

Abundance of phytoseiid mites on *Vitis* species: effects of leaf hairs, domatia, prey abundance and plant phylogeny

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ABSTRACT

We observed the number of predatory mites (Phytoseiidae: *Typhlodromus caudiglans*) on the foliage of 20 North American species of grapes (*Vitis* spp) plus the domesticated European *Vitis vinifera*, all grown in a common garden. We found relatively few phytophagous mites. The numbers of phytophagous mites were not correlated with the plant characteristics that we measured. We found approximately five times as many predatory mites as phytophagous mites and the numbers of these phytoseiid predators were not affected by the availability of prey. Similarly, numbers of phytoseiids were unaffected by plant gender and, hence, the availability of pollen, another source of food. The numbers of phytoseiids were not clustered according to the taxonomic grouping of the tested plant species. Leaf surface characteristics explained over 25% of the variance in the numbers of phytoseiids. Numbers of phytoseiids were positively associated with the density of vein hairs, the density of bristles in leaf axils, and the presence of leaf domatia. These results suggest that sheltered habitats rather than food availability may limit the numbers of phytoseiid mites on grapevines.

Key words: Phytoseiid, predatory mites, *Vitis*, leaf surface, mite domatia.

INTRODUCTION

The size and dynamics of populations of predators can be influenced by characteristics of their prey, one trophic level down and also by characteristics of their prey's food, two trophic levels down. In the case of predatory phytoseiid mites, both their prey, herbivorous mites and the host plants that the herbivorous mites use, have been suggested as major determinants of phytoseiid numbers. The host plants influence phytoseiids by determining the environment in which they live, the population size and dispersal abilities of herbivorous mites (their primary prey),

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as well as providing potentially alternative sources of food such as pollen and plant-parasitic fungi (Huffaker, 1958; Huffaker *et al.*, 1970; McMurtry *et al.*, 1970; Sabelis, 1981, 1985; Overmeer, 1985).

Phytoseiid mites feed primarily on phytophagous mites, particularly tetranychids and eriophyids; many phytoseiid species also use pollen, honeydew, fungi and small arthropods as food sources (Schuster and Pritchard, 1963; McMurtry, 1982, Tanigoshi, 1982; Overmeer, 1985). Because phytoseiid mites are voracious predators of agriculturally important phytophagous spider mites of the family Tetranychidae, they have been reared for release to control these pest species. They are considered as the primary means of biological control of spider mites in many crops (Huffaker *et al.*, 1970; McMurtry *et al.*, 1970). Despite their wide acceptance in agriculture, they have provided only inconsistent control of spider mites (e.g. Chant, 1959; King *et al.*, 1985; Easterbrook, 1992; and see references below).

Several species of phytoseiid mites have been released to control phytophagous spider mites that feed on cultivated grapevines (Kinn and Doult, 1972; Schruft, 1985; Flaherty *et al.*, 1992). These efforts have met with varying degrees of success (McMurtry, 1982; Flaherty *et al.*, 1985; Schruft, 1985; English-Loeb *et al.*, 1993). The reasons for failed control are not well understood, although predator-prey ratios, suboptimal phenological matching of predator and prey, poor overwintering, pesticide applications and alternative prey for the predators have been discussed.

In this study, we wished to determine the importance of prey abundance and host plant characteristics on the abundance of phytoseiid mites on grapevines. We observed the number of predatory phytoseiid mites on the foliage of 20 North American grape species (*Vitis* spp.) plus the domesticated European *Vitis vinifera* L., all grown in a common garden. We used regression techniques to analyse the contributions of (1) the availability of phytophagous mite prey, (2) the availability of pollen, (3) the taxonomic groupings of the grape species and (4) the leaf surface characteristics to explain the numbers of predatory mites on these grapevines.

METHODS

The *Vitis* species used in this experiment were growing in the USDA National Germplasm Repository west of Winters, Solano County, California. All vines were 12 years old, head trained and spur pruned and planted on a 2 × 4 vine × row spacing. We studied from one to 11 accessions of the 21 species. The vines were randomly arranged throughout a large collection of other species that were not studied; each accession was replicated twice.

On 31 May or 1 June 1994, we released 10 adult Pacific mites (*Tetranychus pacificus* McGregor) to a marked shoot of each experimental plant. *Tetranychus pacificus* is a phytophagous mite commonly found on grape foliage in California. We collected two leaves from each of our release shoots on 21 June 1994 (two

leaves per plant, two plants per accession). These sample leaves were placed in moist paper towels and kept in ice chests until they were brought into the laboratory and examined using dissecting microscopes. All mites on the sample leaves were enumerated.

Grapes are dioecious; an individual plant produces either male or female flowers but not both. Cultivated *V. vinifera* is the exception, having hermaphroditic (bisexual) flowers. Plants that are either male exclusively or hermaphroditic (in the case of *V. vinifera*) produce abundant pollen, a resource that is potentially important to phytoseiid mites. The sex and, hence, availability of pollen, was recorded for each plant in our sample.

The *Vitis* species have been aggregated into series by many authors (Viala and Ravaz, 1903; Munson, 1909; Bailey, 1934). These series have undergone revision by Comeaux *et al.* (1987) and Moore (1991) and represent putative phylogenetic relationships, although there is no supportive genetic data. We have used eight groupings of the 21 species studied (Table 1), which correspond with Comeaux *et al.* (1987) and Moore (1991).

TABLE 1

Number of phytoseiid mites on *Vitis* spp.

Species group	Species	Number of accessions	Phytoseiid mites (mean \pm 1 SE per leaf)
1	<i>labrusca</i>	2	0 \pm 0
	<i>mustangensis</i>	3	1.67 \pm 1.20
	<i>doaniana</i>	1	8
2	<i>champinii</i>	5	6.40 \pm 4.52
	<i>aestivalis</i>	1	0
	<i>lincecumii</i>	2	6.50 \pm 1.50
3	<i>smalliana</i>	8	2.00 \pm 1.44
	<i>cinerea</i>	10	6.30 \pm 2.63
4	<i>berlandieri</i>	8	3.63 \pm 1.82
	<i>vulpina</i>	7	7.14 \pm 2.23
5	<i>palmata</i>	1	0
	<i>riparia</i>	11	5.60 \pm 1.63
	<i>rupestris</i>	10	0.20 \pm 0.13
6	<i>acerifolia</i>	10	6.00 \pm 1.45
	<i>californica</i>	3	2.33 \pm 0.67
	<i>girdiana</i>	4	8.75 \pm 4.21
	<i>arizonica</i>	1	0
7	<i>treleasei</i>	3	0.67 \pm 0.67
	<i>monticola</i>	6	1.67 \pm 1.67
	<i>rotundifolia</i>	9	0.11 \pm 0.11
8	<i>vinifera</i>	3	0 \pm 0

We estimated the surface characteristics of each of the two leaves that were sampled for mites. We scored the density of prostrate hairs on the underside of the leaf blade, the main vein and in the axil of the main vein on a scale of 0 (no hairs) to 10 (very dense hairs) and the density of bristles (erect hairs) on the underside of the main vein and in the axil of the main vein on a scale of 0 (no bristles) to 10 (very dense bristles) using the OIV codes 084-1 and 085-1, respectively (IBPGR/OIV, 1989). Two people scored each leaf independently and the mean of the two scores was recorded. Finally we recorded the presence or absence of leaf tissue that formed a pocket or small cavity located in the primary vein axil (O'Dowd and Willson 1989). These pockets, termed domatia, have been hypothesized to serve as important shelters for phytoseiid mites (Lundstroem, 1887; O'Dowd and Willson, 1989; Pemberton and Turner, 1989; Walter and Denmark, 1991).

Multiple regression analyses (MGLH procedure in Systat, Evanston, IL) were performed using the following traits as predictors of numbers of Pacific mites and phytoseiid mites per leaf for each accession: presence of leaf domatia, hairs on the leaf blade, hairs on the leaf veins, bristles on the leaf veins, hairs in the main leaf axil and bristles in the main leaf axil. Plant gender and species grouping were also entered as categorical variables in the multiple regression.

RESULTS

We recovered very few phytophagous Pacific mites (*Tetranychus pacificus* *McGregor*) in our leaf samples (mean \pm 1 SE = 0.71 ± 0.23 mites per leaf; $n = 105$ accessions). The numbers of Pacific mites did not differ on the 17 grape species for which we had more than one accession ($F_{16,86} = 1.00$, $P = 0.46$). None of the leaf traits that we measured explained a significant portion of the variance in the numbers of Pacific mites (data not shown).

Predaceous phytoseiid mites were more common in our leaf samples (mean \pm 1 SE = 3.61 ± 0.54 mites per leaf; $n = 105$ accessions). Most of these were *Typhlodromus caudiglans* Schuster with some individuals of *Metaseiulus pomoides* Schuster and Pritchard and *Metaseiulus* sp. *Typhlodromus caudiglans* has been observed on grapes and orchard trees feeding on mites, pollen and fungal spores (Putman, 1962; Schuster and Pritchard, 1963; McMurtry, 1982).

The numbers of phytoseiid mites per leaf were not related to the number of phytophagous tetranychid mites on that leaf ($F_{1,101} = 0.47$, $P = 0.49$). The number of phytoseiid mites differed on the 17 grape species for which we had more than one accession (Table 1, $F_{16,86} = 2.06$, $P = 0.018$). Since phytoseiid mites eat pollen, we hypothesized that male plants (which produce pollen in abundance) would have more phytoseiid mites than female plants. However, we found no differences in numbers associated with plant gender ($F_{1,91} = 0.002$, $P = 0.96$; 12 accessions were not included because we could not determine gender).

TABLE 2

Results of multiple regression analysis of the mean number of phytoseiid mites per leaf.

Variable	Coefficient	SE	T	P
Domatia	2.48	1.11	2.23	0.028
Vein hairs	0.78	0.18	4.42	0.001
Axil bristles	0.87	0.19	4.65	0.001
Constant	-5.35	1.81	2.95	0.004

 $R^2 = 0.273$, $F_{3,96} = 12.01$, $P < 0.001$.

The 21 species of grapes that we censused for mites can be organized into eight species groups (Table 1). The mean numbers of phytoseiid mites were not more similar for members of these species groups than for other species (Table 1, $F_{7,13} = 0.37$, $P = 0.90$). In other words, the mean number of phytoseiid mites on a grape species did not cluster in a similar fashion as did other traits. For example, the density of axil bristles and the density of hairs on leaf veins closely followed the plant species groupings. (For axil bristles, R^2 associated with species groups = 0.66, $F_{7,13} = 3.57$, $P = 0.023$; for vein hairs, $R^2 = 0.64$, $F_{7,13} = 3.28$, $P = 0.031$.) These results suggest that the number of phytoseiid mites on a grape species was not strongly influenced by that plant's presumed phylogenetic position.

Leaf surface characteristics explained a large fraction of the variation that we observed in numbers of phytoseiid mites. In a multiple regression analysis, the numbers of phytoseiids were positively associated with the density of vein hairs, the density of bristles in leaf axils and the presence of leaf domatia (Table 2). These three variables explained 27% of the variation in numbers of phytoseiid mites ($P < 0.001$). Multiple regression analysis assumes that the independent variables are not highly correlated with one another (Zar, 1984, p. 338). A simple correlation matrix showed that this assumption was satisfied for the three variables that we included in our model (Table 3). Another variable, the density of hairs on the leaf blades, did not satisfy this assumption as it was highly positively correlated with the density of vein hairs and the density of axil bristles and was not correlated with the numbers of phytoseiid mites by simple correlation (Table 3). Therefore, we did not include the density of hairs on the leaf blade in our model.

DISCUSSION

Knowledge of the density and locations of hairs, bristles, and pockets on the leaf surfaces of native grape species provided considerable information about the numbers of phytoseiid mites, *T. caudiglans*, that would be found. These three variables alone accounted for over 25% of the variation in densities of these mites. This striking observation suggests that densities of these phytoseiid mites may be

TABLE 3

Pearson correlation matrix for phytoseiid mites and leaf traits (Pearson coefficient/associated probability)

	Phytoseiids	Hairs on leaf blade	Hairs on veins	Bristles on axil	Domatia
Phytoseiids	1				
Hairs on leaf blade	0.106/0.294	1			
Hairs on veins	0.277/0.005	0.856/0.001	1		
Bristles on axil	0.298/0.003	-0.240/0.016	-0.297/0.003	1	
Domatia	0.181/0.072	-0.013/0.894	0.000/0.997	-0.032/0.749	1

limited by the availability of sheltered habitats. This suggestion is consistent with observations of other phytoseiids generally and of this species in particular. Most individuals of *T. caudiglans* were found in protected places on leaves and the bark of peach trees (Putman, 1962). Similar associations between leaf pubescence, possible shelters and the numbers of *T. caudiglans* have been suggested for apple foliage of several varieties (Downing and Moilliet, 1967). Putman and Herne (1964) tested the hypothesis that the numbers of shelters limited populations of *T. caudiglans* on peach leaves. They clipped small plastic cells onto leaves, providing artificial shelters. Leaves with such shelters had approximately three times the number of this phytoseiid species as paired control leaves without shelters. Other species of phytoseiids have been found in greater numbers close to the physical junctions or protective angles formed by the leaf midribs and major veins (McMurtry *et al.*, 1970).

Grape leaves that had pockets, cavities formed by tissue at the juncture of the main veins, had higher densities of *T. caudiglans* than leaves that lacked pockets. A positive association between these pockets and densities of phytoseiid mites has been made previously for *Vitis munsoniana* Simpson ex Munson and many other unrelated plant species (O'Dowd and Willson, 1989, 1991; Pemberton and Turner, 1989; Walter and Denmark, 1991). Several workers have proposed that leaf pockets and other small foliar cavities may be structures that enable plants to maintain high densities of phytoseiid mites that in turn reduce densities of phytophagous mites and plant pathogens (Lundstroem, 1887; O'Dowd and Willson 1989, 1991; Pemberton and Turner 1989). As mentioned above, the first half of this hypothesis, that leaves with cavities have higher densities of phytoseiids than those without, is well supported by data from this and other studies. The second half of the hypothesis, that leaves with phytoseiids have lower densities of phytophagous mites and other plant parasites is only weakly supported by data at this time from any plant species (Grostal and O'Dowd, 1994). Unfortunately, our data did not address this issue.

One possible advantage of leaf shelters is that they retard dessication. Eggs of phytoseiid mites are particularly sensitive to drying out at low relative humidities

(Sabelis, 1981). For example, eggs of *Phytoseiulus persimilis* Athias-Henriot were very vulnerable to mortality due to desiccation below 70% relative humidity (Stenseth, 1979, Sabelis, 1981).

Our results were noteworthy not only in suggesting that leaf traits influenced the numbers of phytoseiids but also that leaf traits were more important than other factors such as the numbers of phytophagous prey and the taxonomic grouping of the plant species. The observation that predators were more abundant than their prey seems counter-intuitive and potentially unstable. However, this observation may be explained by the broad diet of *T. caudiglans*. This predator also eats pollen and fungal spores, although they will not feed directly on plant tissues or exudates (Putman 1962). Putman (1962) reared mites successfully on diets of pollen only and, with more difficulty, on diets of fungal spores only. In this present study, male plants that presumably had more pollen supported no more mites than did females. However, given that the experimental vines were grown in a mixed collection of males interspersed with females, the females may have been contaminated with some pollen from male vines. Our results follow those of Duso (1992) who found that leaf traits, pubescence in particular, were better predictors of densities of two other phytoseiid species in Italian vineyards than was the availability of tetranychid prey.

The plant traits that affect densities of phytoseiid mites may be affected or even constrained by the evolutionary history of the grape species considered (e.g. Gould and Lewontin, 1979; Derrickson and Ricklefs, 1988; Miles and Dunham, 1993). If evolutionary history was important, we hypothesized that the numbers of phytoseiid mites would be grouped coinciding with the groupings of the grape species. In other words, the numbers of mites would correlate with the hypothesized phylogeny of the grapes. Indeed, the species groupings were good predictors of several leaf characteristics (see above). Since plant phylogeny was correlated with some leaf characters and leaf characters affected mite numbers, we expected the densities of mites to be affected by plant phylogeny. However, densities of phytoseiid mites associated with grape species were not clustered according to the presumed evolutionary history of the plants. This suggests that the plant characteristics that most strongly affect the numbers of phytoseiid mites are evolutionarily labile and have arisen and vanished numerous times. We assume here that the taxonomic classification provides a reliable picture of phylogeny and one that is independent of the characteristics (leaf hairs, numbers of mites) that we are trying to explain.

In conclusion, characteristics of the plant surface were excellent predictors of numbers of phytoseiids on leaves of different grape species. They were more important than were other traits that we measured.

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