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Effects of predation and competition on the population dynamics of *Tetranychus pacificus* on grapevines

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Summary

1. The Pacific spider mite *Tetranychus pacificus* and the Willamette spider mite *Eotetranychus willamettei* are herbivore pests of grapevines in California. The two spider mite species share a common and often effective phytoseiid predator, the Western orchard predatory mite *Metaseiulus occidentalis*. It has been suggested that *E. willamettei* may be beneficial in vineyards because it may have a negative impact on the more damaging *T. pacificus* through their shared predator or through some form of interspecific competition. We conducted field and greenhouse experiments to determine the relative effects of these interactions between the two herbivores on the population dynamics of *T. pacificus* in 'Thompson Seedless' grape vineyards. We also used the field data to generate a functional relationship for the combined impact of *E. willamettei* and *M. occidentalis* on *T. pacificus*.

2. Predation and predator-mediated apparent competition were the only factors affecting *T. pacificus* densities in the field experiment. The addition of the predatory mite *M. occidentalis* alone resulted in a significant reduction in *T. pacificus* densities, while the addition of *E. willamettei* alone had little impact on *T. pacificus* densities. The greatest reductions in *T. pacificus* densities occurred in plots where both the predatory mite *M. occidentalis* and *E. willamettei* were added. The predatory mite occurred earliest and increased at the greatest rate in plots where it was released along with *E. willamettei*. From April to June, *M. occidentalis* abundance was positively correlated with *E. willamettei* abundance while *T. pacificus* abundance in July and August was negatively correlated with *M. occidentalis* abundance in the period April to June.

3. Under greenhouse conditions, the addition of *E. willamettei* to *T. pacificus* vines resulted in a marked decrease in *T. pacificus* population growth rate. In contrast, doubling *T. pacificus* abundance in the absence *E. willamettei* did not affect *T. pacificus* population growth rate, indicating that interspecific competition is more important than intraspecific competition in determining *T. pacificus* abundance.

4. Contrary to the greenhouse data and other studies in 'Zinfandel' vineyards, we found no evidence that *E. willamettei* competed with *T. pacificus* in the absence of predation in a Thompson Seedless vineyard. We suggest that the outcome of interactions between *E. willamettei* and *T. pacificus* may be affected by grape cultivar, growing region, a combination of cultivar and region-specific differences, or size and timing of vine infestations with *E. willamettei*.

5. In Thompson Seedless vineyards, vine infestation with *E. willamettei* would be most useful in increasing the effectiveness of the predatory mite *M. occidentalis* in controlling *T. pacificus*, primarily through an elevated predatory mite abundance prior to the development of large *T. pacificus* populations.

Key-words: Acari, *Eotetranychus willamettei*, *Metaseiulus occidentalis*, predator-mediated apparent competition, predator–prey interactions, *Vitis vinifera*.

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Introduction

Direct effects of predation and interspecific competition have long been implicated as important factors affecting the population dynamics of arthropods in natural systems (e.g. Schoener 1983; Connell 1983; Sih *et al.* 1985). More recently, it has been suggested that indirect effects produced by shared predation (i.e. one or more predator species sharing more than one prey species) may also cause profound effects on prey population dynamics (e.g. Sih *et al.* 1985; Kerfoot & Sih 1987). One class of indirect effects of shared predation results in population and community patterns similar to those produced by interspecific competition (Holt 1977, 1984; Holt & Kotler 1987; Holt & Lawton 1994; Holt, Grover & Tilman 1994). Holt (1977) termed this interaction predator-mediated apparent competition, which arises from strong predator numerical responses to prey densities. Despite the theoretical appeal of apparent competition and the existence of numerous examples of predator–prey interactions that are in line with its predictions (Holt 1984), there have been few experimental demonstrations of its existence (Collyer 1964; Schmitt 1987; Settle & Wilson 1990; Huang & Sih 1990; Karban, Hougén-Eitzman & English-Loeb 1994). Although apparent competition theory was developed for prey that do not compete directly (Holt 1977), competition for resources and predator-mediated apparent competition are not mutually exclusive hypotheses and are likely to be complementary forces determining sizes of animal populations (Holt 1984; Holt *et al.* 1994; Sih *et al.* 1985).

In this paper, we explore the relative effects of predation, interspecific competition, and predator-mediated apparent competition on the population dynamics of the Pacific spider mite *Tetranychus pacificus* McGregor (Acari: Tetranychidae), which is a serious pest of grapevines *Vitis vinifera* L. in the San Joaquin Valley of California. Large populations of this spider mite species are capable of inflicting considerable damage to vine growth and grape yield and quality (Flaherty *et al.* 1992). The Willamette spider mite *Eotetranychus willamettei* (McGregor) (Acari: Tetranychidae) is also commonly found on grapevines, but generally causes considerably less damage than comparable densities of *T. pacificus*, particularly in vineyards of the Southern San Joaquin Valley, California (Flaherty 1969). Both *T. pacificus* and *E. willamettei* are attacked by the predatory mite *Metaseiulus* (= *Typhlodromus* = *Galendromus*) *occidentalis* (Nesbitt) (Acari: Phytoseiidae), which is their principal biological mortality agent in vineyards (Flaherty *et al.* 1985).

That *T. pacificus* and *E. willamettei* co-occur on grapevines and share the same predator has led to speculations that the two species might compete directly (interspecific competition) or through the shared predator (predator-mediated apparent competition). Observations from several vineyards have

led to speculations that the presence of *E. willamettei*, especially during spring, may prevent outbreaks of *T. pacificus*, possibly by leading to an early increase in populations of *M. occidentalis* (Flaherty & Huffaker 1970; Flaherty & Hoy 1971). If this hypothesis is true, then predator-mediated apparent competition between *T. pacificus* and *E. willamettei* may be an important factor in the dynamics of this acarine predator–prey system. More recently, results from greenhouse and field experiments have suggested that negative effects of *E. willamettei* on *T. pacificus* may be caused by interspecific competition or ‘induced resistance’ (English-Loeb & Karban 1988; Karban & English-Loeb 1990). However, these alternative responses were cultivar-specific. While they were apparent on ‘Zinfandel’ and ‘Chardonnay’ cultivars, they were weak or lacking on ‘Thompson Seedless’ grapevines. Also lacking were the relative effects of interspecific and intraspecific competition on spider mite densities.

Clearly, several biological processes may be important in determining population abundance and pest-status of spider mites in vineyards. In this paper we report the results of a field experiment designed to assess the relative significance of predation, interspecific competition, and predator-mediated apparent competition on the short- and long-term dynamics of *T. pacificus* populations in Thompson Seedless vineyards in the San Joaquin Valley of California. We also report on the results of a greenhouse experiment designed to compare the relative significance of interspecific competition (concurrent feeding by *E. willamettei*) and intraspecific competition on the population growth of *T. pacificus*. In conducting this study, we were also motivated by the practical desire (i) to determine the viability of vine infestation with the less damaging *E. willamettei* to increase the effectiveness of *M. occidentalis* in reducing densities of the more damaging *T. pacificus*, and (ii) to generate a functional relationship for predicting the impact of *M. occidentalis* densities on *T. pacificus* populations in the presence of different levels of *E. willamettei*.

Methods

LIFE HISTORY OF THE MITES

Both *T. pacificus* and *E. willamettei* are endemic to the far western United States. They were first reported on grapes in California vineyards by Lamiman (1935). Both species are found throughout California, but *T. pacificus* is most commonly found in the warm interior valleys (Flaherty 1967). *Tetranychus pacificus*, like other members of the acarine genus *Tetranychus*, has a wide host range, infesting a variety of perennial and annual plant species, and is a pest of major crops in the western United States (Pritchard & Baker 1955). In contrast, *E. willamettei* infests only a few perennial plant species including apple *Malus* spp., antelope brush *Purshia tridentata*, box elder *Acer negundo* cali-

fornicum, service berry *Amelanchier* sp., *Quercus garryana*, and both wild and cultivated *Vitis* spp. (Frazier & Smith 1946; Pritchard & Baker 1955). While the biology of *T. pacificus* is well known on several hosts, little is known about the biology of *E. willamettei* on hosts other than grapes.

Both *T. pacificus* and *E. willamettei* are residents of vineyards; they overwinter as mated adult females under loose bark (Flaherty & Huffaker 1970; Kinn & Doult 1972). In late winter and early spring, adult females of both species become active and colonize newly expanded leaves soon after bud break (Flaherty & Huffaker 1970). Generally, *E. willamettei* appears to be more active and able to reproduce faster than *T. pacificus* during the cool spring temperatures (R. Hanna, personal observation). It is not known, however, if the differences in early season activity between the two spider mite species is due to differences in critical temperature thresholds or the shape of the development–temperature curves. Both species produce several generations during the grape growing season and can reach high densities during the summer months.

Metaseiulus occidentalis is the dominant natural enemy of spider mites in California vineyards (Flaherty & Huffaker 1970; Kinn & Doult 1972). Although indigenous to western North America, *M. occidentalis* is now found in many areas of the world (McMurtry 1982). It is associated with many mite species on many annual and perennial host-plants (Schuster & Pritchard 1963). *Metaseiulus occidentalis* can be found in vineyards throughout the year, and is capable of long- and short-range dispersal between crop hosts (Hoy 1982). In vineyards, *M. occidentalis* overwinters under bud scales as diapausing, non-gravid and mated adult females (Hoy & Flaherty 1970). In the spring, overwintering females colonize young leaves where they feed on *E. willamettei*, *T. pacificus* and the tydeid mites *Homeopronematus* (*Pronematus*) *anconai* (Baker) and *Pronematus ubiquitous* McGregor.

Soon after the initiation of vegetative growth, predators and prey colonize the newly emerging leaves, and remain on the lower leaves of the growing shoots for much of the early spring. During mid-to-late spring and in the summer, predators and prey move outwards along the elongating shoots (Hanna *et al.* 1996). *Tetranychus pacificus* and *E. willamettei* overlap considerably in their distribution on the vines but during the summer, *T. pacificus* occurs in greater abundance on sun-exposed areas of the vines, and *E. willamettei* occurs throughout the vines but with slightly greater abundance on shaded leaves (Hanna *et al.* 1996). These overlapping distributions on vines may increase the likelihood of direct or indirect interactions between *T. pacificus* and *E. willamettei*.

FIELD EXPERIMENT

We conducted a field experiment during the 1989 growing season to determine the relative effects of

predation, interspecific competition, and predator-mediated apparent competition on the population dynamics of *T. pacificus*. We conducted this experiment in a section of a 35-year-old Thompson Seedless vineyard (located near Madera, California) where *T. pacificus* reached outbreak levels during the previous year, while *E. willamettei* and *M. occidentalis* were rare (R. Hanna, unpublished data). We used a randomized complete block design with four treatments and three replicate blocks. Each subplot was four vine rows (14.6 m wide) by 10 vines (24.4 m long), and was separated from other subplots within each block by 15 buffer vines (36.6 m). Four vine rows (14.6 m) served as buffers between blocks. This experimental design represented a trade-off between large plot size that minimized between-plot interference, and small plot size that minimized between-plot variability. We chose three replicates of larger plots, as opposed to a greater number of replicates and smaller plots, to minimize between-plot interference. We reduced sampling error by taking a large number of sample units (i.e. grape leaves) from each plot.

Treatments were randomly assigned to plots within each of three blocks. In one treatment, we added *E. willamettei* and *M. occidentalis*. In two other treatments we added either *E. willamettei* or *M. occidentalis*. We did not manipulate predator and prey abundance in the fourth treatment, which served as the control. [Another experiment was conducted to determine the impact of *M. occidentalis* and *T. pacificus* on *E. willamettei* Hanna (1992)]. *Eotetranychus willamettei* needed for our experiment was collected from a nearby vineyard where this mite was abundant. We treated source vines with methomyl (Dupont Co., Richmond, VA) 1 week prior to collecting *E. willamettei* to eliminate naturally occurring individuals of *M. occidentalis*. Methomyl is toxic to *M. occidentalis* (with a residual toxicity of at least 5 days), and relatively harmless to *E. willamettei* (Hoy *et al.* 1979). Vines in the experimental area were not treated with methomyl at any time during the season. On 10 May 1989, we added 156 ± 45 (± 1 SE) immature and adult *E. willamettei* individuals to each vine within each of the *E. willamettei* release plots. We also added 67 ± 19 (± 1 SE) mobile individuals of *M. occidentalis* (Biotactics Inc., Riverside, CA) per vine in predator release plots on 21 May 1989.

We sampled all plots at approximately 3-week intervals between 24 April and 2 June 1989, and at approximately 2-week intervals between 2 June and 14 August 1989. On each sampling date, we collected 20 leaves from the middle six vines of the two centre vine rows within each plot. On the first three sampling dates, we collected leaves from the basal region of vine shoots. During the remainder of the season, leaves were selected from the middle portion of shoots. On all sampling dates, shoot selection was divided equally between four zones of the vine canopy: south, north, top and interior. Although sampling was stratified, shoots

within zones and leaves from each mid-shoot region were selected randomly. All life stages of spider mites and *M. occidentalis* on leaves were counted under a dissecting microscope in the laboratory.

We used univariate repeated measures analysis of variance of the two main effects (*M. occidentalis* addition and *E. willamettei* addition) and their interaction to determine the impact of *M. occidentalis* and *E. willamettei* on the abundance of *T. pacificus*, *E. willamettei* and *M. occidentalis*. We also quantified the effects of sampling date and the interaction of sampling date with the main effects. All analyses were conducted with SAS PROC GLM (SAS Institute 1989). Due to heterogeneity of variance inherent in census data, all analyses were performed on log-transformed values of the dependent variables.

GREENHOUSE EXPERIMENT

We conducted a greenhouse experiment on 2-month-old grapevines to measure the effect of interspecific and intraspecific competition on changes in *T. pacificus* population size. We established two solitary and one mixed species treatments. One solitary treatment received 15 adult *T. pacificus* females, and the other solitary treatment received 30 adult *T. pacificus* females. The mixed-species treatment received 15 adult *T. pacificus* females and 15 adult *E. willamettei* females. There were five replicate vines for each treatment. All vines were uniform in size and age, with a single shoot and a total of seven leaves for each shoot. Vine and mite source and culture were as described by Hanna & Wilson (1991). Eight days after the addition of spider mites to the vines, all leaves were harvested and chilled to 3 °C, and all stages of spider mites were counted in the laboratory.

Changes in *T. pacificus* population size (expressed

as the ratio of final mite and initial mite density) were analysed with a one-way analysis of variance. We used planned contrasts to test for the effects of interspecific and intraspecific competition on changes in *T. pacificus* population size.

Results

FIELD EXPERIMENT

We conducted this field experiment to test the relative effects of predation, interspecific competition, and predator-mediated apparent competition on *T. pacificus* abundance. We assumed that rates of mortality due to predation by *M. occidentalis*, and the effects of interspecific competition, can be inferred from between-treatment differences in *T. pacificus* abundance. Seasonal trends of *T. pacificus*, *E. willamettei* and *M. occidentalis* are presented in Figs 1, 2 and 3. The results of univariate repeated measures analysis of variance on each species are presented in Table 1.

We succeeded in establishing large differences in *E. willamettei* densities in our experimental plots. Our efforts were especially aided by low background levels of *E. willamettei* in the control plots, where *E. willamettei* abundance remained very low throughout the experiment (Fig. 1). The addition of *E. willamettei* explained the greatest proportion of variation in numbers of this species. In plots where *E. willamettei* was added, its seasonal density reached a significant 2.7-fold higher level than in non-addition plots. The addition of *M. occidentalis* appeared to reduce *E. willamettei* population size but this effect was not significant in our experiment (Fig. 1 and Table 1). Furthermore, the effect of *E. willamettei* augmentation on its seasonal density was independent of our efforts to

Table 1. Repeated measures analysis of variance* on mite counts where *E. willamettei* and *M. occidentalis* were simultaneously manipulated to test their impact on the population dynamics of *T. pacificus*

Source of variation	d.f.	<i>T. pacificus</i>		<i>E. willamettei</i>		<i>M. occidentalis</i>	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Between treatments†							
<i>M. occidentalis</i> addition	1	67.50	<0.005	0.85	0.391	32.16	0.001
<i>E. willamettei</i> addition	1	6.59	0.043	107.61	<0.005	4.54	0.077
Interaction	1	3.81	0.098	1.08	0.338	5.36	0.060
Within treatments†							
Date	7	218.30	<0.005	97.97	<0.005	132.70	<0.005
Date × <i>M. occidentalis</i> addition	7	28.70	<0.005	1.84	0.104	21.58	<0.005
Date × <i>E. willamettei</i> addition	7	2.33	0.042	11.69	<0.005	2.12	0.062
Date × <i>M. occidentalis</i> addition × <i>E. willamettei</i> addition	7	2.43	0.035	1.44	0.217	2.24	0.049

*Analysis performed on log-transformed values of the dependent variables.

†All block effects had a *P*-value greater than 0.05. Error degrees of freedom for between-treatment effects = 6. Error degrees of freedom for within-treatment effects were adjusted where necessary with the Huynh–Feldt Epsilon ($\epsilon = 1.066$ for *T. pacificus*, $\epsilon = 1.188$ for *E. willamettei* and $\epsilon = 0.973$ for *M. occidentalis*). Degrees of freedom were not adjusted for $\epsilon > 1$. Unadjusted residual d.f. = 42.

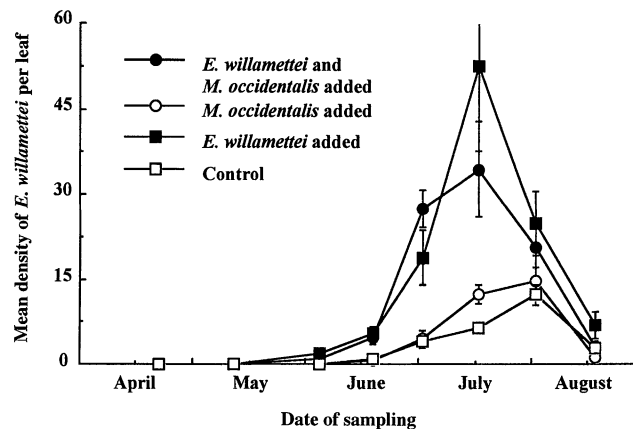


Fig. 1. Abundance of *E. willamettei* on grapevines from 24 April to 14 August 1989. Data are mean density of *E. willamettei* per leaf with standard errors.

manipulate predator densities (Fig. 1 and Table 1). Although *M. occidentalis* is generally capable of controlling *E. willamettei* densities, we cannot make any conclusions on the impact of *M. occidentalis* on *E. willamettei* (when present alone) in this study because *T. pacificus* was present in all plots. This issue is considered in another study that examined the impact of *T. pacificus* and predator addition on the population dynamics of *E. willamettei* (Hanna 1992).

Fluctuations in *E. willamettei* abundance through the season was indicated by a significant overall date effect (Table 1), with these fluctuations being affected most by the addition of *E. willamettei*. Densities of this mite increased earlier and faster where it was added (linear time contrast, $P = 0.007$). Rate of change in *E. willamettei* densities was not affected by predator release ($P = 0.246$), and the temporal dynamics of *E. willamettei* were independent of predator release ($P = 0.591$).

Tetranychus pacificus densities differed considerably between treatments (Fig. 2). The average seasonal density of *T. pacificus* in non-predator release plots was 2.8-fold greater than in predator release plots. *Tetranychus pacificus* densities were also negatively affected by the presence of *E. willamettei*. The

average seasonal density of *T. pacificus* was greater on vines where *E. willamettei* was not added. There were also indications that *E. willamettei* releases might have increased the success of *M. occidentalis* in reducing the size of *T. pacificus* populations ($P = 0.098$). A lack of significant interaction effect was probably due to large subplot variability and the cumulative nature of errors associated with the interaction effect. We cannot interpret the *E. willamettei* effect as evidence for some form of interspecific competition because the effect of *E. willamettei* addition was averaged over predator plots and therefore contained some indirect effects. *Post hoc* comparisons of pairs of cell means (or simple effects) were necessary for partitioning the direct and indirect effects of *E. willamettei* on *T. pacificus* densities. Also, the interaction between sampling dates and treatments provided greater sensitivity for testing the null hypothesis of treatment effects, and allowed subplots to act as their own control to a greater extent than in only main effect analysis (Dr Neil Willits, Statistical Laboratory, University of California, Davis, personal communication).

Since conservatism was desirable for *post hoc* comparisons, we used Tukey's technique (Neter, Wasserman & Kutner 1985) to test each treatment mean

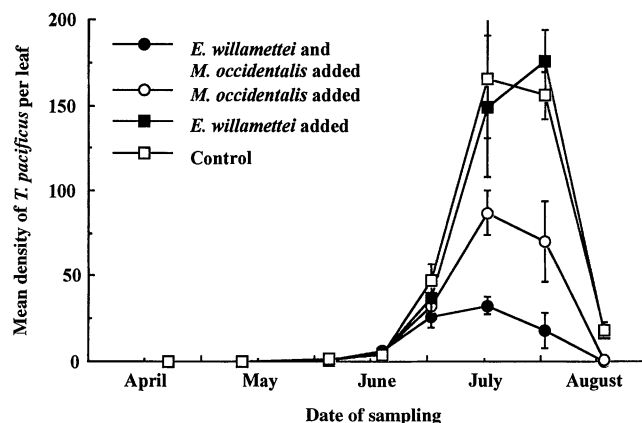


Fig. 2. Abundance of *T. pacificus* on grapevines from 24 April to 14 August 1989. Data are mean density of *T. pacificus* per leaf with standard errors.

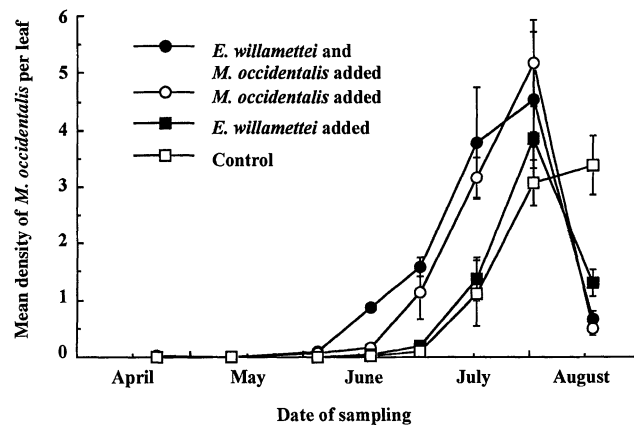


Fig. 3. Abundance of *M. occidentalis* on grapevines from 24 April to 14 August 1989. Data are mean density of *M. occidentalis* per leaf with standard errors.

against the control (which did not receive *M. occidentalis* or *E. willamettei*). Of interest were three comparisons used to test the simple effects on *T. pacificus* by (i) adding only *M. occidentalis*, (ii) adding only *E. willamettei*, and (iii) adding both *E. willamettei* and *M. occidentalis*. The first and second comparisons, respectively, measured the separate direct effects of *M. occidentalis* and *E. willamettei* on *T. pacificus* abundance. The third comparison measured the indirect components in the effects of *M. occidentalis* and *E. willamettei* on *T. pacificus* abundance.

The addition of *M. occidentalis* in the absence of *E. willamettei* releases resulted in a twofold reduction in *T. pacificus* abundance ($P < 0.05$), whereas the addition of *E. willamettei* in the absence of *M. occidentalis* releases resulted in negligible reductions in *T. pacificus* abundance, thus supporting the hypothesis that *E. willamettei* has little direct effect on *T. pacificus*. The greatest reduction in the size of *T. pacificus* populations occurred in the presence of both *M. occidentalis* and *E. willamettei*. Addition of these two species resulted in a 4.7-fold reduction in *T. pacificus* densities.

In addition to differences in the average seasonal abundance of *T. pacificus*, there were also differences in the temporal dynamics of this species resulting from the manipulation of *M. occidentalis* and *E. willamettei* (Fig. 2 and Table 1). Although predator releases explained the greatest proportion of the temporal variation in *T. pacificus* abundance, this effect also depended on *E. willamettei* addition. The addition of *E. willamettei* alone had little effect on the rate of increase of *T. pacificus* compared to the control (linear time contrast, $P > 0.05$), whereas predator addition significantly reduced the rate of increase of *T. pacificus* regardless of *E. willamettei* addition ($P < 0.05$). However, *T. pacificus* abundance appeared to have increased faster in the presence of *M. occidentalis* alone than in the presence of *M. occidentalis* and *E. willamettei* together (Fig. 2).

Average seasonal densities of *M. occidentalis* varied

considerably between treatments (Fig. 3). This predator apparently was able to colonize vines where it was not released or was initially absent. Average seasonal *M. occidentalis* abundance was 1.5-fold higher on release vines compared to non-release vines despite the presence of greater prey abundance on non-release vines. The larger average seasonal abundance of *M. occidentalis* in release plots was the probable cause of lower *T. pacificus* abundance in these plots compared with those where *M. occidentalis* was not added. There was also some indication that the addition of *E. willamettei* to the system resulted in an increase in the average seasonal abundance of *M. occidentalis* (Table 1, $P = 0.077$), and this effect was dependent on whether or not *M. occidentalis* was released (main effects interaction, $P = 0.060$). Again, due to the marginal non-significance of *E. willamettei* addition and the interaction between *E. willamettei* and *M. occidentalis* addition, we performed *post hoc* comparisons of treatment means to clarify the nature of the main effects and their interaction.

The addition of *E. willamettei* alone had little effect on the average seasonal density of this predator ($P > 0.05$). This outcome was expected as predators were almost absent from April to the end of June on non-release vines. The average seasonal abundance of *M. occidentalis* was greatest where this predator was released on vines that also received *E. willamettei* ($P < 0.05$), and was also significantly greater in *M. occidentalis* release plots without *E. willamettei* addition compared with control plots ($P < 0.05$).

Analysis of temporal changes in *M. occidentalis* abundance indicated that there was a highly significant sampling date by treatment effect on this species' abundance, with the greatest effect being due to predator release. There was also an indication that *E. willamettei* addition affected the temporal dynamics of *M. occidentalis* as indicated by the date and *E. willamettei* interaction ($P = 0.062$), and by the three-way interaction between date, *E. willamettei* addition and *M. occidentalis* release ($P = 0.049$). It is therefore

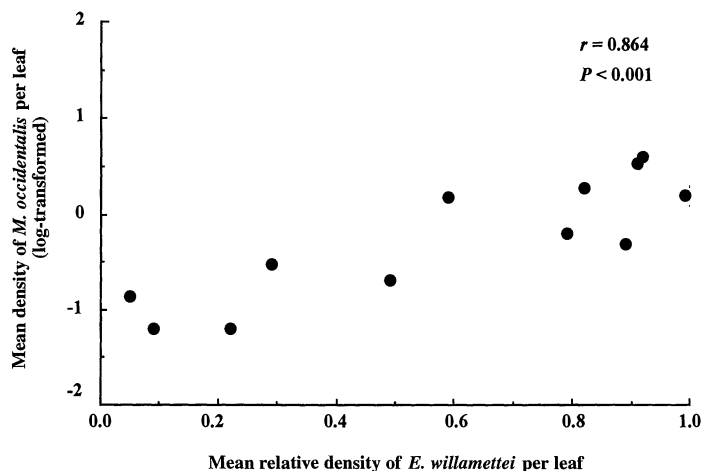


Fig. 4. Relationship between relative *E. willamettei* density (expressed as a proportion of the combined densities of *E. willamettei* and *T. pacificus*) and log-transformed *M. occidentalis* density during the period 24 April to 29 June 1989. Each data point is the mean density of mites per leaf from an experimental unit ($n = 12$).

necessary to interpret changes in predator abundance in terms of this three-way interaction. This was best examined with the analysis of predator abundance during the period 24 April to 29 June, which preceded any appreciable predator increase in plots where they were not released (Fig. 3). Linear time contrasts over the entire experiment were not appropriate because *M. occidentalis* colonized non-release vines and consumed all prey by the end of the experiment. The predator's numerical response (although delayed) in non-release plots masked the effects of early season *E. willamettei* densities on predator release.

Metaseiulus occidentalis was almost completely absent from all plots on 24 April and 11 May. Predator densities began to increase after the 2 June sampling in the release plots, but remained very low in non-predator release plots (predators released on 21 May). There were significant main effects and interaction effects on *M. occidentalis* abundance during the period between 24 April and 29 June. *Metaseiulus*

occidentalis was more abundant in release plots compared with non-release plots (two-factor ANOVA with blocking, $P = 0.002$). *Eotetranychus willamettei* release also resulted in a net increase in *M. occidentalis* ($P = 0.01$), with this effect being greatest where *M. occidentalis* was released together with *E. willamettei* ($P = 0.022$), indicating that the addition of *E. willamettei* as alternative prey for *M. occidentalis* increased the numbers of this predator during April, May and June. This is also indicated by a highly significant correlation between relative *E. willamettei* abundance and *M. occidentalis* abundance during the period from 24 April to 29 June (Fig. 4; $r = 0.864$; $P < 0.001$). Furthermore, there was a highly significant negative correlation between *M. occidentalis* abundance in April, May and June and *T. pacificus* abundance in July and August (Fig. 5; $r = 0.811$; $P = 0.001$). The predator's numerical response to the addition of *E. willamettei* and the resulting increase in the predator's impact on *T. pacificus* densities are both

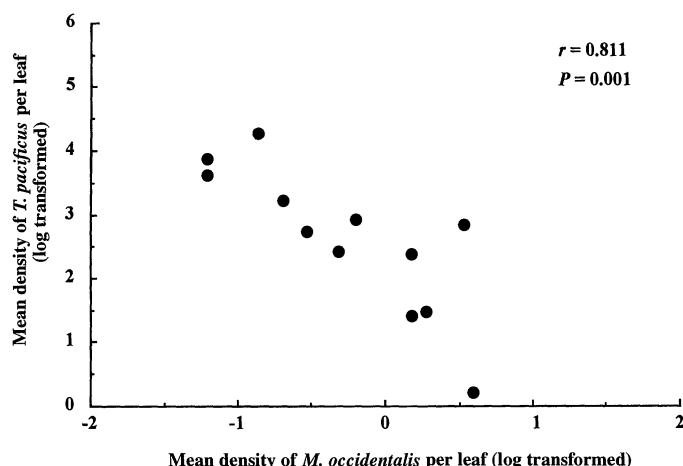


Fig. 5. Relationship between April–June *M. occidentalis* density and July–August *T. pacificus* density. Each data point is the log-transformed mean number of *T. pacificus* or *M. occidentalis* from an experimental unit ($n = 12$). The x-axis represents the mean density of *M. occidentalis* per leaf for the period of 24 April to 29 June, and the y-axis represents the mean density of *T. pacificus* per leaf for the period of 29 June to 14 August.

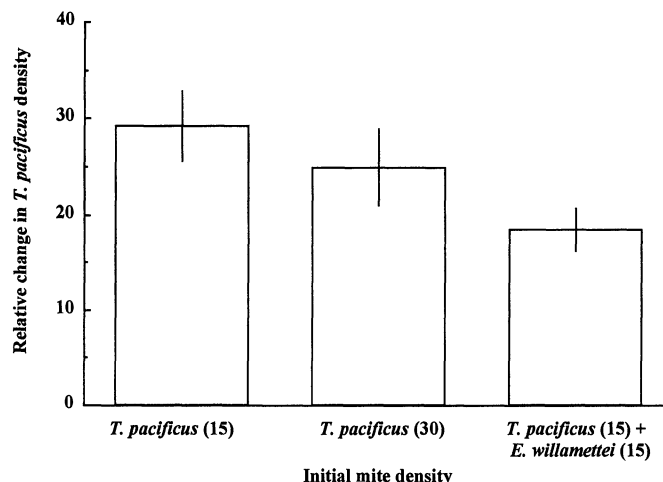


Fig. 6. Relative change in *T. pacificus* density (expressed as the ratio of final and initial *T. pacificus* densities) as affected by interspecific and intraspecific competition in the greenhouse experiment. Vertical bars are standard errors of the means.

evidence of the occurrence of predator-mediated apparent competition between *E. willamettei* and *T. pacificus*.

INTERSPECIFIC AND INTRASPECIFIC COMPETITION IN THE GREENHOUSE

The effects of interspecific and intraspecific competition on the population growth of *T. pacificus* in the greenhouse are summarized in Fig. 6. The presence of *E. willamettei* on vines with *T. pacificus* led to a 37% reduction in the change of *T. pacificus* population size ($F_{1,12} = 5.04$, $P = 0.044$) compared with vines without *E. willamettei*, indicating that some form of interspecific competition occurred between the two species. Furthermore, under the conditions of this experiment *T. pacificus* was not affected by conspecifics ($F_{1,12} = 1.77$, $P = 0.208$), indicating that intraspecific competition is not as important as interspecific competition in determining *T. pacificus* abundance. These results must be interpreted with caution, however, since the ultimate test of competition should be conducted in the field (Schoener 1983). The greenhouse experiment was intended only to help us understand the relative effects of interspecific and intraspecific competition on changes in *T. pacificus* population size under conditions which would have been difficult to achieve in the field.

Discussion

This study has shown that the direct effect of predation and the indirect effect of predator-mediated apparent competition strongly affected the population dynamics of *T. pacificus* in the field. *Tetranychus pacificus* densities were significantly greater in control plots (initially free from predators) compared with *M. occidentalis* release plots. That predation strongly affected *T. pacificus* abundance is not surprising.

Numerous studies have shown that *M. occidentalis* strongly suppresses spider mite densities on several crop plants (McMurtry 1983). On grapevines, this predation effect on *T. pacificus* was caused by strong predator numerical and functional responses that were probably enhanced by the aggregated spatial distribution of *T. pacificus* and area restricted search by *M. occidentalis* (Hanna & Wilson 1991).

This study has also shown that the impact of predation on *T. pacificus* by *M. occidentalis* can be enhanced by the presence of *E. willamettei* as alternate prey, particularly during the early growth phase of *T. pacificus* populations. The observed impact of shared predation on *T. pacificus* abundance was hypothesized by Flaherty (1967), who observed a negative correlation between the abundance of *E. willamettei* and *T. pacificus*. We demonstrated that the addition of both *E. willamettei* and *M. occidentalis* caused the greatest reductions in *T. pacificus* abundance (Fig. 2), which was apparently caused by an enhanced numerical response by *M. occidentalis* (Fig. 4).

Our study is one of only few studies (Collyer 1964; Schmitt 1987; Huang & Sih 1990; Settle & Wilson 1990; Karban *et al.* 1994) that have experimentally demonstrated the existence of predator-mediated apparent competition. We have shown that predator-mediated apparent competition is a significant ecological mechanism affecting the dynamics of spider mites on Thompson Seedless grapevines, and that apparent competition was caused by a strong *M. occidentalis* numerical response to the addition of *E. willamettei*. The potential for apparent competition would have been weakened, however, if the numerical response by *M. occidentalis* had been dampened by intraguild predation (Holt 1977; Holt *et al.* 1994; Holt & Lawton 1994).

Although several insect and mite predators can be found on grapevines in California, the six-spotted thrips *Scolothrips sexmaculatus* (Pergande) is the only

other spider mite predator found in large numbers in vineyards and is primarily associated with high spider mite densities (Flaherty *et al.* 1992). *Scolothrips sexmaculatus* prefers spider mites but it can feed on *M. occidentalis* when spider mites are scarce (R. Hanna, unpublished data). Therefore, intraguild predation is most likely to occur during the declining phase of the seasonal spider mite cycle, when both *M. occidentalis* and *S. sexmaculatus* have consumed most of the spider mite prey. Intraguild predation did not play a role in our experiment because *S. sexmaculatus* was absent during much of the duration of the experiment.

In the greenhouse study, the change in *T. pacificus* population size was significantly lower in the presence of *E. willamettei*, indicating that this species also competes with *T. pacificus* in the absence of predators. This finding is consistent with earlier studies (English-Loeb & Karban 1988; English-Loeb, Karban & Hougén-Eitzman 1993) where previous or concurrent feeding by *E. willamettei* resulted in reductions in *T. pacificus* abundance; however, the mechanisms of these interactions between *T. pacificus* and *E. willamettei* are not well known. *Eotetranychus willamettei* can compete with *T. pacificus* (i) for resources (exploitative competition), (ii) by direct interference, or (iii) by an induced response such as shown by English-Loeb & Karban (1988) and English-Loeb *et al.* (1993). If exploitative competition was more important than other mechanisms of competition between *E. willamettei* and *T. pacificus*, population growth of the latter should have been negatively affected by intra-specific competition. Both species of spider mites have similar physiological effects on grapevines under field and greenhouse conditions (Welter *et al.* 1989), yet *T. pacificus* population growth was lower in the presence of *E. willamettei* than in the presence of equal densities of conspecifics (Fig. 6). If these similar physiological effects are related to depletion of resources, then exploitative competition between *E. willamettei* and *T. pacificus* is not as important as other mechanisms of competition.

Although we were able to document in the greenhouse that *E. willamettei* competed with *T. pacificus* in the absence of predation, we did not obtain any evidence for the presence of competition (other than predator-mediated apparent competition) between the two species in the field, contrary to findings by Karban & English-Loeb (1990) and English-Loeb *et al.* (1993) (but see Karban *et al.* 1994). Working in Zinfandel vineyards in the Northern San Joaquin Valley (Lodi, California), these authors found that *E. willamettei* negatively affected *T. pacificus* abundance independent of the effects of predation. In contrast, we did not find any evidence that *E. willamettei* competed with *T. pacificus* (in the absence of predation) in Thompson Seedless vineyards in the Southern San Joaquin Valley (Madera, California). Several explanations are offered for the lack of concordance between our study and that of Karban & English-

Loeb (1990) and English-Loeb *et al.* (1993). The strength of the negative interactions between the mites (in the absence of predation) may be affected (i) by cultivar-specific differences (Zinfandel vs. Thompson Seedless), (ii) by climatic variables associated with the two geographical regions where the studies were conducted (Lodi is generally cooler than Madera), (iii) by a combination of cultivar and region-specific differences, or (iv) by differences in the timing and size of *E. willamettei* releases [negative effects are more pronounced when *E. willamettei* is present shortly after the initiation of vegetative growth (Hougén-Eitzman & Karban 1995)]. These differences in experimental conditions may have affected the outcome of the experiments and our conclusions regarding the ecological mechanisms affecting the dynamics of this acarine community.

The experiments reported in this paper were conducted in part to test the relative significance of the ecological mechanisms affecting spider mite dynamics in vineyards, and to obtain practical information that can be used by pest management practitioners to reduce the occurrence of damaging *T. pacificus* outbreaks. We have determined that infestation of Thompson Seedless vines with *E. willamettei* is a viable management approach. However, we were unable to show (with the densities and timing of *E. willamettei* infestation) that this mite alone would reduce *T. pacificus* densities. Under the conditions of our experiments, vine infestation with *E. willamettei* was most useful in increasing *M. occidentalis* densities, which increased the effectiveness of this predator in controlling *T. pacificus* populations. Furthermore, as indicated in Figs 4 and 5, this study provides useful information for predicting predator effectiveness in controlling *T. pacificus* populations under varying levels of *E. willamettei*.

Although we have shown that vine infestation with *E. willamettei* was useful in reducing *T. pacificus* infestations, caution should be exercised in using this tactic, because the pest-status of *E. willamettei* depends on the grape cultivar and its geographical location. Vine infestation with *E. willamettei* is unlikely to cause significant problems on Thompson Seedless grapes in the Southern San Joaquin Valley, where *E. willamettei* rarely causes significant losses in grape yield and quality. *Eotetranychus willamettei* is more likely to be a pest on wine grape cultivars (e.g. Zinfandel, Chardonnay and Pinot noir) in dry-land vineyards in the foothills of the Sierra Nevada mountains (Welter *et al.* 1989), the Northern San Joaquin Valley (R. Hanna & F. Zalom, unpublished data), and the coastal valleys (Flaherty *et al.* 1992). If vine infestation with *E. willamettei* is used, augmentative releases and/or conservation of *M. occidentalis* should lower the risk of the development of damaging *E. willamettei* populations on grapes grown in vulnerable regions, while increasing the viability of vine infestation with *E. willamettei* to control *T. pacificus* outbreaks.

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