

Biology and Co-Occurrence of *Psyllobora vigintimaculata taedata* (Coleoptera: Coccinellidae) and Powdery Mildews in an Urban Landscape of California

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ABSTRACT Biological control of powdery mildew (PM) plant pathogens may offer a solution to chemical control problems such as resistance, worker safety, and effects on nontarget organisms. Unfortunately, mildew consumption by arthropods is seldom studied and poorly understood. The coccinellid tribe Halyziini is composed entirely of obligate consumers of various PM fungi and is represented in the Western Hemisphere by members of the genus *Psyllobora* Chevrolat. In western North America *Psyllobora vigintimaculata* Say feeds on PM in natural and managed systems. Here, we report the insect's biology and phenology through the use of a laboratory colony, rectangular degree-day calculation and field sampling in an urban landscape. The natural presence of this beetle in Davis, CA, has been documented over the course of 2 yr through weekly presence-absence and density sampling of native and exotic plants prone to PM. Sampling data indicates activity from late February through mid-December. The insect was observed feeding on the PM of >25 plant species in 13 different plant families. There is a positive relationship between PM severity and the relative density of insects, suggesting an aggregative numerical response. The potential of *P. vigintimaculata* for biological control and the possibility of using this insect as an indicator of PM in horticultural systems are both discussed.

KEY WORDS powdery mildew, *Psyllobora vigintimaculata*, biological control

The fungi belonging to the Erysiphales, Ascomycota, commonly known as powdery mildews (PMs), are all obligate biotrophs. As an order, they have been recorded to infect close to 10,000 species of angiosperm plants in 169 families (Amano 1986). Because many of these host plants are valued in agriculture and as ornamentals, PM is collectively considered one of the most important plant pathogens worldwide. Significant yield losses due to PM infection have been recorded in agronomic crops: soybean, *Glycine max* (L.) Merr.; wheat, *Triticum aestivum* L.; and barley, *Hordeum vulgare* L. (Phillips 1984, Conner et al. 2003, Nordeng et al. 1988), as well as horticultural crops: strawberry, *Fragaria* × *ananassa* Duch.; wine grapes, *Vitis vinifera* L.; and cucumber, *Cucumis sativus* L. (Miller et al. 2003; Ypema and Gubler 1997, Abood et al. 1991). Disease management typically involves regular applications of fungicides. This approach has led to documented resistance to benzimidazoles, sterol inhibitors, demethylation inhibitors, and strobilurins in both laboratory and field experimentation (Gubler

et al. 1996; del Pino et al. 1999, Heaney et al. 2000, McGrath 2001).

Biological control of PM may offer solutions to this resistance phenomenon and other fungicide-related issues, such as residues in food crops and effects to nontarget organisms. There are several commercially available microbial biological control agents including the spore-forming bacterium *Bacillus subtilis* Cohn and the fungal hyperparasite *Ampelomyces quisqualis* Cesati. Little is known, however, of the potential of arthropod agents to control or reduce disease through consumption of PM. Work by English-Loeb et al. (1999) illustrated the ability of a tydeid mite (Acari: Tydeidae) to reduce the incidence of PM in riparian grapevines, *Vitis riparia* Michx, in upstate New York. All members of the Halyziini Casey (Coleoptera: Coccinellidae) are obligate consumers of various PM conidia and hyphae at all mobile life stages (Gordon 1985). No-choice feeding assays by Davidson (1921) highlighted the prey refusal and subsequent death of *Psyllobora vigintimaculata taedata* LeConte individuals offered spider mites (Acari: Tetranychidae), aphids (Hemiptera: Aphididae) or armored scale insects (Homoptera: Diaspididae). However, records of aphidophagy or phytophagy within Halyziini persist in contemporary literature, usually as part of a natural survey (Omkar and Pervez 1999; Yurtsever 2001). In a review of coccinellid taxonomy, Gordon (1985) sug-

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gested records such as these to be a result of inaccurate observation. Clearly, a dearth in the scientific literature addressing the mycophagy exhibited by these insects has led to some biological inaccuracies. The cosmopolitan genus *Psyllobora* Chevrolat is represented in temperate and subtropical regions worldwide, in natural and managed systems, and contains a group of insects with the potential to provide biological control of PM (Prasad and Rai 1988, Cruz et al. 1989, Hoffman et al. 1997, Almeida and Milleo 1998, Tezcan and Uygun 2003). Soylu et al. (2002) recorded a reduction in PM conidia of 92% by comparing leaf areas grazed upon by *P. bisoetonota* Mulsant with nonfed-upon areas, suggesting a real and measurable PM removal through consumption. Further work with this species (Ahmad et al. 2003) revealed a large host range. The insect was recorded feeding on the mildew of 52 different plant species belonging to 24 families. This tendency for wide prey acceptance within Erysiphales and the obligation to feed on mildew at all life stages may prove to be important attributes of *Psyllobora* in relation to biological control.

We observed *P. vigintimaculata* Say (subspecies *taedata* LeConte) colonizing greenhouse and landscape plants infected with PM in Davis, CA, and this generated our curiosity regarding the insect's seasonality and occurrence in the local urban landscape. The objective of this study was to observe and document the biology and natural occurrence of *P. v. taedata* in various managed horticultural systems in Davis, CA, with respect to host plants, PM severity and the environment throughout the course of the year. It is hypothesized that because previous observations of the genus (Soylu et al. 2002, Ahmad et al. 2003) show a wide acceptance of mildew species as food on a variety of plants, then all plants in the landscape infected with PM should harbor *P. v. taedata* during its active seasons. It is expected that if PM severity increases in a specific location, incidence and density of *P. vigintimaculata taedata* also will increase locally.

Materials and Methods

A colony of *P. v. taedata* was maintained in the laboratory in a series of insect rearing cages. Plant material with PM was grown separately under high-pressure sodium lighting (600 W) in a humidified (50–80% RH) and climate-controlled ($25 \pm 5^\circ\text{C}$) growth room by using ebb-and-flood hydroponics. Weekly inoculations with crop-specific PM conidia were made either by an applied spore solution or by brushing off spores from infected plants. Sufficiently infected plants, either *Gerbera jamesonii* Adlam, *Zinnia elegans* Jacquin, or *Rosa* spp., were then exposed to caged adults at weekly intervals for egg deposition. After oviposition, the adults were removed and the egg-laden plants transferred to another cage to facilitate larval development. Toward the end of the beetles' fourth larval stadium, the plants are moved to a final cage and cut at the soil line. An inverted black plastic tray was placed in the pupation cage to act as

a pupation platform. Pupae were harvested by removing those formed on the platform, or adults were captured as they emerged. In this manner, the colony provided harvestable eggs, pupae or adults of uniform age and culture at 5-d intervals.

Biological Observation. Egg masses deposited on the same day were removed from the colony and transferred to an incubator (I-30 BL, Percival Scientific, Perry, IA) kept at $25 \pm 3^\circ\text{C}$ under fluorescent lights. Upon eclosion, the first-instar larvae were individually transferred with a fine paintbrush (#00) to observation petri dishes (55 mm in diameter) containing an excised *Gerbera jamesonii* leaf disc (10 mm in diameter) infected with the PM *Erysiphe chiochocearum* as food on top of filter paper moistened with deionized water. These observation dishes were returned to the incubator and monitored, with recorded observations every 24 h, noting visible exuviae or active molting to establish stadia durations. Fresh water and a new leaf portion containing PM were added and replaced, respectively, each day until successful pupation. Ten randomly selected insects were measured using an ocular scale sensitive to 0.01 mm and a stereomicroscope (M420, WILD, Heerbrugg, Switzerland) at each observation event. Observations were terminated upon adult emergence. These incubator observations were subsequently repeated with a separate cohort of eggs at $20 \pm 3^\circ\text{C}$. Laboratory conditions were assumed to be entirely within the insect's upper and lower developmental thresholds, and so accumulated degree-days (DD) were estimated as the sum of the daily differences in mean temperature and the lower developmental threshold by using the following formula: $\text{DD} = \sum (\text{T}_{\text{mean}} - \text{T}_0)_{\text{day}}$ (Zalom et al. 1983). The lower developmental temperature threshold used was 10.0°C . This is a commonly used standardized lower threshold for insects as recommended by Pruess (1983). While rearing individual insects at constant (20°C and 25°C) temperature in the laboratory, we were able to estimate the required accumulated degree-days for each larval stadium.

Natural Presence Determination. Various landscape plants known to be susceptible to PM were identified in and around the University of California (UC) Davis campus and located on a municipal map to establish a sampling circuit that encompassed some ecological variability and the largest variety of plant species. All sampling areas were managed urban gardens or landscapes, planted with ornamentals (exotic or native) or horticultural food crops. Sampling was designed to describe the presence of *P. v. taedata* in an established urban landscape setting, where many different plant-mildew complexes are likely to be encountered and where desirable management may call for chemical applications or physical disturbances to the plants. The UC Davis Arboretum, a 40-ha (100-acre) public botanical garden, allowed us to observe and sample from different garden types. The UC Davis Student Farm, an organic production operation and public educational resource, allowed use of sites including an organic vineyard of mixed wine and table grape varieties, the subscription garden, and the chil-

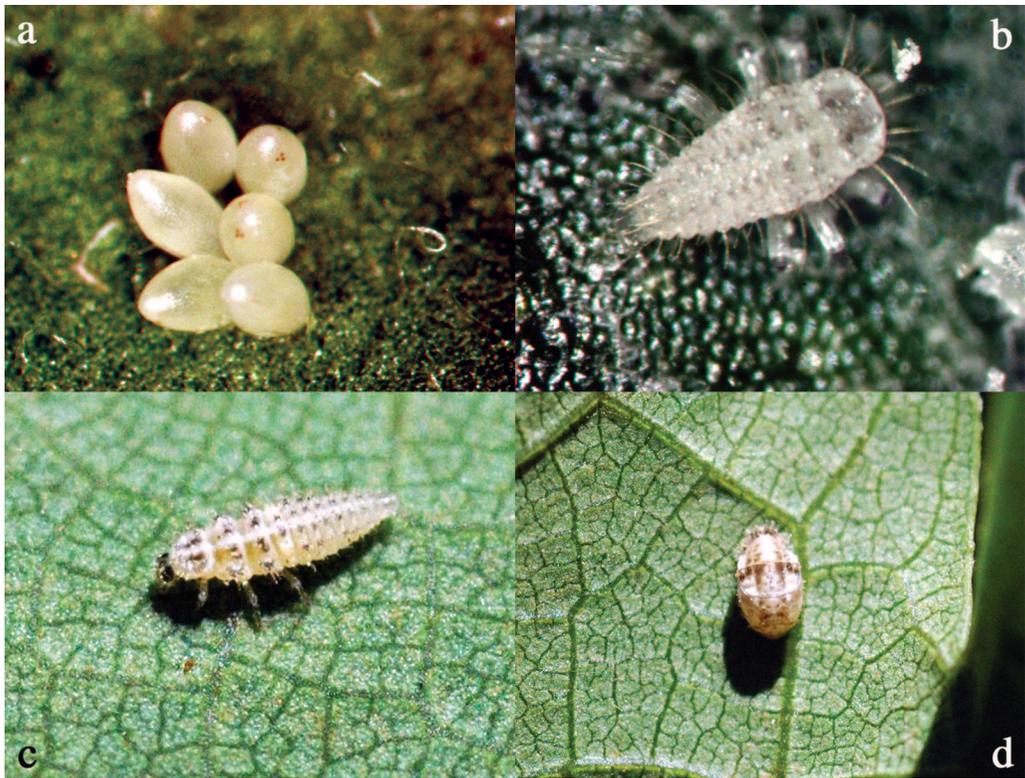


Fig. 1. (a) Top, a typical cluster of *P. v. taedata* eggs deposited on the abaxial surface of a leaf infected with powdery mildew. (b) Newly hatched first instar of *P. v. taedata*. (c) Late second instar of *P. v. taedata* on a grape leaf. (d) Typical pupa of *P. v. taedata* fixed to the abaxial surface of a grape leaf. (Online figure in color.)

dren's ecological teaching garden. Foundation plantings of various shrubs on campus grounds also were included. The final compendium of sampling sites comprised a circuit of ≈ 10 km. A sampling protocol was developed, in which presence/absence and density measurements were recorded for both PM and *P. vigintimaculata* weekly for each plant at every sampling site.

Mildew severity in the field was estimated visually, and an integral PM severity index from 1 (a very slight infection) to 5 (a very heavy infection) was assigned to each sample. Because the sampling circuit involved ≈ 30 different plant species, there was no uniform sampling unit such as a shoot or leaf. Therefore, an easily visualized and spatially constant sampling unit of 0.03 m^3 (1 cubic foot) was used at all sites and for all species, and thus the mean response variable from ten randomly selected sampling units was recorded for each sampling event. Additionally, five leaf samples were collected weekly from each plant species and examined for real PM density in the laboratory to correct and account for possible subjectivity and error surrounding the severity index in the field. Powdery mildew density and severity have been measured in several ways. In some cases, leaves are analyzed visually or digitally to assess a percentage of leaf area occupied by PM mycelia (Miller et al. 2003). In cases where density of conidia is the desired measurement,

a method of counting conidia on a hemocytometer was used as described by Chellemi and Marois (1991) and further adapted by Ypema and Gubler (1997) to ascribe a density measurement expressed in conidia per square centimeter of known leaf area. Because we were working with different mildew species on many hosts, it was decided to combine these approaches by multiplying the measured density within mycelial patches by the percentage leaf area affected to obtain a final density (conidia per square centimeter \times percentage of infection), expressed as an integer. This real density term was then fit to the sample's PM severity index from the field through linear regression to establish its validity and warrant its use as a measurement.

Insect presence or absence was determined through manual examination of ten randomly selected sample units (0.03 m^3) per site or through yellow sticky card trap catches, which were especially used for small-leaved plants and during the cooler season when insect densities were low. Insect presence data also included a separation of observed life stages, so that presence of eggs, larvae, pupae, adults, and mating adults were recorded at each sample site. An estimation of insect density based on the ten sample units per site was used to compare densities among sites. When only eggs were encountered, a subsample of the eggs

was taken back to the laboratory for eclosion and positive identification.

Climatic measurements included the daily high temperature, daily low temperature, average daily relative humidity, and measurable precipitation. These figures were available electronically through the California Irrigation Management Information System weather station located in west Davis. These data were used to characterize and describe the seasonal occurrence of *P. vigintimaculata* in terms of environmental conditions.

Bivariate scatter diagrams and linear regression (JMP IN version 5.1, SAS Institute 2005) were used to establish relationships between PM density and insect occurrence or density. The Median test on rank ordered responses was used for relationships involving response variables with non-Normal distributions. All plants harboring *P. vigintimaculata* life stages actively consuming PM were identified to species and recorded. Mean comparisons by host plant were performed by Student's *t*-tests, by using Bonferroni α adjustment for type I error avoidance (Holm 1979).

Results

Biological Observation. Masses of one to seven elongate, oval whitish eggs (0.7 ± 0.1 by 0.25 ± 0.04 mm; $n = 10$) were deposited directly on the abaxial leaf surface, petiole, or stem of the infected plant, or sometimes on a hard surface in the laboratory, such as the sides of a petri dish, with the long axis always perpendicular to the substrate (Fig. 1a). Laboratory and field observations of hundreds of eggs noted that there were very few hatch failures over a range of conditions, suggesting that virtually all eggs deposited are fertile. There were four larval instars followed by a final ecdysis and subsequent pupation. The first instar hatchling had an oval translucent whitish gray body (0.8 ± 0.12 by 0.25 ± 0.03 mm; $n = 10$), somewhat dorsoventrally flattened, with many white hairs borne from the thoracic and abdominal tubercles (Fig. 1b). After the first molt the larva's color was a much darker gray with a cream colored or yellowish median stripe, but as the larva neared the end of each instar the color gradually paled to that of almost white (Fig. 1c). The size of larvae gradually increased after each molt so that the measure of a new second instar was 1.7 ± 0.33 by 0.55 ± 0.09 mm ($n = 10$), the new third 2.3 ± 0.34 by 0.6 ± 0.11 mm ($n = 10$), and the new fourth 2.8 ± 0.45 by 0.8 ± 0.12 mm ($n = 10$). Just before the final molt the average fourth instar larva measured 3.3 ± 0.53 by 1.3 ± 0.18 mm ($n = 10$). The body shape and markings did not change from the second instar to the fourth instar, but markings did become more pronounced. During the latter parts of the fourth instar, the larva stopped feeding and attached itself to a pupation substrate, usually the abaxial surface of a large leaf or petiole. This process required about a third of the duration of the fourth instar. The pupa that followed the fourth molt was also oval in shape, al-



Fig. 2. An adult *P. v. taedata* feeding on a patch of powdery mildew. (Photo by Jack Kelly Clark. Online figure in color.)

though much shorter and somewhat convex (2.0 ± 0.22 by 1.3 ± 0.16 mm by 1.0 ± 0.12 mm; $n = 10$). Pupae were similar in color to the larvae, with the addition of gray wing pads, and a transverse row of black spots on the abdomen (Fig. 1d). The emerging adult was similar in shape and size to the pupa (female: 2.8 ± 0.35 by 1.5 ± 0.2 by 1.0 ± 0.12 mm; $n = 23$; and male: 2.2 ± 0.28 by 1.3 ± 0.2 by 0.8 ± 0.09 mm; $n = 19$), although more typically convex. The elytra were a base color of cream or yellowish, each marked with three dark brown spots and two light brown blotches (Fig. 2). The pronotum was of similar cream color with five

Table 1. Generalized life cycle of *P. v. taedata* with observed stadia durations (mean \pm SEM, $n = 25$) and approximate degree-day requirements

Life stage	Duration (d) at 20°C	Duration (d) at 25°C	Degree-days requirement
Egg	6.64 \pm 0.25	4.40 \pm 0.15	67
First instar	4.00 \pm 0.18	2.52 \pm 0.12	40
Second instar	3.80 \pm 0.19	2.76 \pm 0.10	40
Third instar	3.36 \pm 0.24	2.28 \pm 0.16	33
Fourth instar	3.32 \pm 0.19	2.16 \pm 0.14	33
Pupa	6.68 \pm 0.31	4.36 \pm 0.17	67
Total (egg-adult)	27.9 \pm 0.62	18.5 \pm 0.35	280

Based on developmental threshold (T_0) of 10.0°C and the formula $DD = \sum(T_{mean} - T_0)_{day}$.

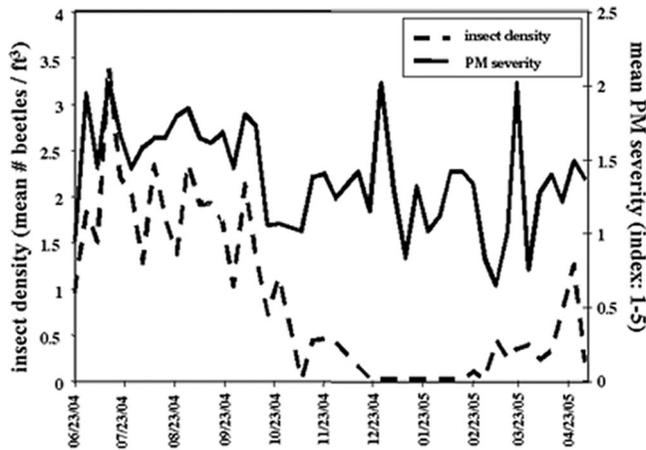


Fig. 3. Seasonal density of powdery mildew (*sensu lato*) and its consumer, *P. v. taedata*, in urban gardens of Davis, CA.

brown spots arranged in an arc. The legs and antennae were golden yellow and all ventral surfaces dark brown to black. Under laboratory conditions ($25 \pm 3^\circ\text{C}$, photoperiod of 12:12 [L:D] h) adults spent a full day virtually immobile and in proximity to the recently exited pupal exuvia. Upon emergence beetles were very pale or white. After several hours the elytra darken and the pattern of maculation becomes visible.

Development from egg deposition to adult required ≈ 280 DD (Table 1). At 20°C , this equals ≈ 7 d for the egg, 4 d each for the first and second instars, three and a third days each for the third and fourth instars, and almost 7 d duration from pupation to emergence, for a total of ≈ 28 d from egg to adult. At 25°C this process is accelerated to 19 d.

Natural Occurrence. Life stages of *P. v. taedata* were observed feeding on the PM of 26 plant species in 13 different families and may be associated with several

other plants where adult beetles were caught on sticky cards in the proximity of mildew infection (Table 2). Activity of the insect was regularly detected until the middle of December, when California's Mediterranean climate yields daily fog, rainfall and sustained low temperatures (daily mean 7°C , 9.5-h photoperiod). Adult beetles were once again encountered in late February and early March (Figs. 2 and 3), as rains became less frequent and temperatures began to rise (daily mean 11.1°C , 11-h photoperiod).

The PM severity index from field assessment was positively correlated to measured PM density ($R^2 = 0.52$, $n = 53$) and one-way analysis of variance (ANOVA) showed a significant positive correlation of the field rating with real (laboratory measured) density ($F = 55.96$; $df = 1, 52$; $P < 0.0001$). Therefore, the field rating was considered a reliable measure of PM density and was further used as a comparative tool.

The Median test for nonparametric data used to detect an aggregative numerical response of *P. vigintimaculata* to increasing PM severity showed a significant positive effect of PM rating on insect density (Fig. 4) ($\chi^2 = 83.8$, $df = 3$, $P < 0.0001$). Additionally, there were more different *P. viginti-*

Table 2. Plant species on which *P. vigintimaculata* was recorded feeding on the powdery mildew in the urban landscape of Davis, CA, 2004–2005

Family	Species	Mo observed
Aceraceae	<i>Acer macrophyllum</i>	July
Asteraceae	<i>Dahlia coccinea</i>	Nov.–Dec.
	<i>Gerbera jamesonii</i>	April–Dec.
	<i>Zinnia elegans</i>	June–Aug.
Bignoniaceae	\times <i>Chitalpa tashkentensis</i>	June–Sept.
Cucurbitaceae	<i>Cucumis sativa</i>	July–Oct.
	<i>Cucurbita</i> spp.	July–Dec.
Dipsacaceae	<i>Scabiosa columbaria</i>	Dec., April–June
Fagaceae	<i>Quercus agrifolia</i>	Dec.
Lamiaceae	<i>Mentha spicata</i>	March
	<i>Monarda punctata</i>	Nov.–Dec.
	<i>Salvia spathacea</i>	June–Dec.
Lythraceae	<i>Lagerstroemia indica</i>	April–Nov.
Oleaceae	<i>Syringa vulgaris</i>	Aug.–Nov.
Plantaginaceae	<i>Plantago lanceolata</i>	July–Sept.
Platanaceae	<i>Platanus</i> \times <i>acerifolia</i>	Aug.–Nov.
Rosaceae	<i>Malus</i> spp.	Sept.
	<i>Prunus persica</i>	June–Nov.
	<i>Rosa</i> spp.	Feb.–Dec.
	<i>Spiraea douglasii</i>	Sept.
	<i>Vitis californica</i>	Aug.–Oct.
Vitaceae	<i>Vitis vinifera</i>	July–Oct.

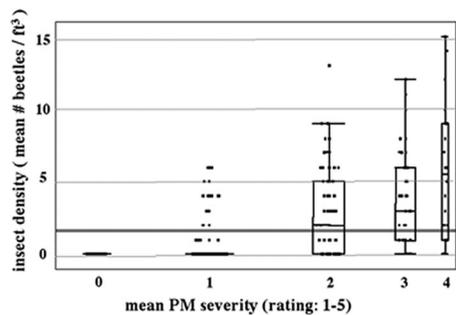


Fig. 4. Relationship between powdery mildew severity in Davis, CA for 29 different plant species and the observed density of *P. vigintimaculata* on the same plant assemblage averaged over time (June 2004–July 2005). Median test: $\chi^2 = 83.8$, $df = 3$, $P < 0.0001$.

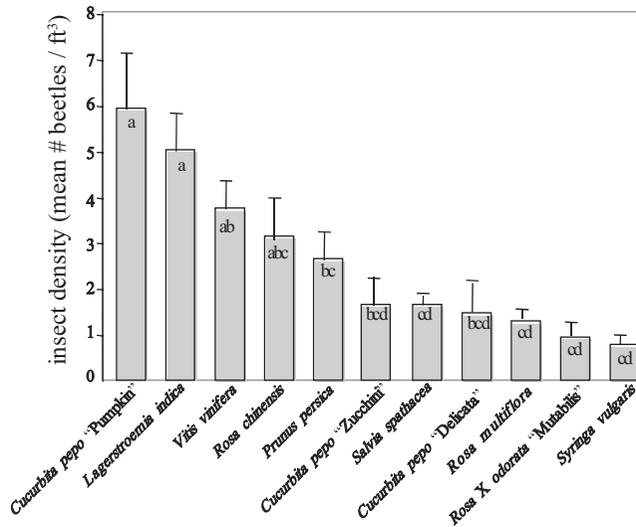


Fig. 5. Mean density of *P. v. taedata* individuals on various plant species infected with powdery mildew (*sensu lato*) during insect's active season. Student's *t* least significant difference mean separation, $t = 2.91$, $\alpha = 0.0038$ or 0.05/13 comparisons.

maculata life stages present as mildew density increased. There were also significant differences in the mean beetle density between plant species (Fig. 5). In early spring, the largest populations were seen on roses, followed by grapevines and crepe myrtle trees in the summer, and field cucurbits in autumn.

Discussion

The mycophagous coccinellid *P. v. taedata* is present in many managed agricultural and horticultural systems in Davis, CA, as a consumer of PM between the end of February and the middle of December through a wide range of temperatures. According to Gordon (1985), in North America this genus can only be morphologically confused with members of tribe Coccinellini, which also belong within the subfamily Coccinellinae. However, *Psyllobora* species are very seldom larger than 3 mm in length, and with one exception (*Anisosticta* Dejean) North American Coccinellini all exceed 3 mm in length at their extreme smallest. Two other species of *Psyllobora* (*Psyllobora borealis* Casey and *Psyllobora renifer* Casey) share parts of the California range of *P. vigintimaculata*, in the Sierra Nevada, but they can be distinguished by dorsal color pattern (Gordon 1985). Previous observation by Davidson (1921) on this subspecies notes that the insects overwinter as adults in small aggregates within leaf litter and field detritus. This is consistent with our records, in which the adult is the last noticeable life stage late in the season and the first noticeable life stage in early spring. In California's hot central valley, mean daily summer air temperature may reach 28°C, and we estimate *P. v. taedata* would complete development from egg to adult in just over 2 wk (15.5 d).

It is interesting to consider that in this series of observations, consisting of 2 yr and involving only a

small smattering of native and exotic landscape plants, *P. vigintimaculata* occurred in many PM complexes. This implies a very large host range and suggests a somewhat generalist feeding habit on Erysiphales fungi. Ahmad et al. (2003) observed a similar wide range of association between *P. bisoctonotata* and PM complexes in Syria. This versatility of *Psyllobora* should prove useful in the implementation of augmentative biological control in various horticultural systems. The insect was never seen on sampled plants not harboring PM. It is interesting to note, however, that these insects were also not detected directly on plants in several chronic PM systems, including *Euonymus japonica* L. and the California native *Eschscholzia californica* Charm. Because these PM complexes in the field lacked the presence of *P. vigintimaculata* throughout the year despite extensive mildew severity it is possible that there are restrictions or preferences in the diet of this insect and/or an undetermined host plant effect.

Insect density increased in response to increasing mildew density. This is a measure of the numerical response of a consumer to its food source. This attribute is an important criterion for effective biological control agents. Our observations of adult insect presence on single or small groups of PM-infected plants in a large and variable landscape suggest the ability to locate PM infections aerially through specific olfaction or by following an aerial spore gradient. There were no eggs observed on plants harboring PM at severity level two or lower, which suggests that the adult insect may not deposit eggs in a location where there is an inadequate food supply for the larvae to complete development. This ability to locate food is a key element to successful biological control (Solomon 1949). In a protected system such as a greenhouse, it is possible that this insect could be used for early detection of PM out-

breaks by conventional insect monitoring methods such as yellow sticky cards. Fluctuating levels of naturally existing populations in an open system, such as a commercial vineyard, could be used as an indicator of dynamic PM populations in the crop, and that monitoring of the insects could support PM treatment decisions. This idea is based on the assumption that areawide sampling for PM, especially at low density and in large agroecosystems, is more labor-intensive than discrete systematic sampling of sticky cards or other monitoring devices.

It is important to recognize *P. v. taedata* as a native natural enemy of a key horticultural disease. It may already be present in many systems unbeknownst to crop managers. Although biological control of PM by using this insect alone may not be adequate for commercial PM control, it may be possible to integrate its natural PM consumption with compatible fungicides and cultural approaches to achieve the level of control desired. Such an integrated approach to PM management could include the augmentation and conservation of this native natural enemy as a PM consumer and an indicator of early, isolated PM infection.

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