

Orius insidiosus (Say) as a predator of the soybean aphid, *Aphis glycines* Matsumura

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Received 13 September 2004; accepted 4 January 2005

Abstract

The soybean aphid, *Aphis glycines* Matsumura, a pest of soybeans in Asia, invaded North America recently. The indigenous generalist predator *Orius insidiosus* (Say) is common in Midwestern US soybean fields throughout the soybean-growing season. From its phenology and abundance, we hypothesize that this predator could act to suppress soybean aphid population growth by attacking aphids during the critical period when aphids are first colonizing soybean fields. Therefore we conducted a series of laboratory assays of *O. insidiosus* to evaluate the conditions under which it may effectively suppress aphid population growth. We conducted a standard functional response experiment and found that *O. insidiosus* had a maximum attack rate of 19.25 (± 0.06 SE) aphids in 24 h. We examined the ability of *O. insidiosus* to suppress aphid population growth over a four-day period in microcosms with different numbers of aphids, plant sizes, and plant numbers. We found that predators were able to effectively suppress aphid population growth, but that their efficacy depended upon the number of prey present and characteristics of the plant on which prey were found. Further, we showed that *O. insidiosus* was able to suppress aphid population growth below starting densities for an extended time period (12 days). These results suggest that under certain conditions, *O. insidiosus* can effectively suppress aphid population growth and that they may be key factors influencing aphid population dynamics in soybeans.

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Keywords: Soybean aphid; *Aphis glycines*; *Orius insidiosus*; Biological control; Population suppression

1. Introduction

The soybean aphid, *Aphis glycines* Matsumura (Homoptera: Aphididae), a pest of soybeans in Asia, recently invaded North America. Soybean aphids were discovered infesting soybean fields in the Midwest in the summer of 2000, and by 2003 had been found in over 21 states and three Canadian provinces (Ragsdale et al., 2004). The soybean aphid reduces yield directly via plant feeding and indirectly through virus transmission and reduction in seed protein content (D'yakonov, 1975; Halbert et al., 1986; van den Berg et al., 1997;

Wang et al., 1994). In a Wisconsin study, high levels of aphid infestation in 2003 were associated with up to 50% reduction in yield (Meyers and Hogg, 2003). We have seen yield reductions of up to 25% in Indiana (RJO unpublished data). The aphid has served as a key-stone pest, triggering insecticide applications in soybean fields throughout the US and Canada. For many locations, this was the first time ever that soybean fields were treated for any insect pest.

In Asia, the soybean aphid is attacked by braconid and aphelinid parasitoids, fungal pathogens, and predatory coccinellids, chamaemyids, syrphids, anthocorids, and chrysopids (Chang et al., 1994; Heimpel et al., 2004; Quimio and Calilung, 1993; van den Berg et al., 1997; Wang and Ba, 1998). In Indonesia, naturally occurring populations of the coccinellid *Harmonia arcuata* (Fab.) and the staphylinid *Paederus fuscipes* Curtis play important roles

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in aphid population dynamics (van den Berg et al., 1997). In the Midwestern United States, surveys of the natural enemies of the soybean aphid have shown that predators commonly dominate the natural enemy community (Rutledge et al., 2004). Although aphid populations can drop precipitously during fungal epizootics (Ragsdale et al., 2004) and occasionally parasitism rates can be locally high, predators remain the most significant natural enemy in midwestern soybean fields (Rutledge et al., 2004).

A common predator in Indiana, and other midwestern soybean fields, is *Orius insidiosus* (Say) (Heteroptera: Anthicoridae) (Bary, 1973; Clements and Yeargan, 1997; Raney and Yeargan, 1977; Rutledge et al., 2004). *O. insidiosus* is a generalist predator, and its population dynamics in soybean fields have been linked to both thrips population levels (Isenhour and Marston, 1981; Kampmeier, 1984; RJO, unpublished data) and soybean flowering (Isenhour and Marston, 1981). Both nymphs and adults have been observed eating soybean aphids in the field (Rutledge et al., 2004), and *O. insidiosus* can complete its life cycle on a diet of soybean aphids in the laboratory (RJO, unpublished data). *O. insidiosus* is generally present in Indiana soybean fields when soybean aphids arrive. During the aphid's initial colonization of the crop *O. insidiosus* is typically the numerically dominant predator (Rutledge et al., 2004).

In annual crop systems, such as soybeans, early season predators have the potential to suppress populations of invading pests before the pests reach high population levels (Chang and Kareiva, 1999; Murdoch et al., 1985; Symondson et al., 2002; Wiedenmann and Smith, 1997). The presence of *O. insidiosus* in soybean fields when soybean aphids arrive suggests that it could have a significant impact on aphid population growth, and potentially suppress aphid outbreaks. In 2001 this potential was indicated by an inverse relationship between number of weeks that *O. insidiosus* colonized a field before soybean aphid arrival, and eventual severity of the soybean aphid infestation (Rutledge et al., 2004). The coincidence of *O. insidiosus* with respect to soybean aphid arrival and subsequent dynamics suggest that predation by *O. insidiosus* early in the invasion cycle can be key to preventing an aphid outbreak (see also Landis and van der Werf, 1997).

Factors other than phenology affect a predator's ability to suppress pest populations. Among these are the density and distribution of prey (Flaherty and Huffaker, 1970; Hassell, 1978; Kareiva and Perry, 1989; Kareiva and Sahakian, 1990; Solomon, 1949). For foliar searching predators like *O. insidiosus* (Coll and Ridgway, 1995; Isenhour and Yeargan, 1981), encounter rate between predators and prey will be influenced by both number of prey present and size of the plant upon which prey are located (see O'Neil, 1997). Because these predators traverse the plant to find prey, density of prey can change either through change in prey number or through

changes in plant size. Although the impact of plant size on *O. insidiosus* predation has been assessed in other systems (Coll et al., 1997), its reaction to changes in soybean plant size is not known.

Distribution of prey can also affect their encounter rate with predators (Evans, 1976). In soybeans, soybean aphids are at first sparsely distributed among plants (Ragsdale et al., 2004). As time continues the frequency of occupied plants increases, but numbers of aphids per plant remains low. It is only after most plants in a field have at least one aphid that numbers of aphids per plant increase. Spatial distribution of aphids therefore changes over time. A searching predator must accommodate these changes to encounter and attack enough aphids to influence the aphid's population growth. It is not known how the aphid's distribution pattern affects *O. insidiosus* predation, but if *O. insidiosus* is to suppress early-season aphid population growth it must be able to locate aphids among plants, particularly when aphid numbers per plant are relatively low.

To better understand the conditions under which *O. insidiosus* might impact population dynamics of soybean aphid, we examined several facets of the interaction between soybean aphids and *O. insidiosus* in the laboratory. We determined the maximum attack rate of *O. insidiosus* preying on soybean aphids by measuring its functional response. We then conducted a series of experiments to assess the ability of *O. insidiosus* to suppress aphid population growth during initial aphid colonization conditions, specifically examining number and distribution of aphids, and size of soybean plants. We created different densities of aphids by changing the number of aphids on a plant, and by changing the size of the plant. We examined how aphid distribution affects the ability of *O. insidiosus* to suppress population growth by measuring aphid population growth when aphids were dispersed among plants. Finally, we assessed the ability of the predator to suppress soybean aphid populations over an extended time period. This time period was approximately equal to the length of time when aphid population density in the field is similar to the densities we tested in the laboratory. Our objectives in these experiments were to better understand how these characteristics of the aphid-predator-soybean dynamic affect aphid population growth and to gain insight into the potential of predators like *O. insidiosus* to influence aphid outbreaks in soybeans.

2. Materials and methods

2.1. Plants and insects

2.1.1. Soybeans

Soybeans (var. Beck 366NRR, Beck Hybrids, Atlanta, IN) were planted four to a pot in 26cm pots using

potting mix (All Purpose Potting Mix, Bennett's Greenhouse, Lafayette, IN). Plants were reared in a greenhouse (L:D 16:8, 24°C, RH ~60%) and watered daily. Plants were fertilized with a slow release fertilizer once they reached cotyledon stage (N:P:K 14:14:14, Osmocote, The Scotts, Marysville, OH).

2.1.2. *Soybean aphids*

Aphids were collected in the field in summer 2002 and reared on soybean plants in a greenhouse (L:D 16:8, 24°C, RH ~60%). New plants were supplied to the colony weekly, and infested by placing an aphid-infested leaflet on the new plant's leaves.

2.1.3. *Orius insidiosus*

Adults were collected in the summer and fall of 2002 and reared following the techniques of Ito and Nakata (1988). All life stages were reared in petri-dishes (14 cm × 2 cm) filled with dry, sterilized, and wheat seeds. The wheat seeds provided a greatly increased surface area in the dish and reduced levels of cannibalism by the predators. All life stages were fed frozen *Euphesitia* spp. eggs (Pyralidae: Lepidoptera) (Beneficial Insectaries, CA), and provided soybean stems with the cut end wrapped in cotton to provide moisture. Soybean stems with cotyledons were supplied to adults for oviposition, and then placed into new dishes. Colonies were kept in an incubator (L:D 16:8, 24°C, RH ~60%). All tests were conducted with adult female *O. insidiosus* that were at least 4 days old. Before the beginning of each experiment, female adults were isolated in individual vials with a moist cotton plug, but no food, for 18 h. Predators were in colonies approximately three generations (4 months) prior to the start of experiments.

2.2. Experimental protocols

All experiments were conducted under laboratory conditions (L:D 16:8, 24°C, RH ~60%) with fluorescent lighting.

2.2.1. Functional response of *O. insidiosus* to soybean aphids

We measured the functional response of *O. insidiosus* to soybean aphids in a petri-dish (9 cm × 1.5 cm) lined with filter paper. A single soybean leaflet (~20 cm²) with its stem placed into a small water-filled vial provided a substrate for the feeding aphids. We tested *O. insidiosus* against 2, 4, 8, 16, 32, and 64 aphids. Predators were introduced 2 h after the aphids were placed on the plant to allow the aphids time to settle on the plant's surface. All aphids were between the second and fourth instar. After 24 h, predators were removed, and the remaining soybean aphids were counted. We assumed missing aphids were eaten, as preliminary study indicated nearly 100% survival of aphids in the absence of predators.

We conducted eight replicates at each aphid number. Replicates were discarded if first-instar aphids were present, indicating that reproduction had taken place. Replicates were also discarded if the predator had escaped, or had died.

Because we did not replace aphids as they were eaten, the prey number decreased with each prey item removed. Therefore, we followed the methods of Juliano (1993) to fit the data to Rogers' (1972) random predator equation. Using this method, the type of functional response (I, II or III) displayed by the data is first determined by linear regression in PROC CATMOD (SAS, 2000). In this method, the polynomial function that describes the relationship between the proportion of aphids eaten at each density and each initial density is determined. If the first term in that function is negative, the predator is displaying a Type II functional response, if positive, a Type III (Juliano, 1993). After the type of functional response was determined, the data were fit to the random predator equation in PROC NLIN (SAS, 2000). Instantaneous search rate and handling time were estimated by fitting Rogers' equation to the data and were not measured independently.

2.2.2. Suppression of soybean aphid population growth by *O. insidiosus*

To assess the ability of *O. insidiosus* to suppress aphid population growth, we measured population growth of soybean aphids on plants in microcosms with and without a predator. Placing a clear acetate cylinder over a potted soybean plant created a microcosm. Cylinders had a mesh top and windows for ventilation, and measured 50 cm high × 15 cm in diameter. Sand was placed on the soil surface to provide a substrate into which the cylinder could be easily pushed to ensure a complete seal. Plants used in these experiments had two unifoliate leaves and one trifoliate leaf (soybean vegetative stage V-1, Herman, 1988) and an average leaf area of 187.3 cm² (SE ± 38.56 cm²). We used leaf area as a measure of plant size as it has been used in other studies of predation in crops (O'Neil, 1997; Wiedenmann and O'Neil, 1992), and we have observed *O. insidiosus* searching soybean leaves for prey in the field (RJO, unpublished data).

Adult apterous aphids were used in all trials. Treatment levels were 12, 24, 48, and 64 aphids. Within each plant, aphids were divided as evenly as possible amongst nodes, and then leaflets. Each plant had 2 nodes and 5 leaflets. Therefore, for example, for a starting number of 24 aphids, the first node, which had 2 leaflets, received 6 aphids per leaflet. The second node, with 3 leaflets, received 4 aphids on each leaflet. All experiments were run for 4 days, which preliminary experiments had shown was sufficient time for aphid populations to double in the absence of predation. At the end of the 4 days all aphids were counted. Replicates in which the

predator was missing, or dead, were excluded from analysis. Control plants had the same aphid number as the treatment plants, but no *O. insidiosus* was introduced into the system. Each treatment and control was repeated until 10 replicates were completed.

The final size of the soybean aphid population was compared between microcosms with and without predators for each starting number of aphids using the Student's *t* test (SAS, 2000).

2.2.3. Impact of plant architecture and number on suppression of soybean aphids by *O. insidiosus*

These experiments followed the same protocol as the experiment above, with the addition of variation in plant number and plant size.

In the first treatment, a single plant with two unifoliate leaves and one trifoliate leaf (soybean vegetative stage V-1, Herman, 1988) and an average leaf area of 187.3 cm² (SE ± 38.56 cm²) was used (Table 1). In the second treatment there were three plants in the microcosm. The plants were the same stage, V-1, as the plants in the first treatment and had a combined leaf area of 438.05 cm² (SE ± 42.54 cm²; Table 1). When aphids first arrive in a soybean field, their distribution is patchy, and it is common to find several aphids on one plant and none on the neighboring plants (Ragsdale et al., 2004). To be an effective predator under low-density conditions, the predator must be able to move between plants and locate plants with aphids, and the aphids on those plants. Therefore in this treatment all aphids were placed on one plant out of the three. In the final treatment, aphids were placed on a single plant with two unifoliate leaves and three trifoliate leaves, soybean vegetative stage V-3, with an average leaf area of 421.4 cm² (SE ± 55.28 cm², Table 1). After each trial we measured the stem length of each plant, and measured its leaf area using a LI-3100 Area Meter (Li-Cor, Lincoln, NE). This allowed us to calculate the surface to edge ratio for the plants. This ratio is important for edge-searching predators such as *O. insidiosus* (Isenhour and Yeorgan, 1981; Shields and Watson, 1980) as low surface area to edge ratios have been shown to reduce predator, and parasitoid, efficiency (Andow and Prokrym, 1990; Cloyd and Sadof, 2000; Frazer and McGregor, 1994; Kaiser, 1983; LeGrand and Barbosa, 2003). The three treatments also differed in the number of junctions. A junction (*sensu*

LeGrand and Barbosa, 2003) is a point where a predator is faced with a decision as to which route to take, such as the junction of a leaf petiole and the stem. The number of junctions per treatment is listed in Table 1.

In all treatments, aphids were distributed within plants as described in the previous experiment. The experiments on the suppression of aphids by *O. insidiosus* on a single plant showed that the predator could suppress aphid population growth for aphid numbers up to, but not including 64 aphids. Therefore, we started with one half, and one quarter, of that number of aphids, 32 and 16 aphids, respectively, in all treatments. This allowed us to see if the predators were as effective on the larger plants, or in more complex arenas, as they were on a single plant.

We used a general linear model, PROC GLM to compare various components of plant architecture, among the three treatments (SAS, 2000). We used least squares means to further discriminate among the treatments. We used a general linear model, PROC GLM, to compare the growth of aphid populations on plants with and without predators within each experiment (SAS, 2000). We used least squares means to examine differences between treatments with and without predators at each starting number of aphids. In order to normalize the data we used the ratio of the number of aphids at the start of the trial to the number of aphids at the end of the trial, the fold-increase, as the response variable instead of the absolute numbers of aphids.

We also used a general linear model to compare the growth of aphid populations on all treatments at the lowest initial starting number of aphids, 16. This allowed us to compare effectiveness of predators at the population level for which they were able to suppress aphid populations in all microcosm treatments. Least squares means were used to examine the difference between fold-aphid increases for each of the three treatments.

2.2.4. Suppression of soybean aphids by *O. insidiosus* over time

In this experiment, we examined the ability of *O. insidiosus* to suppress aphid populations over a longer time period. Single female adult predators were confined in a microcosm with 24 aphids on a V-1 stage plant. Control replicates had no predator. The treatments varied in the number of days they lasted, and were 4, 8, and 12 days

Table 1
Architectural characteristics of soybean plants in the experiments on the impact of plant structure and number on *O. insidiosus* predation

Plant # and stage	# Stems	Average total stem length	# Leaflets	Average leaf surface area	Surface area/edge ratio	# Junctions
1 V-1	1	11.05 (±0.35) ^{a,*}	5	187.3 (±28.56) ^a	2.16 (+0.04) ^a	20
3 V-1	3	34.89 (±0.72) ^b	15	438.1 (±42.54) ^b	1.92 (+0.02) ^b	60
1 V-3	1	18.46 (±0.76) ^c	11	421.4 (±55.28) ^b	1.65 (+0.04) ^c	48

Number of junctions refers to the number of places on the plant where a predator must choose between two or more directions (e.g., the junction between a petiole and stem).

* Values with the same letter are not significantly different from other values in the same column.

long, respectively. Twelve days is roughly equivalent to the time period during which aphid densities in the field are within the density range that we tested in our experiments. For example, in our 2003 experimental plots, the number of aphids increased from 1 per plant to 45 per plant over the course of 2 weeks. The next week there were 500 aphids on the plant. The density of the aphids during this time period was similar to the conditions we tested in the laboratory; aphids increased from 0.01 aphids per cm² of leaf surface to 0.24 aphids per cm² (RJO, unpublished data). Treatments were sampled destructively as they finished (at 4, 8, and 12 days) and the aphids were counted in replicates with and without predators.

We used general linear models, PROC GLM to compare the influence of the length of treatment (4, 8, and 12 days) and presence of predators on aphid population growth rates (SAS, 2000). As the data conformed to a normal distribution, we used the number of aphids at the end of each time period, instead of fold-increase, as the measure of aphid population growth.

3. Results

3.1. Functional response of *O. insidiosus* to soybean aphids

Orius insidiosus showed a Type II functional response to soybean aphid (Fig. 1). This was shown by the negative first term of the linear regression of the proportion of aphids consumed at each density versus each initial density of aphids. In the treatment with the highest number of aphids, 64, *O. insidiosus* attacked an average of 19.25 (± 3.38 SE) aphids in 24 h. Estimated handling time, T_h , was 0.705 (± 0.29 SE) h. The model estimated

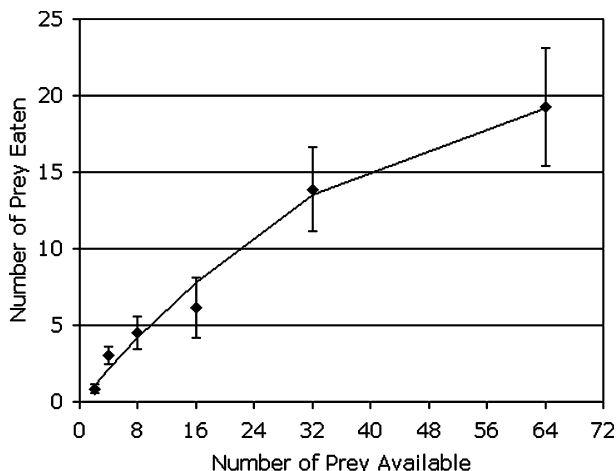


Fig. 1. Functional response of *O. insidiosus* to soybean aphid in a petri-dish arena. Points show average number of aphids eaten by *O. insidiosus* at each level of prey availability. Error bars show standard error. The line shows the fitted model for Rodgers' random predator equation for a Type II functional response.

search rate, a , was 0.035 (± 0.01 SE) h⁻¹. A Type II functional response for *O. insidiosus* has been reported for other prey items, such as soybean thrips (Isenhour and Yeagan, 1981) corn earworm eggs (Coll and Ridgway, 1995) and spider mites (van den Meiracker and Sabelis, 1999).

3.2. Suppression of soybean aphid population growth by *O. insidiosus*

Orius insidiosus was able to suppress soybean aphid population growth as compared to aphid population growth in treatments without predators in treatments with starting numbers of 12, 24, and 48 aphids. When the starting number of aphids was 64, the increase in aphid numbers was not significantly different between the replicates with and without a predator present (Fig. 2).

3.3. Impact of plant architecture and number on suppression of soybean aphids by *O. insidiosus*

Average leaf area, number of leaflets, number of stems, and average stem length for each treatment, as well as the significant differences among plant architectural features, are shown in Table 1. The leaf surface area did not significantly differ between microcosms with one V-3 plant and microcosms with three V-1 plants, and thus the starting density (aphids/cm² of leaf area) of aphids did not significantly differ between the two treatments. However the two treatments differed in several plant architectural characteristics, including leaflet number, stem number, and total stem length (Table 1). In addition to differing plant architectures, the distribution of aphids varied between the three treatments. Aphids were distributed amongst all leaflets and nodes in microcosms with one V-1 plant and one V-3 plant, whereas in microcosms with three V-1 plants, all aphids were placed on only one plant of the three. This meant that there

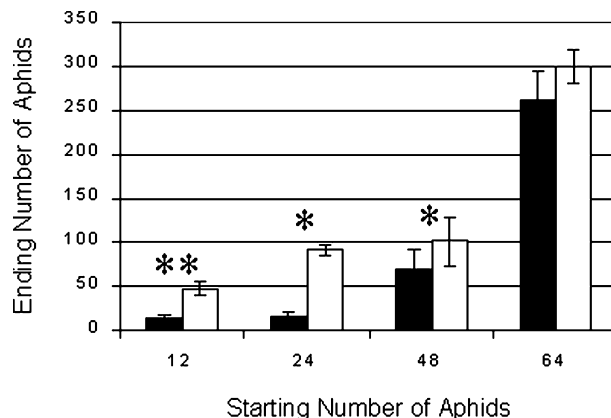


Fig. 2. Average numbers of aphids (\pm SE) at the end of four days with (black bars) or without (open bars) *O. insidiosus*. * $P < 0.05$ and ** $P < 0.001$.

were two 'empty' plants without any aphids, although the aphids were distributed in the same way on the one plant with aphids as they were in the single V-1 plant treatment.

In microcosms with single V-1 plants aphid population growth had a significantly smaller increase when predators were present than in control treatments when the starting number of aphids was 16 or 32 (Table 2). When we increased the number of V-1 plants in the microcosm to three plants, *O. insidiosus* still suppressed aphid population growth compared to controls when the starting number of aphids was 16, but aphid populations in treatments with and without predators increased by the same amount when the starting number of aphids was 32 or 64 (Table 2). Similar results were seen when the size of the soybean plant increased from V-1 to V-3; the predators depressed aphid population growth at 16 aphids, but not when the starting number of aphids was 32 or 64 aphids (Table 2).

When we compared the increase of aphid numbers across treatments at the starting number of 16 aphids, we found *O. insidiosus* suppressed aphid population growth to a greater degree in the treatments with a single plant, regardless of whether it was a V-3 plant or a V-1 plant, than on the treatment with 3 V-1 plants ($df=5$, $F=11.94$, $P=0.0001$). Aphid population increased on average 3.53-fold on the three V-1 plants and only increased an average of 1.07-fold and 1.89-fold on the V-1 and V-3 plants, respectively. The difference between the fold-increase of aphid population size for treatments with predators was significant for treatments 3V-1 and V-3 ($P=0.024$) as well as for treatments 3V-1 and V-1 ($P=0.0036$). The difference in population growth was not different for aphids in trials with predators for V-1 and V-3 ($P=0.389$).

3.4. Suppression of soybean aphids by *O. insidiosus* over time

Orius insidiosus was able to maintain aphid numbers below the initial starting level of 24 aphids for up to 12 days ($df=5$, $F=11.94$, $P=0.0001$, Fig. 3). The difference

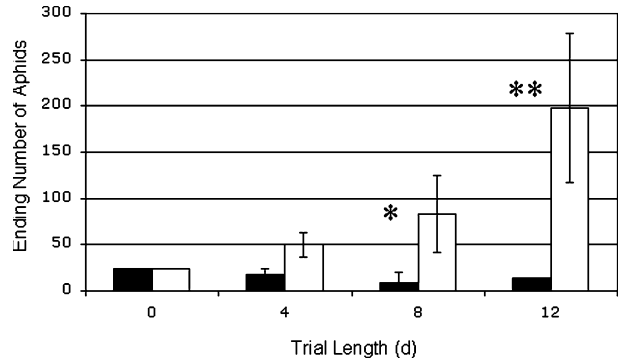


Fig. 3. Average aphid populations (\pm SE) in microcosms with (black bars) and without (open bars) an *O. insidiosus* adult female. Error bars show standard error. * $P < 0.05$ and ** $P < 0.001$.

between the aphid numbers with and without predators was greater in the treatments that lasted longer. Aphid numbers increased 8.2-fold over the course of the 12 days when predators were not present, but decreased 0.58-fold in the treatments with predators. Aphid populations had different growth trajectories over time depending on the presence of the predator as shown by the significant interaction term between predator and time ($df=2$, $F=3.72$, $P=0.044$).

4. Discussion

The ability of *O. insidiosus* to suppress soybean aphid outbreaks depends on its ability to locate, and kill, sufficient number of aphids when they are at relatively low numbers early in the growing season. Our studies help delineate the conditions under which *O. insidiosus* can effectively suppress soybean aphid population growth. For example, the maximum number of aphids attacked measured in the functional response study (ca. 19 aphids per day), provides us with an approximation of the level of aphid reproduction needed to compensate for predation, once *O. insidiosus* have located local patches of aphids in the field. In our experiments, treatments with 16 aphids consistently showed little to no aphid

Table 2

Least squares means comparisons from the test of pre- and post-aphid densities within each of the three aphid suppression experiments

Plant stage	# Plants	# Plants infested	Starting aphids	Without <i>O. insidiosus</i>	With <i>O. insidiosus</i>	<i>P</i> value
V-1	1	1	16	2.56 (± 0.22)	1.07 (± 0.15)	0.0049
			32	3.60 (± 0.36)	2.07 (± 0.51)	0.0019
			64	4.37 (± 0.23)	3.74 (± 0.29)	0.2810
V-1	3	1	16	5.31 (± 0.37)	3.54 (± 0.30)	0.0002
			32	4.41 (± 0.25)	3.72 (± 0.36)	0.3025
			64	4.00 (± 0.32)	3.94 (± 0.14)	0.4144
V-3	1	1	16	5.68 (± 1.21)	1.89 (± 0.24)	0.0001
			32	4.25 (± 0.33)	3.29 (± 0.54)	0.2695
			64	3.97 (± 0.27)	2.66 (± 0.25)	0.1307

Results are from a mixed linear model with the fold-increase in aphid numbers over the course of the experiment as the response variable, and with experiment and starting aphid number as predictor variables.

population growth. Only when aphid number increased to 32 or 64 aphids were the predators unable to prevent aphid population growth in most treatments. It appears therefore that when aphid numbers reach these levels in the field, the predator's maximal attack rate will not be able to compensate for aphid reproduction, and increases in aphid numbers are to be expected.

Besides the absolute number of aphids, aphid density, plant characteristics, and aphid distribution on plants affected the ability of *O. insidiosus* to suppress aphid population growth. While predators could suppress aphid growth in populations of 12–48 aphids on single V-1 plants, predators only suppressed aphid growth when there were initially 16 aphids in the 3 V-1 plants and V-3 plant treatments. Plants in these two latter treatments had approximately twice the leaf area of the single V-1 plant. Thus the density of aphids, the number of aphids per cm² leaf area, was similar when there were 16 aphids on the V-1 plant, and 32 aphids on the 3 V-1 or V-3 plants (each about 0.08 aphids/cm²).

Distribution of aphids within the plant is another issue. On V-3 plants aphids were distributed across 11 leaflets, whereas aphids on V-1 plants were distributed across 5 leaflets. If leaflets represent a "patch" searched by predators, for equal number of aphids per plant, each patch had a larger number of aphids on the V-1 plants than on the V-3 plants. However, the failure of *O. insidiosus* to suppress aphid growth on the V-3 plants with 32 aphids where prey density (ca. 0.08/cm²) and patch size (ca. 3/leaflet) were equal to the V-1 plants with 16 aphids suggest that the number of leaflets mediates the predator's ability to suppress aphid growth. Although the mechanism for this is unknown, if the predator stays within the area where prey were found, they would increase their chances of encountering another prey in the patch (as shown for *Orius tristicolor*, van Laerhoven et al., 2000) but possibly leave less time to find other patches with prey (Hassell and May, 1973, 1974; Hassell et al., 1991). The longer time spent within a patch would therefore provide more time for aphids to reproduce in other patches, potentially providing a mechanism for aphids to escape predation and suppression of aphid population growth by the predator.

Another potential mechanism of aphid escape related to patch size is the reduction of non-consumptive impact of the predator on aphid reproductive rate. Nelson et al., (2004) showed that damsel bugs (*Nabis* spp.) that were rendered unable to kill pea aphids (by amputation of the last segment of their stylets), reduced aphid fertility by forcing aphids to devote time and energy to defensive behaviors rather than to feeding and reproduction. In our experiment, predators may have spent less time per patch in the treatments in which the aphids were spread between more patches. Thus the non-consumptive impact of the *O. insidiosus* may have been reduced in treatments with more patches com-

pared to treatments in which aphids were concentrated in fewer patches.

Predators were more successful at suppressing aphid populations when 16 aphids were on a single V-3 plant than in the three V-1 plants treatments, even though the aphid density (ca. 0.3/cm²) and total leaf area (ca. 430 cm²) were approximately the same in both treatments (Table 1). Plants in these treatments differed in a number of plant structural traits (Table 1). The three V-1 plants had a greater total stem length, and smaller and more numerous leaflets leading to a lower surface area to edge ratio than for the V-3 plants (Table 2). Low surface area to edge ratios have been shown to reduce predator, and parasitoid, efficiency (Andow and Prokrym, 1990; Cloyd and Sadof, 2000; Frazer and McGregor, 1994; Kaiser, 1983; LeGrand and Barbosa, 2003). The increased edge length means that a predator following edges, as does *O. insidiosus* (Isenhour and Yeagan, 1981; Shields and Watson, 1980) will have a longer distance to travel to access the same amount of surface area with its attendant aphids. The increased "travel time" would leave less time to attack aphids, and thereby allow aphids to escape predation on the more architecturally complex plant. Finally, LeGrand and Barbosa (2003) have shown that the number of 'junctions' or points at which a predator must choose between one route or another influences the amount of new surface explored. A high number of junctions can lead to a predator recursively searching the same plant parts and therefore leaving other parts of the plant unexplored. The three V-1 plants microcosms had more junctions than the V-3 plant microcosms (60 vs. 48), and the physical separation of plants in the three V-1 plants added to the difference between the treatments. The time spent traversing plant junctures would reduce the time available to find and attack aphids on these plants.

When confronted with 24 aphids on V-1 plants *O. insidiosus* was able to suppress aphid populations for 12 days, suggesting that *O. insidiosus* may be able to exert sustained pressure on colonizing soybean aphids.

Our studies show that *O. insidiosus*' ability to impact soybean aphid population growth will be affected by the size and architectural characteristics of the crop. This is of practical interest as the timing of aphid invasion relative to crop phenology varies greatly depending on geography. In Indiana, aphids have colonized fields at stages ranging from V-2 to V-9 (Rutledge et al., 2004). Further north in Michigan, aphids are often seen on plants at the cotyledon stage (Rutledge et al., 2004).

The relative numbers of aphids and predators also impact predator effectiveness. Field observations in Indiana show that *O. insidiosus* is often present at the time of aphid invasion into fields and that throughout the season they are more likely to be found on plants with aphids than on plants without aphids (Rutledge et al., 2004). However, *O. insidiosus* abundance and phenology

in soybean fields is often closely tied to that of soybean thrips (Isenhour and Marston, 1981; Kampmeier, 1984; RJO unpublished data). The effect of the relationship between thrips and soybean aphid phenology and abundance on *O. insidiosus*' ability to impact soybean aphid population growth needs to be investigated.

Further study of the soybean aphid-predator-soybean dynamic in larger spatial and temporal scale systems is also needed to better define these relationships and provide additional options to use endemic predators to manage soybean aphids.

Acknowledgments

We thank S. Thomson, S. Fujimura, and C. Butler for their assistance with the experiments. C. Sadof and D. Richmond, and two anonymous reviewers improved the manuscript with their thoughtful comments. This project was partly supported by the Indiana Soybean Board and USDA-NRI competitive Grant # 2003-03334. The project was also supported by the National Research Initiative of the USDA Cooperative State Research, Education and Extension Service, Grant No. 2003-35316-13805. This is Purdue Agricultural Research Program Manuscript No. 2004-17448.

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