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Colonization of New York Vineyards by *Anagrus* spp. (Hymenoptera: Mymaridae): Overwintering Biology, Within-Vineyard Distribution of Wasps, and Parasitism of Grape Leafhopper, *Erythroneura* spp. (Homoptera: Cicadellidae), Eggs

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A study was conducted in New York to identify the *Anagrus* species present in vineyards, to determine the plants in which *Anagrus* species overwinter, and to characterize the dispersal of wasps and level of parasitism of grape leafhopper eggs in vineyards. *Anagrus daanei* S. Triapitsyn and *Anagrus erythroneurae* S. Trjapitzin and Chiappini were the most abundant species reared from *Vitis labrusca* Bailey and *Vitis vinifera* L. cultivars, respectively. *V. labrusca* cultivars are infested predominantly by *Erythroneura comes* (Say), whereas *V. vinifera* cultivars are infested primarily by the *Erythroneura vitifex* Fitch–*Erythroneura bistrata* McAtee complex. *Anagrus tretiakovae* S. Triapitsyn was reared from seven grape cultivars in approximately equal proportions. Thus, *A. daanei* and *A. erythroneurae* appear to possess greater degrees of host specificity than *A. tretiakovae.* These results support the belief that, although *Anagrus* species have relatively broad host associations, host preferences do exist. These preferences may be mediated by the plant associations of particular leafhopper species. *Anagrus* species use alternate hosts that infest several plant species. In particular, diapausing insect eggs in *Acer saccharum* Marshall, *Robinia pseudo-acacia* L., *Rosa multiflora* Thunberg, *Salix nigra* L., *Vitis riparia* Michaux, and *Zanthoxylum americanum* Miller may play important roles in the overwintering biology of the *Anagrus* species that are most abundant in vineyards. Following emergence from overwintering hosts, *Anagrus* adults are aggregated at the vineyard edge early in the season (May and June). By midseason or later (August and September), the pattern of wasp colonization and parasitism indicates that parasitoids are more widely dispersed in the vineyards. This pattern is consistent with colonization from vineyard edges, followed by relatively slow dispersal into the vineyard interior. Further investigations are necessary to identify the alternate host(s) that *Anagrus* exploits during the winter and spring and to delineate the phenology of such alternate hosts, as well as that of the grape leafhoppers and *Anagrus* species in the spring. Habitat management studies could then be conducted to identify strategies that would accelerate population growth of *Anagrus* in the spring and increase the rate of dispersal into vineyards. © 2000 Academic Press

Key Words: **conservation biological control; *Vitis; Anagrus; Erythroneura;* egg parasitoid; leafhoppers; dispersal.**

INTRODUCTION

In western North America and Europe *Anagrus* species are valuable biological control agents of grape leafhoppers (McKenzie and Beirne, 1972; Williams, 1984; Wells *et al.*, 1988; Cerutti *et al.*, 1991; Murphy *et al.*, 1996). These egg parasitoids complete two to three generations for every leafhopper generation (Cate, 1975; Williams, 1984), and parasitism rates increase from 10–20% in the first leafhopper generation to 80–95% in the second generation (Cate, 1975). Because grape leafhoppers overwinter as adults, and *Anagrus* species overwinter in host eggs, *Anagrus* species must rely on alternate host insects that overwinter as diapausing eggs in perennial plants (Doutt and Nakata, 1973; Kido *et al.*, 1984). This requirement for a different overwintering host is important because it means that the agroecosystem must be manipulated if biological control by *Anagrus* is to be enhanced (Corbett and Rosenheim, 1996; Murphy *et al.*, 1998).

Research conducted during the past decade has provided New York grape growers with viable alternatives to calendar-based insecticide treatments for control of grape berry moth, *Endopiza viteana* (Clemens) (Hoffman and Dennehy, 1987; Dennehy *et al.*, 1991; Martinson *et al.*, 1991). As with any change in production

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practices, this reduction in insecticide use has altered the composition of the insect pest complex in vineyards. In particular, the densities of grape leafhoppers, *Erythroneura* species, have increased, and recent studies have focused on determining what adjustments to control programs are needed to prevent economic losses due to grape leafhoppers. Whereas these studies show that reduced insecticide use for control of grape berry moth does not necessarily allow grape leafhoppers to increase (Martinson *et al.*, 1994), biotic and abiotic factors can lead to economically important outbreaks of *Erythroneura* species (Martinson *et al.*, 1994; Martinson and Dennehy, 1995a). Under the current conditions of limited insecticide use, natural enemies can play a major role in preventing outbreaks of leafhoppers in New York vineyards.

Despite the effectiveness of *Anagrus* parasitoids in western North America and Europe, the effect of *Anagrus* species on grape leafhopper densities in eastern North America is unknown. Grape production in eastern North America is very different from that in the western United States, and conclusions about the role of *Anagrus* parasitoids in eastern vineyards based on studies conducted in the west are inappropriate. In the east, *Vitis labrusca* Bailey cultivars and French–American interspecific hybrid varieties are grown under relatively low light intensity and short growing seasons. Both crop phenology and the composition of alternate hosts in which *Anagrus* wasps may overwinter are very different in the eastern United States. Also, a greater proportion of land in grape production regions of the east is in noncrop vegetation, and eastern vineyards are generally smaller than those in the west. The complex of *Erythroneura* species differs between the two regions and even among the different cultivars grown in the east (Martinson and Dennehy, 1995b). Finally, the wetter conditions prevalent in the eastern United States require more intensive use of fungicides, which may adversely affect *Anagrus* parasitoids.

Several key gaps in our understanding of *Anagrus* biology in the northeastern United States must be filled before a successful biological control program for grape leafhoppers can be developed. Knowledge concerning the alternate host associations of *Anagrus*, the between- and within-vineyard dispersal and parasitism, and the effect of pesticides on *Anagrus* parasitoids is crucial for realizing the full potential of biological control in eastern vineyards. Objectives of the present study were to (1) identify the *Anagrus* species that are most abundant in New York vineyards, (2) identify the plants that are used by alternate hosts of *Anagrus* during the winter and early spring in New York, and (3) characterize the colonization of vineyards by *Anagrus* and subsequent parasitism of grape leafhopper eggs.

TABLE 1

Vineyard Characteristics at Research Sites, Finger Lakes Region, New York

Characteristic	Field Sites			
	Niagara	DeChaunac	Castel[a]	GR-7[a]
No. vineyard traps	25	36	18	24
No. edge traps	25	18	5	12
No. woodlot traps	25	18	5	12
Distance between vine 1 and edge trap transects (m)	11.1	13.3	11.4	11.4
Distance between vine 1 and woodlot trap transects (m)	22.9	23.7	18.6	18.6
Distance between vine 1 and intermediate vine transects (m)	32.4	43.2	40.0	40.0
Distance between vine 1 and interior vine transects (m)	64.8	91.8	80.0	80.0
Distance between vines within rows (m)	2.7	2.7	2.5	2.5
Distance between vineyard rows (m)	2.4	2.7	2.8	2.8
Elevation of site (m)	360	335	223	223

[a] Castel and GR-7 are adjacent vineyard blocks and are referred to in the text as the same site.

MATERIALS AND METHODS

Field Sites

This study was conducted from 1993 to 1995 in vineyards and their adjacent woodlots in Yates County (Finger Lakes Region), New York. One of the vineyard sites consisted of adjacent blocks of 'Castel 196-17' and 'GR-7.' The other two vineyard sites consisted of solid cultures of either 'DeChaunac' or 'Niagara.' 'Castel,' 'GR-7,' and 'DeChaunac' are interspecific hybrid varieties, whereas 'Niagara' is a native American (*V. labrusca*) variety. No insecticides were applied during the study, but other pesticide applications, such as pre- and postbloom fungicide applications, were made as usual. Each vineyard block was bordered on the south side by a woodlot. Vineyard rows were on a north–south orientation at all sites. Other characteristics of the vineyards are presented in Table 1.

Anagrus Overwintering Sites

From early December to late April of 1993–1995, shoots and branches were collected from trees and shrubs at three field sites in the Finger Lakes Region and at additional sites in western New York (Chatauqua County). Collections of different plant species had the same relative abundance as that occurring at each site. All collections were made within 30 m of the woodlot edge. Each collection was made by pruning ca.

500 g of shoots and branches (growth from the previous season) and placing this material in a labeled brown paper bag. Collections were made from 0 to 10 m above the ground. Plants from which collections were taken were marked in the field for later identification. In the laboratory, each sample was placed in a 3.8-liter cylindrical paper carton, which served as a rearing chamber. Each container was wrapped with aluminum foil to render it opaque, and a glass vial containing 70% ethanol was secured at the top of the chamber to allow light to enter and attract emerging *Anagrus* wasps. Rearing chambers were held at 30°C, 14:10 h (L:D) cycle, and 50% RH for 4 weeks. *Anagrus* adults that emerged during this time were collected in the glass vials. During the following season, marked plants were collected and pressed. Plants were identified by consulting with specialists and comparing pressed specimens with those in the L. H. Bailey Hortorium (Cornell University). Voucher specimens are deposited in the Hortorium. *Anagrus* adults were identified to species by S. Triapitsyn (University of California, Riverside). Voucher specimens are deposited in the Entomology Research Museum, University of California, Riverside and the Comstock Entomology Museum, Cornell University.

Within-Vineyard Distribution of Anagrus and Erythroneura

Yellow sticky traps were used to monitor adults of *Anagrus* species, as well as those of *Erythroneura* species leafhoppers, on a weekly basis from early July to mid-October in 1993 and from late April to mid-October in 1994. Sticky traps (7.6 by 12.7 cm; Olson Products, Medina, OH) were placed in the vineyard and adjacent woodlot along five transects. One transect ("woodlot traps") was placed in the woodlot adjacent to the vineyard block ca. 10 m from the woodlot edge. An additional transect ("edge traps") was established at the edge of the woodlot and the mown grass alley adjacent to the vineyard block. Both transects were established parallel to the woodlot–vineyard edge. Traps in these transects were stapled 1 m above the ground onto wooden stakes placed at intervals corresponding to the distance between vineyard rows (Table 1). Traps in the vineyards were established at several distances from the woodlot edge (Table 1). Actual distances of traps from the woodlots varied somewhat by site, but the following general description of trap layout applies to all sites. "Vine 1" denotes vines nearest the woodlot, "intermediate" vines were further from the woodlot, and "interior" vines were furthest from the woodlot. Numbers of traps used at each vineyard are given in Table 1. Traps were hung 1 m above the ground on the low trellis wire within the canopy adjacent to a vine. After 1 week, traps were removed, placed on transparent food wrap, and transported to the laboratory. Traps were examined under a dissecting microscope and numbers and gender (based on antennal characteristics) of *Anagrus* wasps were recorded, as were numbers of *Erythroneura* leafhoppers. *Erythroneura* leafhoppers were identified to species by comparison with specimens of known identity (determinations provided by R. Gill, California Department of Food and Agriculture, Plant Pest Diagnostics Center). Voucher specimens were obtained from each site and deposited in the Entomology Research Museum, University of California, Riverside; the Comstock Entomology Museum, Cornell University (*Anagrus*); and the California Department of Food and Agriculture, Plant Pest Diagnostics Center (*Erythroneura*).

Parasitism in Vineyards

During the 1993 season, parasitism of grape leafhopper eggs by *Anagrus* wasps was assessed concurrently with sampling of adults at two times ("early" and "late") during the growing season. These times were chosen to correspond to the first and last generations of *Anagrus* within the vineyard. At each time, one shoot was randomly chosen from each of the vines where sticky traps were placed. The node 4 leaf (counting from the base of the shoot) was removed and placed in a cooler with ice. Martinson and Dennehy (1995b) reported that most grape leafhopper eggs were found on leaves 3–7. At the laboratory, leaf area was measured (Agvision Pseudocolor Image Analysis System; Decagon Devices, Inc., Pullman, WA) and then leaves were held in a freezer until parasitism was determined.

For 'Castel,' 'GR-7,' and 'DeChaunac' leaves, parasitism was assessed by examination of both sides of each leaf via transmitted light with a dissecting microscope. Because 'Niagara' leaves were too large to examine the entire leaf efficiently, we randomly chose half of each leaf, delineated by the midvein, for examination. Counts from each of these half-leaves were multiplied by two to give whole-leaf values. For leaves of all varieties, leafhopper eggs were scored as "parasitized" if either a circular wasp exit hole was present or a clearly visible wasp was observed within the egg (Wells *et al.*, 1988). Proportions of total leafhopper eggs that were parasitized and numbers of parasitized eggs/cm^2 of leaf tissue were calculated. Parasitization values measured in this way provided estimates of cumulative parasitism up to the sample date for each distance class.

In 1994, parasitism was assessed by creating uniform, discrete host patches of leafhopper eggs at the Niagara site. These "sentinel egg" host cohorts were established in mid-June, mid-July, and mid-August. At each of these times, sentinel egg cohorts were established along three transects at different distances from the woodlot. The "woodlot edge" transect was established in vines nearest (11 m) to the woodlot. The "interior" transect was established in the center of the

vineyard block 125 m from the woodlot. Vines farthest from the woodlot (248 m) at the opposite edge of the block comprised the "open edge" transect. Although a woodlot was not adjacent to the "open edge," several species of *Prunus* and *Juglans* were nearby. For each transect, 10 cohorts of sentinel eggs were established on vines, 1 each in 10 adjacent rows.

To create sentinel egg cohorts, adults of *Erythroneura comes* (Say) were collected with a gasoline-powered leaf vacuum (Homelite, Charlotte, NC) in areas of the vineyard outside the study area. Twelve adult leafhoppers were then aspirated into clip cages (4 cm diameter), and clip cages were placed onto leaf 7 (counting from the base of the shoot) of a randomly chosen shoot on each of the 10 vines in each transect. Leafhoppers were caged on the underside of the leaf. After 2 days, the clip cages and leafhoppers were removed. Three weeks later, these leaves and their cohorts of eggs were collected, placed in ziplock freezer bags, and transported on ice to the laboratory. Leaves were frozen until processed. To assess parasitism, host patches on the leaves were examined, and leafhopper eggs were categorized as previously described. Using this "sentinel egg" approach provided point estimates of parasitism and allowed us to determine the effect of distance from woodlot, and time of growing season, on parasitism.

Statistical Analyses

Data were $\log_{10}$ or arcsine transformed to reduce variance heterogeneity. An overall analysis of variance (PROC MIXED; SAS Institute, 1998) was structured to block for between-vineyard variation for numbers of wasps/trap and parasitism in 1993. Also, a linear trend was fitted to means of numbers of wasps/trap as a function of distance from woodlot. Analysis of variance was also conducted for each year–vineyard combination to provide insight on within-vineyard trends. Untransformed means are presented for all variables.

RESULTS AND DISCUSSION

Anagrus Overwintering Sites

A total of 328 collections were made from 43 plant species representing 21 families (Table 2). From these collections, 170 *Anagrus* wasps were reared from 13 plant species in 11 families (Table 2). More than half of the wasps (95) emerged from 2 species, *Rosa multiflora* Thunberg and *Acer saccharum* Marshall. However, based on the number of *Anagrus* reared per collection, *Zanthoxylum americanum* Miller and *Juglans nigra* L. were most productive, yielding an average of 2.0 and 1.8 wasps per collection, respectively (Table 2). Cerutti *et al.* (1991) reared overwintered *Anagrus atomus* (L.) from *Rosa* spp., *Rubus* sp., and *Lonicera* sp., and a subsequent spring generation of *A. atomus* was reared from *Rubus* sp., *Corylus avellana* L., *Rosa* spp., *Betula pendula* Roth, and *Malus domestica* Borkhausen. The work of Cerutti *et al.* (1991), Doutt and Nakata (1973), and Kido *et al.* (1984) indicates that members of the Rosaceae play an important role in the overwintering biology of *Anagrus* species. The present study supports this and alludes to the importance of other plant families, i.e., Aceraceae, Rutaceae, Fabaceae, and Salicaceae, in the northeastern United States.

The systematics of *Anagrus* are poorly understood; members of this genus that inhabit vineyards consist of a complex of species and biotypes (Trjapitzin and Chiappini, 1994; Triapitsyn, 1998). Table 3 presents the designations of *Anagrus* species reared from cultivated grapes and noncrop perennial plants in the vicinity of New York vineyards (Triapitsyn, 1998). Two *Anagrus* species groups, *atomus* and *incarnatus,* were represented. Members of the *atomus* species group included *A. atomus* and *Anagrus erythroneurae* S. Trjapitzin and Chiappini. The *incarnatus* species group was represented by five species, *Anagrus epos* Girault, *Anagrus daanei* S. Triapitsyn, *Anagrus nigriventris* Girault, *Anagrus tretiakovae* S. Triapitsyn, and *Anagrus yawi* Fullaway, in addition to three potential species designated "C," "D," and "K." Designations of several species of *Anagrus* reared from noncrop perennial plants remain unknown.

Martinson and Dennehy (1995b) reported on the species composition of *Erythroneura* leafhoppers infesting the major grape cultivars grown in New York. Based on this knowledge, we can infer the identity of the leafhopper hosts of several of the *Anagrus* species in the present study. It is important to note that these inferences must be confirmed in future studies. The predominant leafhopper in Concord and Niagara grapes is *E. comes,* comprising 99 and 75% of the *Erythroneura* species collected, respectively (Martinson and Dennehy, 1995b). *A. daanei, A. epos, A. nigriventris,* and *A. tretiakovae* were reared from hosts in Concord leaves (Table 3). Thus, these parasitoid species probably attack *E. comes.* Furthermore, our results suggest that *A. daanei* is the most abundant *Anagrus* species on hosts in Concord and Niagara grapes. Two *A. erythroneurae* emerged from Niagara leaves, but it is not clear whether this represents occasional parasitism of *E. comes* by this wasp or parasitization of a species of *Erythroneura* that is relatively uncommon on this cultivar. *Vitis vinifera* cv. Chardonnay is infested primarily (>97% of *Erythroneura* species) by a mixture of the cryptic species *Erythroneura vitifex* Fitch and *Erythroneura bistrata* McAtee. *A. erythroneurae, A. tretiakovae, A. daanei, A. epos,* and "K" were reared from Chardonnay, suggesting that these species can develop in *E. vitifex* and/or *E. bistrata.* In particular, *A. erythroneurae* was most commonly reared from hosts associated with Chardonnay grape leaves (Table 3). Results

TABLE 2

Plant Species Investigated for Harboring Overwintered *Anagrus* spp. in New York, 1993–1995

Species	Family	No. of collections	No. of *Anagrus* reared	No. of *Anagrus* reared/collection
Acer saccharum Marsh.	Aceraceae	50	41	0.82
Rhus typhina L.	Anacardiaceae	9	0	0
Ostrya virginiana (Mill.) K. Koch.	Betulaceae	7	1	0.14
Lonicera tartarica L.	Caprifoliaceae	9	0	0
Cornus racemosa Lam.	Cornaceae	4	1	0.25
Cornus stolonifera Michx.	Cornaceae	2	0	0
Juniperus virginiana L.	Cupressaceae	1	0	0
Robinia pseudo-acacia L.	Fabaceae	9	6	0.67
Fagus grandifolia Ehrh.	Fagaceae	2	0	0
Quercus alba L.	Fagaceae	1	0	0
Quercus rubra Gray	Fagaceae	7	1	0.14
Quercus velutina Lam.	Fagaceae	1	0	0
Hamamelis virginiana L.	Hamamelidaceae	2	0	0
Carya ovata (Mill.) K. Koch.	Juglandaceae	7	0	0
Juglans cinerea L.	Juglandaceae	2	0	0
Juglans nigra L.	Juglandaceae	8	14	1.8
Sassafrass albidum (Nutt.) Nees.	Lauraceae	1	0	0
Morus alba L.	Moraceae	1	0	0
Fraxinus americana L.	Oleaceae	13	2	0.15
Fraxinus nigra Marsh.	Oleaceae	3	0	0
Fraxinus pennsylvanica Marsh.	Oleaceae	2	0	0
Picea glauca (Moench) Voss.	Pinaceae	2	0	0
Pinus resinosa Ait.	Pinaceae	2	0	0
Rhamnus catharticus L.	Rhamnaceae	19	0	0
Crateagus sp. L.	Rosaceae	8	1	0.13
Malus pumila Mill.	Rosaceae	16	9	0.56
Prunus cerasus L.	Rosaceae	2	0	0
Prunus serotina Ehrh.	Rosaceae	37	15	0.41
Prunus virginiana L.	Rosaceae	2	0	0
Pyrus communis L.	Rosaceae	1	0	0
Rosa multiflora Thunb.	Rosaceae	49	54	1.1
Rubus pubescens Raf.	Rosaceae	1	0	0
Rubus strigosus Michx.	Rosaceae	8	0	0
Zanthoxylum americanum Mill.	Rutaceae	11	22	2.0
Populus deltoides Marsh.	Salicaceae	2	0	0
Salix nigra L.	Salicaceae	2	1	0.5
Salix purpurea L.	Salicaceae	1	0	0
Tilia americana L.	Tiliaceae	8	0	0
Tilia heterophylla Vent.	Tiliaceae	2	0	0
Tilia monticola Sarg.	Tiliaceae	1	0	0
Ulmus americana L.	Ulmaceae	1	0	0
Parthenocissus vitacea (Knerr) Hitchc.	Vitaceae	3	0	0
Vitis riparia Michx.	Vitaceae	9	2	0.22

of the present study indicate that >85% of the *Erythroneura* leafhoppers collected in Castel and GR-7 belong to the *vitifex–bistrata* complex. *A. daanei, A. tretiakovae,* and "K" were reared from each of these cultivars, further suggesting that these species utilize the *vitifex–bistrata* complex. Noncrop perennial plants from which *A. daanei* were reared included *A. saccharum, Robinia pseudo-acacia* L., *R. multiflora,* and *Z. americanum. Salix nigra* L. was the only noncrop perennial from which *A. erythroneurae* was reared. In addition to cultivated grapes, *A. tretiakovae* was also reared from *Vitis riparia* Michaux.

Based on limited collections, the relative importance of the different species of *Anagrus* and overwintering plants on grape leafhoppers in eastern vineyards is difficult to determine. However, our data suggest that (1) *A. daanei, A. erythroneurae,* and *A. tretiakovae* are the predominant mymarids parasitizing grape leafhopper eggs in the study area and (2) alternate hosts of these wasps occur on several noncrop perennial plants adjacent to vineyards. It must also be understood that other *Anagrus*–host associations of importance to grape production may exist. Further research is warranted to elucidate the plant–alternate host interac-

TABLE 3

Designations of *Anagrus* spp. Reared from Cultivated Grapes and Perennial Plants Associated with Vineyards in New York, 1993–1995

Anagrus species	*Anagrus* species group	Material examined	Plant species	Plant family
atomus	*atomus*	1 Female	*Ostrya virginiana* (Mill.) K. Koch.	Betulaceae
		3 Females	*Rosa multiflora* Thunb.	Rosaceae
erythroneurae	*atomus*	1 Female	*Salix nigra* L.	Salicaceae
		21 Females	*Vitis vinifera* L. cv. Chardonnay	Vitaceae
		2 Females	*Vitis labrusca* Bailey cv. Niagara	Vitaceae
daanei	*incarnatus*	6 Females, 1 Male	*Acer saccharum* Marsh.	Aceraceae
		2 Females	*Robinia pseudo-acacia* L.	Fabaceae
		2 Females	*Rosa multiflora* Thunb.	Rosaceae
		1 Female	*Zanthoxylum americanum* Mill.	Rutaceae
		29 Females, 25 Males	*Vitis labrusca* Bailey cv. Concord	Vitaceae
		27 Females, 23 Males	*Vitis labrusca* Bailey cv. Niagara	Vitaceae
		7 Females, 4 Males	*Vitis* cv. GR-7	Vitaceae
		1 Female	*Vitis* cv. Castel	Vitaceae
		1 Female	*Vitis* cv. Seyval blanc	Vitaceae
		1 Female	*Vitis vinifera* L. cv. Chardonnay	Vitaceae
epos	*incarnatus*	3 Females	*Robinia pseudo-acacia* L.	Fabaceae
		1 Female	*Vitis vinifera* L. cv. Chardonnay	Vitaceae
nigriventris	*incarnatus*	2 Females	*Robinia pseudo-acacia* L.	Fabaceae
		2 Females	*Vitis labrusca* Bailey cv. Concord	Vitaceae
tretiakovae	*incarnatus*	1 Female, 1 Male	*Vitis riparia* Michx.	Vitaceae
		4 Females, 2 Males	*Vitis labrusca* Bailey cv. Concord	Vitaceae
		1 Female, 2 Males	*Vitis labrusca* Bailey cv. Niagara	Vitaceae
		7 Females, 6 Males	*Vitis labrusca* Bailey cv. Delaware	Vitaceae
		5 Females, 5 Males	*Vitis* cv. GR-7	Vitaceae
		2 Females, 8 Males	*Vitis* cv. Castel	Vitaceae
		1 Female, 4 Males	*Vitis vinifera* L. cv. Chardonnay	Vitaceae
yawi	*incarnatus*	1 Female	*Cornus racemosa* Lam.	Cornaceae
C	*incarnatus*	4 Females, 3 Males	*Juglans nigra* L.	Juglandaceae
D	*incarnatus*	4 Females, 7 Males	*Zanthoxylum americanum* Mill.	Rutaceae
K	*incarnatus*	5 Females, 2 Males	*Vitis* cv. GR-7	Vitaceae
		2 Females, 4 Males	*Vitis* cv. Castel	Vitaceae
Unknown	Unknown	4 Females, 3 Males	*Acer saccharum* Marsh.	Aceraceae
Unknown	Unknown	4 Males	*Robinia pseudo-acacia* L.	Fabaceae
Unknown	Unknown	1 Male	*Quercus rubra* Gray	Fagaceae
Unknown	Unknown	2 Females	*Fraxinus americana* L.	Oleaceae
Unknown	Unknown	1 Female	*Crateagus* sp. L.	Rosaceae
Unknown	Unknown	1 Male	*Malus pumila* Mill.	Rosaceae
Unknown	Unknown	2 Females, 1 Male	*Prunus serotina* Ehrh.	Rosaceae

tions that key *Anagrus* species exploit in the winter and spring in the northeastern United States.

Within-Vineyard Distribution of Anagrus Wasps

Based on the *Anagrus–Erythroneura–Vitis* associations described above, we assume that *A. daanei* was the predominant wasp at the Niagara site and that *A. tretiakovae*, "K," and *A. daanei* were present at the other sites. Table 4 presents results of the analysis that was structured to block across vineyards. The time by distance interaction for analysis of the three vineyard transects (vine 1, intermediate, and interior) was significant for both years (1993; $F = 6.30$; 2, 12.4; $P = 0.0129$) (1994; $F = 30.65$; 2, 10.7; $P < 0.0001$), indicating that distance effect was dependent on time of season in both years. When all five transects were included in the analysis, this interaction was significant only in 1994 ($F = 14.12$; 4, 12.8; $P = 0.0001$). Lack of significance in 1993 ($F = 1.55$; 4, 23.4; $P = 0.2194$) was due to the effects of edge and woodlot transects. In both years, time by distance interaction for the three vineyard transects was significant early

TABLE 4

Distribution of *Anagrus* Wasps in 1993 and 1994, Finger Lakes Region, New York (Mean No. of Wasps per Trap)[a]

Year	Transect	Early	Late
1993	Vine 1	47.2	30.3
	Intermediate vine	24.3 (0.1010)	27.1 (0.6433)
	Interior vine	16.9 (0.0099)	16.6 (0.3792)
	Edge	4.2 (<0.0001)	4.1 (0.0339)
	Woodlot	2.3 (<0.0001)	2.7 (0.0081)
1994	Vine 1	25.2	51.4
	Intermediate vine	5.2 (0.0001)	71.7 (0.1446)
	Interior vine	3.3 (<0.0001)	67.1 (0.2415)
	Edge	3.4 (<0.0001)	6.8 (<0.0001)
	Woodlot	3.3 (<0.0001)	5.5 (<0.0001)

[a] Values in parentheses are significance levels for contrasts between vine 1 and other transects within a year–time combination.

(1993; $F = 28.77$; 2, 10.6; $P < 0.0001$) (1994; $F = 38.15$; 2, 11.4; $P < 0.0001$), but not late (1993; $F = 2.27$; 2, 14.2; $P = 0.1390$) (1994; $F = 2.59$; 2, 11.4; $P = 0.1182$). Wasp densities in the early season were usually higher at vines adjacent to a wooded edge (vine 1) than at vines further removed from woodlots (intermediate and interior vines) (Table 4). The slope of a linear trend fit to the means of the three vineyard transects (log of wasp numbers as a function of distance) differed between early and late season for both years (1993; $F = 13.03$; 1, 6.73; $P = 0.0092$) (1994; $F = 34.21$; 1, 12.6; $P < 0.0001$). In 1993, slope was significant for both times (early; $P < 0.0001$) (late; $P = 0.0439$). In 1994, slope was significant early ($P < 0.0001$) but not late ($P = 0.1785$). These results corroborate those from ANOVA on means that indicate that distance from woodlot had a stronger affect on early season wasp dispersion than on that observed in late season (Table 4).

Table 5 presents distributions of *Anagrus* wasps in each vineyard, thus allowing within-vineyard comparison. At each vineyard, wasp densities in the early season were always significantly ($P < 0.01$) higher at vine 1 than at intermediate or interior vines. Higher overall wasp density in 1993 at the Castel/GR-7 site may be due in part to the fact that trapping at these sites was initiated later in the season than in 1994. Wasps captured at this site in 1993 probably represent the first generation emerging from grapes, whereas wasps captured in 1994 may represent immigrants from woodlots. The onset of *Anagrus* immigration varied between sites and appeared to be related to local climatic conditions. Bud break and wasp immigration occurred at the site of lowest elevation (Castel/GR-7) nearly a month before the highest site (Niagara).

Late season *Anagrus* dispersion differed from that observed in the early season. Overall wasp numbers in vine 1 did not differ from those in the other two vineyard transects in either year (Table 4). In 1993, two of the sites (GR-7 portion of the Castel/GR-7 block and DeChaunac) exhibited trends similar to those observed in the early season (Table 5). Wasp densities at the Castel and Niagara sites, however, were independent of distance from woodlot in both years. This trend was also observed at the DeChaunac site in 1994. Wasp densities were higher at the intermediate and interior vines than at the vine adjacent to the woodlot in 1994 at the GR-7 block. This trend was unlike that observed in 1993 and may be due to within-vineyard differences in host densities. In 1994, adult grape leafhopper densities were relatively high at the interior of the vineyard compared to those at the edge. This was not observed in 1993. High adult leafhopper densities in

TABLE 5

Within-Vineyard Distribution of *Anagrus* Wasps, Finger Lakes Region, New York, 1993 and 1994 (Mean No. of Wasps per Trap)[a]

		Castel		GR-7		Dechaunac		Niagara	
Year	Transect	Early	Late	Early	Late	Early	Late	Early	Late
1993	Vine 1	75.3	4.7	79.2	5.3	13.3	3.9	21.6	109
	Intermediate vine	46.1*	6.7ns	43.0***	3.2**	7.1***	2.3*	5.8***	97.8 ns
	Interior vine	20.2***	5.9ns	40.5***	2.8**	3.2***	1.5**	3.6***	56.4 ns
	Edge	8.2***	3.4*	5.8***	3.4**	0.6***	2.1**	1.7***	7.4***
	Woodlot	3.0***	2.2**	2.4***	2.0***	2.3***	3.7 ns	1.1***	2.6***
1994	Vine 1	36.3	45.0	22.5	14.8	14.3	21.1	28.0	124
	Intermediate vine	6.3**	66.3ns	4.0**	67.8**	4.7**	26.0 ns	5.8***	127 ns
	Interior vine	5.7**	47.0ns	2.5***	60.0**	2.3***	21.0 ns	2.8***	140 ns
	Edge	4.3***	2.6***	4.3***	2.6**	1.2***	4.8***	3.7***	14.3***
	Woodlot	3.4***	5.4***	3.4***	5.4***	2.8***	8.6**	3.6***	6.0***

[a] Significance levels (*$P < 0.05$; **$P < 0.01$; ***$P < 0.0001$; ns, not significant) for comparisons between vine 1 and the other transects within a year–vineyard–time combination.

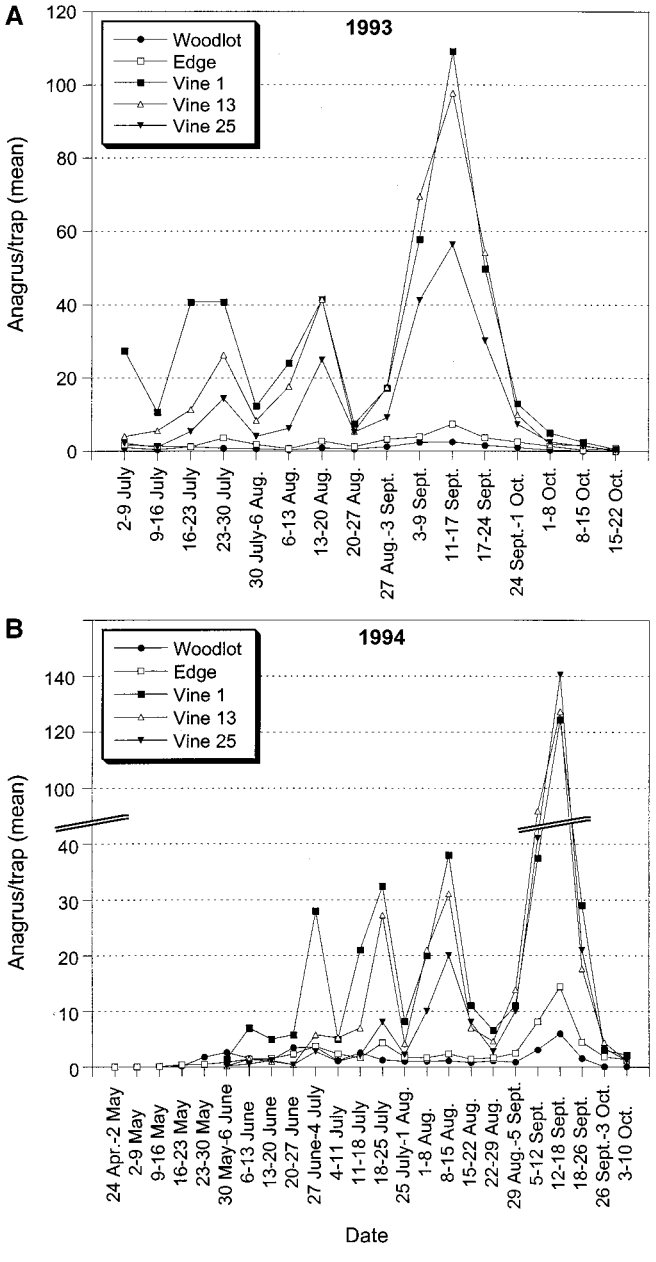

FIG. 1. Seasonal trap catches of *Anagrus* wasps at varying distances from woodlot at the Niagara site in 1993 (A) and 1994 (B).

July and August probably resulted in greater oviposition, i.e., greater host densities for *Anagrus*, thus leading to the observed differences in trap catches of *Anagrus* in early September.

Weekly trap catches of adult wasps at the Niagara site are presented in Fig. 1. Seasonal trends of wasp captures were similar in both years and were characterized by peak captures occurring approximately every 3 weeks throughout the summer, with the greatest number of wasps being captured in mid-September. This 3-week interval corresponds to the time required for *Anagrus* to develop from egg to adult. We attribute the abrupt decline in trap catches in the week following peak catches to the brief longevity of adult wasps under field conditions. This factor led to the highly regular trap catches observed in July and August. As the growing season progressed, this regularity decomposed somewhat, so that the final peak catches occurred in mid-September, 4–5 weeks after the previous peak. Cooler temperatures in late August and September may have slowed the development of *Anagrus* and thus have been a contributing factor. Trap catches dropped precipitously after this peak due to the lack of host eggs. Martinson and Dennehy (1995a) reported that the onset of reproductive diapause for *E. comes* occurs in late July to early August and that few eggs are laid after mid-August.

The relatively slow dispersal of *Anagrus* wasps from vineyard edge to interior suggests that parasitization of grape leafhopper eggs in the interior of the vineyards is limited primarily to the second leafhopper generation. It is difficult to know if, and to what extent, *Anagrus* return to the overwintering sites from the vineyard in the fall. It is possible that overwintering habitat is colonized by *Anagrus* that remain in the woodlot areas adjacent to vineyards throughout the growing season, as well as by wasps that emerge from vines adjacent to woodlots.

Parasitism

Table 6 presents results of ANOVA blocking across vineyards in 1993. The time by distance interaction was significant for proportion of parasitized eggs (F = 3.24; 2, 157; P = 0.0419) but not for mean number of parasitized eggs/cm^2 of leaf tissue (F = 0.20; 2, 327; P = 0.8212). Time by distance interaction was significant at both times for proportion of parasitized eggs (early; F = 23.18; 2, 12; P = 0.0001) (late; F = 6.30; 2, 20.1; P = 0.0075) and for mean parasitized eggs/

TABLE 6

Distribution of *Erythroneura* spp. Eggs Parasitized by *Anagrus*, Finger Lakes Region, New York, 1993

Transect	Early	Late
	Mean proportion of parasitized eggs[a]	
Vine 1	0.212	0.296
Intermediate vine	0.061 (<0.0001)	0.201 (0.0486)
Interior vine	0.064 (<0.0001)	0.170 (0.0020)
	Mean no. of parasitized eggs/cm^2 leaf tissue[a]	
Vine 1	0.025	0.063
Intermediate vine	0.008 (0.0018)	0.049 (0.0167)
Interior vine	0.005 (0.0003)	0.041 (0.0003)

[a] Significance levels for contrasts (vine 1 vs intermediate vine or vine 1 vs interior vine) within time of season.

TABLE 7

Within-Vineyard Distribution of *Erythroneura* spp. Eggs Parasitized by *Anagrus,* Finger Lakes Region, New York, 1993[a]

	Castel		GR-7		DeChaunac		Niagara	
Transect	Early	Late	Early	Late	Early	Late	Early	Late
				Mean proportion of parasitized eggs				
Vine 1	0.370	0.352	0.407	0.375	0.212	0.081	0.192	0.543
Intermediate vine	0.081***	0.181**	0.281 ns	0.275 ns	0.040**	0.072 ns	0.027*	0.364 ns
Interior vine	0.015***	0.159**	0.183 ns	0.297 ns	0.071**	0.037 ns	0[†]	0.218*
				Mean no. of parasitized eggs per cm^2				
Vine 1	0.039	0.080	0.025	0.054	0.013	0.019	0.020	0.106
Intermediate vine	0.006**	0.059 ns	0.022 ns	0.044 ns	0.001**	0.013 ns	0.003 ns	0.074 ns
Interior vine	0.003**	0.069 ns	0.013 ns	0.031*	0.001**	0.004**	0[†]	0.060**

[a] Significance levels (*$P < 0.05$; **$P < 0.01$; ***$P < 0.0001$; ns, not significant) for comparisons between vine 1 and the other transects within a vineyard–time combination.

[†] Means of zero not included in ANOVA due to lack of homogeneity of variance.

cm^2 of leaf tissue (early; $F = 7.81$; 2, 327; $P = 0.0005$) (late; $F = 6.93$; 2, 327; $P = 0.0011$). Parasitism was highest at vine 1 and decreased significantly with distance from the woodlots at both times of the season (Table 6). Early season proportion of parasitism at vine 1 averaged 21% and increased to nearly 30% in the late season.

Within-vineyard distribution of parasitism is presented in Table 7. Early season parasitism of leafhopper eggs was significantly influenced by distance from woodlot at the Castel, DeChaunac, and Niagara sites (Table 7 and Fig. 2A). At each of these sites, parasitism, as measured by the mean number of parasitized eggs/cm^2 of leaf tissue and the proportion of parasitized eggs, was usually higher at vines adjacent to woodlots than at more distant vines. Parasitism was usually lowest at the interior vines, farthest from the woodlots. Early season parasitism ranged from about 20 to 41% at vines closest to woodlots and ranged from 0 to 28% in the intermediate and interior vines (Table 7). Distance from woodlot did not influence densities of total leafhopper eggs ($P > 0.05$), suggesting that resource availability did not influence the pattern of parasitism by *Anagrus.* Early season parasitism in 1994 followed a trend similar to that observed in 1993 (Table 8). In late June, parasitism was significantly greater in vines at both edges than in the interior of the vineyard. At this time, 59% of the sentinel eggs in the vines adjacent to the woodlot edge were parasitized, 35% of the eggs in the vines adjacent to the open edge were parasitized, and 2% of the eggs in the vines in the interior of the vineyard were parasitized. Parasitism was unexpectedly high at the open edge throughout the season in 1994. This suggests that the relatively few perennial plants in the vicinity produced many *Anagrus* and/or *Anagrus* colonized the open edge from more distant (>200 m) woodlots. Corbett and Rosenheim (1996) demonstrated that most (>65%) *Anagrus* colonize California vineyards from areas other than prune tree refuges.

Late season parasitism in 1993 generally decreased with distance from woodlots (Tables 6 and 7 and Fig. 2B). In 1994, the distribution of parasitized eggs/cm^2 was not affected by distance from vineyard edges in late July (Table 8). However, the percentage of eggs parasitized at the open edge in late July was significantly greater than at vines in the interior (49% vs 21%). In late August, a distance effect on parasitism was not observed. Low numbers of parasitized eggs/cm^2 were observed across all distances and were due to a substantially lower rate of leafhopper oviposition in late August as their reproductive cycle was on the decline. Parasitism at this time ranged from 29 to 50%.

Our results suggest that *Anagrus* emerges from alternate hosts in overwintering sites in the spring and possibly completes at least one generation in alternate hosts prior to bud break of cultivated grapes. Colonization of vineyards then proceeds from the edges toward the interior, so that, by the end of the growing season, *Anagrus* abundance and parasitism are similar throughout the vineyard. This knowledge lays the groundwork for other studies that must be conducted before a biological control program for grape leafhopper can be developed in the northeastern United States. First, we must have definitive identification of the alternate hosts utilized by *Anagrus,* and elucidation of *Anagrus*-alternate host life histories and their impact on *Anagrus* population dynamics in the spring. Doutt and Nakata (1965, 1973) first recognized the importance of alternate host habitats on the ability of *A. epos* to overwinter and subsequently colonize vineyards in California. In that agroecosystem, blackberry

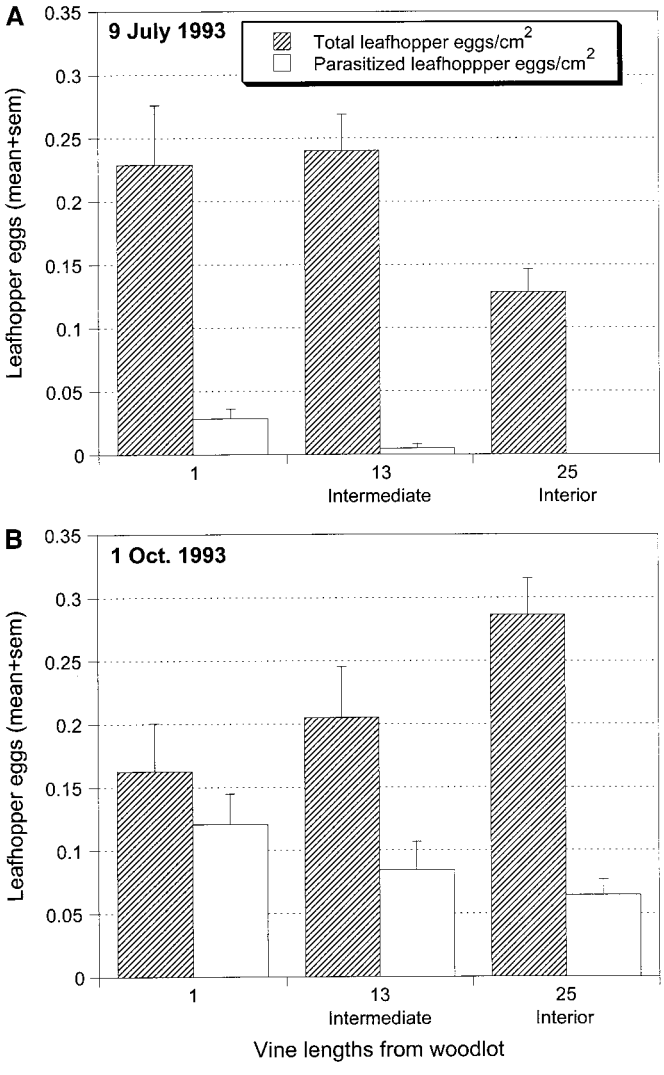

FIG. 2. Effect of distance from woodlot on host density (total *E. comes* eggs/cm^2) and parasitism by *Anagrus* (parasitized *E. comes* eggs/cm^2) at Niagara site in July (A) and October (B) 1993.

brambles harbor the diapausing eggs of a noneconomic leafhopper, *Dikrella californica* (Lawson), in which *A. epos* overwinters. Later, Kido *et al.* (1984) found that prune trees support another leafhopper, *Edwardsiana prunicola* (Edwards), used by *A. epos* during California winters.

In addition to providing overwintering refuges for *Anagrus*, diapausing insect eggs serve as important resources for *Anagrus* populations in the spring. In California and Europe, *Anagrus* emerging from overwintering hosts complete at least one generation in alternate leafhopper hosts in the spring prior to dispersal into the vineyard (Doutt and Nakata, 1973; Williams, 1984; Cerutti *et al.*, 1990, 1991). Further studies will determine if *Anagrus* species in the northeastern United States have the same strategy. The role of alternate host eggs in the spring is twofold. First, they sustain *Anagrus* emerging from overwintering hosts until the onset of grape leafhopper oviposition. Second, the availability of alternate hosts in the spring might allow *Anagrus* populations to increase before dispersal into vineyards. Thus, leafhopper species that overwinter as diapausing eggs play a crucial role in the life history of *Anagrus* in cultivated grape, because they act as an "ecological bridge" which spans the gap between times when grape leafhopper eggs are available.

A more detailed understanding of *Anagrus*–alternate host associations in New York may lead to habitat management strategies that optimize the impact of *Anagrus* on grape leafhopper populations. Establishment of prune tree refuges in the proximity of vineyards enhances early season densities of *A. epos* in California vineyards (Kido *et al.*, 1984; Pickett *et al.*, 1990). Murphy *et al.* (1996, 1998) showed that *A. epos* densities and parasitism in vineyards are directly related to densities of *A. epos* overwintering in nearby prune tree refuges. Vineyards adjacent to these refuges had greater parasitism of *Erythroneura elegantula* Osborn eggs in the early season than vineyards without refuges (Murphy *et al.*, 1998). Increased early season parasitism was further shown to be an important determinant of season-long parasitism rates (Murphy *et al.*, 1998). Corbett and Rosenheim (1996) reported that the number of wasps that emerge from overwintering habitats and the physical characteristics of the habitats strongly influence colonization of vineyards by *Anagrus.* Distance between the overwintering habitat and the vineyards, densities of *Anagrus* in these refuges, and windbreak effects generated by the refuges all play major roles in dispersal of *Anagrus.* These studies indicate that habitat management has great potential for enhancing biological control of grape leafhoppers. Integration of habitat management and pesticide use strategies that optimize the efficacy of *Ana-*

TABLE 8

Within-Vineyard Distribution of *Erythroneura comes* Eggs Parasitized by *Anagrus* at the Niagara Site, Finger Lakes Region, New York, 1994

Transect	Late June	Late July	Late August
	Mean proportion of parasitized *E. comes* eggs[a]		
Woodlot edge	0.593 (<0.0001)	0.307 (0.2822)	0.398 (0.7752)
Interior	0.020	0.209	0.289
Open edge	0.352 (0.0246)	0.490 (0.0287)	0.500 (0.8101)
	Mean no. of parasitized *E. comes* eggs per cm^2 leaf tissue[a]		
Woodlot edge	0.800 (<0.0001)	0.231 (0.3152)	0.056 (0.8347)
Interior	0.040	0.438	0.080
Open edge	0.334 (0.0180)	0.334 (0.8569)	0.048 (0.7793)

[a] Significance levels for comparisons (interior vs woodlot edge, interior vs open edge) within time of season.

grus will be an important step toward the establishment of a biological control program for grape leafhoppers in New York.

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