

Population responses by *Orius insidiosus* to vegetational diversity

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Abstract The abundance of different life stages of *Orius insidiosus* (Say) (Heteroptera: Anthoridae) and its prey were recorded in vegetationally diverse (soybean and agronomic weeds) and monoculture (soybean only) fields. *Orius insidiosus* adults and nymphs were more abundant in diversified plots than in monocultures. A similar number of *O. insidiosus* eggs were found in the two treatments, but twice as many eggs were laid on non-crop plants than on soybeans within the vegetationally diverse plots. Prey densities were equivalent in the two treatments. In olfactometer assays, naïve *O. insidiosus* females were unresponsive to odors from three weed species (morning glory, redroot pigweed and velvetleaf). The current results,

coupled with previous experimental observations, lead us to believe that higher abundance of *O. insidiosus* in vegetationally diverse habitats could be related to improved fitness of the predator, which in turn is related to certain plant qualities (e.g., nutrition, plant architecture, etc.). Proximal cues are likely more influential to oviposition decisions by *O. insidiosus* females than volatile signals.

Keywords *Aphis glycines* · Biological control · Conservation · Habitat diversity · *Orius insidiosus* · Weed

Introduction

Field crop monocultures pervade the agricultural landscape in the United States, and a “clean field” management philosophy often interferes with biological control of pests in these habitats (Croft 1990; Desneux et al. 2007). There is very low tolerance by most farmers to cropland weeds, and herbicides are commonly applied to maintain monocultures of a single crop species. Methods to restore plant and habitat diversity to farmland include reducing the amount of herbicides applied to allow the persistence of small weed populations, using cover crops, and intercropping with several crop species (Altieri and Whitcomb 1979; Andow 1991; Marshall et al. 2003; Norris and Kogan 2005). Typically, crops produced under vegetationally diverse conditions suffer from fewer insect pest problems, and natural enemy

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populations are higher in more diverse habitats (Andow 1991; Bianchi et al. 2006; Root 1973; Tahvanainen and Root 1972; van Emden 1963; Zehnder et al. 2007).

Vegetational diversity may favor natural enemies such as arthropod predators in a variety of ways (Altieri and Whitcomb 1979; Barbosa 1998; Landis et al. 2000, 2005; Norris and Kogan 2005; van Emden 1963). At least two different mechanisms seem to foster the enhancement of a predator species within a given habitat. First, predator fitness could be promoted in some way, leading to greater numbers of larvae/nymphs and adults. Second, predators could oviposit to a greater extent within more diverse habitats which would result in enhanced population growth.

Vegetational diversity can improve predator fitness through both nutritional and climatic diversification of a habitat (Barbosa 1998). The majority of entomophagous species consume plant-based foods (i.e., seeds, pollen, nectar, and vegetation) to augment their diet and improve various aspects of their fitness (Alomar and Wiedenmann 1996; Altieri and Whitcomb 1979; Coll and Guershon 2002; Lundgren et al. 2004, 2005). Diverse plant communities also support alternative prey ordinarily not found in monocultures, and these alternative prey can be used to sustain natural enemies when target pest densities are low (Andow 1991; Holt and Lawton 1994; Murdoch et al. 1985; Symondson et al. 2002). Finally, habitat diversity leads to gradients in microclimates, which allow diverse assemblages of natural enemies to self select spatial niches of maximum suitability and incur less mortality (Orr et al. 1997).

Theoretically, an insect should choose to oviposit on plants that bestow the greatest fitness for developing offspring, and in several cases non-crop plants are preferred over agricultural crops for oviposition by predatory insects (Coll 1996; Cottrell and Yeargan 1999; Griffen and Yeargan 2002; Lundgren and Fergen 2006; Lundgren et al. 2008). A potential driving force behind plant preferences of facultatively phytophagous predators that merits further attention is the contribution of plant nutrients to the reproductive success of females. For *Orius albidipennis* (Reuter) (Heteroptera: Anthocoridae), nitrogen content of their host plants (cotton; *Gossypium hirsutum* L.) did not influence the ovipositional behavior of *O. albidipennis*, nor the survivorship of the nymphs laid on plants of presumably different nutritional quality (Groenteman et al. 2006). Likewise, variance

in the nutritional suitability among different plants for developing *Geocoris punctipes* (Say) nymphs did not apparently drive the reproductive decisions of females (Naranjo and Stimac 1985, 1987). But Lundgren et al. (2008) found a close association with the ovipositional preferences of female *Orius insidiosus* (Say) (Heteroptera: Anthocoridae) for different plants and the longevity of their developing offspring. Whether and how these plant-mediated decisions by *O. insidiosus* affect their demographics in the field remains to be studied.

The recent invasion of *Aphis glycines* Matsumura (Homoptera: Aphididae) in North America and its status as a destructive pest of soybean in the region has prompted research on identifying its endemic natural enemies. One important predator of *A. glycines* is *O. insidiosus* (Desneux et al. 2006; Rutledge et al. 2004), which in addition to feeding on insect prey is also facultatively phytophagous. Ovipositing *O. insidiosus* display distinct preferences for different plant species, and even consistently discriminate plant structures within a given plant species (Lundgren and Fergen 2006). These ovipositional preferences may be manifested in the field, where increasing plant diversity within soybean fields is shown to increase predator populations (J. G. Lundgren unpublished data), but the mechanisms that drive these increases remain poorly understood. Here, we test the hypothesis that soybeans produced in more vegetationally diverse fields (e.g., with low densities of weeds) support higher densities of *O. insidiosus* than monoculture soybeans, and investigate whether *O. insidiosus* females use volatile signals to locate potential oviposition plants.

Materials and methods

Field study

A 6-ha field of Roundup-Ready soybeans (Pioneer hybrid 91M40; 0.75 m between rows; 475,000 seeds ha⁻¹) was planted on 1-June, 2006 on the Eastern South Dakota Soil and Water Research Farm near Brookings, SD (USA) (−96.81° W, 44.35° N). Within this field of soybeans, eight 3.3 m² plots were established in a randomized complete block design. Plots were separated from each other by at least 6 m of soybeans. Weeds were managed in the surrounding field with glyphosate (Round-up Weathermax,

Monsanto Company, St. Louis, MO, USA) and metolachlor (Dual II, Syngenta, Greensboro, NC, USA) at planting and glyphosate on 19-June at label-recommended rates, and were removed by hand (on 30-June) in the areas between the plots.

Two treatments ($n = 4$ plots per treatment) were established, one with high (diversified treatment) and low (monoculture treatment) vegetational diversity. In the diversified plots, 30 seeds of ivyleaf morning glory (*Ipomoea hederacea* Jacq.) and redroot pigweed (*Amaranthus retroflexus* L.), two prominent agronomic weeds of soybeans in North American cropland (Stubbendieck et al. 2003), were planted by hand just beneath the soil surface in each plot. The non-crop plants were established the day after soybean planting. Endemic weeds were allowed to grow in this treatment. In the monoculture treatment, no weeds were planted and naturally occurring non-crop plants were mechanically removed by hoeing 11 days after planting.

On 30-June, 184 *O. insidiosus* adults were collected in a nearby alfalfa (*Medicago sativa*) field using sweep nets. To ensure random mating, *O. insidiosus* were held in the laboratory in sealed plastic containers with a vermiculite substrate and fed *Ephestia kuehniella* eggs with a green bean as a moisture source. The *O. insidiosus* were divided evenly ($n = 23$) into eight 100-mm diam. Petri dishes. These dishes were opened in the center of each plot after 24 h in the laboratory, to increase *O. insidiosus* populations within the experiment. When *O. insidiosus* was released, soybean plants within the plots were approximately 15 cm tall and had 2–3 trifoliate leaves; non-crop plants had emerged to varying degrees.

After 3 weeks (19-July), plots were examined for non-crop plant densities and *O. insidiosus* life stages. The number and species of non-crop plants were enumerated in each plot. A 0.25-m² square quadrat was randomly placed into each plot, and all vegetation within the quadrat was removed. Plants were clipped at the soil line and were examined microscopically in the laboratory for eggs of *O. insidiosus*. These eggs are laid directly beneath the epidermis of the plant and only the operculum is visible externally (Lundgren and Fergen 2006; Lundgren et al. 2008). The crop and non-crop plant material collected in the quadrats was then dried at 60°C for 72 h and weighed to the nearest 0.01 g.

On 31-July, the vegetation was removed from a 1.8 m section of soybean row and the adjacent inter-row area in each plot. The vegetation was examined

microscopically, and the number of *O. insidiosus* adults and nymphs was recorded. Four of the remaining soybean plants in each plot were examined for soybean aphids (*Aphis glycines*), by far the most abundant prey item of *O. insidiosus* in soybean fields. Other alternative prey was conspicuously less abundant (nearly absent, in fact) relative to soybean aphid densities, even when considering the non-crop plants.

Within each plot, the diversity of non-crop plants was quantified using the Shannon index (H' ; Smith 1992) and indices were compared between treatments using Kruskal–Wallis non-parametric ANOVA (SYSTAT Software 2004). The numbers of *O. insidiosus* eggs, nymphs, and adults per plot were compared between treatments using ANCOVA, with plant biomass in each plot used as a covariate. Within subsamples in the vegetationally diverse plots, the number of eggs laid per plant between soybeans and non-crop plants were compared using ANOVA. In this comparison, the number of eggs laid per plant type (crop and non-crop) was standardized by the amount of biomass for each plant type found in each plot.

Olfactometer assay

Individual pots of velvetleaf (*Abutilon theophrasti* L.), redroot pigweed, and ivyleaf morning glory were produced in the greenhouse ($n = 4$ of each species). Multiple seedlings were produced in each pot, and were fertilized with Nutricote (Agrivert Inc., New York, NY) at planting. The soil mix consisted of field soil, peat moss, and vermiculite (4:2:1) and plants were watered as needed. Four pots were filled with soil and treated similarly as the plants to serve as a control group. Plants were approximately 20 cm tall when the assay was conducted.

Two shipments of *O. insidiosus* adults were ordered from Koppert Biological Systems (Scarborough, Ontario, Canada). Upon receipt, females of the first and second shipments were separated into individual 30-ml glass vials and fed on European corn borer (*Ostrinia nubilalis* Hübner) eggs or *Ephestia kuehniella* Zeller eggs, respectively. Vials were kept at $25 \pm 1^\circ\text{C}$, $60 \pm 10\%$ R.H. and 16:8 L:D for up to one week. Glass vials were sealed with a cotton plug that was kept moist throughout the assay. A minimum of 80 females was tested against each plant species.

A Y-tube olfactometer was used to determine whether naïve, mated *O. insidiosus* females responded

to odors from selected non-crop plants. The olfactometer consisted of a Y-shaped glass tube 1 cm in diameter. The base and the two arms of the Y tube were 10 and 11 cm in length, respectively. The airflow through each of the olfactometer arms was kept constant at 600 ml min^{-1} . A vacuum pressure pump pushed room air through activated charcoal and a 250 ml Pyrex Erlenmeyer flask filled with distilled water. Odor containers were 11.3 l glass carboys cut near the top to allow insertion of odor sources. Experiments were done at $21 \pm 1^\circ\text{C}$ and $25 \pm 5\%$ R.H., and observations were made within a box made of white laminated wood. The apparatus was illuminated by a double 40-W fluorescent tube. In one of the odor containers we inserted one planting pot with either one of the following plants: ivy leaf morning glory, redroot pigweed and velvetleaf, while a pot with planting soil only was placed in the other container. We tested the preference of *O. insidiosus* females for volatiles from either plant species, with each assay conducted over two separate days. When predators passed the 'choice line' (4 cm past the intersection of both olfactometer arms) and remained there for at least 15 sec, it was recorded as a choice between odor treatments. Each female was allowed 5 min to decide which tube to enter before she was discarded. The Y tube was turned 180° after every six females that were tested, switching the side from which odors entered the apparatus. This was done to eliminate the effects of any directional bias for one of the arms. The olfactometer was washed with ethanol, rinsed with water and dried after every 12 *O. insidiosus* females. After each day of experiments, all glassware was washed with acetone and distilled water and allowed to dry for at least 36 h. All experiments were conducted 5–12 h after the start of the 16 hr light period of the photoperiod regimen under which predators were reared. The number of choices *O. insidiosus* females made toward odors from non-crop plants versus those of soil was compared using two-way contingency tables (replicate and choice) and Pearson χ^2 test statistics.

Results

Field experiments

The diversity of non-crop plants within the diversified plots was significantly higher than in the monocultures

($\chi^2 = 5.33$, $df = 1$, $P = 0.02$). One-hundred and forty-nine individuals of 10 non-crop species were found in diversified plots ($H = 2.13 \pm 0.13$; mean \pm SE), and 12 individuals of five non-crop species were found in monoculture plots ($H = 0.81 \pm 0.31$). Species encountered were lambsquarters (*Chenopodium album* L.), wild buckwheat (*Polygonum convolvulus* L.), morning glory, redroot pigweed, dandelion (*Taraxacum officinale* G. H. Weber ex Wiggers), wild sunflower (*Helianthus annuus* L.), eastern black nightshade (*Solanum ptychanthum* Dunal ex DC), thistle (*Cirsium* sp.), unidentified grass sp., and a maple seedling (*Acer* sp.). All of these species are frequently found in cropland of the Great Plains (Stubbendieck et al. 2003).

The numbers of eggs laid in the two treatments were similar (trmt: $F_{1,5} = 0.01$; $P = 0.92$; plant biomass: $F_{1,5} = 0.70$; $P = 0.44$) (Fig. 1). However, within the diversified plots, significantly more eggs were laid per plant on weeds than on soybeans ($F_{1,6} = 7.22$, $P = 0.036$) (Fig. 2). Within subsamples, we examined the following non-crop plants for *O. insidiosus* eggs: lambsquarters ($n = 6$), wild buckwheat ($n = 3$), ivyleaf morning glory ($n = 2$), grass ($n = 1$), redroot pigweed ($n = 1$). No eggs were found on the buckwheat, grass, or pigweed plants.

Other life stages of *O. insidiosus* were significantly more abundant in the diversified plots than in monoculture plots. Adults in the diversified plots were nearly 170% of those found in the monocultures (trmt: $F_{1,5} = 6.68$, $P = 0.049$; plant biomass: $F_{1,5} = 0.74$, $P = 0.43$) (Fig. 1). Also, higher numbers of nymphs were found in the diversified plots (140% of monoculture densities) (trmt: $F_{1,5} = 6.53$, $P = 0.05$; plant biomass: $F_{1,5} = 4.25$, $P = 0.09$). The number of aphids per soybean plant per plot did not differ for both treatments ($F_{1,4} = 1.24$, $P = 0.33$). Mean (\pm SE) number of aphids per soybean plant was 1, 253 \pm 364 in the monoculture soybeans and 1, 064 \pm 275 in the diverse treatment.

Olfactometer assay

Of the 80, 80, and 101 trials on velvetleaf, pigweed, and morning glory (respectively), *O. insidiosus* females entered one of the treatment arms 45, 43, and 38 times, respectively. *Orius insidiosus* females did not prefer odors emanating from any of the plants

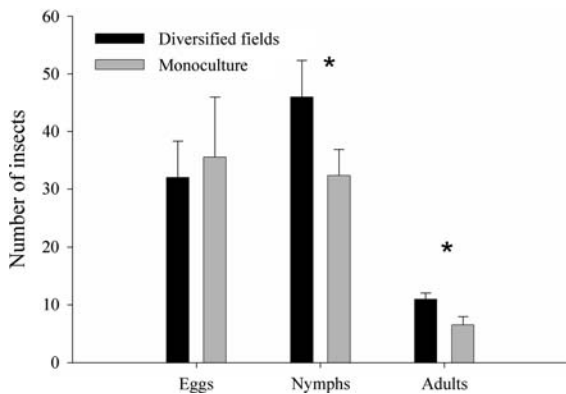


Fig. 1 Mean (+ SE) densities of *Orius insidiosus* life stages in soybeans produced under diversified and monoculture conditions. Data represent the number of eggs per 0.25 m², and the number of nymphs and adults per m of row. ‘*’ indicates significant differences between the treatments ($P \leq 0.05$)

over those from soil (velvetleaf: $\chi^2 = 2.81$, $df = 1$, $P = 0.094$; morning glory: $\chi^2 = 0.24$, $df = 1$, $P = 0.62$; pigweed: $\chi^2 = 1.16$, $df = 1$, $P = 0.28$).

Discussion

Orius insidiosus is more abundant in vegetationally diverse cropland than in soybean monocultures, which is in line with the hypothesis that developing *O. insidiosus* experience higher fitness in more diverse habitats. Non-crop plant volatiles did not invoke a response in gravid *O. insidiosus* females, and it is unlikely that females use long-range cues to locate ideal habitats for oviposition. Previous research (Lundgren et al. 2008) has shown that

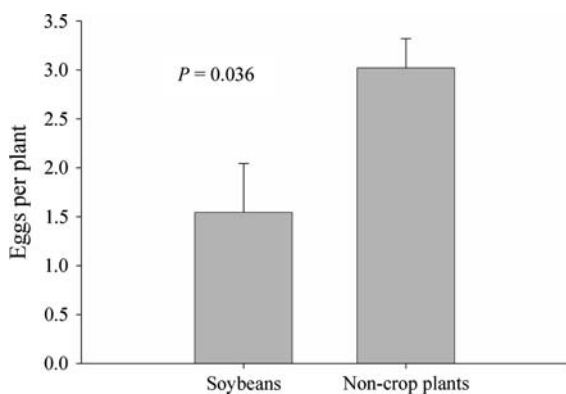


Fig. 2 The mean (+ SE) number of *Orius insidiosus* eggs laid per plant (per plot) on soybeans and non-crop plants within diversified soybean fields

O. insidiosus nymphs live longest on plants that were most frequently used for oviposition, and these results could explain the population trends that we observed. We conclude that non-crop plants provide a favorable environment for nymphs, and this may partially explain the greater densities of this predator within vegetationally diverse plots.

Orius insidiosus females were not attracted to constitutively produced plant volatiles. It is clear that *O. insidiosus* females rely on proximal cues (thickness of external plant tissues and trichome densities) when selecting oviposition sites (Lundgren et al. 2008), but it was not previously clear whether long-range, plant-based cues were influential to ovipositing females. Previous studies have found that *Orius* spp. are attracted to certain volatile infochemicals, particularly from potential food sources. For instance, *O. insidiosus* aggregates to cornfields during anthesis, where it is known to consume corn pollen (Corey et al. 1998; Isenhour and Marston 1981), and is attracted to *A. glycines* infestations in the field (N. Desneux unpublished data). A congener, *O. tristicolor* (White), is attracted to sticky traps baited with a number of herbivory-induced plant volatiles under field conditions (James 2003, 2005). Thus, *O. insidiosus* clearly possesses the capacity for chemoreception of long-range volatile cues. Olfactometer assays indicated that *O. insidiosus* females do not use this strategy for host-plant location in reproductive decisions. Furthermore, there were similar numbers of eggs laid in the monoculture and diversified plots even when more females were present in the diversified areas (Fig. 1). However, within the diversified plots, females laid nearly twice as many eggs on non-crop plants as on soybeans (Fig. 2). Thus, *O. insidiosus* females clearly distinguish among plants in the field as has been demonstrated in the laboratory (Lundgren and Fergen 2006; Lundgren et al. 2008), but the cues involved seem to be perceived only under close quarters. One explanation for the lack of long-range responses may be that *O. insidiosus* is a habitat generalist (Miliczky and Horton 2005), and can make use of numerous plant species as oviposition hosts. As a result of this plasticity, selective pressure for using long-range infochemicals to locate certain plants within a given habitat may be low (Vet and Dicke 1992). Once *O. insidiosus* females find a given habitat, they may assess the plant species present and make oviposition decisions based on short-range cues.

Certain qualities of non-crop plants may be contributing to more abundant *O. insidiosus* populations in vegetationally diverse cropland. In the laboratory, plant-based foods have been shown to sustain the preimaginal development of *O. insidiosus* (Dicke and Jarvis 1962; Kiman and Yeargan 1985), and other predatory heteropterans have increased survival (Legaspi and O'Neil 1993; Stoner 1970, 1972; Stoner et al. 1974, 1975; Vacante et al. 1997), size (Naranjo and Stimac 1985) and fecundity (Cocuzza et al. 1997; Salas-Aguilar and Ehler 1977) when plant tissue is included in their diets. Previous work on this topic showed that nymphs died sooner when reared in the absence of prey on soybeans than on morning glory or green beans, two preferred plants for oviposition (Lundgren et al. 2008). In the field trials, morning glory was selected as an oviposition site more than twice as frequently (3.67 eggs plant⁻¹) in the field than soybeans (1.55 eggs plant⁻¹), and green bean is also a preferred plant for oviposition (Lundgren and Fergen 2006). Future research should address the role of other factors (e.g., enhanced microclimate, arrested foraging behavior of adults, alternative prey on non-crop plants, etc.) associated with plant diversity that may also contribute to the increased numbers of *O. insidiosus* in diverse habitats. These findings might also have implications for mass production of this predator, where the provision of optimal insect diets and oviposition substrates is crucial (De Clercq et al. 2005; Murai et al. 2001).

This paper supports the notion that vegetational diversity can be used as a tool for conserving natural enemies within farmland and enhancing their potential as biological control agents. Shaltiel and Coll (2004) found that *Anthocoris nemoralis* F. preferred to oviposit on non-crop plants in pear orchards, and recommended intercropping with preferred host trees to increase predation within pear orchards. Similarly, Seagraves and Yeargan (2006) found that sweet corn fields had higher numbers of *Coleomegilla maculata* DeGeer (Coleoptera: Coccinellidae) when bordered by tomato (*Lycopersicon esculentum* Miller) plants, a preferred oviposition plant of this predator. In our relatively small study plots, we did not observe significant reductions in the target prey populations (*Aphis glycines*) resulting from plant diversity. The reason for this is likely related to the fact that *O. insidiosus* performs best as a predator of *A. glycines* at low prey densities (30–60 aphids

plant⁻¹) (Rutledge and O'Neil 2005), and aphid populations at the time of our study were >1,000 per plant. In line with Rutledge and O'Neil's findings, aphid outbreaks are shown to be delayed in vegetationally diverse cropland, possibly as a result of predation during early aphid infestation (J. G. Lundgren unpublished data). It was striking that, even when potential prey was extremely abundant for this predator, we still observed a population increase in response to plant diversity. Thus, the contributions of vegetational diversity overwhelm the sole benefit of having adequate prey for this predator's life history.

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