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Direct effects of soybean varietal selection and *Aphis glycines*-resistant soybeans on natural enemies

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Abstract The direct effects of three soybean parentages, each represented by an *Aphis glycines*-resistant and susceptible isoline, on the fitness and performance of two key predators (*Orius insidiosus* and *Harmonia axyridis*) were evaluated in the laboratory. Predators were reared from hatch through adulthood in Petri dishes with cut trifoliolate leaves of the designated soybean variety, using eggs of *Ephestia kuehniella* as surrogate prey to eliminate prey-mediated effects of the host plant. Preimaginal survival and development, sex ratio, adult longevity, fecundity, and size were compared among treatments and a no-plant control. An additional experiment compared life-history parameters of predators caged with soybean versus *Ipomoea hederacea* (ivyleaf morning glory). Aphid resistance reduced the adult longevity of *H. axyridis,* but *O. insidiosus* was unaffected by resistance traits. However, adult *O. insidiosus* lived longer on soybeans with Group C base genetics than the other soybean varieties. Other parameters were not affected by soybean base genetics or resistance, but both predators generally performed worse on soybean than on *I. hederacea* or no-plant controls. The results suggest that soybean varietal selection, particularly with respect to *A. glycines*-resistance, may directly affect biological control agents. Also, implications of the generally poor suitability of soybean for natural enemies are discussed within the context of current crop production practices.

Keywords Biological control · *Glycine max* · *Orius insidiosus* · *Harmonia axyridis* · Host plant resistance · Integrated pest management · *Ipomoea hederacea* · Omnivory · Predator

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Introduction

Substantial intraspecific variation in chemistry and architecture occurs in crops, and heterogeneity in these traits creates a continuum in the suitability of a crop plant for pests and natural enemies alike. Selecting for herbivore resistance within crops is predicated upon this inherent genetic variability, and this tactic is frequently employed as a cornerstone of integrated pest management (IPM) programs for insect pests (Panda and Khush 1995; Smith 2005). Host plant resistance (HPR) is often compatible with biological control, sometimes even leading to a synergistic or additive lowering of pest densities (Pair et al. 1986; Starks et al. 1972; van Emden 1986; van Emden 1995; Wyatt 1970). Although they are best appreciated for their ability to consume prey, arthropods assigned to higher trophic levels frequently rely on plant-based resources for food and habitat (Barbosa 1998; Landis et al. 2000; Lundgren 2009; Pickett and Bugg 1998). The reliance of natural enemies on crop plants for food and shelter sometimes results in direct adverse effects of crop characteristics on biological control agents (Hare 1992). Thus, there is a need to establish which crop varieties, especially those that

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express HPR, are compatible with predators and parasitoids within IPM systems.

Natural enemies may interact with crop phenotype directly or through prey (van Emden 1995). Reduced prey quality and availability resulting from HPR have an obvious effect on natural enemies, and these are irrefutably the most commonly documented adverse interactions of crop phenotypes with higher trophic levels (Kauffman and Flanders 1985; Kennedy et al. 1975; Orr and Boethel 1986; van Emden 1995). Phenotypic variation in plant architecture and morphology also may influence natural enemies via traits such as trichome density or structure and leaf-surface texture or waxiness (Eigenbrode et al. 1996; Eigenbrode et al. 1995; Simmons and Gurr 2004; Treacy et al. 1987). Finally, phytochemistry varies greatly within a plant species, and differences in synomone production and plant nutrition have been documented to differentially affect the foraging and fitness of omnivorous natural enemies (Hagen 1986; Lundgren 2009; Lundgren and Wiedenmann 2004; van Emden 1995).

Soybean (*Glycine max* L.) is a prevalent crop in North America, and the soybean aphid, *Aphis glycines* Matsumura, is its primary pest (Venette and Ragsdale 2004). Several soybean lines show resistance to *A. glycines* (Hesler and Dashiell 2007; Hesler and Dashiell 2008; Hesler et al. 2007; Hill et al. 2004; Li et al. 2004; Mensah et al. 2005), and resistant varieties of soybean are likely to be available to farmers soon. Even so, few studies have examined the effects of different soybean genotypes or HPR on key natural enemies of *A. glycines*.

Harmonia axyridis (Pallas) and *Orius insidiosus* (Say) represent two abundant natural enemies in soybean that are implicated in reducing *A. glycines* populations (Brosius et al. 2007; Butler and O'Neil 2007; Costamagna and Landis 2006; Costamagna and Landis 2007; Costamagna et al. 2007; Fox et al. 2004; Harwood et al. 2007; Harwood et al. 2009; Mignault et al. 2006; Rutledge and O'Neil 2005; Schmidt et al. 2008). However, their seasonal phenologies and feeding ecologies differ in ways that could affect their relative direct exposure to potentially harmful characteristics of soybean. Both predators consume plant tissue (at least during the larval stage for *H. axyridis*) (Corey et al. 1998; Dicke and Jarvis 1962; Lundgren et al. 2008; Lundgren et al. 2004; Moser et al. 2008), but ostensibly *O. insidiosus* relies on non-prey foods more heavily than *H. axyridis*. Feeding style also differs between these predators, as *H. axyridis* has chewing and *O. insidiosus* has sucking mouthparts. Finally, *O. insidiosus* is phenologically most abundant during the vegetative stages of soybean, and *H. axyridis* numbers swell during the middle and late reproductive stages of the crop. Consequently, *O. insidiosus* is believed to be most important as a biological control agent before *A. glycines* populations surge and *H. axyridis* responds to the prevalent aphids later in the season.

The effects of aphid resistance and other variable traits of soybean have not been evaluated against key natural enemies of *A. glycines*. The fact that the target herbivore is affected by HPR challenges the separation of direct and prey-mediated effects on natural enemies. The current study focuses specifically on *direct* effects of soybean base genetics and aphid resistance on *H. axyridis* and *O. insidiosus* using surrogate prey (*Ephestia kuehniella* Zeller eggs) of high nutritional quality that is inherently unaltered by the plants. Specifically, the research tests the hypotheses that 1) soybean base genetics do not directly affect the life-history parameters of these two predators, and 2) that predator life histories are comparable between aphid-resistant and susceptible soybean.

Methods

Insects

Orius insidiosus adults were obtained from Koppert Canada Limited (Scarborough, ON, Canada), and maintained on *E. kuehniella* (Lepidoptera: Pyralidae) eggs and 1–2 cm green bean (*Phaseolus vulgaris* L.) sections for moisture. Eggs laid into green beans were checked daily, and newly eclosed nymphs were isolated. *Harmonia axyridis* adults were collected from an overwintering site in Brookings, SD, USA. Collected adults were maintained for <60 d on *A. glycines* (soybean aphids), *E. kuehniella* eggs, honey, and water. Mated females were isolated from the colony, sexed (McCornack et al. 2004), and allowed to lay eggs on their plastic dish. Larvae were isolated on the days they hatched. Neonate nymphs and larvae were randomly assigned to treatments described below.

Plants

Six soybean lines were compared that represent three distinct parentages, each containing an *A. glycines*-resistant and a susceptible isoline. These are designated here as Group A: lines LD05-16118 (LD05; resistant) and SD01-76R (SD01; susceptible); Group B: lines LDXG04-18-2-4 (IL-4; resistant) and LDXG04018005-21 (IL-105; susceptible); and Group C: lines LDXG04-23-2-11 (IL-35; resistant) and LDXG04-23-2-22 (IL-46; susceptible). The aphid-resistant varieties all expressed the *Rag1* gene and shared a Dowling parent.

For each soybean line, 20 pots (25.4 cm diam.) with individual plants were maintained in a single greenhouse with climatic conditions representative of early soybean development in our region: 24 and 13°C for 12 h periods each diel cycle, and a photoperiod of 15:9 (L:D). Plants were grown in 2:1:1 parts soil:peat:vermiculite, and were

watered as needed. The assays were timed to reflect when these two predator species are believed to be most important in terms of *A. glycines* suppression. Thus, plants were initially staged at the V4 and R1 stages for the *O. insidiosus* and *H. axyridis* assays, respectively. For each individual predator, a randomly selected trifoliolate leaf was snipped at the petiole base and immediately placed through a hole in the cap of a water-filled, 1.5-ml microcentrifuge tube.

Ipomoea hederacea (L.) Jacq. (ivyleaf morning glory) plants were used in a follow-up experiment to assess the general suitability of soybeans as a habitat for natural enemies. These plants were grown individually in 10-cm square pots under identical growing conditions to those described above. Plants were ≥25 cm long when assays were conducted.

Orius insidiosus *assays*

Neonates (N = 210) were evenly and randomly assigned to one of seven treatments, including each of the six soybean lines and a no-plant control. Each experimental arena consisted of a 15 cm diam Petri dish containing a water-soaked cotton wick and *E. kuehniella* eggs (initially 10 and increasing to 20 eggs as the nymphs aged), which were replaced every 96 h. Single trifoliolate soybean leaves per arena were changed every 48 h, and the Petri dishes were sealed with a strip of Parafilm® (Pechiney Plastic Packaging, Menasha, WI, USA) to reduce escape by the nymphs. The arenas were held at 27°C, with a 16:8 (L:D) photoperiod and 80% relative humidity. Arenas were checked daily, noting whether the nymph had died or completed development to adulthood. Arenas with missing nymphs were excluded from analyses, and the sample size per treatment was adjusted accordingly.

Adult *O. insidiosus* were sexed and were maintained in an identical experimental arena as those they developed in, except that a 1-cm long section of green bean was provided to the no-plant control as an oviposition substrate. Each female was mated with a male of their treatment (who was at least 72 h old) for 24 h within 48 h of eclosion, and subsequently every 72 h with a different male for the rest of their lives. The plant tissue in each dish was examined daily for the number of eggs laid. Upon their death, the head capsule width (posterior to the eyes) was measured microscopically at 50–80×.

The mean development time, adult longevity, fecundity, and head widths were calculated for each treatment and were compared using Kruskal-Wallis non-parametric ANOVA. The percent survival to adulthood and sex ratio (proportion female) were compared among treatments using two-way contingency tables and Pearson chi-square analyses. The treatment means for each of these parameters were compared to assess the effects of soybean base genetics ($n = 2$ each treatment) and resistance ($n = 3$ each treatment) on *O. insidiosus* using separate non-parametric assays. Mann-Whitney *U* tests were applied to resistance-susceptible comparisons involving continuous variables, and Kruskal-Wallis ANOVA to the base genetics comparisons with continuous variables.

Harmonia axyridis *assays*

A nearly identical experimental procedure was used to assess the effects of soybean base genetics and *A. glycines* resistance on *H. axyridis.* Some exceptions to the protocol outlined above are that the durations of each stadium and the pupal stage were noted in addition to total preimaginal development. Adult *H. axyridis* can live for many weeks, and the experiment was terminated at 15 d after the last adult eclosed. Thus, adult survival was necessarily measured as a proportional value (% alive at 15 d) rather than a continuous variable as in the *O. insidiosus* assay. Finally, the length of the metatibia, measured microscopically at 50–80×, was used as an index of adult size.

Soybean versus I. hederacea *assays*

Due to poor performance of both predators reared on all soybean lines, an additional set of assays was performed to determine whether plant tissue was generally harmful to developing *O. insidiosus* and *H. axyridis*. *Orius insidiosus* performs well and preferentially oviposits on *I. hederacea* leaves (Lundgren and Fergen 2006; Lundgren et al. 2008), so this plant species was chosen to evaluate the efficacy of our experimental design. The experimental design was similar to that outlined above, but only 20 individuals of each predator were tested per treatment, and the experiments were terminated at eclosion. The three treatments evaluated in this experiment were soybean IL-105 petioles (randomly selected from the susceptible varieties), *I. hederacea*, and a no-plant control. Equivalent leaf areas of *I. hederacea* and soybean were used. For *O. insidiosus* assays, preimaginal development times and the proportion surviving to adulthood were compared among treatments with Kruskal-Wallis non-parametric ANOVA and a two-way contingency table with Pearson chi-square test, respectively (sample sizes were adjusted for nymphs lost during the experiment). For *H. axyridis*, the mean duration of each stadium and total larval development were compared among treatments using Kruskal-Wallis ANOVA, and the proportion surviving to adulthood was analyzed with a two-way contingency table.

Results

Orius insidiosus *preimaginal assays*

There were differences in the preimaginal survival ($\chi^2_6 = 15.62$, $P = 0.02$) and developmental rates ($\chi^2_6 = 15.41$, $P = 0.02$) of *O. insidiosus* nymphs among the different treatments when the no-plant controls were included in the analysis (Table 1). When comparisons were made exclusively among the soybean treatments, there were no differences in nymphal survival or development time among base genetics (survival: $\chi^2_2 = 1.65$, $P = 0.44$; development: $\chi^2_2 = 3.92$, $P = 0.14$) or between resistant and susceptible varieties (survival: $\chi^2_1 = 0.73$, $P = 0.39$; development time: $\chi^2_1 = 0.50$, $P = 0.48$).

Orius insidiosus *adult assays*

There was an effect of treatment on the longevity ($\chi^2_1 = 0.73$, $P < 0.001$), and fecundity ($\chi^2_6 = 14.08$, $P = 0.02$) when analysis included the no-plant control (Table 1). There were no effects of treatment on adult head capsule width ($\chi^2_6 = 5.66$, $P = 0.34$) and sex ratio ($\chi^2_6 = 4.42$, $P = 0.62$). When the no-plant control was excluded from the analysis, there were no varietal effects on these parameters. There was an effect of base genetics on adult longevity ($\chi^2_2 = 10.40$, $P < 0.01$), but aphid resistance did not affect adult longevity ($\chi^2_1 = 0.56$, $P = 0.45$). There were no effects of base genetics ($\chi^2_2 = 3.64$, $P = 0.16$) or aphid resistance ($\chi^2_1 = 0.41$, $P = 0.52$) on fecundity.

Harmonia axyridis *preimaginal assays*

Developmental rates ($\chi^2_6 = 52.13$, $P < 0.001$) and survival ($\chi^2_6 = 36.53$, $P < 0.001$) of *H. axyridis* larvae differed significantly among treatments when analysis included the no-plant control (Table 2). When the no-plant controls were removed from analyses, there was no effect of variety on development time ($\chi^2_6 = 5.99$, $P = 0.31$) and survival ($\chi^2_5 = 9.49$, $P = 0.09$). Aphid resistance did not affect development time ($\chi^2_1 = 0.19$, $P = 0.66$) and the survival ($\chi^2_1 = 1.77$, $P = 0.18$) of *H. axyridis* larvae. Base genetics also did not affect development time ($\chi^2_2 = 3.82$, $P = 0.15$) and larval survival ($\chi^2_2 = 2.91$, $P = 0.23$).

Harmonia axyridis *adult assays*

When analysis included the no-plant control, there was a treatment effect on fecundity ($\chi^2_6 = 14.11$, $P = 0.03$), proportion of adults surviving for 15 d post-eclosion ($\chi^2_6 = 25.02$, $P < 0.001$), post-eclosion longevity ($\chi^2_6 = 50.83$, $P < 0.001$), adult weight ($\chi^2_6 = 24.52$, $P < 0.001$), and hind tibial length ($\chi^2_6 = 18.26$, $P < 0.001$), but not adult sex ratio ($\chi^2_6 = 5.84$, $P = 0.44$) (Table 2). When the no-plant control was excluded from analysis, there was no varietal effect on adult weight ($\chi^2_5 = 3.82$, $P = 0.56$), adult tibial length ($\chi^2_5 = 6.47$, $P = 0.26$), post-eclosion longevity ($\chi^2_5 = 9.96$, $P = 0.07$), proportion surviving 15 d post-eclosion ($\chi^2_5 = 9.12$, $P = 0.11$) and fecundity ($\chi^2_5 = 7.30$, $P = 0.20$).

There were no effects of aphid resistance on fecundity ($\chi^2_1 = 0.45$, $P = 0.50$), adult tibial length ($\chi^2_1 = 0.37$, $P = 0.54$), or adult weight ($\chi^2_1 = 0.27$, $P = 0.60$), but aphid-resistant soybean varieties reduced adult longevity ($\chi^2_1 = 4.86$, $P = 0.03$) and the proportion of adults that survived 15 d post-eclosion ($\chi^2_1 = 5.85$, $P = 0.02$). Base genetics of the soybean did not affect adult weight ($\chi^2_2 = 2.94$, $P = 0.23$), adult tibial length ($\chi^2_2 = 2.43$, $P = 0.30$), post-eclosion longevity ($\chi^2_2 = 2.37$, $P = 0.31$), the proportion surviving 15 d post-eclosion ($\chi^2_2 = 1.35$, $P = 0.51$) and fecundity ($\chi^2_2 = 4.80$, $P = 0.09$).

Soybean versus Ipomoea hederacea

There was a treatment effect on preimaginal survival of *O. insidiosus* when analysis included the no-plant control ($\chi^2_2 = 12.96$, $P = 0.002$), but not on developmental rates

Table 1 The influence of soybean genotypes on *Orius insidiosus* performance (mean values ± SE)

Variety	Base genetics	Resistant/ susceptible	Nymphs		Adults			
			Development; d	Survival; % (n)	Longevity; d (n)	Sex ratio; % female	Fecundity; eggs per female (n)	Size; head capsule widths; μm (n)
SD01	A	Susceptible	9. 6 ± 0.6	36.0 (25)	3.3 ± 0.6 (9)	44.4 (9)	0.3 ± 0.3 (4)	300.0 ± 12.5 (2)
LD05	A	Resistant	9.3 ± 0.4	36.4 (22)	4.8 ± 0.9 (8)	50.0 (8)	7.5 ± 6.2 (4)	312.5 ± 0 (2)
IL-105	B	Susceptible	9. 6 ± 0.4	36.0 (25)	5.1 ± 0.6 (9)	33.3 (9)	7.0 ± 4.4 (3)	303.1 ± 3.1 (4)
IL-4	B	Resistant	10.3 ± 0.6	33.3 (24)	4.0 ± 0.7 (8)	50.0 (8)	10.0 ± 5.7 (4)	306.3 ± 6.2 (2)
IL-46	C	Susceptible	8.8 ± 0.3	34.8 (23)	9.1 ± 1.5 (8)	12.5 (8)	51.0 (1)	314.6 ± 3.8 (6)
IL-35	C	Resistant	9.4 ± 0.4	61.9 (21)	6.2 ± 1.9 (5)	40.0 (5)	4.5 ± 3.5 (2)	312.5 (1)
No-plant control			8.4 ± 0.2	77.3 (22)	20.1 ± 1.7 (17)	52.9 (17)	88.4 ± 20.7 (9)	318.4 (17)

Table 2 The influence of soybean genotypes on *Harmonia axyridis* performance (mean values ± SE)

Variety	Base genetics	Resistant/ susceptible	Larvae		Adults					
			Total preimaginal development; d (n)	Survival; % (n)	Longevity; d (n)*	15 d survival; %	Sex ratio; % female	Adult weight; mg (n)	Hind tibial length; mm (n)	Fecundity; eggs per female (n)
SD01	A	Susceptible	13.4 ± 0.5 (11)	36.7 (30)	13.6 ± 1.3 (11)	81.8	25.0 (11)	11.4 ± 0.9 (8)	1.68 ± 0.02 (8)	124.5 ± 109.5 (2)
LD05	A	Resistant	13.5 ± 0.3 (13)	43.3 (30)	11.2 ± 1.4 (13)	53.9	50.0 (13)	10.5 ± 0.9 (10)	1.70 ± 0.02 (10)	68.0 ± 33.9 (6)
IL-105	B	Susceptible	13.9 ± 0.3 (8)	27.6 (29)	12.5 ± 1.7 (8)	75.0	62.5 (8)	9.0 ± 1.1 (5)	1.68 ± 0.02 (5)	128.4 ± 55.0 (5)
IL-4	B	Resistant	13.4 ± 0.2 (7)	23.3 (30)	7.3 ± 2.2 (7)	28.6	42.9 (7)	8.7 ± 0.6 (2)	1.58 ± 0.03 (2)	22.0 ± 11.9 (3)
IL-46	C	Susceptible	13.3 ± 0.2 (14)	46.7 (30)	11.2 ± 1.6 (13)	61.5	35.7 (13)	11.0 ± 1.1 (7)	1.70 ± 0.04 (7)	10.6 ± 9.4 (5)
IL-35	C	Resistant	13.2 ± 0.4 (5)	16.7 (30)	5.4 ± 2.5 (5)	20.0	20.0 (5)	9.1 ± 3.4 (2)	1.65 ± 0.01 (2)	0 (1)
No-plant control			11.7 ± 0.1 (25)	83.3 (30)	15.0 ± 0 (24)	100.0	52.0 (24)	18.2 ± 0.8 (11)	1.80 ± 0.02 (11)	18.5 ± 13.0 (13)

*Study terminated after 15 d

Table 3 Comparisons of ivyleaf morning glory and soybean (line IL-105) on the development and survival of immature *Orius insidiosus* and *Harmonia axyridis* (mean ± SEM)

	Orius insidiosus			*Harmonia axyridis*							
	Nymphal development; d (n)	Preimaginal survival; % (n)	Head capsule width; μm	First instar; d (n)	Second instar; d (n)	Third instar; d (n)	Fourth instar; d (n)	Preimaginal development; d (n)	Preimaginal survival; % (n = 20)	Adult dry weight; mg (n)	Hind tibial length, mm (n)
Morning glory	9.7 ± 0.3 (15)	78.9 (19)	294.2 ± 4.0 (15)	2.0 ± 0.1 (18)	1.4 ± 0.2 (18)	1.8 ± 0.2 (17)	3.7 ± 0.2 (12)	12.0 ± 0.2 (12)	60.0	8.2 ± 0.4 (12)	1.69 ± 0.04 (12)
Soybean	10.8 ± 1.0 (6)	31.8 (19)	295.8 ± 5.3 (6)	2.6 ± 0.1 (14)	1.4 ± 0.2 (13)	1.9 ± 0.2 (10)	4.3 ± 0.2 (6)	13.1 ± 0.3 (8)	40.0	6.1 ± 0.2 (8)	1.69 ± 0.02 (8)
No-plant control	9.4 ± 0.1 (14)	82.4 (17)	284.8 ± 3.0 (14)	2.0 ± 0 (19)	1.0 ± 0 (19)	1.7 ± 0. 1 (19)	3.5 ± 0.1 (19)	11.4 ± 0.1 (19)	95.0	9.9 ± 0.4 (19)	1.71 ± 0.03 (19)

($\chi^2_2 = 2.32$, $P = 0.31$) (Table 3). When nymphal survival is directly compared between *I. hederacea* and soybean, those nymphs reared on *I. hederacea* survive better ($\chi^2_1 = 8.66$, $P = 0.003$), but nymphs developed at similar rates in these two treatments ($\chi^2_1 = 33$, $P = 0.33$) (Table 3). Head widths of adult *O. insidiosus* were unaffected by treatment ($\chi^2_2 = 4.45$, $P = 0.11$) (Table 3).

There was a treatment effect on preimaginal survival of *H. axyridis* ($\chi^2_2 = 13.63$, $P = 0.001$), and on preimaginal developmental rates ($\chi^2_2 = 17.66$, $P < 0.001$) when the analysis included the no-plant control (Table 3). *Harmonia axyridis* survived equally well on *I. hederacea* and soybean ($\chi^2_1 = 1.60$, $P = 0.21$), but larvae reared with *I. hederacea* developed faster than those with soybean ($\chi^2_1 = 15.5$, $P = 0.006$) (Table 3). The differences between *H. axyridis* reared on *I. hederacea* and soybean were only present during the first and fourth stadia (first instars: $\chi^2_1 = 62$, $P = 0.004$; second instars: $\chi^2_1 = 120$, $P = 0.89$; third instars: $\chi^2_1 = 79$, $P = 0.73$; fourth instars: $\chi^2_1 = 79$, $P = 0.047$). There was no treatment effect on *H. axyridis* hind tibial lengths ($\chi^2_2 = 1.33$, $P = 0.51$), but there was on dry weight ($\chi^2_2 = 21.39$, $P < 0.001$) (Table 3). Beetles exposed to *I. hederacea* were heavier than those exposed to soybean ($\chi^2_1 = 89$, $P = 0.002$) (Table 3).

Discussion

Base genetics and aphid resistance in soybean were shown to directly affect key predators of *A. glycines* in laboratory assays for three out of 13 traits measured (when no-plant controls were excluded). However, soybean irrespective of genotype was a relatively poor plant for *O. insidiosus* and *H. axyridis*, as both predators performed substantially better when reared with leaves of *I. hederacea* than with soybean. Direct adverse effects of soybean traits on predators may partially explain the poor performance of predators reared in laboratory studies with soybeans and prey (Butler and O'Neil 2007a; Butler and O'Neil 2007b, but see Naranjo and Stimac 1985; Mignault et al. 2006). Rogers and Sullivan (1986, 1987) found that adverse effects of soybean on omnivorous predators differed depending on whether whole plants or leaf sections were used in the assays. In their research, resistant soybeans only affected *Geocoris punctipes* (Say) when the leaves were attached to the plant. That detached leaves reduced *H. axyridis* performance in our study suggests that the *Rag1* gene operates differently than some other forms of herbivore resistance currently known in soybeans. Variable suitability among soybean varieties for these different predators could potentially be manipulated to favor predators of *A. glycines* (Bottrell et al. 1998). Adult *O. insidiosus* lived longer on soybeans possessing Group C base genetics, and aphid resistance in soybean was associated with reduced longevity in *H. axyridis* adults. The direct effects of soybean genetics on biological control should be considered when integrating HPR and varietal selections into IPM systems.

The mechanisms that operate in this HPR system are largely unknown, but our data are in line with the hypothesis that plant chemistry or nutrition at the level of plant variety may reduce predator performance. Although confined with plant tissue, there was sufficient space within the arenas that the predators could have avoided contact with the plant tissues (indeed, the prey were not in contact with the soybean leaves). This possibly suggests that nutritional requirements of the predators necessitated that they consume plant-based foods that were ultimately toxic to them. Alternatively, the predators may not have consumed plant material, but were affected through direct contact with soybean or by volatile emissions from soybean plants. Soybean and other legumes possess an array of secondary chemicals that aid in their defense against herbivores (Chiang and Norris 1983; Pusztai et al. 1983; Seigler 2003). Although the genes responsible for *A. glycines* resistance in soybean have been isolated, the mechanism that confers resistance has not been determined (Hill et al. 2006a; Hill et al. 2006b). However this resistance trait operates against *A. glycines*, it also functions against *H. axyridis* to produce shorter-lived adults.

It is striking that for both predators, the life stage most affected by soybean treatments was the adult stage. In both predator species, evidence indicates that the immature stages are more phytophagous than the adult stages (Lundgren et al. 2008; Lundgren et al. 2004). This would suggest that either the adult stage uses soybean differently than the immatures in ways that increases their exposure to lethal characteristics of the soybean, or that the physiology of adults renders them particularly prone to the effects of the crop. An additional explanation is that some of the effects of the soybean varieties may be chronic, and only manifest themselves after prolonged exposures. It seems likely that the high mortality (usually >50%) incurred by immatures of these predators on soybean masks treatment effects experienced by this life stage.

Finally, the fact that natural enemies performed poorly on soybean makes a defensible argument for the inclusion of non-crop plants within soybean fields as a means of conserving natural enemies of *A. glycines*. Predators reared with soybean developed more slowly, had lower survival, and had reduced size compared to those reared with *I. hederacea* leaves. Currently, conventional production practices entail the use of herbicides to maintain large monocultures of soybean, and these practices may be exacerbating problems with *A. glycines*. While it is true

that predators are able to colonize soybean monocultures, additional plant diversity at the landscape and within-field levels favors natural enemies in cropland (Landis and Menalled 1998; Landis et al. 2005; Thies and Tscharntke 1999). For example, *Orius insidiosus* is known to preferentially oviposit on plants that best support developing nymphs, and they lay eggs on non-crop plants more frequently than on the crop within soybean fields (Lundgren et al. 2008; Lundgren et al. 2009). Whether and how non-crop plants can be implemented in order to reduce *A. glycines* densities remains to be established.

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References

Barbosa P (ed) (1998) Conservation Biological Control. Academic Press, Ltd, San Diego, CA 396pp

Bottrell DG, Barbosa P, Gould F (1998) Manipulating natural enemies by plant variety selection and modification: a realistic strategy? Annu Rev Entomol 43:347–367. doi:10.1146/annurev.ento.43.1.347

Brosius TR, Higley LG, Hunt TE (2007) Population dynamics of soybean aphid and biotic mortality at the edge of its range. J Econ Entomol 100:1268–1275. doi:10.1603/0022-0493(2007)100[1268:PDOSAA]2.0.CO;2

Butler CD, O'Neil RJ (2007a) Life history characteristics of *Orius insidiosus* (Say) fed *Aphis glycines* Matsumura. Biol Control 40:333–338. doi:10.1016/j.biocontrol.2006.12.006

Butler CD, O'Neil RJ (2007b) Life history characteristics of *Orius insidiosus* (Say) fed diets of soybean aphid, *Aphis glycines* Matsumura and soybean thrips, *Neohydatothrips variabilis* (Beach). Biol Control 40:339–346. doi:10.1016/j.biocontrol.2006.12.005

Chiang H-S, Norris DM (1983) Phenolic and tannin contents as related to anatomical parameters of soybean resistance to agromyzid bean flies. J Agric Food Chem 31:726–730. doi:10.1021/jf00118a012

Corey D, Kambhampati S, Wilde GE (1998) Electrophoretic analysis of *Orius insidiosus* (Hemiptera: Anthocoridae) feeding habits in field corn. J Kans Entomol Soc 71:11–17

Costamagna AC, Landis DA (2006) Predators exert top-down control of soybean aphid across a gradient of agricultural management systems. Ecol Appl 16:1619–1628. doi:10.1890/1051-0761(2006)016[1619:PETCOS]2.0.CO;2

Costamagna AC, Landis DA (2007) Quantifying predation on soybean aphid through direct field observations. Biol Control 42:16–24. doi:10.1016/j.biocontrol.2007.04.001

Costamagna AC, Landis DA, DiFonzo CD (2007) Suppression of soybean aphid by generalist predators results in a trophic cascade in soybeans. Ecol Appl 17:441–451. doi:10.1890/06-0284

Dicke FF, Jarvis JL (1962) The habits and seasonal abundance of *Orius insidiosus* (Say) (Hemiptera: Heteroptera: Anthocoridae) on corn. J Kans Entomol Soc 35:339–344

Eigenbrode SD, Castagnola T, Roux MB, Steljes L (1996) Mobility of three generalist predators is greater on cabbage with glossy leaf wax than on cabbage with a wax bloom. Entomol Exp Appl 91:335–343. doi:10.1007/BF00187043

Eigenbrode SD, Moodie S, Castagnola T (1995) Predators mediate host plant resistance to a phytophagous pest in cabbage with glossy leaf wax. Entomol Exp Appl 77:335–342. doi:10.1007/BF02383068

Fox TB, Landis DA, Cardoso FF, DiFonzo CD (2004) Predators suppress *Aphis glycines* Matsumura population growth in soybean. Environ Entomol 33:608–618

Hagen KS (1986) Ecosystem analysis: plant cultivars (HPR), entomophagous species and food supplements. In: Boethel DJ, Eikenbary RD (eds) Ecosystem analysis: plant cultivars (HPR), entomophagous species and food supplements. Ellis Horwood Publishers, Chichester, UK, pp 151–197

Hare JD (1992) Effects of plant variation on herbivore-natural enemy interactions. In: Fritz RS, Simms EL (eds) Effects of plant variation on herbivore-natural enemy interactions. University of Chicago Press, Chicago, IL, pp 278–298

Harwood JD, Desneux N, Yoo HJS, Rowley DL, Greenstone MH, Obrycki JJ, O'Neil RJ (2007) Tracking the role of alternative prey in soybean aphid predation by *Orius insidiosus*: a molecular approach. Mol Ecol 16:4390–4400. doi:10.1111/j.1365-294X.2007.03482.x

Harwood JD, Yoo HJS, Greenstone MH, Rowley DL, O'Neil RJ (2009) Differential impact of adults and nymphs of a generalist predator on an exotic invasive pest demonstrated by molecular gut-content analysis. Biol Invasions. doi:10.1007/s10530-008-9302-6

Hesler LS, Dashiell KE (2007) Resistance to *Aphis glycines* (Hemiptera: Aphididae) in various soybean lines under controlled laboratory conditions. J Econ Entomol 100:1464–1469. doi:10.1603/0022-0493(2007)100[1464:RTAGHA]2.0.CO;2

Hesler LS, Dashiell KE (2008) Identification and characterization of new sources of resistance to *Aphis glycines* Matsumura (Hemiptera: Aphididae) in soybean lines. Appl Entomol Zool (Jpn) 43:197–206. doi:10.1303/aez.2008.197

Hesler LS, Dashiell KE, Lundgren JG (2007) Characterization of resistance to *Aphis glycines* in soybean accessions. Euphytica 154:91–99. doi:10.1007/s10681-006-9273-6

Hill CB, Li Y, Hartman GL (2004) Resistance to the soybean aphid in soybean germplasm. Crop Sci 44:98–106

Hill CB, Li Y, Hartman GL (2006a) A single dominant gene for resistance to the soybean aphid in the soybean cultivar Dowling. Crop Sci 46:1601–1605. doi:10.2135/cropsci2005.11-0421

Hill CB, Li Y, Hartman GL (2006b) Soybean aphid resistance in soybean Jackson is controlled by a single dominant gene. Crop Sci 46:1606–1608. doi:10.2135/cropsci2005.11-0438

Kauffman WC, Flanders RV (1985) Effects of variably resistant soybean and lima bean cultivars on *Pediobius foveolatus* (Hymenoptera: Eulophidae), a parasitoid of the Mexican bean beetle, *Epilachna varivestis* (Coleoptera: Coccinellidae). Environ Entomol 14:678–682

Kennedy GG, Kishaba AN, Bohn GW (1975) Response of several pest species to *Cucumis melo* L. lines resistant to *Aphis gossypii* Glover. Environ Entomol 4:653–657

Landis DA, Menalled FD (1998) Ecological considerations in teh conservation of effective parasitoid communities in agricultural systems. In: Barbosa P (ed) Ecological considerations in teh conservation of effective parasitoid communities in agricultural systems. Academic Press, London, UK, pp 101–123

Landis DA, Menalled FD, Costamagna AC, Wilkinson TK (2005) Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes. Weed Sci 53:902–908. doi:10.1614/WS-04-050R1.1

Landis DA, Wratten SD, Gurr GM (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. Annu Rev Entomol 45:175–201. doi:10.1146/annurev.ento.45.1.175

Li Y, Hill CB, Hartman GL (2004) Effect of three resistant genotypes on the fecundity, mortality, and maturation of soybean aphid (Homoptera: Aphididae). J Econ Entomol 97:1106–1111. doi:10.1603/0022-0493(2004)097[1106:EOTRSG]2.0.CO;2

Lundgren JG (2009) Relationships of natural enemies and non-prey foods. Progress in Biological Control, vol 7. Springer Science

Lundgren JG, Fergen JK (2006) The oviposition behavior of the predator *Orius insidiosus:* Acceptability and preference for different plants. BioControl 51:217–227. doi:10.1007/s10526-005-0609-2

Lundgren JG, Fergen JK, Riedell WE (2008) The influence of plant anatomy on oviposition and reproductive success of the omnivorous bug, *Orius insidiosus*. Anim Behav 75:1495–1502. doi:10.1016/j.anbehav.2007.09.029

Lundgren JG, Razzak AA, Wiedenmann RN (2004) Population responses and food consumption by predators *Coleomegilla maculata* and *Harmonia axyridis* (Coleoptera: Coccinellidae) during anthesis in an Illinois cornfield. Environ Entomol 33:958–963

Lundgren JG, Wiedenmann RN (2004) Nutritional suitability of corn pollen for the predator *Coleomegilla maculata* (Coleoptera: Coccinellidae). J Insect Physiol 50:567–575. doi:10.1016/j.jinsphys.2004.04.003

Lundgren JG, Wyckhuys KAG, Desneux N (2009) Population responses by *Orius insidiosus* to vegetational diversity. BioControl. doi:10.1007/s10526-008-9165-x

McCornack BP, Ragsdale DW, Venette RC (2004) Demography of soybean aphid (Homoptera: Aphididae) at summer temperatures. J Econ Entomol 97:854–861. doi:10.1603/0022-0493(2004)097[0854:DOSAHA]2.0.CO;2

Mensah C, DiFonzo CD, Nelson RL, Wong D (2005) Resistance to soybean aphid in early maturing soybean germplasm. Crop Sci 45:2228–2233. doi:10.2135/cropsci2004.0680

Mignault M-P, Roy M, Brodeur J (2006) Soybean aphid predators in Quebec and the suitability of *Aphis glycines* as prey for three Coccinellidae. BioControl 51:89–106. doi:10.1007/s10526-005-1517-1

Moser SE, Harwood JD, Obrycki JJ (2008) Larval feeding on Bt hybrid and non-Bt corn seedlings by *Harmonia axyridis* (Coleoptera: Coccinellidae) and *Coleomegilla maculata* (Coleoptera: Coccinellidae). Environ Entomol 37:525–533. doi:10.1603/0046-225X(2008)37[525:LFOBHA]2.0.CO;2

Naranjo SE, Stimac JL (1985) Development, survival, and reproduction of *Geocoris punctipes* (Hemiptera: Lygaeidae): effects of plant feeding on soybean and associated weeds. Environ Entomol 14:523–530

Orr DB, Boethel DJ (1986) Influence of plant antibiosis through four trophic levels. Oecologia 70:242–249. doi:10.1007/BF00379247

Pair SD, Wiseman BR, Sparks AN (1986) Influence of four corn cultivars on fall armyworm (Lepidoptera: Noctuidae) establishment and parasitization. Fla Entomol 69:566–570. doi:10.2307/3495391

Panda N, Khush GS (1995) Host Plant Resistance to Insects. CABI Publishers, Oxon, UK

Pickett CH, Bugg RL (eds) (1998) Enhancing biological control: habitat management to promote natural enemies of agricultural pests. University of California Press, Berkeley, CA 448pp

Pusztai A, Croy RRD, Grant G, Stewart JC (1983) Seed lectins: distribution, location and biological role. In: Daussant J, Mosse J, Vaughan J (eds) Seed lectins: distribution, location and biological role. Academic Publishers, London, UK, pp 53–82

Rogers DJ, Sullivan MJ (1986) Nymphal performance of *Geocoris punctipes* (Hemiptera: Lygaeidae) on pest-resistant soybeans. Environ Entomol 15:1032–1036

Rogers DJ, Sullivan MJ (1987) Growth of *Geocoris punctipes* (Hemiptera: Lygaeidae) on attached and detached leaves of pest-resistant soybeans. J Entomol Sci 22:282–285

Rutledge CE, O'Neil RJ (2005) *Orius insidiosus* (Say) as a predator of the soybean aphid, *Aphis glycines* Matsumura. Biol Control 33:56–64. doi:10.1016/j.biocontrol.2005.01.001

Schmidt NP, O'Neal ME, Dixon PM (2008) Aphidophagous predators in Iowa soybean: a community comparison across multiple years and sampling methods. Ann Entomol Soc Am 101:341–350. doi:10.1603/0013-8746(2008)101[341:APIISA]2.0.CO;2

Seigler DS (2003) Phytochemistry of *Acacia- sensu lato*. Biochem Syst Ecol 31:845–873. doi:10.1016/S0305-1978(03)00082-6

Simmons AT, Gurr GM (2004) Trichome-based host plant resistance of *Lycopersicon* species and the biocontrol agent *Mallada signata*: are they compatible? Entomol Exp Appl 113:95–101. doi:10.1111/j.0013-8703.2004.00210.x

Smith CM (2005) Plant Resistance to Arthropods. Springer, Dordrecht, The Netherlands

Starks KJ, Munippan R, Eikenbary RD (1972) Intearction between plant resistance and parasitism against the greenbug on barley and sorghum. Ann Entomol Soc Am 65:650–655

Thies C, Tscharntke T (1999) Landscape structure and biological control in agroecosystems. Science 285:893–895. doi:10.1126/science.285.5429.893

Treacy MF, Benedict JH, Lopez JD, Morrison RK (1987) Function respons of a predator (Neuroptera: Chrysopidae) to bollowrm (Lepidoptera: Noctuidae) eggs on smoothleaf, hirsute, and pilose cottons. J Econ Entomol 80:376–379

van Emden HF (1986) The interaction of plant resistance and natural enemies: effects on populations of sucking insects. In: Boethel DJ, Eikenbary RD (eds) The interaction of plant resistance and natural enemies: effects on populations of sucking insects. Ellis Horwood Publishers, Chichester, UK, pp 138–150

van Emden HF (1995) Host plant-aphidophaga interactions. Agric Ecosyst Environ 52:3–11. doi:10.1016/0167-8809(94)09001-N

Venette RC, Ragsdale DW (2004) Assessing the invasion by soybean aphid (Homoptera: Aphididae): where will it end? Ann Entomol Soc Am 97:219–226. doi:10.1603/0013-8746(2004)097[0219:ATIBSA]2.0.CO;2

Wyatt IJ (1970) The distribution of *Myzus persicae* (Sulz.) on year-round chrysanthemums. II. Winter season: the effect of parasitism by *Aphidius matricariae* Hal. Ann Appl Biol 65:31–41. doi:10.1111/j.1744-7348.1970.tb04559.x