Oecologia (1994) 97:508–511

ORIGINAL PAPER

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Predator-mediated apparent competition between two herbivores that feed on grapevines

Received: 9 June 1993 / Accepted: 20 January 1994

Abstract We have been releasing economically unimportant herbivorous mites of one species early in the season and protecting grapevines against another, more damaging herbivorous mite throughout the growing season. In this experiment, releases of economically unimportant Willamette mites alone, or of predatory mites alone, failed to reduce populations of the damaging Pacific spider mite. However, where both herbivorous Willamette mites and predatory mites were released together populations of Pacific mites were reduced. This interaction between effects of Willamette mites and predatory mites suggests that predation against Pacific mites was more effective where alternate prey (Willamette mites) were available for the predators. The "apparent competition" between Willamette mites and Pacific mites, mediated through their shared predator, can be an important force in the agroecosystem although its importance varies from year to year and vineyard to vineyard.

Key words Apparent competition · Spider mites Tetranychidae · Predatory mites · *Vitis*

Introduction

According to classical definitions, interspecific competition has occurred when the addition of one species reduces the population size of another species (Begon et al. 1986; Ricklefs 1990). Such competition is assumed to involve a resource that is in short supply for both species. Even if two species of herbivores do not use the same plant resources or occur at the same time, they may interact indirectly by changing the quality of their shared host plant. Recently many studies have found evidence for host-mediated interactions between herbivore species (Karban and Myers 1989; Tallamy and Raupp 1991). Two species that use non-overlapping sets of resources may also compete if they share a predator. Such a situation has been termed apparent competition (Holt 1977, 1984) and, in such cases the "limiting resource" may be thought of as "enemy-free space" (Jeffries and Lawton 1984). According to this model, the predator becomes more numerous or more efficient at consuming species 1 in the presence of species 2. Examples of apparent competition have been relatively few (Schmitt 1987; Price et al. 1988; Huang and Sih 1990; Settle and Wilson 1990; Grosholz 1992), although several authors have hypothesized that the process is common in nature (Holt 1984; Jeffries and Lawton 1984).

We have been working with two herbivorous mite species, Willamette mites (Acari: Tetranychidae: *Eotetranychus willamettei*) and Pacific mites (Acari: Tetranychidae: *Tetranychus pacificus*), that both feed on the foliage of grape plants. The two species are negatively associated; vineyards that have large populations of one species tend not to have many of the other (Flaherty and Hoy 1971; English-Loeb and Karban 1988). In the northern San Joaquin Valley of California, Pacific mites are considered an economic pest of grapevines whereas Willamette mites cause much less damage (Flaherty and Huffaker 1970; Flaherty et al. 1992). We have been exploiting this situation by intentionally releasing Willamette mites into commercial Zinfandel vineyards that have experienced chronic economic problems with Pacific mites (Karban and English-Loeb 1990; English-Loeb et al. 1993). Results of these releases have been very encouraging (personal observation) although we have only a sketchy understanding of the mechanisms responsible for the population suppression of Pacific mites following our introductions of Willamette mites (English-Loeb et al. 1993).

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In addition to these two species of herviborous mites, a predatory mite, *Metaseiulus occidentalis* (=*Galendromus occidentalis*; Acari: Phytoseiidae), is also common in vineyards. Previous workers hypothesized that these predators increase when populations of Willamette mites are abundant, early in the growing season. Later in the season, when conditions are more favorable for Pacific mites, the predatory mites prevent populations of Pacific mites from increasing (Flaherty and Huffaker 1970; Flaherty and Hoy 1971).

Evidence suggests that several mechanisms may play a role in the reduction of populations of Pacific mites on grapevines inoculated with Willamette mites. Introducing predatory mites is the method of control for Pacific mites that is currently recommended (Flaherty et al. 1992). Observations suggested that *M. occidentalis* was a more effective predator of Pacific mites when alternate prey was also available (Flaherty and Huffaker 1970; Flaherty and Hoy 1971), although apparent competition has not been demonstrated conclusively in this system. Our own previous results indicated that predators were not the only cause of the negative association. Introducing Willamete mites to vines made them less suitable as hosts for Pacific mites in the absence of predators in both the greenhouse and field (English-Loeb and Karban 1988; Karban and English-Loeb 1990). On Zinfandel vines without predators, Pacific mite populations were depressed on new leaves of vines that had previously had Willamette mites on their lower leaves only (English-Loeb and Karban 1988; Karban and English-loeb 1990). This separation in time and space indicated that induced resistance was also involved. In this paper, we describe a field experiment to test the relative importance of direct predation, direct and indirect competition, and predator-mediated apparent competition in reducing populations of Pacific mites on vines inoculated with Willamette mites.

Methods

We conducted a field experiment in which we established four treatments: (1) a release of predatory mites; (2) a release of Willamette mites; (3) a release of both Willamette and predatory mites; and (4) a control where we made no releases. We selected a 25-year-old Zinfandel vineyard on St. George rootstocks owned by Mr. Ron Mencarini, north of Lodi, California for this work. Mr. Mencarini had experienced chronic problems with Pacific mites in this vineyard and had tried releases of predatory mites and applications of miticides unsuccessfully in the past. Each of the four treatments in this experiment consisted of three vines and each was replicated ten times (two replicates in each of five blocks). Experimental units were separated from one another by three buffer vines which were not treated in any way.

Willamette mites were introduced to plants scheduled to receive them on 29 March 1992 just as the overwintering shoots were beginning to elongate. Each vine received 400 ± 50 active mites (mean adults and immature ± 1 SE) by placing rolled leaves which had mites under the bark scales and into shoot axes of the designated vines. Each experimental vine that was scheduled to receive predacous mites (from Biotactics, Riverside, CA) was inoculated with 22.1 ± 2.3 active mites on 14 May and again on 16 June.

The desity and species of mites was estimated for the center plant of each of the 40 experimental units at approximately 5-day intervals from 21 April to 31 August and again on 23 September. At each sampling date two leaves from the cener of each vine and two leaves from the ends of shoots that extended away from each vine were collected and brought back to the lab for counting with the help of dissecting microscopes. This sampling protocol takes into account the tendency for Pacific mites to concentrate on exposed leaves and Willamette mites to be randomly distributed and not clumped (English-Loeb et al. 1986). For each census date, we averaged the mite counts on the four leaves.

Since the vines varied in size, we determined three estimates of size that we used as covariates in our analyses. We measured (1) the trunk diameter 1 cm below the first branch, (2) the number of shoots on the upper half of the vine, and (3) the lengths of two shoots, haphazardly selected on each vine.

We examined the success of our releases of Willamette mites and predaceous mites by comparing numbers recovered on the census dates immediately following the releases and during the first three months of the season (April, May, June). Since mite densities were censused repeatedly throughout the season, we tested for effects of Willamette mites, predaceous mites and the interaction between the two species on numbers of Pacific mites using profile analysis of repeated measures (Proc GLM, SAS Institute 1990; Morrison 1990). "Between-subject effects" in repeated-measures analysis tests whether the main factors explained a significant fraction of variation in the response variable, averaged over all sample dates. Densities of mites were log-transformed to normalize the distributions and correct for heterogeneity of variance in all of our analyses.

Results

Our experimental introductions of Willamette mites were successful. The first census was conducted on 21 April, 23 days after the release. At this time Willamette mites were collected in greater numbers from vines to which they had been released ($F_{1,24} = 4.78$, $P = 0.04$). Previous work demonstrated that Willamette mites must be present during the early part of the season if they are to be effective at reducing numbers of Pacific mites (Hougen-Eitzman and Karban, pers. obs.). Numbers of Willamette mites remained higher on release vines than on vines which had not been inoculated

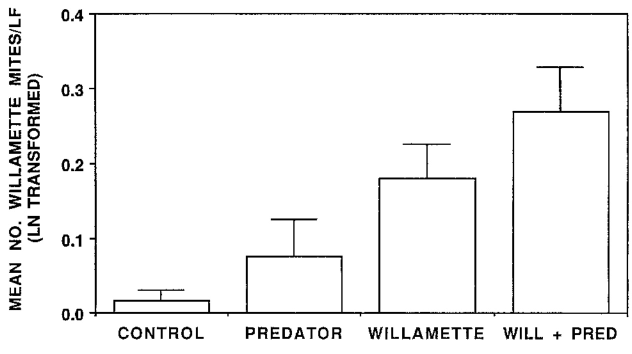

Fig. 1 Mean number of Willamette mites per leaf in censuses conducted during the early season: April, May, and June. Numbers are log-transformed and *bars* indicate 1 SE

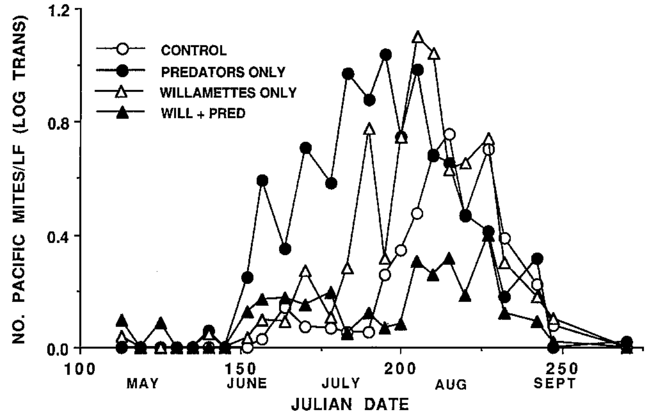

Fig. 2 Mean number of Pacific mites per leaf for the four treatments over the season. Numbers are log transformed

Table 1 Analysis of Variance of the Number of Pacific mites per vine. Numbers were log-transformed

Source	*df*	SS	MS	*F*	*P*
Block	4	0.91	0.23	0.20	0.93
Willamette Release	1	1.70	1.70	1.51	0.23
Predator Release	1	0.03	0.03	0.03	0.87
Block × Willamette	4	0.65	0.16	0.14	0.96
Block × Predator	4	6.37	1.59	1.42	0.26
Willamette × Predator	1	9.31	9.31	8.26	0.01
Error	24	27.04	1.13		

throughout April, May, and June (Repeated measures analysis on mainframe SAS, $F_{1,24}=4.49$, $P=0.04$; Fig. 1).

We can be less confident about the success of our releases of predatory mites. We did not recover significantly more predatory mites immediately following our releases on 17 May ($F_{1,24}=0$ because no predators were found on non-release vines) nor on 24 June ($F_{1,24}=1.27$, $P=0.27$). Similarly over April, May, and June predatory mites were no more abundant on release vines than on vines to which they were not released ($F_{1,24}=0.63$, $P=0.43$). These results probably indicate that predatory mites move to those vines with prey (English-Loeb et al. 1993) rather than reflecting an inability to establish or the existence of high numbers of predators, independent of our releases. Consistent with this suggestion, we noticed that during April, May, and June the release of Willamette mites explained a larger portion of the variance in predator numbers ($F_{1,24}=3.82$, $P=0.06$).

Populations of Pacific mites began to increase in July, although densities on all treatments remained below those experienced in this vineyard during previous years (Ron Mencarini, personal communication). Our releases of predatory mites to vines without Willamette mites did not reduce populations of Pacific mites (Fig. 2, Table 1). Similarly, vines to which we released only Willamette mites had high densities of Pacific mites (Fig. 2, Table 1). Only where Willamette mites and predatory mites were both released did we observe reductions in populations of Pacific mites (Fig. 2). This was reflected in a significant Willamette X predator interaction term in the analysis of variance ($F_{1,24}=8.26$, $P=0.01$, Table 1).

Although the vines varied in the three measures of size that we used, adding these measures as covariates into our analyses of mites populations did not change any of our conclusions.

Discussion

This is one of the first experimental demonstrations of apparent competition, although it has been argued that the phenomenon is widespread and important (Holt 1984; Jeffries and Lawton 1984). Flaherty and Huffaker (1970) hypothesized that this phenomenon of competition mediated by a shared predator was operating in California's vineyards. In this Zinfandel vineyard, neither releases of predatory mites nor releases of Willamette mites reduced populations of Pacific mites. We have rarely observed predatory mites to be effective agents of control in Zinfandel vineyards, despite their widespread use (English-Loeb et al. 1993). This is the first field experiment of seven that we have conducted in Zinfandel vineyards in which introductions of Willamette mites alone did not reduce populations of Pacific mites (English-Loeb and Karban 1987; Karban and English-Loeb 1990; English-Loeb et al. 1993, manuscript in prep).

When both Willamette mites and predatory mites were released together, populations of Pacific mites were lowered. Several mechanisms could produce this effect. (1) Predators could be more effective per individual at reducing Pacific mite numbers in the presence of Willamette mites. (2) Willamette mites could be more effective at reducing Pacific mite numbers in the presence of predatory mites. (3) There may be more predatory mites on vines to which we released Willamette mites than on vines without them. Our data do not allow us to test these various potential mechanisms.

It is useful to identify the processes that affect populations of economically damaging hervibores but even more informative to ask questions about the relative importance of those processes in differing ecological situations (Quinn and Dunham 1983). We conducted similar experiments to this one in Zinfandel vineyards in the Lodi area during the previous 3 years (Karban and English-Loeb 1990; English-Loeb et al. 1993). This was the only one of the four in which predator-mediated apparent competition was found. Because so many factors differ from year to year we have little power to distinguish those that encouraged predator-mediated apparent competition in this season more so than in previous years. These observations indicate that this process can be a significant force in the grape ecosystem but that its importance varies considerably.

Acknowledgements We thank Rowena Richter, Chris Chan, and Lauretta Hougen-Eitzman for assistance with field work and mite counting. We appreciate the cooperation of Paul Verdegaal and Ron Mencarini. We were supported by USDA competitive grants 90-37153-5264 and 92-01998 and by a grant from the growers of the Lodi-Woodbridge district.

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