-old 'Thompson Seedless' vineyard grown for sun-dried raisin production on Hanford sandy loam soils near Madera, California (36°49′51.3″N, 120°01′25.9″E). The vineyard was surrounded by other vineyards in all four compass directions, and was planted with a standard vine and row spacing of 3.7 m between vinerows and 2.4 m within vinerows. Vegetation under all vinerows was controlled with mechanical cultivators. Between rows, the ground was either planted with a cover crop (see description below) or was maintained free of vegetation by periodic cultivation. Nitrogen fertilizer was applied on 25 May 1992 at the rate of 22 kg N ha^{-1}. Water was applied by flooding row middles at approximately 3-week intervals from early March through July. Powdery mildew *Uncinula necator* (Schwein.) Burrill was controlled with five applications of sulfur dust in April and May, and two applications of fenarimol (DowElanco, Inc.) in June. Cryolite (Atochem) was used for the control of lepidopterous pests. Although formal studies have not been conducted to determine the impact of these disease and insect control chemicals on leafhoppers and their natural enemies, we have not observed any impact on leafhoppers in 12 years of research in vineyards (R. Hanna, F. G. Zalom, and W. J. Roltsch, pers. obs.).

Relative effects of cover crop and spiders on leafhopper abundance: open-vine spider exclusion experiments

The field experiment consisted of two factors, cover crop (main plots) and spider exclusion (subplots), arranged in a split-plot design with three replicate blocks, which were 10 vinerows (37 m) wide and 110 vines (264 m) long. Main plots (cover crop and bare ground) consisted of two adjacent vinerows located three vinerows from block borders. The location of cover crop rows was chosen at random within the first block, and maintained at the same position relative to the bare ground plots in the second and third blocks. This plot arrangement maintained a constant distance of five vinerows between main plots, within, and between blocks. In one main treatment level, the area between the two vinerows (row middles) consisted of a fall-planted mix of 30% (by weight) purple vetch (*V. benghalensis*), 30% common vetch (*V. sativa*), and 40% 'Cayuse' oat (*A. sativa*). In the other main treatment level and in all buffer areas, row middles were maintained free of vegetation by periodic cultivation. The cover crop was seeded on 7 November 1991 at a rate of 132 kg of seeds (total of the three cover crop species) per planted hectare in 1.5 m beds between vinerows, and allowed to grow without disturbance until 4 April 1992, at which time it was mowed with a rotary mower to a height of approximately 20 cm. This was necessary as mowing the ground vegetation in early spring reduces the risk of spring frost (Snyder & Connell, 1993) and delays seed set and cover crop senescence. The cover crop was then allowed to grow to maturity. It was tilled on 15 July, 45 days prior to grape harvest. All plots were thereafter kept free of vegetation by periodic cultivation.

To separate the effect of spiders from other cover crop effects (e.g., effects on vine nutrient and water status) on *E. variabilis*, we established two subplot levels – spider exclusion and control – in each of the cover crop and bare ground plots. Subplots were randomly assigned to each of two six-vine plots within each main plot, and were located 30 vines from row ends and at least 30 vines apart. Spider exclusion was initiated on 8 March just prior to the beginning of the vines' vegetative growth. Because several spider species are found under loose bark on vine trunks (R. Hanna and F. G. Zalom, unpubl. data), we stripped all loose bark from vine trunks with a wire brush to remove all existing spiders and to facilitate the retrieval of spiders that had colonized the vines during the remainder of the experiment. To reduce subsequent cursorial colonization of spider-exclusion vines from the ground or from adjacent non-exclusion vines, we placed an 8 cm wide band of duct tape around the center of the trunk and supporting wood post, and a 15 cm band on the trellis wire (outside of plot border vines). The duct tape bands were generously coated with tanglefoot (Tanglefoot Co., Grand Rapids, MI) which was applied again to barriers as needed to maintain their 'stickiness'. We recognized that sticky trunk bands could restrict the movement of other predators. We believe this was unlikely in our experiments, as 'other' predators were rare on vines where we did not restrict movement from the cover. To further reduce the cursorial colonization of exclusion vines by spiders, we trimmed the grapevine shoots at slightly above ground or cover crop levels to prevent the formation of 'bridges' between the vines and the ground or the cover crop. Shoot trimming at approximately 0.5 m above ground level is also a standard practice during the summer months in 'Thompson Seedless' vineyards. For the remainder of the experiment, exclusion vines were thoroughly searched during the day for spiders at 14–20 day intervals. Two additional night searches were conducted on 27 April and 18 June

Although we did not control for spider removal (e.g., we did not establish plots where we removed and returned spiders to the same vines), we determined the impact of disturbance caused by vine inspection by establishing a six-vine plot between each exclusion and non-exclusion plot. These vines were inspected at four different dates, but

spiders were not intentionally removed. We conducted a census of *E. variabilis* densities in these plots during the peak of each of the three leafhopper generations (see sampling sections for details).

We determined vegetation biomass and species composition in the cover crop plots on three occasions from three haphazardly selected 0.25 m^2 quadrates from each plot. We present average dry weight by species for *A. sativa* and *Vicia* spp., and combined dry weights for other vegetation types (i.e., weeds).

In each plot, leafhopper densities were determined from counts of nymphs on 24 grape leaves at 14–18 day intervals from May through September; and adults on three yellow vinyl cards (7.6 cm × 10.7 cm) coated with Stickem (Seabright Enterprises, Emeryville, CA, USA) placed in the middle canopy of randomly selected vines and replaced at approximately 14-day intervals from April to September. Five leaves – one leaf from the north aspect of each of five vines – were removed at 14–18 day intervals to estimate leafhopper egg densities and levels of parasitism by *Anagrus* spp. Eggs was determined following the method used by Settle & Wilson (1990).

Spider densities were determined from monthly samples taken from each plot using the shake-funnel method (developed and tested by Roltsch et al., 1998). Spider densities were also counted on grape leaves during each leafhopper census, but here we report only spider densities in shake funnel samples, as this was more reliable than counts on leaves for estimating densities of most spider species found on grapevines (Roltsch et al., 1998). Shake-funnel samples consisted of a 0.58 m^2 funnel placed under the vine canopy, which was then shaken vigorously for 10 s. Spiders were collected in plastic bags, chilled immediately, and stored at 3 °C until counting. Shaking was conducted at approximately monthly intervals between 7 and 13 h. Two shake-funnel samples were collected from each plot on each sampling date.

Counts of spiders in shake-funnel samples, leafhopper eggs and nymphs on leaves, proportion of *E. variabilis* eggs parasitized by *Anagrus* spp., and adult *E. variabilis* on sticky cards were used as dependent variables in univariate repeated measures analysis of variance, with cover crop as the between-subject factor and spider exclusion and sampling date as within-subject factors. We used a logarithmic transformation of the response variables (except for the proportion of leafhopper eggs parasitized by *Anagrus* spp., which required the use of angular transformation) where needed to reduce the heterogeneity of variance. Where date and cover crop, or date and spider exclusion interactions occurred, we used a two-factor ANOVA stratified by date to determine statistical differences in factor effects on each sampling date. Probability values in the stratified analyses were adjusted with the Bonferroni procedure (Milliken & Johnson, 1984).

Relative effects of cover crop and spiders on leafhoppers: enclosure experiments

Within each main plot, a nylon organdy enclosure (1 m long × 42 cm wide, enclosing 8–10 grape leaves from the middle to distal end of the shoots) was fitted over each of 10 randomly selected shoots per plot on 30 May, for an experiment total of 60 enclosures. Enclosures were placed within sampling rows and between main plot/subplot sampling zones to minimize plot disturbance. At the time of enclosure placement, we inspected all the leaves and removed all insects and spiders. Enclosures were then closed for 19 days to allow sufficient time for leafhopper nymphs to emerge from eggs that were already present on the enclosed leaves. On 18 June, we removed all leafhoppers (and other insects) and spiders present in the enclosures. We then introduced 45 female and 20 male leafhoppers into each enclosure. Males were added to ensure that all females had the opportunity to mate, and the sex ratio of leafhoppers released in enclosures was similar to the sex ratio of the source leafhopper population obtained from the same study site. We allowed leafhoppers to feed and reproduce for 10 days.

On 28 June we randomly selected two enclosures from each plot (i.e., 12 out of 60 enclosures) and counted all leafhopper eggs in the laboratory under a dissecting microscope using light transmitted through the leaf, as *E. variabilis* eggs are inserted deep in the leaf tissue. The sum of eggs in each enclosure provided a value for estimating the effect of cover crop and bare ground on *E. variabilis* reproduction on vines. After determining egg densities, we used a leaf area meter (Li-Cor Inc., South Royalton, VT, USA) to measure total leaf area in each enclosure. We then dried the leaves at 70 °C for 7 days to estimate leaf dry weight. We report leafhopper egg densities in units of numbers per enclosure, numbers per gram of leaf dry weight, and numbers per cm^2 of leaf area.

After collection of the first set of enclosures, we incubated the leafhopper eggs in the remaining enclosures for an additional 8-day period to ensure sufficient leafhopper nymph emergence (and hence sufficient leafhopper nymph levels) prior to the introduction of spiders into the enclosures. On 6 July, we divided the remaining eight enclosures in each replicate into two groups of four enclosures: one group received one individual of each of the five common species of spiders found in the study vineyard and most other raisin vineyards in the San Joaquin Valley, while the other group of enclosures was kept free of spiders. Spiders used in the enclosures were collected from

non-experimental vines in the study site. All were juveniles and representative of the age structure of the spiders found in the vineyard at that time. Individuals of *T. pacificus*, *C. inclusum*, and *H. nedra* were of approximately similar body size, but larger than *T. dilutum* and *T. melanurum*, which were similar in size. *Hololena nedra* (a funnel web spider) preys primarily on adult leafhoppers (and several other arthropods), but has been observed feeding on 4th and 5th instar leafhopper nymphs, while the other species have been observed on numerous occasions feeding on leafhopper adults and all nymph stages (R. Hanna, pers. obs.). The inclusion of all five spider species in the enclosures provided a realistic representation of the species composition of canopy-dwelling spiders found in the study vineyard.

On 22 July and 9 August (16 and 34 days, respectively, after the addition of spiders), we collected four enclosures (two with spiders and two without) from each plot. On each collection date, all enclosures were cooled at 1 °C for a maximum of 1.5 h following collection to facilitate the counting of adult *E. variabilis* present on the leaves. In the laboratory, the leaves were sequentially removed from a chilled enclosure and all *E. variabilis* nymphs and adults were counted. Enclosures (without the leaves) were then placed in a freezer (−20 °C) to kill all the remaining leafhoppers and spiders, which were later separated and counted. All leaves from each enclosure were examined under a dissecting microscope to count the number of *E. variabilis* live eggs and nymph exit holes.

We used a single-factor ANOVA with blocking to determine treatment effects on *E. variabilis* egg densities on enclosure leaves collected on 28 June, and a split-plot (with blocking) ANOVA to determine the relative effects of spiders and cover crop on *E. variabilis* nymph and adult densities in enclosures collected on 22 July and 9 August.

Effect of cover crop on vine nutrient status

We were interested in the question of whether the cover crop had any effect on vine nutrient status (macronutrients), as vegetative ground cover has been shown to affect crop plant nutrient (and water) status (Merwin & Stiles, 1994), which might in turn affect leafhopper biology (Mayse et al., 1991). To determine the impact of cover crop on vine nutrient status, we collected 60 leaf petioles from each plot at véraison (beginning of berry softening), which is a key phenological stage in the assessment of vine nutrient status (Christensen et al., 1978). Leaf petiole is the most appropriate tissue for nitrogen, phosphorus, and potassium (NPK) determination at véraison (Christensen et al., 1978). Leaf blades collected from enclosures on 28 June were also tested for NPK. Leaf petioles (collected at véraison) and leaf blades (from enclosures on 28 June) were dried for 7 days at 70 °C to prepare them for determination of their NPK content. Leaf blade N, and phosphorus and potassium in leaf blades and petioles are reported as per cent dry weight, whereas N content in petioles is reported as nitrate-nitrogen (p.p.m.). We used a split-plot ANOVA to determine the effects of cover crop and spider exclusion on the levels of each of the nutrient elements (NPK) from all plots at véraison; and a single-factor ANOVA with blocking to determine the effect of cover crop on leaf blade NPK in enclosures. All statistical analyses were performed using the SAS statistical program (SAS Institute Inc., 1996).

Results

Cover crop growth

We report details of vegetation composition and management because the variability in the experimental results on the effects of vegetation diversity on spiders and leafhoppers could be partially explained by differences in cover crop species composition and management (Hanna et al., 1995).

We succeeded in establishing a nearly pure stand of *A. sativa*, *V. sativa*, and *V. benghalensis*. The three species comprised 94% of total vegetation from 26 April to 10 July. The average proportion of each vegetation type consisted of 56%, 38%, and 6% *Vicia* spp., *A. sativa*, and 'weeds', respectively (Table 1). Weed species composition varied between sampling dates. On 26 April, three species of winter annual weeds comprised nearly 100% of the weed biomass, while four summer annual weeds comprised nearly 100% of the two samples taken on 2 June and 10 July (Table 1).

Effect of cover crop on vine nutrient status

Nitrate-nitrogen (p.p.m.) and phosphorus (per cent of dry weight) in grape leaf petioles were not affected by cover crop or spider exclusion ($P = 0.340–0.736$). Average nitrate-nitrogen and phosphorus, respectively, ranged from 141.7 ± 37.4 p.p.m. to 166.7 ± 21.9 p.p.m and $0.38 \pm 0.03\%$ to $0.43 \pm 0.09\%$. In contrast, potassium levels (% of dry weight) were significantly higher in the leaf petioles of vines in cover crop plots ($0.46 \pm 0.01\%$) compared with vines in bare ground plots ($0.36 \pm 0.01\%$) ($F_{1,4} = 19.45$, $P = 0.048$).

Relative effects of cover crop and spiders: open-vine spider exclusion experiment

Spider densities followed seasonal patterns similar to those previously reported in this vineyard (Roltsch et al., 1998). Averaged over all sampling dates, spider densities were 1.4-fold higher on vines in the cover crop compared

Table 1 Plant weight and height[a] of cover crop and other vegetation in row middles of cover crop plots[b]

	A. sativa		*V. sativa* and *V. benghalensis*		Weeds[c]
Date	Weight (g/0.25 m^2)	Height (cm)	Weight (g/0.25 m^2)	Height (cm)	Weight (g/0.25 m^2)
26 April	11.1 ± 0.9	14.2 ± 1.3	16.3 ± 0.4	12.0 ± 1.2	1.0 ± 0.2
2 June	33.6 ± 2.9	26.3 ± 2.2	44.5 ± 6.1	18.3 ± 1.2	3.5 ± 0.1
10 July	18.7 ± 1.6	20.0 ± 1.0	33.3 ± 2.7	17.3 ± 0.3	6.4 ± 0.8

[a]Plant measurements were based on dry weight means of two 0.25 m^2 quadrats per plot in the cover treatments.

[b]Bare ground plots were kept free of vegetation with periodic cultivation.

[c]Weeds were separated and weighed by species, but here we report combined weight of all species. The following weed species were found: *Calandrinia ciliata* (R. & P.), *Stellaria media* (L.), and *Erodium* spp. on 26 April; and *Conyaza canadensis* (L.), *Lactuca serriola* (L.), *Setaria glauca* (L.), and *Digitaria sanguinalis* (L.) on 2 June and 10 July.

with bare ground plots (Figure 1, Table 2). Because the cover crop effect was averaged over spider exclusion, we compared the simple effects of cover crop and bare ground on each sampling date in non-exclusion plots. For these post hoc comparisons, we used a conservative Bonferroni adjustment (Milliken & Johnson, 1984). Averaged over all four census dates, spider densities were 1.6-fold higher on vines in non-exclusion cover crop plots compared with vines in non-exclusion bare ground plots ($P < 0.05$). Stratification of the analysis by date revealed a strong trend toward higher spider densities (all species combined) over three consecutive sampling dates (June, July, and August) on vines in cover crop plots compared with bare ground plots. However, this difference was only statistically significant in July and August (Figure 1, $P < 0.05$).

Although the cover crop appears to have enhanced spider densities, spider species composition did not change, and their relative abundance was only slightly affected by cover crop. In July, average abundance of *H. nedra*, *Theridion* spp., *C. inclusum*, and *T. pacificus* were, respectively, 2.06 ± 0.32, 5.89 ± 1.13, 1.22 ± 0.11, and 2.44 ± 0.59 (mean ± SE) per shake-funnel sample on vines in cover crop plots, and 1.31 ± 0.35, 3.89 ± 0.11, 1.22 ± 0.40, and 0.89 ± 0.36 per shake-funnel sample on vines in bare ground plots. *Cheiracanthium inclusum* was the only species that was not affected by the presence of the cover crop.

Because the exclusion vines were open, it was impossible to keep them free of spiders without continuous inspection and excessive vine disturbance. We were successful, however, in maintaining spider densities on exclusion vines at a

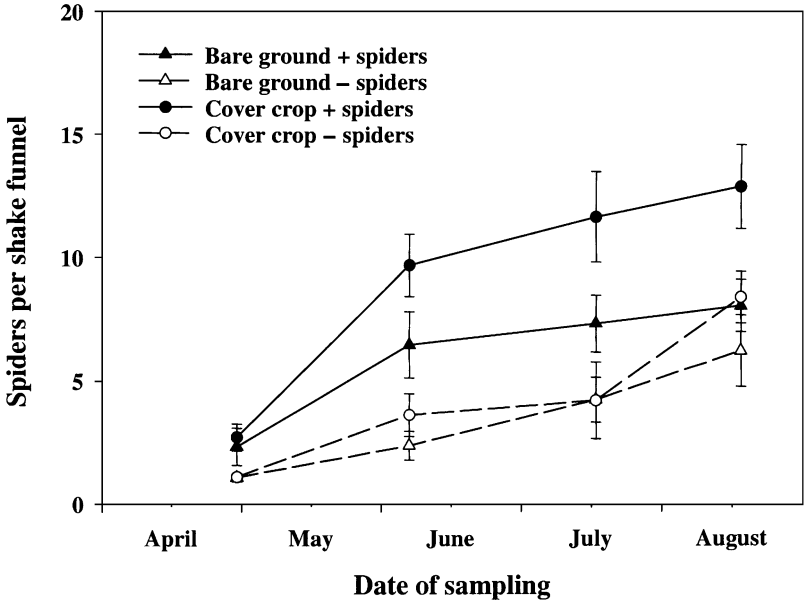

Figure 1 Seasonal patterns of spiders (all species combined) on vines in cover crop and spider exclusion plots from April to August. Data points are mean spider densities per shake sample; error bars are standard errors of the means. Treatment means (± SE; n = 12) over all four sampling dates were as follows: 6.01 ± 1.28, 3.44 ± 1.21, 9.2 ± 2.27, and 4.30 ± 1.51 for bareground + spiders, bareground – spiders, cover + spiders, and cover – spiders, respectively.

Table 2 Univariate repeated measures analysis of variance of cover crop and spider exclusion effects on total spider densities on vines

Source [a]	d.f.	Mean square	F	P
Cover crop	1	53.0	16.1	0.057
Block	2	11.9	3.59	0.218
Error	2	3.30		
Spiders	1	160.3	115.7	0.009
Spiders × cover crop	1	18.6	13.4	0.067
Spiders × block	2	4.13	2.98	0.251
Error	2	1.39		

[a]For brevity, date effects are not included in the table. Significant effects are reported in the text.

seasonal average of 50% of their densities on non-exclusion (Figure 1, Table 2); but our ability to exclude spiders was variable over the course of the experiment (Figure 1, date by spider interaction: $F_{1,6} = 4.69$, $P = 0.151$; $P = 0.052$ before Greenhouse–Geisser adjustment). We maintained spider densities on exclusion vines at 37–44% of their densities on non-exclusion vines from April through July (linear contrasts of exclusion vs. non-exclusion plots: $F_{1,6} = 8.05$–65.8, $P < 0.05$); but spider densities increased on exclusion vines to nearly equal levels with non-exclusion vines (in bare ground plots only) in August ($F_{1,6} = 5.42$, $P = 0.145$).

The impact of cover crop and spider exclusion on *E. variabilis* densities was determined from counts of *E. variabilis* eggs and nymphs on leaves, and adults on yellow sticky cards. *Erythroneura variabilis* densities followed the typical pattern of three generations per growing season in San Joaquin Valley vineyards. None of the censused three leafhopper life stages (eggs, nymphs, and adults) was affected by cover crop (Figure 2, Table 3). In contrast, spider exclusion had a significant overall impact on densities of *E. variabilis* nymphs and adults, independent of cover crop (Figures 2 and 3, Table 3). Overall egg densities were not affected by spider exclusion (Figure 4, Table 3).

Over the season, *E. variabilis* nymphs were 1.5-fold higher on spider exclusion vines compared with non-exclusion vines (Figure 2, Table 3), with the highest (and statistically significant) difference occurring during the peak of the 1st *E. variabilis* generation (1.6-fold higher on exclusion than on non-exclusion vines, $F_{1,4} = 55.72$, $P < 0.05$ after Bonferroni adjustment). Nymph densities during the 2nd generation peak (average of 17 and 25 July) were higher on exclusion than non-exclusion vines, but were not statistically significant ($F_{1,4} = 8.56$, $P > 0.05$). Third generation nymphs were near zero and were not affected by spider exclusion.

Unlike nymph densities, adult densities on sticky cards (Figure 3) were only significantly higher on exclusion vines compared with non-exclusion vines on 8 and 22 June, which coincided with peak densities of first generation adults ($F_{1,4} = 12.34$, $P < 0.05$ on 8 June; $F_{1,4} = 11.30$, $P < 0.05$ on 22 June). The higher adult densities in the spider exclusion plots were probably the result of higher first generation nymph densities and likely lower spider predation on adult *E. variabilis* as spider densities were substantially lower on exclusion compared with

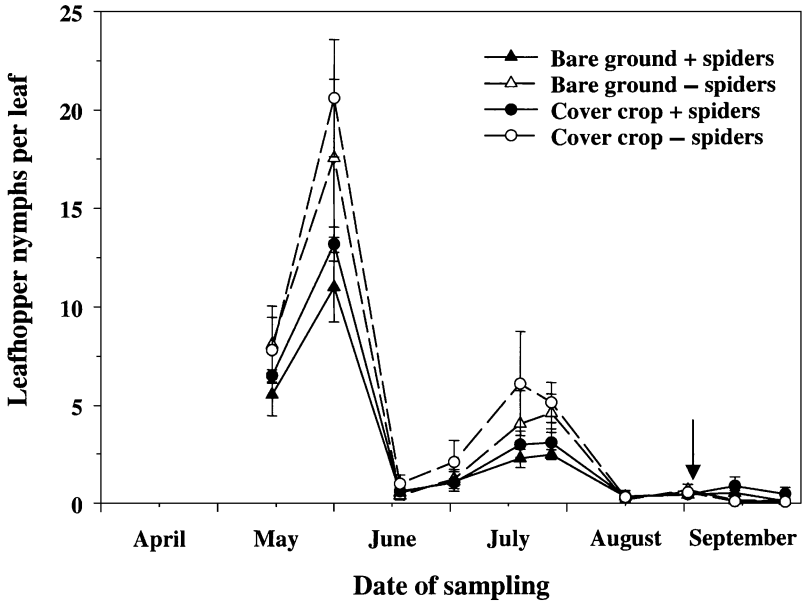

Figure 2 Seasonal patterns of *E. variabilis* nymph densities on vines in cover crop and bare ground plots from May through September. Data points are mean nymph densities per leaf; error bars are standard errors of the means. Treatment means (± SE; n = 30) over all 10 sampling dates were as follows: 2.40 ± 0.62, 3.68 ± 1.06, 2.94 ± 0.73, and 4.36 ± 1.18 for bareground + spiders, bareground – spiders, cover + spiders, and cover – spiders, respectively. Vertical arrow indicates date of grape harvest.

Table 3 Univariate repeated measures analysis of variance of cover crop and spider exclusion effects on densities of *E. variabilis* eggs, nymphs, and adults

Source	d.f.	Mean square	F	P
Live eggs[a]				
Cover crop	1	0.0002	0.05	0.841
Block	2	0.316	34.31	0.028
Error	2	0.008		
Spiders	1	0.734	0.55	0.534
Spiders × cover crop	1	0.180	0.14	0.748
Spiders × block	2	0.362	0.27	0.786
Error	2	1.326		
Nymphs[a]				
Cover crop	1	0.399	2.77	0.238
Block	2	0.691	4.80	0.172
Error	2	0.144		
Spiders	1	0.378	27.26	0.035
Spiders × cover crop	1	0.0001	0.0001	0.994
Spiders × block	2	0.343	24.74	0.039
Error	2	0.014		
Adults[a]				
Cover crop	1	0.003	0.11	0.767
Block	2	0.718	25.69	0.038
Error	2	0.028		
Spiders	1	1.685	45.10	0.022
Spiders × cover crop	1	0.000	0.000	0.987
Spiders × block	2	0.028	0.75	0.572
Error	2	0.037		

[a]Analyses were conducted on log-transformed values of the independent variables. For brevity, date effects are not included in the table. Date effect was significant ($P < 0.01$) for all three independent variables. Date by spider interactions was significant ($P < 0.05$) for both nymphs and adults but not for live eggs ($P > 0.10$). Date by cover crop interaction was not significant for any of the three leafhopper life stages ($P > 0.10$).

non-exclusion vines. Second generation adult *E. variabilis* densities were similar in all the plots (Figure 3, $P > 0.05$). We did not census third generation *E. variabilis* adults.

Densities of *E. variabilis* eggs were not affected by cover crop or spider exclusion, although there was a trend toward higher egg densities in the spider exclusion plots in the mid-June and early July samples (Figure 4). Unlike nymph and adult densities, we did not take leaf samples to estimate *E. variabilis* egg densities until after peak nymph emergence (30 May). Therefore, we are less certain about the indirect impact of cover crop and spider exclusion on first generation egg densities (through predation on overwintering adults). However, the number of first generation leafhopper nymph and *Anagrus* spp. exit holes (data not shown) were similar in all treatments ($P > 0.10$). Total number of exit holes (leafhopper and *Anagrus* spp.) can be reliably used for comparing leafhopper egg densities when background egg mortality is generally low (Murphy et al., 1998).

Parasitism by *Anagrus* spp. was the only additional biotic mortality factor (other than spiders) that affected *E. variabilis* populations in this study. Parasitism of *E. variabilis* eggs by *Anagrus* spp. was not affected by cover crop or by spider exclusion (Figure 5; except for the date effect, none of the other factors were significant). Leafhopper egg parasitism by *Anagrus* spp. varied considerably during the season, ranging from 20% in early June (first leafhopper generation) to nearly 85% at the end of August (peak third generation eggs). *Anagrus* spp. parasitism of *E. variabilis* eggs was density independent, as indicated by regressions of proportion of *E. variabilis* eggs parasitized by *Anagrus* spp. on corresponding *E. variabilis* egg densities at the scale of a plot (means of five leaves per plot) on each of the seven census dates (slope = –0.00008 – 0.001; $r^2 = 0.001–0.171$; $P = 0.181–0.924$; $n = 12$).

In addition to determining the impact of cover crop and spider exclusion on *E. variabilis* densities, we carried out a census of *E. variabilis* nymph densities in plots that had simulated search and disturbance similar to the treatment of exclusion vines during spider removal. Comparisons of *E. variabilis* densities on 30 May, 17 July, and 10 September indicated that *E. variabilis* nymph densities on 'disturbed' vines were not different from their densities on 'undisturbed' vines in both cover crop and bare ground plots (single-factor ANOVA with blocking and stratified by census date: $F_{1,2} = 0.015–3.158$, $P = 0.150–0.909$).

Relative effects of cover crop and spiders: enclosures experiments

Leafhopper egg counts on 28 June, along with leaf area and dry weight measurements are summarized in Table 4. During the 10-day oviposition period, *E. variabilis* females (all females in one enclosure) laid over 1000 eggs per enclosure. Oviposition was similar in both cover crop and bare ground plots (Table 4). In addition, leaf area and leaf dry weights in enclosures were similar in the two treatments on 28 June ($P > 0.05$), thus eliminating the need to correct for these factors for the other enclosures. Determination of nitrogen, phosphorous, and potassium (all expressed as a percentage of dry weight) indicated that on 28 June, vine foliage in enclosures in cover crop and bare ground plots, respectively, contained similar levels of total nitrogen (2.807 ± 0.012 and 2.842 ± 0.03) and phosphorus (0.325 ± 0.022 and 0.287 ± 0.049) (single-factor ANOVA with blocking, $F_{1,2} = 0.932–1.732$, $P = 0.294–0.382$). However, vine foliage in cover crop plots contained significantly higher potassium levels (0.833

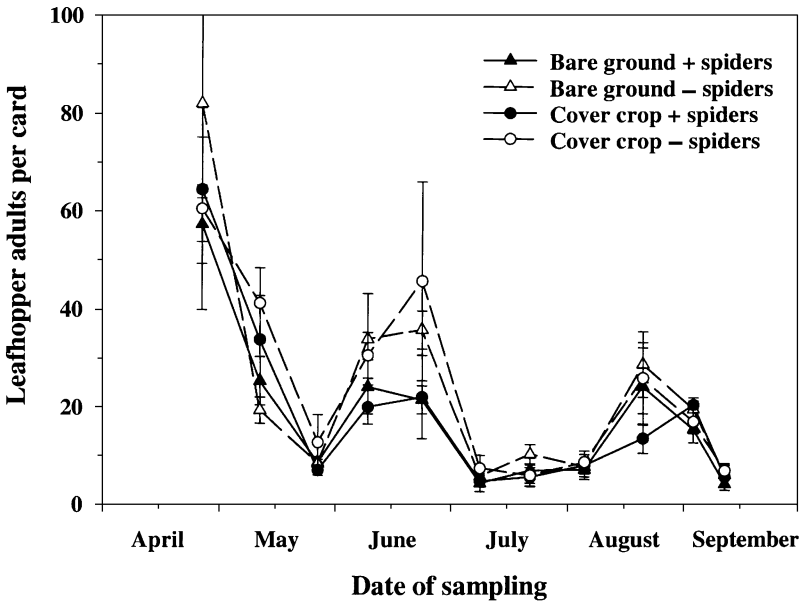

Figure 3 Seasonal patterns of *E. variabilis* adults densities on vines in cover crop and bare ground plots from mid-April through mid-September. Data points are mean adult densities per sticky card trap; error bars are standard errors of the means. Treatment means (± SE; n = 33) over all 11 sampling dates were as follows: 18.0 ± 2.83, 23.3 ± 4.17, 18.6 ± 3.26, and 23.8 ± 3.96 for bareground + spiders, bareground – spiders, cover + spiders, and cover – spiders, respectively.

± 0.026) compared with vine foliage in bare ground plots (0.695 ± 0.006) (single-factor ANOVA with blocking, $F_{1,2}$ = 49.46, P = 0.015), which were similar to differences in potassium levels in cover and bare ground plots in petiole tissue at bloom.

Densities of *E. variabilis* nymphs per enclosure at the time the spiders were added to the enclosures were similar in both cover crop and bare ground plots [cover crop: 118.0 ± 14.1 (mean per enclosure ± SE); bare ground: 88.5 ± 26.9; single-factor ANOVA with blocking: $F_{1,2}$ = 0.561, P = 0.532]. Survivorship of *E. variabilis* (as indicated by nymph, adult, and combined nymph and adult densities) in enclosures was not affected by cover crop or bare ground on 22 July (Table 5). The addition of spiders, however, resulted in a substantial reduction in *E. variabilis* survivorship, as indicated by nymph densities, which were 2.6-fold higher in the absence than in the presence of spiders (Table 5). Adult densities on 22 July were not affected by spider addition (Table 5), probably because only a small proportion of nymphs had reached the adult stage by that time.

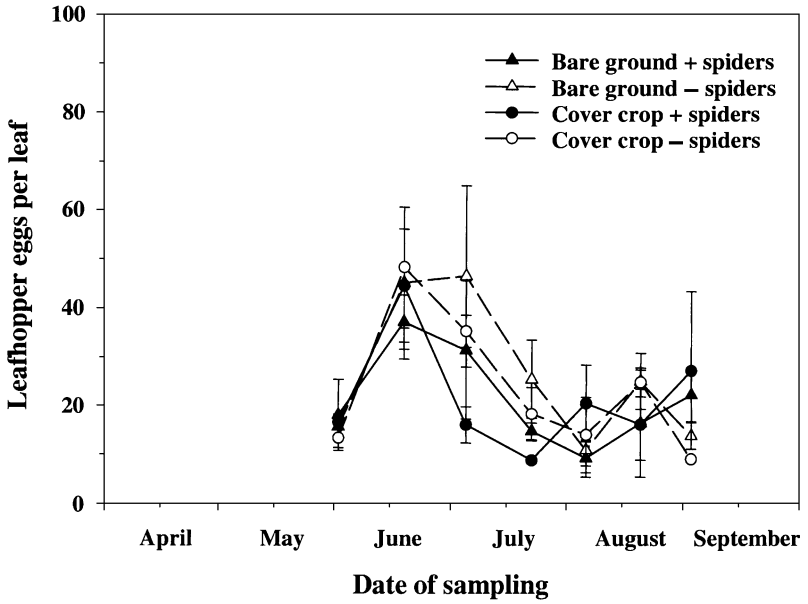

Figure 4 Seasonal patterns of *E. variabilis* egg densities on vines in cover crop and bare ground plots from early June through August. Data points are mean egg densities per leaf; error bars are standard errors of the means.

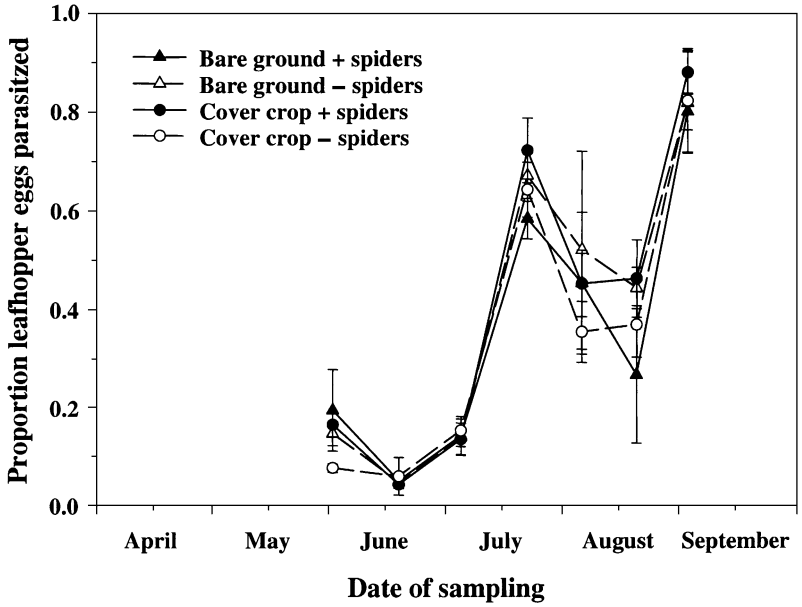

Figure 5 Seasonal dynamics of *E. variabilis* egg parasitism by *Anagrus* spp. on vines in cover crop and bare ground plots from early June to early September. Data points are the mean proportion leafhopper eggs parasitized by *Anagrus* spp. per leaf; error bars are standard errors of the means.

On 9 August, nymph densities in all enclosures were very low (3–8.7 nymphs per enclosure) and most were early instar nymphs (Table 6). The presence of cover crop had little impact on leafhopper survivorship, as indicated by adult densities (P = 0.534) and combined adult and nymph densities (P = 0.560). In contrast, the addition of spiders to enclosures resulted in a substantial reduction in leafhopper survivorship (Table 6), independent of the presence or absence of cover crop (spider by cover crop interaction P > 0.40). Adult leafhopper densities were 5.3-fold greater in the absence than in the presence of spiders.

Spider densities in cages declined through time. On 22 July, enclosures had either two (six enclosures) or three (six enclosures) surviving spiders. None of the enclosures had all four or five spiders. Additional mortality occurred between 22 July and 9 August, as indicated by a lower frequency of enclosures with three spider species and a higher frequency of enclosures with one spider species.

Table 4 Oviposition of *E. variabilis* in enclosures on vines in cover crop and bare ground plots from 18 to 28 June

	Eggs/enclosure[b]	Eggs/g[b]	Eggs/cm^{2}[b]
Treatments[a]	(all leaves)	(leaf dry weight)	(leaf area)
Cover crop	1435.3 ± 91.8	134.3 ± 10.0	0.028 ± 0.014
Bare ground	1186.0 ± 68.8	114.0 ± 11.9	0.015 ± 0.008

[a]Oviposition of *E. variabilis* in enclosures was similar in both cover crop and bare ground plots for eggs per enclosure, eggs/g of leaf dry weight, and eggs/cm^{2} of leaf area (single-factor ANOVA with blocking, P > 0.05 for each variable).

[b]Values are means ± SE. Mean total leaf area and mean total leaf dry weight in enclosures were similar in both cover crop and bare ground plots (single-factor ANOVA with blocking, P > 0.5 for each variable).

Discussion

In this study, we intended to determine the relative effects on *E. variabilis* abundance on grapevines by cover crops [as used in our previous studies (Roltsch et al., 1998)] and predation by the spider assemblage commonly found in 'Thompson Seedless' vineyards in California's San Joaquin Valley. With open-vine spider exclusion and enclosures, our study demonstrated that the spider assemblage found in 'Thompson Seedless' vineyards can cause substantial *E. variabilis* mortality and hence lead to significantly lower *E. variabilis* abundance on the cover-cropped vines. Furthermore, findings from the present study support our previous findings that increasing vegetation diversity with a cover crop mixture of *V. sativa*, *V. benghalensis*, and *A. sativa* (managed as specified in this experiment) enhances densities of four out five of the spider species commonly found in San Joaquin Valley 'Thompson Seedless' vineyards.

In the open vine experiments, spider exclusion clearly resulted in higher *E. variabilis* nymph and adult densities at their respective first generation peaks (May for nymphs and June for adults). That the effect of spider exclusion on leafhopper nymphs was not clearly apparent until late May suggests that spider abundance was still too low before that date to have a measurable impact on relatively low-density leafhopper populations. Low spider densities on vines in

Table 5 The impact of spider predation on *E. variabilis* in enclosures on vines associated cover crop or bare ground from 6 to 22 July

Treatments	Nymphs	Adults	Total
***E. variabilis* densities (mean ± SE) in enclosures on 22 July[a]**			
Bare ground – spiders	550.8 ± 162.9	34.5 ± 16.5	585.3 ± 179.1
Bare ground + spiders	214.7 ± 81.5	22.3 ± 6.27	237.0 ± 87.5
Cover crop – spiders	394.0 ± 88.0	32.7 ± 18.2	426.7 ± 94.4
Cover crop + spiders	154.2 ± 40.2	15.8 ± 4.59	170.0 ± 44.8

	Nymphs[b]			Adults[b]			Total[b]		
Source (d.f.)	MS	F	P	MS	F	P	MS	F	P
ANOVA									
Cover crop (1)	0.15	0.96	0.430	0.03	0.39	0.597	0.15	1.05	0.422
Block (2)	0.96	6.23	0.138	0.90	11.7	0.079	0.92	6.36	0.136
Error (2)	0.15			0.01			0.15		
Spiders (1)	3.18	16.7	0.015	0.74	3.81	0.123	2.94	16.3	0.015
Spiders × cover crop (1)	0.02	0.10	0.764	0.19	0.61	0.480	0.01	0.06	0.826
Error (4)	0.19			0.20			0.18		

[a]Means are based on two enclosures per plot (n = 3).
[b]ANOVAS were performed on log-transformed plot means to correct for heterogeneity of variance.

April and early May had no measurable impact on relatively abundant overwintering adult leafhoppers during that period (Figure 3). Since we started with equal overwintering adult leafhopper and later with equal first generation leafhopper egg densities across treatments (Figures 3 and 4), most of the differences in first generation nymph abundance must have been due to differences in spider predation on exclusion and non-exclusion vines, especially since parasitism rates by *Anagrus* spp. were similar in all plots (Figure 5), and other natural enemies (e.g., *Chrysoperla* spp., *Orius* spp. and *A. agilis*) were rare (data not shown). That these generalist natural enemies (other than spiders) were rare in our vineyard is consistent with findings from numerous other surveys showing that spiders represented about 98% of the generalist predator fauna in Californian grape vineyards (e.g., Costello & Daane, 1999).

Table 6 The impact of spider predation on *E. variabilis* in enclosures on vines associated cover crop or bare ground from 6 July to 9 August

Treatments	Nymphs	Adults	Total
***E. variabilis* densities (mean ± SE) in enclosures on 9 August[a]**			
Bare ground – spiders	4.67 ± 1.21	457.5 ± 29.8	462.2 ± 28.7
Bare ground + spiders	3.00 ± 1.81	68.7 ± 20.1	71.7 ± 18.5
Cover crop – spiders	8.67 ± 0.93	294.0 ± 75.2	302.7 ± 74.5
Cover crop + spiders	7.33 ± 3.67	64.7 ± 22.1	72.0 ± 25.3

	Nymphs[b]			Adults[b]			Total[b]		
Source (d.f.)	MS	F	P	MS	F	P	MS	F	P
ANOVA									
Cover crop (1)	0.83	2.64	0.246	0.28	0.56	0.534	0.24	0.48	0.560
Block (2)	0.72	2.29	0.304	0.13	0.26	0.796	0.17	0.32	0.754
Error (2)	0.31			0.51			0.51		
Spiders (1)	0.94	1.03	0.367	9.36	60.9	0.002	8.82	65.4	0.001
Spiders × cover crop (1)	0.01	0.01	0.943	0.12	0.79	0.426	0.12	0.88	0.401
Error (4)	0.96			0.15			0.14		

[a]Means are based on two enclosures per plot (n = 3).
[b]ANOVAS were performed on log-transformed plot means to correct for heterogeneity of variance.

The impact of spider exclusion diminished during the second generation (July), and was absent during the third generation (in September) despite 2.3–2.7-fold differences in spider densities between exclusion and non-exclusion vines. The lower impact of spider exclusion on leafhopper nymph densities during the second and third generation was most likely the result of lower overall leafhopper densities during the summer months. The overall decline of *E. variabilis* to low levels during the second and third generation (July–September) was probably caused by the combination of spider predation as already discussed, *Anagrus* spp. parasitism, and poor vine nutritional quality. Parasitism by *Anagrus* spp. played a much greater role in limiting *E. variabilis* densities during the second and third generations than during the first generation. Parasitism rate by *Anagrus* spp. ranged from 16–22% during the first generation to 80–87% during the third generation. Vine nitrogen status was low across treatments during the summer months, and this may have contributed in part to the overall decline in leafhopper densities observed throughout the vineyard site, as low nitrogen levels are known to negatively affect several aspects of *E. variabilis* reproduction and survivorship (Mayse et al., 1991).

Our study presents clear evidence that the specific cover crop used in this experiment enhances spider abundance; however, this enhancement appears to be spider species-dependent (*T. pacificus* > *Theridion* spp. > *H. nedra* > *C. inclusum*, based on differences in densities in July between cover crop and bare ground vines) and is most pronounced during the middle of the summer (i.e., July and August). In a 3-year experiment in a table grape vineyard in California's San Joaquin Valley, total spider densities were not affected by the presence of ground cover, but the abundance of one species, *T. pacificus*, was consistently higher on vines in ground cover plots compared with vines in bare ground plots (Costello & Daane, 1998). In our study, *T. pacificus* abundance was also higher in cover crop plots compared with bare ground plots, and in both studies, *T. pacificus* showed the greatest response to the presence of cover crop. The two studies contrasted, however, in the different response to cover crop by *H. nedra* and *Theridion* spp. – these species increased in abundance in the presence of cover crop only in our study. The differences in the response to the presence of cover crop by *H. nedra* and *Theridion* spp. are likely due to differences in the relative abundance of the these species in the two vineyards [70% in our study and 4% in that of Costello & Daane (1998)], and perhaps to other factors related to specific cover crop management, vineyard age, and differences in spider species composition on grapevines and ground cover. That *H. nedra* and *Theridion* spp. were relatively rare in the study by Costello and Daane may indicate that factors inherent to the particular environment in that study site limited the abundance of those two species, and would therefore have limited their capacity to respond to the presence of cover crop. Of the spiders reported on vines in our study and that of Costello & Daane (1998), *C. inclusum* was the only species that did not respond to the presence of cover crop in both studies, where it was also equally represented relative to the abundance of other spiders on the vines. See Costello & Daane (1999) for a plausible explanation for the lack of response of *C. inclusum* to the presence of cover crop.

Despite this positive evidence concerning the enhancement of spider populations and their impact on *E. variabilis* densities, we are not able to support, based on the present results, the idea that enhanced spider densities on vines in cover crop plots would necessarily result in a greater suppression of *E. variabilis* densities, which underscores the complex and variable nature of trophic interactions within vineyard agroecosystems. Although a spring and early summer cover crop in this study enhanced spider abundance, and spider exclusion resulted in elevated *E. variabilis* densities, overall densities of this pest on vines in cover crop plots were similar to those on vines in bare ground treatments. In contrast, *E. variabilis* densities were considerably lower on vines adjacent to cover crop in this same vineyard over the previous two growing seasons (Roltsch et al., 1998), and this difference was not due to the effects of cover crop on vine nutrient status, as NPK levels were similar on vines in cover crop and bare ground areas (R. Hanna and F.G. Zalom, unpubl. data). There are several possible unknown factors which could cause the differences in the results of the two studies. Here we explore one explanation related to the level of spider enhancement needed to obtain a measurable impact on leafhopper densities.

Spider densities in the present study were only 1.6-fold higher on vines in cover crop plots compared with vines in bare ground plots. In all other studies (Hanna et al., 1996b; Roltsch et al., 1998) in which spider enhancement on cover cropped vines resulted in significant reductions in leafhopper densities, there were greater than twofold differences in spider densities between cover crop and bare ground vines realized. This is also evident in the present study, where an average difference in spider densities of 2.1-fold between exclusion and non-exclusion vines, resulted in significant differences in leafhopper densities during the first generation, when leafhoppers were still abundant. It is therefore likely that differences in (or enhancement of) spider densities in excess of twofold would be needed for a measurable impact on leafhopper populations. Additional field experiments with cover crop and spider exclusion might be needed to lend further support to our conclusions. The absence of a measurable link between spider enhancement

and leafhopper suppression in cover crop plots notwithstanding, the fact remains that the cover crop system used in this study consistently resulted in greater population densities of four out of five spider species on vines adjacent to the cover crop compared with those in bare ground plots (this study and Roltsch et al., 1998). These results add to mounting evidence showing that greater habitat complexity, such as that obtained with cover cropping, leads to an enhancement in spider densities (e.g., Rypstra, 1983; Greenstone, 1984; Roltsch et al., 1998 reviewed by Sunderland & Samu, 2000). Several possible mechanisms have been proposed for the increase in spider densities with increasing habitat structure and complexity, but these mechanisms have not been well elucidated experimentally. Here we explore two of the mechanisms relative to the enhancement of spider densities observed in our study.

First, it is possible that spider enhancement was related to an increase in alternative prey and to the movement of spiders between vines and ground vegetation in cover crop plots. If the cover crop augmented the food resources available to the spiders, and the spiders 'shuttled' between cover crop and vines, the cover crop could have indirectly enhanced spider numbers on the vines (and of course in the cover crop) [but see Riechert & Bishop (1990) for lack of response of spiders to the addition of plants that presumably increased prey densities]. In our study, densities of arthropods, particularly thrips, flies, and several homopteran insects trapped on yellow sticky cards in the vine canopy, were substantially higher on vines in cover crop plots compared with bare ground plots (R. Hanna and F. G. Zalom, unpubl. data), and may have affected several elements of spider behavior and life history [e.g., dispersal behavior, residence time, aggregative response, and reproduction and survivorship (Provencher & Vickery, 1988)], leading to an enhancement of spider abundance on vines adjacent to the cover crop. Evidence from elemental marking studies using foliar applications of rubidium chloride to the cover crop also provided evidence that spiders in the vine canopy feed on arthropods originating from the cover crop [44.1 and 47% of spiders, and 17.1 and 56.3% of herbivores collected from the vines and the cover, respectively, contained elevated levels of rubidium (R. Hanna, F. G. Zalom, M. Stimmann, A. Corbett, and L. Martin, unpubl. data)]. It is not clear if the spiders consumed these additional (marked) food resources when they moved or passed through the vines, or if the spiders consumed the marked prey in the cover and moved between vine and cover. Second, it is also possible that enhancement of spider abundance on covercropped vines was aided by a favorable thermal environment for spiders and alternate prey (Riechert & Tracy, 1975). Although we did not measure temperature and humidity in the experimental plots, vine canopy temperature was only slightly affected by cover crop in a similar experiment [1–2 °C cooler on cover cropped vines for a brief period in the afternoon on days when maximum temperature exceeded 33 °C (R. Hanna and F.G. Zalom, unpubl. data)]. We are less certain, however, about the impact of the cover crop on relative humidity, which is much more difficult to measure accurately. We believe that it is unlikely that relative humidity in the vine canopy was substantially affected by the cover crop because the vines were bordered by cover crop from one side and bare ground on the other, and where cover crop was planted it covered approximately 60% of row middles. The impact of cover crop on canopy temperature (and presumably relative humidity) is minimal when > 30% of the ground is free of vegetation (R. Snyder, Department of Land, Air and Water Resources, University of California, Davis, pers. comm.).

While we can only speculate at this time on how spiders were enhanced by the cover, it is unlikely that only one of the scenarios discussed above fully explains this enhancement. We believe, however, that the extra food resources provided by the cover crop plays the greatest role in enhancing spider densities, and for some species, this enhancement might be facilitated by the utilization of the cover crop for protection from extreme thermal environments.

While our experimental vineyard was representative of most raisin grape vineyards in the San Joaquin Valley, the relative impact of cover crop and spiders on *E. variabilis* would probably depend on several factors, including specific cover crop management, spider species composition, and abundance; grape variety, age, and specific cultural management practices; environmental conditions associated with specific regions, and pesticide history (Costello & Daane, 1995; Hanna et al., 1995, 1996b; Costello & Daane, 1998; Roltsch et al., 1998). Additionally, the overall effect of spiders on *E. variabilis* may depend on the strength of other biotic mortality factors (e.g., *Anagrus* spp. parasitism and predation by other generalist predators), and abiotic factors such as microclimate and vine-related factors such as nitrogen and water status that can potentially affect *E. variabilis* abundance. These factors can be region- and vineyard-specific, and can vary from year to year (Hanna et al., 1995; Roltsch et al., 1998). While it is well acknowledged, however, that the impact of spiders and cover crop should be studied under a range of cultural conditions and over several years and regions in order to draw generalized conclusions, this one-year study has clearly determined that, if sufficiently abundant, the spider assemblage found in the study site can negatively influence *E. variabilis* densities in vineyards. To our knowledge, this

is the first experimental demonstration that spiders can reduce leafhopper densities in vineyards.

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