

# Conservation Biological Control of Rosy Apple Aphid, *Dysaphis plantaginea* (Passerini), in Eastern North America

M. W. BROWN<sup>1</sup> AND CLARISSA R. MATHEWS<sup>2</sup>

Environ. Entomol. 36(5): 1131–1139 (2007)

**ABSTRACT** Because of the potentially serious damage rosy apple aphid, *Dysaphis plantaginea* (Passerini) (Homoptera: Aphididae), can cause to apple fruit and branch development, prophylactic insecticides are often used for control. If biological control could be relied on, the amount of pesticide applied in orchards could be reduced. This study examined biological control of rosy apple aphid in eastern West Virginia and the potential for enhancement through conservation biological control, in particular, the effect of interplanting extrafloral nectar-bearing peach trees. By 20 d after first bloom, only 2% of fundatrices initially present survived to form colonies based on regression of data from 687 colonies. Exclusion studies showed that many of the early colonies were probably destroyed by predation; the major predator responsible seemed to be adult *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). Mortality before apple bloom was most important in controlling rosy apple aphid population growth but by itself is not sufficiently reliable to prevent economic injury. Interplanting of extrafloral nectar-bearing trees did not increase biological control, and interplanting with 50% trees with extrafloral nectar glands reduced biological control. The number of leaf curl colonies in the 50% interplanted orchards was lower than in monoculture orchards, suggesting a preference of alate oviparae for more diverse habitats, supporting the resource concentration hypothesis but not at a level sufficient to prevent injury. Predation and parasitism after the formation of leaf curl colonies was not adequate to control rosy apple aphid populations.

**KEY WORDS** interplanting, extrafloral nectar, *Harmonia axyridis*, *Malus x domestica*, *Prunus persica*

Habitat management to increase conservation biological control has been a popular topic in recent years (Barbosa 1998, Landis et al. 2000). It has been relatively easy to show that by adding alternate food resources to a system, the abundance of predators and parasitoids can be increased (Nentwig 1988, White et al. 1995, MacLeod 1999, Nicholls et al. 2001). Showing an impact on biological control, although more difficult, has been shown (Baggen and Gurr 1998, Stephens et al. 1998, Carmona and Landis 1999). In apple [*Malus x domestica* (Borkh.)] orchards, several researchers have tested the potential for companion plants to increase biological control (Bugg and Waddington 1994, Wyss 1995, Stephens et al. 1998, Brown and Glenn 1999, Jenser et al. 1999, Bostanian et al. 2004). Interplanting species of fruit trees with extrafloral nectaries into apple orchards has also been suggested (Brown and Mathews 2005). Mathews et al. (2007) showed that extrafloral nectaries can increase biological control of oriental fruit moth [*Grapholita molesta* (Busck) (Lepidoptera: Tortricidae)] in peach (*Prunus persica* Batsch). Extrafloral nectar from peach also has been shown to increase fitness of *Tri-*

*chogramma minutum* (Hymenoptera: Trichogrammatidae) in the laboratory (Shearer and Atanassov 2004) and the residence time of *Chrysoperla plorabunda* (Fitch) (Neuroptera: Chrysopidae) on almond, *Prunus amygdalus* Batsch, in the field (Limburg and Rosenheim 2001). Interplanting trees bearing extrafloral nectaries to manipulate biological control in apple orchards has yet to be tested.

The rosy apple aphid, *Dysaphis plantaginea* (Passerini) (Homoptera: Aphididae), is a major pest of apple in North America and Europe (Hull and Starner 1983, Hemptinne et al. 1994). Rosy apple aphids spend the winter as eggs on apple, the primary host. Egg hatch coincides with apple bud break in early spring (Hull and Starner 1983). The first generation or two are exposed on apple buds and expanding leaves, but by the time trees bloom, the leaves begin to curl, thus providing protection to the remaining generations. There are five to seven generations on apple in the spring and early summer (Baker and Turner 1916), with migration to the secondary host, *Plantago* spp., especially *P. lanceolata* L. (Blommers 1999), occurring from mid-May through June. The aphids return to apple in late summer to early fall, where there is a sexual generation that produces oviparous females. Injury to apple can occur by deformation of growing shoots and fruit that develop on those shoots through the secretion of plant hormone-mimicking com-

<sup>1</sup> Corresponding author: USDA-ARS, Appalachian Fruit Research Station, 2217 Wiltshire Rd., Kearneysville, WV 25430 (e-mail: mark.brown@ars.usda.gov).

<sup>2</sup> Shepherd University, Institute for Environmental Studies, 35 Snyder Hall, Shepherdstown, WV 25443.

pounds in the aphids' saliva (Parrott et al. 1919). The rosy apple aphid is a difficult pest to control in all but the first few generations because of the protection provided by the tightly curled leaves in which it feeds (Blommers 1999). Although chemical control can be effective, it must be applied before the formation of curled leaves (Hull and Starner 1983, Hemptinne et al. 1994).

Recently there have been several studies on the biological control of rosy apple aphid in apple orchards. In Europe, the most abundant natural enemies in the spring have been the predators *Episyrphus balteatus* (DeGeer) (Diptera: Syrphidae), *Adalia bipunctata* L. (Coleoptera: Coccinellidae), and *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) (Wyss et al. 1999b, Miñarro et al. 2005). Both *E. balteatus* and *A. bipunctata* were effective in reducing rosy apple aphid populations in field cages (Wyss et al. 1999b), but none of the predators provided sufficient control in orchards of northwest Spain (Miñarro et al. 2005). Habitat manipulation in the form of flowering companion plant strips was effective in reducing rosy apple aphid populations by increasing predation rates in the spring and fall (Wyss 1995). Augmentative release of larval *A. bipunctata* in early spring (Wyss et al. 1999a) and autumn (Kehrli and Wyss 2001) has also shown positive results. It was suggested that the planting of rowan trees (*Sorbus aucuparia* L.) could increase biological control of rosy apple aphids by increasing the abundance of the parasitoid *Ephedrus persicae* Froggatt (Hymenoptera: Braconidae) by providing the alternate, congeneric host *Dysaphis sorbi* Kaltenbach (Bribosia et al. 2005).

The predator *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) has been dominant in eastern North American apple orchards since 1995 (Brown and Miller 1998). This coccinellid is the most effective predator of spirea aphid, *Aphis spiraeicola* Patch (Homoptera: Aphididae), in West Virginia (Brown 2004). Adult *H. axyridis* were found to be the most effective predator in controlling spirea aphid because it arrives early during the aphid colonization phase on apple and is very mobile and voracious (Brown 2004). This study was conducted to assess the adequacy of biological control of rosy apple aphid populations in eastern North American apple orchards and the potential of interplanting peach trees into apple orchards to promote its biological control.

### Materials and Methods

All studies were conducted in research orchards that were not treated with insecticides, located at the Appalachian Fruit Research Station in Kearneysville, WV, from 1997 to 2006. The orchards were managed the same and received standard horticultural treatments other than insecticides; including mowing, weed control in the tree rows, pruning, and fungicides for disease management. Rosy apple aphid populations in six orchards were studied: three were apple monocultures paired with three similar apple orchards interplanted with peach. Two of the interplanted or-

chards had 50% of the trees as peach ('Loring/Lovell') or sweet cherry, *Prunus avium* L., all having extrafloral nectaries; and 50% apple ('Granny Smith/EMLA 26' and 'Royal Empire/M9/EMLA 111') or pear, *Pyrus communis* L. The paired monoculture for these two interplanted orchards only had a mixture of the two apple species. These four orchards were planted in April 1997 and each was 0.5 ha in size. The other interplanted orchard had 9% peach trees ('Crimson Rocket' on its own roots) and the apple cultivars Enterprise/EMLA26 and Liberty/EMLA26. The paired monoculture had the two apple cultivars and was separated from the interplanted orchard by five apple trees. These two orchards were planted in April 2002 and each was 0.15 ha in size.

Four studies were done to evaluate the effect of interplanting on biological control of rosy apple aphid and to identify the primary species involved. Colony abundance estimates were made to compare the abundance of colonies in apple monoculture orchards with abundance in orchards interplanted with 50% peach. Nondestructive sampling was used to track the fate of cohorts of colonies from egg hatch to the formation of leaf-curling to estimate early spring population development. An exclusion study was done to separate the effects of predators from other possible population regulating factors during the early egg hatch to leaf-curl colony stage. Destructive sampling was done after leaf curling began to estimate the possible impact of biological control in these larger, protected colonies and identify natural enemies involved.

**Colony Abundance.** On 13–14 May 1998 and 11–14 May 2001, all rosy apple aphid colonies (leaf curl stage) on all apple trees in the two 50% interplanted orchards and the two paired monocultures were counted. All shoots or flower clusters with curled leaves from rosy apple aphid feeding were counted without determining if aphids were present to include all active and inactive colonies.

Colony abundance data were analyzed with a 2 by 4  $\chi^2$  because of the lack of normality in the distribution of colony counts (a large number of zero counts resulted in a truncated distribution). The variable used for analysis was number of rosy apple aphid colonies per 100 trees to standardize for the different number of apple trees in each orchard ( $n = 114$ – $140$ ). The  $\chi^2$  table had monocrop or interplanted as the two columns and year by orchard pair as the four rows. The expected matrix was calculated using fixed row totals.

**Nondestructive Sampling.** Rosy apple aphid colonies were randomly selected as soon as eclosion was observed in the orchard in early April 2002, 2004, and 2005. These colonies were marked with colored thread so that the same colonies could be observed until they either disappeared or formed the leaf curl colony stage in early May. In 2002, a preliminary sample 61 colonies were initially observed on 2 April, all in one of the 0.5-ha monoculture block of apples. In 2004, 86 colonies were initially observed on 6 April and another 219 colonies were first observed on 17–18 April: 109 colonies were in the 50% interplanted blocks, 44 colonies in the 9% interplanted block, and a total of 152 were

in the three apple monoculture blocks. In 2005, 318 colonies were initially observed on 10–11 April: 111 colonies were in 50% interplanted blocks, 50 colonies in the 9% interplanted block, and a total of 157 in the three apple monoculture blocks. Colonies were observed at 3- to 10-d intervals depending on weather conditions and were recorded as present or absent. Also, at each observation, the presence of any predators or parasitoids was noted. A 2 by 2  $\chi^2$  test to examine the effect of spider presence on disappearance of aphid colonies was performed on a subset of the 2004 data. Regression analysis was done on each year by orchard type, monoculture or interplanted, using a logistic transformation to normalize the residuals and linearize the data (Neter and Wasserman 1974). Differences between survivorship, standardizing for annual differences in phenology by using days from first bloom for the cultivar Golden Delicious (a standard cultivar in West Virginia with an average bloom phenology among the cultivars examined), in monoculture and interplanted orchards across years was tested by *t*-tests of the slope estimates between the interplanted orchards and their matched controls for each concentration of interplanting and between the two controls (Steel and Torrie 1960) using pooled SE of the slopes.

**Exclusion Study.** On 14–17 March 2006, 191 newly eclosed rosy apple aphid fundatrices were identified and marked for repeated observations in the three monoculture apple orchards. Of the initial 191 putative colonies, 29 disappeared before treatment and thus were not included in the exclusion study. On 27–28 March, four treatments were applied randomly to the putative colonies and monitored until 24 April. The control treatment was left with just a string marking the location of 40 colonies. An exclusion treatment was applied to 40 buds to prevent walking predators from feeding on the colony and to quantify the extent of migration by the rosy apple aphid fundatrices. This treatment was composed of a band of tangle trap (Tanglefoot Co., Grand Rapids, MI) on the twig around the bud on which the aphid was located; if the bud was in the middle of a twig, a band of tangle trap was placed around the twig on either side of the bud. Flying predators were excluded by placing a 15- to 30-cm-long by 15-cm-diameter cloth mesh cage, 10 by 50 threads/cm (BioQuip Products, Gardena, CA), around 41 colonies. One colony was enclosed in each cage after each twig was searched to ensure no predators were within the cage. A third exclusion treatment, composed of both the mesh cage and tangle trap bands, was applied to 41 colonies.

All colonies were observed at 5- to 8-d intervals, and the presence or absence of aphids was recorded. Any contributing causes to the loss of a colony; such as presence of a predator, aphid stuck on the tangle trap band, or damage to the bud, was also noted. Because it could not be determined at eclosion if the fundatrix was a rosy apple aphid or an apple grain aphid, *Rhopalosiphum fitchii* (Sanderson), all apple grain aphids were eliminated from further analysis once the aphid was large enough to be identified in the field. A 4 by

2  $\chi^2$  analysis was conducted with the four treatments as rows and the total number of colonies that disappeared from unknown cause as one column and the number of surviving colonies on 24 April as the other column.

**Destructive Sampling.** During 5 yr, between 1997 and 2005, colonies of rosy apple aphid were destructively sampled after bloom when the colonies were large and exhibited tightly curled leaves. In 1997, there were three samples of 10 colonies per sample date. In 2001, there were four samples of 40 colonies per sample. In the other years, there were 20 colonies per sample with eight samples in 2002, three samples in 2004, and four samples in 2005. Samples were taken in equal proportions from the four 0.5-ha orchards. To standardize for differences in annual phenology, data were converted to days after 'Golden Delicious' petal fall. Destructive sampling started from 2 May to 28 May (1–23 d after petal fall) and continued as late as 21 June in 2002 (60 d after petal fall). Sampling intervals were at approximately weekly intervals but were as long as 17 d at one sample interval in 2005. At each sample, branches with curled leaves from rosy apple aphid feeding were randomly selected, cut and placed into resealable plastic bags in a cooler for transport to the laboratory, where they were refrigerated until processing. In the laboratory, the sample bags were opened and the presence or absence of ants and their species identity were recorded, as was the number of curled leaves, number of leaves with rosy apple aphids present, presence of alate forms of rosy apple aphids, and the presence of any other arthropods within the colony. Parasitoids were reared from aphid mummies and identified by E. E. Grissell (Megaspilidae) and P. M. Marsh (Braconidae) from the USDA-ARS Systematic Entomology Laboratory, U.S. National Museum, Washington, DC. Data from the 5 yr of sampling were combined into one data set and summarized by week after petal fall; samples from weeks 1 and 2 and weeks 7 and 8 were combined because of limited samples.

The interaction between ants and the more abundant taxa of predators was tested with a  $\chi^2$  test for association by year. Taxa that were abundant enough for testing were syrphids, coccinellids, *A. aphidimyza*, and aphid mummies. The phenology of the various predator groups was compared graphically with the percentage of rosy apple aphid infested leaves from the samples by week to identify which, if any, predator group might be capable of controlling the leaf curling stage of rosy apple aphid.

## Results

**Colony Abundance.** There was a consistent and significant difference in the number of rosy apple aphid leaf curl colonies between the monoculture and 50% interplanted orchards postbloom ( $\chi^2 = 29.22$ , *df* = 3, *P* < 0.05). In all four paired orchards (two orchard pairs in each of 2 yr), there were more aphid colonies per apple tree in the monoculture than in the interplanted orchards. The average infestation in the

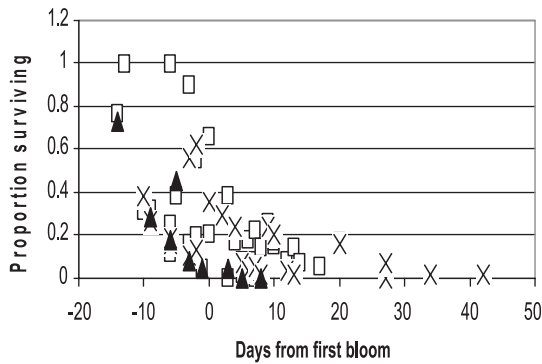


Fig. 1. Survivorship of rosy apple aphid from eclosion from eggs to 40 d after first bloom in 2002, 2004, and 2005: open squares, apple monoculture,  $n = 44$ ; crosses, apple interplanted with 50% peaches,  $n = 25$ ; solid triangles, apple interplanted with 9% peaches,  $n = 9$ .

monoculture was 1.38 rosy apple aphid colonies per tree (range, 0.97–1.60) and 0.95 per tree in the interplanted orchards (range, 0.76–1.38).

**Nondestructive Sampling.** There was a steady decrease in the number of rosy apple aphid colonies in the prebloom to 1-mo postbloom period (Fig. 1). Using the regression for the data set as a whole (Fig. 1), only 2% of the initial 687 colonies were still alive by 20 d after first bloom. The slope for the 9% interplanted treatment ( $-0.3634$ ) was not significantly different from its control ( $-0.3777$ );  $t = 0.13$ ,  $P > 0.05$  (Table 1). The slope for the 50% interplanted treatment ( $-0.0748$ ) was significantly less negative than its control ( $-0.1591$ );  $t = 2.26$ ,  $P < 0.05$  (Table 1). The slope for the two controls was significantly different with the control for the 9% interplanted being more negative than the 50% interplanted control;  $t = 3.60$ ,  $P < 0.01$  (Table 1).

Only three aphid predators were observed during the nondestructive sampling: *H. axyridis* adults, syrphid eggs, and spiders. *H. axyridis* adults were the most abundant predator and were observed as early as 7 April foraging among the apple buds whenever the temperature was above  $\approx 10^{\circ}\text{C}$ . Syrphid eggs were infrequent ( $< 1$  per 20 colonies) during the prebloom period, and the presence of an egg had no noticeable effect on the persistence of the nearby rosy apple aphid colony. There was no effect of the presence of spiders on the disappearance of rosy apple aphid col-

Table 1. Regression, logistic transformed data, and statistics for survivorship of orchard treatment cohorts and the matching control (monoculture) across years for rosy apple aphid from eclosion from egg to formation of leaf curl colony (based on a total of 684 colonies)

Orchard	slope ( $\pm$ CI)	$r^2$	df	$P$ ( $r^2 > 0$ )
9% Interplanted	$-0.3634$ (0.2956)	0.8620	7	$< 0.01$
Control for 9% interplanted	$-0.3777$ (0.2115)	0.8602	8	$< 0.01$
50% interplanted	$-0.0784$ (0.0862)	0.4296	23	$< 0.05$
Control for 50% interplanted	$-0.1591$ (0.0607)	0.5878	32	$< 0.01$

Table 2. Number (%) of rosy apple aphid colonies in the four exclusion treatments by cause of colony disappearance and no. (%) surviving, 27 Mar. to 24 April 2006

Colony fate	Treatment				Total
	Control	Cage	Sticky	Cage plus sticky	
Initial cohort	40	41	40	41	162
Unknown/predation	26 (65.0)	2 (4.9)	12 (30.0)	0 (0.0)	40 (24.7)
Damaged	6 (15.0)	13 (31.7)	11 (27.5)	12 (29.3)	42 (25.9)
Migration	1 (2.5)	2 (4.9)	0 (0.0)	0 (0.0)	3 (1.8)
Apple grain aphid	1 (2.5)	1 (2.4)	4 (10.0)	3 (7.3)	9 (5.6)
Survived	6 (15.0)	23 (56.1)	13 (32.5)	26 (63.4)	68 (42.0)

onies ( $\chi^2 = 0.211$ ,  $df = 1$ ,  $P > 0.05$ ). There were 11 branch terminals with both spiders and aphids and 10 with spiders and no aphids. A total of 226 terminals were without spiders, 112 had aphids, and 114 did not have aphids. The spiders observed were all crab spiders (Thomisidae and Philodromidae).

**Exclusion Study.** The initial number of fundatrices treated and the fate of the putative colonies are given in Table 2. To calculate the magnitude of colonies with an unknown fate (potentially attributable to predation), we first subtracted the number of colonies that were identified as apple grain aphid, 5.6% overall (Table 2). Damaged colonies, those that exhibited signs of physical damage from either the treatment or other causes, accounted for 15% of the colonies in the control treatment and 29.5% of colonies in the exclusion treatments (Table 2). The 15% loss of colonies in the control treatment could have been from wind damage, vertebrate browsing, other natural physical factors, or repeated observation and manipulation of the branch to facilitate observation. Migration was observed in both the cage and control treatment at 4.9 and 2.5% of the colonies, respectively. In these cases, the aphid was found on an adjacent bud that previously had no aphid (control) or was found on the inside of the cage. There was no migration noted in either treatment with sticky material (Table 2). The category of most interest was unknown loss of colonies. There was no unexplained loss of colonies in the cage plus sticky treatment and only 4.9% unknown loss in the cage treatment. The sticky treatment had 30% and the control had 65% unknown loss. There were significantly more colonies lost to unknown causes in the control treatment than any of the exclusion colonies ( $\chi^2 = 51.98$ ,  $df = 3$ ,  $P < 0.001$ ).

**Destructive Sampling.** There was a large and diverse guild of arthropods associated with the leaf curl phase of rosy apple aphid colonies (Table 3). The most abundant group, Formicidae, was not quantified because of their high level of activity and aggressiveness. Four species constituted the ant tending guild: *Pre-nolepis imparis* (Say), *Formica subsericea* Say, *Lasius neoniger* Emery, and *Paratrechina vividula* (Nylander). *Aphidoletes aphidimyza* was the predominant predator species, accounting for 50% of the individuals

**Table 3.** Abundance of arthropods (all stages combined), other than Aphididae, found inhabiting leaf curl rosy apple aphid colonies from destructive sampling of 490 colonies in 1997, 2001, 2002, 2004, and 2005

Taxon	Number of individuals
<b>Insecta</b>	
<b>Heteroptera</b>	
Anthocoridae	3
Miridae	1
Geocoridae	1
<b>Orthoptera</b>	
Oecanthinae	6
<b>Dermaptera</b>	
<i>Forficula auricularia</i> L.	62
<b>Neuroptera</b>	
Chrysopidae	14
<b>Coleoptera</b>	
<b>Coccinellidae</b>	
<i>Harmonia axyridis</i> (Pallas)	77
<i>Coleomegilla maculata</i> Timberlake	1
<i>Coccinella septempunctata</i> L.	11
<i>Cycloneda munda</i> (Say)	2
<i>Scymnus</i> sp.	1
Cantharidae	5
Carabidae	
<i>Harpalus</i> sp.	1
Elateridae	3
<b>Diptera</b>	
Syrphidae <sup>a</sup>	117
<b>Cecidomyiidae</b>	
<i>Aphidoletes aphidimyza</i> (Rondani)	678
<b>Hymenoptera</b>	
<b>Formicidae<sup>b</sup></b>	
Braconidae and Megaspilidae combined <sup>c</sup>	
	311
<b>Araneida</b>	
	55
<b>Total</b>	1,349

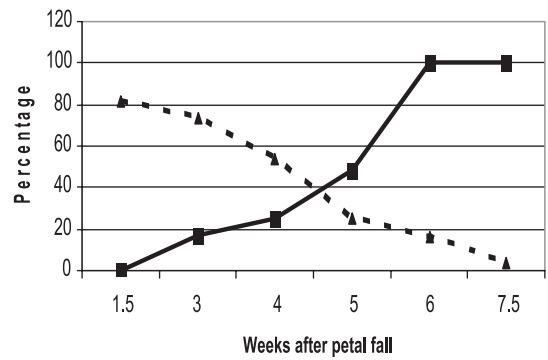
<sup>a</sup> Includes *Syrphus rectus* Osten Sacken, *Eupeodes americanus* Wiedemann, and *Allograpta obliqua* (Say).

<sup>b</sup> Includes *Prenolepis imparis* (Say), *Formica subsericea* Say, *Lasius neoniger* Emery, and *Paratrechina vividula* (Nylander).

<sup>c</sup> Includes Braconidae, *Diaeretiella* sp. and *Ephedrus* sp. prob. *persicae* Froggatt; Megaspilidae, *Asaphes suspensus* Nees, and one unidentified species.

encountered. The other abundant groups were parasitic Hymenoptera (23%), syrphids (9%), *H. axyridis* (6%), *Forficula auricularia* L. (4%), and spiders (4%). Individual species of parasitic Hymenoptera were not quantified separately, but four species were reared from collected mummies: two Braconidae, *Diaeretiella* sp. and *Ephedrus* sp. prob. *persicae*, and two hyperparasitic Megaspilidae, *Asaphes suspensus* Nees and one unidentified species. Three species of syrphids were identified but not quantified individually: *Syrphus rectus* Osten Sacken, *Eupeodes americanus* Wiedemann, and *Allograpta obliqua* (Say).

By 2 mo after petal fall, all rosy apple aphids disappeared from the leaf curls (Fig. 2). The most rapid decline in the apple infestation occurred from 3 to 5 wk after petal fall in West Virginia (Fig. 2). The most rapid increase in formation of alatae was from 4 to 6 wk after petal fall (Fig. 2). Of the most abundant natural enemies, abundance of parasitized mummies peaked earliest in the first 2 wk, with a second peak in the sixth week after petal fall (Fig. 3). Syrphids peaked in the third week and *A. aphidimyza* in the fourth



**Fig. 2.** Percentage of rosy apple aphid leaf curl colonies infested with rosy apple aphids, dotted line, and percentage of colonies with alate rosy apple aphids, solid line; based on destructive sampling of 490 colonies in 1997, 2001, 2002, 2004, and 2005.

week after petal fall (Fig. 3). Coccinellids did not become abundant until 4–6 wk after petal fall (Fig. 3). Chrysopids, Heteroptera, Orthoptera, Dermaptera, and spiders combined did not peak until 6–8 wk after petal fall (data not shown).

Ants were abundant throughout all 8 wk of destructive sampling. In all years, there was no significant association of ants with the presence of syrphids. Coccinellids had only a weak negative association with ants in 1 (2002) of the 4 yr ( $\chi^2 = 3.97$ ,  $df = 1$ ,  $P < 0.05$ ). *A. aphidimyza* had a significantly positive association with ants in all 4 yr (1997:  $\chi^2 = 4.06$ ,  $df = 1$ ,  $P < 0.05$ ; 2001:  $\chi^2 = 4.16$ ,  $df = 1$ ,  $P < 0.05$ ; 2002:  $\chi^2 = 28.94$ ,  $df = 1$ ,  $P < 0.001$ ; 2004:  $\chi^2 = 16.50$ ,  $df = 1$ ,  $P < 0.001$ ). Parasitized mummies were not observed in 1997, but in 2001 and 2004, there was no association of mummies with ants and a significantly positive association with ants in 2002 ( $\chi^2 = 13.15$ ,  $df = 1$ ,  $P < 0.001$ ).

**Discussion**

There was a significant effect of host density on the mortality rates of young rosy apple aphid colonies before apple bloom. Orchards with 50% of the trees having extrafloral nectar glands had lower rates of mortality than orchards with 0 or 9% interplanted trees with extrafloral nectaries (Table 1). It was shown previously that the presence of peach shoots with extrafloral nectar in a cage with aphid-infested apple shoots reduced predation by *H. axyridis* over a short time period (Spellman et al. 2006). The reduction in predation of aphid colonies in the presence of abundant nectar sources apparently occurred in the field (Table 1) as it did in the small cage trials. This reduced predation could be a result of predator satiation or interference in host finding. There was a high degree of site to site variation in rosy apple aphid mortality shown by the significant difference in the two control data sets (Table 1). This difference could be because of differences in site characteristics, surrounding habitat, age of trees, or cultivar.

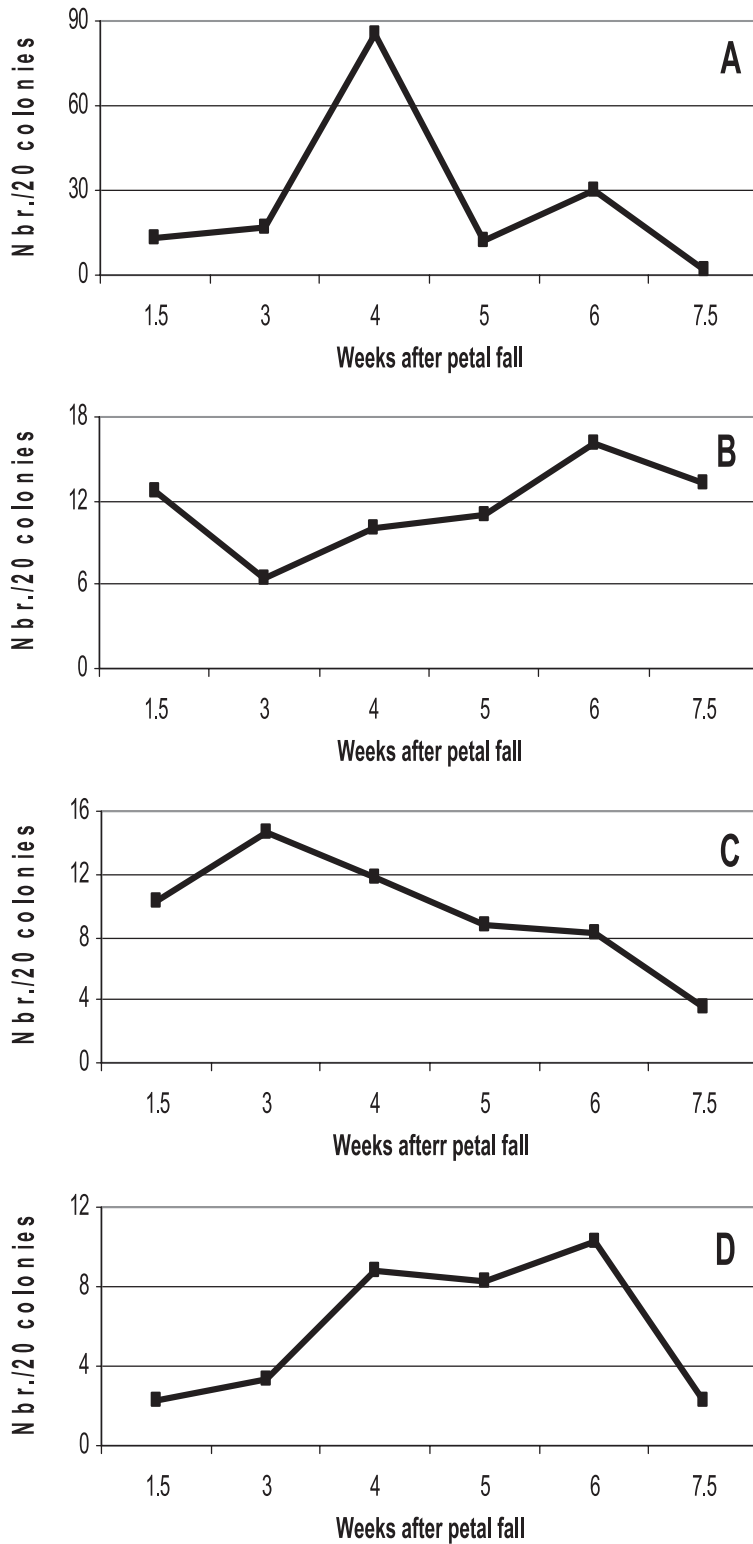


Fig. 3. Number of major predators of rosy apple aphids per 20 colonies from destructive sampling of 490 leaf curl colonies: (A) *Aphidoletes aphidimyza*; (B) parasitized aphid mummies; (C) Syrphids (all species combined); and (D) Coccinellids (all species and stages combined).

Concentration of host plants also had an effect on the dynamics of rosy apple aphid populations. The number of leaf curl colonies after bloom was lower in orchards interplanted with 50% nonhost plants (peach) than in monoculture orchards. However, rates of mortality during the early stages of rosy apple aphid population growth were lower in the 50% interplanted orchards than in the monoculture (Table 1). Lower rosy apple aphid populations in the 50% interplanted orchard than in the monoculture, despite lower mortality, support the resource concentration hypothesis (Kareiva 1983) rather than the enemies hypothesis (Russell 1989). Rosy apple aphid oviparae returning to apple in the fall seem to be attracted to high concentrations of host plants rather than more diverse interplanted orchards.

Disappearance of young rosy apple aphid colonies was high (Fig. 1). By 20 d after bloom, an estimated 2% of the initial 687 founding colonies had survived, as calculated by the overall logistic regression equation. However, even 2% of the colonies surviving 3 wk after bloom would continue the life cycle because alatae begin forming by the third week after petal fall (Fig. 2). Predators and parasitoids do exert some pressure on the larger, postbloom, leaf curl colonies (Fig. 3). There are a large number of natural enemies that obviously feed on large numbers of aphids, but the formation of alatae beginning at 3 wk postbloom (Fig. 2) indicates that there are sufficient numbers of aphids leaving apple to continue the life cycle on alternate hosts. Also, these leaf curl colonies, which occur after petal fall, are large and rapidly growing with very high numbers of aphids per colony; as many as  $7 \times 10^9$  after six generations, using the average reproduction rate reported by Baker and Turner (1916). It would, therefore, be difficult for the combined predators and parasitoids to exert a regulating effect on these large colonies (Blommers 1999). Reductions in postbloom rosy apple aphid infestations are more likely explained by the formation of alatae (Fig. 2) and subsequent migration to the summer host, *Plantago* spp.

Tending ants had a surprisingly small impact on the natural enemies of postbloom leaf curling rosy apple aphid colonies. There was a highly significant positive association of ants with *A. aphidimyza* abundance, as was shown previously for *A. aphidimyza* in spirea aphid colonies (Brown 2004). Both ants and this predator midge are attracted to large aphid colonies. Only the abundance of coccinellids had a slight negative association with ants in this study, showing some degree of interference of predation by ants. Although it is generally assumed that ants interfere with biological control of aphids (Buckley 1987), in this study, ants had minimal impact on the effectiveness of aphid predators.

In the exclusion study, there was no migration in the presence of sticky barriers that could be a result of repellency to the material. However, without the sticky barrier, migration was minimal, at 2.5 and 4.9%. Aphids were rarely found within the cage off of the bud, so it is unlikely that dropping off the bud would contribute to any of the unknown mortality. Any

aphid nymphs that would have dropped off the bud would likely be lost to the population by predation or environmental stress. Environmental factors such as extremes in temperature or moisture are also not likely to have caused any of the mortality recorded as unknown because of the negligible amount of unknown mortality in the two caged treatments. Having removed most apparent causes of colony loss, it is concluded that much of the colonies lost caused by an unknown fate (Table 2) were because of predation. The exclusion study showed that the presence of cages eliminated all but 4.9% of unknown mortality (Table 2). The cages eliminated predators from finding the rosy apple aphid colonies but had no effect on the abiotic factors [the same cage material was shown to have no effect on temperature inside the cage in a prior study (Brown 2004).] The presence of a sticky barrier eliminated walking predators from finding the aphid colonies but not flying predators. The sticky treatment reduced the unknown loss to 30% compared with 65% in the control (Table 2).

Only three predator groups were observed during the early, preleaf curl colony stage. Spiders and syrphids were neither abundant enough nor effective at foraging for the small rosy apple aphid colonies, which were often composed of a single fundatrix. *Harmonia axyridis* adults, however, were observed early, and their ability to find and consume many colonies before rosy apple aphid reproduction could have a significant impact on further population growth, as was shown for spirea aphid on apple (Brown 2004). In early spring, *H. axyridis* adults would have just come out of their overwintering sites (Koch 2003), and, although small colonies of rosy apple aphids are scattered in apple orchards, this lady beetle has a high ability to track aphid resources (Osawa 2000). Adult *H. axyridis* would be inhibited partially by a sticky barrier because much of their foraging is done by walking up and down branches in search of prey (MWB and CRM, unpublished data). About one half of the presumed predation would be attributed to walking predators, because of the 30% unknown loss in the sticky treatment, and one half to flying predators, those eliminated by the cage treatments. Predation by adult *H. axyridis* either walking or flying among early colonies seems to be the most likely cause of the large reduction in early rosy apple aphid populations (Fig. 1).

Given aphids' high reproductive rate, it is critical there be an early response to their infestations before entering the exponential growth stage of population growth (Frazer and Gill 1981, Elliott and Kieckheffer 1990, Blommers 1999). Adult *H. axyridis* seem to be the key predator contributing to the early mortality of rosy apple aphid in these orchards. It has been concluded in European studies that natural levels of biological control are not sufficient to control rosy apple aphid (Wyss et al. 1999b, Miñarro et al. 2005). In those studies, however, *H. axyridis* was not present. *Adalia bipunctata* did not arrive in the Spanish study until after rosy apple aphid populations had reached peak abundance (Miñarro et al. 2005). Although releases of larval *A. bipunctata* were effective in controlling rosy

apple aphid in Switzerland, they had to be made before the coccinellid arrived naturally in the orchard (Wyss et al. 1999b). The appearance of adult *H. axyridis* in eastern North American orchards before exponential aphid population growth seems to be the key to effective biological control for rosy apple aphid populations (Blommers 1999).

Clearly, most of the mortality in rosy apple aphid populations occurs before the development of leaf curl colonies before apple bloom (Fig. 1). This is fortunate for orchard pest management considerations because this precedes damage to fruit or tree limbs (Baker and Turner 1916). This early mortality is largely caused by predation (Table 2), particularly by adult *H. axyridis*. In some cases, predation may be sufficient to control rosy apple aphid as shown in the 9% interplanted orchard and its control (Table 1), but biological control cannot be relied on, as in the 50% interplanted orchard and its control. Interplanting with trees bearing extrafloral nectar glands does not seem to be a reliable option for enhancing biological control of rosy apple aphids in eastern North America.

### Acknowledgments

We thank B. Short for assistance with the field work and identification of the ants and syrphids; E. E. Grissell for identification of the Megaspilidae; P. M. Marsh for identification of the Braconidae; and M. Miñarro, A. Agnello, B. Short, E. Wyss, and two anonymous reviewers for comments on an earlier draft of the manuscript. This project was supported in part by the National Research Initiative of USDA Cooperative State Research, Education and Extension Service Grant 2003-35316-13773.

### References Cited

- Baggen, L. R., and G. M. Gurr. 1998. The influence of food on *Copidosoma koehleri* (Hymenoptera: Encyrtidae), and the use of flowering plants as a habitat management tool to enhance biological control of potato moth, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). *Biol. Control* 11: 9–17.
- Baker, A. C., and W. F. Turner. 1916. Rosy apple aphid. *J. Agric. Res.* 7: 321–344.
- Barbosa, P. 1998. Conservation biological control. Academic, New York.
- Blommers, L.H.M. 1999. Probing the natural control of rosy apple aphid *Dysaphis plantaginea* (Hemiptera: Aphididae). *IOBC WPRS Bull.* 22: 53–56.
- Bostanian, N. J., H. Goulet, J. O'Hara, L. Masner, and G. Racette. 2004. Towards insecticide free apple orchards: flowering plants to attract beneficial arthropods. *Biocont. Sci. Tech.* 14: 25–37.
- Bribosia, E., D. Bylemans, M. Migon, and B. van Impe. 2005. In-field production of parasitoids of *Dysaphis plantaginea* by using the rowan aphid *Dysaphis sorbi* as substitute host. *BioControl* 50: 601–610.
- Brown, M. W. 2004. Role of aphid predator guild in controlling spirea aphid populations on apple in West Virginia, USA. *Biol. Control* 29: 189–198.
- Brown, M. W., and S. S. Miller. 1998. Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. *Entomol. News* 102: 136–142.
- Brown, M. W., and D. M. Glenn. 1999. Use of ground cover plants as a pest management tool in apple orchards. *J. Econ. Entomol.* 92: 899–905.
- Brown, M. W., and C. R. Mathews. 2005. Components of an ecologically and economically sustainable orchard. *Proceedings of the 6th International Conf. Integrated Fruit Production. IOBC/WPRS Bull.* 28: 73–76.
- Buckley, R. C. 1987. Interactions involving plants, Homoptera, and ants. *Annu. Rev. Ecol. Syst.* 18: 111–135.
- Bugg, R. L., and C. Waddington. 1994. Using cover crops to manage arthropod pests of orchards: a review. *Agric. Ecosyst. Environ.* 50: 11–28.
- Carmona, D. M., and D. A. Landis. 1999. Influence of refuge habitats and cover crops on seasonal activity-density of ground beetles (Coleoptera: Carabidae) in field crops. *Environ. Entomol.* 28: 1145–1153.
- Elliott, N. C., and R. W. Kieckheffer. 1990. Dynamics of aphidophagous coccinellid assemblages in small grain fields in eastern South Dakota. *Environ. Entomol.* 19: 1320–1329.
- Frazer, B. D., and B. Gill. 1981. Hunger, movement, and predation of *Coccinella californica* on pea aphids in the laboratory and in the field. *Can. Entomol.* 113: 1025–1033.
- Hemptinne, J.-L., A.F.G. Dixon, P. Guillaume, and C. Gaspar. 1994. Integrated control programme of the apple aphid, *Dysaphis plantaginea* Passerini (Homoptera: Aphididae): forecasting seasonal and yearly changes in abundance. *Med. Fac. Landbouws. Univ. Gent.* 59: 529–537.
- Hull, L. A., and V. R. Starner. 1983. Effectiveness of insecticide applications timed to correspond with the development of rosy apple aphid (Homoptera: Aphididae) on apple. *J. Econ. Entomol.* 76: 594–598.
- Jenser, G., K. Balázs, Cs. Erdélyi, A. Haltrich, F. Kádár, F. Kozár, V. Markó, V. Rác, and F. Samu. 1999. Changes in arthropod population composition in IPM apple orchards under continental climatic conditions in Hungary. *Agric. Ecosyst. Environ.* 73: 141–154.
- Kareiva, P. 1983. Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement, pp. 259–289. *In* R. F. Denno and M. W. McClure (eds.), *Variable plants and herbivores in natural and managed systems*. Academic, New York.
- Kehrli, P., and E. Wyss. 2001. Effects of augmentative releases of the coccinellid, *Adalia bipunctata*, and of insecticide treatments in autumn on the spring population of aphids of the genus *Dysaphis* in apple orchards. *Entomol. Exp. Appl.* 99: 245–252.
- Koch, R. L. 2003. The multicolored Asian lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control, and non-target impacts. *J. Insect Sci.* 3: 32.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45: 175–201.
- Limburg, D. D., and J. A. Rosenheim. 2001. Extrafloral nectar consumption and its influence on survival and development of an omnivorous predator, larval *Chrysoperla plorabunda* (Neuroptera: Chrysopidae). *Environ. Entomol.* 30: 595–604.
- MacLeod, A. 1999. Attraction and retention of *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) at an arable field margin with rich and poor floral resources. *Agric. Ecosyst. Environ.* 73: 237–244.
- Mathews, C. R., M. W. Brown, and D. G. Bottrell. 2007. Leaf extrafloral nectaries enhance biological control of a key economic pest, *Grapholita molesta* (Lepidoptera: Tortricidae), in peach (Rosales: Rosaceae). *Environ. Entomol.* 36: 383–389.



- Miñarro, M., J.-L. Hemptinne, and E. Dapena. 2005. Colonization of apple orchards by predators of *Dysaphis plantaginea*: sequential arrival, response to prey abundance and consequences for biological control. *BioControl* 50: 403–414.
- Nentwig, W. 1988. Augmentation of beneficial arthropod by strip management. 1. Succession of predacious arthropods and long-term change in the ratio of phytophagous and predacious arthropods in a meadow. *Oecologia* (Berl.) 76: 596–606.
- Neter, J., and W. Wasserman. 1974. Applied linear statistical models. Richard D. Irwin, Homewood, IL.
- Nicholls, C. I., M. Parella, and M. A. Altieri. 2001. The effects of a vegetational corridor on the abundance and dispersal of insect biodiversity within a northern California organic vineyard. *Landscape Ecol.* 16: 133–146.
- Osawa, N. 2000. Population field studies on the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): resource tracking and population characteristics. *Pop. Ecol.* 42: 115–127.
- Parrott, P. J., H. E. Hodgkiss, and F. A. Hartzell. 1919. The rosy aphid in relation to abnormal apple structures. U. S. Dept. Agric. Tech. Bull. 66. 29 pp.
- Russell, E. P. 1989. Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. *Environ. Entomol.* 18: 590–599.
- Shearer, P. W., and A. Atanassov. 2004. Impact of peach extrafloral nectar on key biological characteristics of *Trichogramma minutum* (Hymenoptera: Trichogrammatidae). *J. Econ. Entomol.* 97: 789–792.
- Spellman, B., M. W. Brown, and C. R. Mathews. 2006. Effect of floral and extrafloral resources on predation of *Aphis spiraeicola* by *Harmonia axyridis* on apple. *BioControl* 51: 715–724.
- Steel, R.G.D., and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill, New York.
- Stephens, M. J., C. M. France, S. D. Wratten, and C. Framp-ton. 1998. Enhancing biological control of leafrollers (Lepidoptera: Tortricidae) by sowing buckwheat (*Fagopyrum esculentum*) in an Orchard. *Biocont. Sci. Tech.* 8: 547–558.
- White, A. J., S. D. Wratten, N. A. Berry, and U. Weigmann. 1995. Habitat manipulation to enhance biological control of *Brassica* pests by hover flies (Diptera: Syrphidae). *J. Econ. Entomol.* 88: 1171–1176.
- Wyss, E. 1995. The effects of weed strips on aphids and aphidophagous predators in a apple orchard. *Entomol. Exp. Appl.* 75: 43–49.
- Wyss, E., M. Villiger, J.-L. Hemptinne, and H. Müller-Schärer. 1999a. Effects of augmentative releases of eggs and larvae of the ladybird beetle, *Adalia bipunctata*, on the abundance of the rosy apple aphid, *Dysaphis plantaginea*, in organic apple orchards. *Entomol. Exp. Appl.* 90: 167–173.
- Wyss, E., M. Villiger, and H. Müller-Schärer. 1999b. The potential of three native insect predators to control the rosy apple aphid, *Dysaphis plantaginea*. *BioControl* 44: 171–182.

Received for publication 13 December 2006; accepted 21 June 2007.