Seasonal Abundance of Resident Parasitoids and Predatory Flies and Corresponding Soybean Aphid Densities, with Comments on Classical Biological Control of Soybean Aphid in the Midwest

TAKUJI NOMA¹ AND MICHAEL J. BREWER

Integrated Pest Management Program, Department of Entomology, Michigan State University, East Lansing, MI 48824

J. Econ. Entomol. 101(2): 278-287 (2008)

ABSTRACT Seasonal abundance of resident parasitoids and predatory flies, and corresponding soybean aphid, Aphis glycines Matsumura (Hemiptera: Aphididae), densities were assessed in soybean fields from 2003 to 2006 at two locations in lower Michigan. Six parasitoid and nine predatory fly species were detected in 4 yr by using potted plants infested with soybean aphid placed in soybean fields. The parasitoid Lysiphlebus testaceipes Cresson (Hymenoptera: Braconidae) and the predatory flies Aphidoletes aphidimyza Rondani (Diptera: Cecidomyiidae), and Allograpta obliqua Say (Diptera: Syrphidae) were most numerous. Generally, L. testaceipes was more abundant late in the soybean growing season, but it also occurred during soybean vegetative growth; A. obliqua was more abundant during vegetative growth; and A. aphidimuza was common throughout the season. Sovbean plants were visually inspected to estimate densities of soybean aphid, mummified aphids, and immature predatory flies. From 2003 to 2006, parasitism rates were inversely correlated with aphid density: percentage of parasitism was always very low ($\leq 0.1\%$) at high aphid densities (>100 aphids per plant), and higher parasitism, up to 17%, was observed at very low aphid densities (<1 aphid per plant). Populations of immature predatory flies, particularly A. aphidimyza, generally increased in soybean fields with increasing soybean aphid populations, but aphids always outnumbered immature flies by 100–21,000fold when flies were detected. Rearing field-collected aphid in 2006 substantiated that parasitism varied widely, with parasitism in most cases <10%. Based on findings of low parasitism and predation, positive response to changing aphid densities by predatory flies but not parasitoids, early season abundance primarily of predatory flies, and past findings on these taxa's diversity and abundance, we discuss the potential use of exotic parasitoids and predatory flies to enhance soybean aphid biological control.

KEY WORDS Aphis glycines, classical biological control, parasitoids, predatory flies

Soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is a pest of soybean from Asia that recently established and spread across the soybean production regions of the United States and Canada (Ragsdale et al. 2004). The aphid can increase rapidly and reach much higher densities than the recommended economic threshold of ≈250 aphids per plant under common commercial soybean production conditions (Ragsdale et al. 2007). Michigan is one of the states experiencing periodic outbreaks of soybean aphid since 2000, and insecticide application targeting this new aphid is widespread in outbreak years (Di-Fonzo and Hines 2002).

Biological control is a potential tactic for sustainable management of soybean aphid, because of soybean's ability to sustain modest densities of soybean aphid without economic damage. It is desirable for activity peaks of natural enemies to occur during early vegetative growth and early reproductive stages of soybean

A large number of resident natural enemies (native or long-term residents of the region) that prey on soybean aphid have been documented in North America, including predators, parasitoids, and pathogens (Rutledge et al. 2004, Fox et al. 2005, Nielsen and Hajek 2005, Desneux et al. 2006, Kaiser et al. 2007). Generalist predators have been observed to suppress soybean aphid populations, with two predators, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) and *Orius insidiosus* (Say) (Hemiptera: Anthocoridae), particularly important (Fox et al. 2004, Rutledge et al. 2004, Costamagna and Landis 2006, Desneux et al. 2006). Epizootics of fungal pathogens have been associated with declines of soybean aphid populations in New York (Nielsen and Hajek 2005). Infections of

growth, which are most susceptible to soybean aphid (Ragsdale et al. 2007). Positive responsiveness to changing soybean aphid densities also is relevant to within-season control of soybean aphid, which has high reproductive capacity and short generation time (McCornack et al. 2004, Wu et al. 2004).

¹ Corresponding author, e-mail: noma@msu.edu.

soybean aphid also were observed during this study in Michigan (T.N., unpublished data).

A complex of parasitoids (Aphelinidae and Braconidae) and predatory flies (Cecidomyiidae, Chamaemyiidae, and Syrphidae) have been reported attacking soybean aphid in the midwestern and eastern United States. Parasitized soybean aphid (mummies) were rarely found in Illinois in 2001 and 2002, in Michigan from 2001 through 2004, and across the upper Midwest and Ontario, Canada (Lin and Ives 2003, Fox et al. 2004, Rutledge et al. 2004, Costamagna and Landis 2006, Kaiser et al. 2007). More recently, parasitism rates of soybean aphid through rearing fieldcollected aphids were estimated up to 15.7% in New York in 2003 and 2004 (Nielsen and Hajek 2005). In addition, aphid predatory flies have been associated with soybean aphid in Michigan and New York (Rutledge et al. 2004, Nielsen and Hajek 2005, Costamagna and Landis 2006, Kaiser et al. 2007).

Although suppression of soybean aphid by parasitoids and predatory flies is suspect in the United States, studies in Asia suggest these aphid enemies play a role in soybean aphid control. In China, >50% soybean aphid parasitism by Lysiphlebus sp. and 10.3-52.6% parasitism by Lysiphlebia japonica (Ashmead) (Hymenoptera: Braconidae) were reported (Gao 1994, Liu et al. 2004). Presence of parasitoids, Aphelinus albipodus Hayat & Fatima (Hymenoptera: Aphelinidae) in Japan, and Lysiphlebus fabarum (Marshall) and Lipolexis gracilis Förster (Hymenoptera: Braconidae) in China, were associated with very low densities of soybean aphid in soybean fields (Heimpel et al. 2004). Syrphids were regarded as important predators of soybean aphid in China along with coccinellids and lacewings (Wu et al. 2004). Seven species of syrphids were documented from sovbean fields in China, and syrphids numerically responded to increasing soybean aphid density (Liu et al. 2004, Wu et al. 2004). Because of the control potential seen in Asia and the interest in classical biological control for sovbean aphid (Heimpel et al. 2004), we pursued more detailed work on estimating seasonal abundance of parasitoids and predatory flies and corresponding soybean aphid densities. Because seasonal abundance of aphid parasitoids, predatory flies, and their aphid hosts can vary greatly between species and years (e.g., Brewer et al. 2005), our study was conducted over a 4-vr period bridging across aphid outbreak and nonoutbreak years in Michigan. Based on our results and previous findings on taxonomic diversity and abundance, we discuss the merits and desirable attributes of exotic parasitoids and predatory flies when considering classical biological control of soybean aphid in the Midwest.

Materials and Methods

Sampling Sites. Soybean plots were sampled for parasitoids and predatory flies at the Kellogg Biological Station, Long-Term Ecological Research site, Hickory Corners, MI (42° 24′ N, 85° 23′ W) from 2003 to 2006 and the Entomology Farm, East Lansing, MI

(42° 41′ N, 84° 29′ W) in 2003, 2004, and 2006. Both sites were managed by Michigan State University, they were separated by 80 km, and they were at least 3 km from greenhouse facilities, which may be an unintentional source of aphid enemies. At the Hickory Corners site, sampling occurred in four replicated large plots (100 by 100 m) in 2003, in four replicated small plots (9 by 27 m) in 2004 and 2005, and again in four large plots in 2006. The plot size variation was due to sampling in a large-scale rotational experiment where each crop entry point was represented once every 3 yr (2003 and 2006) and sampling in smaller plots in intervening years (Kellogg Biological Station 2006). The soybean variety Northup King S20-F8 was planted at a row width of 38 or 76 cm. At the East Lansing site, sampling was conducted in one large plot (100 by 50 m) that was divided into four subplots in 2003 and 2006, and five replicated small plots (18 by 6 m) in 2004. The soybean varieties and row spacing used in this site were Pioneer 92B38 and 38-cm row spacing in 2003, Pioneer 92B13 RR and 76-cm row spacing in 2004, and Pioneer 92M61 and 38-cm row spacing in 2006. All plots at both sites were planted in May and they were free of pesticide application.

Seasonal Prevalence of Parasitoids and Predatory Flies. Parasitoids and predatory flies attacking soybean aphid were sampled using potted soybean plants infested with laboratory-reared soybean aphid (outplanted soybean plants). This method has been previously used to detect parasitoids and predatory flies attacking Diuraphis noxia (Mordvilko) (Hemiptera: Aphididae) in wheat, at various field aphid densities (Noma et al. 2005). Preparation of out-planted soybean plants was fully described in Kaiser et al. (2007). In brief, ≈ 12 soybean plants (V2 stage on the scale of Fehr and Caviness (1977)) planted in round plastic pots (17 cm in height and 15 cm in diameter) were infested with roughly 1,000 aphids. On each sampling date, four to eight units of out-planted soybean plants were exposed to ovipositing parasitoids and predatory flies at five preset plot stations for 3 to 4 d. This sampling was conducted two to four times per year between June and September: 1) mid-June, during early vegetative growth of soybean (V2-V3) when aphids may first migrate to soybean; 2) mid-July, during flowering (R1–R2) when aphids may be multiplying on soybean; 3) mid-August, during soybean pod fill (R3-R5) when aphids may be reaching peak densities; and 4) early September, during plant senescence (R6) when aphids may be declining in density.

After field exposure, the out-planted soybean plants were incubated in the laboratory under supplemental lighting (1,000-W Metal Halide Plant Grow Light System, Sunlight Supply, Inc., Vancouver, WA) at \approx 21°C and a photoperiod of 16:8 (L:D) h for 1 wk to allow oviposited parasitoids and predatory flies to mature. Then plants were clipped, placed into emergence canisters with a collection vials attached, and incubated for 2 wk in the laboratory to allow adults to emerge (Kaiser et al. 2007). The contents of the collection vials and canisters were examined under a dissection microscope for species identification and counts using

keys and other materials found in Heiss (1938), Gagné (1981), Vockeroth (1992), and Pike et al. (1997). An additional four pots of infested soybean plants were kept in the laboratory to check for possible parasitoid or predatory fly contamination in the laboratory; no contamination was detected during this study. Although this sampling method is effective in detecting aphid parasitoids and predatory flies at various field aphid densities, we acknowledge potential sampling bias associated with the out-planted soybean plants that were different in aphid infestation level (often higher) and plant age (often younger) from the soybean plants in the surrounding fields. This concern was mitigated by visual inspection of field soybean plants for aphids, parasitoids, and predatory flies conducted concurrently (see below).

Voucher specimens of parasitoids and predatory flies were deposited in the United States National Museum Collection, Washington, DC (*Leucopis gly-phinivora* Tanasijtshuk [Diptera: Chamaemyiidae], SDG dissection 1258-1270) and in the A. J. Cook Arthropod Research Collection of the Entomology Department, Michigan State University (parasitoids and all other predatory flies, VC 2006-01).

Aphid Enemy Abundance and Corresponding Soybean Aphid Densities. To assess the relationship between soybean aphid density and aphid enemy abundance, we inspected soybean plants for soybean aphid, mummified soybean aphid, and immature (larvae and pupae) predatory flies. In 2006, we also reared field-collected aphids to detect parasitism before mummification.

Visual inspection occurred on the same dates when out-planted soybean plants were set in the same field, and on some additional dates. We selected 20-25 plants from each of four to five plots or subplots (a total of 100 plants per site) for nondestructive sampling, in which leaves of an entire plant was inspected for aphids and aphid enemies. On each plant, a series of count ranges were used to estimate an approximate aphid density per plant at high infestations. In 2003, up to five aphids were counted, after which aphid counts were estimated using the ranges 6-10, 11-25, 26-50, 51–100, 101–500, and 501–5,000 aphids per plant. The high-end range was based on our field observations and past studies (DiFonzo and Hines 2002) that indicated aphid densities varied widely once populations surpassed several hundreds per plant but did not exceed 5,000 per plant during this period. From 2004 to 2006, the count ranges were modified to refine estimates of low- and high-end counts: up to 50 aphids were counted, after which ranges of 51–100, 101–500, 501–1,000, and 1,001–5,000 aphids per plant were used. Counts of aphid mummies and immature predatory flies were also recorded. In 2003, aphid mummies (aphelinid and braconid types) and immature predatory flies (cecidomyiids and syrphids) were counted and identified to family in the field. From 2004 to 2006, all mummies and immature symphids were counted, brought back to the laboratory, and reared to adults for species identification. The data were used to estimate mean number of soybean aphid per plant (the midpoint of the count ranges were used to calculate aphid means), percentage of parasitism of soybean aphid per plant (using the sum of soybean aphids and mummies as the divisor), and number of immature predatory flies per plant. Growth stages of soybean plants were noted using the scale of Fehr and Caviness (1977).

An additional assessment of soybean aphid parasitism was made from June through August 2006 by rearing field-collected aphids as a check on sampling using the out-planted soybean plants and field parasitism by visual inspection for mummies (Day 1994, Nielsen and Hajek 2005). During the visual inspection of the soybean plots, up to 100 aphids were collected by clipping aphid-infested leaves from at least 20 plants scattered across the study site. The aphids were kept cool while being transported to the laboratory. The aphids were incubated on fresh soybean leaflets encaged in 30-ml plastic portion cups lined with 2% water agar (Nielsen and Hajek 2005). Aphids, in groups of five individuals per cage, were incubated at ≈21°C and a photoperiod of 16:8 (L:D) h. Mummified aphids were removed from the cages and kept in gelatin capsules at the room temperature. Emerged adult parasitoids were examined under a dissection microscope for species identification. The percentage of parasitism of soybean aphid was calculated by dividing the number of mummified aphids by the number of field-collected aphids that were encaged for rearing.

Data Analysis. Data from out-planted soybean plants were used to graphically visualize general seasonal patterns of parasitoids and predatory flies. A mean number of aphid enemies caught per pot was calculated for each taxon (species whenever possible) and for each soybean growth state sampled (June-September), averaging across four sampling years and two soybean sites. Aphid enemy counts were averaged across the pots set in each plot or subplot. Detailed analysis focused on seasonality were performed for the most numerous enemy species. Relative abundance of aphid enemies (per pot basis) was compared among different soybean growth stages across the growing season using analysis of variance (ANOVA) (PROC GLM, SAS Institute 2000). The count data (number of aphid enemies per pot [X]) were transformed into a logarithmic scale ($\log [100 \times + 1/6]$) to satisfy the assumption of normality for ANOVA (Mosteller and Tukey 1977). When differences in abundance across the soybean growing season were detected, Tukey's multiple comparison test was used to separate means.

For visual inspection data, percentage of parasitism and density of immature flies per plant were separated at family or species level based on ability to identify species and forms of mummies. Regression analyses were run between estimates of soybean aphid densities and percentage of parasitism of soybean aphid, and between estimates of soybean aphid densities and densities of predatory flies (PROC REG, SAS Institute 2000). Data used for these analyses included all sampling sets across 4 yr and both soybean sites in which

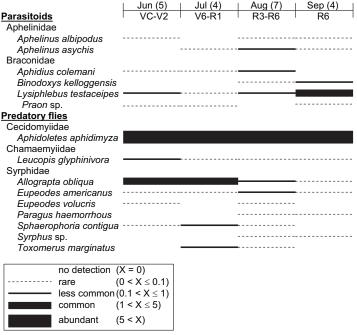


Fig. 1. Generalized seasonal occurrence (June–September) and relative abundance of parasitoids and predatory flies detected on out-planted soybean plants across the four study years. Relative abundance is shown by line thickness. Number following the month is the number of samples taken. Codes below months are soybean growth stages (Fehr and Caviness 1977). V, vegetative stages; R, reproductive stages. X, mean number of parasitoids or predatory flies recovered per pot.

both aphids and enemies (mummies or flies) were detected. Although there were insufficient means to test for regression differences across the season, a seasonality perspective was maintained by labeling means graphically with seasonal information. All variables (soybean aphid density, percentage of parasitism, and predatory fly density) were transformed into a logarithmic scale using the formula by Mosteller and Tukey (1977).

Results and Discussion

Seasonal Activity: Parasitoid Prevalence. Six species of parasitoids were detected on out-planted soybean plants placed in soybean fields of Michigan, with L. testaceipes the most abundant across the soybean growing season (Fig. 1). L. testaceipes was most common after late August during soybean maturation (R6), but it also was present during early vegetative growth of soybean (VC-V2) (Figs. 1 and 2a and b). Other parasitoids were detected more sporadically between years and sites: Aphelinus asychis Walker (Hymenoptera: Aphelinidae), Aphidius colemani Viereck, and Binodoxys kelloggensis Pike, Starý & Brewer (Hymenoptera: Braconidae) tended to be more common late in the soybean growing season, and Aphelinus albipodus Hayat & Fatima (Hymenoptera: Aphelinidae) and *Praon* sp. were rarely detected across the season (Fig. 1). This taxonomic diversity was consistent with the species list generated by Kaiser et al. (2007). As a regional comparison, in New York only two genera of braconids, *Aphidius* and *Praon*, were found parasitizing soybean aphid (Nielsen and Hajek 2005).

Seasonal Activity: Predatory Fly Prevalence. Of nine species of predatory flies found on out-planted soybean plants, Aphidoletes aphidimyza Rondani (Diptera: Cecidomyiidae) and Allograpta obliqua Say (Diptera: Syrphidae) were the most abundant species detected (Fig. 1), which was consistent with previous findings (Kaiser et al. 2007). A. aphidimyza was generally abundant throughout the soybean growing season, and A. obliqua was most abundant early in the season when soybean was at vegetative to early reproductive stages (VC-R1) (Figs. 1 and 2c-f). Other dipteran species were more sporadically detected attacking soybean aphid: L. glyphinivora, Sphaerophoria contigua Macquart, Toxomerus marginatus Say, and Eupeodes americanus Wiedemann (Diptera: Syrphidae). Three other species were rarely detected: Eupeodes volucris Osten Sacken, Paragus hemorrhous Meigen, and Syrphus sp. (Diptera: Syrphidae) (Fig. 1). Similar seasonal occurrence of predatory flies in sovbean fields has been reported previously. In Michigan, syrphid and other predatory fly larvae were found from late June through mid-August, whereas in New York, syrphid and cecidomyiid larvae were found in July and August (Rutledge et al. 2004, Nielsen and Hajek 2005, Costamagna and Landis 2006).

Aphid Enemy Abundance and Corresponding Soybean Aphid Densities. Field Parasitism. Most mummies found in 2003 were braconid type (85%),

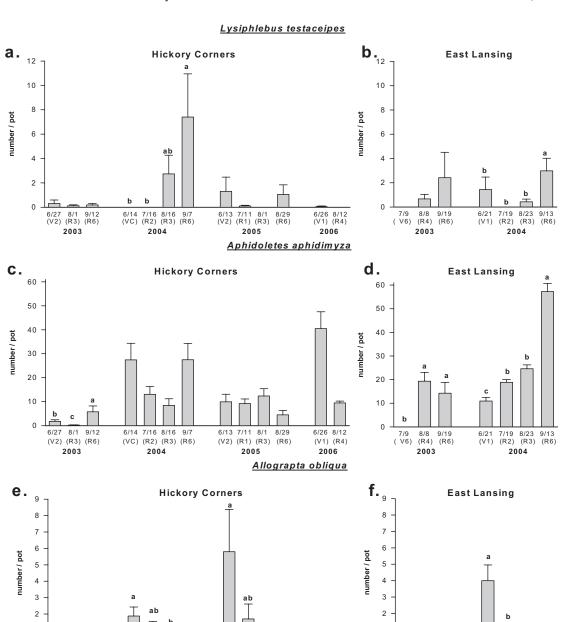


Fig. 2. Seasonal changes in abundance of the most common parasitoid (*L. testaceipes*) and predatory flies (*A. aphidimyza* and *A. obliqua*) detected using out-planted soybean plants at two soybean sites in Hickory Corners and East Lansing, MI, from 2003 to 2006. Error bars are standard errors of means. Codes in parentheses are soybean growth stages (Fehr and Caviness 1977). V, vegetative stages; R, reproductive stages. Different letters within the year indicate significant differences by Tukey's test ($\alpha = 0.05$).

8/29

(R6)

6/26 8/12

(V1) (R4)

2006

6/13 7/11 8/1

(V2) (R1) (R3)

2005

whereas most mummies found in 2004, 2005, and 2006 were aphelinid type (86%) (Fig. 3). From 2004 to 2006, 24% of mummies were successfully reared to adults and identified as *A. asychis* and *L. testaceipes* (Fig. 3). Overall, mummified soybean aphid was infrequently observed during this study, which is consistent with

6/14 7/16 8/16

(VC) (R2) (R3) (R6)

2004

9/7

0

6/27 8/1 9/12

(V2) (R3) (R6)

2003

the previous reports in the Midwest (Lin and Ives 2003, Rutledge et al. 2004, Costamagna and Landis 2006, Kaiser et al. 2007). Parasitoids seemed not to respond positively to changes in aphid densities in that percentage of parasitism (measured as percentage of aphids found on plants that were mummies) was in-

0

7/9 8/8 9/19

(V6)

(R4) (R6)

2003

6/21 7/19 8/23 9/13

(V1)

(R2) (R3)

2004

(R6)

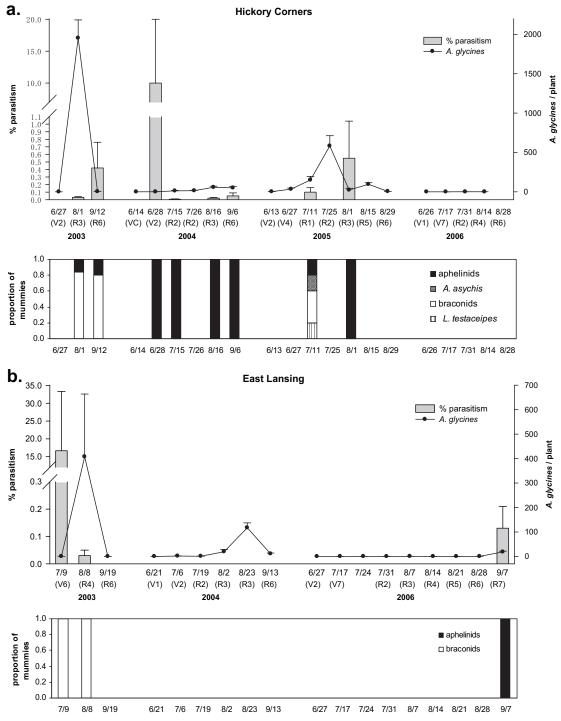
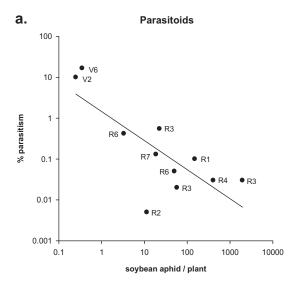


Fig. 3. Seasonal abundance of soybean aphid and parasitized soybean aphid (mummies) detected at two soybean sites in Hickory Corners (a) and East Lansing (b), MI, from 2003 to 2006. Percentage of parasitism (bars) was scaled on the primary y-axis and soybean aphid (lines) was scaled on the secondary y-axis. Error bars are standard errors of means. Codes in parentheses are soybean growth stages (Fehr and Caviness 1977). V, vegetative stages; R, reproductive stages. Boxes show proportions of different parasitoids involved in mummification detected on each sampling date.



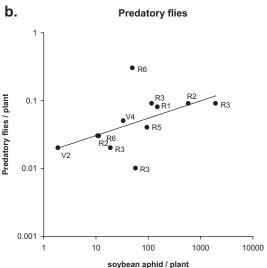


Fig. 4. Relationship between soybean aphid density and percentage of parasitism (measured as percentage of aphids found on plants that were mummies) (a), and predatory fly density (measured as number of fly larvae and pupae per plant) (b) across four sampling years and two soybean sites. All variables were transformed into a logarithmic scale. Soybean growth stages corresponding to data points were indicated using the scale of Fehr and Caviness (1977). V, vegetative stages; R, reproductive stages.

versely correlated with aphid densities (y = -0.71x + 3.59; $R^2 = 0.61$; F = 13.74; df = 1, 9; P = 0.005; Fig. 4a). Thus, the way in which parasitoid abundance corresponds to soybean aphid density is not conductive to soybean aphid control.

In contrast, Gao (1994) reported 10.3–52.6% parasitism of soybean aphid by *L. japonica* in China, considerably exceeding rates seen in our study and elsewhere in the Midwest (Lin and Ives 2003, Rutledge et al. 2004, Costamagna and Landis 2006). Although aphid densities that corresponded to parasitism sam-

pled were not explicitly provided in this Chinese study, the article indicated in a couple occasions that percentage of parasitism, 34 and 11%, were associated with low aphid densities of \approx 2.3 aphids per plant (Gao 1994). In Japan and China, high aphid densities were not encountered, and aphid suppression at least partly due to parasitism was assumed because of region-wide low aphid densities, including during vegetative growth and early reproductive stages of soybean (Heimpel et al. 2004).

Nielsen and Hajek (2005) noted that rearing of field-collected aphids was more sensitive in detecting parasitism of soybean aphid than field observation of mummies. In 2006, mummified soybean aphid was not found during our visual inspection except for 0.1% parasitism found in September in East Lansing (Fig. 3). In comparison, rearing field-collected soybean aphid yielded a few more parasitoid recoveries. Parasitism rates varied widely (0–35%) because of the very low aphid densities, but the majority of cases were < 10%. Rearing field-collected aphids in 2006 substantiated the view that parasitoids were general low in activity, and they were not positively responsive to aphid density changes.

Based on overall low parasitism rates found consistently in out-planted soybean plants, visual inspection, and rearing field-collected aphids, potential for within-season suppression of soybean aphid was not high for any of the resident parasitoids encountered. Of the group, *L. testaceipes* had the greatest, although at best modest, abundance during vegetative growth. This species has a wide aphid host range (Kaiser et al. 2007), and it is well known in annual cropping systems (Brewer and Elliott 2004). Thus, aphid host and crop habitat preferences by *L. testaceipes* and seasonal availability of other aphids and crops in the soybean production areas may have influenced seasonal abundance of this parasitoid in soybean fields.

Field Predatory Fly Densities. Immature predatory flies, especially cecidomyiids, were most often observed on soybean plants (Fig. 5). Predatory fly densities tended to increase as aphids increased (y = 0.25x - 0.23; $R^2 = 0.27$; F = 3.41; df = 1, 10; P = 0.09; Fig. 4b). Similar observations have been noted in China in which syrphid densities increased with increasing soybean aphid densities (Wu et al. 2004). Despite the numerical responses seen, the impact of predatory flies on aphid populations seemed to be minor, because aphids always outnumbered immature flies by 100–21,000-fold when flies were detected. Immature predatory flies have been observed in previously studies, with variable abundance estimates. In Michigan, Rutledge et al. (2004) documented that predatory fly larvae made up 16.4% of potential soybean aphid predators in 2002, but they made up only 1% of predators in 2001. In another Michigan study in 2003, Costamagna and Landis (2006) found that syrphid and other predatory fly larvae made up 8.7% of foliar natural enemies they sampled. In New York, Nielsen and Hajek (2005) reported up to 0.7 predatory fly larvae per plant.

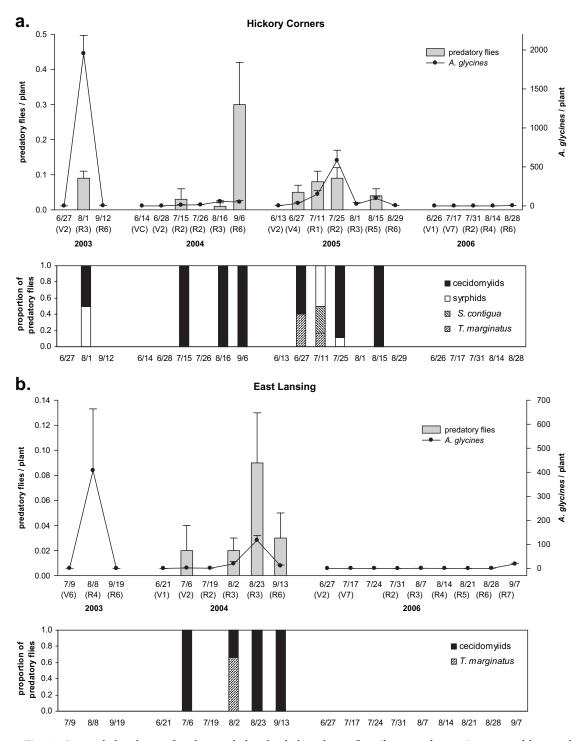


Fig. 5. Seasonal abundance of soybean aphid and aphid predatory flies (larvae and pupae) monitored by visual inspection at two soybean sites in lower Michigan from 2003 to 2006. Predatory flies (bars) were scaled on the primary y-axis and soybean aphid (lines) was scaled on the secondary y-axis. Error bars are standard errors of means. Codes in parentheses are soybean growth stages (Fehr and Caviness 1977). V, vegetative stages; R, reproductive stages. Boxes show proportions of different predatory flies detected.

Based on results from the out-planted soybean plants and visual inspection, potential for within-season suppression of soybean aphid was limited to two species. A. obliqua was abundant during vegetative growth, and A. aphidimyza was common throughout the season (Figs. 1 and 2c-f). And there was positive population response to changing aphid densities (Fig. 4b), although aphid population increase currently far exceeds predatory fly increase (Fig. 5). Both these species have a wide aphid host range (Kaiser et al. 2007), and their seasonal patterns in soybean fields may be partly shaped by their aphid host preferences and availability of other aphids in the soybean production areas.

Implications for a Classical Biological Control Effort. Introduction of exotic aphid parasitoids targeting soybean aphid is currently under consideration, and risks of introducing exotic parasitoids against soybean aphid in North America have been considered previously (Heimpel et al. 2004). Here, we add information on taxonomic diversity (Kaiser et al. 2007; Fig. 1), seasonality (Figs. 3 and 5), and parasitoid responsive to aphid population changes of the resident enemies (Fig. 4) as a basis to consider classical biological control of soybean aphid in the Midwest.

Introduction of additional exotic parasitoids into the existing fauna should be considered, with focus on achieving substantial parasitism at low aphid densities during soybean vegetation growth and early reproductive stages. Parasitoid taxa diversity in Michigan is about same as seen in Asia (Kaiser et al. 2007; Fig. 1), but none of the resident parasitoids seemed to contribute to reduced risk of aphid outbreaks. Detection of parasitoid mummies and adults from visual inspection and rearing field-collected aphids were overall low through the 4 yr. In China and Japan, some parasitoid species, L. japonica, L. fabarum, L. gracilis, and Lysiphlebus sp., were reported to be associated with very low soybean aphid densities, and at least L. japonica and Lysiphlebus sp. have been documented parasitizing soybean aphid early in the season (Gao 1994, Heimpel et al. 2004, Liu et al. 2004). These and other species being considered do not fill taxonomic gaps of the resident fauna, but they may hold promise as strategic additions to slow or suppress soybean aphid population growth at low aphid densities during the susceptible soybean stages. Risks to nontargets and other risk factors also should be considered (Heimpel et al. 2004).

There is a diverse predatory fly fauna found attacking soybean aphid in Michigan, and most species have a broad aphid host range (Kaiser et al. 2007; Fig. 1). Two species, A. aphidimyza and A. obliqua, were present during the susceptible soybean phenology (Figs. 1 and 2c-f), and immature flies, mostly consisting of cecidomyiid larvae (Fig. 5), often responded positively to increasing soybean aphid densities (Fig. 4b). However, low predatory fly abundance compared with that of soybean aphid reflected their current minor impact compared with coccinellids and O. insidiosus (Fox et al. 2004, Rutledge et al. 2004, Costamagna and Landis 2006, Desneux et al. 2006). Higher

densities of predatory fly *Paragus tibialis* (Fallén) (Diptera: Syrphidae) were observed in soybean of China compared with this study, but heavy syrphid parasitism also was detected (Liu et al. 2004). On balance, these results suggest that introduction of additional predatory flies may have risks associated with potential broad host aphid ranges and have unknown potential for adding to the current fly predation on soybean aphid in the Midwest.

Overall, additions to the enemy fauna of soybean aphid seem warranted in the Midwest, with special focus on parasitoids. We found low parasitism and low abundance of predatory flies relative to aphid abundance. But there was positive response to changing aphid densities by predatory flies, and early season abundance presence of some predatory flies. Predatory fly observations from Asia and their potential broad host ranges also do not make additions to the fauna appealing. In contrast, resident parasitoids seem to not respond to changes in soybean aphid population dynamics, and their presence is mostly later in the soybean growing season. A parasitoid that has potential to suppress soybean aphid at low aphid densities during the susceptible soybean stages and has minimal effect on nontargets (Heimpel et al. 2004) may be a beneficial addition to the resident parasitoid fauna.

Acknowledgments

We are grateful to Michigan State University (MSU) student workers Matt Kaiser, Ananda Jenkins, Jared Natzke, Momoko Minakawa, and Paul Thomas for assistance during this study. We also thank Drew Corbin, Joe Simmons, and Chris Sebolt (MSU) for the access and maintenance of soybean plots. Support for this study was provided by National Science Foundation Long-Term Ecological Research Program at the Kellogg Biological Station, USDA North Central Region IPM Program Competitive Grants Program, and the Project GREEEN initiative of Michigan State University.

References Cited

Brewer, M. J., and N. C. Elliott. 2004. Biological control of cereal aphids in North America and mediating effects of host plant and habitat manipulations. Annu. Rev. Entomol. 49: 219–242.

Brewer, M. J., T. Noma, and N. C. Elliott. 2005. Hymenopteran parasitoids and dipteran predators of the invasive aphid *Diuraphis noxia* after enemy introductions: temporal variation and implication for future aphid invasions. Biol. Control 33: 315–323.

Costamagna, A. C., and D. A. Landis. 2006. Predators exert top-down control of soybean aphid across a gradient of agricultural management systems. Ecol. Appl. 16: 1619– 1628.

Day, W. H. 1994. Estimating mortality caused by parasites and diseases of insects: comparisons of the dissection and rearing methods. Environ. Entomol. 23: 543–550.

Desneux, N., R. J. O'Neil, and H.J.S. Yoo. 2006. Suppression of population growth of the soybean aphid, Aphis glycines Matsumura, by predators: the identification of a key predator and the effects of prey dispersion, predator abundance, and temperature. Environ. Entomol. 35: 1342–1349.

- DiFonzo, C., and R. Hines. 2002. Soybean aphid in Michigan. Extension Bulletin E-2748. Michigan State University, East Lansing, MI.
- Fehr, W. R., and C. E. Caviness. 1977. Stages of soybean development. SR 80. Iowa State University, Ames, IA.
- Fox, T. B., D. A. Landis, F. F. Cardoso, and C. D. DiFonzo. 2004. Predators suppress Aphis glycines Matsumura population growth in soybean. Environ. Entomol. 33: 608– 618
- Fox, T. B., D. A. Landis, F. F. Cardoso, and C. D. DiFonzo. 2005. Impact of predation on establishment of the soybean aphid, Aphis glycines in soybean, Glycine max. Biocontrol 50: 545–563.
- Gagné, R. J. 1981. Cecidomyiidae, pp. 257–292. In J. F. McAlpine, B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood [eds.], Manual of Nearctic Diptera. Agriculture Canada, Ottawa, ON, Canada.
- Gao, J. 1994. Biological characteristics and control effect of Lysiphlebia japonica (Hym.: Braconidae) on Aphis glycines (Hom.: Aphididae). Chin. J. Biol. Control 10: 91–92.
- Heimpel, G. E., D. W. Ragsdale, R. Venette, K. R. Hopper, R. J. O'Neil, C. E. Rutledge, and Z. Wu. 2004. Prospects for importation biological control of the soybean aphid: anticipating potential costs and benefits. Ann. Entomol. Soc. Am. 97: 249–258.
- Heiss, E. M. 1938. A classification of the larvae and puparia of the Syrphidae of Illinois exclusive of aquatic forms. Ill. Biol. Monogr. 16: 1–142.
- Kaiser, M. E., T. Noma, M. J. Brewer, K. S. Pike, J. R. Vockeroth, and S. D. Gaimari. 2007. Hymenopteran parasitoids and dipteran predators found using soybean aphid after its Midwestern United States invasion. Ann. Entomol. Soc. Am. 100: 196–205.
- Kellogg Biological Station. 2006. Experimental design. (http://lter.kbs.msu.edu/experimentalDesign.htm).
- Lin, L. A., and A. R. Ives. 2003. The effect of parasitoid host-size preference on host population growth: an example of *Aphidius colemani* and *Aphis glycines*. Ecol. Entomol. 28: 542–550.
- Liu, J., K. Wu, K. R. Hopper, and K. Zhao. 2004. Population dynamics of Aphis glycines (Homoptera: Aphididae) and its natural enemies in soybean in northern China. Ann. Entomol. Soc. Am. 97: 235–239.

- McCornack, B. P., D. W. Ragsdale, and R. C. Venette. 2004. Demography of soybean aphid (Homoptera: Aphididae) at summer temperatures. J. Econ. Entomol. 97: 854–861.
- Mosteller, F., and J. W. Tukey. 1977. Data analysis and regression: a second course in statistics. Addison-Wesley, Reading, MA.
- Nielsen, C., and A. E. Hajek. 2005. Control of invasive soybean aphid, Aphis glycines (Hemiptera: Aphididae), populations by existing natural enemies in New York State, with emphasis on entomopathogenic fungi. Environ. Entomol. 34: 1036–1047.
- Noma, T., M. J. Brewer, K. S. Pike, and S. D. Gaimari. 2005. Hymenopteran parasitoids and dipteran predators of *Diu-raphis noxia* in the west-central Great Plains of North America: species records and geographic range. Biocontrol 50: 97–111.
- Pike, K. S., P. Starý, T. Miller, D. Allison, L. Boydston, G. Graf, and R. Gillespie. 1997. Small-grain aphid parasitoids (Hymenoptera: Aphelinidae and Aphidiidae) of Washington: distribution, relative abundance, seasonal occurrence, and key to known North American species. Environ. Entomol. 26: 1299–1311.
- Ragsdale, D. W., B. P. McCornack, R. C. Venette, B. D. Potter,
 I. V. Macrae, E. W. Hodgson, M. E. O'Neal, K. D. Johnson,
 R. J. O'Neil, C. D. DiFonzo, et al. 2007. Economic threshold for soybean aphid (Hemiptera: Aphididae). J. Econ. Entomol. 100: 1258–1267.
- Ragsdale, D. W., D. J. Voegtlin, and R. J. O'Neil. 2004. Soybean aphid biology in North America. Ann. Entomol. Soc. Am. 97: 204–208.
- Rutledge, C. E., R. J. O'Neil, T. B. Fox, and D. A. Landis. 2004. Soybean aphid predators and their use in integrated pest management. Ann. Entomol. Soc. Am. 97: 240–248.
- SAS Institute. 2000. SAS/STAT user's guide, version 8. SAS Institute, Cary, NC.
- Vockeroth, J. R. 1992. The flower flies of the subfamily Syrphinae of Canada, Alaska, and Greenland. Diptera: Syrphidae. The insects and arachnids of Canada part 18. Agriculture Canada, Ottawa, ON, Canada.
- Wu, Z., D. Schenk-Hamlin, W. Zhan, D. W. Ragsdale, and G. E. Heimpel. 2004. The soybean aphid in China: a historical review. Ann. Entomol. Soc. Am. 97: 209–218.

Received 25 July 2007; accepted 28 September 2007.