

SUPPRESSION OF SOYBEAN APHID BY GENERALIST PREDATORS RESULTS IN A TROPHIC CASCADE IN SOYBEANS

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Abstract. Top-down regulation of herbivores in terrestrial ecosystems is pervasive and can lead to trophic cascades that release plants from herbivory. Due to their relatively simplified food webs, agroecosystems may be particularly prone to trophic cascades, a rationale that underlies biological control. However, theoretical and empirical studies show that, within multiple enemy assemblages, intraguild predation (IGP) may lead to a disruption of top-down control by predators. We conducted a factorial field study to test the separate and combined effects of predators and parasitoids in a system with asymmetric IGP. Specifically we combined ambient levels of generalist predators (mainly Coccinellidae) of the soybean aphid, *Aphis glycines* Matsumura, with controlled releases of the native parasitoid *Lysiphlebus testaceipes* (Cresson) and measured their impact on aphid population growth and soybean biomass and yield. We found that generalist predators provided strong, season-long aphid suppression, which resulted in a trophic cascade that doubled soybean biomass and yield. However, contrary to our expectations, *L. testaceipes* provided minor aphid suppression and only when predators were excluded, which resulted in nonadditive effects when both groups were combined. We found direct and indirect evidence of IGP, but because percentage parasitism did not differ between predator exclusion and ambient predator treatments, we concluded that IGP did not disrupt parasitism during this study. Our results support theoretical predictions that intraguild predators which also provide strong herbivore suppression do not disrupt top-down control of herbivores.

Key words: agroecosystems; *Aphis glycines*; biological control; *Coccinella septempunctata*; *Harmonia axyridis*; intraguild predation; invasive herbivore; multiple enemy assemblage; *Orius insidiosus*; parasitism; top-down control; trophic interactions.

INTRODUCTION

Top-down regulation of herbivores has been strongly debated since it was postulated as a major force organizing terrestrial ecosystems by Hairston et al. (1960). This view of three defined trophic levels that interact directly and indirectly with lower trophic levels has led to the concept of trophic cascades, in which organisms in higher-order trophic levels affect the abundance, biomass, or productivity of other species across more than one link in a food web (Pace et al. 1999). Empirical evidence shows that trophic cascades frequently occur in simple systems (i.e., less reticulated food webs) with many cases having been documented in aquatic environments (Strong 1992, Pace et al. 1999). However, other studies have demonstrated trophic cascades in terrestrial ecosystems (Schmitz et al. 2000, Halaj and Wise 2001), and particularly in agroecosystems (Carter and Rypstra 1995, Snyder and Wise 1999, Colfer and Rosenheim 2001, Snyder and Wise 2001, Cardinale et al. 2003, Lang 2003, Matsumoto et al. 2003,

Rypstra and Marshall 2005). Several characteristics of agroecosystems contribute to the development of trophic cascades, including homogeneous habitat, faster prey than predator turnover, uniformly edible prey, and simple trophic stratification of the system (Polis et al. 2000, Müller and Brodeur 2002). Moreover, trophic cascades in agroecosystems form the theoretical foundation of biological control, i.e., a reduction of plant damage (with expected increased in crop yield) through deleterious effects of natural enemies (native or imported) on herbivore pests (Polis et al. 2000, Rosenheim et al. 2004a).

However, despite the relative trophic simplicity suggested for agroecosystems, the consumer assemblages present in them typically have multiple natural enemies, and thus interactions such as predator interference, cannibalism, predator avoidance behavior, and intraguild predation may modify the strength of top-down control of herbivores (Sih et al. 1998, Snyder and Wise 1999, Halaj and Wise 2001, Symondson et al. 2002, Rosenheim and Corbett 2003, Rosenheim et al. 2004a). Multiple consumers within an assemblage may interact with synergistic, additive, or nonadditive effects on herbivore populations (Polis et al. 1989, Sih et al. 1998, Dixon 2000). Intraguild predation (IGP hereafter), i.e., trophic interactions among members of the same guild within multiple natural enemy assemblages, may be

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particularly important in determining the overall impact of predators on herbivores (Polis et al. 1989). Within agroecosystems, empirical studies show that the presence of multiple natural enemies that engage in IGP can enhance (Cardinale et al. 2003), have no effect on (Colfer and Rosenheim 2001, Lang 2003, Snyder and Ives 2003, Rosenheim et al. 2004b), or disrupt (Rosenheim et al. 1993, Snyder and Ives 2001, Snyder and Wise 2001, Yasuda and Kimura 2001, Persad and Hoy 2004, Philpott et al. 2004, Rosenheim et al. 2004a) biological control. Disruptions are caused by negative nonadditive interactions that cascade down, producing an increase in the population of the herbivore (Rosenheim et al. 1995). In this case, the IG predator exerts stronger pressure on an IG prey that in turn is effectively suppressing an herbivore, releasing the herbivore from control, thus acting functionally as a fourth trophic level (Polis and Holt 1992, Rosenheim and Corbett 2003).

In natural ecosystems top-down control is commonly exerted by predators, whereas parasitoids are postulated as more important control agents in agroecosystems (Hawkins et al. 1999). Interactions between parasitoids and predators often result in asymmetric IGP, with all the stages of the parasitoid vulnerable to the predator, but with no attack of the predator by the parasitoid (Brodeur and Rosenheim 2000). As a result, IGP has been suggested as a possible mechanism to explain the failure of aphid parasitoids to regulate their hosts (Ferguson and Stiling 1996, Rosenheim 1998, Brodeur and Rosenheim 2000, Colfer and Rosenheim 2001). Although IGP is likely to occur within most of the natural enemy communities present in agroecosystems, relatively few studies have been conducted to quantify IGP's impact on herbivore regulation (Rosenheim et al. 1995). Colfer and Rosenheim (2001) and Snyder and Ives (2003) found no impact of IGP on herbivore suppression, while Snyder and Ives (2001) documented a disruptive effect on biological control.

Even in relatively simplified agroecosystems many factors may influence the extent of herbivore suppression by multiple natural enemies. However, there is a lack of studies manipulating natural enemies in experiments that allow distinction among their separate and combined direct effect on herbivores and indirect effect on plants (Lang 2003). A notable exception is the study performed by Cardinale et al. (2003), that showed synergistic interactions between predators and parasitoids, resulting in a reduction of herbivore abundance and an increase of plant biomass, although they did not directly test for IGP interactions. The recent invasion in North America by the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae) provides an ideal system to test the impact of assemblages of multiple natural enemies. Several studies demonstrate that assemblages of naturally occurring generalist predators can provide effective top-down control of *A. glycines* in North America (Fox et al. 2004, 2005, Costamagna and Landis 2006). Parasitoids were observed at very low

levels in these studies, and the most common species collected was *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae; Brewer and Noma 2004, Costamagna and Landis 2006). *L. testaceipes* is a generalist parasitoid that has been shown to be the target of intense IGP by coccinellids in cotton agroecosystems, although it remains as an important biocontrol agent of the cotton aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae; Colfer and Rosenheim 2001). Moreover, in a previous study we found significantly greater numbers of *L. testaceipes* mummies in cages that excluded *A. glycines* predators than in sham cages and open treatments. We hypothesized that exclusion cages provided refuge from IGP (Costamagna and Landis 2006). These results suggest that in the *A. glycines* system, IGP may be limiting the impact of parasitoids, and may impair future attempts to establish additional parasitoid species by importation biological control.

We conducted a field study to test the impact of ambient levels of generalist predators and controlled releases of the native parasitoid *L. testaceipes* on *A. glycines* suppression and soybean biomass and yield. Using exclusion cages we separated the effects of large predators vs. *L. testaceipes*, and tested whether their combined effect resulted in additive control. In addition, we directly measured intraguild predation on parasitoid mummies to assess to what extent IGP disrupts biological control by *L. testaceipes*. Specifically, we asked (1) can ambient levels of generalist predators provide season-long suppression of *A. glycines*, (2) can parasitoids alone suppress *A. glycines*, (3) does the combined impact of predators and parasitoids result in synergistic, additive or nonadditive control of *A. glycines*, (4) does IGP disrupt biological control by parasitoids, and finally, (5) do predators, parasitoids or their combined impacts on *A. glycines* populations indirectly increase soybean biomass and yield?

MATERIALS AND METHODS

The experiment was conducted in a 99 × 94 m soybean field at the Michigan State University Entomological Research Farm, Ingham County, Michigan, USA. Soybean (Pioneer 92B13) was planted on 7 May 2004, using a Great Plains Seed Drill planter (Great Plains Manufacturing, Salina, Kansas, USA) on 38 cm wide rows, at a population of 494 209 seeds/ha, and weeds were controlled using Roundup WeatherMax (Monsanto St. Louis, Missouri, USA) tank-mixed with ammonium sulfate at standard rates. The experiment was designed as a 2 × 2 factorial in six completely randomized blocks, with predator and parasitoid manipulations as main factors. The four treatments were: (1) aphid control, with added aphids only; (2) parasitoid, in which parasitoids were released and large predators were excluded; (3) predator, in which ambient levels of predators were allowed access to the aphids; and (4) predator + parasitoid, similar to the predator, but with parasitoids released as in the parasitoid

treatment. The rationale for this approach was that parasitoid immigration into the aphid and predator treatments would be minimal due to the very low background levels of field parasitism found in the study area (Costamagna 2006). To further ensure low levels of parasitism in the aphid and predator treatments, we recorded and then removed any mummies observed during the weekly samplings. Thus, our treatments contrasted ambient levels of generalist predators vs. increased levels of parasitoids.

The predator exclusion cage consisted of a PVC frame ($1 \times 1 \times 1$ m) covered by fine-mesh white no-see-um netting (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 (Fig. 1a; after Fox et al. 2004, Costamagna and Landis 2006). To allow alate aphid and parasitoid emigration from cages, the upper 10 cm of the lateral walls consisted of a band of mesh with coarse openings (2 mm). A second band of the same coarse mesh (30 cm height) was placed at the canopy level after the third sampling to mimic the openings on the sham cages (see below). This design prevented large predators from entering cages and was used for the aphid and parasitoid treatments. We utilized sham cages to allow access of predators in the predator and predator + parasitoid treatments. The sham cage had the same design as the exclusion cage, but with the upper and canopy level windows completely uncovered (Fig. 1b). To ensure parasitoid establishment, all cage windows were covered during the five initial days of the experiment by an external band of the fine mesh secured by Velcro, and this was performed to all treatments to avoid bias.

To this design we added three control treatments. First, one open reference area of 1 m^2 (open treatment) was flagged in each block as a control for potential cage effects. Second, to estimate effects on plant biomass and yield we included an exclusion cage treatment completely closed (i.e., without lateral bands of coarse mesh) that was maintained free of aphids by weekly inspections and removal of any aphids present (no-aphid treatment). The four treatments and the two controls were located in blocks separated by at least 10 m. Within blocks, all treatments were separated by at least 3 m from each other. In all treatments we included Raid Ant Baits II (S. C. Johnson and Son, Racine, Wisconsin, USA) to prevent ants from establishing and tending aphids. Finally, we established a third control consisting of totally unmanipulated 1-m^2 areas located 30 m distant from the main experiment to avoid contamination by our insect manipulations (field reference).

In all but the field reference, we initially removed by hand all resident predators and aphids and then reinfested with aphids at similar densities to those found at the beginning of the season during outbreak years (100 aphids/m^2 , Fox et al. 2004, Costamagna and

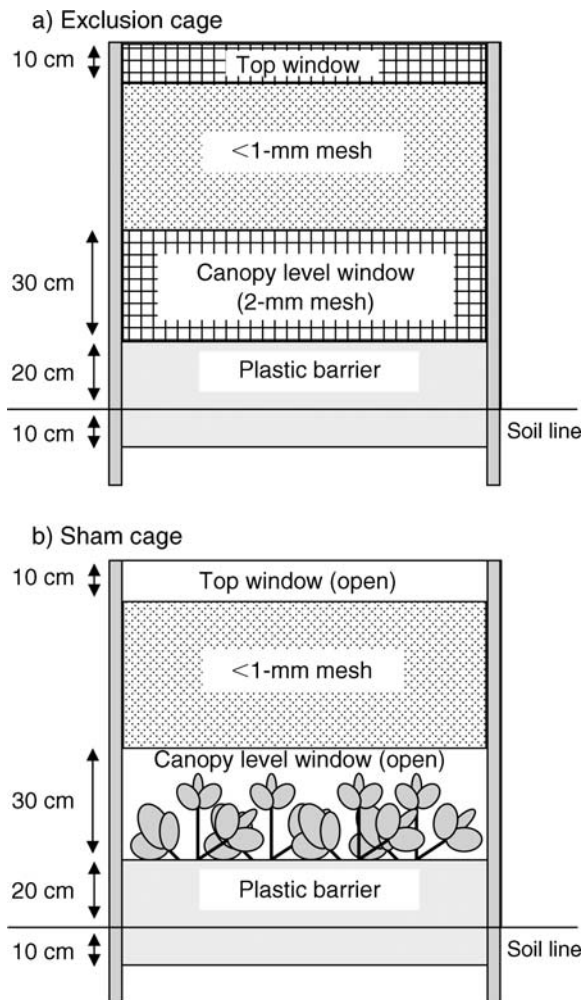


FIG. 1. Design of (a) predator exclusion cages used in aphid and parasitoid treatments, and (b) sham cages used in predator and predator + parasitoid treatments. The fine mesh (<1 mm) prevents aphid, parasitoid, and predator movement, whereas the coarse mesh (2-mm openings) prevents only large predator access (i.e., mainly Coccinellidae). All cages were covered on top by fine mesh. Ground-dwelling predator movement was reduced by means of a transparent plastic barrier buried in the soil (see details in the *Materials and Methods*).

Landis 2006). In the no-aphid treatment the same manipulation was performed, but no aphids were added. Aphids reared on soybeans in the laboratory were released on 16 June 2004, at a rate of 10 aphids per plant on 10 random plants per cage. The soybean plants were at the V3 stage and cages enclosed 29.1 ± 2.0 plants/ m^2 (mean \pm SD). Parasitoids were established in the parasitoid and predator + parasitoid treatments using mummies obtained from a colony of *L. testaceipes* maintained by the USDA APHIS PPQ Laboratory at Niles, Michigan, USA. Mummies were placed in 2-oz plastic cups (59 mL; Sweetheart Cup, Owings Mills, Maryland, USA) covered by a coarse mesh (2-mm openings) at the top that allowed parasitoid emigration

from the cup but protected them from large predators. Cups were held 20 cm above ground level by a wooden stake and were protected from rainfall by an inverted white plastic cup (7.5×8 cm). Three consecutive releases were performed on 16, 23, and 25 June, at a rate of one cup per cage. For each release, 20 mummies were placed in each cup, which generated a 1:5 (parasitoid to aphid) ratio for the first release. This ratio was successfully used in preliminary tests in the same field establishing *L. testaceipes* in small mesh cages. During each release, we deployed control release cups completely closed by a fine mesh ($n = 15$ randomly selected cages), that were checked daily for four days to assess parasitoid emergence.

Aphid and natural enemy populations were assessed weekly in all cages for six weeks following aphid and parasitoid establishment. By week 3 it was evident that, contrary to our expectations, the sham cages were interfering with predator activity, resulting in higher aphid densities than in the open control (see *Results*). Thus, on 9 July we opened windows at the canopy level for both exclusion and sham cages (previously described), which resulted in a significant reduction in aphid abundance. After the sixth week of the experiment, cages were no longer effective at excluding coccinellids, and aphid populations declined in predator exclusion treatments during the following two weeks; thus these data were excluded from statistical analysis. Aphid populations in the sham cages and open and field controls were maintained below the economic threshold level of 250 aphids per plant (Hodgson et al. 2004), and monitoring of aphids and their natural enemies was discontinued after the eighth week of the experiment. To assess the effects of the natural enemy manipulations on the plants, cages were maintained in all treatments until harvest (see below).

Natural enemies were sampled by conducting visual counts in cages for three minutes (Fox et al. 2004), followed by aphid and parasitoid sampling, which consisted of total counts of aphids and mummies on 4–10 plants within the cage (reducing sampling effort with aphid density increase, Costamagna and Landis 2006). Mummies were classified as intact (fully closed mummy), emerged (with openings made by emerging adult parasitoids), or damaged by predation (mummies opened in irregular patterns, consistent with damage by coccinellid feeding observed in preliminary laboratory trials). We assessed parasitism based on the number of intact mummies, and therefore our measure of parasitism is conservative, because some aphids could have been parasitized but not yet mummified. No attempt was made to measure hyperparasitism in this experiment, but other studies conducted in the same field revealed no hyperparasitoids attacking *L. testaceipes* (Brewer and Noma 2004). Soybean plants were harvested for total aboveground biomass in three randomly selected blocks on 16 August, and the remaining three blocks were harvested on 13 October to estimate yield.

Plants were dried at 60°C until no change in mass was detected and then dry masses for whole plants and seeds were recorded.

Statistical analysis

The effects of predator and parasitoid manipulations on aphid, predator, and parasitoid populations were analyzed as a 2×2 factorial ANOVA using a complete randomized block design (CRBD) with time as a repeated factor (Proc Mixed, SAS Institute 2001). Significant interactions were further explored by slicing main effects (Quinn and Keough 2002), and individual means were compared by the least square means difference adjusted by the Tukey-Kramer method for multiple comparisons (LSMD-TK, SAS Institute 2001). We also assessed (1) effects of caging by comparing the predator treatment with the open reference plots, and (2) effects of predator and parasitoid manipulations on soybean yield and biomass, using one-way ANOVAs on a CRBD with time as a repeated factor. Predator, mummy, and aphid counts, and plant biomass and yield data, were log-transformed, whereas percentage parasitism and proportion of damaged mummies (mummies damaged/[mummies damaged + new mummies]) were arcsine-transformed, to meet assumptions of normality and homoscedasticity. Additionally, using log-transformed data in the analysis allowed testing interactions using a multiplicative risk model, which avoids bias when predation levels are high (Sih et al. 1998). We did not record predators and mummies during the first two weeks of sampling in most samples, and therefore these weeks were not included in statistical analyses for those variables.

RESULTS

Effectiveness of predator manipulations

The assemblage of *A. glycines* predators was dominated by coccinellids (Coleoptera: Coccinellidae; 53.7% of total number of predators sampled), with the most abundant species being *Harmonia axyridis* (Pallas) (69.9%), followed by *Coccinella septempunctata* L. (4.2%), *Coleomegilla maculata* (De Geer) (2.2%), and *Hippodamia variegata* (Goeze) (2.2%). First and second instar coccinellid larvae (21.5% of total coccinellid counts) were not identified to species, but were most likely also dominated by *H. axyridis*. Predator and predator + parasitoid treatments had significantly higher abundance of coccinellids than did aphid and parasitoid treatments after the opening of the canopy-level windows (significant predator \times date interaction in Table 1, Fig. 2a), indicating successful manipulation of this group of predators. During the last week of sampling, this trend reversed, with coccinellids occurring in higher abundances on the aphid and parasitoid treatments (Fig. 2a) where higher numbers of aphids occurred (Fig. 3). Small predators including midge larvae (Diptera: Cecidomyiidae and Chamaemyiidae; 58.1%) and *Orius insidiosus* (Say) (41.9%) accounted for

TABLE 1. ANOVA results for effects of predator and parasitoid manipulations on the abundance of predators, parasitoids, and aphids using field cages in Michigan during 2004.

Factor	df	Coccinellids		Small predators		<i>L. testaceipes</i> †		<i>Aphis glycines</i>		
		F	P	F	P	F	P	df	F	P
Block	5, 15	0.49	0.7764	2.99	0.0455	1.82	0.1695	5, 15	1.16	0.3744
Predator	1, 15	11.55	0.004	1.16	0.2985	16.47	0.001	1, 15	181.39	<0.0001
Parasitoid	1, 15	1.32	0.2689	0.16	0.693	32.72	<0.0001	1, 15	2.4	0.1419
Predator × parasitoid	1, 15	1.88	0.1901	1.05	0.3221	4.82	0.0444	1, 15	9.54	0.0075
Date	3, 60	16.24	<0.0001	7.7	0.0002	4.7	0.0052	5, 100	203.08	<0.0001
Date × predator	3, 60	27.52	<0.0001	1.88	0.1432	9.65	<0.0001	5, 100	76.74	<0.0001
Date × parasitoid	3, 60	0.02	0.9972	0.12	0.9451	2.14	0.105	5, 100	0.58	0.7122
Date × predator × parasitoid	3, 60	0.37	0.7761	0.01	0.997	5.94	0.0013	5, 100	1.21	0.3113

† A native parasitoid, *Lysiphlebus testaceipes*.

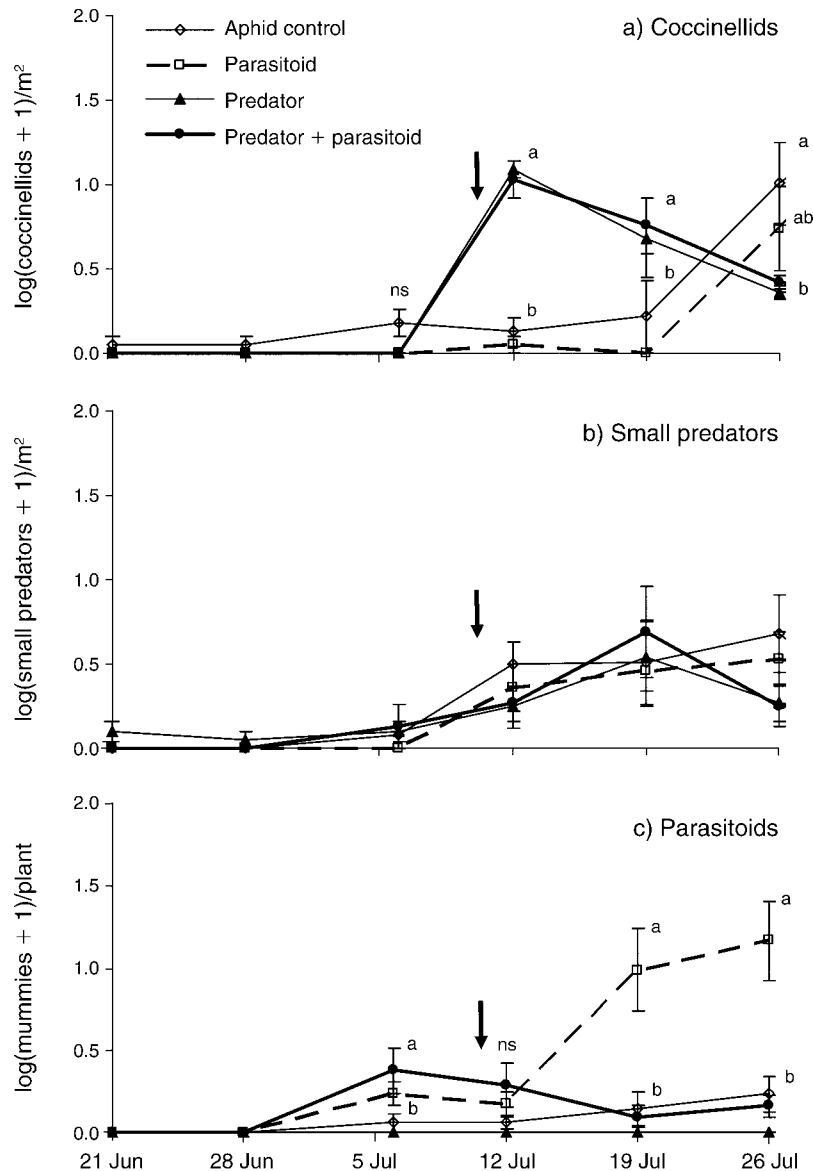


FIG. 2. Abundance (mean ± SE) of (a) coccinellids, (b) small predators (midge larvae and *O. insidiosus* combined), and (c) parasitoid mummies in field cages with *A. glycines* that combine predator and parasitoid manipulations. The arrow indicates the opening of a canopy-level window (see *Materials and Methods*). Different letters within each sampling date represent significant differences ($P < 0.05$) using slicing tests for the two- and three-way significant interactions (Table 1); “ns” indicates that differences were not significant.

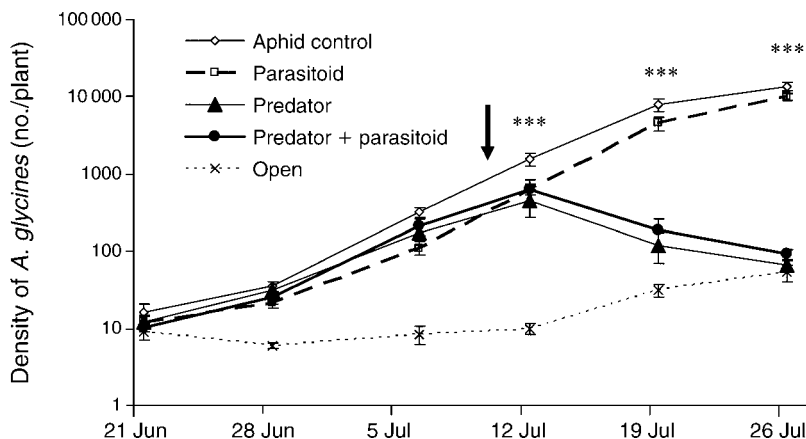


FIG. 3. Number (mean \pm SE) of *Aphis glycines* in field cages with different combinations of predators and parasitoids. The arrow indicates the opening of a canopy-level window (see *Materials and Methods*). Asterisks indicate significant differences between treatments with ambient levels of predators vs. predator exclusion treatments (predator \times date slicing tests, $P < 0.0005$).

34.3% of total predators. In contrast to coccinellids, small predators were not affected by our predator and parasitoid manipulations (Table 1, Fig. 2b). Although our visual sampling method may have underestimated small predators hidden in the canopy of the plants, the detection of small predators at low densities in all treatments indicates an absence of bias among treatments.

Both coccinellids and small predators increased significantly throughout the season, following the increase in *A. glycines* densities (Table 1, Fig. 2). Other predator groups were also sampled, but low abundance and irregular distribution among samples prevented statistical analysis. However, none of these groups showed trends of association with any of the treatments, suggesting that they probably played only a minor role in aphid suppression. Those predators included (in order of abundance): syrphid larvae (Diptera: Syrphidae, 7.4%), lacewing larvae (Neuroptera: Chrysopidae, 2.6%), and nabids (Hemiptera: Nabidae, 0.9%), followed by carabids (Coleoptera: Carabidae), spiders (Arachnidae: Araneae), and staphylinids (Coleoptera: Staphylinidae) (1.1% combined). Because our sampling was conducted during the day, predators with nocturnal habits such as carabids and spiders were undoubtedly underestimated. Finally, parasitoid manipulations did not affect coccinellid or small predator abundance in the cages (Table 1).

We assessed the effects of cage manipulations on the abundance of natural enemies by comparing the predator treatment with uncaged (open controls) and unmanipulated plots (field controls). We observed significantly lower coccinellid abundance in the field (0.38 ± 0.10 individuals/m²; mean \pm SE averaged across weeks 3–6, $n = 40$) and open (1.79 ± 0.33 individuals/m², $n = 24$) controls with respect to the predator treatment (7.38 ± 2.18 individuals/m², $n = 24$) during weeks 4 and 5 (LSMD-TK tests, $P < 0.01$), and no differences between open and field controls. Small

predators showed the same pattern, being significantly lower in abundance in the field (2.17 ± 0.54 individuals/m², $n = 40$), and open (2.56 ± 0.73 individuals/m², $n = 24$) controls with respect to the predator treatment (48.96 ± 26.55 individuals/m², $n = 24$) for weeks 4 and 5 (LSMD-TK tests, $P < 0.05$), and no differences between open and field controls. These results suggest a numerical response of the predators to the higher aphid densities observed in the predator treatment until week 6, during which aphid densities in the three treatments did not differ (see *Results: Aphis glycines control*).

Parasitoid effectiveness and intraguild predation

Data from the control release cups indicated that $46.7\% \pm 12.0\%$ (mean \pm SD) of the *L. testaceipes* mummies emerged successfully within four days. Releases resulted in parasitoid establishment in the cages and a significant increase of *L. testaceipes* mummies (Table 1, Fig. 2c). This effect was consistent through time, as indicated by the nonsignificant parasitoid \times date interaction (Table 1). The presence of predators significantly reduced mummy abundance, but only during the last two sampling dates, after opening the canopy-level window (Table 1, Fig. 2c). There was a significant predator \times parasitoid interaction, indicating nonadditive effects of predator and parasitoid manipulations. Slicing tests of the significant three-way interaction revealed a significant reduction in the number of mummies when predators and parasitoids were combined, in comparison with the parasitoid alone treatment, for the last two dates ($F_{1,60} = 32.90$, $P < 0.0001$, and $F_{1,60} = 42.01$, $P < 0.0001$, respectively; Fig. 2c). Parasitoid abundance increased significantly over time in the parasitoid treatment (Table 1, Fig. 2c). No parasitoids were recovered in the predator treatment and in the field control, and only five mummies were observed in open treatments during the six weeks of the experiment, indicating an almost complete absence of background levels of parasitism.

To test whether predators disrupted aphid control by parasitoids, we compared the percentage parasitism between the parasitoid and the predator + parasitoid treatments. Despite the significantly lower number of parasitoid mummies found in the treatments with predators, we did not detect significant differences in percentage parasitism between treatments with parasitoids exposed vs. protected from large predators ($F_{1,5} = 0.01$, $P = 0.9455$), indicating that predators did not reduce parasitism by *L. testaceipes*. Overall, parasitism was very low (parasitoid, $0.46\% \pm 0.16\%$; predator + parasitoid, $0.59\% \pm 0.21\%$; mean \pm SE averaged across weeks 3–6, $n = 24$) and did not vary among blocks ($F_{5,5} = 1.34$, $P = 0.3774$). In addition, parasitism decreased significantly over time ($F_{3,30} = 4.67$, $P = 0.0085$), indicating a lack of response of *L. testaceipes* to aphid increase. We observed very low levels of damaged mummies throughout the season, and despite a trend for higher total number of mummies damaged per plant in the predator + parasitoid treatment (1.8 ± 1.4 no. mummies damaged/plant, mean \pm SE) than in the parasitoid treatment (1.1 ± 0.6 no. mummies damaged/plant), differences were not significant for total ($F_{1,5} = 0.01$, $P = 0.9104$) or proportion of mummies damaged ($F_{1,5} = 0.86$, $P = 0.3950$). Thus, these results indicate that parasitism by *L. testaceipes* was not disrupted by predators through IGP.

Aphis glycines control

Our natural enemy manipulations resulted in large and significant differences in *A. glycines* populations after six weeks (Fig. 3). Large predators (mainly Coccinellidae) significantly reduced aphid populations (Table 1), resulting in an average 176-fold aphid reduction compared with the aphid control and parasitoid addition treatments. Predator impacts on aphid abundance were underestimated during the initial part of the experiment due to the restrictive size of the sham cage openings, which resulted in significant differences between predator and open treatments ($F_{1,5} = 52.18$, $P = 0.0008$; Fig. 3). However, predator effectiveness increased in both treatments after opening the canopy-level windows, which resulted in a significant predator \times date interaction (Table 1, Fig. 3). Ultimately, the predator treatment did not differ significantly from the open treatment during the last sampling date (slicing by date, last date test, $F_{1,50} = 0.61$, $P = 0.4379$; Fig. 3). In contrast, parasitoid addition resulted in a weak reduction of *A. glycines* populations and only when predators were excluded (Fig. 3). Aphid abundance was not affected by the opening of the canopy-level windows in the parasitoid treatment (Fig. 3). Natural *A. glycines* abundance was very low in the field references, reaching a maximum of 2.3 ± 0.6 aphids/plant at the end of July, and was significantly lower in the field references than in the open treatment ($F_{1,14} = 211.70$, $P < 0.0001$, Fig. 3).

There was a significant predator \times parasitoid interaction, indicating nonadditive effects, and those were

consistent among sampling dates (nonsignificant predator \times parasitoid \times date interaction, Table 1). Slicing the interaction by main effects indicates that predators reduced the number of aphids per plant, with or without added parasitoids ($F_{1,15} = 53.86$, $P < 0.0001$, and $F_{1,15} = 137.07$, $P < 0.0001$, respectively), whereas parasitoids reduced aphids when predators were excluded ($F_{1,15} = 10.76$, $P = 0.0051$) but not when predators were present ($F_{1,15} = 1.18$, $P = 0.2937$). These last two tests indicate a disruptive effect of predators on aphid suppression by the parasitoids that results in a nonsignificant parasitoid main effect. Overall, these results show that generalist predators (mainly coccinellids) provided strong suppression of *A. glycines* and that their presence eliminated the small impact of *L. testaceipes*, resulting in significant nonadditive effects of the two groups of natural enemies.

Trophic cascade

Our predator manipulations resulted in a trophic cascade that restored plant biomass and yield ($F_{4,8} = 7.70$, $P = 0.0075$; and $F_{4,8} = 12.08$, $P = 0.0018$, respectively) to the same levels as the no-aphid control (Fig. 4). Exposure to ambient levels of predators resulted in a twofold biomass and a 1.6-fold yield increase over the aphid control. Adding parasitoids alone resulted in an intermediate increase in biomass, but did not improve plant yield over the aphid control (Fig. 4). Block was not significant in either analysis. Open controls showed lower plant biomass (16.17 ± 4.05 g/plant) and yield (14.36 ± 1.36 g/plant) than in sham cages ($F_{1,4} = 0.56$, $P = 0.0995$; and $F_{1,4} = 15.46$, $P = 0.0171$, respectively), indicating beneficial effects of the cages on plant growth. Although cage effects have been observed in other systems (Hinz and Schroeder 2003), another study on this system conducted by A. C. Costamagna, M. J. Brewer, and D. A. Landis (*unpublished results*) showed similar effects of predator manipulations on plant biomass and yield, without observing differences between sham and open treatments, suggesting that cage effects in this study did not alter the effect of natural enemies. These results indicate that the strong suppression of *A. glycines* by generalist predators cascades down to result in levels of plant biomass and yield similar to plants where aphids were excluded.

DISCUSSION

Our study shows that the established assemblage of generalist predators can significantly impact *A. glycines* populations, and that this control occurred throughout the entire field season. By contrast, controlled releases of the native parasitoid *L. testaceipes* had only minor effects in *A. glycines* suppression when large predators were excluded and did not add control when combined with them. Significant impacts of generalist predators on *A. glycines* were previously shown in Asia (Van den Berg et al. 1997, Liu et al. 2004) and North America (Fox et al. 2004, 2005, Costamagna and Landis 2006), but our

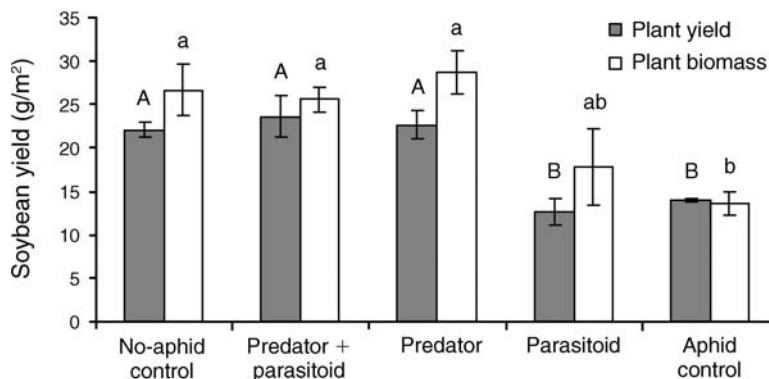


FIG. 4. Soybean yield and aboveground dry biomass (mean \pm SE) in field cages without *A. glycines* (no-aphid control), and with *A. glycines* and different combinations of predators and parasitoids. Different letters above histogram bars represent significant differences at $P < 0.05$ using LSMD-TK (least square means difference with Tukey-Kramer adjustment). Uppercase letters refer to plant yield, and lowercase letters refer to plant biomass.

results extend these findings by spanning an entire field season, and by demonstrating for the first time that this control cascades down to increase plant biomass and yield.

The use of exclusion cages to test for the impact on natural enemies has been extensively used for aphids in general (e.g., Chambers et al. 1983, Hopper et al. 1995, Ferguson and Stiling 1996, Jervis and Kidd 1996, Brown 2004) and also recently for *A. glycines* (Fox et al. 2004, Costamagna and Landis 2006; A. C. Costamagna, M. J. Brewer, and D. A. Landis, *unpublished results*). However, others have criticized cages as potentially preventing aphids from emigrating and thus artificially inflating apparent predation impacts (e.g., Kindlmann et al. 2005). Several lines of evidence support the role of predator exclusion rather than aphid enclosure in explaining higher aphid abundances in predator exclusion cages. Brown (2004) demonstrated similar levels of increased spirea aphid populations by excluding predators with cages or with insecticide treatments in open plots. Chambers et al. (1983) showed that removal of alates from exclusion cages did not result in lower aphid populations in comparison with cages in which alates were confined. In our study, we did not observe significant accumulation of alates in exclusion cages even at high aphid populations, suggesting that alates were able to successfully emigrate from the cages. Finally, a significant reduction in aphid abundance has been shown for treatments with both aphids and predators enclosed together in comparison to controls in which only aphids were enclosed, demonstrating the ability of predators to control aphid populations (e.g., Cardinale et al. 2003, Snyder and Ives 2003). Thus, we feel confident that the reduction in *A. glycines* in our study was due to predation rather than to artificial confinement of aphids.

The different mesh sizes used in our cages allowed us to separate the effects of large vs. small predators on *A. glycines*. Small predators, such as midge larvae and *O. insidiosus*, did not differ in abundance between exclusion

and sham cages. Because aphids increased exponentially in the exclusion cages in the presence of small predators, these results suggest a minor role for small predators in *A. glycines* control at this location. This result contrasts with other studies that suggest that *O. insidiosus* is an important predator of *A. glycines* (Rutledge et al. 2004, Rutledge and O'Neil 2005).

Although extensive data support the importance of coccinellids as aphid predators (Frazer 1988, Hodek and Honěk 1996, Obrycki and Kring 1998), there is still debate concerning their ability to suppress aphid populations (Dixon 2000). Our results demonstrate strong aphid suppression by unmanipulated ambient levels of coccinellids. Both predator treatments resulted in significant *A. glycines* control during the six weeks monitored during the 2004 field season, which mimicked unmanipulated field populations. Further sampling and significant differences in soybean biomass and yield indicate that this suppression was effective throughout the entire field season. By contrast, in treatments that excluded predation by large predators, *A. glycines* increased exponentially, indicating that abiotic factors were suitable and did not limit aphid growth. The similarity in abiotic conditions in exclusion vs. sham cages and open controls was previously demonstrated (e.g., Hopper et al. 1995, Schmidt et al. 2003, Fox et al. 2004). Thus, the absence of outbreak aphid populations in commercial fields during 2004 was not directly attributable to unfavorable abiotic conditions. As in previous reports (Fox et al. 2004, 2005, Costamagna and Landis 2006), our results suggest that the coccinellids *H. axyridis* and *C. septempunctata*, are the main predators responsible for *A. glycines* suppression in our study area.

Controlled releases of the native parasitoid *L. testaceipes* failed to suppress *A. glycines* population growth, even when large predators were reduced. We observed only a small impact of *L. testaceipes* on *A. glycines*, and this effect disappeared when ambient levels of large predators were combined with parasitoids, resulting in nonadditive interactions. Although we

obtained evidence of predator interference on parasitism, the very low impact of *L. testaceipes* on *A. glycines* in predator exclusion cages indicates that this disruption was trivial in comparison with the strong impact of large predators in suppressing *A. glycines*. However, one important caveat of our experiment is that the low efficiency of *L. testaceipes* prevents us from making a generalized conclusion regarding the disruptive effect of IGP on more effective parasitoids. Nevertheless, the strong top-down control exerted by coccinellids suggests that even more efficient parasitoids will add little control and most likely suffer high IGP (Colfer and Rosenheim 2001) under similar conditions as in our experiment. Therefore, our results confirm the theoretical prediction that IG predators that have strong impacts on the primary prey (i.e., the herbivore) will not disrupt top-down control, regardless of how much suppression they exert upon the IG prey (Polis et al. 1989, Holt and Polis 1997).

The failure of *L. testaceipes* to suppress *A. glycines* was unexpected. Previous reports show that *L. testaceipes* significantly suppressed aphid populations in cotton (Colfer and Rosenheim 2001), sorghum (Fernandes et al. 1998), and cereals in general (Brewer and Elliott 2004), and is the most abundant parasitoid attacking *A. glycines* at our study area (Brewer and Noma 2004, Costamagna and Landis 2006). Moreover, laboratory colonies of *L. testaceipes* developed successfully on *A. glycines* for several generations (A. C. Costamagna, *personal observation*) indicating that *A. glycines* is a suitable host for this parasitoid. Field observations suggest that the lack of control of *A. glycines* by *L. testaceipes* cannot be explained by unsuitable abiotic factors. Visual inspections of releases performed in completely closed sleeve cages in the same field two weeks prior to the main experiment revealed continued high levels of parasitism throughout the season, with a cumulative number of 512.2 ± 152.1 mummies/plant (mean \pm SE, $n = 4$). In contrast, the cumulative number of mummies observed in the parasitoid treatment was significantly lower (73.4 ± 32.5 mummies/plant, $t = -3.61$, $df = 8$, $P = 0.0068$). Thus, it is likely that the lower parasitism levels obtained in our field cages were due to parasitoid emigration rather than from potential unfavorable weather conditions. Why *L. testaceipes* would leave a patch with abundant suitable hosts is unclear, but may include a preference to search in other habitats where it is adapted to find hosts (Vinson 1976), imperfect host discrimination (Rosenheim and Mangel 1994), variability in host suitability across scales (Ives et al. 1999), and different responses to cues from different host species (Grasswitz and Paine 1992).

Predator manipulations resulted in a significantly different number of mummies due to several potential causes. We observed a higher number of mummies in the parasitoid treatment, but because percentage parasitism was not affected by predation, mummy increase may be

a response to increased host density rather than the effect of a refuge from predation. We did not estimate predation on parasitized aphids before mummy formation or on adult parasitoids, both of which have been shown as potential sources of IGP (Heimpel et al. 1997, Meyhöfer and Klug 2002). In addition, we cannot rule out a more general, indirect effect of intraguild interference (sensu Lang 2003) as another potential factor reducing mummy numbers in the treatment combining parasitoids and predators. Recent studies showed that female parasitoids spend less time, attack fewer aphids, and avoid leaves on which coccinellids or their semiochemicals are present (Taylor et al. 1998, Nakashima et al. 2004).

This study adds to the growing body of evidence that generalist predators have strong effects on prey, and is novel in demonstrating that these effects cascade down to increase plant biomass and yield. Trophic cascades are pervasive in terrestrial ecosystems (Schmitz et al. 2000, Halaj and Wise 2001, but see Polis et al. 2000), and have been demonstrated in agricultural systems, including vegetable (Snyder and Wise 1999, 2000, 2001), perennial (Cardinale et al. 2003), and annual crops (Carter and Rypstra 1995, Colfer and Rosenheim 2001, Rypstra and Marshall 2005), although some studies fail to show significant impacts (e.g., Vichitbandha and Wise 2002). Our findings showed that strong top-down control by lady beetles can completely release soybean plants from aphid pressure and restore plant biomass and yield. Our study differs from previous experiments investigating top-down control and trophic cascades in agroecosystems in two aspects. Previously it has been argued that strong trophic cascades in agroecosystems may be at least partially an artifact of increasing the levels of natural enemies above ambient levels, and by measuring plant damage, which may not be an adequate surrogate of plant fitness (Polis et al. 2000, Halaj and Wise 2001). We addressed these concerns by conducting factorial natural enemy manipulations that allowed ambient levels of predation to respond to aphid density and avoided forcing interactions by allowing free emigration of aphids and parasitoids from all treatments. This also makes us confident that aphid pressure on plants was not artificially inflated. Finally, we directly measured plant biomass and yield, this last being a good surrogate for plant fitness.

In summary, we observed that strong suppression of soybean aphid by generalist predators led to a trophic cascade that restored soybean biomass and yield. On the other hand, the most abundant native parasitoid attacking soybean aphid, *L. testaceipes*, was ineffective in reducing aphid populations. Although we obtained direct evidence of IGP in field conditions, the low suppression exerted by *L. testaceipes* is not currently limited by IGP. However, we still have a very poor knowledge of factors leading to *A. glycines* outbreaks, and thus it is still an open question whether despite potential IGP more effective parasitoids may add

control during seasons in which aphids escape predation.

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