Habitat Diversification for Improving Biological Control: Abundance of *Anagrus epos* (Hymenoptera: Mymaridae) in Grape Vineyards

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ABSTRACT A frequently cited habitat diversification tactic is the use of prune tree refuges that support overwintering populations of *Anagrus epos* (Girault), a mymarid egg parasite of the western grape leafhopper, *Erythroneura elegantula* Osborn, in vineyards. Here we test the effect of prune trees on early-season abundance of adult *A. epos* in vineyards. *A. epos* was found in vineyards downwind of prune trees at more than twice the densities of vineyards lacking prune trees, despite significant variation in *A. epos* immigration from sources outside the prune tree-vineyard system. Densities of *A. epos* trap capture in vineyards. Furthermore, another factor associated with prune trees was found to influence *A. epos* abundance in vineyards: a windbreak effect created by the prune trees concentrated dispersing *A. epos* on the leeward side of the prune trees, thereby further enhancing *A. epos* numbers.

KEY WORDS Anagrus epos, Erythroneura elegantula, habitat diversification, conservation biological control, grape

HABITAT DIVERSIFICATION HAS long been promoted as a tactic to conserve natural enemies and enhance biological control of insect pests and as a integrated method of developing sustainable pest control systems in production agriculture. Both approaches argue that habitat diversification can provide essential resources for natural enemies, such as feeding sites, alternate hosts or prey, or overwintering sites, that can enhance their abundance in the surrounding environment and help prevent pest outbreaks (Herzog and Funderburk 1985, National Research Council 1989, van Emden 1990, Altieri 1992).

Whether viewed as a biological control tactic or as an integrated approach to sustainable pest control, habitat diversification in or around crop fields can have a profound effect on how insect herbivore and natural enemy populations interact. An understanding of the ecological mechanisms involved will also provide a rich resource for the development of pest management tactics in production agriculture (Herzog and Funderburk 1985).

One of the key hypotheses underlying the concept of habitat diversification is that many pest problems are the result of a loss of habitat critical for supporting natural enemy populations (Letourneau 1987, Russell 1989, Andow 1991). Although the ecological basis behind habitat diversification and natural enemy effectiveness has been discussed for many years, and many proposed systems have been evaluated in a preliminary way (reviewed by Flint and Roberts 1988, Russell 1989, Altieri 1992), most studies have been qualitative rather than quantitative in nature. Furthermore, there are no current tactics that have been widely adopted for pest control in production agriculture. Here, we test and examine the ecological mechanisms associated with prune tree habitats planted adjacent to grape vineyards on a key natural enemy species.

Anagrus epos-Erythroneura elegantula System. A frequently cited example used to illustrate the effect of habitat diversification on natural enemy effectiveness is the planting of overwintering habitats for Anagrus epos (Girault) near grape vineyards to enhance biological control of the western grape leafhopper, Erythroneura elegantula Osborn.

Erythroneura elegantula is a major pest of grapes in many regions of the western United States. High leafhopper numbers result in economic losses caused by cosmetic damage to grape berries from leafhopper frass, reduced vine vigor from heavy leaf feeding and leaf loss, and fruit damage from sun exposure. Furthermore, high densities of adult leafhoppers can disrupt harvest by flying into the eyes, nose, and mouth of field laborers.

A key natural enemy of the grape leafhopper is A. epos, an important egg parasite of E. elegantula as well as other leafhopper species (Gordh and Dunbar 1977, Williams 1984). A. epos has been reported to parasitize a significant proportion of E. elegantula eggs within commercial vineyards

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(Doutt and Nakata 1973). A major factor hypothesized to be associated with the abundance and effectiveness of *A. epos* is the presence of nearby habitat that supports alternate leafhopper hosts (Doutt and Nakata 1965, 1973). *A. epos* overwinters within leafhopper eggs. *E. elegantula* overwinters as an adult, thus, an alternate source of leafhopper eggs is required to support overwintering *A. epos* numbers.

Doutt and Nakata (1965) first observed that vineyards located downwind from riparian habitats had higher levels of *E. elegantula* egg parasitism and lower E. elegantula numbers relative to vineyards located distant from these habitats. They found that blackberry brambles, Rubus spp., abundant in riparian habitats, support Dikrella californica (Lawson), a year-round host of A. epos. They observed that early spring emergence of A. epos from blackberry results in earlier vineyard colonization by parasites, which coincided with oviposition of overwintered E. elegantula. They also speculated that earlier vineyard colonization at higher densities produced a stronger numerical response and thereby improved biological control (Doutt and Nakata 1973). Unfortunately, field trials determined blackberry brambles grown away from riparian habitats did not maintain abundant populations of A. epos, and further attempts were abandoned (Flaherty et al. 1985)

Kido et al. (1984) demonstrated that prune trees support the prune leafhopper, Edwardsiana prunicola (Edwards), which overwinters in the egg stage and serves as an overwintering host for A. epos. Emergence of overwintering A. epos from overwintering E. prunicola eggs laid beneath the bark of prune twigs also was found to coincide with 1st-generation E. elegantula oviposition in vineyards, suggesting that prune trees also serve as an overwintering habitat for A. epos. Studies in both commercial and experimental plantings of prune trees demonstrated that A. epos populations could be supported year-round. Williams (1984) and Kido et al. (1984) also showed that A. epos reared from E. prunicola or D. californica can parasitize E. elegantula eggs successfully, and vice versa. Finally, it has been shown that elevated A. epos populations were associated with higher E. elegantula egg parasitism in vineyards near prune trees (Kido et al. 1984, Pickett et al. 1990). Although these studies established the basic framework of the grape leafhopper—A. epos interaction, there have been no replicated field trials that assess the efficacy of prune tree habitats or that test the ecological mechanisms underlying the effect.

Anagrus epos Abundance. Doutt and Nakata (1973) and Kido et al. (1984) hypothesized that overwintering refuges near vineyards increase early-season A. epos vineyard colonization as a result of overwintering A. epos emerging from refuges and dispersing into nearby vineyards. They tested these predictions in field trials using yellow sticky traps to measure early-season abundance of adult A. epos in vineyards or by examining *E. elegantula* eggs and comparing rates of egg parasitism. Colonization appeared to be enhanced in vineyards downwind from prune orchards or riparian habitats containing blackberry brambles. They concluded that the greater abundance seen in field trials supported the overwintering refuge hypothesis. However, because these initial experiments used unreplicated comparisons, the results, although consistent with the refuge hypothesis, were preliminary in nature.

The interpretation presented by Doutt and Nakata (1973) and Kido et al. (1984) also rested on an untested assumption; namely, that an increase in parasite captures or egg parasitism near refuges was the direct result of A. epos emergence from overwintering sites. A 2nd potential mechanism that could explain increased parasite captures downwind of prune trees or trees found in riparian habitats is a windbreak effect generated by the physical structure of these habitats. A windbreak effect occurs when a structural barrier creates turbulence in the airflow and a sheltered zone on the leeward side of the barrier. The turbulent airflow may act to increase the probability that a dispersing insect will settle into these sheltered zones, thereby enhancing colonization. Dispersing insects from many families, including wasps in the family Mymaridae, have been shown to accumulate behind windbreaks (Lewis and Stephenson 1966). Wilson et al. (1989) showed that A. epos reach higher densities in prunes when artificial windbreaks are positioned on the upwind side of prune trees. Corbett and Rosenheim (in press) have also recently demonstrated a pattern of A. epos captures in vineyards downwind of prune trees that is consistent with the operation of a windbreak. Thus, enhanced A. epos abundance could be the result of overwintering populations within the prune trees, a windbreak effect, or some combination of those 2 factors.

In the current study, we tested 2 key hypotheses with respect to the effect of overwintering sites on *A. epos* abundance in vineyards as follows: (1) that prune trees adjacent to vineyards enhance earlyseason *A. epos* numbers in vineyards, and (2) that differences in abundance are the result of differences in the densities of overwintering *A. epos* emerging from prune trees. In addition to those 2 hypotheses, we also analyzed capture data for evidence of a windbreak effect influencing *A. epos* abundance downwind of prune trees.

Materials and Methods

Experimental Design. A. epos colonizes virtually all grape vineyards at some point during the growing season; the time and density of abundance can, however, be highly variable. E. elegantula populations also can be variable among vineyard sites in a given year. Because of the variation of both parasite and leafhopper numbers, a rigorous



vineyards might be more likely to have experienced severe leafhopper problems, motivating growers to look for enhanced means of control, and (2) growers using prune tree plantings might be a relatively "progressive" subset of all growers and might also differ in other aspects of vineyard management. Because 10 of the 12 prune tree sites were commercial prune orchards and were not planted for pest control, we feel that the lack of true randomization is unlikely to introduce a systematic bias into the analysis.

Vineyard A. epos Abundance. Vineyard plots were monitored to estimate densities of immigrating A. epos and E. elegantula during the early season, before parasites or leafhopper adults began emerging from the 1st generation of reproduction in vineyards. For both prune tree and control vineyard plots, 2 yellow sticky traps (75 by 125 mm yellow plastic cards, Hilcor Plastics, Los Angeles, CA) coated with Tanglefoot were attached to each of 6 wooden poles (12 traps total per site). Poles were placed in a transect at 10-m intervals along the 3rd vine row from the upwind edge of each vineyard block. Traps were oriented perpendicular to the predominant wind direction and positioned 0.6 and 1.2 m above the vine canopy to minimize any influence of vine canopies on trap capture. Traps were deployed beginning 1 April (7 paired sites), 15 April (3 additional pairs), and 1 May (2 final pairs), and were replaced twice monthly through 15 June 1992. All traps were taken to the laboratory and examined under a dissection microscope to count the number of adult A. epos captured.

Four vineyard plots were monitored weekly beginning 15 April to estimate the beginning of leafhopper oviposition and the 1st-generation (F_1) nymphal emergence. The beginning of oviposition was determined by examining field-collected grape leaves under a dissection microscope for the presence of E. elegantula eggs. The presence of nymphs was determined by examining grape leaves in the field.

Prune Tree Effect. The prune tree sites varied with respect to tree number, tree size, and orchard management practices. These differences in turn could influence overwintering A. epos densities and cause variation in the treatment effect within our design. Therefore, to control for variation in the prune refuge effect, and to test hypotheses about the contribution of A. epos overwintering in prunes to vineyard abundance, we sampled prune twigs to estimate overwintering A. epos densities (details below). We also recorded the number of trees and orchard management practices and estimated the average rate of tree growth to determine if these factors influence densities of overwintering A. epos (details below).

Fig. 1. Paired vineyard plot locations in northern and central California. The exploded view shows the orientation of prune tree and control vineyard plots.

PRUNE TREES

TREATMENT

PLOT

> 0.4 km

< 4.0 km

evaluation of prune tree-enhanced biological control required a large number of replicates. Surveys were conducted throughout the major wine grape viticultural regions of central and northern California to locate 26 paired commercial vineyards, one with adjacent upwind prune trees and the other lacking prune trees (Fig. 1). Paired vineyards were matched for grape cultivar, trellising, and management practices. Control (nonprune tree) vineyards were positioned 0.4-4.0 kilometers from refuge sites and either parallel to or upwind of prune tree vineyard sites to minimize movement of leafhoppers or parasites between treatment and control vineyards. The paired plots were grouped into 2 viticultural growing regions defined by the cumulative degree days occurring between April and October (Winkler et al. 1974). Comparisons were made between cooler growing regions (<3,000 DD) and warmer regions (>3,000 DD). Two of the prune tree sites used in the study were planted specifically for leafhopper control; the remainder were commercial or remnant prune orchards growing adjacent to the vineyard plots.

Given the nature of the prune tree habitat being tested, we were unable to ensure true randomization within our experimental design. True randomization would have required us to assign prune tree plantings randomly to plots and would have required a delay of 3-5 yr for the prune trees to become established and support large populations of the alternate leafhopper host. As a result, we used vineyard sites located near previously established prune trees. Had we chosen to work priThe primary difference in management practices found among sites was whether or not trees were irrigated. Seven of the 12 sites used in the study received little or no supplemental water during the growing season. We classified prune tree sites that had a permanent irrigation system as irrigated trees. Prune trees that were occasionally provided supplemental irrigation using portable systems, or that were never irrigated, were classified as nonirrigated.

Overwintering A. epos Densities. Anagrus epos emerge from overwintering prune leafhopper eggs oviposited beneath the bark of 1-6-yr-old branch wood (Mulla 1957). Because 2-6-yr-old branch wood can accumulate A. epos emergence holes over several years, we sampled only 1-yr-old branch wood to distinguish the current year's emergence holes from those of previous years. Prune twigs were collected in late June and early July, after the completion of A. epos emergence. A minimum of 4 prune twigs (1-yr-old) sampled from 10 randomly selected prune trees at each site was examined (see twig sampling details described below). The length and diameter of twigs were measured to calculate the surface area of 1-yr-old growth (area = $\pi * d * l$, where d is 1-yr-old twig diameter, l is twig length). Prune twigs were then examined under dissection microscopes for the presence of A. epos emergence holes. These data were then used to estimate the average number of emergence holes per square centimeter of twig surface area for each refuge site.

Prune Tree Growth. Average tree growth varied substantially among prune tree sites. To evaluate the possible influence of this factor on *A. epos* densities, we recorded the following 3 parameters as measures of tree growth: average length, diameter, and number per tree of 1-yr-old twigs. The average length and diameter of twigs were determined by randomly selecting 10 trees within each prune tree site for sampling. A main branch was removed from each compass direction of each tree for a total of 40 branches per site. Branches were taken to the laboratory, and the length and diameter of each 1-yr-old twig were recorded.

The total number of 1-yr-old twigs per tree was estimated by randomly selecting 4 trees from each prune tree site for sampling. Each tree was divided in half vertically and horizontally to establish 4 quadrants. One quadrant position was randomly chosen in each of the 4 trees to count twigs. The 4 twig counts, 1 example from each quadrant position, were pooled to estimate the mean number of twigs per tree.

Prune Tree Site Traps. Yellow sticky traps also were used to monitor *A. epos* and *E. prunicola* adult numbers within prune trees. For each prune site, 1 trap was placed in 3 randomly selected prune trees 2.0–2.5 m from the ground. Traps were replaced twice monthly as described above.

Statistical Procedures. The average number of *A. epos* caught on traps within the vineyard plots

was analyzed using a split-plot analysis of variance (ANOVA) model. Growing region was the main factor within the model, and presence or absence of a prune tree site was the subfactor. Each vineyard pair was treated as a statistical block to control for spatial variability in *A. epos* densities. Because the number of vineyard pairs sampled increased as the season progressed, separate univariate analyses were conducted for each sampling period. The analyses were conducted to test the null hypothesis that *A. epos* abundance rates in vineyards are independent of the presence or absence of prune trees.

Prune Tree Effect. To test if differences in vineyard parasite abundance can be explained by the emergence of overwintering *A. epos* from prune trees, multiple regression analyses were performed using *A. epos* emergence hole densities from prunes and *A. epos* capture in control vineyards as independent variables and *A. epos* capture in prune tree vineyards as the response variable. We interpret *A. epos* trap capture in a control vineyard as an estimate of the local abundance of parasites moving into vineyards in the absence of prune trees (area-wide *A. epos* numbers). We tested the null hypothesis that differences in *A. epos* abundance are independent of variation in overwintering *A. epos* densities within prune trees.

Multiplicative Effects. We evaluated the potential influence of a windbreak effect on A. epos abundance in vineyards using model II regression analyses (Sokal and Rohlf 1981) to examine the relationship between A. epos captures in the control vineyards (the independent variable) and A. epos captures in prune tree vineyards (the dependent variable) (statistical model: prune tree vineyard captures = β^* control vineyard captures + c + error). If overwintering A. epos within prune trees were the only factor affecting A. epos trap capture, we would expect the slope of the regression equation (β) to approximate 1.0, with an increase in the intercept (c) reflecting an additive increase in the number of A. epos contributed by prune trees. If, on the other hand, the slope parameter is significantly greater than 1.0, a multiplicative effect in prune tree vineyard trap capture is present, indicating the presence of another factor, such as a windbreak effect, increasing A. epos capture independent of any contribution from overwintering A. epos emerging from prune trees.

This analysis was used because model I regression produces a biased estimate of the slope for low values of the correlation coefficient (Sokal and Rohlf 1981, Pagel and Harvey 1988). Model II analysis is also the most appropriate method for analyzing the functional relationship between 2 variables when both variables are subject to experimental error (Sokal and Rohlf 1981). A principal axis (major axis) model II regression estimates the slope parameter by estimating the principal axis between 2 normally distributed random variables (Pagel and Harvey 1988). We used this analysis to



Fig. 2. Seasonal patterns of A. *epos* and E. *elegantula* in vineyard plots. (A) A. *epos* adult trap captures (mean \pm SE) in control and treatment plots. (B) E. *elegantula* adult trap captures (mean \pm SE) in control and treatment plots. (C) Period of E. *elegantula* oviposition in vineyard plots. (D) Period of A. *epos* F₁ emergence. (E) Period of F₁ nymphal emergence. Hatched lines indicate early appearance in some vineyard plots. Solid lines indicate appearance in all plots.

test the null hypothesis that there is no multiplicative increase in *A. epos* trap capture in prune tree vineyards relative to control vineyard captures.

For all statistical analyses except the model II regressions, trap captures were subjected to a $\log(x + 1)$ transformation, and *A. epos* emergence hole data were square root-transformed to normalize the distribution of means. Mean comparisons tests were accomplished using single degree of freedom tests (orthogonal contrasts), and all statistical analyses except the model II regressions were performed using the JMP statistical program for the Macintosh (SAS institute 1989). A Bonferroni correction for multiple comparisons was used to maintain the total experimentwise a error rate at 0.05 for the ANOVA and regression analyses (Sokal and Rohlf 1981).

Results

Seasonal Patterns. Examination of the earlyseason pattern of parasite and leafhopper trap captures revealed that during the 1st sample period in early to mid-April, 1 or more *A. epos* were caught in 7 of the 14 vineyard plots monitored (Fig. 2). During the 2nd sample period, *A. epos* was detected in 18 of 20 vineyard plots. The increasing A. epos capture over time indicated that parasites began moving into vineyards in April, several weeks after overwintered E. elegantula adults begin moving into vineyards. Overwintered adults typically begin moving into vineyards from their overwintering habitats during March (Doutt and Nakata 1965, Williams 1984). E. elegantula eggs were detected in vineyards beginning in late April (Fig. 2C), demonstrating that the appearance of A. epos coincided with the beginning of the oviposition period of overwintering leafhopper adults. The large increases in A. epos capture during the 4th sample period in late May coincided with the 1st appearance of A. epos emergence holes in grape leaves, marking the emergence of adults of the F₁ parasite generation (Fig. 2D). Also during the 4th sample period, F_1 leafhopper nymphs began appearing on grape leaves in most vineyards (Fig. 2E).

Regression analyses were done to assess the relationship between the final density of A. epos emergence holes in 1-yr-old prune twigs and trap capture in prune trees to estimate the time of A. epos emergence from prune twigs. During the 1st sample period (15-18 April), only a single prune tree site had an A. epos capture. Regression analyses for the 2nd (24 April-1 May) and 3rd (8-15 May) periods revealed that A. epos emergence holes explained a significant amount of the variation in trap captures ($R^2 = 0.88$, n = 9, P = 0.002and $R^2 = 0.42$, n = 12, P = 0.022, respectively). No relationship was found between area-wide trap captures in control vineyards and trap capture within prune trees ($R^2 = 0.05$, n = 9, P = 0.56 for the 2nd sample period; $R^2 = 0.17$, n = 12, P =0.18 for the 3rd sample period). The conclusion from these analyses is that sticky traps in prune trees reflect the A. epos emergence pattern from prune trees and are not influenced significantly by area-wide A. epos moving from outside sources. The high degree of correlation during the 2nd sample period suggests that peak overwintering emergence of A. epos from prune twigs occurred between 18 April and 1 May.

Vineyard A. epos Abundance. We confined our analyses of A. epos abundance to the 1st 3 sample dates when A. epos captured on traps were most likely to have originated from sources outside the vineyard. Traps in prune tree vineyards captured >2 times the number of parasites as did traps in control vineyards during the 2nd and 3rd sample dates (Fig. 2A; Table 1). No significant differences in capture were detected between the 2 growing regions, but variation in A. epos captures was substantial across the paired vineyards as indicated by the significant block effect.

Prune Tree Effect. Model I regression analyses revealed that captures of *A. epos* in prune tree vineyards were closely correlated with captures in control vineyards for the 2nd and 3rd sample dates $(R^2 = 0.53, n = 10, P = 0.016, R^2 = 0.65, n = 12,$

Table 1. Nested ANOVA of the number of A. epos (log₁₀ transformed) captured on traps in vineyards with respect to prune refuges, growing regions, and paired vineyard plots (block effect)

Date	Source of variation	df	F	Pa
15-18 Apr	Treatment	1	3.93	0.094
•	Blocks (region)	5	6.17	0.023*
	Region	1	0.13	0.735
24 Apr-1 May	Treatment	1	6.47	0.032*
. ,	Blocks (region)	8	5.14	0.012*
	Region	1	4.60	0.061
8–15 May	Treatment	1	11.32	0.006*
,	Blocks (region)	10	5.72	0.004*
	Region	1	3.56	0.086

^{*a*} One-tailed tests for hypothesis testing; *, P <critical value after Bonferroni correction (P < 0.033).

P = 0.001, respectively), but not for the 1st sample date ($R^2 = 0.48$, n = 7, P = 0.09). The significant regressions of *A. epos* capture between the treatment and control plots underlines the importance of blocking by vineyard pair, a key feature of our experimental design. This result also confirms that area-wide *A. epos* numbers were a significant source of parasites in vineyards whether prune trees were present or not.

The multiple regression analyses indicated that *A. epos* emergence from prunes was a factor explaining *A. epos* trap captures in prune tree vineyards, after controlling for area-wide abundance from control plot trap captures, during the 2nd sample period (Table 2). This coincided with the estimated time of *A. epos* emergence from prune twigs as determined by sticky traps in prune trees. The partial regression coefficients indicated that emergence from prunes explained a substantial amount of the variation in *A. epos* capture during the first 2 sample periods in April, but by the 3rd sample period in early May, area-wide *A. epos* captures.

Variation in Overwintering A. epos Densities. Prune tree sites varied in terms of the number of trees per site, the rate of tree growth, the number of 1-yr-old twigs per tree, and the density of A. epos emergence holes (Table 3). Much of this variation was generated by variation in irrigation practices (Table 4). Irrigated trees were associated with greater tree growth (average surface area of 1-yrold twigs) and lower twig numbers than nonirrigated trees. Irrigation was also associated with higher A. epos overwintering densities as well as higher trap captures of E. prunicola and A. epos adults in tree canopies. ANCOVA revealed that both irrigation (F = 23.06, df = 1, 12, P = 0.001) and prune tree number (F = 11.21, df = 1, 12, P = 0.009) had significant influences on the density of A. epos emergence holes in prune trees. There was a positive linear relationship between the number of prune trees and the density of A. epos emergence holes in trees (intercept = -0.0496, slope = 0.0773). Nevertheless, neither prune tree number nor irrigation had detectable effects on parasite catch in associated vineyards during the 3 sample periods (P > 0.047).

We also estimated the average number of A. epos emergence holes per tree and the total number of emergence holes per prune tree site to test if these parameters could explain captures in adjacent vineyards. The number of emergence holes per tree was nonsignificant during the 1st sample period (F = 8.9; df = 1, 6; P = 0.041), significant during the 2nd period (F = 7.21; df = 1, 9; P =0.031), and non-significant during the 3rd period (F = 0.26, df = 1, 11, P = 0.625). The number per prune tree site was, however, nonsignificant during all 3 sample periods ($P \ge 0.096$).

Multiplicative Effects. The principal axis analyses (model II regression) of *A. epos* trap captures in control and prune tree vineyards suggest that a multiplicative effect was present during the 2nd and 3rd sample periods, when both slope parameters were significantly >1.0 (Fig. 3 B and C). During the 1st sample period, the estimated slope was similar to the other sample periods, but not significantly different from 1.0 (Fig. 3A). These results suggest that independent of any contribution from *A. epos* overwintering in prune trees, prune trees were associated with a multiplicative effect augmenting *A. epos* capture on the downwind side of prune trees.

Table 2. Multiple regression analysis of the relationship between the dependent variable, $\log_{10} (A. epos \text{ trap catch})$ in prune tree plots, and the independent variable, square root (A. epos emergence density) from prune sites and $\log_{10} (A. epos \text{ trap catch})$ in control plots

Sample date	Source of variation	dſ	Slope (± SE)	F	R ² a	Pb
15-18 Apr.	Whole model test	2, 7		11.9	0.86	0.026
	Emergence density	1, 7	$1.06 (\pm 0.325)$	10.6	0.75	0.031
	Control captures	1, 7	$0.67 (\pm 0.237)$	8.0	0.69	0.047
24 Apr–1 May	Whole model test	2, 10	—	16.8	0.83	0.002*
	Emergence density	1, 10	$2.37 (\pm 0.717)$	10.9	0.73	0.013*
	Control captures	1, 10	$0.84 (\pm 0.242)$	11.9	0.75	0.011*
8–15 May	Whole model test	2, 12		10.15	0.69	0.005*
	Emergence density	1, 12	$0.91 (\pm 0.825)$	1.21	0.35	0.299
	Control captures	1, 12	$1.48 (\pm 0.363)$	16.74	0.81	0.003*

^a R^2 for individual factors are partial correlation coefficients (r^2).

^b*, P < critical value after Bonferroni correction (P < 0.017).

Variable	Mean	SE	Range
No. prune trees per site	422.5	111.9	27-1,216
No. 1-yr-old twigs per tree	1,121.7	177.4	435-2,238
1-yr-old twig surface area, cm ²	20.3	4.0	3.7-122.5
A. <i>epos</i> emergence density/cm ²	0.021	0.0056	0.0023-0.0640

Table 3. Descriptive parameters of prune trees among experimental plots

Discussion

The goal of this research was to assess the influence of prune trees on early-season A. epos abundance in vineyards and to test the hypothesized ecological mechanisms underlying this system. Prune trees were associated with significant increases in the density of A. epos captured in nearby grape vineyards relative to vineyards lacking prune trees. Prune tree vineyards were found, on average, to receive twice the number of early-season parasite captures. Overwintering A. epos emergence from prune trees was a significant predictor of A. epos trap capture in nearby vineyards during the 2nd sample period, which coincides with our estimated period of A. epos emergence from prune twigs. Examination of the functional relationship between control and prune tree vineyard parasite captures also revealed a multiplicative response in trap capture on the downwind side of prune tree vineyard plots. This suggests that another factor associated with prune trees, other than overwintering A. epos populations, enhanced parasite numbers in refuge vineyards.

Seasonal Patterns. Based on limited field data, Doutt and Nakata (1973) and Kido et al. (1984) speculated that the effectiveness of overwintering refuges near vineyards was, at least in part, caused by the time of A. epos emergence from overwintering hosts. They based this hypothesis on the observation that parasite emergence from prune trees or blackberries occurs during mid-April, at the approximate time overwintered E. elegantula begin oviposition in vineyards. They further speculated that enhancing early-season A. epos colonizers, coupled with the high numerical response of the parasite (A. epos completes 3 generations for each E. elegantula generation), improves biological control of leafhoppers in vineyards. The seasonal pattern of leafhoppers and parasites seen in the curwith rent study concurs these previous observations. Across the replicated vineyard pairs, our data show a consistent pattern of both areawide A. epos captures and A. epos emergence from prune trees coinciding with the onset of oviposition by overwintered E. elegantula in vineyards. Thus, parasite abundance appears to be synchronized with the appearance of host eggs in grape vineyards.

Vineyard A. epos Abundance. The replicated comparisons of A. epos abundance in vineyards showed that the presence of overwintering habitats produced a substantial early-season increase in the density of A. epos trapped in grape vineyards, a result consistent with the observations reported by Doutt and Nakata (1973) and Kido et al. (1984). The elevated capture rates were seen despite differences in geographical regions and variation in the number of area-wide A. epos captures, which indicates that the prune tree effect operated under a wide variety of vineyard management and environmental conditions. Based on these results, we concluded that the presence of prune trees was associated with elevated A. epos numbers, and as a result, parasites may colonize these vineyards at higher rates than vineyards lacking nearby prune trees.

Ecological Mechanisms. Doutt and Nakata (1973) and Kido et al. (1984) assumed that any increase in parasite abundance in vineyards (inferred using trap data or egg parasitism rates) was the direct result of overwintering emergence from nearby habitats. In the current study, we tested this assumption by comparing the density of overwintering A. epos emergence holes with A. epos trap capture in prune tree vineyards after controlling for area-wide colonizers. The significant regression during the 2nd sample period indicated prune trees were a significant source of parasite captures during the period of A. epos emergence from overwintered E. prunicola eggs. These results reveal 2 important points regarding the influence of prune trees on parasite abundance in vineyards. The 1st is that overwintering emergence is a significant ecological factor determining early-season parasite

Table 4. Effect of irrigation on prune tree growth and populations of E. prunicola and A. epos.

	Growth rate, cm ^{2a}	No. twigs (±SE)	A. epos emergence holes/cm ²	A. epos trapped ^b	E. prunicola trapped ^b
Irrigated Nonirrigated	$30.4 \pm 4.98*$ 13.1 ± 4.20	$642 \pm 176^{**}$ 1,475 ± 163	$\begin{array}{c} 0.0325 \pm 0.0063 * \\ 0.0105 \pm 0.058 \end{array}$	$9.50 \pm 2.09 **$ 1.10 ± 1.93	$\begin{array}{c} 22.16 \pm 5.48^{**} \\ 0.59 \pm 5.07 \end{array}$

^a Surface area of 1-yr-old prune twigs (mean \pm SE).

^b Numbers of adults caught on traps within prune tree canopies. * Significantly different, 0.01 < P < 0.05.

** Significantly different, P < 0.01.



Fig. 3. Scatterplots of the functional relationship between A. *epos* capture in prune tree refuge vineyards against A. *epos* capture in control vineyards. (A) 15–18 April (B = 1.705; 97.5% CL, L = 0.58, U = nonestimatable). (B) 24 April–1 May (B = 2.38; 97.5% CL, L = 2.05, U = 2.79). (C) 8–15 May (B = 3.10; 97.5% CL, L = 2.23, U = 4.85). Confidence limits were established for 97.5% as a correction for multiple comparisons.

numbers. The 2nd is that the effect of prune trees on *A. epos* abundance was dependent not only on the presence of prune trees themselves, but on the density of overwintering parasites residing within the trees. This latter point may have important implications for using prune trees as a commercial pest control tactic (discussed below).

Lewis and Stephenson (1966) showed that flying insects dispersing in the surrounding environment accumulate in sheltered regions near physical barriers (natural or artificial windbreaks). They also found that insects aggregate behind windbreaks as a multiplicative function of the number of insects dispersing in the surrounding environment. This effect was particularly pronounced for mymarid wasps. Using elemental labeling techniques, Corbett and Rosenheim (in press) found a pattern of A. epos capture suggesting that area-wide A. epos numbers accumulate at a rate 4 times greater immediately downwind of prune trees than found upwind of trees. Based on these results, they hypothesized that a windbreak effect may also be a mechanism enhancing abundance within the prune tree-vineyard system. We tested this hypothesis across our replicated study by examining the functional relationship between control vineyard trap captures (area-wide colonizers in the surrounding environment) and prune tree vineyard captures (number of colonizers behind windbreaks). Our results revealed that during each of the 3 sample periods, the slope of the relationship was ≥ 1.7 . Thus, a multiplicative increase in capture was associated with the presence of prune trees but independent of any contribution from overwintering A. epos densities. This result supported the windbreak hypothesis and demonstrated the effect may be consistent for vineyards with a windbreak present. Furthermore, this result identifies an important additional mechanism that may be affecting *A. epos* vineyard colonization in this system.

These results underscore the importance of investigating the ecological mechanisms underlying systems of habitat diversification in addition to tests of overall effectiveness of diversification. Understanding the mechanisms involved will enhance our ability to manipulate these systems to maximize their effectiveness and provide a useful framework to begin analyses of new systems.

Variation in the Prune Tree Effect. Because overwintering A. epos densities varied among the prune tree sites, we were interested in how the management of prune trees affects overwintering A. epos populations and their subsequent abundance in vineyards. Irrigation practices were found to be a significant factor explaining much of the variation in overwintering A. epos densities observed in prune trees (Table 4) and some of the variation in trap catches in prune tree vineyards. The number of prune trees within a site also affected overwintering A. epos density. How tree number exerts an influence on the density of overwintering A. epos (per square centimeter of prune bark) is not known, but we speculate that greater numbers of trees may create a more favorable microhabitat, increasing the number of A. epos that successfully emerge from their overwintering hosts.

Although tree number had a strong positive influence on the density of *A. epos* emergence holes per square centimeter of prune tree bark, it was not a predictor of *A. epos* captures in prune tree vineyards. This is an enigmatic result. At the outset

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of the study, we expected that prune tree sites containing more trees would produce a larger pool of migrants for the downwind vineyards. The increased density (per square centimeter of bark) of overwintering A. epos in prune tree sites with larger tree numbers only strengthened our expectation that tree number would be a major determinant of early-season abundance in prune tree vineyards. Indeed, we expected that we would be able to estimate the minimum number of trees needed to generate the level of augmentation of A. epos necessary to achieve pest management. Instead, what we found is that tree number is less a predictor of abundance in vineyards than is the number of A. epos produced per centimeter of bark. We also calculated the total number of A. epos emerged from overwintering sites within an entire prune tree site (a composite estimate, obtained as the product of A. epos density per square centimeter of bark the total area per tree, and the number of trees per site) as the estimate for A. epos contributions from prune tree sites. This estimate was, however, a weaker predictor of early-season abundance in vineyards than either the number of A. epos per square centimeter of bark or per prime tree. How can we explain this result? One possibility is that trees within the larger prune tree sites may have contributed unequally to the number of vineyard migrants, with the rows of trees directly adjacent to the vineyard producing the bulk of the wasps trapped in vineyards. Additional experimentation will be needed to test this and other potential explanations for the lack of a tree number effect.

These results have 2 implications for establishing and managing prune tree refuges for pest control. The 1st is that enhanced A. *epos* abundance may be attainable with a relatively small number of trees. The 2nd is that irrigation of prune trees will be of primary importance for supporting high densities of overwintering A. *epos* populations. More detailed recommendations for establishing prune tree refuges will be presented in future papers.

Questions about the effect of vegetational diversity on the diversity and abundance of insect populations recently have received considerable attention from ecologists and pest control specialists. The results of the current study not only supported the hypothetical effect of prune tree refuges on A. *epos* abundance, but in a broader context, provide a test of the effect of vegetational diversity on natural enemy abundance. As a result, this study has satisfied the 1st of 3 hypothesized natural enemy responses which predicts greater natural enemy abundance in diversified systems (Russell 1989, Andow 1991). In addition, our study identified the following 2 mechanisms underlying the influence of prune trees: the presence of an overwintering host, and a windbreak effect.

Future papers will examine the effect of overwintering refuges on the remaining 2 hypotheses the effect of prune trees on *E. elegantula* egg mortality, and *E. elegantula* population densities within grape vineyards.

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