Predators Suppress *Aphis glycines* Matsumura Population Growth in Soybean

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Environ. Entomol. 33(3): 608–618 (2004)

ABSTRACT The soybean aphid, *Aphis glycines* Matsumura, is an invasive pest of soybean, first discovered in North America in 2000. We studied the ability of the existing predator community in soybean to suppress *A. glycines* population growth during June–August 2002, in field studies using predator exclusion and sham cages or no-cage controls. Cages were infested with uniform initial densities of *A. glycines* adults, and subsequent populations of aphids and predators were monitored. After 2 wk, exclusion and sham cages were switched, with aphid and predator density followed for additional 2 wk. The experiment was repeated a second time, allowing observation of predator community response to both low and high density aphid populations over several time periods and stages of soybean development. Cages had minimal effects on temperature, relative humidity, or soybean growth. In contrast, predator communities and aphid populations were strongly affected by cage treatments. In the first trial, the activity of foliar-foraging predators effectively prevented *A. glycines* population growth maintaining populations below 10 aphids per plant (adult + nymphs) in sham cages, while populations exceeded 200 aphids per plant in exclusion cages. After cage switch, these high *A. glycines* populations in the former exclusion cages were rapidly colonized and reduced by nearly an order of magnitude within 2 wk by a combination of generalist and specialist predators. The second trial produced qualitatively similar results, but at much lower aphid densities. The most abundant predators in both trials included: *Harmonia axyridis* Pallas, *Orius insidiosus* (Say), and *Leucopis* spp. These studies demonstrate that existing predator communities comprised of a mixture of indigenous and naturalized species can suppress *A. glycines* population density in soybean. The impact of existing predator communities should be further investigated as a component of *A. glycines* management in United States soybean production systems.

KEY WORDS biological control, invasive species, predator community

THE SOYBEAN APHID (*Aphis glycines* Matsumura) (Hemiptera: Aphididae) is an invasive herbivore new to North America. It was first discovered in North America in Wisconsin in late July 2000 infesting soybean (*Glycine max* L.) (Wedburg 2000) and is currently distributed in 19 US states and parts of Canada, from Mississippi to Quebec and Delaware to Nebraska. In these new environments, *A. glycines* interacts with both native and naturalized predators that were present in soybean ecosystems before its arrival. Understanding the role of existing predator communities in *A. glycines* population dynamics is a critical step in the development of effective management systems for this new pest.

A. glycines has a heteroecious holocyclic life cycle with sexual stages found on the primary host plants, various species of buckthorn (Rhamnaceae: *Rhamnus* spp.), and asexual stages occurring on the secondary host plant, soybean (Wang et al. 1962). Five species of *Rhamnus* occur widely in the northcentral United States, including one native species *R. alinifolia* L'Her. In Michigan, the exotic invasive *R. cathartica* L. appears to be the key overwintering host for *A. glycines.* Fall migration to *R. cathartica* by *A. glycines* gynoparae and males, and production of oviparae and overwintering eggs have been observed in the field with subsequent production of fundatrices and alate viviparous females and migration to soybean the following spring (DiFonzo and Hines 2001; C.D.D., unpublished data). The prior invasion of *R. cathartica* and *R. frangula* L. into the northcentral United States may have paved the way for the establishment of *A. glycines* in a fashion consistent with invasional meltdown (Simberloff and Von Holle 1999).

NC-502 was the United States Department of Agriculture/CSREES North Central Region Soybean Aphid Committee, now incorporated into S-1010 Dynamic Soybean Pest Management for Evolving Agricultural Technologies and Cropping Systems. NCR-125 is the United States Department of Agriculture/CSREES North Central Region Arthropod Biological Control Committee.

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0046-225X/04/0608–0618$04.00/0

Soybean aphids reproduce parthogenetically while on soybeans, increasing their numbers rapidly. As plants become crowded, alate aphids are produced that disperse to colonize new host plants (Dixon 1998). Fields infested early in the season (June) are most likely colonized by soybean aphids migrating from primary hosts, whereas fields infested later in the season (July) are most likely colonized by alate aphids dispersing from soybean plants. Fields infested earlier in the season generally reach higher numbers than those infested later (Rutledge et al. 2004). This may be due in part to the influence of host plant quality on *A. glycines* fecundity, or to the composition of early season natural enemy communities.

In Asia, *A. glycines* feeding on soybean can cause up to a 20-cm reduction in growth and a 27.8% reduction in seed yield (Wang et al. 1996). In the United States, populations in excess of 13,000 aphids per plant and 40% loss in seed yield were recorded in Michigan (DiFonzo and Hines 2002). Macedo et al. (2003) measured up to 50% reduction in photosynthetic rates for soybean leaves infested with *A. glycines.* Feeding by *A. glycines* can also indirectly harm soybeans by vectoring alfalfa mosaic, soybean dwarf, soybean stunt, soybean mosaic, tobacco ringspot, and bean yellow mosaic viruses (Van den Berg et al. 1997, Clark and Perry 2002, Wang and Ghabrial 2002). Epidemics of soybean mosaic potyvirus in summer-sown soybean fields in Jiangsu, China, were closely associated with the timing of *A. glycines* immigration (Li and Pu 1991). Soybean aphids also cause indirect damage by excreting honeydew, which promotes the growth of sooty molds that reduce plant photosynthetic capacity (Lenné and Trutmann 1994, Hirano et al. 1996).

After the detection of *A. glycines,* scientists affiliated with NC-502 and NCR-125[1] initiated studies of its natural enemies in the United States and Asia during 2001. In United States soybeans, generalist predators dominated the natural enemy community while parasitoids and pathogens were virtually absent (Fox 2002, Fox and Landis 2003, O'Neil and Rutledge 2002, Herbert et al. 2002, Puttler and Bailey 2002). The predators *Harmonia axyridis* (Pallas) and *Orius insidiosus* (Say) were the most numerous, and most commonly observed attacking aphids (Fox 2002, O'Neil and Rutledge 2002). Densities of *H. axyridis* as high as 7 adults or 46 larvae per m^2, and up to 1.3 *O. insidiosus* per soybean terminal, have been recorded in Michigan (Fox 2002).

Initial foreign exploration in Asia in 2001 revealed that *A. glycines* populations were extremely low in portions of the native range corresponding to north-central United States latitudes. In China, *H. axyridis* was the most common natural enemy observed (G. Heimpel, personal communication) while in Japan the most common natural enemies were chamaemyiids and cecidomyiids (D. Voegtlin, personal communication). In Asia, coccinellid predators (*Harmonia* spp.) play an important role in suppressing *A. glycines* populations in soybean fields (Van den Berg et al. 1997). Likewise, aphidophagous predators, such as *Nabis* spp., *H. axyridis, Coccinella septempunctata* L., *Chrysopa* spp., and the syrphid *Ischiodon escutellaris* (F.), were reported to aid in *A. glycines* control during the mid to late season in China (Han 1997). The role of predation in suppression of *A. glycines* populations in the United States is not known. The objectives of the following studies were to determine whether predation was an important factor in the population dynamics of *A. glycines* in Michigan.

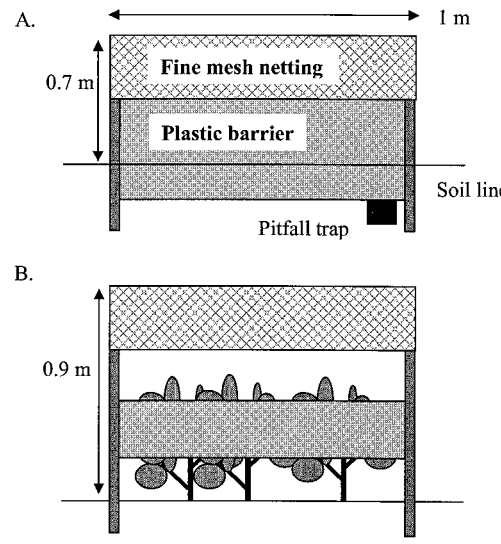

Fig. 1. Design of exclusion (A) and open (B) cages used to assess predation effects on *A. glycines* in 2002. Two pitfall traps in each exclusion cage aid in removal of unwanted predators. A third treatment consisting of the plastic cage support frame alone was used as a control for cage effects.

Materials and Methods

Field Site. Experiments were conducted on the Michigan State University Entomology Research Farm, Ingham County, Michigan. On 20 May 2002, a 99 × 94-m field was planted to soybean (Pioneer 93B82) at a rate of 70,900 seeds/ha in 38-cm rows. Experiments were conducted in this field with individual plots isolated at least 9 m from any border to minimize edge effects. The crop area was managed using reduced primary tillage (chisel plow, disc), followed by secondary tillage (field cultivation). Herbicides (lactofen [Cobra, Valent USA Corporation, Walnut Creek, CA] [1 liter/ha], bentazon [Basagran, BASF, Mt. Olive, NJ] [2 liters/ha], sethoxydim + dash [Poast Plus, BASF] [2 liters/ha], and crop oil concentrate [2 liters per ha]) were applied on 5 June 2002 to control broadleaf and grass weeds.

Predator Exclusion Trials. Predator and *A. glycines* densities were compared in cages with or without ground and foliar-foraging predators. Cage supports were constructed of PVC pipe (1.3 cm outside diameter; Cresline Plastic Pipe, Evansville, IN). Supports for exclusion cages (Fig. 1A) were 1 m^2 (top view) with legs 0.90 m long, with 20 cm placed in the soil and 0.70 m extending above the soil line to exclude ground-

foraging predators. To remove any preexisting predators, exclusion cages each contained two 8.5-cm-diameter × 13-cm-deep pitfall traps placed in opposite corners of the cage. Pitfalls contained 50% ethylene glycol as a killing agent. The top of the cage was covered with fine-mesh white no-see-um netting (Balson-Hercules, New York, NY) sewn to fit the support exterior and draped 27 cm down the side of cages. At the soil line, the frame was surrounded by a 3-ml clear plastic sheet that extended 10 cm below and 27 cm above the ground to meet the bottom of the mesh cage to exclude foliar-foraging predators. The mesh and plastic were joined with a 2-cm strip of Velcro that allowed cages to be opened for sampling. Supports for open cages (Fig. 1B) were also 1 m^2 (top view), but legs were 1 m long, with 0.10 m below the soil surface. This allowed for an 18-cm gap between the plastic and the soil line to allow ground-foraging predators to enter, and a 10-cm gap between the plastic and the mesh for foliar-foraging predators to enter. Both exclusion and open cages contained the same amount of screen and plastic materials above the soil level. A control cage consisting of only the PVC support with no plastic or screen netting was included as a control for cage effects. Cages enclosed three soybean rows and contained 30–42 plants.

The plot layout was a completely randomized block design, with one cage per 6 × 6-m area. There were five replications of the three treatments, for a total of 15 cages. Cages were established and plants infested with *A. glycines* on 26 June when natural infestations of *A. glycines* were <1 per plant. We selected an infestation method to balance the competing aims of assuring establishment while mimicking the low natural infestation level. We targeted initial densities of ≈1–2 adults per plant by assuming up to 50% preestablishment mortality and potential aphid dispersal among all plants in the cage. To achieve this, 10 randomly selected plants per cage each received an average of 11 ± 1 adult lab-reared *A. glycines* adults by transferring them from infested soybean plants using a fine camel hair brush. Only adult, apterous *A. glycines* with a visible cauda were used. The trial was sampled five times from 28 June to 12 July. On 12 July, four of the five replicates were randomly selected, and the open and exclusion cage treatments were switched. This was done by carefully removing the support and cage materials and transferring to the opposite plot area. The fifth replicate was left intact to provide an estimate of aphid population trajectory if the cage treatment was not manipulated. Control cages were left in place. The trial was then continued for another five sample dates from 15 to 29 July.

The experiment was repeated a second time beginning on 10 July. Cages were artificially infested with 13 ± 1 adult *A. glycines* per plant using the methodology described above. Overall, natural infestation of *A. glycines* in the field remained very low, with scattered colonies found at densities of <10 per plant. The second trial was sampled five times between 12 and 26 July, when open and exclusion cages were switched. The trial continued from 29 July to 12 August. To accommodate the increased soybean height, when cages were switched, exclusion cages were raised ≈10 cm with the added height offset by burying less plastic below the soil line.

In both trials, data were collected on Mondays and Fridays. On each sample date, the temperature and relative humidity inside and outside of each cage were measured at canopy height by inserting the probe though a small slit before opening the cage. This was followed by a 3-min nonintrusive visual examination of the soybeans to determine predator abundance and species composition, followed by a detailed examination of all soybean foliage in the cage to detect any additional predators. Any predators found inside exclusion cages were removed. Next, 10 plants were randomly selected in each cage and whole plant counts were conducted to assess adult and nymphal *A. glycines* population density. Finally, 5 additional plants were randomly selected, measured, and staged using the method of Ritchie et al. (1989). Representative specimens of all predators were collected and identified, and voucher specimens were deposited in the A.J. Cook Arthropod Research Collection at Michigan State University (East Lansing, MI).

Data Analysis. Repeated measures analysis of variance (ANOVA) and a type III *F* test were used to assess the statistical significance of treatment effects on temperature, humidity, and plant variables. Adult and nymphal *A. glycines* and predator counts were analyzed by Poisson regression with a type III *F* test for overall treatment effects, using the GLIMMIX Macro link of SAS statistical program (SAS Institute 2000). From these analyses, treatment, date, and treatment date interaction are reported. Where significant ($P < 0.05$) treatment date interactions occurred, data were sliced to reveal treatment differences by date. Significance of pairwise mean comparisons (from LS MEANS of SAS output) was determined using the Tukey-Kramer adjustment for multiple comparisons ($P < 0.05$).

Results

Cage Effects

Temperature, Relative Humidity, and Soybean Growth. Cage treatment had little effect on temperature inside cages or frame controls (Table 1; Fig. 2). As expected, temperature varied significantly by date through both trials. In trial 1, temperatures ranged from 22 to 34°C and were significantly warmer in exclosure versus other cages, primarily because of a large difference on the initial sample date. In trial 2, temperatures ranged from 22 to 33°C with no significant treatment effects. Cage treatment also had little effect on relative humidity inside cages or frame controls (Fig. 2). In trial 1, relative humidity varied significantly by date, ranging from 35 to 95% (Table 1). The only significant treatment difference in humidity in trial 1 occurred on 12 July, when exclusion cages had significantly higher relative humidity when compared with open cages. In trial 2, relative humidity

Table 1. Sources of variation, degrees of freedom (numerator, denominator), *F* statistics, and probabilities for the effects of cage treatment and date on temperature, relative humidity, and soybean growth in cages during *A. glycines* predation trials, 2002

Effect	Trial 1			Trial 2		
	df	*F*	*P*	df	*F*	*P*
Temperature before cage switch						
Treatment	2, 8	37.7	<0.0001	2, 8	2.6	0.1367
Date	4, 48	56.1	<0.0001	4, 48	44.5	<0.0001
Trt. date	8, 48	0.5	0.8413	8, 48	1.3	0.2533
Temperature after cage switch						
Treatment	2, 4.9	0.1	<0.9077	2, 6.7	1.4	0.3126
Date	4, 32	13.3	<0.0001	4, 40	12.6	<0.0001
Trt. date	8, 32	0.3	0.9451	8, 40	0.5	0.8376
Relative humidity before cage switch						
Treatment	2, 8	0.2	0.8171	2, 8	24.0	0.0004
Date	4,48	8.5	<0.0001	4,48	230.1	<0.0002
Trt. date	8, 48	2.4	0.0269	8, 48	0.8	0.6179
Relative humidity after cage switch						
Treatment	2, 6.3	20.2	0.0018	2, 2.8	3.2	0.1886
Date	4, 40	89.1	<0.0001	4, 32	4.8	0.0037
Trt. date	8, 40	0.8	0.6264	8, 32	0.8	0.6303
Plant height before cage switch						
Treatment	2, 8	1.3	0.3303	2, 11.9	0.0	0.9926
Date	4, 48	256.2	<0.0001	4, 46.2	120.5	<0.0001
Trt. date	8, 48	2.4	0.0263	8, 46.2	1.8	0.1132
Plant height after cage switch						
Treatment	2, 5.3	2.2	0.240	2, 6.8	3.8	0.0801
Date	4, 40	106.3	<0.0001	4, 39.2	70.1	<0.0001
Trt. date	8, 40	1.1	0.4192	8, 39.2	1.0	0.4339

Trt. = Treatment.

again varied significantly by date, ranging from 22 to 33°C with no significant differences between treatments on any date (Table 1; Fig. 2). Soybean height varied significantly by date, but was not significantly affected by cage treatment in either trial (Table 1; Fig. 2). During trial 1, plants were in V5 stage on the first sample date (28 June), and the R1 stage on the last sample date before cages were switched (12 July). After cages were switched, plants were in R1 stage on 15 July and R2 on 29 July. During trial 2, plants were in R1 stage on 15 June, and R2 on 26 July before cages were switched. After cages were switched, plants were in the R2 stage on 29 July and R4 on 9 August.

Aphid and Predator Effects

Trial 1, Aphids. Cage treatment significantly influenced the numbers of *A. glycines* adults and nymphs before cage switch and nymph number after cage switch (Table 2). In the first half of the experiment, adult *A. glycines* populations in exclusion cages increased steadily, reaching ≈100 aphids per plant by 12 July (Fig. 3A). In contrast, in open and frame cages, populations remained below 5 aphids per plant. Similar trends occurred for nymphal *A. glycines* (Fig. 3B). Statistically, exclusion cages contained greater numbers of adult and nymphal *A. glycines* than open and frame cages on all but the first two sample dates before cage switch (Fig. 3, A and B).

In the second half of the experiment, the two unmanipulated replicates (exclusion control and open control) indicate the trends in *A. glycines* populations if original treatments were left in place (Fig. 3, A and B). In unmanipulated exclusion cages, *A. glycines* populations increased dramatically, peaking at 1,534 adult and 2,492 nymphal *A. glycines* per plant on 26 July, while in the unmanipulated open cage densities fluctuated between 1 and 40 aphids per plant. These observations stand in sharp contrast to those cages that were switched on 12 July. High populations of *A. glycines* in the former exclusion treatment were exposed to predators, and the low aphid populations in former open treatments were protected from predation. When predators were excluded from formerly open cages, there was an increase in both adult and nymphal *A. glycines* populations, indicating that predators previously were keeping these *A. glycines* populations low (Fig. 3, A and B). In the newly opened cages, adult and nymphal *A. glycines* populations remained constant for ~1 wk, then decreased from an average of 103 adult *A. glycines* per plant on 15 July, to 11 adults per plant on 26 July (Fig. 3A), and from 159 to 40 *A. glycines* nymphs per plant (Fig. 3B). For both adults and nymphs, populations remained higher in the former exclusion cages until 22 July when they were approximately equal. While there was a significant treatment effect, there were no statistical differences of pairwise treatment comparisons after cages were switched. The significant treatment date interaction reveals the diverging treatment effects over time (Table 2).

Trial 1, Predators. In the first half of the experiment, predator abundance was consistently low and not significantly different in any treatment (Table 3; Fig. 4A). Overall, 13 ground and 11 foliar-foraging predator species were observed (Fox 2002). In exclusion cages, *O. insidiosus* adults and *Chrysoperla* spp. were occasionally detected and removed. In open and frame

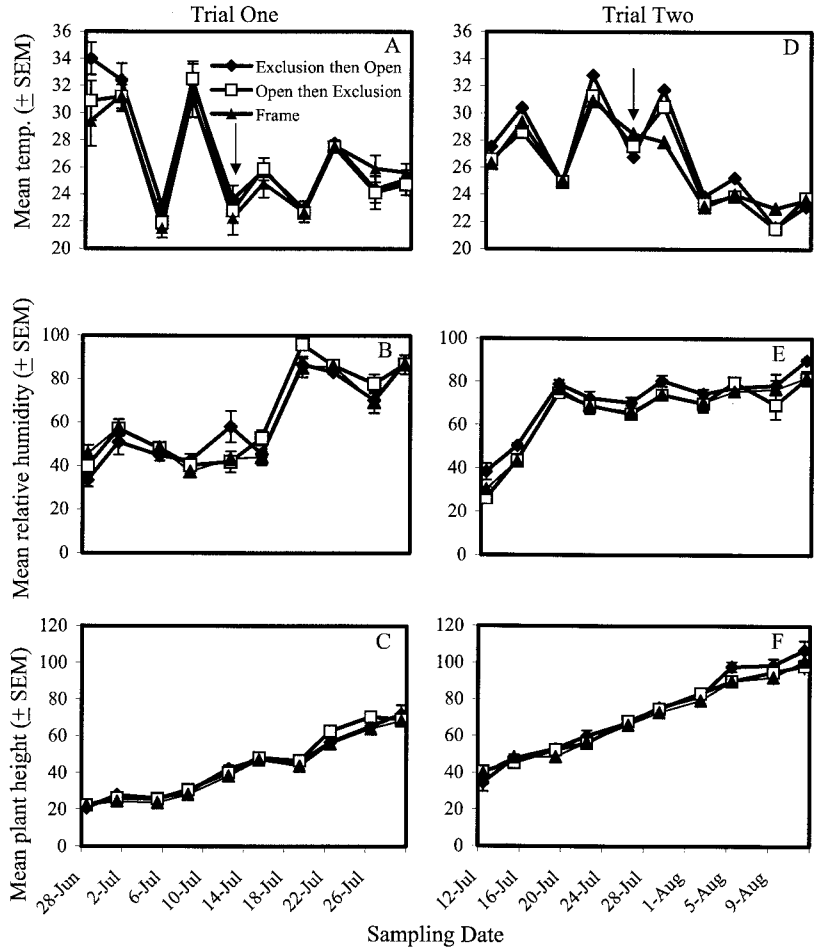

Fig. 2. Mean temperature (°C), relative humidity (%), and plant height (cm) in exclosure, open, and frame cage treatments in trial 1 (A–C) and trial 2 (D–F), 2002. The arrow indicates the date in which open and exclusion cages were switched in four of five replications.

treatments, *O. insidiosus* adults constituted 61.7 and 55.2% of the observed predators. *Coccinella septempunctata* (L.), *Nabis* spp., and *H. axyridis* also were observed at low densities (Fox 2002, Rutledge et al. 2004). After the cages were switched, predator abundance increased significantly in the former exclusion treatments, in which aphid populations were now accessible to predators (Table 3; Fig. 4A). In these treatments, predator abundance increased from below 5 to over 60 predators per m^2 (Fig. 4A). The most abundant predators were *H. axyridis* adults (Fig. 4B), *O. insidiosus* adults (Fig. 4C), and *Leucopis* spp. larvae (Fig. 4D) that made up 22.9, 14.0, and 30.6% of the total predator counts, respectively (Fox 2002, Rutledge et al. 2004). The population of *H. axyridis* remained elevated throughout the rest of the trial, while the *O. insidiosus* and *Leucopis* spp. increase was confined to 19 July.

Trial 2, Aphids. Cage treatment again significantly influenced adult and nymphal *A. glycines* numbers before and after cage switch (Table 2). In the first half of the experiment, overall results were similar to trial 1; however, aphid density was uniformly lower (Fig. 5). Adult *A. glycines* populations in exclusion cages increased rapidly, reaching ≈50 aphids per plant by 30 July, while those in open and frame cages remained below 5 aphids per plant (Fig. 5A). Similar trends occurred for nymphal *A. glycines* (Fig. 5B). By 22 July, exclusion cages contained statistically more adult and nymphal *A. glycines* than open or frame cages (Fig. 5, A and B). In contrast to trial 1, in the second half of the experiment *A. glycines* populations did not continue to rise in the unmanipulated exclusion cage, nor did populations in the formerly open treatment rise more than in the unmanipulated control after exclusions were established (Fig. 5, A and B). Rather, populations of both adult and nymphal aphids in the now open and exclusion treatments gradually converged until they became statistically indistinguishable on the final two sample dates of 9 and 12 August. The lack of a rapid rise in the exclusion treatments after cage

Table 2. Sources of variation, degrees of freedom (numerator, denominator), *F* statistics, and probabilities for the effects of cage treatment and date on adult and nymph populations during *A. glycines* predation trials 1 and 2, 2002

Time period	Adults			Nymphs		
Effect	df	*F*	*P*	df	*F*	*P*
Trial 1						
Before cage switch						
Treatment	2, 47.8	31.3	0.002	2, 10.5	46.2	<0.0001
Date	4, 44.5	7.9	<0.0001	4, 48.3	9.5	<0.0001
Trt. date	8, 44.5	3.5	0.004	8, 48.5	3.5	0.003
After cage switch						
Treatment	2, 10.2	2.7	0.110	2, 10	3.4	0.010
Date	4, 41.7	0.4	0.840	4, 41.2	0.8	0.570
Trt. date	8, 41.7	4.4	0.006	8, 41.6	4.2	0.001
Trial 2						
Before cage switch						
Treatment	2, 10.9	10.8	0.003	2, 11.2	19.3	0.002
Date	4, 50.2	4.6	0.003	4, 50.2	5.3	0.001
Trt. date	8, 50.1	0.9	0.520	8, 50.2	0.9	0.560
After cage switch						
Treatment	2, 8	35.4	0.001	2, 8.5	35.8	0.001
Date	4, 36.7	4.5	0.004	4, 42.1	8.3	<0.0001
Trt. date	8, 42	4.0	0.001	8, 42	2.6	0.020

Trt. = Treatment.

switch may have been related to difficulty in removing all predators from this treatment.

Trial 2, Predators. In comparison with the first trial, overall predator numbers were slightly higher in all treatments during the first half of the experiment, but failed to reach as high a level in the second half of the experiment (Fig. 4E). The predator community was similar to that of trial 1 (Fig. 4A), consisting of 13 ground and 8 foliar-foraging predator species (Fox 2002). In the first half of the trial, *H. axyridis* (Fig. 4G) and *Leucopis* spp. (Fig. 4H) were present in very low numbers. The most abundant predator before cage switch was *O. insidiosus* (Fig. 4F), which made up 69.9, 58.5, and 61.5% of predators observed in exclusion, open, and frame cages. During this time, the exclusion cages prevented entry by most predators; however, *O. insidiosus* was difficult to exclude, as evidenced by the persistent numbers observed in the exclusion cages in contrast to trial 1 (Fig. 4G). This was most likely caused by the difficulty in observing and removing *O. insidiosus* from these cages in which plants were now taller and filling the rows.

Table 3. Sources of variation, degrees of freedom (numerator, denominator), *F* statistics, and probabilities for the effects of cage treatment and date on total predator populations during *A. glycines* predation trials 1 and 2, 2002

Effect	Trial 1			Trial 2		
	df	*F*	*P*	df	*F*	*P*
Before cage switch						
Treatment	2, 15.9	0.9	0.410	2, 10.1	5.8	0.020
Date	4, 50.5	6.4	0.003	4, 48.3	10.8	<0.0001
Trt. date	8, 50.7	1.4	0.230	8, 48.3	1.2	0.340
After cage switch						
Treatment	2, 8.7	31.5	0.001	2, 6.7	55.2	<0.0001
Date	4, 38	1.8	0.150	4, 36.2	3.3	0.020
Trt. date	8, 38.1	2.2	0.050	8, 32.2	1.7	0.130

Trt. = Treatment.

After cage switch, predator abundance increased in the former exclusion, now open cages (Fig. 4E), but the increase was not as dramatic as in trial 1 (Fig. 4A). The same three species (*H. axyridis*, *Leucopis* larvae, and *O. insidiosus*) were again the most abundant species in the open cages, and reached peak abundance ~1 wk after cages were switched. While *H. axyridis* reached similar levels to trial 1, both *O. insidiosus* and *Leucopis* larvae were not as prevalent.

Discussion

In predator manipulation experiments, it is important to evaluate the potential for cage effects to bias the outcome (Luck et al. 1999). In our experiments, temperature, relative humidity, and plant height did not differ greatly among cage treatments. While significant cage effects were found for temperature and relative humidity on one occasion each, the absolute value of these differences was small. Mean temperatures between cage treatments generally varied by <2°C, while relative humidity generally varied by <10%. Mean plant height, as a measure of overall conditions for plant growth in the cages, did not differ significantly among any of the treatments in either trial.

While we cannot rule out that cage effects may have influenced *A. glycines* growth or survival, the direction of these impacts appears to favor predation as the primary explanation for our overall result. The optimum temperature for *A. glycines* development is reported to be between 22 and 25°C (Wang et al. 1962). During both trials, the average temperature inside all cages was generally above this optimum; thus, it might be expected that *A. glycines* population growth rate may have been slightly slower in the exclusion cages on dates they were warmer than open or frame treatments. As such, our trials may tend to underestimate the impact of predation on *A. glycines* population increase. Humidity effects are more difficult to interpret. Higher relative humidity is known to favor fungal pathogens of aphids (Tanada and Kaya 1993); however, no evidence of pathogen infection was noted in any treatment. If subtle pathogen mortality was occurring, it should have been greater in exclusion treatments, again possibly contributing to an underestimate of the population growth of *A. glycines* in the absence of predation.

In addition to excluding predators, exclusion cage treatments could also unnaturally confine *A. glycines* on the plants. It is known that production of alate aphids increases under crowding and plant stress conditions (Dixon 1998). Thus, emigration may be an alternative explanation for a decrease in aphid abundance after the cages are switched. However, several lines of evidence argue against this. First, even under the most crowded conditions, i.e., in unmanipulated exclusion controls, alates only became abundant, reaching thousands, on 22 July, when adult aphid populations were averaging over 1,000 aphids per plant. In

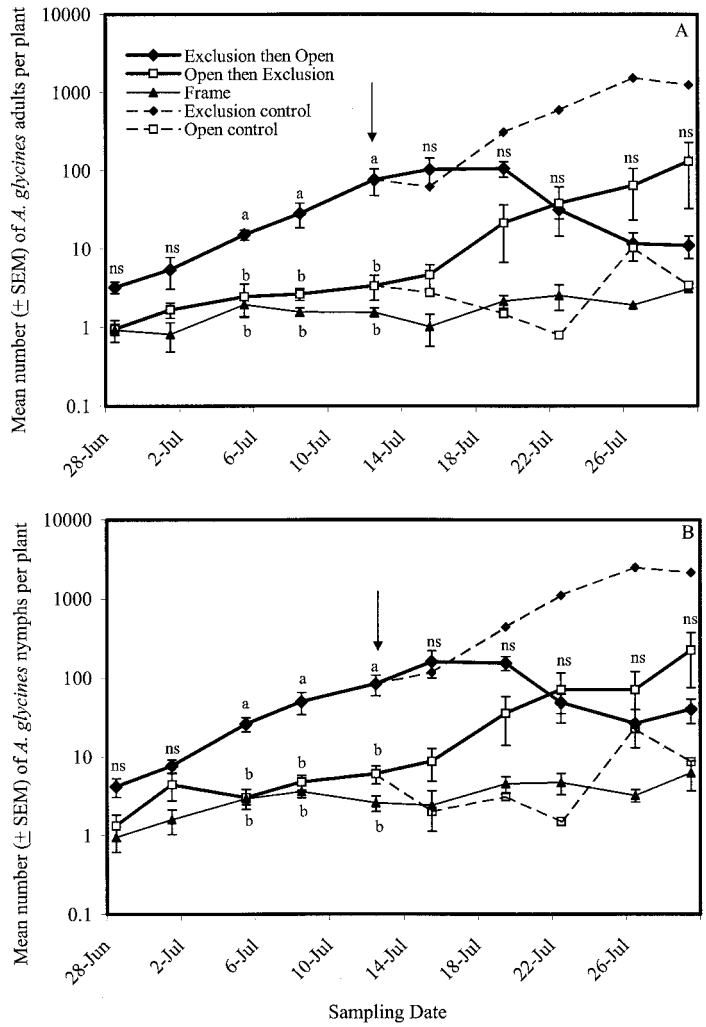

Fig. 3. Mean (±SEM) adult (A) and nymph (B) *A. glycines* population (log scale) per plant in open, exclusion, and frame cages in trial 1, 2002. The arrow indicates when open and exclusion cages were switched. One randomly selected replicate of open and exclosure cages was left in place (dashed line) to show the trend if cages were not switched. Means with the same letter on a given date are not significantly different ($P < 0.05$, LS MEANS).

other treatments, alate *A. glycines* were rarely observed. No alates were observed in trial 1 until 12 July, when a total of three alates was found in the exclusion treatment, when aphid numbers averaged >50 per plant. In trial 2, there was only one observation of alates in exclusion cages on 26 July. Similarly, we did not see evidence that large numbers of apterous aphids wandered from open or sham cage areas. Because foliage outside of cages did not touch that within, it would be very difficult to leave cages by walking. Coupled with observations of a large increase in predator abundance after cage switch, emigration is unlikely to be the predominant explanation for *A. glycines* reductions in the former exclusion treatments.

Finally, the overall context of the experiments may have impacted our result. Perhaps 2002 was a poor/good year for aphid increase, making predator suppression of *A. glycines* populations more/less likely. Or perhaps the low natural density of aphids in the field may have resulted in stronger/weaker predator impacts. Conditions of low natural density of *A. glycines* are a valid environment for testing predator impacts, as our short experience with this insect indicates that regionally low densities have occurred in 1 of 4 years. In such years, aphids are not absent, and studying the impacts of predators under these conditions is vital to a full understanding of aphid predator dynamics. In this context, our tests indicate that in two separate trials in 2002, excluding predators created an order of magnitude difference in *A. glycines* populations from a common initial density in 2 wk. While this clearly demonstrates that predation was an important factor in population suppression under the conditions tested, additional tests over many environments will be re-

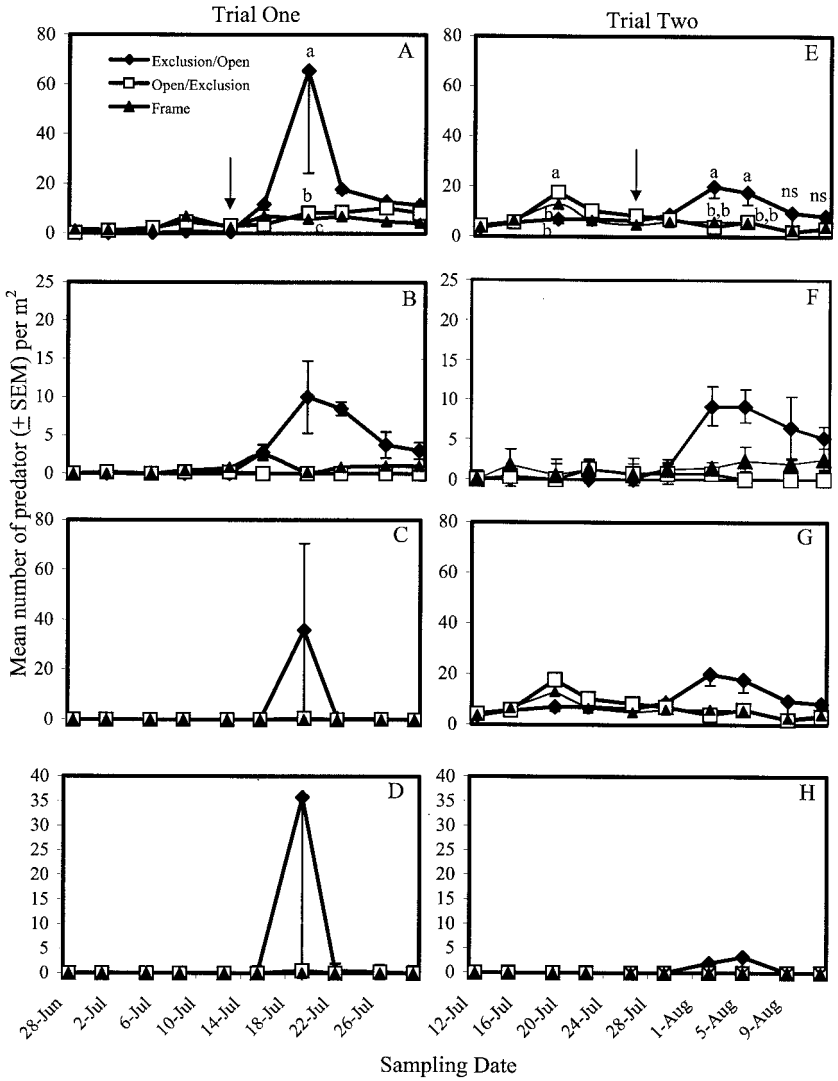

Fig. 4. Mean (±SEM) abundance of foliar-foraging predators based on a combination of nonintrusive visual examination, followed by close examinations of foliage in the open, exclusion, and frame treatments during trial 1 (A–D) and trial 2 (E–H), 2002. Total number of predators (A, E), and individual species abundance, *Harmonia axyridis* (B, F), *Orius insidious* (C, G), and *Leucopus* spp. (D, H), are shown. The arrow indicates when open and exclusion cages were switched.

quired to determine the overall parameters under which such impacts may occur.

The density of most predator species was successfully reduced by the exclusion cage treatment, and *A. glycines* population dynamics in the contrasting open and frame treatments provide strong evidence that predators were important in suppressing aphid populations. Low densities of actively foraging predators, particularly *H. axyridis*, *O. insidiosus*, and *C. septempunctata*, were continually present in open and frame treatments. In both trials, there were modest increases in predator numbers in these treatments on the second to fourth sample dates, apparently in response to the occurrence of *A. glycines* (Fig. 4, A, C, and E–G). The impact of this subtle response becomes evident only in comparison with the exclusion treatment. Where predators had free access to plants they prevented aphid increase, while adjacent plots with predator exclusions reached hundreds of aphids per plant during the same time period. Subsequently, switching the cage types resulted in a reversal in aphid populations. Collectively, the predator community showed the ability to keep initial *A. glycines* populations low (both trials), respond to increased prey availability when cages were switched, and quickly reduce high *A. glycines* populations (trial 1). These findings suggest that predation was among the primary factors regulating *A. glycines* population dynamics.

Previous studies have also shown that foliar-foraging predators can control a variety of aphid species

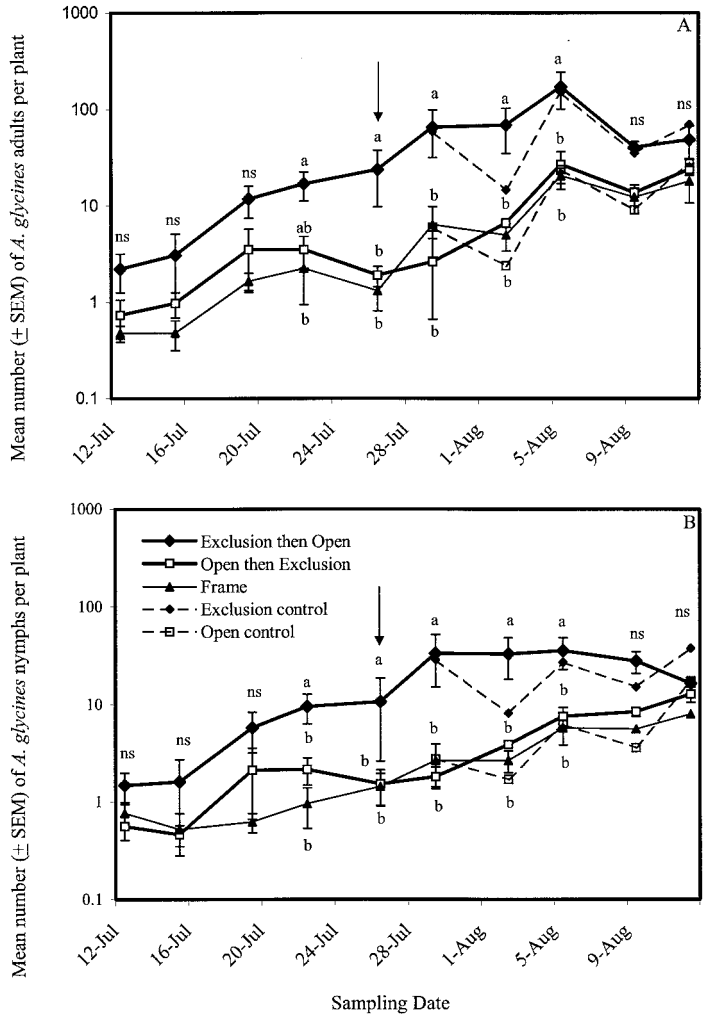

Fig. 5. Mean (±SEM) adult (A) and nymph (B) *A. glycines* population (log scale) per plant in open, exclusion, and frame cages in trial 2 during 2002. The arrow indicates when open and exclusion cages were switched. One randomly selected replicate had cages that were not switched (dashed line) to show the trend if cages were not switched. Means with the same letter on a given date are not significantly different ($P < 0.05$, LS MEANS).

(Grasswitz and Burts 1995, Starý 1995, Chen and Hopper 1997, Landis and Van der Werf 1997, Obrycki and Kring 1998). Overall, this study supports the findings of Van den Berg et al. (1997), which indicated that predators, in particular *Harmonia* spp., contributed to the reduction of *A. glycines* populations in Indonesia. During our trials, *H. axyridis* and *O. insidiosus* were consistently the most abundant predators. *Leucopis* midge larvae were only abundant during one sample date. It is possible that they have an ephemeral period of abundance, or that they suffered intraguild predation by larger predators.

The overall increase in *A. glycines* populations in the absence of predators and the reduction of *A. glycines* populations when predators were allowed access were greater in the first trial when plants were smaller and at an earlier phenological stage. Van den Berg et al. (1997) showed that the intrinsic rate of increase of *A. glycines* decreased as soybean ages. It may be that in the first trial *A. glycines* populations were able to respond to protection from predation because of more suitable host plant quality. In addition, predators may have had an easier time foraging for *A. glycines* on these smaller plants. When plants are smaller and canopies less dense, prey have fewer places to hide and predators have less leaf area to search. The opposite may be true when plants mature, as in trial 2. Garcia and O'Neil (2000) found that predation by the coccinellid *Cryptolaemus montrouzieri* Mulsant on the citrus mealybug, *Planococcus citri* Risso, decreased as *Coleus* plants increased in size. They suggested that plant characteristics were the most likely reason for this decrease in predator efficiency found in their study.

A final observation relates to the apparently low density of predators required to suppress *A. glycines*

population growth. In trial 1, total predator populations never exceed 5/m^2 and yet were able to completely suppress *A. glycines* population growth in the first half of the trial. By attacking aphids before they reach high populations, even a low density of predators was able to suppress this pest. This is consistent with the theoretical models (Chang and Kareiva 1999) and empirical results (Symondson et al. 2002), which suggest that when pest populations are low, generalist predators may be as, or more effective in pest regulation than more specialized natural enemies. In our system, specialized predators (e.g., *Leucopis* spp.) appeared and reproduced only after exclusion cages containing large numbers of aphids were opened. It remains to be seen whether in the future specialized natural enemies will respond at time and densities sufficient to prevent economic damage.

These studies indicate an important role for existing predators in *A. glycines* control in Michigan. With apparently strong *A. glycines* suppression by existing predators already in place, introduction of additional biological control agents should be carefully considered. It is likely that existing predator communities would interact with introduced parasitoids via intraguild predation (Colfer and Rosenheim 2001). More data need to be collected to determine whether existing natural enemies will influence establishment of introduced agents, or alternatively, whether combinations of existing and introduced natural enemies will provide more complete or more reliable aphid suppression. Consideration of these potential interactions before the release of additional natural enemies is appropriate.

Acknowledgments

We thank Suzanne Thiem and Kurt Thelen for their advice on this research. We also thank Chris Sebolt, Alejandro Costamagna, Sandra Clay, Alison Gould, Andrea McMillian, Andre Ball, Meghan Burns, Michelle Smith, Christy Hemming, Kathy McCamant, Allison Lewinski, Ben Nessia, and Kevin Newhouse for their field assistance. Soybean aphids were provided by the United States Department of Agriculture APHIS PPQ Invasive Species Laboratory (Niles, MI). This work was funded by a Cooperative Agreement with United States Department of Agriculture APHIS PPQ and by the Michigan Agricultural Experiment Station.

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Received 17 June 2003; accepted 7 November 2003.