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Research article

Biological Control—Parasitoids and Predators

Host Plant Associations of *Anagrus* spp. (Hymenoptera: Mymaridae) and *Erythroneura elegantula* (Hemiptera: Cicadellidae) in Northern California

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Abstract

Anagrus erythroneurae S. Trjapitzin & Chiappini and *Anagrus daanei* Triapitsyn are the key parasitoids of the western grape leafhopper (*Erythroneura elegantula* Osborn) in northern California vineyards. *Erythroneura elegantula* overwinters as an adult in reproductive diapause. To successfully overwinter, *Anagrus* spp. must locate an alternate leafhopper host that overwinters in an egg stage that they can parasitize. These alternate leafhopper hosts are thought to be primarily located in the natural habitats surrounding vineyards. This study identifies the noncrop host plants utilized by *Anagrus* spp. not only during the overwintering period but throughout the entire year, as well as the leafhopper species associated with these host plants. Over a 2-yr period, *Anagrus* spp. and leafhoppers were sampled from numerous plants in natural and cultivated habitats surrounding vineyards. Results from this study confirm previously known *Anagrus* spp. host plants, but also identify new host plant species. Some of the host plants harbored *Anagrus* spp. year-round while others were utilized only during certain periods of the year. Leafhoppers associated with *Anagrus* spp. host plants may potentially serve as the alternate host utilized by *Anagrus* spp. on these plants, but this was not confirmed in the current study. Records of *E. elegantula* demonstrate their cyclical movement between the vineyard floor (winter), temporary noncrop hosts (spring/fall), and the grape vine canopy (summer).

Key words: *Anagrus*, *Erythroneura*, overwintering, parasitoid, leafhopper

The western grape leafhopper (*Erythroneura elegantula* Osborn; Hemiptera: Cicadellidae) is a common pest of wine grapes in coastal California and the Pacific Northwest (Daane and Costello 2000, Daane et al. 2013). *Erythroneura elegantula* feed and reproduce on grape leaves throughout the grape (*Vitis vinifera* L.)-growing season (March to October), typically completing two to three generations per year in this region. Feeding by *E. elegantula* causes leaf stippling that can reduce yield and fruit quality. High populations of *E. elegantula* adults in the fall can also be a nuisance, flying into the eyes, nose, and mouth of workers manually harvesting grapes. As grape vines senesce and their leaves drop in the fall, *E. elegantula* adults move onto the vineyard floor or surrounding vegetation where they overwinter in reproductive diapause on grasses, weedy vegetation, and perennial evergreen plants, such as citrus. In the spring, as grape vines begin to produce new shoots and leaves, the adults move back onto the grape vines to feed and deposit eggs (Daane and Costello 2000, Daane et al. 2013).

The key parasitoids of *E. elegantula* are *Anagrus erythroneurae* S. Trjapitzin & Chiappini and *Anagrus daanei* Triapitsyn (Hymenoptera: Mymaridae). Both species attack the eggs of *E. elegantula* throughout the grape-growing season. Whereas *E. elegantula* overwinter as adults, *Anagrus* wasps overwinter in host eggs and must find alternate leafhopper host species that overwinter in the egg stage (Doutt and Nakata 1965). These alternate leafhopper hosts for the *Anagrus* spp. are thought to reside primarily in natural habitats outside of vineyards (Doutt and Nakata 1965, 1973; Kido et al. 1984; Lowery et al. 2007).

Previous studies have identified a number of plant species, and in some cases even the alternate leafhopper host species, which *Anagrus* wasps utilize to overwinter. Doutt and Nakata (1973) observed that vineyards adjacent to stands of wild blackberry (*Rubus* spp.) had greater early-season populations of *Anagrus* wasps (at that time referred to as *A. epos* Girault) as well as increased *E. elegantula* egg parasitism rates, presumably due to the proximity to *Anagrus* overwintering habitat. They concluded that the alternate leafhopper host was the blackberry leafhopper (*Dikrella californica* [Lawson]). Kido et al. (1983) observed the same relationship in vineyards adjacent to French prune orchards (*Prunus domestica* L.) and,

similar to the previous work on blackberries, proposed that *Anagrus* overwintered in the eggs of the prune leafhopper (*Edwardsiana prunicola* [Edwards]) in these trees (Kido et al. 1984, Wilson et al. 1989). Based on the findings of these initial studies, it was recommended that grape growers establish stands of wild blackberry and/or French prune adjacent to their vineyards to enhance biological control of *E. elegantula*, although this was met with little success, in part, due to the difficulty of establishing blackberry stands outside of riparian areas (Flaherty et al. 1985) and the limited feasibility of establishing large refuges in commercial vineyards (Mills and Daane 2005).

A major taxonomic revision of *Anagrus* occurred in the 1990s, when a global survey to evaluate the systematics of this genus revealed that a number of unique species were all being referred to as *A. epos* (Triapitsyn 1998). For instance, re-examination of voucher specimens from the Doutt and Nakata work (Doutt and Nakata 1965, Doutt et al. 1966, Doutt and Nakata 1973) found that what was described as *A. epos* reared from *D. californica* on wild blackberry and from *E. elegantula* on cultivated grape were actually two different species, *A. daanei* (commonly reared from *D. californica* on *Rubus* spp.) and *A. erythroneurae* (commonly reared from *E. elegantula* and *Erasmoneura variabilis* [Beamer] on grape; Trjapitzin 1995). Although both of these species are known to attack *E. elegantula*, this re-examination confounded results from the earlier studies that had concluded that the *Anagrus* wasps overwintering on blackberry were the same as those attacking *E. elegantula* in vineyards. Furthermore, these findings may explain why previous attempts to augment *Anagrus* overwintering habitat by planting either blackberries or prunes near vineyards were not entirely successful, as these plants may have been supporting populations of an *Anagrus* species that was not actually the dominant species attacking *Erythroneura* leafhoppers in vineyards.

Following these revisions by Triapitsyn (1998), further studies to identify *Anagrus* overwintering habitat were conducted in New York (Williams and Martinson 2000), Washington and Oregon (Wright and James 2007), and British Columbia (Lowery et al. 2007). In a related effort, Prischmann et al. (2007) identified the *Anagrus* species attacking *E. elegantula* and *E. ziczac* Walsh (Virginia creeper leafhopper) in Washington and Oregon vineyards. They found that *E. elegantula* was attacked by *A. daanei*, *A. erythroneurae*, and *A. tretiakovae* Triapitsyn whereas *E. ziczac* was attacked only by *A. daanei* and *A. tretiakovae*.

Anagrus erythroneurae and *A. daanei* are present in northern California vineyards, but no definitive studies have been conducted to identify their alternate host plant preferences in this region. Although many of the leafhopper hosts and host plants identified in previous surveys can be found in this area (such as *D. californica* and *Rubus* spp.), there are a number of plant species unique to the region that have never been surveyed (such as *Baccharis pilularis* DC., *Ceanothus* spp., and *Aesculus californica* [Spach] Nutt.). Therefore, a survey was conducted during 2012–2014 to identify vegetational resources utilized by *Anagrus* in California's North Coast wine-grape-growing region, as well as to identify the leafhoppers associated with these plants that may be serving as the alternate host for *Anagrus* wasps.

Materials and Methods

Study sites consisted of 19 separate patches (>400 m^2 each) of natural and cultivated habitats found near vineyards in Napa, Sonoma, and Mendocino County, CA. The primary natural habitats sampled were oak woodland and riparian, which are the dominant natural habitats in this study region. Cultivated habitats such as hedgerows, gardens, and landscape plantings adjacent to vineyards were also included in the survey.

From February to May 2012 and January 2013 to March 2014, vegetation was sampled approximately every 4 wk from plant species in these habitats. *Anagrus* wasps were reared following methods adapted from Lowery et al. (2007). Plant material was brought to the greenhouse, weighed, and then placed into opaque cylindrical paper cartons and held under controlled conditions (24°C, 40% RH, and a photoperiod of 16:8 [L:D] h) for 4 wk to allow for the emergence of any *Anagrus* wasps. A vial was secured to the top of the container to let light enter the chamber and attract and capture emerging wasps. Emergence chambers were checked daily. All emerging adult *Anagrus* were collected and stored in 95% ETOH. All specimens were then identified to species or genus.

At these same sites, leafhoppers were sampled following methods adapted from Summers et al. (2004). Sampling took place approximately every 4 wk from December 2012 to March 2014. Leafhoppers were sampled from individual plant species using a D-vac-type suction sampling machine, which consisted of a 25 cc gasoline blower/vacuum fitted with a 18.9-liter (5 gallon) bucket on the vacuum tube to create a 0.093 m^2 (1 ft^2) sampling cone. Each selected plant species in a given habitat was sampled three times, with each sample consisting of five thrusts with the D-vac running at full throttle. Samples were held in a cooler and brought to the laboratory for processing. All leafhopper specimens were sorted and identified to species or genus.

Results

Anagrus Collection

Over the course of this survey, 1,124 collections of plant material were made from 78 different plant species found in and around North Coast vineyards. A total of 1,957 *Anagrus* specimens were reared from 20 plant genera across 13 families (Tables 1 and 2). *Anagrus* species collected in this survey include *A. atomus* (L.), *A. avalae* Soyka, *A. daanei*, *A. erythroneurae*, *A. nigriventris* Girault, and *A. tretiakovae*. Some specimens could only be identified to genus, often because of physical damage. Both ethanol-preserved and slide-mounted voucher specimens of the *Anagrus* wasps identified in this study were deposited in the Entomology Research Museum, University of California, Riverside, CA.

Leafhopper Collection

Overall 1,348 D-vac samples were taken from 45 plant species across 42 plant genera. A total of 7,856 leafhoppers were collected, of which 3,663 were *E. elegantula*. The remaining 4,193 leafhopper specimens included 30 species or genera collected from 30 different plant species or genera, including all of the plants that yielded *Anagrus* wasps (Tables 1 and 2). Point-mounted voucher specimens were deposited both in the Essig Museum of Entomology, University of California, Berkeley, CA, and the Illinois Natural History Survey, University of Illinois, Urbana-Champagne, IL.

Data Summary and Presentation

The host plants identified in this study are classified as either "natural" or "cultivated." Natural plant species are those that are endemic to the study region while cultivated plants are maintained as part of a hedgerow, garden, or some other form of aesthetic and/or productive planting near vineyards. This distinction serves to

Table 1. Alternate host plants (natural) used by *Anagrus* spp. (per kg) and co-occurring leafhopper adults (presence/absence)

Host plant	Insect	Winter	Spring	Summer	Fall
Aesculus californica (Sapindaceae)	*Anagrus atomus*		2.1		
	Anagrus erythroneurae		0.8		
	Anagrus nigriventris		1.6		
	Anagrus spp.		0.4	2.4	
	Aceratagallia obscura		x		
	Alconeura sp.		x		
	Alconeura unipuncta		x		
	Caladonus coquilletti		x		
	Colladonus montanus reductus		x		
	Dikrella californica		x		
	Empoasca spp.	x	x	x	
	Erythroneura caetra		x		
	Erythroneura elegantula		x		
	Graphocephala atropunctata				x
	Neocoelidia sp.			x	
	Scaphytopius sp.			x	
	Thamnotettix zelleri		x		
Alnus rhombifolia (Betulaceae)	*Anagrus atomus*			3.7	
	Anagrus avalae	0.7	2.3	1.6	3.7
	Anagrus erythroneurae	8.9	2.3	3.7	3.6
	Anagrus spp.		2.6	1.6	0.6
	Alconeura sp.		x		
	Alconeura unipuncta			x	x
	Caladonus coquilletti			x	x
	Edwardsiana commisuralis		x	x	x
	Empoasca cerea				x
	Empoasca sp.		x	x	x
	Erythroneura elegantula		x		
	Graphocephala atropunctata				x
Archtostaphylos spp. (Ericaceae)	*Anagrus erythroneurae*	0.6			
	Empoasca spp.		x		
Baccharis pilularis (Asteraceae)	*Anagrus atomus*	1.3			
	Anagrus erythroneurae	36.6	20.2	4.8	4.1
	Anagrus spp.	0.4	0.2		
	Aceratagallia obscura			x	
	Alconeura nudata		x		
	Caladonus coquilletti				x
	Colladonus montanus reductus			x	
	Deltocephalus fuscinervosus				x
	Empoasca cerea	x	x	x	x
	Empoasca spp.	x	x	x	x
	Stragania sp.			x	
Populus sp. (Salicaceae)	*Anagrus* spp.			2.9	
	Erythroneura elegantula				x
Quercus agrifolia (Fagaceae)	*Anagrus erythroneurae*		0.3		
	Alconeura spp.		x		
	Empoasca spp.	x	x		
	Macropsis sp.		x		
	Thamnotettix zelleri		x		
Rubus spp. (Rosaceae)	*Anagrus atomus*	6.5	12.8	23.3	6.7
	Anagrus avalae		0.5		
	Anagrus daanei				1.7
	Anagrus erythroneurae	37.2	17.9	14.9	16.4
	Anagrus nigriventris	0.6	0.5		
	Anagrus spp.	5.3	1.1	8.7	
	Alconeura unipuncta		x		
	Dikraneura rufula				x
	Dikrella californica	x	x	x	x
	Edwardsiana commisuralis				x
	Empoasca spp.		x	x	x
	Erythroneura elegantula		x		
	Graphocephala atropunctata			x	
	Ribautiana tenerrima		x		x

(continued)

Table 1. continued

Host plant	Insect	Winter	Spring	Summer	Fall
	Thamnotettix zelleri		x	x	
Salix sp. (Salicaceae)	*Anagrus erythroneurae*	1.6			
	Anagrus nigriventris	1.6			
	Anagrus spp.	1.8		20.2	22.1
	Alconeura unipuncta			x	x
	Caladonus coquilletti			x	x
	Deltocephalus fuscinervosus				x
	Dikraneura rufula				x
	Empoasca calcara			x	x
	Empoasca cerea		x		
	Empoasca spp.			x	x
	Erythroneura caetra			x	x
	Erythroneura rosa		x		
	Euscelidius schenki			x	
	Idiocerus sp.	x		x	x
	Macropsis sp.			x	
	Rhytidodus decimusquartus		x		
Umbellularia californica (Lauraceae)	*Anagrus* spp.	5.4			
	Empoasca spp.			x	
	Idiocerus sp.			x	
Vinca major (Apocynaceae)	*Anagrus nigriventris*	4.4			
Vitis californica (Vitaceae)	*Anagrus atomus*				0.9
	Anagrus daanei				4.6
	Anagrus erythroneurae			1.6	5.6
	Anagrus spp.				0.9
	Deltocephalus fuscinervosus			x	x
	Dikraneura rufula				x
	Dikrella californica				x
	Empoasca spp.			x	x
	Erasmoneura nigerrima				x
	Graphocephala atropunctata			x	
	Neocoelidia sp.			x	
	Osbornellus sp.			x	x
	Ribautiana tenerrima				x
	Scaphytopius sp.				x

differentiate host plant species that are frequently found throughout this region (natural) from those that are only occasionally encountered (cultivated). This is important to note because natural host plant species are likely supporting *Anagrus* and leafhopper populations on a regional scale, whereas cultivated species are only making minor contributions. In a few rare cases, a plant species classified as natural was sometimes sampled from a cultivated setting, such as a stand of *Alnus rhombifolia* Nutt. or *B. pilularis* that was part of a hedgerow, garden, or landscape planting.

To adjust the data for sampling effort, the *Anagrus* species reared from host plants are displayed in terms of total wasps per kilogram of plant material sampled (Tables 1 and 2) and *E. elegantula* densities are presented as total number per D-vac sample (Table 3). Densities were not recorded for any of the other leafhopper species and so these data are shown as presence/absence (Tables 1 and 2). All data are delineated by seasonal period, which consists of "Winter" (December to February), "Spring" (March to May), "Summer" (June to August), and "Fall" (September to November).

Co-occurrence of *Anagrus* and leafhopper species on specific host plants during each seasonal period is summarized in Table 4. The purpose of this is to evaluate possible relationships between *Anagrus* spp. and leafhoppers found on the same host plants. While co-occurrence does not necessarily imply utilization, if the same species of *Anagrus* and leafhopper frequently co-occur on the same plant at the same time, it may be more likely that the leafhopper is an alternate host of *Anagrus* spp. That said, this study does not definitively identify which leafhopper species are being utilized by *Anagrus* spp. on any individual host plant.

Discussion

Alternate Host Plants Used by *Anagrus* spp

This survey confirmed results from previous studies of *Anagrus* host plant associations and identified a number of new hosts. Host plant families that have not previously been reported include Apocynaceae, Asteraceae, Ericaceae, Lauraceae, Rhamnaceae, and Sapindaceae; genera include *Arctostaphylos*, *Umbellularia*, *Ceanothus*, *Heteromeles*, *Populus*, and *Aesculus*; and species include *B. pilularis*, *A. californica*, *Vinca major* L., *Umbellularia californica* (Hook. & Arn.) Nutt., and *Heteromeles arbutifolia* (Lindl.) M. Roem (Tables 1 and 2). The dominant *Anagrus* species identified in this survey were *A. erythroneurae* and *A. atomus*; *A. avalae*, *A. daanei*, *A. nigriventris*, and *A. tretiakovae* were far less frequently encountered (Tables 1 and 2).

Anagrus atomus was reared from 12 plant species or genera from six different families (Tables 1 and 2). It was primarily collected from *Nepeta* sp., *Mentha* sp., and *Rubus* spp., and to a lesser extent from *A. californica*, *A. rhombifolia*, *B. pilularis*, *Lavandula angustifolia* Mill., *Malus domestica* Borkh., *Rosa* spp., *Rosmarinus officinalis* L., *Salvia* spp., and *Vitis californica* Benth. (Tables 1 and

Table 2. Alternate host plants (cultivated) used by *Anagrus* spp. (per kg) and co-occurring leafhopper adults (presence/absence)

Host plant	Insect	Winter	Spring	Summer	Fall
Ceanothus spp. (Rhamnaceae)	*Anagrus erythroneurae*	6.5	1.7	18.1	204.1
	Anagrus tretiakovae				24.6
	Anagrus spp.		1.7	1.3	
	Alconeura nudata		x	x	
	Alconeura spp.	x	x		
	Deltocephalus fuscinervosus		x		
	Dikrella californica	x			
	Empoasca sp.	x	x	x	
	Erythroneura elegantula		x		
	Scaphytopius (*Scaphytopius*) sp.			x	x
	Thamnotettix zelleri		x		
Lavandula angustifolia (Lamiaceae)	*Anagrus atomus*		2.8	5.8	
	Erythroneura elegantula		x		
	Eupteryx decemnotata		x		
Malus domestica (Rosaceae)	*Anagrus atomus*	2.5			
	Anagrus erythroneurae		8.1		1.9
	Anagrus spp.			1.3	
	Colladonus spp.				x
	Dikrella californica				x
Malus domestica (Rosaceae)	*Edwardsiana rosae*				x
	Empoasca spp.				x
	Eupteryx decemnotata	x			
Mentha sp. (Lamiaceae)	*Anagrus atomus*		4.8	11.5	6.8
	Anagrus erythroneurae		139.7	234.5	167.6
	Anagrus spp.		8.6		4.3
	Aceratagallia obscura	x		x	x
	Aceratagallia spp.			x	
	Acinopterus angulatus			x	x
	Caladonus coquilletti			x	
	Colladonus montanus reductus		x		
	Deltocephalus fuscinervosus		x	x	
	Empoasca (Hebata) sp.		x		
	Empoasca cerea				x
	Empoasca spp.	x	x	x	x
	Erythroneura elegantula	x	x		
	Eupteryx decemnotata	x	x	x	x
	Euscelidius schenki		x		
	Macrosteles quadrilineatus		x	x	
	Scaphytopius sp.		x	x	
	Thamnotettix zelleri		x		
Nepeta sp. (Lamiaceae)	*Anagrus atomus*	47.1	19	11.8	20
	Anagrus erythroneurae	437.6	1029.9	41.5	270.6
	Anagrus spp.	29.4	18.9	17.9	18.2
	Aceratagallia obscura				x
	Amblysellus grex				x
	Deltocephalus fuscinervosus		x	x	
	Empoasca arida				x
	Empoasca spp.			x	
	Eupteryx decemnotata		x	x	x
Pyrus communis (Rosaceae)	*Anagrus erythroneurae*	12.9			3.1
	Anagrus spp.	6.5			
	Empoasca spp.				x
	Idiocerus sp.				x
Rosa spp. (Rosaceae)	*Anagrus atomus*	0.5			
	Anagrus daanei				0.7
	Anagrus nigriventris			1.1	
	Dikrella californica	x			
	Edwardsiana rosae				x
	Empoasca cerea				x
	Empoasca spp.	x	x		x
	Erythridula occidua		x		
	Erythroneura elegantula		x		
Rosa spp. (Rosaceae)	*Exitianus exitiosus*			x	

(continued)

Table 2. continued

Host plant	Insect	Winter	Spring	Summer	Fall
	Thamnotettix zelleri		x		
Rosmarinus officinalis (Lamiaceae)	*Anagrus atomus*	7.3			
	Alconeura unipuncta		x		
	Empoasca spp.		x		
	Erythroneura elegantula	x	x		
	Erythroneura rosa		x		
	Eupteryx decemnotata	x	x	x	
Salvia spp. (Lamiaceae)	*Anagrus atomus*	1.5	7.4	14.6	
	Anagrus erythroneurae	7.7	82.2	107.6	3.2
	Aceratagallia obscura		x		
	Aceratagallia spp.		x		
	Acinopterus angulatus				x
	Alconeura spp.		x		
	Caladonus coquilletti			x	
	Colladonus montanus reductus		x		
	Deltocephalus fuscinervosus		x		
	Draeculaphala sp.		x		
	Empoasca (Hebata) sp.	x	x	x	x
	Empoasca spp.		x	x	x
	Erythroneura elegantula	x	x		
	Erythroneura rosa	x			
Salvia spp. (Lamiaceae)	*Eupteryx decemnotata*	x	x	x	
	Scaphytopius sp.		x		
	Xerophloea peltata				x

Table 3. Abundance of adult *E. elegantula* (per D-vac sample) on noncrop hosts (N/C = "natural" and "cultivated"), cultivated grape vines, and the vineyard floor

N/C	Family	Plant	Winter	Spring	Summer	Fall
N	Adoxaceae	*Sambucus* sp.	–	1.3	0	–
N	Asteraceae	*Baccharis pilularis*	0	0.2	0.4	0.3
C		*Calendula* sp.	–	0.3	–	–
N	Betulaceae	*Alnus* sp.	0	1.2	0.4	0.2
C		*Corylus cornuta*	–	9	1.3	1.7
N	Ericaceae	*Arctostaphylos* spp.	0	0.1	–	0
N	Fagaceae	*Quercus agrifolia*	0	0.1	0	1
C	Lamiaceae	*Lavandula angustifolia*	–	1.8	0.3	–
C		*Mentha* sp.	12.1	10.1	0	8.7
C		*Nepeta* sp.	–	0	1.3	0.3
C		*Rosmarinus officinalis*	0.6	0.1	0.3	–
C		*Salvia* spp.	1	0.2	1.2	0.3
N	Lauraceae	*Umbellularia californica*	0	0.0	0	0.3
C	Malvaceae	*Tilia* sp.	–	0	42	119.7
C	Oleaceae	*Olea europaea* L.	0	0.2	0	0
N	Papaveraceae	*Eschscholzia californica* Cham.	–	2	–	–
N	Rhamnaceae	*Ceanothus* spp.	0	2.7	0.3	0
N	Rosaceae	*Heteromeles arbutifolia*	0.6	0	0.3	1.3
C		*Prunus* spp.	0	0.2	0	0.2
C		*Rosa* spp.	0.3	40.1	5.3	16.5
N	Rosaceae	*Rubus* sp.	0.2	7.7	0	1.7
C	Rutaceae	*Citrus limon* (L.) Burm. f.	0	0	0.3	1.3
N	Salicaceae	*Populus* spp.	–	–	0	0.6
N		*Salix* spp.	0	21.3	1	0.2
N	Sapindaceae	*Aesculus californica*	0	13.8	0	0
C	Ulmaceae	*Ulmus* sp.	0	0.3	0	0
C	Vitaceae	*Parthenocissus quinquefolia*	–	55.3	20	6.3
N		*Vitis californica*	–	–	3.6	21
C		*Vitis vinifera*	–	1.9	37	112.6
–	Vineyard floor	–	3	5.7	0.1	7.9
	Total		17.8	175.6	115.1	302.1

Table 4. Co-occurrence of leafhopper adults and *Anagrus* spp. reared from undetermined hosts on the same host plant within the same seasonal period (atom. = atomus, ava. = avalae, daan. = daanei, eryth. = erythorneurae, nigri. = nigriventris, tret. = tretiakovae)

Leafhopper	*atom.*	*ava.*	*daan.*	*eryth.*	*nigri.*	*tret.*	*A.* spp.	Total
Aceratagallia obscura	5	0	0	6	1	0	3	15
Aceratagallia spp.	2	0	0	2	0	0	0	4
Acinopterus angulatus	2	0	0	3	0	0	1	6
Alconeura nudata	0	0	0	3	0	0	3	6
Alconeura spp.	2	1	0	6	1	0	3	13
Alconeura unipuncta	3	3	0	4	2	0	6	18
Amblysellus grex	1	0	0	1	0	0	1	3
Caladonus coquilletti	4	2	0	6	1	0	5	18
Colladonus m. reductus	3	0	0	4	1	0	2	10
Colladonus spp.	0	0	0	1	0	0	0	1
Deltocephalus fuscinervosus	6	0	1	9	0	0	6	22
Dikraneura rufula	2	0	2	2	0	0	2	8
Dikrella californica[a]	7	1	2	8	3	0	5	26
Draeculaphala sp.	1	0	0	1	0	0	0	2
Edwardsiana commisuralis	2	3	1	4	0	0	3	13
Edwardsiana rosae[a]	0	0	1	1	0	0	0	2
Empoasca (Hebata) sp.	4	0	0	5	0	0	1	10
Empoasca arida	1	0	0	1	0	0	1	3
Empoasca calcara	0	0	0	0	0	0	2	2
Empoasca cerea	2	1	1	6	0	0	4	14
Empoasca spp.	14	4	3	26	2	0	17	66
Erasmoneura nigerrima	1	0	1	1	0	0	1	4
Erythridula occidua	0	0	0	0	0	0	0	0
Erythroneura caetra	1	0	0	1	1	0	3	6
Erythroneura elegantula[a]	7	2	0	7	2	0	5	23
Erythroneura rosa	1	0	0	1	0	0	0	2
Eupteryx decemnotata	12	0	0	9	0	0	5	26
Euscelidius schenki	1	0	0	1	0	0	2	4
Exitianus exitiosus	0	0	0	0	1	0	0	1
Graphocephala atropunctata	1	1	0	3	0	0	2	7
Idiocerus sp.	0	0	0	2	1	0	3	6
Macropsis sp.	0	0	0	1	0	0	1	2
Macrosteles quadrilineatus	2	0	0	2	0	0	1	5
Neocoelidia sp.	0	0	0	1	0	0	1	2
Osbornellus sp.	1	0	1	2	0	0	1	5
Rhytidodus decimusquartus	0	0	0	0	0	0	0	0
Ribautiana tenerrima[a]	3	1	2	3	1	0	2	12
Scaphytopius sp.	4	0	1	4	0	1	3	13
Stragania sp.	0	0	0	1	0	0	0	1
Thamnotettix zelleri	4	1	0	6	2	0	5	18
Xerophloea peltata	0	0	0	1	0	0	0	1

[a] Known host.

2). The host plants *B. pilularis* and *A. californica* are both new records for *A. atomus*. *Alnus rhombifolia* is also a new record, although *A. atomus* has been collected from other genera in the Betulaceae, including *Betula* spp. and *Ostrya* sp. (Tables 1 and 2; Williams and Martinson 2000, Lowery et al. 2007). *Anagrus atomus* is globally distributed with a wide range of hosts (Chiappini and Triapitsyn 2007, Triapitsyn 2015, Noyes 2016). In Europe and Asia, *A. atomus* is commonly found attacking *Empoasca* spp. leafhoppers on grape vines (Chiappini et al. 1996, Triapitsyn and Berezovskiy 2004, Chiappini and Triapitsyn 2007, Triapitsyn 2015). In the Nearctic it is frequently encountered on plants in the Rosaceae, where it has been documented attacking *Zonocyba pomaria* (McAtee) on *Malus* spp. and *Prunus* spp., *Kyboasca maligna* (Walsh) on *Malus* spp., *E. prunicola* on *Rosa* spp. and *Prunus* spp., *E. rosae* on *Rosa* spp., *Malus* spp. and *Rubus* spp., and *Dikrella* sp. on *Rubus* spp. (Triapitsyn 1998). This species has also been recovered from unknown hosts on *Acer glabrum* Torr., *L. angustifolia*, *Mentha* spp., *Nepeta* spp., *Ostrya virginiana* (Mill.) K. Koch., *Prunus virginiana* L., *Purshia* sp., *R. multiflora* Thunb., *Salix* sp., *Salvia officinalis* L., and *Ulmus pumila* L. (Williams and Martinson 2000, Lowery et al. 2007, Wright and James 2007).

Anagrus avalae was primarily collected from *A. rhombifolia*, but a few specimens were also reared from *Rubus* spp. (Tables 1 and 2). Similar to *A. atomus*, the specimens of *A. avalae* reared from *A. rhombifolia* also represent a new host plant record for this species, although it has been previously recovered from other plants in the same family (Betulaceae), including *Betula occidentalis* Hook., *Carpinus betulus* L., and *Corylus avellana* L. (Chiappini and Triapitsyn 1997, Lowery et al. 2007). *Anagrus avalae* can be found throughout the Holarctic as well as Australasia (Triapitsyn 2015, Noyes 2016) and is known to attack a number of leafhoppers on plants in the Rosaceae, including *Edwardsiana rosae* (L.) on *Rosa* spp., *E. prunicola* on *Prunus* spp., *E. crataegi* (Baker) and *Z. pomaria* on *Malus* spp., and *Ribautiana tenerrima* (Herrich-Schäffer) on *Rubus* spp. (Triapitsyn 1998, Triapitsyn and Berezovskiy 2004, Lowery et al. 2007, Wright and James 2007, Noyes 2016). This species has also been recovered from *Zonocyba* sp. on *Ulmus* sp., *Empoasca vitis* (Göthe) on *V. vinifera*, and from an unknown host on *Sambucus nigra* L. (Chiappini and Triapitsyn 1997, Triapitsyn 1998, Triapitsyn and Berezovskiy 2004, Noyes 2016).

Anagrus daanei was reared from only three plant hosts in two families (Tables 1 and 2). This species is commonly found attacking *E. elegantula* in North Coast wine grape vineyards. Outside of the vineyard it could only be found on *Rubus* spp., *Rosa* spp., and *V. californica* (Tables 1 and 2). *Anagrus daanei* has been documented attacking *Erythroneura* leafhoppers in Washington state and British Columbia (Lowery et al. 2007, Prischmann et al. 2007). In western North America, *A. daanei* has also been found on *Prunus* sp. (Triapitsyn 1998) and *Parthenocissus quinquefolia* (L.) Planch. (Lowery et al. 2007). Surveys in the eastern United States have collected *A. daanei* from unknown leafhopper eggs on *Acer saccharum* Marshall, *Robinia pseudoacacia* L., *Rosa multiflora* Thunb., and *Zanthoxylum americanum* Mill. (Williams and Martinson 2000).

Anagrus erythroneurae was collected from 14 plant species or genera from 10 families (Tables 1 and 2). Specimens primarily came from *A. rhombifolia*, *B. pilularis*, *Ceanothus* spp., *Mentha* sp., *Nepeta* sp., *Rubus* spp., *Salvia* spp., and to a lesser extent from *A. californica*, *Archtostaphylos* spp., *Malus* sp., *Pyrus communis* L., *Quercus agrifolia* Née, *Salix* spp., and *V. californica* (Tables 1 and 2). Most of these host plant associations match with previous Nearctic surveys (Triapitsyn 1998, Williams and Martinson 2000, Lowery et al. 2007, Wright and James 2007), although *B. pilularis*, *Archtostaphylos* spp., and *Ceanothus* spp. are all new records for this species. A survey in British Colombia reported *A. erythroneurae* from *Cornus stolonifera* L. and *Prunus* spp. as well (Lowery et al. 2007). This species has been reported to attack *Z. pomaria* on *Malus* spp., *E. prunicola* on *Prunus* spp., *Dikrella* spp. (most likely *D. californica*) on *Rubus* spp. and a variety of leafhoppers on *Vitis* spp., including *D. cockerellii* (Gillette) in New Mexico, *Erythroneura bistrata* McAtee and *E. comes* (Say) in New York, and *E. elegantula* and *E. variabilis* in California and British Columbia (Triapitsyn 1998).

Anagrus nigriventris was encountered on five plant genera across four families, including *A. californica*, *Rubus* spp., *Rosa* spp., *Salix* spp., and *V. major* (Tables 1 and 2). Both *V. major* and *A. californica* are new host plant associations for this species. Previous surveys have identified *A. nigriventris* attacking *Erythroneura* leafhoppers

on cultivated and wild grape in New York state as well as on leafhopper eggs on *R. pseudoacacia* (Williams and Martinson 2000). In California, Oregon, and Washington, it has been reared from leafhopper eggs on *Rubus* spp. in multiple surveys (Triapitsyn 1998, Lowery et al. 2007, Wright and James 2007).

Anagrus tretiakovae was recovered only from *Ceanothus* spp., which is a new host plant association for this species (Tables 1 and 2). *Anagrus tretiakovae* has previously been found attacking *Erythroneura* leafhoppers on grape in New York (Williams and Martinson 2000), Delaware and Maryland (Triapitsyn 1998), Washington (Prischmann et al. 2007), California (Segoli and Rosenheim 2013), and Arizona, New Mexico and Baja California Mexico (Triapitsyn 1998). This species has also been collected from *P. virginiana*, *Rosa* spp., and *Rubus* spp. in Oregon and Washington (Wright and James 2007).

Timing of *Anagrus* spp. Host Plant Use

Records on the timing of host plant use are not absolute due to differences in sampling effort over the years, but some conclusions can still be inferred. Certain *Anagrus* species appeared to make use of leafhoppers on specific host plants throughout the majority of the year. This includes *A. atomus* from *Mentha* sp., *Nepeta* sp., *Rubus* spp., and *Salvia* spp.; *A. avalae* from *A. rhombifolia*; and *A. erythroneurae* from *A. rhombifolia*, *B. pilularis*, *Ceanothus* spp., *Mentha* sp., *Nepeta* sp., *Rubus* spp., and *Salvia* spp. (Tables 1 and 2). It is unclear whether the more cryptic species that were documented on these plants are able to utilize them throughout the year as well, due to their overall low abundance. This includes *A. daanei* and *A. nigriventris* on *Rubus* spp. and *A. tretiakovae* on *Ceanothus* spp.

Alternately, some host plants appeared to be utilized by *Anagrus* spp. only during very specific periods of the year, such as *A. atomus*, *A. erythroneurae*, and *A. nigriventris* on *A. californica* in Spring and *A. atomus*, *A. erythroneurae*, and *A. daanei* on *V. californica* from late summer through fall (Tables 1 and 2). Both of these plant species are deciduous, and although they were sampled multiple times throughout the year, *Anagrus* specimens were only recovered when there was foliage on these plants. This is especially true for *A. californica*, which is drought-deciduous and thus in a Mediterranean climate has a very narrow window of time during which leaves are present (typically March to May, although leaves can persist as late as August when soil moisture is sufficient). Similarly, while *A. avalae* and *A. erythroneurae* were collected from *A. rhombifolia* throughout the entire year, *A. atomus* was collected from this host plant only in summer. *Alnus rhombifolia* is winter-deciduous and thus collections of *A. avalae* and *A. erythroneurae* between December to February indicate the likely use of a leafhopper host that deposits eggs into the woody material of the plant while *A. atomus* (collected only in the summer when leaves are present) are suspected of attacking leafhopper host eggs primarily found on the leaves.

Anagrus Movement Between Overwintering Habitat and Vineyards

Doutt and Nakata (1973) outlined a two-phase cycle in which *Anagrus* parasitoids were primarily found in commercial grape vineyards attacking *E. elegantula* throughout the growing season (March to October) but when the grape vines lose their leaves and become dormant (November to March) the *Anagrus* disperse to other plant species and attack alternate leafhopper hosts to successfully overwinter. While this is generally accurate, it is likely that *A. erythroneurae* and *A. daanei* actually make use of a number of intermediate host plants during their seasonal dispersal between overwintering habitat and commercial vineyards. For example, they may utilize *A. californica* in the spring as they move from overwintering habitat into vineyards and *V. californica* in the fall as they move from vineyards into overwintering habitat. A similar process, but with different host plants, was suggested by Cerutti et al. (1991) for *A. atomus* attacking *E. vitis* (Göthe) in European vineyards.

Alternate host plants are critical for the support of overwintering populations of *A. erythroneurae* and *A. daanei*, and also appear to provide refugia for these parasitoids throughout the year. Both *A. erythroneurae* and *A. daanei* were consistently observed attacking *E. elegantula* in vineyards during the summer and were simultaneously collected from a number of alternate host plants, including *B. pilularis*, *Rubus* spp., *Salvia* spp., *Nepeta* sp., and *Ceanothus* spp. (Tables 1 and 2). This indicates that some portion of the *Anagrus* population remains outside of the vineyard throughout the year, even when *E. elegantula* is available on wine grapes. These alternate summer host plants likely serve as refugia when vineyard conditions become inhospitable for the *Anagrus* (i.e., low/no *E. elegantula* population, nontarget impacts of chemical controls, lack of water or floral resources) and/or provide individuals to re-colonize vineyards following a localized reduction in the *Anagrus* population.

Regional Dynamics of *E. elegantula* Parasitoids

Anagrus erythroneurae and *A. daanei* are the key egg parasitoids of *E. elegantula* in North Coast wine grape vineyards and arguably the most important natural enemy for biological control of this pest. While large quantities of *A. erythroneurae* were reared from *Nepeta* sp., *Mentha* sp., and *Salvia* spp., it is thought that *B. pilularis* and *Rubus* sp. are the primary overwintering host plants supporting regional populations of this parasitoid, as these two plants are very abundant in the natural habitats of the North Coast region. *Baccharis pilularis* is a drought-tolerant woody perennial shrub and are typically found growing in field margins, along roadways, and in other disturbed habitats. While *Rubus* spp. are more restricted to riparian habitats, they can thrive outside of these areas given the proper soil moisture requirements and are therefore also found along drainage ditches and in low-lying pastures. Similarly, out of the three *A. daanei* host plants documented in this survey, *Rubus* spp. is likely the key species supporting regional *A. daanei* populations. The other two host plants (*Rosa* spp. and *V. californica*) are either restricted in their abundance (*Rosa* spp., mostly found in small-scale garden plantings) or serve as a suitable plant host only in the summer and fall when foliage is present (*V. californica*, which is winter deciduous). As mentioned, *Rubus* spp. is widely abundant throughout the North Coast and has foliage throughout the entirety of the year.

Leafhoppers on the Alternate Host Plants

Results from the leafhopper survey revealed 30 species across 30 genera (Tables 1, 2, and 4). Some of the species or genera had not been previously reported from California, and a number of new host plant records are presented here (Tables 1 and 2). Excluding *E. elegantula*, the most frequently encountered species were *Eupteryx decemnotata* Rey, *Deltocephalus fuscinervosus* Van Duzee, and *D. californica*, and the most frequently encountered genera were *Empoasca* spp., *Alconeura* spp., *Colladonus* spp., and *Aceratagallia* spp. (Tables 1 and 2). What follows is a description of the various leafhopper species collected in this survey. For many of them there are no reports of host plants, key parasitoids, and/or overwintering biology. Descriptions are only given for species, not genera.

Aceratagallia obscura Oman can be found in Arizona, California, and Oregon (Oman 1933, 1949). It was originally described as a pest of truck-crops and legumes in California (Oman 1933), and has been shown to transmit potato yellow dwarf virus (Black 1944, Nielson 1968), but is not currently considered a pest of economic significance. No other information exists about alternate host plants for *A. obscura* specifically, although the *Aceratagallia* are commonly encountered on a number of annual plants, including forbs, grasses, sedges, amaranths, chenopods, composites, legumes, mallows, mint, mustards, phlox and spurge (Hamilton 1998). Oman (1933) also reported the genus on spruce trees. While Lakin (1985) found that *A. obscura* is attacked by *Polynema* spp. (Hymenoptera: Mymaridae) the *Aceratagallia* overwinter as adults, thus making *A. obscura* an unlikely candidate to support overwintering *Anagrus* spp. (Hamilton 1998).

Acinopterus angulatus Lawson is commonly found in California and the southwest United States and is widely distributed throughout Central and South America as well as the Caribbean (DeLong and Severin 1947). This species can typically be found on alfalfa (*Medicago sativa* L.), and has also been collected from Spanish clover (*Acmispon americanus* [Nutt.] Rydb.), ladino clover (*Trifolium repens* L. var. *latum* McCarthy), wild licorice (*Glycyrrhiza lepidota* [Nutt.] Pursh), and on weeds and grasses in pasture primarily composed of *Bidens pilosa* L. (DeLong and Severin 1947, Nielson 1968).

Alconeura unipuncta (Gillette) can be found throughout the continental United States as well as in Cuba and has been reported on *Pluchea sericea* Nutt. (Ball and DeLong 1925, Metcalf 1968). *Alconeura nudata* Ball & DeLong has been reported in the same region but from a more limited range that includes just Wyoming, Montana and California (Ball and DeLong 1925, Griffith 1938).

Amblysellus grex (Oman) is found in the United States west of the Mississippi River. Krugner et al. (2008) reported that *A. epos* could successfully complete development on eggs of *A. grex*, thus indicating it as a possible alternate host for other species of *Anagrus*. This species has been recovered in California almond orchards (Daane et al. 2011) as well as on various rangeland grasses in Montana (Spangler and Macmahon 1990, Bess et al. 2004).

Caladonus coquilletti (Van Duzee) is found throughout the southwest United States, primarily on *Salix* spp. (Van Duzee 1890, Oman 1949).

Colladonus montanus reductus (Van Duzee) is found throughout the United States and Canada west of the Rocky Mountains, although it is most abundant in California, where it was first described (Van Duzee 1917). This species vectors California aster yellows and has been commonly recovered on alfalfa and clover, although it is not considered a pest of economic importance. It has also been collected from *Malva parviflora* L. and *Atriplex* sp. (Nielson 1957). No parasitoids of this species have been documented to date. It has been shown that shorter photoperiods induce *C. m. reductus* adults to produce diapausing eggs that do not complete development until the following spring (Marsh 1965). Overwintering in an egg stage makes this species a candidate host for overwintering *Anagrus* wasps.

Deltocephalus fuscinervosus is found in the United States west of the Mississippi River as well as in Canada (Metcalf 1968, Kramer 1971).

Dikraneura rufula Gillette can be found west of the Rocky Mountains in the United States as well as in southern British Columbia and Quebec (Beamer 1943, Metcalf 1968). Leafhoppers in this genus have been recovered from vineyards in Canada (Saguez et al. 2014).

Dikrella californica is found along the West Coast of the United States and in southern British Columbia, primarily on *Rubus* spp. (Lawson 1930, Beirne 1956). This was the first species to be identified as an overwintering host for *Anagrus* spp. in vineyards (Doutt and Nakata 1965) and has been the focus of many subsequent studies to further investigate the ecology of the *Rubus-Dikrella-Anagrus* system and the influence of vineyard proximity to *Rubus* spp. on parasitism of *Erythroneura* leafhoppers (Doutt et al. 1966, Doutt and Nakata 1973, Williams 1984, Flaherty et al. 1985). Here, *D. californica* was consistently recovered from *Rubus* spp., indicating its likely role as the primary host plant for this leafhopper. *Dikrella californica* was also present at various times of the year on *A. californica*, *Ceanothus* spp., *M. domestica*, and *V. californica*, all of which yielded *Anagrus* spp. during the same period.

Edwardsiana commissuralis (Stål) is common throughout North America and Canada. Its host plants include *Alnus* spp. and *Cornus* spp. (Christian 1953, Hamilton 1997). This species has also been reported from Siberia (Metcalf 1968). No information is available about which parasitoids specifically attack *E. commissuralis*, although it is likely to have some overlap with the *Anagrus* spp. that are known to attack *E. rosae*.

Edwardsiana rosae is a European species introduced to North America and it can now be found throughout the entire Northern Hemisphere. This species has previously been collected from a number of host plants, including *Alnus* sp., *Corylus* sp., *Crataegus* sp., *Fragaria* sp., *Malus* sp., *Prunus* spp., *P. communis*, *Quercus* spp., *Rhus coriaria* L., *Rosa* sp., *Rubus* sp., *Salix* sp., *Sorbus* sp., and *Styrax officinalis* L. (Le Quesne and Payne 1981, Ossiannilsson 1981, Hamilton 1985, Lahoud 1995, Abdul-Nour 2005, Nickel 2008). This species is known to be attacked by mymarid parasitoids (Mulla 1956), in particular *A. atomus*, *A. avalae*, *A. daanei*, and *A. ustulatus* Haliday (Triapitsyn 1998). Nymphs of this species are also attacked by the endoparasitoids *Chalarus* spp. (Diptera: Pipunculidae) and *Aphelopus* spp. (Hymenoptera: Dryinidae). Previous studies have indicated that this species is likely an overwintering host utilized by *Anagrus* wasps that attack *Erythroneura* and other leafhoppers in vineyards (McKenzie and Beirne 1972, Prischmann et al. 2007, Zanolli and Pavan 2011).

Empoasca arida DeLong is found in the United States west of the Rocky Mountains as well as in Texas (Oman 1949, Metcalf 1968, Dmitriev 2014). Crop hosts include alfalfa and sugar beets and it has been noted as a pest of various truck crops in California (DeLong 1938). Wild hosts include *Quercus* sp., *Conium maculatum* L., and *Parthenium argentatum* Gray (Lange 1944, Goeden and Ricker 1982).

Empoasca calcara DeLong is primarily found in the American Southwest, although specimens have been recovered in Florida as well (Metcalf 1968, Dmitriev 2014). *Platanus occidentalis* L. is the only host plant reported for this species (Dmitriev 2014).

Empoasca cerea DeLong has been widely collected in the United States west of the Rocky Mountains, but specimens have also been recovered in Texas, Alabama, Florida, and Mexico (DeLong 1931, Metcalf 1968). This species has been found on alfalfa (*M. sativa*), sugar beets (*Beta vulgaris* L.), and sweet potato (*Ipomoea batatas* [L.] Lam.) (Dmitriev 2014), although it is not necessarily a key pest of these crops relative to other *Empoasca* species, such as *E. fabae* (Harris), *E. solana* DeLong, and *E. mexara* Ross & Moore. *Empoasca cerea* has also been collected from various perennial shrubs and subshrubs, including *Ericameria cooperi* (A. Gray) H.M. Hall, *E. paniculata* (A. Gray) Rydb., *Gutierrezia* sp., and *Salix* sp., as well as on the annual *Hemizonia* sp. (Dmitriev 2014).

Erasmoneura nigerrima (McAtee) has previously only been documented in the central and northeastern United States (Dmitriev and Dietrich 2007).

Erythridula occidua (Beamer & Griffith) was first described from specimens collected in northern California, where it is thought to be endemic (Dmitriev and Dietrich 2009).

Erythroneura caetra McAtee is found throughout the western United States and southwest Canada, primarily on *Salix exigua* Nutt. and other *Salix* spp. as well as on *Prunus* spp. and *Rosa* spp. (Dmitriev and Dietrich 2007).

Erythroneura elegantula is native to the western United States and southwest Canada. The species is also found in Panama, where it was apparently introduced. It can be found primarily on *Vitis* spp. (Dmitriev and Dietrich 2007). The eggs are attacked by *A. erythroneurae* and *A. daanei* and the nymphs by *Aphelopus* spp. (Daane and Costello 2000, Daane et al. 2013). This species overwinters as adults.

Erythroneura rosa Robinson is found in central and southern United States and in central Canada. Host plants include *Salix* spp., *Aesculus* sp., *Populus tremuloides* Michx., *Viburnum* sp., *Crataegus* sp., *Medicago* sp., *P. occidentalis*, *Rubus* sp., *Vitis* sp., and *Toxicodendron radicans* (L.) Kuntze (Dmitriev 2014).

Eupteryx decemnotata was originally described from Mediterranean regions of France and Italy, but expanded its range throughout Europe in the 1990s (Nickel and Holzinger 2006). The species was first reported in North America in 2009, when it was found in Florida on a shipment of rosemary from California, where it is reported from Napa County and Riverside County (Rung et al. 2009). This species has been found on, and considered a pest of, various plants in the Lamiaceae, including rosemary (*R. officinalis*), sage (*Salvia officinalis* L.), catmint (*Nepeta cataria* L.), thyme (*Thymus vulgaris* L.), balm (*Melissa officinalis* L.), pepper mint (*Mentha* x *piperita* L.), basil (*Ocimum basilicum* L.), marjoram (*Origanum majorana* L.), and oregano (*O. vulgare* L.) (Vidano and Arzone 1976, Maczey and Wilson 2004, Nickel and Holzinger 2006). The species overwinters as eggs (Nickel and Holzinger 2006).

Euscelidius schenkii (Kirschbaum) is endemic to Europe, although it has been reported in southern British Columbia on creeping thistle (*Cirsium arvense* [L.] Scop.) (Maw 1976).

Exitianus exitiosa (Uhler) has been reported in the New World from Paraguay, Mexico, the United States, and British Columbia, primarily on grasses, but also on tarragon (*Artemesia dracunculus* L.) and in vineyards where it may use grapevines as a secondary host (Beirne 1956, Kirfman et al. 1986, Saguez et al. 2014, Servín et al. 2014, Silvie et al. 2014).

Graphocephala atropunctata (Signoret) is native to California and is a vector of *Xylella fastidiosa* Wells et al., the bacterium that causes Pierce's Disease in grape vines (Purcell and Finlay 1979, Hill and Purcell 1995). This species can be found throughout the West Coast and as far east as Arizona (Delong and Severin 1949). It has been reported from a number of weeds, woody vines, and shrubs (Delong and Severin 1949, Winkler 1949), but the most common host plants include blackberry (*Rubus* spp.), elderberry (*Sambucus* spp.), wild grape (*V. californica*), willow (*Salix* spp.), mugwort (*Artemesia douglasiana* Besser), and nettle (*Urtica* spp.) (Purcell 1976). In California, it is attacked by the egg parasitoids *Gonatocerus latipennis* (Girault) and *Polynema* spp. (Boyd and Hoddle 2006, Boyd et al. 2008). This species overwinters as an adult, thus making it an unlikely candidate as alternate host for *Anagrus* wasps (Severin 1949).

Macrosteles quadrilineatus (Forbes) is widely distributed throughout North America and Hawaii (Hamilton 1983, Le Roux and Rubinoff 2009). This is a polyphagous species that has been documented on over 300 plant species, primarily grasses and various weeds, along with small grain and vegetable crops (Wallis 1960, Hagel and Landis 1967). This species can overwinter in the egg stage (Hagel and Landis 1967), but the only reported parasitoids are *Pachygonatopus minimus* Fenton, *Neogonatopus ombrodes* Perkins, and *Epigonatopus plesius* Fenton (Hymenoptera: Dryinidae), which are known only to attack the nymph stage (George 1959, Barrett et al. 1965, Freytag 1977, Capinera 2008).

Rhytidodus decimusquartus (Schrank) is endemic to Europe, but has been introduced into North America (Arzone et al. 1987). This species has primarily been collected on *Populus nigra* L., but also *Salix* spp. and *B. vulgaris* (Labonne et al. 1998, Helden and Stewart 2008, Moosavi and Namaghi 2012). It has also been reported in European vineyards (Özgen et al. 2009). The species is thought to overwinter in the egg stage (Stöckmann et al. 2013).

Ribautiana tenerrima is found throughout Europe, North America, and Oceania (Metcalf 1968, Larivière et al. 2010). It is very common on cane berries (*Rubus* spp.) and considered an economic pest of these crops when in commercial production (Raine 1960, Hamilton 1983). It has also been reported from *Agrimonia eupatoria* L., *Alnus* sp., *Betula* spp., *Corylus* spp., Prunus sp., *Quercus* sp., *Salix* sp., *Ulmus* sp., and *Vitis* sp. (Le Quesne and Payne 1981, Saguez et al. 2014). This species overwinters in the egg stage (Raine 1960) and has been implicated as an alternate host for overwintering *Anagrus* wasps (Raine 1960, Ponti et al. 2005).

Thamnotettix zelleri (Kirschbaum) is endemic in North America and Europe (Nast 1987, Hamilton 2014). The species has been reported from vineyards in Europe (Bosco et al. 1997, Özgen et al. 2009) and Israel (Orenstein et al. 2003) and on grasses adjacent to almond orchards in California (Daane et al. 2011). It has also been collected from mint (*Mentha* spp.), anise (*Pirnpinella anisum* L.), and oregano (*Origanum* spp.) (Giray 1980, 1982, Tezcan et al. 2003).

Xerophloea peltata (Uhler) can be found throughout the west and midwest of the United States and Canada (Nielson 1962, Hamilton 2004). This species has been reported from vineyards (Saguez et al. 2014), on various grasses (Beirne 1956, DeLong 1965, Hamilton 2004, Nemec and Bragg 2008), as well as on *Helianthus annus* L. (Gillette and Baker 1895), *Atriplex semibaccata* R.Br., *Chenopodium murale* (L.) S. Fuentes, Uotila & Borsch, *Amaranthus retroflexus* L., *Tribulus terrestris* L., *Franseria acanthicarpa* (Hook.) Coville, *Centaurea solstitialis* L., *M. sativa*, *Vitis* sp., *Vicia* spp. (Severin et al. 1945), *Artemisia* sp., *Gutierrezia* sp., *Salsola pestifer* A. Nelson, *B. vulgaris*, *Apium graveolens* L. (Nielson 1962), *Ambrosia* spp. (Goeden and Ricker 1976), *Solidago* spp. (Whitcomb et al. 1987), *Cirsium* spp. (Goeden and Ricker 1987), *Dicoria canescens* Torrey & Gray and *Iva axillaris* Pursh (Goeden and Teerink 1993). There are no reports on the overwintering biology or key parasitoids of *X. peltata*.

Alternate Leafhopper Hosts of *Anagrus* spp

The *Anagrus* spp. recovered in this study are known to utilize a number of Nearctic leafhopper hosts, which includes *Dikrella* sp, *Empoasca* spp., *E. prunicola*, *E. rosae*, *K. maligna*, and *Z. pomaria* for *A. atomus*; *E. avellanae* (Edwards), *E. crataegi* (Douglas), *E. prunicola*, *E. rosae*, *R. tenerrima*, and *Z. pomaria* for *A. avalae*; *E. rosae*, *E. bistrata*, *E. comes*, *E. elegantula*, *E. variabilis*, *E. ziczac*, and *Z. pomaria* for *A. daanei*; *D. californica*, *D. cockerellii*, *E.*

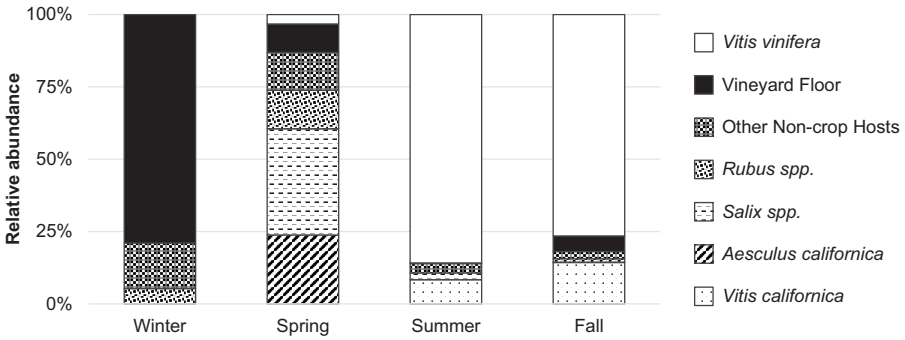

Fig. 1. Relative abundance of *E. elegantula* adults changes over the year as they move between the vineyard floor and grape vine canopy, making use of intermediate host plants such as *A. californica, Rubus* spp, and *Salix* spp. in the spring and *V. californica* in the fall. Data show relative densities only from alternate host plant species classified as natural, *V. vinifera* and the vineyard floor, which together represents the plant composition of a typical vineyard and its surrounding landscape.

prunicola, *E. bistrata*, *E. comes*, *E. elegantula*, *E. variabilis*, and *Z. pomaria* for *A. erythroneurae*; *E. comes* for *A. nigriventris*; and *Erythridula plena* (Beamer), *E. bistrata*, *E. comes*, *E. variabilis*, and *E. ziczac* for *A. tretiakovae* (Triapitsyn 1998, 2001, 2015; Triapitsyn and Berezovskiy 2004).

Further evaluation is necessary to definitively confirm the alternate leafhoppers being utilized as hosts by the *Anagrus* spp. on the various plant species, but the five leafhoppers with the highest frequency of co-occurrence with *Anagrus* spp. are *Empoasca* spp., *E. decemnotata*, *D. californica*, *E. elegantula*, and *D. fuscinervosus* (Table 4). More specifically, *A. atomus* had a relatively high frequency of co-occurrence with *A. obscura*, *D. fuscinervosus*, *D. californica*, *Empoasca* spp., *E. elegantula*, and *E. decemnotata*; *A. avalae* with *Empoasca* spp., *A. unipuncta* and *E. commissuralis*; *A. daanei* with *D. rufula*, *D. californica*, *Empoasca* spp., and *R. tenerrima*; *A. erythroneurae* with *Alconeura spp.*, *C. coquilletti, D. fuscinervosus*, *D. californica*, *E. cerea*, *Empoasca* spp., *E. decemnotata*, *E. elegantula*, and *T. zelleri*; *A. nigriventris* with *A. unipuncta*, *D. californica*, *Empoasca* spp., *E. elegantula*, and *T. zelleri*; and *A. tretiakovae* with *Scaphytopius* sp. See Table 4 for additional records.

Additionally, it may be useful to evaluate the leafhopper species that were consistently recovered (present in >2 seasonal periods) from key host plants that consistently yielded *Anagrus* spp., such as *Alnus* sp. (*E. commissuralis*, *Empoasca* spp.), *B. pilularis* (*E. cerea*, *Empoasca* spp.), *Ceanothus* spp. (*Empoasca* spp.), *Mentha* sp. (*A. obscura*, *Empoasca* spp., *E. decemnotata*), *Nepeta* sp. (*E. decemnotata*), *Rubus* spp. (*D. californica*, *Empoasca* spp.), and *Salvia* spp. (*Idiocerus* spp., *Empoasca* (Hebata) sp., *Empoasca* spp., *E. decemnotata*; Tables 1 and 2).

As egg parasitoids, using the co-occurrence of leafhopper adults and *Anagrus* wasps emerging from undetermined host eggs is an imperfect means of identifying alternate hosts, as it is unclear whether the presence of adults during a given seasonal period also implies the presence of eggs, much less their utilization by *Anagrus* spp. As such, no definitive conclusions about alternate leafhopper hosts for the *Anagrus* spp. can be drawn until less ambiguous experimental data are obtained. The data presented here could serve as a guide for such investigations.

Seasonal Habitat Use of *E. elegantula*

Erythroneura elegantula densities on noncrop hosts followed seasonal patterns that have been previously outlined (Doutt and Nakata 1973, Cate 1975, Daane and Costello 2000, Daane et al. 2013). During the winter *E. elegantula* primarily resided in leaf litter and debris on the vineyard floor. As temperatures increased in the spring *E. elegantula* were found on numerous noncrop host plants, including *A. californica*, *Rubus* spp., and *Salix* spp. before moving onto cultivated wine grapes (*V. vinifera*) in the summer (Fig. 1) . These intermediate hosts are most likely used for feeding but not reproduction, as *E. elegantula* reproductive organs do not fully mature until they feed on grape leaves (Cate 1975, Daane and Costello 2000). As the vines senesce in the fall *E. elegantula* can again be found on temporary noncrop hosts before ultimately returning to the vineyard floor to overwinter (Fig. 1). *Erythroneura elegantula* was also recovered from a number of cultivated host plants, notably *Corylus cornuta* Marshall, *Mentha* sp., *P. quinquefolia*, *Rosa* spp., and *Tilia* sp. (Table 3).

In conclusion, results from this survey provide new information on the host plants that support *Anagrus* spp., the timing of host plant use, and the leafhoppers associated with these host plant species in northern California. Since both *A. erythroneurae* and *A. daanei* are known to attack *E. elegantula*, identification of their alternate host plants has implications for the use of on-farm habitat diversification to enhance biological control of this pest in wine grape vineyards. For example, growers could potentially augment habitat in and around their vineyard with the plant species identified in this survey that were shown to be hosts for *A. daanei* and *A. erythroneurae*. Alternately, preexisting natural habitats could be managed to promote the growth of overwintering host plants for these two *Anagrus* species.

Subsequent studies are needed to better elucidate the timing and distance of *Anagrus* spp. movement between commercial vineyards and overwintering sites. Previous research has indicated that *Anagrus* wasps may disperse great distances (Corbett et al. 1996, Corbett and Rosenheim 1996), which could imply that overwintering habitat may not necessarily need to be directly adjacent to vineyards. Furthermore, it would also be useful to evaluate how *Anagrus* spp. population densities change as they seasonally move between agricultural and overwintering habitats, as it has been suggested that the effectiveness of providing overwintering habitat for *Anagrus* spp. may be influenced by the total area of habitat relative to that of the vineyard (Mills and Daane 2005). Finally, definitive studies are needed to ascertain which leafhopper species are utilized by *Anagrus* spp. on these host plants. The data on host plant association (Tables 1 and 2) and co-occurrence (Table 4) could guide such efforts. Such insight into the ecology of these wasps and their alternate hosts could aid in the development of more reliable conservation biological control programs for control of *E. elegantula* in commercial wine grape vineyards.

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