

BioControl **48:** 363–378, 2003. © 2003 *Kluwer Academic Publishers. Printed in the Netherlands.*

Establishment of multicolored Asian lady beetle in Eastern North Carolina: Seasonal abundance and crop exploitation within an agricultural landscape

Brian A. NAULT^{1,*} and George G. KENNEDY²

¹Department of Entomology, Cornell University, New York State Agricultural Experiment Station, Geneva, NY 14456, USA; ²Department of Entomology, Box 7630, North Carolina State University, Raleigh, NC 27695, USA *Author for correspondence; e-mail: ban6@cornell.edu

Received 17 April 2002; accepted in revised form 8 November 2002

Abstract. Seasonal abundance and crop exploitation of the multicolored Asian lady beetle, Harmonia axyridis (Pallas) (Coccinellidae: Coleoptera), were identified during its initial establishment in the eastern North Carolina agroecosystem. Densities of H. axyridis adults and larvae were compared with densities of previously established predaceous coccinellids in wheat, potato, corn and soybean, which are the predominant crops in this region. One-hundredfifty whole plant samples were visually inspected for coccinellid adults and larvae in each crop on six farms every 7 to 14 days. H. axyridis adults colonized wheat, potato and corn, but reproduced only in wheat and potato. Soybean fields were not colonized. The presence of H. *axyridis* in a crop was typically associated with an abundance of aphids, with the exception of potato, and no aphids were encountered in soybean. In addition to H. axyridis, four other lady beetle species, Coccinella septempunctata L., Coleomegilla maculata (DeGeer), Hippodamia convergens (Guerin) and Cycloneda munda L., were encountered in the landscape. In wheat, potato and corn, densities of H. axyridis adults averaged throughout the 1995 and 1996 seasons were seven, ten and 28 times lower, respectively, than the season average density of the least abundant species of previously established lady beetle, whereas these densities averaged 82, 42 and 356 times lower, respectively, than the average density of the most abundant established coccinellid species. H. axyridis is commonly encountered in the eastern North Carolina agricultural landscape, but its impact on the existing coccinellid assemblage cannot yet be determined. The results presented provide a baseline against which the results of future studies can be compared to determine if H. axyridis is displacing established species.

Key words: biological control, Coccinellidae, Coleoptera, habitat utilization, *Harmonia axyridis*, landscape

Introduction

The potential for exotic biological control species to adversely impact non-target organisms has been largely neglected until relatively recently (Howarth, 1991; see Follett and Duan, 2000). One major concern is that the introduced species may compete with and potentially displace indigenous ones and thereby threaten biodiversity. In the United States, the seven-spotted lady beetle, *Coccinella septempunctata* L., was introduced into 11 states from 1957 to 1973 to control several aphid species (Angalet et al., 1979) and has since spread throughout most of North America (Schaefer et al., 1987). *C. septempunctata* has been implicated in reducing populations of native coccinellids such as *Adalia bipunctata* (L.) and *C. transversoguttata richardsoni* Brown in agricultural crops in eastern South Dakota (Elliott et al., 1996) as well as *C. novemnotata* Herbst in the northeastern United States (Wheeler and Hoebeke, 1995). Interestingly, no studies in North America have documented a significant reduction of aphid populations by *C. septempunctata* (Obrycki et al., 2000).

The exotic multicolored Asian lady beetle, Harmonia axyridis (Pallas) (Coccinellidae: Coleoptera), also may threaten existing coccinellid assemblages in the United States. H. axyridis is predominantly arboreal, but also will exploit alfalfa, soybean, corn, winter wheat and tobacco (Colunga-Garcia and Gage, 1998; Wells and McPherson, 1999). H. axyridis is primarily aphidophagous, but it has been recorded to prey on insects from two other orders and nine other families (Tedders and Schaefer, 1994). H. axyridis was intentionally released multiple times throughout the 20th century to control aphids (Gordon, 1985; McClure, 1987; Tedders and Schaefer, 1994); however, its first documented establishment in the United States, which occurred in Louisiana in 1988 (Chapin and Brou, 1991), may have been accidental (Day et al., 1994). H. axyridis was first reported throughout central and western North Carolina in 1992 and most regions of Virginia in 1993, but its distribution had not reached the eastern region of North Carolina until 1994 (Kidd et al., 1995). It is currently distributed throughout much of North America (Tedders and Shaeffer, 1994; LaMana and Miller, 1996; Krafsur et al., 1997).

Colunga-Garcia and Gage (1998) compared coccinellid species diversity and abundance in an agricultural landscape in Michigan before and after *H. axyridis* became established. In their study, *H. axyridis* became a dominant coccinellid species in the landscape four years after its arrival. During that four-year period, indigenous populations of *Brachiacantha ursina* (F.), *Cycloneda munda* (Say) and *Chilocorus stigma* (Say) declined. The circumstantial evidence that *H. axyridis* was responsible for the decline of these native coccinellid species warrants further evaluation of its impact on coccinellid populations in other regions of North America. To date, little is known about the diversity of coccinellid species and their interactions in the Mid-Atlantic United States. The purpose of our research was to document the crops in which *H. axyridis* is found and to compare its relative abundance in these crops with the abundance of established predaceous coccinellids in eastern North Carolina's agricultural landscape. This study was initiated one year after *H. axyridis* was first reported in the region (Kidd et al., 1995). Thus, we provide baseline comparisons of relative coccinellid abundance and species richness for this region.

Materials and methods

Populations of predaceous coccinellids were surveyed in several crops that dominate the eastern North Carolina agroecosystem. One commercial field each of wheat, potato, corn, and early- and late-planted soybean was randomly selected from each of six farms (n = 6) in Pasquotank and Washington Counties in 1995 and 1996. Fields were sampled weekly for coccinellid adults and larvae until the crop was either harvested or was mature enough that coccinellids were no longer present. Adults were identified to species, but only Coleomegilla maculata (DeGeer) and H. axyridis larvae were identified to species. Sampling periods in the various crops were as follows: wheat (mid-March through early June), potato (late March or late April through mid to late June), corn (late May to early June through late August), early- and late-planted soybean (late June through late September or early October). One-hundred-fifty whole plant samples were taken in each field in a U-shaped pattern covering ≈ 0.61 ha. In wheat and soybean, each sample was two rows $\times 0.91$ m (area = 0.32 m²), whereas in potato and corn each sample was 1 row \times 0.91 m (area = 0.84 m²). Samples in all crops were inspected visually and data were transformed to a per m² basis. Using the same sampling method in all crops enabled densities of insects among crops to be compared. For each crop on each farm, the average number of insects per sample was determined. Population dynamics of each coccinellid species were compared within each crop using a repeated measures analysis of variance (PROC GLM; SAS Institute, 1990). Additionally, the mean season total number of adults within each crop was analyzed using a one-way analysis of variance (PROC GLM) and means were compared by LSMEANS (P < 0.05). Means were transformed by $log_{10} (x + 1)$ before analysis, but untransformed means are presented.

Results

H. axyridis adults were observed in wheat, potato and corn (Figure 1A–F), but not in soybean. Adults colonized wheat in mid-April in 1995, while the

subsequent generation of adults was active in wheat and potato in mid-May and another generation was evident in wheat, potato and corn during the first half of June. In early August 1995, a single *H. axyridis* adult was observed in a corn field, suggesting that a third generation may develop within the agroecosystem. *H. axyridis* larvae were only observed in wheat and potato (Figure 2A–D). The first generation of larvae in wheat was produced from late April through early May and a subsequent larval generation was observed in wheat and potato from late May through early June. The habitats exploited by *H. axyridis* from July until it overwinters in the fall are not known.

The presence of *H. axyridis* in a crop was typically associated with an abundance of aphids, with the exception of potato. *H. axyridis* was not found in soybean, perhaps because aphids did not colonize that crop. In wheat, the bird cherry-oat aphid, *Rhopalosiphum padi* (L.), and the English grain aphid, *Macrosiphum avenae* (F.) were most common, whereas *R. padi* was prevalent in corn. In potato, however, very few aphids were seen, but Colorado potato beetle, *Leptinotarsa decemlineata* (Say), and European corn borer, *Ostrinia nubilalis* (Hübner), eggs and small larvae were relatively abundant in some fields. In wheat, potato and corn, *H. axyridis* was observed feeding on other predaceous coccinellid eggs and larvae.

In addition to H. axyridis, four other species of lady beetles, C. septempunctata, C. maculata, Hippodamia convergens (Guerin) and C. munda, were observed in the crops sampled. Because C. munda was rarely observed in this survey, data of its abundance are neither presented nor discussed. The mean season total numbers of coccinellid adult species sampled in wheat, potato, corn, early- and late-planted soybean differed significantly (wheat, 1995: F = 29.27; df = 3, 15; P < 0.0001; wheat, 1996: F = 31.22; df = 3, 15; P < 0.0001; potato, 1995: F = 3.66; df = 3, 15; P = 0.0368; potato, 1996: F = 20.69; df = 3, 15; P < 0.0001; corn, 1995: F = 76.67; df= 3, 15; P < 0.0001; corn, 1996: F = 17.28; df= 3, 15; P < 0.0001; early-planted soybean, 1995: F = 13.41; df = 3, 15; P = 0.0002; early-planted soybean, 1996: F = 5.00; df = 3, 15; P = 0.0134; late-planted soybean, 1995: F = 7.76; df = 3, 15; P = 0.0023). The only exception was the 1996 late-planted soybean data set in which no differences among means existed (F = 1.50; df= 3, 15; P = 0.2551). The mean season total numbers of *H. axyridis* adults sampled in wheat, potato, corn, early- and late-planted soybean were significantly lower than mean season total numbers of all or most other species (Table 1).

Densities of *H. axyridis* adults averaged over the 1995 and 1996 seasons in wheat, potato and corn were seven, ten and 28 times lower, respectively, than the average densities of the least abundant species of previously established lady beetle. Further, season total densities averaged over 1995 and 1996 in the same crops were 82, 42 and 356 times lower, respectively,

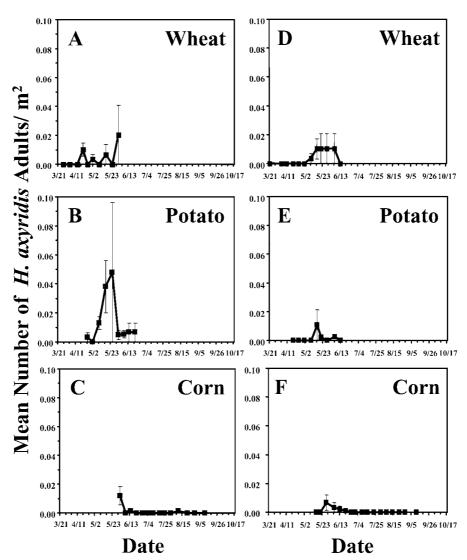


Figure 1. Mean (\pm SEM) number of *H. axyridis* adults per m² sampled in winter wheat, potato and corn in 1995 (A, B and C, respectively) and in 1996 (D, E and F, respectively).

than the average season densities of the most abundant existing coccinellid species. The number of *C. septempunctata*, *C. maculata*, *H. convergens*, and *H. axyridis* adults encountered in this survey represented 38% and 36%, 58% and 46%, 2% and 17%, and 2% and 1% of the overall predaceous adult coccinellid population in 1995 and 1996, respectively. In 1995, the greatest percentage of the adult coccinellid population that consisted of *H. axyridis* in

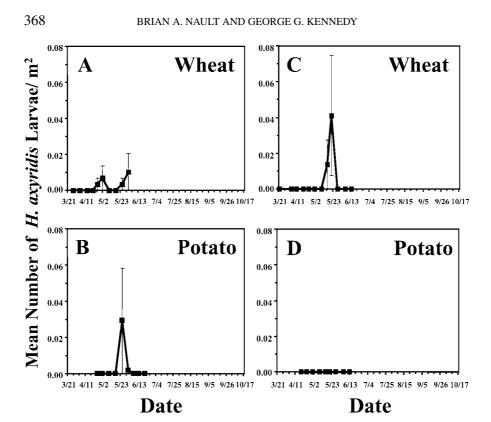


Figure 2. Mean (\pm SEM) number of *H. axyridis* larvae per m² sampled in winter wheat and potato in 1995 (A and B, respectively) and in 1996 (C and D, respectively).

wheat, potato and corn on a single sampling date was only 8%, 21% or 2%, respectively (Figure 3A–C). In 1996, the greatest percentage in these crops on a single date was only 2%, 11% or 1%, respectively. (Figure 3D–F).

The number of *C. maculata, H. axyridis* and other coccinellid larvae encountered in this survey represented 72% and 84%, 2% and 1%, and 26% and 15% of the overall predaceous larval coccinellid population in 1995 and 1996, respectively. In 1995, the greatest percentage of the larval coccinellid population that consisted of *H. axyridis* in wheat and potato on a single sampling date was 5% and 21%, respectively (Figure 4A and B). The relatively high mean percentage of *H. axyridis* larvae in potato was a result of many larvae in just 1 of the 6 fields sampled. In this particular field, Colorado potato beetle and European corn borer infestations were high because no synthetic insecticides had been used during the season. In 1996, the greatest percentage of larvae in wheat on a single date was 5%, whereas no larvae were observed in potato (Figure 4C and D).

Сгор	Species	Mean season total number of adults/m ^{2*}	
		1995	1996
Wheat	C. septempunctata	1.74 a	3.06 a
	C. maculata	1.04 b	1.48 b
	H. convergens	0.03 c	0.46 c
	H. axyridis	0.02 c	0.04 d
Potato	C. septempunctata	0.39 ab	0.62 a
	C. maculata	0.63 a	0.24 b
	H. convergens	0.07 bc	0.17 b
	H. axyridis	0.03 c	0.01 c
Corn	C. septempunctata	0.23 b	0.54 b
	C. maculata	3.93 a	3.19 a
	H. convergens	0.03 b	0.75 b
	H. axyridis	0.01 b	0.01 c
Soybean (early)	C. septempunctata	0.02 b	0.01 bc
	C. maculata	0.07 a	0.04 ab
	H. convergens	0.00 c	0.05 a
	H. axyridis	0.00 c	0.00 c
Soybean (late)	C. septempunctata	0.04 a	0.03 a
	C. maculata	0.06 a	0.03 a
	H. convergens	0.01 b	0.03 a
	H. axyridis	0.00 b	0.00 a

Table 1. Mean season total number of predaceous coccinellid adults sampled from prevalent crops in eastern North Carolina during 1995 and 1996

*Means within a crop followed by the same letter are not significantly different (P > 0.05; LSMEANS).

In wheat, *C. septempuncta* adults were the most abundant throughout the season, followed by *C. maculata*, *H. convergens* and *H. axyridis* (Table 1). Adult densities of these species differed through time (1995: F = 3.14; df = 24, 120; P < 0.0001; 1996: F = 4.72; df = 30, 150; P < 0.0001) (Figure 5A and B). Although *C. septempunctata*, *C. maculata* and *H. convergens* adults colonized wheat earlier than *H. axyridis*, the timing of adult emergence from the first generation produced in wheat was similar among species (2 through 9 May). In 1996, *C. maculata* populations peaked approximately one week after the others. In 1995, *C. maculata* populations were increasing at the time wheat fields were harvested and therefore comparisons between peak abundance of *C. maculata* and other species cannot be made.

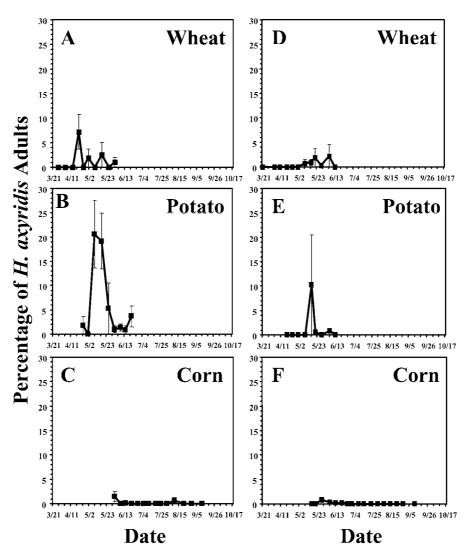


Figure 3. Mean (\pm SEM) percentage of the overall predaceous coccinellid adult assemblage that consisted of *H. axyridis* in wheat, potato and corn in 1995 (A, B and C, respectively) and in 1996 (D, E and F, respectively).

In potato, *C. septempuncta* adults were the most abundant throughout the season, although the total number sampled did not differ significantly from the number of *C. maculata* in 1995 (Table 1). The mean total number of *H. convergens* adults encountered in potato was intermediate between the numbers of *H. axyridis* and other coccinellid adults observed. Densities of adults were significantly affected by a species \times time interaction (1995: *F* =

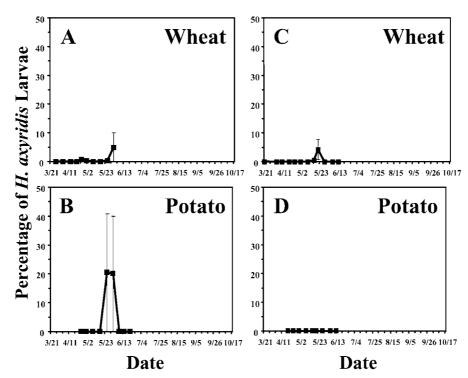


Figure 4. Mean (\pm SEM) percentage of the overall predaceous coccinellid larval population that consisted of *H. axyridis* in wheat and potato in 1995 (A and B, respectively) and in 1996 (C and D, respectively).

1.92; df = 15, 75; P = 0.0343; 1996: F = 4.30; df = 15, 75; P < 0.0001) (Figure 6A and B). *C. septempunctata*, *H. convergens* and *H. axyridis* adults colonized potato earlier than *C. maculata*, resulting in a 1 to 2 week earlier emergence of first-generation adults (7 through 16 May). Prior to this study, Hilbeck and Kennedy (1996) identified *C. maculata*, *C. septempunctata*, and *H. convergens* as the only predaceous coccinellid species to colonize potato in eastern North Carolina.

The mean season total number of *C. maculata* adults encountered in corn was significantly greater than the numbers of all other species (Table 1). *C. septempunctata* and *H. convergens* adults were more abundant throughout the season than *H. axyridis*, but these differences were not significant in 1995. Densities of *C. maculata* adults changed differently through time than the changes in densities for the other species (1995: F = 2.07; df = 18, 90; P = 0.0133; 1996: F = 6.05; df = 24, 120; P < 0.0001) (Figure 7A and B). Initial colonization of corn by coccinellid adults could not be determined in 1995, but in 1996 all four species were first observed on 21 May. Adult populations

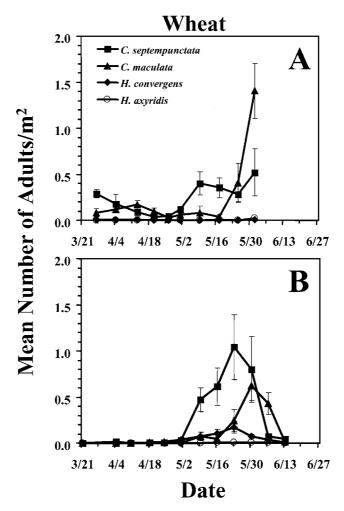


Figure 5. Mean (\pm SEM) numbers of adult coccinellids per m² in wheat fields in 1995 (A) and 1996 (B). Sampling was initiated during tillering stage and ended near harvest.

of *C. septempunctata*, *H. convergens* and *H. axyridis* peaked in late May, whereas *C. maculata* adult populations peaked 2 weeks later. Coccinellid adults were rarely observed in corn after mid June, with the exception of *C. maculata*, which was present until harvest.

Few predaceous coccinellids were encountered in early- and late-planted soybean (Table 1). *C. septempunctata* and *C. maculata* adults were most prevalent in soybean in 1995 and *H. convergens* was encountered in this crop in 1996. Population densities of coccinellid adults were not affected by a species \times time interaction (early-planted soybean, 1995: *F* = 1.16; df = 24,

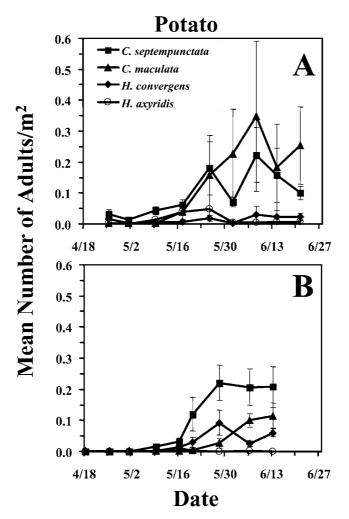


Figure 6. Mean (\pm SEM) numbers of adult coccinellids per m² in potato fields in 1995 (A) and 1996 (B). Sampling begun during the early pre-bloom stage and finished at harvest.

120; P = 0.2969; 1996: F = 1.23; df = 27, 135; P = 0.2187; late-planted soybean, 1995: F = 1.05; df= 27, 135; P = 0.4127; 1996: F = 1.05; df = 21, 105; P = 0.4157). A comprehensive survey of arthropods encountered in soybean fields in North Carolina in 1973–1974 included at least five lady-bird beetle species: *C. maculata, C. munda, Diomous terminatus* (Say), *H. convergens* and *Scymnus* sp. (Deitz et al., 1980).

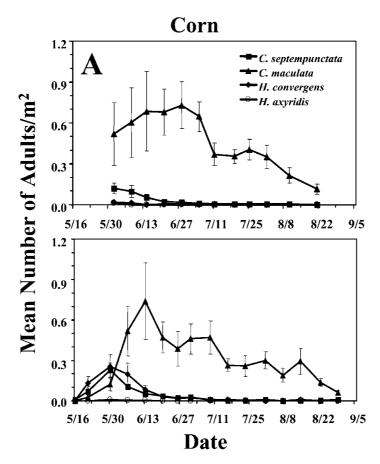


Figure 7. Mean (\pm SEM) numbers of adult coccinellids per m² in corn fields in 1995 (A) and 1996 (B). Sampling was initiated when the crop was in the early whorl stage and concluded at harvest.

Discussion

The multicolored Asian lady beetle has become established in eastern North Carolina's agroecosystem and utilizes significant acreages of wheat, potato and corn, but not soybean. *H. axyridis* reproduces in wheat and potato and they are often associated with aphids, with the exception of potato in which Colorado potato beetle and European corn borer eggs and small larvae are potential prey. *H. axyridis* completes at least two generations in eastern North Carolina. A generation is completed in wheat from late April through early May and another occurs in wheat and potato from mid-May through early June. It is not known if *H. axyridis* exploits additional resources and

reproduces prior to colonization of wheat fields in the spring or between the time adults emerge from wheat and potato and the time they migrate to overwintering sites in the fall.

The composition of coccinellid communities in agricultural crops typically includes relatively few species (Hodek and Honek, 1996). In the Midwestern US during the late 1980s and early 1990s, Obrycki et al. (2000) reported that two to five species of lady beetles were commonly encountered (>5% of total species sampled) in alfalfa and wheat. The five most commonly encountered species were *H. convergens*, *Hippodamia tredecimpunctata* (Say), *Hippodamia parenthesis* (Say), *C. maculata* and *C. septempunctata*. In 1989 and 1990 in Michigan, Maredia et al. (1992) reported six species of coccinellids in an agricultural habitat that consisted of alfalfa, wheat, triticale, soybean and corn. *C. septempunctata* and *C. maculata* were the most abundant species and were the only ones observed in all of these crops. In our study, *C. septempunctata* and *C. maculata* also were the most abundant species. *H. axyridis* could be considered common (>5% of total species sampled) in wheat and in some potato fields, but rare (<1% of total) in corn and absent in soybean (0% of total).

A reduction in size and diversity of coccinellid communities due to interspecific competition may be more likely to arise if species occur together and reproduce in the same habitats, especially if habitat use within a field or even on the same plant is similar in space and time (Obrycki et al., 2000). Although interspecific competition among coccinellids can occur during adult and immature stages, the relative immobility of larvae compared with adults may make competition more intense among them than among adults. In eastern North Carolina, H. axyridis larvae occurred together with other predaceous coccinellid larvae primarily in wheat where larval populations of coccinellids were relatively synchronous, suggesting that negative effects of interspecific competition among species in this crop could occur. Cottrell and Yeargan (1998) demonstrated in the laboratory that H. axyridis can complete development solely on C. maculata eggs and that H. axyridis larvae often have a competitive advantage over C. maculata larvae that often results in H. axyridis devouring C. maculata. In other laboratory competition experiments, Yasuda et al. (2001) reported that H. axyridis larvae were more likely to attack C. septempunctata larvae than the reverse, and that H. axvridis larvae were more likely to escape from C. septempunctata than the reverse situation. Additionally, fewer C. septempunctata that were fed H. axyridis larvae survived than when they were provided aphids, whereas H. axyridis larvae survived equally well on a diet of either aphids or C. septempunctata larvae (Yasuda and Ohnuma, 1999). The more aggressive behavior and potentially greater polyphagy of *H. axyridis* compared with *C. maculata* and *C.*

septempunctata may lead to it becoming a dominant species in eastern North Carolina wheat fields.

Interspecific competition between an introduced coccinellid and established coccinellids may or may not cause the established species to become displaced. C. septempunctata has been implicated several times in displacing indigenous coccinellids in agricultural crops in eastern North America (Wheeler and Hoebeke, 1995; Obrycki et al., 2000). The likelihood that an exotic coccinellid such as H. axyridis will displace established coccinellid species depends on abiotic and biotic factors that operate at various spatial scales (Obrycki et al., 2000). Certainly, interspecies competition for resources may be important, but food abundance and availability, composition of plant species in the region, overwintering habitat, microclimate and mobility are likely to be important as well (Hagen, 1962; Honek, 1985). The lack of understanding how these factors and their potential interactions may affect coccinellid communities make predicting the possibility of established coccinellid displacement by H. axyridis in eastern North Carolina difficult. Perhaps, additional knowledge in the areas mentioned above combined with a historical comparison of H. axyridis abundance and coccinellid diversity in this region could enable such predictions on ladybird beetle displacement to be made in the future.

Acknowledgements

We thank B. Bumgarner, M. Campbell, C. Cheshire, K. Coward, V. Covington, R. Groves, M. Hanzlik, and N. Storer for their assistance in field sampling. We also appreciate valuable comments by F. Musser on and earlier version of this paper. This work was supported by the USDA CSRS NRI CGP, grant number 94-37312-0628.

References

- Angalet, G.W., J.M. Tropp and A.N. Eggert, 1979. Coccinella septempunctata in the United States: recolonization and notes on its ecology. Environ. Entomol. 8: 896–901.
- Colunga-Garcia, M. and S.H. Gage, 1998. Arrival, establishment, and habitat use of multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. *Environ. Entomol.* 27: 1574–1580.
- Cottrell, T.E. and K.V. Yeargan, 1998. Intraguild predation between an introduced lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). J. Kansas Entomol. Soc. 71: 159–163.
- Chapin, J.B. and V.A. Brou, 1991. *Harmonia axyridis* (Pallas), the third species of the genus to be found in the United States (Coleoptera: Coccinellidae). *Proc. Entomol. Soc. Wash.* 93: 630–635.

376

- Day, W.H., D.R. Prokrym, D.R. Ellis and R.J. Chianese, 1994. The known distribution of the predator *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae) in the United States, and thoughts on the origin of this species and five other exotic lady beetles in eastern North America. *Entomol. News* 105: 244–256.
- Deitz, L.L., J.W. Van Duyn, J.R. Bradley, Jr., R.L. Rabb, W.M. Brooks and R.E. Stinner, 1980. A guide to the identification and biology of soybean arthropods in North Carolina. North Carolina Agricultural Research Service, Raleigh, Tech. Bull. No. 238.
- Elliott, N., R. Kieckhefer and W. Kauffman, 1996. Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologia* 105: 537–544.
- Follett, P.A. and J.J. Duan, 2000. *Nontarget effects of biological control*. Kluwer Academic Publishers, Norwell, MA.
- Gordon, R.D., 1985. The Coccinellidae (Coleoptera) of America north of Mexico. J. N.Y. Entomol. Soc. 93: 1–912.
- Hagen, K.S., 1962. Biology and ecology of predaceous coccinellidae. *Annu. Rev. Entomol.* 7: 289–326.
- Hilbeck, A. and G.G. Kennedy, 1996. Predators feeding on the Colorado potato beetle in insecticide-free plots and insecticide-treated commercial potato fields in eastern North Carolina. *Biol. Control* 6: 273–282.
- Hodek, I. and A. Honek, 1996. *Ecology of Coccinellidae*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Honek, A., 1985. Habitat preferences of aphidophagous coccinellids (Coleoptera). *Entomo-phaga* 30: 253–264.
- Howarth, F.G., 1991. Environmental impacts of classical biological control. Annu. Rev. Entomol. 36: 485–509.
- Kidd, K.A., C.A. Nalepa, E.R. Day and M.G. Waldvogel, 1995. Distribution of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in North Carolina and Virginia. *Proc. Entomol. Soc. Am.* 97: 729–731.
- Krafsur, E.S., T.J. Kring, J.C. Miller, P. Nariboli, J.J. Obrycki, J.R. Ruberson and P.W. Schaefer, 1997. Gene flow in the exotic colonizing ladybird *Harmonia axyridis* in North America. *Biol. Control* 8: 207–214.
- LaMana, M.L. and J.C. Miller, 1996. Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. *Biol. Control* 6: 232–237.
- Maredia, K.M., S.H. Gage, D.A. Landis and T.M. Wirth, 1992. Ecological observations on predatory coccinellidae (Coleoptera) in southwestern Michigan. *The Great Lakes Entomol.* 25: 265–270.
- McClure, M.S., 1987. Potential of the Asian predator, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), to control *Matsucoccus resinosae* Bean and Goodwin (Homoptera: Margarodidae) in the United States. *Environ. Entomol.* 16: 224–230.
- Obrycki, J.J., N.C. Elliott and K.L. Giles, 2000. Coccinellid introductions: potential for evaluation of nontarget effects. In: P. Follett and J. Duan (eds), *Nontarget effects of biological control*. Kluwer Academic Publishers, Norwell, MA. pp. 127–145.
- SAS Institute, 1990. SAS/STAT user's guide, version 6.12. Cary, NC.
- Schaefer, P.W., R.J. Dysart and H.B. Spect, 1998. North American distribution of *Coccinella* septempunctata (Coleoptera: Coccinellidae) and its mass appearance in coastal Delaware. *Environ. Entomol.* 16: 368–373.
- Tedders, W.L. and P.W. Schaefer, 1994. Release and establishment of *Harmonia axyridis* (Coleoptera: Coccinellidae) in the southeastern United States. *Entomol. News.* 105: 228–243.

- Wells, M.L. and R.M. McPherson, 1999. Population dynamics of three coccinellids in flue-cured tobacco and functional response of *Hippodamia convergens* (Coleoptera: Coccinellidae) feeding on tobacco aphids (Homoptera: Aphididae). *Environ. Entomol.* 28: 768–773.
- Wheeler, A.G., Jr. and E.R. Hoebeke, 1995. Coccinella novemnotata in northeastern North America: historical occurrence and current status (Coleoptera: Coccinellidae). Proc. Entomol. Soc. Wash. 97: 701–716.
- Yasuda, H. and N. Ohnuma, 1999. Effect of cannibalism and predation on the larval performance of two ladybird beetles. *Entomol. Exper. et Appl.* 93: 63–67.
- Yasuda, H., T. Kikuchi, P. Kindlmann and S. Sato, 2001. Relationships between attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. J. Insect Behavior. 14: 373–384.