

PREDATORS EXERT TOP-DOWN CONTROL OF SOYBEAN APHID ACROSS A GRADIENT OF AGRICULTURAL MANAGEMENT SYSTEMS

ALEJANDRO C. COSTAMAGNA¹ AND DOUGLAS A. LANDIS

Department of Entomology, 204 Center for Integrated Plant Systems, Michigan State University,
East Lansing, Michigan 48824-1311 USA

Abstract. The discovery of soybean aphid, *Aphis glycines* Matusumura, in North America in 2000 provided the opportunity to investigate the relative strength of top-down and bottom-up forces in regulating populations of this new invasive herbivore. At the Kellogg Biological Station Long Term Ecological Research site in agroecology, we contrasted *A. glycines* establishment and population growth under three agricultural production systems that differed markedly in disturbance and fertility regimes. Agricultural treatments consisted of a conventional-tillage high-input system, a no-tillage high-input system, and a zero-chemical-input system under conventional tillage. By selectively restricting or allowing predator access we simultaneously determined aphid response to top-down and bottom-up influences. Irrespective of predator exclusion, our agricultural manipulations did not result in bottom-up control of *A. glycines* intrinsic rate of increase or realized population growth. In contrast, we observed strong evidence for top-down control of *A. glycines* establishment and overall population growth in all production systems. Abundant predators, including *Harmonia axyridis*, *Coccinella septempunctata*, *Orius insidiosus*, and various predaceous fly larvae, significantly reduced *A. glycines* establishment and population increase in all trials. In contrast to other systems in which bottom-up forces control herbivore populations, we conclude that *A. glycines* is primarily controlled via top-down influences of generalist predators under a wide range of agricultural management systems. Understanding the role of top-down and bottom-up forces in this context allows agricultural managers to focus on effective strategies for control of this invasive pest.

Key words: agroecosystems; aphid; *Aphis glycines*; biological control; *Coccinella septempunctata*; generalist predators; *Harmonia axyridis*; invasive herbivore; lady beetles; Michigan, USA; *Orius insidiosus*; top-down vs. bottom-up effects.

INTRODUCTION

Ecologists have long been interested in understanding the relative strength of top-down and bottom-up forces in shaping natural communities (Hairston et al. 1960, Hunter and Price 1992, Power 1992, Walker and Jones 2001). In terrestrial ecosystems both forces are widespread (Gruner 2004), and several factors have been shown to significantly affect the relative strength of their effects, including plant morphology (Kareiva and Sahakian 1990), productivity (Power 1992, Fraser and Grime 1998, 1999, Dyer and Letourneau 1999, Moran and Scheidler 2002), consumer efficiency (Power 1992), temporal vs. spatial variation of herbivore populations (Hunter et al. 1997), herbivore life stages (Walker and Jones 2001), seasonal and year-to-year changes in abiotic and biotic conditions (Walker and Jones 2001, Boyer et al. 2003, Gratton and Denno 2003a, b), differential predation risk among herbivore species (Denno et al. 2003), and herbivore body size (Sinclair et al. 2003). Although not explicitly framed in a bottom-

up vs. top-down context, several studies in agroecosystems have tested the effects of fertility regimes and host plant resistance vs. the effects of natural enemies on pest control (Walker and Jones 2001). Agroecosystems often consist of highly simplified food webs with strong reciprocal influences between adjacent trophic levels (Polis et al. 2000), resulting in ideal systems to manipulate bottom-up vs. top-down forces. Despite this potential, no simultaneous manipulations of both forces have been conducted in agroecosystems (but see Dyer and Stireman 2003). Furthermore, understanding the relative strength of top-down vs. bottom-up forces in agricultural systems has the potential to provide insights into fundamental ecological questions, as well as help guide agroecosystem management.

We tested the relative strength of top-down vs. bottom-up influences on the population growth of soybean aphid, *Aphis glycines* Matsumura (Homoptera: Aphididae). *Aphis glycines* is an important pest of soybean (*Glycine max* L.) in China and Southeast Asia, causing yield losses of up to 70% (Wang et al. 1962, Hirano et al. 1996, Van den Berg et al. 1997, Wu et al. 2004). In the year 2000, *A. glycines* was discovered for the first time in North America and as of 2004 was reported present in 21 states in the United States and

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¹ E-mail: costamag@msu.edu

three provinces of Canada (Hunt et al. 2003, Landis et al. 2003, Venette and Ragsdale 2004). In 2003, $>2.8 \times 10^6$ ha of soybean were sprayed with insecticides against *A. glycines*, which infested $>20 \times 10^6$ ha of soybean in the United States (Landis et al. 2003). Before the arrival of *A. glycines*, soybean in the north central United States had few serious insect pests and was not usually treated with insecticides. Thus, soybean has played an important role as reservoir of natural enemies for other crops (Heimpel and Shelly 2004). Previous studies have detailed significant impacts of natural enemies on *A. glycines* in Asia (Van den Berg et al. 1997, Liu et al. 2004, Wu et al. 2004), suggesting potential for top-down control. Generalist predators currently dominate the assemblage of *A. glycines* natural enemies in the United States, with parasitoids only rarely observed from 2000 to 2002 (Fox 2002, Fox and Landis 2003, Fox et al. 2004, Rutledge et al. 2004).

In the soybean aphid system, we manipulated different agricultural management systems as a potential source of bottom-up forces under realistic agronomic practices. At the same time, we manipulated the existing natural enemy assemblage as a source of top-down control by using exclusion cages. Specifically, we tested the relative strength of bottom-up vs. top-down influences in determining *A. glycines* (1) early season establishment and (2) population increase. In addition, we tested the effects of agricultural management systems on (3) *A. glycines* survival and intrinsic rate of increase and on (4) unmanipulated populations of aphids and their natural enemies during the entire season.

MATERIALS AND METHODS

Study site

Experiments were conducted at the Kellogg Biological Station Long Term Ecological Research in Row Crops Agriculture site (KBS-LTER) in 2003. The site contains seven different cropping systems, representing levels of disturbance from secondary succession to high-input agriculture plots that have been managed under these practices since 1988. These differing production systems are known to significantly affect weed (Menalled et al. 2001) and natural enemy populations, including ground beetles (Clark et al. 1997) and lady beetles (Mareida et al. 1992, Colunga-Garcia and Gage 1998), but their influence on herbivore populations has not previously been studied.

We utilized three of the annual crop treatments that were planted to soybean and represent a broad range of agricultural practices. The high-input treatment utilizes conventional tillage and standard chemical inputs to simulate typical grower inputs in the region (conventional). A second high-input treatment is identical to the first except for the use of a no-tillage regime (no-till). These were contrasted to a conventionally tilled treatment that received no chemical input of any kind (zero-chemical input) but which utilizes a winter leguminous cover crop to help maintain fertility. These treatments

effectively bracket the range of practices used to produce soybean in the region and are likely to affect soybean plant quality to herbivores. Crop yields obtained in this site are representative of yields reported by the U.S. Department of Agriculture for the north central region (Robertson et al. 2000). All treatments were planted between 26 and 29 May 2003, at a rate of 72 845 seeds/ha, using the cultivar NK S20-F8 (NK Brand Syngenta Seeds, Golden Valley, Minnesota, USA). Conventional and no-till treatments were planted on a 38-cm row spacing and were fertilized at a rate of $N = 1.0$ kg/ha, $P = 4.8$ kg/ha, $K = 11.0$ kg/ha on 26 April 2003. No insecticides were applied in any of the treatments during 2003. The zero-chemical-input treatment was planted in 76-cm rows, with no previous fertilization and weed control by cultivation only. Treatments were replicated six times in 1-ha plots arranged in a randomized complete block design. Using these plots we conducted five studies to assess the impact of agricultural management system and predation on *A. glycines*.

Soybean aboveground net primary production and yield

We assessed the effects of our bottom-up manipulations on the soybean plants by comparing aboveground net primary production (ANPP) and yield among the three agricultural management systems. This information is collected systematically as part of the LTER-KBS sampling protocol (detailed procedures as well as raw data are *available online*).² Sampling of ANPP was performed on 2 September 2003, during soybean peak biomass, on five quadrates (1 m²) per plot. On each quadrate soybeans were clipped at ground level and then dried at 60°C for 48 h to obtain dry mass. Yield was determined by harvesting with conventional techniques on 6 October 2003 and standardized to 13% moisture.

Aphid establishment

We first tested the effects of agricultural management system and predation on aphid survival during the establishment phase in the field. On 26 June, we placed *A. glycines* within clip cages in the three agronomic treatments described previously at a rate of five apterous adults per clip cage. Clip cages were cylinders of 1.8 (diameter) \times 1 (length) cm Cresline PVC pipe (Cresline Plastic Pipe, Evansville, Indiana, USA), covered on the top by a fine-mesh brass screen (33 threads/cm, openings of 0.53×0.53 mm) that allow air exchange but prevent aphid movement (Fox et al. 2005). The clip cage was secured to the abaxial surface of a leaflet of the first or second trifoliate by a metallic clip, which allowed cage removal with minimal disturbance of the aphids. Naturally occurring aphids are common on these plant parts at this crop stage (A. C. Costamagna, *personal observation*). After a 3-h acclimatization period, the

² (<http://lter.kbs.msu.edu>)

groups of five aphids were indiscriminately assigned to one of three predator treatments: (1) predator exclusion, in which aphids were protected from predators by clip cages; (2) emigration control, in which aphids were enclosed by clip cages with a 3-mm opening (covered by a cork during the acclimatization period) that allowed aphid emigration but restricted predator access; and (3) open, in which clip cages were removed, allowing both predation and aphid emigration. The 3-mm opening prevents entry by large predators (i.e., Coccinellidae), but small predators such as *Orius insidiosus* (Heteroptera: Anthracoridae) may theoretically enter cages, although this was never observed by us or in previous studies (Fox et al. 2005). Therefore, predation measured as the difference between the open and the emigration control treatments represents a conservative estimation (Fox et al. 2005). After 24 h the numbers of live *A. glycines* adults and nymphs were quantified separately. The experiment was conducted on the six replicates of agricultural treatments, with five clip cages per agricultural and predator treatment combination, for a total of 270 clip cages.

Aphid population increase

In a second experiment, we tested the effects of agricultural management system and predation on the population growth of *A. glycines* enclosed in 1-m² areas during the population increase phase. In each agricultural treatment plot we established 1-m² areas with (1) a field cage that excluded predators, (2) a sham field cage that allowed predator access, and (3) a 1-m² open area as a no-cage control. The predator exclusion field cage consisted of a PVC frame (1 × 1 × 1 m) covered by fine-mesh white no-see-um netting (openings of 0.65 × 0.17 mm; Kaplan Simon, Braintree, Massachusetts, USA) on the upper portion to exclude foliar predators and a basal plastic barrier (10 cm buried in the soil, 20 cm above soil surface), connected to the netting by Velcro, to exclude ground-dwelling predators (after Fox et al. [2004]). The sham treatment consisted of a similar field cage, but open from 0 to 15 cm above the soil and with a second 20 cm wide opening at the canopy level, allowing access to both ground and foliar predators. The open treatment consisted of a 1-m² area delimited by wire flags. In each plot of the three agricultural treatments, three 1-m² areas were arranged as the vertices of a triangle, separated by 3 m, and were randomly assigned using a table of random numbers to a predator manipulation treatment. In each 1-m² area we removed resident predators and aphids and then reinfested at the mean aphid density in the field at large (110 aphids/m²). Aphids were released at a rate of 11 aphids per plant on 10 plants interspersed throughout the 1-m² area. Five blocks were infested using naturally occurring aphids from the same or nearby block, and one block was infested using artificially reared aphids from the USDA Niles Plant Protection and Quarantine laboratory at Niles, Michigan, USA. No subsequent difference in the

performance of natural vs. artificially reared aphids was detected and therefore all blocks were considered for data analysis. The experiment was initiated on 14 July with aphid and natural enemy populations assessed in all cages 6 and 14 d after infestation. Natural enemy sampling consisted of 3-min nonintrusive visual counting of larger predators (Fox et al. 2004), followed by a more-detailed search on 6–10 plants within the cage (reducing sampling effort with aphid density increase over time) to detect small or cryptic natural enemies (i.e., predaceous fly larvae, syrphid larvae, lacewing larvae, *O. insidiosus*, and first- and second-instar coccinellid larvae; see *Results*). Sample plants were selected without bias as to size, presence of natural enemies and aphids, or previous sampling history. The numbers of small-size predators and parasitoid mummies per plant were adjusted for the total number of plants per cage to compare with the number of large-size predators. Aphid sampling consisted of total counts of aphids on the same 6–10 plants.

Aphid intrinsic rate of increase

A third experiment was conducted to assess the effect of differing agricultural practices on survival, longevity, fecundity, and intrinsic rate of increase (*r*) of *A. glycines*. We followed *A. glycines* cohorts using clip cages in the three agricultural treatments utilized in the previous studies during the same time period as the large cage study (16 July to 21 August). Clip cages were the same as previously described (see *Aphid establishment*) but ventilated with the addition of a 3-mm cylindrical opening covered with the same fine-mesh screen as above to reduce potential heat stress. Three to five apterous adult *A. glycines* were enclosed in a clip cage to produce offspring. After 24 h all but three nymphs were removed. These nymphs were followed until we observed the first adults (indicated by the presence of newborn nymphs). At this point we removed all but one adult aphid in order to obtain estimates of per capita fecundity (van den Berg et al. 1997). From the survivorship, longevity, and fecundity data we estimated the intrinsic rate of increase (*r*) for each block using the method developed for aphids by Wyatt and White (1977). The experiment was replicated in the six blocks, with 10 clip cages per agricultural treatment plot.

Natural population sampling

We further assessed the effect of agronomic management system on *A. glycines* and natural enemy populations by conducting weekly sampling of unmanipulated populations in the six plots of each agricultural treatment from 24 June to 18 August 2003. There were other herbivores present, mostly thrips (Insecta: Thysanoptera) and leafhoppers (Homoptera: Cicadellidae), but due to their low abundance, no attempt was made to quantify them. Sampling consisted of three samples of one linear meter of soybean plants within a row (14.6 ± 2.7 plants/linear m; mean ± SD) in each plot. New

sampling points were interspersed in each field plot, for each sampling date. In each sample, foliar natural enemies were sampled by 3-min nonintrusive visual counts, followed by a more detailed inspection of plant foliage (as described in *Aphid population increase* above). Whole-plant counts of 4–10 plants were used to assess *A. glycines* populations (reducing sampling effort as aphid density increased over time).

Statistical analysis

Soybean ANPP and yield were analyzed using ANCOVA on a completely randomized block design with number of plants per square meter and number of plants per hectare as covariates, respectively. The number of surviving aphids in the aphid establishment experiment was analyzed using a split-plot design with agricultural treatment as the whole-plot factor and predator manipulation as the subplot factor. Numbers of adults and nymphs were analyzed independently to separate adult mortality/emigration from reproduction. Number of aphids, predators, and parasitoid mummies in the aphid population increase experiment were analyzed using a split-split-plot design, with agricultural treatment as whole-plot factor and predator manipulation and time as subplot factors. A Poisson regression using the GLIMMIX Macro link of SAS in PROC MIXED (SAS Institute 2001) was used to analyze these data due to the absence of a suitable transformation to normalize them, except in the aphid counts within large cages, which were $\ln(x + 1)$ -transformed and analyzed by ANOVA. The effect of agricultural treatments on *A. glycines* longevity, fecundity, and r was assessed by one-way ANOVA. The effect of agricultural treatments on unmanipulated populations was assessed by one-way ANOVA (aphids) and MANOVA (natural enemies) utilizing sampling date as a repeated-measures factor. Due to the large number of samples with zeros, natural enemy data were condensed in three ways: (1) subsamples within each sample were combined (addition of all individuals per group), (2) the first two sampling dates were excluded from the analysis, and (3) groups representing <5% of the natural enemies collected were not used in the analysis. We used standardized canonical coefficients to interpret the discriminant function of the MANOVA (Scheiner 2001).

Significant interactions in the ANOVA models were further explored via slicing by main effects (Quinn and Keough 2002), and means were separated using least squares means difference (LSMD, SAS Institute 2001). A significant agricultural treatment \times date interaction obtained in the MANOVA was explored using preplanned contrasts among agricultural practice treatments within each sampling date. When necessary to meet the assumptions of the ANOVA and MANOVA, variables were $\ln(x + 1)$ -transformed before analysis. Blocks and the interaction terms involving them were modeled as random effects in all models. ANOVAs were

performed using PROC MIXED, and MANOVA was performed using PROC GLM (SAS Institute 2001).

RESULTS

Soybean aboveground net primary production and yield

Agricultural management systems significantly affected soybean ANPP and yield. Aboveground net primary production was significantly lower in the zero-chemical-input treatment ($322.2 \pm 22.3 \text{ g/m}^2$) than in the conventional treatment ($515.9 \pm 9.5 \text{ g/m}^2$), with an intermediate response in the no-till treatment ($462.3 \pm 14.1 \text{ g/m}^2$; $F_{2,9} = 5.10$, $P = 0.0331$; LSMD test, $P < 0.02$). The number of plants per square meter was not a significant covariate ($F_{1,9} = 0.00$, $P = 0.9971$), and blocking did not affect the results ($F_{5,9} = 1.07$, $P = 0.4374$). Yield also differed among treatments ($F_{2,9} = 5.54$, $P = 0.0271$), with significantly higher levels in the no-till ($1854.7 \pm 35.7 \text{ kg/ha}$) and in the conventional treatments ($1620.8 \pm 78.5 \text{ kg/ha}$) than in the zero-chemical-input treatment ($1009.5 \pm 78.7 \text{ kg/ha}$; LSMD tests, $P < 0.04$). The number of plants per hectare and block effects were not significant ($F_{1,9} = 0.04$, $P = 0.8406$ and $F_{5,9} = 1.39$, $P = 0.3139$, respectively).

Aphid establishment

We observed significant effects of predator manipulation on adult survivorship ($F_{2,30} = 8.77$, $P = 0.0010$) and nymph production ($F_{2,30} = 4.41$, $P = 0.0210$) after 24 h of establishment (Fig. 1, Appendix A). Exposure to predation significantly reduced adults and nymphs ($\sim 32\%$) in the open vs. the emigration control treatment (Fig. 1). Adults and nymphs were 12% and 6% less abundant in the emigration control vs. the predator exclusion treatment; however, these differences were not significant (Fig. 1). There was no significant effect of agricultural management system on either adults ($F_{2,10} = 0.48$, $P = 0.6314$) or nymphs ($F_{2,10} = 0.35$, $P = 0.7103$) or the agricultural management system \times predator manipulation interaction (adults, $F_{4,30} = 0.39$, $P = 0.8156$; nymphs, $F_{4,30} = 1.02$, $P = 0.4125$), indicating an absence of bottom-up effects in this test.

Aphid population increase

Top-down control significantly reduced aphid numbers in the large field cages during the two weeks of the experiment (predator manipulation effect, $F_{2,27} = 94.63$, $P < 0.0001$; Fig. 2, Appendix B). Aphids increased significantly from the first to the second week ($F_{1,42} = 644.46$, $P < 0.0001$), but differences among predator treatments ranging from four- to seven-fold more aphids in the exclusion cages were persistent between weeks (Fig. 2). The significant impact of predation on aphid population growth was consistent despite a marginally significant interaction between agricultural management system and predator manipulation ($F_{4,27} = 2.50$, $P = 0.0661$), with higher numbers of aphids in predator exclusion cages under all agricultural management systems (all slicing tests with $P < 0.001$, Appendix B).

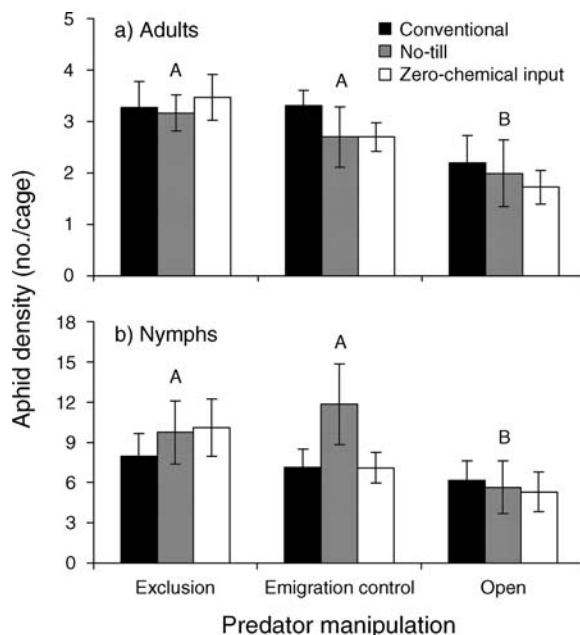


FIG. 1. Effect of natural enemies and agricultural management system on the number of *Aphis glycines* (mean \pm SE) alive after 24 h at the Kellogg Biological Station Long Term Ecological Research site, Michigan, USA, during 2003 (see *Materials and Methods: Aphid establishment*). Different letters above bars indicate significant differences among predator manipulation treatments ($P < 0.05$, least squares means difference, SAS Institute 2001).

Agricultural treatments did not affect significantly the number of aphids in exclusion ($F_{2,27} = 1.43$, $P = 0.2572$) and open ($F_{2,27} = 2.03$, $P = 0.1508$; Fig. 2) treatments, but significantly higher aphid suppression in sham cages in the no-till treatment in comparison with conventional and zero-chemical-input treatments ($F_{2,27} = 8.28$, $P = 0.0016$) was observed. Sham and open treatments differed in the no-till treatment (LSMD, $P = 0.0144$), suggesting a cage effect rather than an effect of the different agricultural management systems. No cage effects were observed in conventional or zero-chemical-input treatments. Therefore, we obtained evidence of strong top-down control on *A. glycines* population growth, but no evidence of bottom-up effects due to differing crop management systems.

The natural enemy assemblage of *A. glycines* was dominated by generalist predators and a generalist parasitoid species. Large-size predators sampled within the field cages consisted of the lady beetles (Coleoptera: Coccinellidae) *Coccinella septempunctata* ($9.4\% \pm 4.4\%$ of total predators sampled) and *Harmonia axyridis* ($5.5\% \pm 2.8\%$), whereas small-size predators consisted of *O. insidiosus* ($23.3\% \pm 6.3\%$), first- and second-instar coccinellid larvae not identified to species ($18.4\% \pm 4.9\%$), syrphid larvae (Diptera: Syrphidae) ($20.5\% \pm 6.1\%$), and predaceous fly larvae (Diptera: Cecidomyiidae and Chamaemyiidae) ($7.9\% \pm 3.7\%$) (Appendix C). Mummies of the native parasitoid *Lysiphlebus testa-*

ceipes (Hymenoptera: Braconidae) were also detected at low levels (Appendix C). Exclusion cages significantly reduced the abundance of large-size predators ($F_{2,27} = 4.81$, $P = 0.0163$), but they had no significant effect on small-size predators ($F_{2,27} = 1.39$, $P = 0.2662$; Appendix C). By contrast, parasitoid mummies showed the opposite trend, with significantly more mummies found in exclusion than in open cages ($F_{2,27} = 3.29$, $P = 0.0525$; Appendix C), suggesting that exclusion cages may have protected parasitoids from intraguild predation. Although parasitoids were not able to enter the mesh of the exclusion cages, some parasitism may have occurred within exclusion cages if field-collected aphids used to initially infest the cages had already been parasitized. Agricultural treatments significantly affected the abundance of small-size predators ($F_{2,10} = 6.21$, $P = 0.0177$), with a higher number of predators in the conventional treatment (Appendix C), but did not affect the abundance of large-size predators ($F_{2,10} = 0.62$, $P = 0.5569$) or parasitoids ($F_{2,10} = 0.61$, $P = 0.5649$; Appendix C). These results suggest that the significant increase in aphid density obtained in predator exclusion cages was associated with reduction in the action of large-size predators (mainly Coccinellidae) rather than small-size predators and mummies.

Aphid intrinsic rate of increase

Rearing aphid cohorts with clip cages confirmed the absence of effects of agricultural management system on

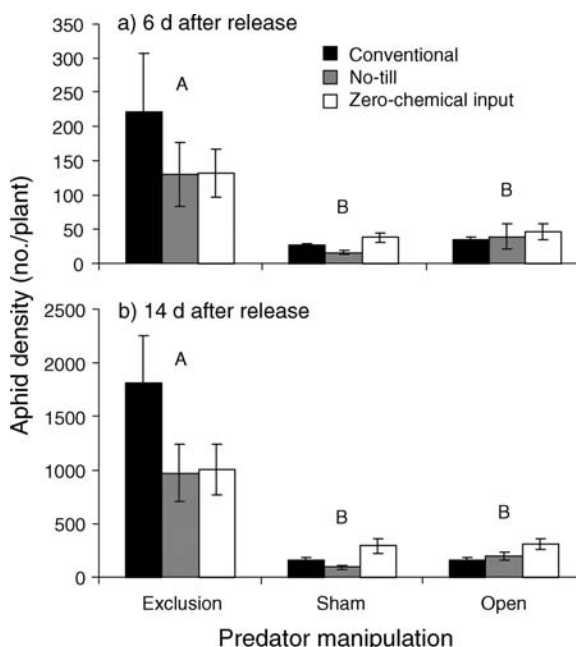


FIG. 2. Effect of natural enemies and agricultural management systems on the number of *Aphis glycines* (mean \pm SE) after (a) 6 d and (b) 14 d of manipulation using large field cages in 2003. Different letters above bars indicate significant differences among predator manipulation treatments ($P < 0.0001$, least squares means difference, SAS Institute 2001).

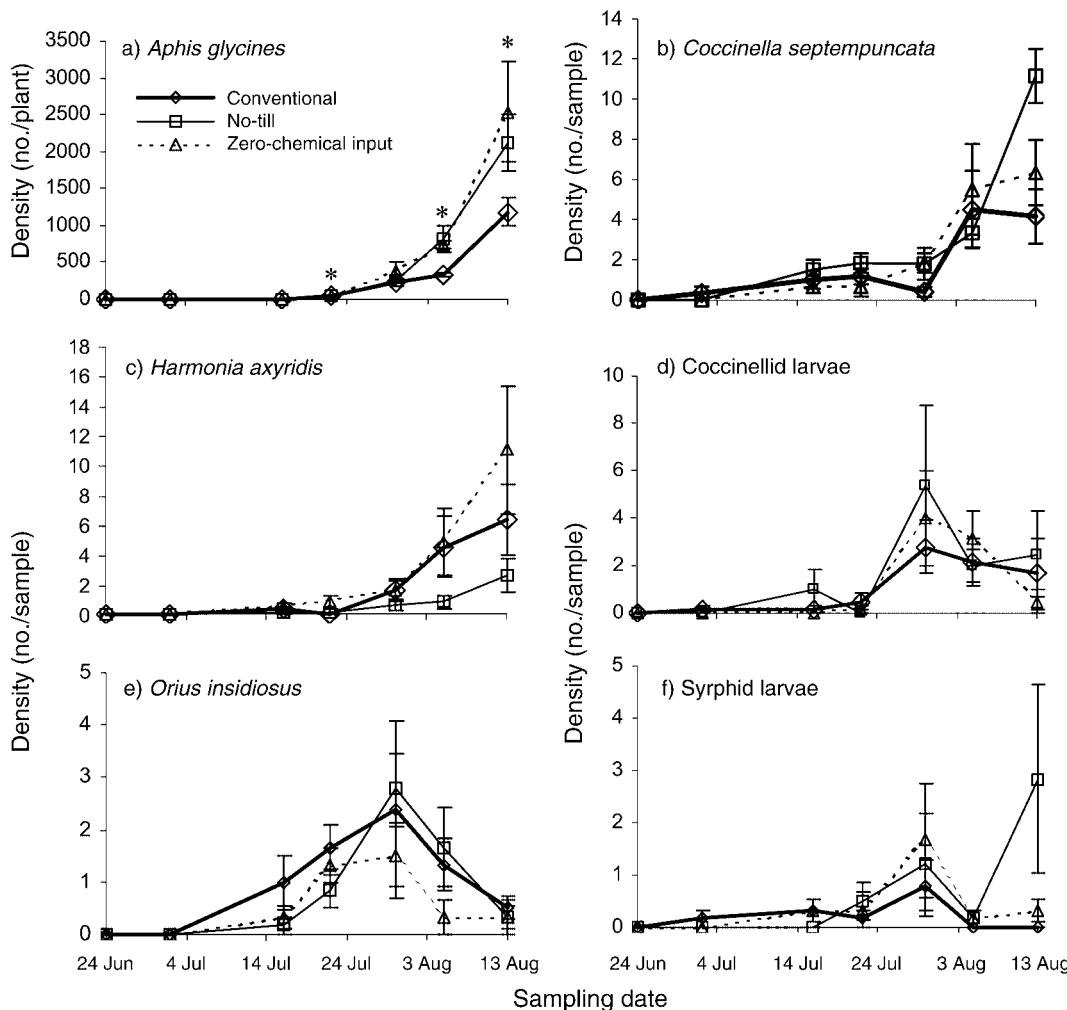


FIG. 3. Unmanipulated density (mean \pm SE) of (a) *Aphis glycines* and (b–f) natural enemy populations in soybeans under

A. glycines life history parameters. Agricultural management systems did not affect significantly *A. glycines* longevity (18.4 ± 0.6 d, $n = 179$; $F_{2,10} = 1.93$, $P = 0.1954$), fecundity (28.9 ± 1.6 females/female, $n = 174$; $F_{2,10} = 0.68$, $P = 0.5287$), or intrinsic rate of increase (0.32 ± 0.01 females-female $^{-1}$ ·d $^{-1}$, $n = 18$; $F_{2,10} = 2.38$, $P = 0.1423$; Appendix D). Our estimates ($r = 0.30$ – 0.33) are consistent with other field estimates of $r = 0.310$ reported by van den Berg et al. (1997).

Natural population sampling

Unmanipulated field populations of *A. glycines* differed among agricultural management systems on three of the seven dates of sampling (agricultural management system \times date interaction: $F_{12,88} = 2.21$, $P = 0.0175$), but there was no main effect of agricultural treatment ($F_{2,10} = 2.36$, $P = 0.1446$). Aphids increased exponentially from the end of July to mid-August (sampling date, $F_{6,88} = 638.95$, $P < 0.0001$), and slicing

by the interaction between agricultural management system and date revealed significantly fewer aphids in the no-till treatment on 16 July ($F_{2,88} = 4.29$, $P = 0.0167$). This trend later reversed, with significantly fewer aphids in the conventional treatment on 5 August ($F_{2,88} = 6.85$, $P = 0.0017$) and 13 August ($F_{2,88} = 3.87$, $P = 0.0246$; Fig. 3a).

Five groups of natural enemies were included in the analysis: *C. septempunctata* (29.4%), *H. axyridis* (23.1%), coccinellid larvae (16.0%), *O. insidiosus* (10.1%), and syrphid larvae (Diptera: Syrphidae; 5.5%), accounting for 84.1% of the total foliar natural enemies observed during the five sampling dates included in the analysis (Fig. 3b–f). The rest of the natural enemies included *L. testaceipes* (3.2%), predaceous fly larvae (3.2%), nabids (Heteroptera: Nabidae; 2.8%), other coccinellid species (2.6%), spiders (Arachnida: Araneae; 1.7%), lacewing larvae (Neuroptera: Chrysopidae; 1.1%), opilionids (Arachnida: Opiliones;

0.9%), and carabids (Coleoptera: Carabidae; 0.3%). The results for the MANOVA showed significant agricultural management system ($F_{10, 148} = 2.25$, $P = 0.0176$), date ($F_{4, 75} = 20.73$, $P < 0.0001$), and management system \times date interaction ($F_{8, 152} = 2.84$, $P = 0.0057$) effects on the assemblage of *A. glycines* natural enemies (Fig. 3b–f, Appendix E). Preplanned contrasts showed that natural enemies assemblages in the no-till treatment differed significantly from the zero-chemical-input treatment (22 July and 30 July, $P = 0.05$) and from the conventional treatment (13 August, $P = 0.01$). The standardized canonical coefficients (SCC) of the first canonical variate showed that *C. septempunctata* (SCC = 0.5110) and syrphid larvae (SCC = 0.4004), which were more abundant in the no-till treatment, explained most of the variability and were negatively correlated with *H. axyridis* (SCC = -0.4876), which was less abundant in the no-till plots. There was an increase of all the abundant foliar predators late in the season, following the increase in aphid populations, with the exception of *O. insidiosus*, which declined in the last two samples (Fig. 3e).

DISCUSSION

Our results provide strong evidence of top-down regulation of *A. glycines* due to predator assemblages, but only weak evidence of bottom-up effects under the range of conditions tested. Generalist predators dominated the natural enemy assemblages, with parasitoids only accounting for <4% of the natural enemies sampled in the unmanipulated study. However, parasitoids showed increased numbers within exclusion cages (46% of total natural enemies in the big cages study), suggesting that cages may have reduced intraguild predation (Colfer and Rosenheim 2001). Ground predators (i.e., spiders and carabids) were probably underestimated by our sampling methods; however, the absence of dropping behavior in *A. glycines* (A. C. Costamagna and D. A. Landis, *personal observations*) suggests a prevalent role of foliar predators in this system. The assemblage of generalist predators was dominated by the coccinellids *C. septempunctata* and *H. axyridis*, which were the dominant species previously reported attacking *A. glycines* in North America (Fox et al. 2004, Rutledge et al. 2004). Both species responded numerically to the increase in *A. glycines* natural populations later in the season; however, *C. septempunctata* was more abundant in the no-till system, whereas *H. axyridis* predominated in the conventional and zero-chemical-input systems (Fig. 3b, c). *Harmonia axyridis* has been shown to be a strong intraguild predator of other coccinellids and in particular of *C. septempunctata* larvae (Yasuda et al. 2001). Thus, the different agricultural-system preferences found for these coccinellids may result in an attenuation of negative interactions between them.

Despite the significant differences in the assemblages of natural enemies in different agricultural production

systems, overall suppression of *A. glycines* did not differ, suggesting a complementary role of the different predator species. Suppression of *A. glycines* occurred both during aphid establishment early in the season and during aphid population increase at mid-season. In the aphid establishment experiment, only a third of the aphids survived when there was no protection against predation. The large impact on aphid survivorship obtained in the relatively short time frame of this experiment (24 h) suggests that this is a conservative measure of predation on aphid establishment. Our results are in agreement with other studies that showed significant effects of predation on establishing pest populations. Using a simple theoretical model, Chang and Kareiva (1999) demonstrated that early predation by generalist predators has a similar effect as later immigration of more specialized natural enemies. Landis and Van der Werf (1997) showed that the assemblage of generalist predators present in sugar beet fields early in the season significantly diminished the population of aphids and the impact of viruses transmitted by the aphids. In *A. glycines*, Fox et al. (2005) also found a significant reduction of aphid establishment due to generalist predators, independent of the presence of predator refuge strips within the field. Östman et al. (2001) found significant impacts of farming practices on bird cherry oat aphid (*Rhopalosiphum padi* [L.]) (Homoptera: Aphididae) establishment on barley, but there was no subsequent difference in aphid population growth between farming practices mediated by natural enemies.

Top-down control by generalist predators significantly reduced *A. glycines* population increase (four- to seven-fold) across all agricultural production systems. Top-down control of herbivores has been shown to be important in several terrestrial systems, leading to trophic cascades that release plants from herbivory pressure (Spiller and Schoener 1990, Carter and Rypstra 1995, Moran and Hurd 1998, Schmitz et al. 2000, Halaj and Wise 2001, Snyder and Wise 2001). In agroecosystems, both parasitoids and predators have been shown to be effective in suppressing several aphid species (Hopper et al. 1995, Obrycki and Kring 1998, Colfer and Rosenheim 2001, Symondson et al. 2002, Cardinale et al. 2003, Lang 2003, Schmidt et al. 2003, 2004). Natural enemies suppress *A. glycines* in its original area of distribution (Van den Berg et al. 1997, Liu et al. 2004, Wu et al. 2004) and in its invaded range in North America (Fox et al. 2004). Our results expand these findings by showing that generalist predators suppressed *A. glycines* establishment and growth across a wide gradient of agricultural production systems.

Several factors have been shown to independently lead to bottom-up effects on aphid population growth in agroecosystems. Among them are significant impacts of fertilization (Cisneros and Godfrey 2001, Morales et al. 2001, Nevo and Coll 2001), tillage (Andersen 2003, Hesler and Berg 2003, Gencsoylu and Yalcin 2004), and

cover crops (Tillman et al. 2004). On *A. glycines*, Van den Berg et al. (1997) observed a negative impact of plant age on population increase, whereas Myers et al. (2005) found positive effects of soil potassium deficiency. In our study, differing input regimes (treatments) resulted in significant differences in ANPP and soybean yield, confirming successful manipulation of bottom-up resources; however, aphid population increase was not significantly affected. This suggests that manipulation of chemical inputs and tillage under realistic agricultural production systems does not change the quality of the soybean plant sufficiently to cause significant bottom-up effects on *A. glycines* establishment or population growth, even in the absence of top-down controls. Although other studies have shown significant bottom-up effects on aphid population growth within shorter time frames than our experiments (Van den Berg et al. 1997, Nevo and Coll 2001, Myers et al. 2005), we cannot rule out that bottom-up effects may become more evident over longer periods of time.

In our study, field populations of *A. glycines* eventually exceeded the economic threshold (250 aphids/plant; University of Wisconsin Soybean Plant Health, *available online*).³ However, our experiment demonstrates that if predators were not continually suppressing aphids, damaging aphid populations would have occurred much earlier in the season (Fig. 2). In other studies we have documented that season-long predator suppression of *A. glycines* can occur as well (Fox et al. 2004). Understanding the mechanism of aphid escape in some but not all years is the focus of ongoing studies.

Our results showed that top-down controls dominated the dynamics of the invasive *A. glycines* populations during the period of this study. Our findings differ from results obtained in natural systems in which bottom-up forces have been shown to exert the primary control on herbivore populations (Stiling and Rossi 1997, Denno et al. 2002), but supports the prevalence of top-down control in determining herbivore populations found in other studies (Dyer and Letourneau 1999, Walker and Jones 2001). The two high-input production systems utilized in our study represent the most common strategies to grow soybean in North America while the zero-chemical-input system represents an extreme of low inputs. Given this wide range, our results suggest that there is little scope to manage *A. glycines* impacts via such bottom-up influences. However, other sources of bottom-up control on *A. glycines*, such as manipulation of plant phenology (Van den Berg et al. 1997) and plant resistance (Hill et al. 2004a, b, Li et al. 2004), should be investigated.

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³ (<http://www.plantpath.wisc.edu/soyhealth/aglycine.htm>)

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APPENDIX A

Tables showing Poisson regression results of the effect of agricultural management system and predator manipulation treatments on the establishment of *Aphis glycines* at the Kellogg Biological Station Long Term Ecological Research site, Michigan, USA, during 2003 (*Ecological Archives* A016-055-A1).

APPENDIX B

A table showing ANOVA results for fixed and random effects and slicing tests results of the effect of agricultural management system and predator manipulation treatments on *Aphis glycines* within large field cages at the Kellogg Biological Station Long Term Ecological Research site, Michigan, USA, during 2003 (*Ecological Archives* A016-055-A2).

APPENDIX C

A table showing large- and small-size predators and parasitoids for different combinations of agricultural management system and predator manipulation treatments within the large field cages in the aphid population increase experiment at the Kellogg Biological Station Long Term Ecological Research site, Michigan, USA, during 2003 (*Ecological Archives* A016-055-A3).

APPENDIX D

A table showing longevity, fecundity, and intrinsic rate of increase of *Aphis glycines* reared on soybean produced under three different agricultural management systems in the Kellogg Biological Station Long Term Ecological Research site, Michigan, USA, during 2003 (*Ecological Archives* A016-055-A4).

APPENDIX E

A table showing MANOVA results for the effect of agricultural practices on the five more-abundant *Aphis glycines* foliar predators at the Kellogg Biological Station Long Term Ecological Research site, Michigan, USA, during 2003 (*Ecological Archives* A016-055-A5).