Chapter 8
Habitat Diversity at the Field and Landscape Level: Conservation Biological Control Research in California Viticulture

Albie Miles, Houston Wilson, Miguel Altieri, and Clara Nicholls

8.1 Introduction: The Need for Ecologically Based Viticulture in California

The intensification of viticulture in California has led to the creation of grape monocultures characterized by an absence of non-crop plant diversity in and around vineyards. The continued expansion of vineyards into California native plant communities has also led to an aggregate reduction of non-crop habitats at the landscape scale (Heaton and Merenlender 2000). Such increased concentration of plant host resources and the reduction of non-crop habitats supporting natural enemies have been shown to increase pest densities, with associated crop losses and reduced overall crop productivity (Root 1973; Russell 1989; Corbett and Rosenheim 1996a; Altieri and Nicholls 2004). To manage recurring pest problems, California grape growers rely principally on the use of synthetic pesticides, including organophosphate and carbamate insecticides, known to pose a range of environmental quality and human health risks (Bentley 2009; CDPR 2009; UC IPM 2010b; Eskenazi et al. 2010).

With increasing concern over the environmental impacts of viticulture, rising production costs, and increased regulation of pesticides, the demand for research driven by ecologically-based pest management (EBPM) strategies has steadily grown (Broome and Warner 2008; Meadows 2008; Ross and Golino 2008; Brodt et al. 2009). In addition to the use of insecticides accepted under the United States Department of Agriculture, National Organic Program, California grape growers have sought to use EBPM strategies, including on-farm diversification to promote

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A. Miles (✉) • H. Wilson • M. Altieri • C. Nicholls
Department of Environmental Science, Policy and Management, University of California,
130 Mulford Hall #3114, Berkeley, CA 94720-3114, USA
e-mail: albiemiles@berkeley.edu; houston@berkeley.edu; agroeco3@berkeley.edu;
nicholls@berkeley.edu

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biological control (Altieri et al. 2005; Ross and Golino 2008). Despite growing interest and adoption, few field and farm-scale EBPM strategies in use today have been scientifically evaluated for their ability to consistently regulate pest populations below economic thresholds. With the exception of the general principles (Altieri et al. 2011), California grape growers lack specific guidelines on how to successfully diversify their vineyards or conserve non-crop habitats in the surrounding landscapes to ensure biological control of important arthropod pests.

8.2 Key Hypotheses Informing Research in Vineyard Diversification in California: Natural Enemies and Resource Concentration

Two main hypotheses have been used for evaluating the effect of on-farm vineyard diversification strategies on biological control in California: (1) the Natural Enemies Hypothesis (NEH) (Andow 1991a), and (2) the Resource Concentration Hypothesis (RCH) (Root 1973). The NEH predicts a positive correlation between plant species richness, natural enemy abundance and the regulation of herbivore pests through increased predation and parasitism. The RCH predicts that herbivore pests are more likely to find and remain on agricultural host plants grown in pure stands (monocultures) than in more biologically diversified (polycultures) cropping systems. The RCH predicts that most specialized herbivore species are likely to attain the highest relative densities in monocultures when compared to diversified farming systems (Root 1973). In more complex agroecosystems, the dilution of plant host resources, interspecific competition, and more favorable environmental conditions for natural enemies are understood to be complementary factors that serve to regulate herbivore pest densities (Russell 1989; Altieri and Nicholls 2003; Andow 1991b; Costello and Daane 2003).

8.3 Vineyard Diversification Studies in California: Field-Level Research

Multiple on-farm diversification studies have measured the impact of overwintering and summer cover crops on biological control of *Erythroneura* leafhoppers (Table 8.1).

In a 2-year study, Flaherty (1969) measured the impact of the weedy Johnson grass (*Sorghum halepense* (L.) Persoon) on population densities of the Willamette mite (*Eotetranychus willamettei* Ewing) in a Tulare County ‘Thompson Seedless’ vineyard. Researchers measured population densities of predators and pests in both weed infested and grass-free vines, concluding that the Johnson grass supported populations of alternate prey (the twospotted spider mite) which moved between the weedy vegetation and the vine canopy. Provided with an alternate food source, the

Table 8.1 Summary of research on effects of vineyard diversification on biological control in California vineyards: 1998–2005

Description of study	Reference	Main effect	Economically important level of biocontrol?	Reported mechanism influencing biocontrol
Effect of weedy vegetation (Johnson grass) on population densities of Willamette mites (*Eotetranychus willamettei*)	Flaherty (1969)	98% reduction in Willamette mites	Yes	Natural enemies: weedy grasses support populations of alternate prey used by predatory mites (*Metaseiulus occidentalis*). Predatory mites were maintained at high density and well dispersed in system thus able to respond rapidly to increased abundance of pest mites, controlling pest at lower densities
Effect of cover crops (vetch and oats) on population densities of *Erythroneura variabilis*	Roltsch et al. (1998)	40–50% reduction in 2nd and 3rd generation leafhopper density (year 1), 2nd generation only (year 2)	No	Natural enemies: spider densities negatively correlated with leafhopper densities in presence of cover crop
Effect of cover cropping (vetch and barley) on *Erythroneura* leafhoppers	Costello and Daane (1998)	15–20% reduction in nymph leafhopper density	No	Resource concentration: reduced vine vigor influencing plant host quality. No significant difference in natural enemy abundance
Effect of cover cropping (vetch and barley) on *Erythroneura* leafhoppers.	Costello and Daane (2003)	15–20% reduction in nymph leafhopper density	No	Resource concentration and natural enemies: reduced vine vigor influencing plant host quality. Predation by spiders suggested as contributing factor to enhanced biocontrol
Effect of cover cropping (vetches and oats) on *Erythroneura* (variegated) leafhoppers	Hanna et al. (2003)	35% higher density of 1st generation of leafhopper nymphs in exclusion sub-plots	No	Natural enemies: 35% higher density of 1st generation leafhopper nymphs were found in exclusion sub-plots, suggesting role of spiders in regulating leafhoppers. Higher density of spiders in cover crop plots, but no significant effect on biocontrol. Suggested as resulting from intraguild predation and low seasonal density of leafhoppers
Effect of floral resource provisioning (*Helianthus annuus* and *Fagopyrum esculentum*) on *Erythroneura* leafhoppers and thrips	Nicholls et al. (2000) and Altieri et al. (2005)	15% reduction in nymph leafhopper densities (for periods). 32% reduction in thrips	No (leafhoppers) Yes (thrips)	Natural enemies: spiders correlated with low leafhopper densities, and *Orius* spp. correlated with reduced thrips densities in treatment plots

predatory mites (*Metaseiulus occidentalis* (Nesbitt)) were maintained at higher densities and were better dispersed throughout the vineyard area influenced by the weedy vegetation when compared to plots with no Johnson grass. Predatory mites were thus able to respond more rapidly to an increased abundance of the Willamette mite pest and control them at lower densities resulting in significantly lower Willamette mite densities in the diversified (with Johnson grass) versus the simple (no Johnson grass) plots. To further substantiate that enhanced predation by predatory mites was the cause of lower pest mite densities, researchers evaluated the impact of insecticide applications (thus reduced predatory mite populations) on population densities of Willamette mites. Plots with and without Johnson grass that were treated with insecticide showed both lower densities of predatory mites and consistent and significantly higher populations densities of Willamette mite, indicating ecological release of herbivore mites from predation (Flaherty 1969).

Roltsch et al. (1998) conducted several experiments to determine the effect of resident weedy vegetation and cover crops on spider densities and biological control of the variegated leafhopper (*Erythroneura variabilis* Beamer) in a San Joaquin Valley 'Thompson Seedless' vineyard. Building upon prior studies suggesting that vineyard spiders could be influenced by the ground cover habitats, researchers sought to evaluate the impact of the planted cover crops, common vetch (*Vicia sativa* L.), purple vetch (*Vicia benghalensis* L.) and oat (*Avena sativa* L.) on leafhopper densities and spider abundance and diversity. Agelenid (*Holonena nedra* Chamberlin & Ivie), and theridiid (*Theridion* spp.) spiders were found to be more abundant in the vine canopy in ground cover plots. A corresponding inverse relationship was found for leafhopper densities, with the highest densities found in control plots (no cover). Further corroboration of spiders playing a key role in regulating leafhopper densities was found with a strong positive correlation between high late-season leafhopper densities and low spider abundance in insecticide (dimethoate) treated vineyards, indicating an ecological release of leafhoppers from predation by spiders (Roltsch et al. 1998). No further mechanistic studies were conducted to empirically validate enhanced predation by spiders in the presence of ground covers.

A field diversification study examining the impact of overwintering cover crop mixtures and resident weedy vegetation on the variegated leafhopper (*E. variabilis)* was reported by Hanna et al. (2003). Prior research had established that spiders are the most abundant generalist natural enemy in vineyards and other agroecosystems. Furthermore, they are the only natural enemy, other than *Anagrus* spp. (Mymaridae), present in sufficient densities to regulate *Erythroneura* leafhoppers (Costello and Daane 1999, 2003). Researchers thus set out to evaluate the impact of cover cropping on spider and leafhopper abundance using a fall planted mixture of purple vetch (*V. benghalensis*), common vetch (*V. sativa*) and 'Cayuse' oat (*A. sativa*). Using the cover crop mixture and bare-ground as main plots and vine exclusion as sub-plots (to restrict spiders), researchers evaluated the relative impact of each treatment on spider and *E. variabilis* densities. Parasitism rates by *Anagrus* spp. were found to be similar in all plots throughout the year and other generalist natural enemies were found to be rare. Spider exclusion resulted in an average 35% increase in the density of first generation *E. variabilis* nymphs only. Yet, despite a 1.6-fold increase in spider densities on vines with cover crops (no exclusion), the cover crop did not significantly affect the density of *E. variabilis* on grape vines. Researchers suggest that this was due to insufficient spider enhancement from the cover crop and low overall leafhopper abundance during the study period. Interestingly, the cover crop mix had no significant impact on vine vigor/nutrient status, in contrast to the findings of Costello and Daane (1999, 2003). While this study provided support for the hypothesis that in-field diversification can enhance spider abundance, it does not always lead to lower pest densities, perhaps because of the complexity and variability of trophic interactions (e.g. inter and intraguild predation) in agroecosystems (Hanna et al. 2003).

Nicholls et al. (2000) conducted a 2-year comparative study of the effect of floral resource provisioning on biological control in an organic wine grape vineyard in Hopland, California. Comparing two 1-ha vineyard blocks (with and without flowers), researchers measured the impact of the summer cover crops, annual sunflower (*Helianthus annuus* L.), and annual buckwheat (*Fagopyrum esculentum* Moench), on population densities of western grape leafhopper (*Erythroneura elegantula* Osborn), western flower thrips (*Frankliniella occidentalis* (Pergande)), and key natural enemies (parasitoids and generalist predators). Researchers reported an estimated 15% lower density from mid to late season (July–August) leafhopper nymphs in cover cropped vineyards when compared to monocultures and a significantly lower density of thrips (32%) for both years of the study. The study also found a greater abundance and richness of generalist natural enemies (*Orius* spp., Coccinellid beetles, and thomisid spiders) in the treated vs. control plot. Although researchers found a higher density of *Anagrus* spp.[1] wasps in the control plots, no significant difference in rates of parasitism were found between treatment and control plots. Lower density of leafhopper nymphs in the treatment plot (with cover crops) was attributed to impacts of generalist predators, namely spiders and *Orius* spp. anthocorids. Lower density of thrips in treatment plots was attributed to the impact of the generalist *Orius* spp. predators. The researchers also studied the impact of mid-season mowing of the flowering cover crops on pest and beneficial insects, reporting a significant but temporary increase in density (18%) of both generalist predators and *Anagrus* parasitoids, and a subsequent lower (27%) leafhopper nymph density in the vine canopy after mowing (Nicholls et al. 2000; Altieri et al. 2005).

Daane and Costello (1998) assessed the influence of purple vetch (*V. benghalensis*) and barley (*Hordeum vulgare* L.) cover crops and resident weedy vegetation on vine vigor, natural enemy and leafhopper abundance in four San Joaquin Valley vineyards. They found that season-long cover cropping reduced late season leafhopper

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[1] Early research referred to all species of *Anagrus* wasps, a key egg parasitoid of *Erythroneura* leafhoppers, found in vineyard as '*Anagrus epos* Girault.' Recent taxonomic revisions of *Anagrus epos* by Triapitsyn (1998) have revealed a complex of species, including the two most common grape leafhopper parasitoids in California: *A. erythroneurae* and *A. daanei.* As such, *Anagrus* spp. will hereafter be referred to as simply '*Anagrus*.'

nymph densities by 15–20%. Though a treatment effect was clearly determined, the level of leafhopper reduction was not considered economically important and the mechanisms leading to pest reduction were not clearly established. No significant differences in the density of leafhopper predators or *Anagrus* spp. parasitoids were found on vines in cover cropped versus control plots. Additionally, no consistent differences in parasitism rates by *Anagrus* spp. wasps were observed between treatments and control plots, leading researchers to conclude that natural enemy fitness, behavior and density were not significantly enhanced by cover cropping and therefore did not play an important role in regulating leafhopper densities. Assessments of the impact of cover cropping on vine vigor (indicated by petiole nitrogen and vine shoot biomass) however, showed significantly lower vigor and the lowest late season leafhopper density on vines with season long cover crops and resident weedy grasses. Additionally, researchers found the lowest total number of leafhopper eggs on grape vines in cover cropped plots (Daane and Costello 1998). In a follow-up study, Costello and Daane (2003) re-evaluated the influence of the same cover crops (purple vetch and barley) on leafhopper abundance to determine how their presence had reduced leafhopper density, and to isolate the relative influence of cover crops on the nutrient status of vines (i.e. plant host quality) from the impact of cover crops on natural enemy fitness on biological control. Three treatments were established and compared in the 2-year study: ground cover (vetch and barley), no-cover (tilled control) and ground cover with exclusion (i.e. with barriers limiting arthropods and spiders moving into the vine canopy). They showed mid- and late season leafhopper densities were significantly reduced in plots with the ground cover compared with the no-cover. Neither leafhopper egg parasitism by *Anagrus* spp. nor spider density (on vines or ground) could explain differences in leafhopper density. Vine vigor, however, was determined to be significantly lower in cover crop than in the no-cover plots, and late season leafhopper density was highest in ground cover/exclusion plots. Grapevine vigor had the strongest correlation with leafhopper density, with low vigor resulting from the apparent competition between the cover crops, resident weedy vegetation and grapevines and not from the impact of natural enemies. Higher late season leafhopper density in the cover/exclusion plots was, however, attributed to the reduced predation by spiders. The study suggests that cover crops may have a significant impact on soil quality and vine growth, complementing any function they serve in enhancing the natural enemies of vineyard pests (Costello and Daane 2003; Daane et al. 2005).

8.4 Landscape Ecology and Conservation Biological Control in California Vineyards

The intensification of production has not only produced simplified individual cropping systems (i.e., monocultures), but in addition the regional adoption of such practices has led to the aggregate simplification of entire agricultural landscapes (Tscharntke et al. 2005). The process of agroecosystem simplification is particularly acute in wine grape regions as the geographic branding of wine (e.g. premiums paid for wine produced in Napa County) further encourages regional land use conversion from natural habitat to high-value wine grape production. This loss of both agrobiodiversity and natural habitats that surround agroecosystems can lead to the loss of multiple ecosystem services, including biological control (Kremen et al. 2002; Altieri and Nicholls 2004).

The term landscape 'heterogeneity' (alternately landscape 'complexity' or 'diversity') has been used in the ecology and conservation literature to describe the area, arrangement and/or composition of natural habitats surrounding agroecosystems (Bianchi et al. 2006). Studies of landscape effects on ecosystem services typically quantify ecological features within a 1–3 km radius around a crop field, although some studies have measured landscape features at scales ranging from as little as 0.4 km to at most 25 km (Thies and Tscharntke 1999; Östman et al. 2001; Steffan-Dewenter et al. 2002). Landscapes are generally quantified in terms of the relative proportion of various habitat types within a given area (e.g., 32% oak woodland within a 1.5 km radius of a crop field), although some studies simply utilize categorical terms to describe a landscape (e.g., 'complex' and 'simple' landscapes) (Thies and Tscharntke 1999).

While researchers previously hypothesized that landscape heterogeneity could have a significant impact on biological control (van Emden 1965), it is only more recently that they have begun to address this relationship empirically. Bianchi et al. (2006) conducted a review of the ecological literature measuring the influence of landscape heterogeneity on arthropod populations and biological control in agriculture. Their analysis showed that in 74% of the cases studied, increased natural enemy diversity and abundance were correlated positively with increased landscape heterogeneity. However, in only 45% of the studies reviewed, increased landscape heterogeneity correlated positively with decreased pest densities, reduced crop damage or increased yield. While landscape heterogeneity has been shown to have a significant and positive influence on natural enemy diversity and abundance at the field level, meta-analyses conducted to date have shown that landscape heterogeneity does not consistently result in enhanced biological control (Bianchi et al. 2006; Chaplin-Kramer et al. 2011). The relationship between landscape heterogeneity and enhanced pest regulation in agriculture is therefore considered to be specific to the cropping system and life-history characteristics of key pests and their natural enemies (With et al. 2002; Hunter 2002; Tscharntke et al. 2007). A more detailed understanding of how specific biophysical features of landscapes influence arthropod populations will be essential for the development of cost-effective habitat enhancement strategies aimed at improving biological control and other ecosystem services to agriculture.

8.4.1 Research on Overwintering Habitat for Anagrus *spp.*

Several studies have evaluated the contribution of natural enemy refuges to pest regulation in California grape systems. A majority of the existing work has focused on the effect of *Anagrus* overwintering habitat and whether its proximity to vineyards influences biological control of *Erythroneura* leafhoppers. This is because this parasitoid must locate alternate leafhopper host eggs to complete winter diapause. Although *Anagrus* can complete multiple generations by parasitizing *Erythroneura* eggs during the spring and summer, these pest leafhoppers overwinter as adults while *Anagrus* overwinters as larvae (UC IPM 2010a). Overwintering habitat that supports alternate leafhopper host(s) may be limited (due to plant community composition) or lie at a great distance from vineyards. Low quality or distant overwintering habitat for *Anagrus* may lead to delayed spring colonization of vineyards, allowing early grape leafhopper populations to develop unchecked. This can result in leafhopper damage to young grape shoots and/or large populations of adult leafhoppers at the end of the growing season, which can interfere with harvest activities (UC IPM 2010a).

Researchers have attempted to address this management problem by investigating how habitat patches that serve as natural enemy refuge can contribute to early-season control of grape leafhoppers. Studies primarily evaluate the use of blackberry and prune refuges (*Rubus* spp. and *Prunus* spp., respectively) around California vineyards. Although some of this section draws from the broader North American literature, many of the known alternate host plants for overwintering *Anagrus* can be found in California. An overview of known alternate host plants (and associated leafhoppers) for overwintering *Anagrus* wasps is included in Table 8.2.

8.4.1.1 Studies of Wild Blackberry Refuges

A 1966 study of blackberry refuges revealed a gradient of parasitoid activity that declined with increasing distances from the refuges. Leafhopper egg parasitism was observed up to 6.4 km away from the blackberry stands. Beyond this distance egg parasitism rates declined substantially. Researchers concluded that the observed trend was likely due to *Anagrus* dispersing outward from the blackberry refuge. The study did not include any direct measurements of dispersal (e.g. mark/recapture) or quantitative assessments of *Anagrus* densities (Doutt et al. 1966).

In a related survey of *Anagrus* dispersal, Doutt and Nakata (1973) monitored vineyards for parasitoid activity at increasing distances from a large riparian area. It was assumed that the riparian habitat harbored a high density of wild blackberry, although no formal information on plant species composition was reported for the riparian area. Sampling vineyards at increasing distances from the riparian habitat (up to 32 km), researchers observed leafhopper egg parasitism 3–4 weeks earlier in vineyards located at closer proximity (<8 km) to the riparian forest. This finding again led researchers to conclude that *Rubus* spp. were harboring overwintering populations of *Anagrus* wasps and that these parasitoids were dispersing into nearby vineyards earlier in the spring. In addition, researchers observed earlier leafhopper egg parasitism in vineyards located downwind from the riparian ecosystem when compared with vineyards upwind at similar or closer distances. This finding led to the suggestion that dominant wind direction also plays an important role in *Anagrus* dispersal (Doutt and Nakata 1973).

Table 8.2 Summary of plant and leafhopper host associations for *Anagrus* spp.

Plant species	Common name	*Anagrus* species	Host species	Region	Reference
Aceraceae					
Acer glabrum	Douglas maple	*A. atomus*	?	BC	1
Acer saccharum	Sugar maple	*A. daanei*	?	NY	2, 3
		Anagrus spp.	?	NY	3
Betulaceae					
Alnus sp.	Alder	*A. erythroneurae*	?	BC	1
Betula occidentalis	Water birch	*A. atomus*	?	BC	1
		A. avalae	?	BC	1
		A. erythroneurae	?	BC	1
Betula pendula	European white birch	*A. atomus*	?	BC	1
Ostrya virginiana	Hophornbeam	*A. atomus*	?	NY	3
Cornaceae					
Cornus racemosa	Gray dogwood	*A. yawi*	?	NY	3
Cornus stolonifera	Red osier dogwood	*A. daanei* (?)	?	BC	1
		A. erythroneurae	?	BC	1
Fabaceae					
Robinia pseudo-acacia	Black locust	*A. daanei*	?	NY	3
		A. epos	?	NY	3
		A. nigriventris	?	NY	3
		Anagrus spp.	?	NY	3
Fagaceae					
Quercus rubra	Northern red oak	*Anagrus* spp.	?	NY	3
Juglandaceae					
Juglans nigra	Black walnut	*Anagrus* spp.	?	NY	3
Lamiaceae					
Lavendula angustifolia	Lavender	*A. atomus*	?	BC	1

(continued)

Table 8.2 (continued)

Plant species	Common name	*Anagrus* species	Host species	Region	Reference
Mentha spp.	Garden mint	*A. atomus*	?	BC	1
		A. erythroneurae	?	BC	1
	Mint	*A. atomus*	?	BC	1
		A. erythroneurae	?	BC	1
Nepeta cataria	Catnip	*A. atomus*	?	BC	1
		A. erythroneurae	?	BC	1
Nepeta x *mussinii*	Persian catnip	*A. atomus*	?	BC	1
		A. erythroneurae	?	BC	1
Salvia officinalis	Garden sage	*A. atomus*	?	BC	1
		A. erythroneurae	?	BC	1
Oleaceae					
Fraxinus americana	White ash	*Anagrus* spp.	?	NY	3
Rosaceae					
Crateagus sp.	Hawthorn	*Anagrus* spp.	?	NY	3
Fragaria x *ananassa*	Strawberry	*A. atomus* or *A. erythroneura*	?	BC	1
Malus domestica	Apple	*A. atomus*	?	BC	1
		A. avalae	?	BC	1
		A. erythroneurae	?	BC	1
Malus pumila	Apple	*Anagrus* spp.	?	NY	3
Malus spp.	Apple	*A. atomus*	*Typhlocyba pomaria*	BC, ON	2
			Empoasca maligna	MI	2
			?	BC	2
		A. avalae	*T. pomaria*	ON	2
		A. daanei	*T. pomaria*	MI	2
			?	MI	2

		A. erythroneurae	*T. pomaria*	CA, WA	2
		Anagrus sp.	*T. pomaria*	MI	2
		A. tretiakovae	?	MI	2
Prunus avium	Sweet cherry	*A. erythroneurae*	?	BC	1
Prunus domestica	Cultivated plum	*A. erythroneurae*	?	BC	1
Prunus dulcis	Almond	*A. atomus*	?	CA	2
		A. daanei	?	CA	2
		A. erythroneurae	?	CA	2
Prunus persica	Peach	*A. atomus*	*Edwardsiana prunicola*	CA	2
			Typhlocyba quercus (?)	CA	2
			?	CA	2
		A. avalae	*E. prunicola*	CA	2
			?	CA	2
		A. erythroneurae	*E. prunicola*	CA	2
			?	CA	2
		A. tretiakovae	*Erythroneura plena*	MD	2
Prunus serotina	Black cherry	*Anagrus* spp.	?	NY	3
Prunus virginiana	Choke cherry	*A. atomus*	?	BC	1
		A. avalae	?	BC, OR, WA	1, 4
		A. daanei	?	BC	1
		A. tretiakovae	?	OR, WA	4
Purshia tridentata	Antelope bitterbrush	*A. atomus*	?	OR, WA	4
Rosa eglanteria	Sweetbrier	*A. atomus*	?	OR, WA	4
		A. erythroneurae	?	OR, WA	4
Rosa multiflora	Multiflora rose	*A. atomus*	?	NY	3
		A. daanei	?	NY	3
Rosa rugosa	Rugose Rose	*A. atomus*	?	OR, WA	4
		A. erythroneurae	?	OR, WA	4
		A. tretiakovae	?	OR, WA	4

(continued)

Table 8.2 (continued)

Plant species	Common name	*Anagrus* species	Host species	Region	Reference
Rosa spp.	Rose	*A. atomus*	*Edwardsiana rosae*	CA, NY,	2
			?	BC, NY, OR, WA	1, 4
		A. avalae	*E. rosae*	BC, OR(?)	2
			?	BC, OR, WA	1, 4
		A. daanei	*E. rosae*	CA, NY	2
		A. erythroneurae	?	BC, OR, WA	1, 4
		A. nr. sp. *daanei*	?	OR, WA	4
		A. tretiakovae	?	OR, WA	4
Rosa woodsii	Wood's rose	*A. atomus*	?	OR, WA	4
		A. erythroneurae	?	OR, WA	4
Rubus armeniacus (*R. discolor, R. procerus*)	Himalayan blackberry	*A. atomus*	?	OR, WA	4
		A. avalae	?	OR, WA	4
		A. erythroneurae	?	OR, WA	4
		A. nigriventris	?	OR, WA	4
		A. nr. sp. *columbi*	?	OR, WA	4
		A. tretiakovae	?	OR, WA	4
Rubus laciniatus	Evergreen blackberry	*A. atomus*	?	OR, WA	4
Rubus spp.	Blackberry	*A. atomus*	*Dikrella* spp.	CA	2
			?	BC, CA	1, 2
		A. daanei	*Dikrella* spp. (?)	CA	2
			?	CA	2
		A. erythroneurae	*D. californica* (?)	CA	2
			D. cruentata (?)	CA	2
			Dikrella spp.	CA	2
			?	BC, CA	1, 2
		A. nigriventris	?	CA	2
Rubus spp.	Tayberry	*A. atomus*	?	BC	1
		A. erythroneurae	?	BC	1

Rutaceae					
Zanthoxylum americanum	Common prickly ash	*A. daanei*	?	NY	3
		Anagrus spp.	?	NY	3
Salicaceae					
Salix babylonica	Weeping willow	*A.* nr. sp. *avalae*	?	OR, WA	4
Salix nigra	Willow	*A. erythroneurae*	?	NY	3
Salix spp.	Willow	*A. atomus*	?	OR, WA	4
		A. erythroneurae	?	OR, WA	4
		A. nr. sp. *nigriventris*	?	BC, OR, WA	1, 4
		Anagrus sp.	?	BC	1
Ulmaceae					
Ulmus pumila	Siberian elm	*A. atomus*	?	BC	1
Vitaceae					
Parthenocissus quinquefolia	Virginia creeper	*A. daanei*	?	BC	1
Vitis cv. Castel	Grape	*A. daanei*	*Erythroneura* spp. (?)	NY	3
		Anagrus spp.	*Erythroneura* spp. (?)	NY	3
		A. tretiakovae	*Erythroneura* spp. (?)	NY	3
Vitis cv. GR-7	Grape	*A. daanei*	*Erythroneura* spp. (?)	NY	3
		Anagrus spp.	*Erythroneura* spp. (?)	NY	3
		A. tretiakovae	*Erythroneura* spp. (?)	NY	3
Vitis cv. Seyval blanc	Grape	*A. daanei*	*Erythroneura* spp. (?)	NY	3
Vitis labrusca Bailey cv. Concord	Grape	*A. daanei*	*Erythroneura* spp. (?)	NY	3
		A. nigriventris	*Erythroneura* spp. (?)	NY	3
		A. tretiakovae	*Erythroneura* spp. (?)	NY	3
Vitis labrusca Bailey cv. Delaware	Grape	*A. tretiakovae*	*Erythroneura* spp. (?)	NY	3

(continued)

Table 8.2 (continued)

Plant species	Common name	*Anagrus* species	Host species	Region	Reference
Vitis labrusca Bailey cv. Niagara	Grape	*A. daanei*	*Erythroneura* spp. (?)	NY	3
		A. erythroneurae	*Erythroneura* spp. (?)	NY	3
		A. tretiakovae	*Erythroneura* spp. (?)	NY	3
Vitis riparia	Grape	*A. tretiakovae*	*Erythroneura* spp. (?)	NY	3
Vitis spp.	Grape	*A. daanei*	*Erythroneura bistrata*	NY	2
			E. comes	NY	2
			E. elegantula	CA	2
			Erythroneura spp.	CA, NY	2
			E. variabilis	CA	2
			E. ziczac	BC, NY	2
			?	BC, CA, NY	2
		A. epos	*Dikrella*. sp.	NM	2
			E. comes	NY	2
			Erythroneura spp.	BCA, SON	2
			E. variabilis	SON	2
			E. vulnerata	CO	2
			?	NM, SON	2
		A. erythroneurae	*D. cockerellii*	NM	2
			Dikrella sp.	NM	2
			E. bistrata	NY	2
			E. comes	NY	2
			E. elegantula	CA	2
			Erythroneura spp.	BCA, CA	2
			E. variabilis	BCA, CA	2
			?	BCA, CA, NY, SON	2
		A. flaveolus	?	SON	2
		A. nigriventris	*E. comes*	NY	2

		A. tretiakovae	*D. cockerellii* (?)	COA	2
			E. bistrata	NY	2
			E. comes	DE, NY	2
	Grape	*A. tretiakovae*	*Erythroneura* spp.	AZ, COA, NY	2
			E. variabilis	AZ, SON	2
			E. ziczac	NY	2
			?	AZ, BCA, MI, NM, NY, SON	2
		A. yawi	*E. comes*	NY	2
Vitis vinifera	Grape	*A. daanei*	?	BC	1
Vitis vinifera L. cv. Chardonnay	Grape	*A. daanei*	*Erythroneura* spp. (?)	NY	3
		A. epos	*Erythroneura* spp. (?)	NY	3
		A. erythroneurae	*Erythroneura* spp. (?)	NY	3
		A. tretiakovae	*Erythroneura* spp. (?)	NY	3

State and province abbreviations used: Canada: *BC* British Columbia, *ON* Ontario; United States: *AZ* Arizona, *CA* California, *CO* Colorado, *DE* Delaware, *MD* Maryland, *MI* Michigan, *NM* New Mexico, *NY* New York, *OR* Oregon, *WA* Washington; Mexico: *BCA* Baja California, *COA* Coahuila, *SON* Sonora

[1] Lowery et al. (2007)

[2] Triapitsyn (1998)

[3] Williams and Martinson (2000)

[4] Wright and James (2007)

(?) Unverified species or region of collection

Although none of the studies above measured whether early season parasitism significantly influenced pest densities, the findings led to the development of recommendations that growers establish blackberry refuges around their vineyards to promote early season biological control of leafhoppers. More than a decade after the recommendations were made, further scientific evaluation of the plantings showed that the blackberry refuges did not consistently enhance biological control (Flaherty et al. 1985). Researchers posited that the on-farm blackberry refuges were unsuccessful because many were planted outside of their native riparian habitats, and that reduced canopy cover and lower soil moisture levels reduced the quality of the refuges which contributed to lower populations of both blackberry leafhopper (*Dikrella cruentata* (Gillette)) and *Anagrus*. Flaherty et al. (1985) attempted to substantiate this hypothesis by providing shade structures to *Rubus* plantings. Findings suggest that while the shade treatment did enhance *D. cruentata* populations on the blackberry, *Anagrus* densities were not significantly increased.

Due to its inability to consistently control leafhopper populations, California growers largely abandoned the planting of blackberry around Central Valley vineyards by the late 1980s. Additionally, identification of *Rubus* spp. as a systemic host of Pierce's Disease (*Xylella fastidiosa* Wells et al.) led to its removal from many riparian habitats of the Northern and Central Coast grape growing regions (Purcell and Saunders 1999; Baumgartner and Warren 2005).

8.4.1.2 Experiments Involving Prune Refuges

Counter to previous findings, Kido et al. (1983) reported high early season leafhopper parasitism in vineyards adjacent to prune orchards and revealed an additional alternate host for overwintering *Anagrus*, the prune leafhopper (*Edwardsiana prunicola* (Edwards)), which was reproducing in French prune (*Prunus* spp.) orchards neighboring vineyards. Following this discovery, Kido et al. (1984) conducted a non-replicated 2-year study quantifying population densities of *E. prunicola* and *Anagrus* in two vineyards adjacent to prune orchards. Only one vineyard-orchard pair was studied each year. Based on observations of leafhopper egg parasitism 3–4 weeks earlier in vineyards adjacent (<30 m) to the prune orchards, researchers concluded that *Anagrus* populations remained active in the prune trees throughout the growing season and dispersed into the nearby vineyards to parasitize grape leafhoppers eggs in the spring. Kido et al. (1984) concluded that French prunes could be used like *Rubus* spp. to enhance overwintering habitat for *Anagrus* wasps and thereby increase biological control of leafhoppers.

Building upon the above assessments, Wilson et al. (1989) monitored *Anagrus* activity in two vineyards, one adjacent and the other located at some distance away from a prune orchard (exact distance not reported). The study showed that the prune orchard harbored high densities of *Anagrus* wasps, and that leafhopper egg parasitism occurred approximately 3–4 weeks earlier in the nearby vineyard. Like others, the study concluded that *Anagrus* could successfully overwinter in French prune refuges and potentially contribute to early-season control of grape leafhoppers.

The effect of wind speed was also measured on *Anagrus* colonization. Prune trees subjected to low velocity winds were found to have a higher abundance of *Anagrus*. Based on these and the findings of Doutt and Nakata (1973), researchers advised growers to plant French prune trees upwind from their vineyards to augment populations of *Anagrus* and enhance biological control of leafhoppers.

Prior to 1990, all research conducted on the *Anagrus*-leafhopper system had been based on non-replicated comparisons and indirect assessments of *Anagrus* dispersal from overwintering refuges. While early season leafhopper egg parasitism was reported to be enhanced with proximity to *Rubus* spp. and *Prunus* spp. refuges, no assessment of vineyards pest densities were conducted.

The first direct assessment of *Anagrus* movement was carried out by Corbett and Rosenheim (1996a) using rubidium (Rb) to mark prune refuges adjacent to two vineyard sites over a 2-year period. Early season *Anagrus* populations were monitored at increasing distances away from the refuges to quantify the proportion of the *Anagrus* population found in the vineyard that originated in the Rb-marked prune trees. Consistent with the previous prune refuge studies, a higher density of *Anagrus* was found in vine rows directly adjacent (10–20 m) and downwind from prune trees. Only a small percentage of these parasitoids, however, were positively marked with Rb. Given the conflicting evidence, the authors concluded that although prune trees did directly contribute to vineyard *Anagrus* populations, the presence of regional riparian habitats appeared to be a greater source of *Anagrus*. The apparent 'prune tree effect' was partially the result of the prune stands acting as windbreaks for aerially dispersing *Anagrus* assumed to be coming from nearby riparian habitats (Corbett and Rosenheim 1996a).

Murphy et al. (1996, 1998a, b) completed a more comprehensive evaluation of the effect of prune refuges on biological control. In these studies, 18–24 pairs of vineyard blocks with and without nearby prune orchards were evaluated over 2 years. Researchers tested the hypotheses suggested in previous studies by evaluating the influence of prune trees on *Anagrus* abundance in vineyards, measuring leafhopper parasitism rates, and quantifying the abundance of leafhopper nymphs at increasing distances away from the prune refuge plantings. These studies again showed that *Anagrus* was more abundant approximately 3–4 weeks earlier in vineyards adjacent to prune orchards (Murphy et al. 1996). A similar effect was seen in parasitism rates, where leafhopper egg parasitism was significantly higher and occurred approximately 3–4 weeks earlier in vineyards adjacent to the prune orchards (Murphy et al. 1998a). Although significant differences in *Anagrus* density and parasitism rates between treatment and control blocks diminished later in the growing season (second and third leafhopper generations), early season effects of prune refuges could potentially influence late-season leafhopper populations. The final component of this study showed, however, that leafhopper nymph densities were not found to be significantly different between treatment and control sites (Murphy et al. 1998b). These results raised additional questions about the source habitats for *Anagrus* and highlighted the need to carry out more thorough evaluations of alternate overwintering habitat, and conduct further mark-recapture studies to better understand *Anagrus* dispersal across the landscape.

Corbett and Rosenheim (1996b) conducted another mark/recapture study of *Anagrus*, this time using fluorescent dust to mark wasps emerging from vineyard grape leaves. While not a study of *Anagrus* dispersal from any type of refuge *per se*, this study did provide new information on *Anagrus* movement within a vineyard. The study revealed that *Anagrus* appeared to disperse up to 24.5 m/day and contrary to all prior evidence, it had a significant tendency to disperse upwind. However, these novel findings are not definitive. In their discussion, Corbett and Rosenheim (1996b) suggested that, because their data on dominant wind speed and direction was from a nearby weather station, it may not have been representative of wind characteristics within the study vineyard itself. Like the prune refuges, the vineyard canopy structure may have altered wind speed and direction within the vineyard and this might have subsequently influenced *Anagrus* dispersal.

Prune orchards can still be found near some commercial vineyards in California. While these orchards could potentially provide a patchwork of overwintering habitat for *Anagrus* wasps, their area relative to the vineyards is small and their contribution to biological control is likely negligible. Researchers have suggested that small refuges (prune, blackberry or otherwise) may not be viable over the long term, as their entire population of alternate overwintering hosts risk being eliminated by overwhelming populations of *Anagrus* produced in large vineyards during the summer (Mills and Daane 2005).

8.4.1.3 North American Research on Alternate Overwintering Habitat for *Anagrus* spp.

Studies evaluating the impact of habitat patches on biological control of leafhoppers examined only two plant genera, *Rubus* spp. and *Prunus* spp., both in the Rosaceae. This limited range of known overwintering host plants for *Anagrus* has encouraged researchers to seek out new alternate host plants that could be utilized for habitat enhancement in proximity to vineyards. This work is especially important in light of recent taxonomic revisions to the *Anagrus* complex, which revealed that not all *Anagrus* species overwintering near vineyards are necessarily the same as those found parasitizing *Erythroneura* leafhoppers in vineyards during the growing season (Triapitsyn 1998).

Overwintering habitat assessments have been conducted in various viticulture regions in North America, revealing a range of new plant and host associations for *Anagrus* (Table 8.2). While *Anagrus* is consistently encountered on plants in the Rosaceae, this parasitoid also appears to be associated with plants in many other families. At present, *Anagrus* appears to reproduce exclusively on eggs from species in the Ciccadellidae. A summary of known plant and leafhopper host associations for *Anagrus* spp. is presented in Table 8.2.

8.4.2 Measuring the Effect of Plant Corridors, Flower Islands, and Native Vegetation

Nicholls et al. (2001) evaluated the influence of non-crop habitat on biological control in a northern California organic vineyard. They focused on two separate

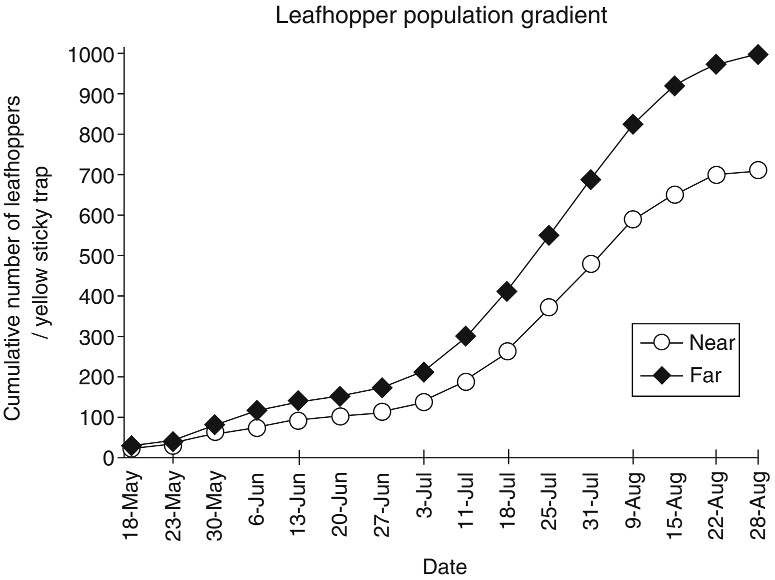

Fig. 8.1 Season patterns of adult leafhoppers in a vineyard 'Near' and 'Far' from a corridor of flowering vegetation (Hopland, California 1996) (From Altieri et al. 2005)

non-crop habitats: (1) a vegetational corridor bisecting the vineyard, and (2) a riparian forest abutting the vineyard. The corridor consisted of 65 different species of flowering plants. No description of plant species composition was provided for the riparian forest. Natural enemy and pest populations were monitored at increasing distances away from the corridor and the riparian forest. The study found that the abundance of generalist predators decreased at increasing distances away from both the forest and corridor, while *Anagrus* densities increased towards the center of the vineyard plots. Leafhopper egg parasitism rates did not exhibit any significant spatial trends relative to the two non-crop habitats, although parasitism rates were generally higher towards the center of the vineyard blocks. Thrips, *F. occidentalis*, and grape leafhopper adult densities both increased at greater distances away from the two non-crop habitats (Fig. 8.1). *Anagrus* dispersal was evaluated through an indirect assessment of movement, and no clear information was provided about dominant wind direction relative to non-crop habitats. In that study, Nicholls et al. (2001) concluded that the distribution of *Anagrus* was likely following that of the leafhoppers resulting from a density-dependent relationship between the parasitoid and host rather than any influence from non-crop habitat.

To further understand the spatial patterns of biological control in vineyards, Altieri et al. (2005) evaluated population densities of pest and beneficial insects at increasing distances away from a 0.25 ha on-farm 'flower island' in a Northern California vineyard. The island was composed of 33 species of flowering shrubs

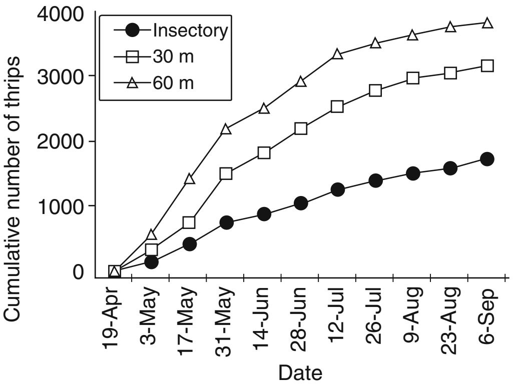

Fig. 8.2 Cumulative number of thrips per yellow sticky trap in 2004 at Benziger vineyard (Glen Ellen, California)

and herbs predominantly from the Asteraceae, Agavaceae, and Lamiaceae. The assemblage of flowering plants was selected to provide floral resources from April to late September. Natural enemy populations (*Orius* spp., Coccinellidae, Syrphidae, *Anagrus* wasps), leafhopper egg parasitism, and thrips density were recorded at increasing distances away from the island (10, 30 and 60 m) over a single growing season. Results showed that natural enemy densities, and leafhopper egg parasitism rates both decreased and abundance of thrips increased at greater distances away from the island (Fig. 8.2). The researchers thus suggested that the flower island may have served as a source of pollen, nectar or alternate prey for natural enemies which led to the observed changes in leafhopper egg parasitism and thrips densities.

While much conservation biological control research in California viticulture has focused on the *Anagrus*-leafhopper system, other research has been conducted to evaluate the relationship between natural habitats and vineyard spider populations. Spiders are known to be the most abundant generalist predator in vineyards and natural habitats could be contributing to these vineyard populations (Costello and Daane 1995, 1999; Roltsch et al. 1998). Hogg and Daane (2010, 2011) evaluated how oak woodland-chaparral, and riparian habitats contributed to vineyard spider populations. Spiders were sampled throughout the growing season in natural habitats and at multiple distances into vineyards. They reported that spider dispersal into vineyards appeared to occur later in the growing season (July and August) and that spider species diversity and abundance significantly differed between natural and vineyard habitats. The observed differences in species composition became more pronounced with increasing distance away from the natural habitats (up to 250 m), and vineyards were found to be dominated by just a few spider species. Researchers suggested that natural habitats serve as an important source of vineyard spider populations. While no assessment of pest densities was conducted in these two studies, the researchers noted that the observed changes in vineyard spider species composition relative to distance away from adjacent source habitats likely has implications for biological control.

8.4.3 Landscape Restoration to Enhance Ecosystem Services to California Vineyards

Habitat restoration in California agriculture is characterized by the establishment of mixed-use hedgerows intended to promote biological control, pollination and other ecosystem services. Hedgerows typically consist of combinations of annuals, herbaceous, and woody perennial shrubs and trees. These plantings have been found to attract populations of important natural enemies of vineyard pests, including *Orius* spp., *Geocoris* spp., Coccinellidae, Chrysopidae, Nabidae, Syrphidae and various spiders (Dufour and Appropriate Technology Transfer for Rural Areas Organization 2000; Robins et al. 2001; Earnshaw 2004). Despite the limited data on the aggregation of natural enemies, the impact on biological control of vineyard pests remains largely unexplored. Given the lack of scientific data on the impact of such plantings, growers and government programs supporting such efforts may not be fully realizing the outcomes they are intended to achieve.

Additionally, the inconsistent findings of many of the previous vineyard diversification studies described above may be in part due to a failure of researchers to adequately account for the influence of the surrounding landscape on biological control. Identifying the key qualities and quantities of non-crop habitats that support natural enemies will be an essential step in developing scientifically based landscape restoration programs that effectively enhance biological control and other ecosystem services to vineyards. Despite the many important contributions of ecologists and biological control specialists to date, many research gaps remain. Filling these gaps will be essential in providing the empirical evidence needed to define the specific types of habitat enhancement that leads to cost-effective regulation of important vineyard pests.

8.5 Current Diversification Research at UC Berkeley: Field-Scale Analysis

Building upon the prior field and landscape-scale studies in conservation biological control in vineyards discussed above, researchers at the university of California, Berkeley, have recently initiated the first comprehensive, multi-scalar study of the impact of floral resource provisioning (FRP) and landscape complexity in Napa, Sonoma, San Joaquin and Fresno County wine grape systems.

The floral resource provisioning theory predicts that the addition of flowering plants to simplified agroecosystems improves biological control by providing insect parasitoids or predators with key food sources (e.g., nectar, pollen) that would otherwise limit fitness of natural enemies (Barbosa 1998; Landis et al. 2000; Altieri and Nicholls 2004; Heimpel and Jervis 2005; Lee and Heimpel 2008). The floral resource provisioning systems attract the interests of researchers and growers because of its theoretical appeal and success in some cropping systems

(Tonhasca and Byrne 1994; Gurr and Wratten 2000; Letourneau et al. 2010). The floral resource provisioning schemes also attract some skepticism in the scientific community as the outcomes of hundreds of on-farm diversification studies have been mixed (Andow 1991a; Lavandero et al. 2005; Wäckers et al. 2005; Straub et al. 2008). However, in a recent meta-analysis, Letourneau et al. (2010) showed that on-farm diversification strategies consistently supported a greater abundance, and diversity of natural enemies and increased pest control. Further, when FRP strategies do appear successful, the ecological processes underlying enhanced pest regulation often remains unsubstantiated or not fully understood (Gurr et al. 2000, 2004; Landis et al. 2000; Nicholls et al. 2000). Finally, the relationship between FRP and pest densities in vineyards and other cropping systems may also be explained by multiple alternative hypotheses (Wratten et al. 1998; Corbett 1998; Costello and Daane 2003; Gurr et al. 2004; Heimpel and Jervis 2005; Bianchi et al. 2006). The current scientific consensus is that FRP can enhance biological control, but its success is both context and system specific (Altieri and Nicholls 2004; Tscharntke et al. 2007). Moreover, while FRP programs have the potential to decrease reliance on pesticides, the uncertainty of the effectiveness of this and other diversification schemes restricts large-scale implementation.

Prior studies in field-scale diversification in California vineyards were limited by a number of key factors. First, in Costello and Daane (1998, 2003), non-flowering cover crops (i.e., barley) were used, and less consideration was given to seasonal availability of floral resources, flower morphology and accessibility, and/or the quality of floral resources needed to enhance the fitness of natural enemies (Wäckers 2004; Begum et al. 2006; Vattala et al. 2006). The findings of Nicholls et al. (2000) were limited to a comparative analysis of two large vineyard blocks without full substantiation of the cause of enhanced biological control. Additionally, in all the prior on-farm diversification research in California, the landscape context (i.e., the area and diversity of non-crop habitat) was not fully taken into account (Tscharntke et al. 2005, 2007; Chaplin-Kramer et al. 2011).

To address some of the limitations and build upon prior studies in vineyard diversification, the current UC Berkeley conservation biological control project will assess the impact of floral resource provisioning and landscape complexity in several key grape producing regions. At the field level, the study will measure the impact of five flowering ground covers (annual buckwheat (*F. esculentum*), lacy phacelia (*Phacelia tanacetifolia* Bentham), sweet alyssum (*Lobularia maritima* (L.) Desvaux), bishop's weed (*Ammi majus* L.), and wild carrot (*Daucus carota* L.)) on biological control of *Erythroneura* leafhoppers (*E. elegantula* and *E. variabilis*) and vine mealybug (*Planococcus ficus* (Signoret)) by the parasitoid wasps *Anagrus* spp. and *Anagyrus pseudococci* (Girault) (Hymenoptera: Encyrtidae) in California vineyards. The research includes eight split-block trials on commercial vineyards in Napa and Sonoma County and two fully replicated research designs, one located in Lodi and the other at the UC Kearney Agriculture Center in Fresno County. The research will test multiple hypotheses (i.e., natural enemies and resource concentration) of biological control in vineyards to advance scientific knowledge of cost-effective and ecologically-based pest management. The study will quantify the impacts of FRP on population densities of pest and beneficial insects and analyze the biological mechanisms (e.g., longevity, fecundity, parasitism rates) theorized to be enhanced through FRP. Comparative cost-benefit analyses (FRP vs. conventional practices) will evaluate the cost-effectiveness of the tested strategies. In addition, the study will measure natural enemy movement from flowering cover crops to the vine canopy and substantiate nectar feeding through laboratory studies and anthrone testing. In a separate replicated and complementary study, researchers are testing the effect of methyl salicylate lures (a beneficial insect attractant) on natural enemies, pest densities and biological control (James 2003, 2006; Cook et al. 2006; James and Price 2004). Data from laboratory studies indicate that FRP has a significant positive impact on the longevity of *A. pseudococci* females (A. Miles et al., unpubl. data).

8.6 Current Diversification Research at UC Berkeley: Landscape Analysis

The landscape component of the UC Berkeley conservation biological control project will evaluate the influence of landscape heterogeneity on the effectiveness of a field-scale FRP treatment to enhance biological control of grape leafhopper (*E. elegantula*) in northern California wine grape vineyards. A field FRP treatment plot will be compared to a control plot in 20 separate vineyards situated along a gradient of landscape heterogeneity. The FRP treatment will consist of three annual flowering plant species: lacy phacelia (*P. tanacetifolia*), bishop's weed (*Ammi majus* L.) and wild carrot (*D. carota*). This combination of species was selected to provide floral bloom throughout the entire growing season. These species are also drought tolerant, require no additional irrigation and can readily be integrated with standard vineyard management practices in northern California. Populations of the leafhopper pest and its key natural enemies will be monitored along with parasitism rates, crop damage and yield. Vine vigor will also be assessed in order to evaluate the influence of plant nutrient status on pest densities. Additionally, an assessment of *Anagrus* dispersal from natural habitats into adjacent vineyards will be conducted. Finally, *Anagrus* overwintering habitat will be assessed. Plant species commonly found in northern California vineyard landscapes will be sampled and evaluated for overwintering parasitoids. Plant material found to support significant *Anagrus* populations will be further evaluated to determine the associated insects that serve as alternate-hosts for the parasitoid. In combination, these studies are intended to generally evaluate how vineyard landscape composition influences the ability of field-scale FRP to enhance biological control of key wine grape pests. The goal of this research is to determine thresholds of landscape heterogeneity within which the use of field-scale FRP is most cost-effective for enhancing biological control.

8.7 Conclusion: Field and Landscape Level Diversification for Conservation Biological Control

Results of the California studies reviewed above show a pattern consistent with the larger national and international conservation biological control literature: treatment effects from diversification strategies are discernable, yet cost-effective biological control is not consistently achieved (Andow 1991a) (English-Loeb et al. 2003; Begum et al. 2006; Berndt et al. 2006; Straub et al. 2008). Nevertheless, meta analyses showed that diversification had a moderate effect on the abundance of plant herbivores (Tonhasca and Byrne 1994; Letourneau et al. 2010). Other meta-analyses of landscape factors have also shown that while natural enemy abundance, richness, predation and parasitism rates do increase significantly with landscape heterogeneity, pest densities are not found to be consistently lower (Bianchi et al. 2006; Chaplin-Kramer et al. 2011). Despite the large body of existing research, significant gaps remain in the conservation biological control literature. Findings from the research proposals outlined herein will help provide the necessary information for advancing the science of conservation biological control and developing more cost-effective ecologically-based pest management strategies for California vineyards.

8.8 Proposals and Considerations for Future Research: Conservation Biological Control in California Vineyards

The following are guidelines and specific proposals for research that would serve to advance the science and practice of conservation biological control in California viticulture. Proposals include both natural and social science studies.

As the effect of field-scale habitat enhancement strategies can be influenced by features in the surrounding landscape, future research must consider the influence of non-crop habitats that lie beyond the individual field or vineyard boundary. Broad correlative studies of landscape heterogeneity, natural enemy and pest density must be conducted along with detailed evaluations of the ecological processes theorized to influence biological control. To provide reliable data for use in developing effective pest management strategies, studies must be conducted for a minimum of 2 years and include full replication at the field and landscape scale. Field-scale evaluations of diversified cropping systems should assess both natural enemies and pest densities along with empirical tests of parasitism and predation (Bianchi et al. 2006). Measures should be taken to determine the impact of treatments on herbivore population densities, crop yield and quality. Studies measuring the impact of intercropping must account for the influence of non-crop vegetation on plant nutrient status along with impacts on the fitness of natural enemies (Daane and Costello 1998; Altieri and Nicholls 2003). Multi-trophic interactions must also be considered as increased diversity, and abundance of natural enemies in complex agricultural habitats can lead to intraguild predation and subsequent release of pests from biological control (Finke and Denno 2004; Straub et al. 2008).

Studies involving habitat manipulation should evaluate both the natural enemies and resource concentration hypotheses. Invertebrate response to landscape heterogeneity should be evaluated in a way that can address both of these hypotheses. At a minimum, this would require separately examining insect response to the relative area, diversity and connectivity of both natural habitat and agricultural land at the landscape scale. The high probability of idiosyncratic and species specific response to the landscape will require that observed trends be evaluated relative to a number of alternate measures of landscape heterogeneity, including perimeter to area ratio, mean patch size, and distance away from natural habitats (for details see Concepción et al. 2008). As non-crop habitats cannot be assumed to benefit only predators and parasitoids, studies should simultaneously measure the impact of non-crop vegetation on the fitness of insect pests (van Emden 1965; Baggen et al. 1999; Roschewitz et al. 2005).

As habitat diversity will influence insect movement at both the field and landscape scale, researchers are encouraged to consider the movement and distribution of arthropods in relation to the elements of heterogeneity under study (Corbett 1998; Dover and Settele 2009). The results of Corbett and Rosenheim (1996a) demonstrate the importance of empirical assessments of parasitoid dispersal from non-crop habitats. Quantifying insect movement between in-field habitat and crop and from non-crop habitats into cropping systems will be critical to developing a more nuanced understanding of the impact of heterogeneity at multiple spatial scales. Recent advances with relatively inexpensive marking systems (Hagler and Jones 2010) will help make this a reality.

Controlled field and laboratory trials are essential for determining the physiological influence of non-crop vegetation on key pests and natural enemies (Wäckers et al. 2005). Quantifying the influence of multiple species of flowering plants on parasitoid longevity, fecundity, parasitism rates and sex ratios of key biological control agents can help form the empirical basis for understanding enhanced biological control in field trials. To further substantiate nectar feeding, researchers should consider anthrone or HPLC testing to determine changes in parasitoid gut-sugar levels in the presence of flowers (Steppuhn and Wäckers 2004; Heimpel and Jervis 2005). Ideally, such work would be conducted under conditions most resembling the vineyard environment (Lee and Heimpel 2008).

It is important for applied research in conservation biological control to include on-farm and participatory trials in commercial vineyard settings. Such dialog with growers encourages the development of practices suitable for large-scale implementation and facilitates a social learning process between researchers, and growers that may improve the relevancy of research, and advance grower adoption of successful ecologically-based pest management practices (Röling and Wagemakers 2000; Warner 2007a, b). Cost-benefit analysis, including data on impact to other ecosystem services (e.g., soil quality, etc.) will provide a more holistic basis for grower decision making regarding the true costs and benefits of vineyard diversification (Fiedler et al. 2008; Gurr et al. 2003; Jackson et al. 2007).

Habitat enhancement tactics may also be successfully combined with the many new chemical ecology approaches (e.g., pheromones) to further enhance biological control (Daane et al. 2008). 'Attract and reward' strategies, for example, combine the use of herbivore-induced plant volatile (HIPV) compounds with in-field FRP and has shown much promise in enhancing the effectiveness of diversification schemes (James 2006; Khan et al. 2008). One such HIPV compound, methyl salicylate (MeSA) has been shown to increase abundance of some natural enemies in grape vineyards as well as in other cropping systems (James and Price 2004; James 2006; Lee 2010).

Future research must also include relevant economic and social assessments which may assist in developing ecologically-based pest management practices suitable for commercial adoption and provide a sound basis for the formulation of public policy (Cullen et al. 2008). To date, little work has been done to evaluate the impacts of public policy on vineyard habitat management or the ability of public institutions to adequately respond to grower research needs and coordination of agricultural restoration efforts at the regional scale. Finally, it will be critical to gather information on consumer perceptions of product quality and value associated with agricultural goods produced using ecologically-based farming practices (Forbes et al. 2009; Zucca et al. 2009; Howard and Allen 2010; Delmas and Grant 2010).

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