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Habitat diversification tactic for improving biological control: parasitism of the western grape leafhopper

Brook C. Murphy[1], Jay A. Rosenheim[1], Robert V. Dowell[2] & Jeffrey Granett[1]
[1]*Department of Entomology, University of California, Davis, CA 95616, USA;* [2]*California Department of Food and Agriculture, Sacramento, CA 95814, USA*

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Abstract

In a previous study we demonstrated greater abundance of the parasitoid *Anagrus epos* (Girault) in grape vineyards located downwind of prune trees that function as overwintering habitats. This study examines whether these higher *A. epos* numbers translated into higher egg parasitism rates of the grape leafhopper, *Erythroneura elegantula* (Osborn). Paired commercial wine-grape vineyard plots, one with and one without adjacent prune trees, were studied within a complete block design in northern and central California. *A. epos* was the key mortality factor affecting *E. elegantula* eggs. Point estimates of *A. epos* parasitism rates were significantly greater in vineyards associated with prune trees during the first *E. elegantula* generation in both 1991 and 1992. No consistent differences in parasitism rates were observed during the second or third generations. The results indicated that prune trees enhance early season parasitism rates. Cumulative estimates of egg parasitism across *E. elegantula* generations demonstrated that enhanced early-season parasitism resulted in a net season-long increase in the degree of mortality imposed by *A. epos* on *E. elegantula* eggs. Two factors were found to influence parasitism rates: the abundance of early-season *A. epos* adults moving into vineyards and the density of *E. elegantula* eggs in vineyards. Our results indicate that diversification of vineyards using prune trees supports overwintering populations of a specialist parasitoid and thereby alters host-parasitoid interactions to favor enhanced parasitism in vineyards.

Introduction

There is a growing interest in the development of agricultural pest management systems that rely less on synthetic pesticides and more on culturally and biologically based controls. This has placed greater emphasis on how factors such as resource enrichment, disturbance and vegetational diversity affects arthropod species richness and population abundance. The role these factors play in affecting community structure will help explain agricultural problems including the development of herbivores as pests and the development of effective biological control programs, especially in annual crops (Price, 1984; Herzog & Funderburk, 1985).

Of particular interest has been the effect of vegetational diversity in agroecosystems on herbivore and natural enemy abundance (Russell, 1989; Letourneau, 1990; Andow, 1991; Altieri, 1992). Theoretical predictions and empirical data generally support the notion that herbivore abundance tends to be lower in diverse systems relative to artificially simplified systems (Risch et al., 1983; Price, 1984). Two hypotheses have been proposed to explain the underlying causes of differences in arthropod abundance between simple and complex systems (reviewed by Russell, 1989 and Andow, 1991). The first is the resource concentration hypothesis, which predicts that specialist herbivores more easily locate and successfully colonize simple systems. The second is the enemies hypothesis, which predicts predators and parasites are more effective at colonizing complex systems (Root, 1973; Letourneau, 1987).

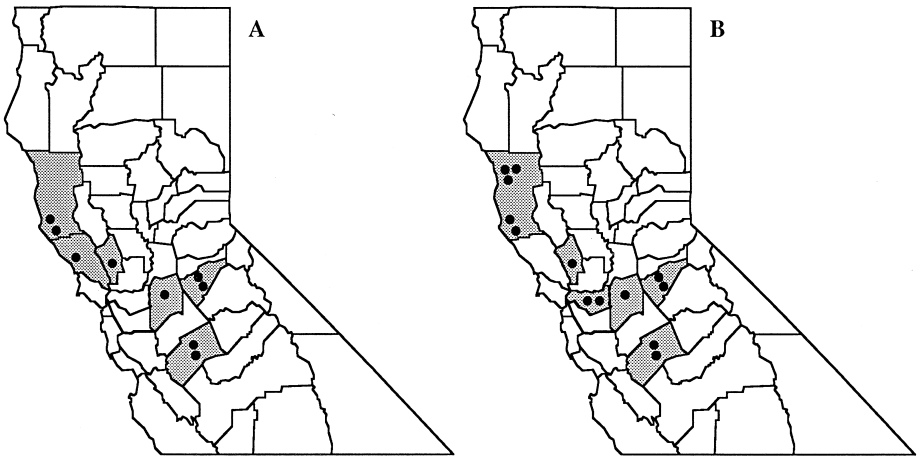

Figure 1. Map of northern and central California showing location of paired vineyard sites used in (A) 1991 and (B) 1992.

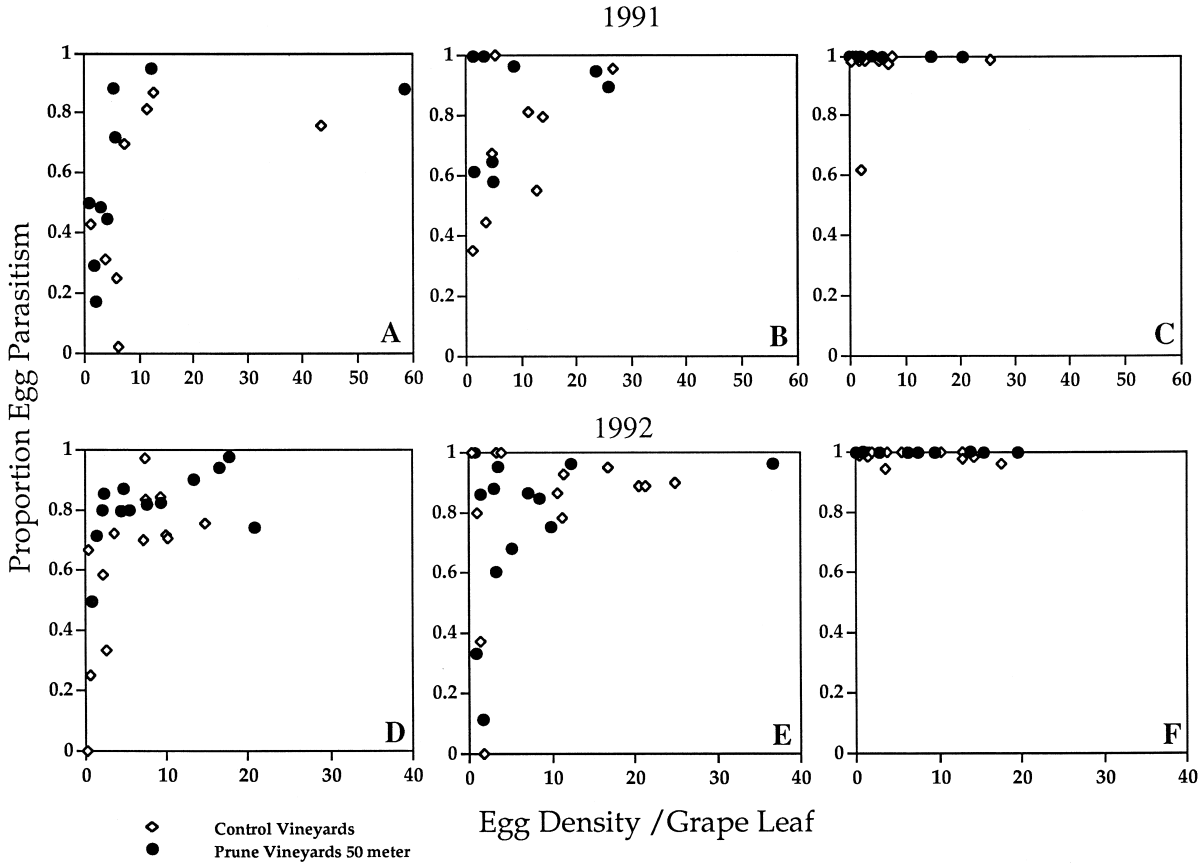

Figure 2. Relationship between *E. elegantula* egg density per grape leaf and proportion of eggs parasitized by *A. epos*. Season 1991, (A) the first leafhopper generation, (B) the second leafhopper generation and (C) the third leafhopper generation. Season 1992, (D) the first leafhopper generation, (E) the second leafhopper generation and (F) the third leafhopper generation.

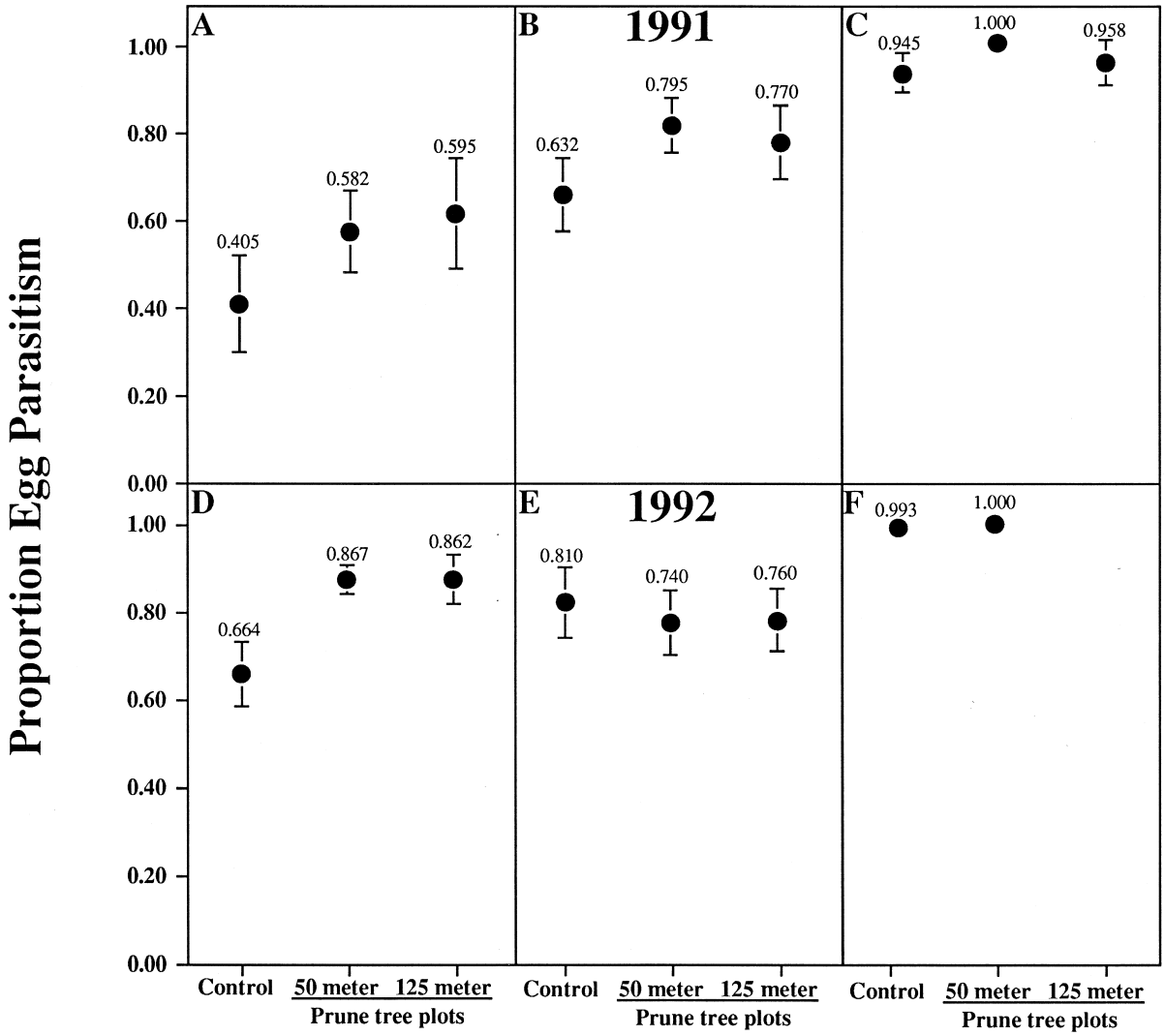

Figure 3. Mean ± S.E. point estimates of egg parasitism. Season 1991, (A) the first leafhopper generation, (B) the second leafhopper generation and (C) the third leafhopper generation. Season 1992, (D) the first leafhopper generation, (E) the second leafhopper generation and (F) the third leafhopper generation.

The degree of vegetational diversification in an environment can profoundly affect how insect herbivore and natural enemy populations interact. A central question underlying both the resource concentration and enemies hypotheses, as they pertain to agroecosystems, is by what mechanism(s) does vegetational diversification (or simplification) influence colonization of insect herbivore and natural enemy populations. Developing an understanding of the colonization process in agroecosystems may explain why some herbivore species reach pest status, but many natural enemy species have difficulty colonizing crops. Here we examine the role of habitat diversification in the colonization of grape vineyards by *Anagrus epos* (Girault), (Hymenoptera: Mymaridae) an important egg parasitoid of the western grape leafhopper, *Erythroneura elegantula* (Osborn), (Homoptera: Cicadellidae) a major pest of grapes throughout the western United States.

Anagrus epos – Erythroneura elegantula *system.* Neither *A. epos* nor *E. elegantula* maintain year-round populations within grape vineyards. After leaf fall, *E. elegantula* spends the winter in the adult stage among winter weeds and leaf litter surrounding vineyards. *Anagrus epos* overwinters within host eggs and

therefore requires a host other than *E. elegantula* for successful overwintering. Each spring *E. elegantula* adults move into vineyards as the first leaves begin to appear on grape vines in March. *Anagrus epos* emerge from their overwintering host eggs and migrate into vineyards as *E. elegantula* begin laying eggs beneath the epidermal layer of grape leaves in April (Doutt & Nakata, 1973; Murphy et al., 1996). In this way vineyards are analogous to annual agroecosystems where each spring the system must be re-colonized by both herbivores and natural enemies.

Doutt & Nakata (1965, 1973) postulated that *A. epos* is unable to control *E. elegantula* populations in vineyards that lack nearby alternate host eggs for overwintering. They hypothesized that vineyards distant from overwintering habitats experience reduced rates of *A. epos* colonization in the early spring because parasites must migrate longer distances. Because fewer parasites are present, *E. elegantula* is released from an important mortality factor, thus allowing them to reach pest status. They hypothesized that establishing habitat supporting overwintering host eggs near vineyards will enhance early-season *A. epos* colonization and thereby improve biological control of *E. elegantula*.

Testing a habitat diversification tactic. Doutt & Nakata (1965, 1973) and later Kido et al. (1984) showed that vineyards located downwind of blackberry (*Rubus* spp.) or French prune trees (*Prunus domestica* L.) had higher levels of early-season *E. elegantula* egg parasitism. Blackberry supports *Dikrella californica* (Lawson), the blackberry leafhopper, a year-round host of *A. epos* (Williams, 1984), and French prune supports the prune leafhopper, *Edwardsiana prunicola* (Edwards), which overwinters in the egg stage and serves as an overwintering host of *A. epos* (Mulla, 1957). Although the results of their studies were consistent with the refuge hypothesis, their conclusions were based on unreplicated comparisons and therefore were preliminary in nature.

We began a field study in 1991 using the prune tree/vineyard system to test the effect of habitat diversification on colonization of *A. epos* in grape vineyards and their subsequent impact on *E. elegantula* numbers. This study examines three responses of *A. epos* to the presence of an overwintering habitat near vineyards: (1) the early-season abundance of adult *A. epos*, (2) the rate of *E. elegantula* egg parasitism and, (3) the density of *E. elegantula*. We reported previously that a greater abundance of *A. epos* is found during the early season in vineyards associated with prune trees (Murphy et al., 1996). Here, we evaluate the impact of prune tree overwintering habitats on parasitism of *E. elegantula* eggs.

In evaluating the effect of prune trees on *E. elegantula* egg parasitism we had three objectives: (1) to determine the effect of prune trees near vineyards on parasitism rates, (2) to determine the relative importance of *A. epos* as a mortality factor for *E. elegantula* eggs and (3) to determine if variation in early-season adult *A. epos* abundance is linked to early-season *E. elegantula* egg parasitism.

Material and methods

Experimental design. Study sites were located throughout the major wine-grape viticultural regions of central and northern California, USA. The effect of overwintering habitats on host egg mortality was examined by comparing egg parasitism rates between paired grape vineyard sites, one with adjacent prune trees and the other lacking prune trees. Eighteen paired vineyard plots were monitored in 1991, and 26 in 1992 (Figure 1). Fourteen of the paired vineyards used during 1991 were also used in 1992. Paired vineyard sites were matched for grape cultivar, trellising and management practices. Control (non-prune tree) vineyards were established 0.4 to 4.0 km away from and either upwind or parallel to vineyards with prune trees to minimize movement of *E. elegantula* or *A. epos* between paired vineyards. The vineyard sites were located in two viticultural regions defined by the cumulative degree days occurring between April and October (Winkler et al., 1974). Comparisons were made between cooler growing regions ($<$3000 deg days) and warmer regions ($>$3000 degree days).

During the course of the study, pesticides were periodically applied against *E. elegantula* nymph and adult populations at some sites. During 1991, one vineyard pair received a pesticide application after the first sample period. During 1992, four sites were sprayed after the first sample period, four additional sites were sprayed after the completion of the second sample period. With one exception, all pesticides were applied to both plots of a pair at approximately the same time. No significant impact on *E. elegantula* egg density or egg parasitism was detected in the plot receiving the additional pesticide application. Because treatment and control vineyards within pairs received simultaneous pesticide applications, we believe our data to be a valid measure of relative parasitism rates.

No pesticides were applied directly to prune trees during the study.

Two of the prune tree sites used in the study were planted specifically for *E. elegantula* control; the remainder were either commercial prune orchards or remnant orchards growing adjacent to vineyards. Given the nature of the prune refuge habitat being tested, we were unable to ensure true randomization of treatments among vineyard plots (see Murphy et al., 1996, for a complete discussion). True randomization would have required random assignment of prune trees to vineyards, and a 3 to 5 year delay until the prune trees could become established and mature. Nevertheless, because seven of the nine sites used during 1991, and 11 of 13 sites used during 1992 were remnant or commercial prune orchards and thus established for reasons other than leafhopper control, we feel that the non-random treatment selection is unlikely to introduce a systematic bias into the analysis.

The taxonomy of mymarid wasps of the genus *Anagrus* reared from leafhopper eggs in the western United States is currently under review. Revisions in the taxonomic status of *Anagrus* spp., including *A. epos* do not impact the interpretation of the biological relationships presented in this study.

Grape leaf sampling. Grape leaves were collected to estimate *E. elegantula* egg parasitism in vineyards downwind of prune trees (henceforth referred to as 'prune tree vineyards') by sampling 30 leaves along each of two transects, the first at 50 m and the second at 125 m downwind from the prune trees. Four prune tree vineyard plots during 1991 and three during 1992 were less than 125 m long. Therefore, only five and ten 125-m transects were monitored during 1991 and 1992, respectively. In control vineyards lacking prune trees, 30 leaves were sampled across vineyard blocks without using transects. For each transect or control vineyard plot three leaves were sampled from each of ten randomly selected grape vines. Only fully expanded, mature grape leaves were collected. During 1991, one grape leaf from each of three vine shoots on a single vine was removed without regard to the position of the leaf on the shoot. A similar procedure was used for 1992 except that vine shoots were divided into three positions, a basal position, mid-shoot position and a top position. One leaf was sampled from each position. Only grape vines that were at least 10 vines from the edge of the vineyard block were sampled to avoid an influence of edge effects on leafhopper density.

Vineyards were sampled for egg parasitism three times during both 1991 and 1992. Each sample period coincided approximately with one of the three *E. elegantula* generations. During 1991 the first generation was sampled between 2 and 16 July, the second between 14 and 31 August and the third between 10 and 21 October. During 1992 leaves were sampled between 11 and 22 June, 17 and 28 August, and 1 and 9 October for the first, second and third generations, respectively.

Measures of egg parasitism. Egg parasitism in vineyards was determined by examining grape leaves under a dissection microscope for the presence of parasitized or healthy *E. elegantula* eggs. Leaves were scored for egg parasitism using two methods. The first method determined egg parasitism for unhatched eggs only. Unhatched eggs were visually examined for the presence of a developing *A. epos* or *E. elegantula* following the method of Settle & Wilson (1990). The second method examined hatched leafhopper eggs, which are recognizable as distinctive scars on the surface of grape leaves. The egg scars were examined and scored as one of three types: (1) egg scars with a round exit hole, indicating *A. epos* emergence; (2) egg scars with a small tear in the egg and leaf epidermis, indicating healthy *E. elegantula* nymphal emergence and (3) egg scars with no signs of emergence. Egg scars without signs of emergence were dissected for evidence of parasitism or mortality from factors other than parasitism.

The examination of unhatched eggs provided a point estimate in time of *E. elegantula* egg parasitism by *A. epos*. Development of *A. epos* from egg to adult requires ≈244 deg-days above a developmental threshold of 7.2 °C (Williams, 1984), which translates into a developmental time of approximately 12 days during late spring and summer (Murphy, unpubl. data). *E. elegantula* requires ≈ 673 deg-days above 10.3 °C and approximately 21 days to complete development during the egg stage (Williams, 1984). Thus, the point estimates are an indicator of relative parasitism rates within 12 days of the sample date. Hatched egg scars remain visible on leaves for the entire season (Murphy, unpubl. data). Thus, hatched egg scars provide an estimate of cumulative egg parasitism over the life of the grape leaf up to the time of collection.

Monitoring A. epos *abundance.* Prune tree and control vineyard plots were monitored early during the 1992 season to estimate density of immigrating *A.*

epos. Two yellow sticky traps (75 by 125 mm yellow plastic cards (Hilcor Plastics Inc., Los Angeles, California) coated with Tangle-Trap adhesive (Tanglefoot Co., Grand Rapids, MI, USA)) were attached to six, 2.4 m long wooden poles (12 traps total). Poles were positioned along a transect at 10 m intervals in the third vine row from the upwind edge of each vineyard. Traps were oriented perpendicular to the wind direction and positioned above the vines to minimize any influence of vine canopy on trap capture. Traps were deployed in vineyards beginning 1 April (7 paired sites), 15 April (3 additional pairs), and 1 May (2 additional pairs), and were replaced twice monthly through 15 June 1992. All traps were examined in the laboratory under a dissection microscope and the number of adult *A. epos* recorded. In a previous study we demonstrated that captures of *A. epos* in vineyards between 1 April and 15 May reflect the number of immigrants moving into vineyard plots from outside sources (Murphy et al., 1996).

Statistical procedures. The mean percentage of *E. elegantula* egg parasitism was analyzed within a split-plot ANOVA model. Growing region was the main factor and the sub-factor was the presence of prune trees sampled 50 or 125 m downwind into vineyards or the absence of prune trees. Each vineyard pair was treated as a statistical block to control variability in *A. epos* and *E. elegantula* numbers across vineyard pairs. Regional differences were tested by nesting blocks within viticultural growing region. Preliminary analysis revealed that parasitism rates were influenced by the host egg density (mean number of eggs per leaf) in vineyards (Figure 2). As a result, we used mean *E. elegantula* egg density as a covariate within our analyses to control for effects of egg density on parasitism rates. Because the number of replicates varied across sample dates, separate univariate analyses were conducted for each sampling period. One-tailed tests were used to test the hypothesis that prune tree vineyards had higher parasitism rates. A Bonferroni correction for multiple comparisons was used to maintain the total α error rate at 0.05 (Sokal & Rohlf, 1981). Mean comparisons were made using single degree of freedom tests (contrast tests) among treatment levels (control vineyards versus prune tree vineyards at 50 and 125 m downwind) (Sokal & Rohlf, 1981). The analyses were conducted to test the null hypothesis that *E. elegantula* egg parasitism by *A. epos* is independent of the presence of prune trees.

To test if cumulative parasitism rates were related to *A. epos* trap capture within vineyards, multiple regression analyses were performed using *E. elegantula* egg density and *A. epos* trap capture as the independent variables and egg parasitism as the dependent variable. We tested the null hypothesis that first generation parasitism rates in vineyards were independent of the density of *A. epos* adults moving into vineyards early in the season.

For all statistical analyses, *A. epos* trap capture and *E. elegantula* egg density were subjected to a $\log(x + 1)$ transformation, and percentage egg parasitism was subjected to an arcsine square root transformation to normalize the distribution of means. The statistical analyses were performed using the JMP statistical program (SAS Institute, 1989).

Results

Point estimates of parasitism. The mean point estimates revealed high levels of parasitism across leafhopper generations for both 1991 and 1992 (Figure 3). Prune tree vineyards were associated with greater egg parasitism rates at the 50-m transect for the first and second sample periods and for the second sample period at the 125-m transect during 1991 (Table 1). Similarly, the 1992 data revealed greater parasitism at the 50- and 125-m transect during the first sample period and the 50-m transect during the third sample period (Table 1). (No data for the 125-m transect were available for the third sample period during 1992.) No regional differences in parasitism were detected during 1991 or 1992. Results of both years demonstrated that vineyards with prune trees had higher mean parasitism rates during the first sample period. However, differences between treatments narrowed or disappeared during the second sample period, and all treatments approached 100 percent parasitism by the third sample period (Figures 3C and 3F).

Cumulative parasitism. Examinations of hatched *E. elegantula* egg scars revealed that parasitism was the single largest egg mortality factor across all vineyards tested during both years and across all sample dates (Figure 4). Furthermore, the proportion of eggs parasitized tended to increase as the season progressed while the proportion killed from other factors remained essentially constant.

Table 1. Analyses of covariance of point estimates of *E. elegantula* parasitism (log_{10} transformed) for vineyards with and without prune trees for 1991 and 1992

Generation	Source	1991				1992			
		df	MS	*F*	P[a]	df	MS	*F*	P[a]
First	[b]Control-50 m	1	1.4590	8.86	0.0033 *	1	1.8930	12.17	0.0006 *
	Control-125 m	1	1.0960	6.64	0.0110 *	1	1.6069	10.33	0.0015 *
	Blocks(region)	7	2.0560	12.47	0.0000 *	11	0.4696	3.02	0.0009 *
	Region	1	0.2455	1.49	0.2237	1	0.3475	2.23	0.1363
	Egg density	1	2.8400	17.22	0.0000 *	1	1.1127	7.15	0.0080 *
	Region × Parasitism	2	0.6785	4.12	0.0177 *	2	0.0497	0.32	0.7266
Second	Control-50 m	1	1.3230	10.54	0.0014 *	1	0.4679	2.99	0.4679
	Control-125 m	1	0.9764	7.74	0.0060 *	1	0.3203	2.05	0.3203
	Blocks (region)	6	1.7670	14.00	0.0000 *	11	0.7404	4.74	0.0000 *
	Region	1	2.6020	20.62	0.0000 *	1	6.1670	39.54	0.0000 *
	Egg density	1	1.2530	9.93	0.0019 *	1	0.0577	0.37	0.5441
	Region × Parasitism	2	0.1079	0.86	0.4270	2	0.0072	0.05	0.9553
Third	Control-50 m	1	0.3308	8.33	0.0045 *	1	0.0073	1.860	0.1754
	Control-125 meter	1	0.1079	2.72	0.1079	–	–	–	–
	Blocks (region)	6	0.2927	7.37	0.0000 *	11	0.0015	0.39	0.9574
	Region	1	0.1762	4.44	0.0370	1	0.0006	0.16	0.6890
	Egg density	1	0.0274	0.69	0.4074	1	0.0142	3.63	0.0588
	Region × Parasitism	2	0.0895	2.25	0.1088	1	0.0033	0.84	0.3612

[a]One-tailed tests for hypothesis testing. * = P < critical value after Bonferroni correction (P < 0.033).
[b]Orthogonal contrasts between control vineyards and prune tree vineyard transects.

We tested for season-long differences in cumulative parasitism rates among vineyards using data collected for the third sample period. Season-long cumulative mean parasitism was greater in prune tree vineyards at both the 50- and 125-m transects during 1991 and at the 50-m transect for 1992 (Table 2; Figure 5). No data for the 125-m transect were available for 1992. Examination of the earlier sample periods for both years also revealed that differences in cumulative parasitism tended to be greatest in prune tree vineyards during the first sample period and narrowed as the season progressed. Differences in parasitism rates between growing regions were detected only during the second sample period for both 1991 and 1992. Egg density was a factor only for the first sample period during 1991.

Comparison of both the point estimate and cumulative parasitism rates between prune tree and control vineyards revealed consistently higher parasitism associated with prune trees during both years of the study. Thus, the presence of prune trees was determined to be associated with greater *E. elegantula* egg parasitism in vineyards.

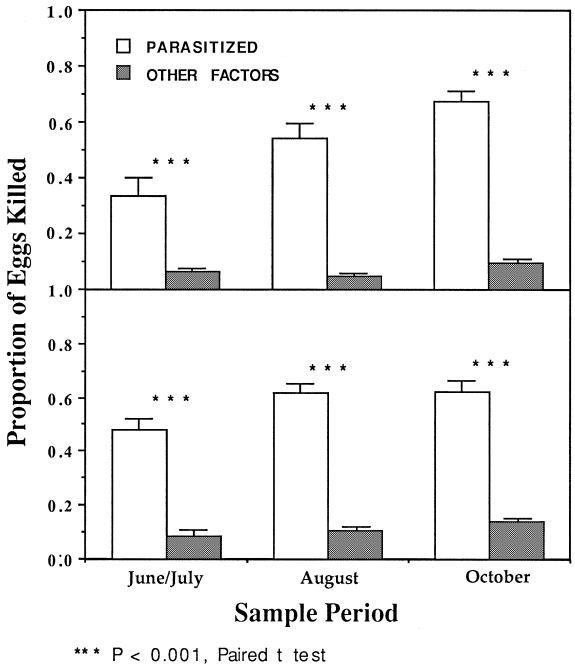

Figure 4. Proportion of *E. elegantula* eggs parasitized and proportion killed by other factors for treatment and control plots combined for 1991 and 1992.

Table 2. Analyses of covariance of cumulative *E. elegantula* parasitism ($\log_{10}$ transformed) for vineyards with and without prune trees for 1991 and 1992

Generation	Source	1991				1992			
		df	MS	*F*	P[a]	df	MS	*F*	P[a]
First	[b]Control-50 m	1	2.7433	24.32	0.0000*	1	4.3780	35.61	0.0000*
	Control-125 m	1	0.2143	2.42	0.1206	1	2.0860	16.97	0.0000*
	Blocks (region)	7	0.8671	7.69	0.0000*	11	1.7440	14.18	0.0000*
	Region	1	0.9447	8.37	0.0042*	1	0.0474	0.39	0.5353
	Egg density	1	4.0565	35.97	0.0000*	1	1.9632	15.96	0.0001*
	Region × Parasitism	2	0.0594	0.53	0.5912	2	0.0085	0.69	0.5007
Second	Control-50 m	1	0.5510	6.12	0.0141*	1	2.2767	23.03	0.0000*
	Control-125 m	1	0.4794	5.32	0.0220*	1	0.4643	4.69	0.0309*
	Blocks (region)	6	1.2374	13.74	0.0000*	11	1.4470	14.64	0.0000*
	Region	1	0.7521	8.36	0.0042*	1	4.8597	49.16	0.0000*
	Egg density	1	1.6222	18.02	0.0000*	1	0.0057	0.06	0.8098
	Region × Parasitism	2	0.2757	3.06	0.0488	2	0.2360	2.38	0.0935
Third	Control-50 m	1	1.3160	21.60	0.0000*	1	1.9539	30.59	0.0000*
	Control-125 m	1	0.3458	5.67	0.0181*	–	–	–	–
	Blocks (region)	6	0.6407	10.51	0.0000*	11	0.6515	10.19	0.0000*
	Region	1	0.4860	7.98	0.0052*	1	3.1400	49.29	0.0000 *
	Egg density	1	0.4879	8.00	0.0051*	1	0.1535	2.40	0.1224
	Region × Parasitism	2	0.4384	7.20	0.0009*	1	0.0012	0.02	0.8907

[a]One-tailed tests for hypothesis testing. * = P < critical value after Bonferroni correction (P < 0.033).
[b]Orthogonal contrasts between control vineyards and prune tree vineyard transects.

Early-season A. epos *abundance.* Multiple regression analyses comparing early-season *A. epos* trap captures in vineyard plots with cumulative egg parasitism rates through the first sample period resulted in significant regressions during the first and third trap sample periods (Table 3). The significant relationships found for two of the three trapping periods indicate that early-season abundance of adult *A. epos* in vineyards was correlated with cumulative parasitism rates from the beginning of *E. elegantula* oviposition in early spring through the first leafhopper generation. Egg density was a non-significant factor during each of the trap sample periods.

Discussion

Our study has demonstrated that prune trees were associated with increased parasitism of *E. elegantula* eggs during the early season of both years as measured by the point estimates of parasitism. Thereafter the incidence of egg parasitism in prune tree vineyards and control vineyards approached unity (Figure 3). The point estimates of parasitism measure the impact of parasites over a relatively short period of time (approximately 14 days). Therefore, our results indicated that prune trees enhance *E. elegantula* egg parasitism primarily during the early season.

The cumulative parasitism data collected during the third sample period showed that prune tree vineyards received significant increases in season-long cumulative parasitism rates relative to control vineyards to a distance of at least 125 meters downwind of trees. Thus, the enhanced parasitism seen in the point estimate data during the first sample period translated into a net season-long increase in egg parasitism across generations in the prune tree vineyards (Figure 5). These tests validated the hypothesis of Doutt & Nakata (1965, 1973) and Kido et al. (1984) that vineyards located near overwintering habitats supporting *A. epos* enhance biological control of *E. elegantula.*

Previously we showed that vineyards with adjacent prune trees had more *A. epos* captures than vineyards lacking prune trees (Murphy et al., 1996). The magnitude of this increase was determined in part by the density of *A. epos* overwintering in *E. prunicola* host eggs in nearby prune trees. The increase in *A. epos* immigration occurred primarily during April, more than a month before the first generation *E. elegantula* completed oviposition. In the present study, our analyses revealed that the higher numbers of *A. epos* captured

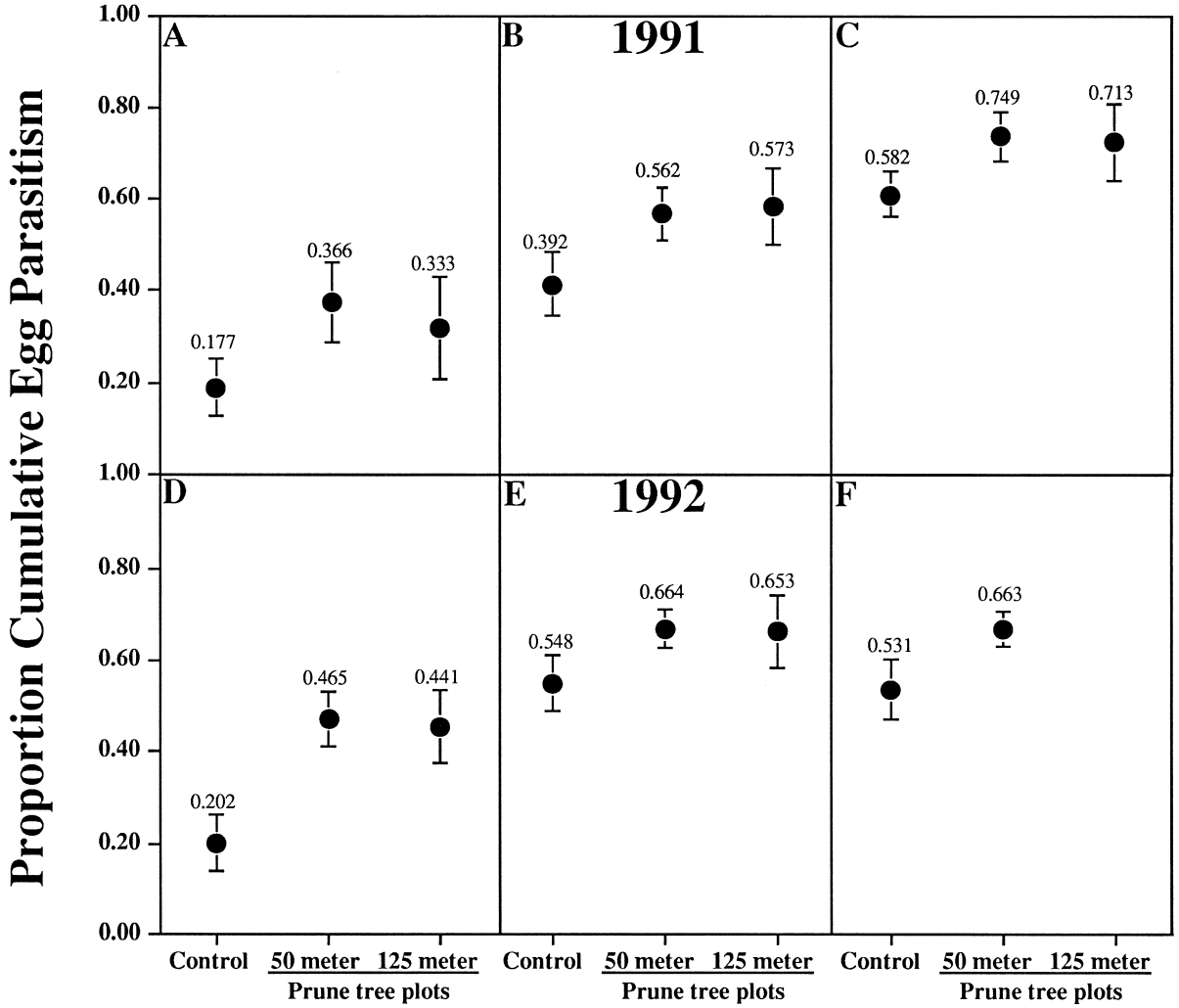

Figure 5. Mean ± S.E. cumulative egg parasitism during 1991 for (A) the first leafhopper generation, (B) the second leafhopper generation and (C) the third leafhopper generation and 1992 for (D) the first leafhopper generation, (E) the second leafhopper generation and (F) the third leafhopper generation.

on vineyard interception traps early in the spring in prune tree vineyards largely explained cumulative parasitism rates through the first leafhopper generation. The strongest relationship and therefore the most important period for enhancing the colonization of *A. epos* was identified to occur in mid April. This analysis demonstrated the ecological linkage between *A. epos* adult migration into vineyards and the level of parasitism generated in vineyards. Both the number of colonizing parasitoids and their density-dependent response to hosts appear to be important determinants of the impact of *A. epos* on leafhopper populations in vineyards.

Together these results demonstrate that diversified agroecosystems using overwintering habitats for natural enemies can enhance colonization and parasitism rates in agroecosystems. Our data provide evidence that a diverse system can increase specialist natural enemy colonization relative to simple systems, and that in disturbed agricultural systems the difficulty many natural enemies have in colonizing crops may be reduced by locating sources of colonists closer to crop fields.

Altieri et al. (1978) and Letourneau (1990) examined the response of *Anagrus* sp. attacking *Empoasca* spp. in monocultures versus polycultures and found no differences in parasitism rates among treatments.

Table 3. Relationship between cumulative percentage *E. elegantula* egg parasitism during the first generation (the dependent variable) and *E. elegantula* egg density in the first generation ($\log_{10}$ transformed) and *A. epos* trap catch early season ($\log_{10}$ transformed) in vineyards (independent variables)

Trap catch sampling period	Source of variation	df	Slope (± S.E.)	*F*	R^{2a}	P
4/15–4/18	Whole model test	2, 14	–	11.38	0.67	0.002*
	A. epos abundance	1, 14	2.77 (± 0.682)	16.48	0.66	0.002*
	E. elegantula egg density	1, 14	0.12 (± 0.155)	0.57	0.19	0.465
4/24–5/1	Whole model test	2, 20	–	4.53	0.35	0.027
	A. epos abundance	1, 20	0.36 (± 0.324)	1.23	0.10	0.283
	E. elegantula egg density	1, 20	0.49 (± 0.193)	6.56	0.30	0.020
5/8–5/15	Whole model test	2, 26	–	8.81	0.43	0.001*
	A. epos abundance	1, 26	0.66 (± 0.236)	7.94	0.34	0.010*
	E. elegantula egg density	1, 26	0.32 (± 0.165)	3.77	0.24	0.065

* = P < critical value after Bonferroni correction (P < 0.017).
[a] R^2 for individual factors are partial correlation coefficients (r^2).

Andow & Risch (1987) and Letourneau (1990) reported that specialist natural enemy numbers were influenced more by host density than by plant diversity, concluding that diversity per se may not be important in determining the abundance and effectiveness of specialist predators. Our results have shown that indeed *A. epos* was influenced by host density. However, our study also showed that a diversified system which incorporates habitat that increases the range of prey for *A. epos* (prune trees supporting overwintering *E. prunicola* eggs) also increases the pool of potential immigrants and thereby increases *A. epos* colonization of vineyards.

Our evaluation of the impact of habitat diversification on the *A. epos*/*E. elegantula* system has satisfied two of the three hypotheses postulated to underlie the response of natural enemies to diversified systems. In a final paper we will examine whether increased parasitism of *E. elegantula* eggs results in enhanced suppression of *E. elegantula* populations.

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