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Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis*

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Abstract. The effects of the invasion of an exotic predator, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), were investigated using three experiments on the ecology of aphid predators on apple. One experiment, 1992, was collected prior to the *H. axyridis* invasion, and two others, 1996 to 1997 and 1999 to 2000, were collected after the invasion. Except for one year, 1999, *H. axyridis* was the dominant coccinellid, replacing the formerly dominant *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), another exotic species. The dominance of *H. axyridis* was greater among larvae than among adults. There was no apparent effect of the *H. axyridis* invasion on abundance of the predator, *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) and a possible positive effect on the abundance of chrysopids (Neuroptera: Chrysopidae). Principal component analysis indicated that although individual species were affected, the overall effect of *H. axyridis* invasion on the predator guild as a whole was negligible. The data indicate that the interaction between the two exotic species, *H. axyridis* and *C. septempunctata*, may be allowing native coccinellids to become more abundant on apple than when *C. septempunctata* was the dominant coccinellid.

Key words: *Aphidoletes aphidimyza*, apple, biological control, Chrysopidae, *Coccinella septempunctata*, *Harmonia axyridis*, North America

Introduction

The problem of invasive species disrupting natural ecosystems has attracted much attention (Elton, 1958; Mooney and Drake, 1986; Enserink, 1999; Levine, 2000). There are a large number of alien species around the world, including both serious pest and vital crop species, but most of the environmental and economic impact is attributable to a small proportion of the total (Pimentel et al., 2001). The practice of classical biological control relies on the intentional introduction of exotic species into an ecosystem. It has recently been realized that classical biological control can have unintended ecological consequences by releasing additional exotic species to control introduced pests (Simberloff and Stiling, 1996; Louda et al., 1997; Strong and Pemberton, 2000; Ehler, 2000; Wajnberg et al., 2001). For example, native thistle species are attacked by *Rhinocyllus conicus* Froeh. (Coleoptera: Curculionidae), which was introduced to control exotic thistles (Louda et al., 1997). Howarth (1991) and Follett and Duan (1999) reviewed the non-target effects of biological control actions enumerating how negative impacts can come about and providing suggestions for maintaining better control of future biological control activity. Follett et al. (2000) concluded their analysis of the risks of biological control introductions by calling for more case histories on the impacts of past introductions.

Apple, *Malus domestica* (Borkh.), is a very successful introduced species in North America. Since its introduction in the early 17th century, it has been widely planted as a food crop and has become successfully naturalized, growing wild in much of eastern North America (Hedrick, 1988). The entomofauna associated with apple in North America is a mixture of exotic species, introduced at various times over the past 4 centuries, and native species that have adapted to apple from related hosts native to North America. The aphidophagous predator guild exemplifies this well. The primary host aphid for the predator guild studied is the exotic spirea aphid, *Aphis spiraecola* (Patch), long known to feed on apple in North America (Patch, 1914). Historically, the major predators of aphids on apple in eastern North America have been *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae), and chrysopids (Neuroptera) (Adams and Prokopy, 1980; Tracewski et al., 1984; Knowles, 1997; Brown and Lightner, 1997). Prior to the invasion of *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), coccinellids were not dominant in the aphid predator guild in North America. The most abundant coccinellids on apple were *C. transversoguttata* Falderman, *C. novemnotata* (Herbst) and *Adalia bipunctata* (L.) (Putman, 1964; Horsburgh and Asquith, 1968; Travis et al., 1978; Carroll and Hoyt, 1984). *Coccinella septempunctata* was first found in North America in 1973 (Angalet et al., 1979), and by the early 1980s it was the most abundant coccinellid in the apple ecosystem in West Virginia (Brown and Miller, 1998). *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) was first recovered in North America in Louisiana in 1988 (Chapin and Brou, 1991) and began colonizing West Virginia apple orchards in 1994 (Brown and Miller, 1998).

A number of studies have documented the impact of *C. septempunctata* invasion on native coccinellids into the small grain ecosystems of the Midwest, USA. Elliot et al. (1996) found that *C. transversoguttata richardsoni* Brown and *A. bipunctata* populations were reduced by the introduction of *C. septempunctata* into grain fields of North Dakota. Overall there were equal numbers of coccinellids on grain before and after the *C. septempunctata* introduction, indicating no change in biological control potential (Elliot et al., 1996). On caged potatoes in the field, coexistence between exotic *C. septem-*

punctata and native *Coleomegilla maculata* (DeGeer) larvae was maintained (Obrycki et al., 1998a). Obrycki et al. (1998b) reported that larval *C. septempunctata* were competitively superior to *C. maculata* larvae at low aphid populations, but at higher aphid populations there was no difference in predation between the two species. The invasion of *C. septempunctata* into North America has been implicated in an overall reduction in *C. novemnotata* and *Hippodamia convergens* Guerin (Wheeler and Hoebeke, 1995; Ellis et al., 1999). After arriving in North America, *H. axyridis* rapidly dominated arboreal habitats in Oregon (LaMana and Miller, 1996), pecan in Georgia (Tedders and Schaefer, 1994), and many habitats in Michigan (Colunga-Garcia and Gage, 1998). *Harmonia axyridis* has a competitive advantage over *C. septempunctata* through both interference competition and predation (Yasuda and Shinya, 1997). Michaud (2000) showed that *H. axyridis* was able to complete development on a diet of *A. spiraecola* on citrus whereas *C. septempunctata* could not. In an examination of a larger guild of native predators in the laboratory, Lucas et al. (1998) found *A. aphidimyza* to be vulnerable to intraguild predation but found a symmetrical interaction between chrysopids and *C. maculata*. Chang (1996) also found no evidence of intraguild predation of *C. septempunctata* on chrysopid larvae.

In this paper, I document the invasion of *H. axyridis* into the apple ecosystem of eastern North America and the effects of this invasion on the preexisting guild of aphid predators on apple. The apple ecosystem is typical of agricultural ecosystems in North America. The host plant is an introduced species supporting a fauna of a mixture of introduced and native species. Plant diversity is low, with the host plant planted in monoculture and a minimum of other plant species being allowed to persist. The responses of this type of ecosystem to invasion may not be typical of a natural ecosystem, but they could be typical of most managed ecosystems in North America.

Materials and methods

Data for this study were taken from 3 separate experiments on the aphid predator guild on apple in West Virginia, however, sampling methodology was similar enough throughout to allow comparisons. Age, location, insect management practices, and year of sampling of each orchard is presented in Table 1. All orchards were 0.5 to 2.0 ha in size. The first experiment was designed to determine appropriate experimental plot size for spirea aphids, *A. spiraecola*, and predators in apple (Brown and Lightner, 1997). Five orchards (A, B, C, D, and E in Table 1) were sampled 6 times during the year using two 15-tree transects from the edge of the orchard toward the center. The entire tree was observed for aphids and predators for orchards A and B.

Table 1. Characteristics of orchards sampled for spirea aphid and aphid predators, 1992 to 2000

Orchard	Year Planted	Location	Management	Year Sampled
A	1992	AFRS [1]	Reduced insecticides	'92, '96, '97
B	1992	AFRS	Conventional	'92, '96, '97
C	1985	AFRS	Reduced insecticides	'92
D	1985	AFRS	Conventional	'92
E	1985	10 km from AFRS	Conventional	'92
F	1990	AFRS	Conventional	'96, '97
G	1984	AFRS	No insecticides	'96, '97
H	1997	AFRS	Conventional	'99, '00
I	1997	AFRS	Reduced insecticides	'99, '00
J	1997	AFRS	Reduced insecticides	'99, '00
K	1997	AFRS	Reduced insecticides	'99, '00

[1] AFRS, Appalachian Fruit Research Station, Jefferson Co., West Virginia, USA.

Orchards C, D, and E had 20 randomly selected branch terminals surveyed on each of 15 transect trees. The second experiment was designed to examine the interaction between predators and aphids on apple (Brown, 1999). Four orchards (A, B, F, and G of Table 1) were sampled for aphids and aphid predators with each sample consisting of 20 randomly selected branch terminals on 20 randomly selected trees in the orchard. Sampling was done weekly from mid-May through June and biweekly from July to September. The third experiment was designed specifically to monitor the relative abundance of coccinellids and other aphid predators on apple. Four orchards (H, I, J, and K of Table 1) were sampled 3 times in 1999 and 6 times in 2000. Each sample consisted of surveying 10 randomly selected branch terminals on 20 randomly selected trees.

For each sample in all 3 experiments, the number of branch terminals infested with spirea aphids and the total number and species of all predators per branch terminal were recorded. To compare the relative abundance of each predator among years, the number per aphid colony was calculated for each orchard over the full season. The variance of the number of predators per aphid colony for each orchard was used as the standard error of the mean for the overall yearly mean. Therefore, all comparisons between years, and between data sets, were based on unbiased mean estimates from 4 or 5 different orchard populations. All data comprising these mean estimates were based on branch terminal counts, even the complete tree counts from

Table 2. Abundance of the major members of the aphidophaga guild on apple in the two orchards sampled before (1992) and after (1996 and 1997) invasion of *H. axyridis*

Predator	No. predators per aphid colony					
	Orchard A			Orchard B		
	1992	1996	1997	1992	1996	1997
H. axyridis	0	0.1743	0.0407	0	0.0396	0.0520
C. septempunctata	0.1745	0.0204	0.0051	0.0654	0.0073	0.0027
Other coccinellids	0	0	0	0	0	0
A. aphidimyza	0.0443	0.7166	0.0034	0.0681	0.2002	0.1026
Chrysopids	0.0554	0.1896	0.0949	0.0872	0.2315	0.0164

the young orchards in 1992 were recorded per infested branch terminal. The similarity in sampling methods and the calculation of yearly means from mean population estimates per orchard permit statistical comparisons among the different data sets. A chi-square test for the number of native versus exotic coccinellids was done comparing each year with 1992 as the pre-invasion control. Statistical comparisons for the abundance of each predator taxa were with 95% confidence intervals around the abundance of each predator in 1992, the pre-invasion control. Principal component analysis was used to examine the effect of *H. axyridis* on the entire aphidophaga guild. Annual mean abundance of coccinellids (all species pooled), *A. aphidoletes*, and chrysopids were used as the variables for plotting the location of each yearly orchard sample in the 2-dimensional space defined by the first 2 principal components.

Results

The effect of *H. axyridis* invasion on the aphidophaga guild on apple in the two orchards sampled both before and after invasion is presented in Table 2. The only obvious impact is a decline in *C. septempunctata* population density after *H. axyridis* entered the guild. No other species of coccinellids were observed in these two orchards. The effect on the other two primary aphid predators, *A. aphidimyza* and chrysopids, is variable (Table 2) and no conclusions can be made based on these two orchards.

The composition of the aphidophagous coccinellid fauna from 1992 to 2000 in the larger data set, larvae and adults combined, is presented in Table 3. The sample prior to the invasion of *H. axyridis* into apple orchards of West

Table 3. Composition of the aphidophagous coccinellid assemblage (larvae and adults combined) on apple prior to (1992) and after (1996–2000) invasion by *Harmonia axyridis*

Year	No. Observed	Relative abundance of Coccinellids (%)		
		Coccinella septempunctata	*Harmonia axyridis*	Other Coccinellids[1]
1992	192	99.5	0.0	0.5
1996	271	10.0	86.3	3.7**
1997	196	6.6	85.7	7.7**
1999	509	57.8	40.9	1.3
2000	301	7.6	90.7	1.7*

[1] Other coccinellids are comprised of the native species *Coleomegilla maculata lengi*, *Hippodamia convergens*, *Adalia bipunctata, Anatis labiculata* and *Cycloneda munda*. Statistically different proportion of "other coccinellids" between 1992 and the year indicated using chi-square contingency table, $^{**}P < 0.05$; and *at $P < 0.10$.

Virginia in 1992, shows a numerical dominance of the aphidophagous coccinellid guild by *C. septempunctata*. In 1996 and 1997, *H. axyridis* dominated this guild, comprising over 85% of individuals (Table 3). In 1999, *C. septempunctata* populations rebounded to comprise 57.8% of individuals in the guild, but in 2000 *H. axyridis* was again dominant with 90.7% of individuals (Table 3). The other coccinellids observed were native species: *Coleomegilla maculata lengi* Timberlake, *H. convergens*, *A. bipunctata*, *Anatis labiculata* (Say), and *Cycloneda munda* (Say). The data show a small but statistically significant increase in the proportion of these native coccinellids after the arrival of *H. axyridis* (Table 3). The only year the proportion of native coccinellids was not significantly greater than in 1992 was in 1999, which was also the only year after the arrival of *H. axyridis* in which *C. septempunctata* was also dominant.

The dominance of *H. axyridis* in the aphidophagous coccinellid guild on apple after 1992 was even more pronounced considering only larval coccinellids. In 1992, 99 larval coccinellids were observed, all being *C. septempunctata*. Since its arrival, *H. axyridis* has been the most abundant coccinellid larvae, comprising 100% of larval coccinellids in 1996 (n = 186), 99.2% in 1997 (n = 120), 80% in 1999 (n = 20), and 96.6% in 2000 (n = 88). The few individual *C. septempunctata* larvae that were found indicate that they have not been completely displaced by *H. axyridis*, but have been reduced numerically.

The impact of the *H. axyridis* invasion on the rest of the aphidophagous guild on apple from the larger data set is documented in Table 4. The abundance of *A. aphidimyza* per aphid colony after the invasion of *H. axyridis* varies around its abundance prior to invasion, (Table 4), similar to the trend seen in just the two orchards sampled before and after invasion (Table 2). Chrysopids were more abundant in 1996 and 1999 than they were prior to the *H. axyridis* invasion (Table 4). The total abundance of aphidophagous coccinellids has not significantly changed since 1992 with the addition of *H. axyridis* into the guild, except for 1999 when the total number of coccinellids was significantly higher. Even though there was an order of magnitude reduction in *C. septempunctata* abundance for the years 1996, 1997, and 2000, the difference was not significantly different from the abundance in 1992 because of high variance. However, if the confidence interval around *C. septempunctata* abundance had been calculated for each year 1996 to 2000 individually, abundance of *C. septempunctata* each year was significantly different from 1992 ($P < 0.05$).

The overall effect on the entire aphidophaga guild on apple is shown in Figure 1 A and B. The location of the guild composition in 2-dimensional space shows that orchards A and B (a and b in Fig. 1A), the only two orchards sampled both before and after invasion by *H. axyridis*, do not show much annual variation beyond the range shown by the other orchard samples. The position of the other orchards sampled prior to *H. axyridis* invasion is also within the range of variation demonstrated by the post-invasion samples (orchards 2 compared with all other orchards, Figure 1B).

Discussion

The greatest impact of *H. axyridis* invasion into West Virginia apple was on the relative abundance of *C. septempunctata* (Tables 2 and 3), especially among larvae. An earlier review of aphidophagous coccinellids in West Virginia (Brown and Miller, 1998) showed a distinct change in coccinellid species abundance prior to *H. axyridis* invasion compared with after the invasion. In just the first full year after the arrival of *H. axyridis*, it had replaced *C. septempunctata* as the most abundant coccinellid (Brown and Miller, 1998). It was also suggested that the abundance of native coccinellids increased after *H. axyridis* arrival, a conclusion supported by the data in Table 3. That *C. septempunctata* may be a stronger competitor to the native coccinellids than is *H. axyridis* is further supported by the lack of a significant difference in the proportion of native coccinellids between 1992 and 1999 (Table 3), the only year post *H. axyridis* invasion when *C. septempunctata* was abundant. In several habitats, *C. septempunctata* has been shown to displace native coccinellids (Wheeler and Hoebeke, 1995; Elliott et al., 1996; Ellis et al., 1999). Like the small grain ecosystem in North Dakota studied by Elliott et

Table 4. Abundance of the major taxa of aphid predators on apple relative to the abundance of spirea aphids (standard error of the mean in parentheses), 1992–2000

Year	No. Colonies Sampled	% Terminals Infested	No. per aphid colony				
			A. aphidimyza	Chrysopids	Total Coccinellids	*C. septempunctata*	*H. axyridis*
1992	4489	–[1]	0.0896	0.0342	0.0617	0.0617	0.0000
			(0.0367)	(0.0323)	(0.0699)	(0.0699)	(0.0000)
1996	3055	43.10	0.2392*	0.1499*	0.1187	0.0069	0.0715*
		(14.08)	(0.2856)	(0.0633)	(0.0659)	(0.0083)	(0.0612)
1997	3727	41.52	0.0589	0.0491	0.0808	0.0034	0.0715*
		(12.04)	(0.0569)	(0.0395)	(0.0732)	(0.0012)	(0.0694)
1999	1788	46.40	0.0058*	0.2757*	0.2852*	0.1657	0.1154*
		(6.50)	(0.0101)	(0.1261)	(0.0492)	(0.0381)	(0.0224)
2000	3240	67.50	0.0695	0.0158	0.0880	0.0070	0.0794*
		(7.30)	(0.0433)	(0.0043)	(0.0376)	(0.0045)	(0.0362)

[1] Data not collected in a manner to allow calculation of percentage aphid infestation.

* Statistically different ($P<0.05$) from abundance of the same taxon in 1992, using 95% confidence intervals around the 1992 mean abundance.

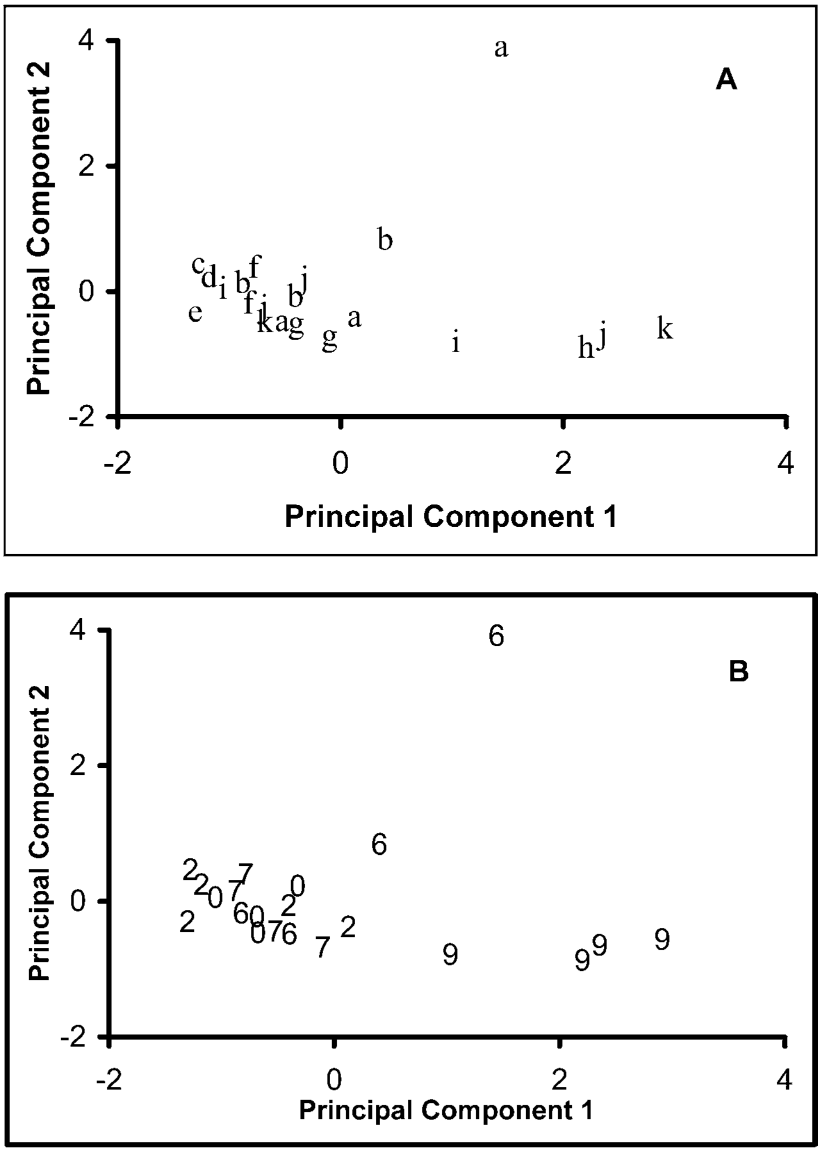

Figure 1. Scatter plots of the first two principal components of the spirea aphid predator guild on apple in West Virginia, USA, using annual mean abundance of coccinellids (all species pooled), chrysopids, and *Aphidoletes aphidimyza*. A, plot indicating location of the predator guild by orchard with orchard identification as indicated in Table 1; and B, plot indicating predator guild location by year with the number corresponding to the last digit of the year in which the data set was collected.

al. (1996), the addition of a new species, in this case *H. axyridis* into West Virginia apple orchards, did not increase the overall number of coccinellids, except in one year (Table 4). As documented in this study, *H. axyridis* has been shown to become the dominant coccinellid in many other ecosystems (Tedders and Schaefer, 1994; LaMana and Miller, 1996, Colunga-Garcia and Gage, 1998). The mechanism by which *H. axyridis* maintains dominance is through interference competition and intraguild predation (Yasuda and Shinya, 1997), and *H. axyridis* is better adapted to the species of host aphid than is *C. septempunctata* (Michaud, 2000). Larval *H. axyridis* are also better adapted to arboreal habitats due to the presence of an adhesion gland on the last abdominal segment, which is lacking on *C. septempunctata* (Hodek, 1973; Lövei et al., 1991).

In 1999, populations of *C. septempunctata* and the other most abundant species in the aphid predator guild were greater, except for *A. aphidimyza*, which had very low abundance. The differences in the guild structure in 1999 are visible in Figure 1B. The reduction in *A. aphidimyza* populations was probably due to the relatively low abundance of aphids in 1999 (Brown, unpublished data) rather than being due to intraguild competition. Large numbers of *A. aphidimyza* usually occur near the peak of aphid abundance, when most colonies are large (Brown, 1999). In 1999, the aphid colonies died out quickly, before they became large enough to attract *A. aphidimyza*. Although Lucas et al. (1998) found *A. aphidimyza* to be susceptible to intraguild predation by coccinellids, I found no direct effect on *A. aphidimyza* populations on apple that could be attributed to *H. axyridis*. The impact of *H. axyridis* invasion on chrysopids was to allow more chrysopids to occur on apple, as in 1996 and 1999 (Table 4). Other studies have also found no negative impact of coccinellids on chrysopid populations (Chang, 1996; Lucas et al., 1998). In spite of the effects on *C. septempunctata* and chrysopids, the overall impact of invasion on the entire guild of spirea aphid predators was negligible when considering all coccinellids as one group (Figure 1).

Ecological effects of invading species have not been well documented for most species. By reviewing 3 separate experiments on the aphid predator guild on apple, I have been able to document some of the effects on this guild caused by the invasion of an exotic predator species. The results of this study indicate that the reduction in *C. septempunctata* abundance is correlated with the invasion of *H. axyridis* (Table 3), and through the interactions between these two dominant species, more native coccinellids seemed to be able to survive on apple. The overall structure of the spirea aphid predator guild, however, is relatively unchanged (Figure 1). The ability of *C. septempunctata* to regain dominance in 1999 (Table 3) shows that it has not, however, completely lost apple as a foraging habitat. There has been little effect of *H. axyridis* on *A. aphidimyza* and a possible positive effect on chrysopids, the other most abundant predators of aphids on apple. Since the invasion of *H. axyridis* occurred relatively recently, in 1994, it is likely that the aphid predator guild on apple is still adjusting to the presence of this invader.

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