

## Oviposition Preference for Water-Stressed Plants in *Orius insidiosus* (Hemiptera: Anthocoridae)

Michael P. Seagraves · Walter E. Riedell ·  
Jonathan G. Lundgren

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**Abstract** Plant species affect the oviposition behavior of the zoophytophagous predator *Orius insidiosus*. This study was conducted to determine whether manipulating plant quality, via stress, within a single plant species (*Phaseolus vulgaris* L.) would affect the oviposition behavior of *O. insidiosus* and the subsequent performance of its offspring. Plants that had water withheld (water-stressed treatment) had about 20% less total dry weight than plants that were watered to alleviate the drought stress (unstressed treatment). In comparison to unstressed plants, unifoliolate leaves and petioles of water-stressed plants had about 20 and 12% less relative water content, 54 and 29% greater sap osmotic potential, and 19 and 70% greater concentrations of amino-nitrogen, respectively. Reproductive *O. insidiosus* were then presented stressed and unstressed plants in a two choice test to determine oviposition preference. First instar survival on the two treatments was evaluated in no-choice tests. *Orius insidiosus* laid 70% more eggs per cm<sup>2</sup> on the stressed plants. The lifespan of newly-hatched nymphs was the same in both treatments. Eggs were more frequently laid on the leaf vein than the petiole of unstressed plants, whereas in stressed plants oviposition on these parts occurred at equal frequency. These findings suggest that physiological changes in water-stressed bean plants created conditions more favorable for *O. insidiosus* oviposition. As there was no increase in offspring performance, it is hypothesized that females chose oviposition sites near preferred feeding sites or plant tissues that were less prone to desiccation.

**Keywords** *Orius insidiosus* · reproduction · oviposition · omnivory · biological control · drought stress · plant-stress hypothesis · turgor pressure · water-stressed plants · predator

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W. E. Riedell · J. G. Lundgren (✉)  
USDA-ARS, North Central Agricultural Research Laboratory, 2923 Medary Avenue,  
Brookings, SD 57006, USA  
e-mail: Jonathan.Lundgren@ars.usda.gov

*Present Address:*  
M. P. Seagraves  
Driscoll's Strawberry Associates, Watsonville, CA 95077, USA  
e-mail: michael.seagraves@driscolls.com

## Introduction

Several climatic and societal concerns regarding impending water abundance and availability, (e.g., decline of aquifers, loss of agricultural water rights, and global warming), could lead to situations of frequent plant water stress or locations where water-stressed plants and unstressed plants are in close proximity. Thus there is a need to fully understand how insect pests and their omnivorous natural enemies respond to these differences. Water stress produces increased levels of nitrogenous compounds in plants due to increased protein hydrolysis and the accumulation of osmoprotectants (Hsiao 1973; Aspinall and Paleg 1981; Brodbeck and Strong 1987). The increased concentration of available nutrients in drought stressed plants is in some circumstances beneficial to herbivores (White 1984, Huberty and Denno 2004). However, increased nutritive value in water-stressed plants can be compromised by elevated levels of alleochemicals (Gershenson 1984, Mattson and Haack 1987, Inbar et al. 2001); these are concentrated in the leaves and are thought to affect leaf feeders more strongly than those feeding on vascular sap (Raven 1983). The trade-offs between changes in nutrient content and phytoprotectant concentration necessitates direct empirical experiments to determine the relative suitability of water-stressed and unstressed plants for insects, particularly omnivores.

Insects use several cues to assess the quality of an oviposition site to maximize their reproductive success. In omnivorous and herbivorous insects, reproductive females weigh the importance of plant-based resources for their developing offspring as part of their oviposition decisions (Jaenike 1978, Craig et al. 1989, Stein and Price 1995, Craig and Ohgushi 2002, but also see Scheirs et al. 2003). The physiological status of a plant changes continuously, and how insects that rely on plant-based resources respond to plants under various levels of stress is poorly understood.

Plants and the nutrients they provide affect beneficial natural enemies of arthropod pests in agricultural systems (Landis et al. 2000; Landis et al. 2005; Lundgren 2009). While it is known that plant water stress strongly affects the population growth of pests, particularly aphids (Archer et al. 1990), there is little understanding of its effect on their omnivorous natural enemies. The zoophytophagous predator *Orius insidiosus* (Say) is a habitat generalist found in many agroecosystems (Miliczky and Horton 2005), where it is a natural control agent of arthropod pests and also feeds on plant material (e.g., vascular sap, pollen) facultatively to replace and complement prey items (Kiman and Yeargan 1985; Naranjo and Gibson 1996; Coll 1998; Corey et al. 1998). These predators require moisture, usually from plant feeding to utilize prey in their diet (Gillespie and McGregor 2000), and eggs of other anthocorids quickly desiccate without some form of hydration (Anderson 1962; Chu 1969). *Orius* populations are affected by available plant nutrients such as leaf soluble protein, nectar, and pollen (Yokoyama 1978; Stone et al. 1984). This dietary breadth makes *O. insidiosus* valuable for biological control efforts, since it can persist in crop fields feeding on alternative prey and plant sources at low pest densities. For example, this bug feeds on thrips and weeds in soybean early in the season, and is already present in soybean when

soybean aphids (*Aphis glycines* Matsumura) colonize (Isenhour and Yeargan 1981; Harwood et al. 2007; Yoo and O'Neil 2009; Lundgren et al. 2009).

Although *O. insidiosus* is known to consume plant material, the exact tissues and nutrients consumed remain unknown. Armer et al. (1998) documented that *O. insidiosus* feeds frequently on xylem and to an unknown extent on mesophyll of soybeans (*Glycines max* L). However, Lundgren et al. (2008) contended that all stages of *O. insidiosus* had mouth parts capable of accessing many plant tissues and that xylem and phloem sieves are bundled together in soybean plants such that both vascular tissues would be encountered when feeding. The tissues consumed by *O. insidiosus* will dictate what nutrients and allelochemicals are gleaned from plant material, and what plant materials are the most important for conserving *O. insidiosus* within cropland.

Many predators use prey-based cues to make oviposition decisions (Seagraves 2009) but plant cues can also be important, and understanding these plant-based cues can assist in developing cropping systems that favor beneficial natural enemies (Seagraves and Yeargan 2006; Lundgren et al. 2009). *Orius insidiosus* lays eggs beneath the epidermis of plants leaving only an operculum exposed (Isenhour and Yeargan 1982; Lundgren et al. 2008). Prey quality does not affect the oviposition decisions of *Orius laevigatus* (Venzon et al. 2002), but plant quality (i.e., species) is evaluated by other *Orius* spp. (including *O. insidiosus*) during reproductive decisions (Coll 1996; Lundgren and Fergen 2006, Lundgren et al. 2008, Seagraves and Lundgren 2010). Moreover, oviposition preferences for specific plants are positively correlated with performance of newly hatched nymphs (Lundgren et al. 2008). In this current research, we manipulated the physiological status of green bean (*Phaseolus vulgaris* L.) by creating water-stressed and unstressed cohorts, and evaluated how *O. insidiosus* responded reproductively to these changes in plant quality, and how water stress affects the suitability of a plant species for developing nymphs.

## Methods

### Preparation of experimental plants

Plastic pots (3.8 cm diam. by 21 cm height; Model SC-10; Stuewe & Son Inc., Tangent OR) were filled to capacity with a compost-peat moss-perlite based potting media (MiracleGro Inc., Marysville, OH) containing a slow-release fertilizer. Two green bean (*Phaseolus vulgaris* L., cv 'Jade') seeds were placed in each pot (this species is a preferred oviposition plant for *O. insidiosus*; Lundgren & Fergen 2006). Pots were thoroughly watered, covered with aluminum foil, and placed into a growth chamber (Model 3245; Conviron Inc., Winnipeg, Canada) at constant 20 °C temperature and 50% relative humidity. High pressure sodium and metal halide lamps in a 20:80 mixture were set to provide a 14:10 L:D photophase at 550  $\mu\text{Mol sec}^{-1}\text{m}^{-2}$  of photosynthetically active radiation. Foil covers were removed 6 d after planting. Seedlings, which began to emerge from the soil after about 4 or 5 d, were thinned to one uniform plant per pot about 8 d after planting. Pots were watered regularly until 13 d after planting.

## Imposition of water stress

Thirteen days after planting, when plants had expanded unifoliolate leaves as well as trifoliolate leaf buds, all pots were watered to saturation. Pots containing plants were weighed and returned to the growth chamber. Water was then withheld from all pots for a period of 3 d. Pots were weighed regularly during this time. Plant pots were then randomly assigned to one of two treatments: water-stressed or unstressed. Plants in the water-stressed treatment did not receive water and pots of the unstressed treatment were watered to soil saturation. All plant measurements and preference tests were taken or initiated approximately 24 h after these treatments were imposed, or 17 d after planting (nymphal survival assays were initiated 18 d after planting).

## Plant measurements

Plants produced using the treatments above were dissected into three components: unifoliolate leaves, unifoliolate leaf petioles, and the remaining stem and trifoliolate leaves. For dry weight determination, these organs were dried to constant weight at 60 ° C in a forced-air oven and weighed to the nearest 0.1 mg. Relative water contents (RWC) of fresh unifoliolate leaves and unifoliolate leaf petioles were measured using the method of Gonzalez and Gonzalez-Villar (2001). Leaf disks of 1 cm diameter were cut with a cork borer from interveinal areas on unifoliolate leaves while unifoliolate leaf petioles were excised with a scalpel. After measuring fresh weights, these organs were suspended over ice-cold distilled water contained in a Petri dish. Petri dishes were stored at 4 ° C for 24 h, after which the water-saturated weight was measured. Organs were then dried to constant weight at 60 ° C in a forced-air oven and weighed. Relative water content, expressed as a percentage of water content at the time of measurement compared to that at full turgor, was then determined using the equation:

$$RWC = \left( \frac{FW - DW}{SATWT - DW} \right) \times 100$$

where FW is fresh weight, DW is dry weight, and SATWT is saturated weight.

Osmotic potentials of sap expressed from fresh unifoliolate leaves and unifoliolate leaf petioles were measured using the methods of Markhart and Lin (1985) and Gonzalez and Roger (2001). Sap from two 1-cm leaf disks or two petioles was expressed with a Markhart plant press (Model LP-27; Wescor Inc., Logan UT) and read immediately with a vapor pressure osmometer (Model 5500; Wescor Inc., Logan UT).

Plant amino nitrogen (amino-N) was measured on the day plants were exposed to *O. insidiosus* females. A subset of plants ( $n=3$  per treatment) in the two treatments were divided into unifoliolate leaves, unifoliolate petioles, and the remainder of the plant (main stem and trifoliolate leaves and buds). Organs were dried at 60 ° C to a constant weight and were ground to pass through a 0.85 mm screen in a Wiley mill (Arthur Thomas Co., Philadelphia, PA). The ground material was suspended in distilled water, shaken for 15 min, and centrifuged at a relative centrifugal force of

about 650 X g for 10 min. The resulting supernatant was passed through 0.45- $\mu\text{m}$  nylon filters (Alltech Associates Inc, Deerfield IL). Amino-N concentration in the filtrate was measured with the method of Yemm and Cocking (1955), using glycine as a standard.

The mean dry weights of the individual plant organs, total dry weights, leaf and petiole RWC, and leaf and petiole solute concentration were compared between stressed and unstressed plants using a two-tailed Student's *t*-test. The analyses were done using PROC TTEST (SAS 2003). Amino-N concentration in leaf and petiole were compared across treatments using a two-tailed Student's *t* test.

### Oviposition choice

Reproductive *O. insidiosus* were offered water-stressed and unstressed plants under choice conditions. An *O. insidiosus* colony (originating from insects produced by Koppert, Romulus, Michigan, USA) was established and reared for four generations using *Ephestia kuehniella* Zeller (Lepidoptera: Phycitidae) eggs and green beans as food. Cylindrical cages (43 cm tall and 23 cm in diameter with square muslin mesh 0.33 mm squares;  $n=25$  final sample size) were assembled with paired plants, one of each treatment, still in their pots. Six female and two male *O. insidiosus*, excess *E. kuehniella* eggs, and a moistened cotton dental wick were housed in each cage for 48 h. Experimental conditions were 25 ° C, 50% r.h., and 14:10 (L:D). After the exposure period, the remaining females per cage were recorded, as were the number of eggs laid in the following tissue categories: internode, petiole, leaf petiole, and leaf vein (adapted from Ritchie et al., 1997). The categories of internode and leaf petiole were combined to create the “stem” category to match tissue categories used in the plant measurements. After eggs were counted, the two-dimensional surface area of each plant was measured using a hand held surface area meter (CID Bio-Science, Inc., Camas, WA). Eggs per plant (square-root transformed) were compared using a paired *t* test; additionally eggs per  $\text{cm}^2$  was examined between treatments as is commonly done in studies examining oviposition choice in insects (Abera et al. 1999, Alyokhin et al. 2004, Holland et al. 2004, Paukku and Kotiaho 2008). The observed proportions of eggs found on each plant part in the water-stressed treatment were compared to those in the unstressed plants using Pearson's chi-square test. Within a treatment, the proportion of eggs occurring on the different plant parts was compared using a Wilcoxon signed rank test with the Proc Univariate function of SAS (SAS 2003).

### Nymphal survival

Survival of *O. insidiosus* nymphs on water-stressed and unstressed plants was evaluated under no-choice conditions. Prey-free, 18-d-old plants ( $n=15$  per treatment) were caged individually in a plastic container (11.25 in diameter by 15.25 cm in depth) sealed with plastic wrap. Single *O. insidiosus* nymphs (less than 12 h old) were transferred into each cage using a fine paintbrush, and their activity was confirmed after the transfer. Nymphal survival was checked at 24, 48, and 72 h after trial initiation. A survival Kaplan-Meyer model was used to test for differences in lifespan between nymphs on the two plant treatments, with data from lost nymphs censored in the model (Systat 11; Systat Software, Inc., Richmond, CA).

## Results

### Plant measurements

Unstressed plants had a greater total dry weight than the water-stressed plants ( $t=6.15$ ,  $P<0.01$ ,  $df=18$ ). This relationship was consistent for each of the individual plant organs (Leaf:  $t=7.50$ ,  $P<0.01$ ,  $df=18$ ; Stem:  $t=2.22$ ,  $P=0.04$ ,  $df=18$ ; Petiole:  $t=3.57$ ,  $P<0.01$ ,  $df=18$ ) (Table 1). Unifoliolate leaves and petioles of the unstressed plants had higher relative water concentration (RWC) than the water-stressed plants (Leaf:  $t=9.12$ ,  $P<0.01$ ,  $df=18$ ; Petiole:  $t=9.45$ ,  $P<0.01$ ,  $df=18$ ) (Table 1). The concentration of solute was 33 to 50% higher in the water-stressed treatments (Leaf:  $t=4.31$ ,  $P<0.01$ ,  $df=12$ ; Petiole:  $t=5.11$ ,  $P<0.01$ ,  $df=12$ ) (Table 1).

All parts of the water-stressed bean plant had numerically greater concentrations of amino-N than unstressed plants and these differences were significant with the exception of unifoliolate leaves (Leaf:  $t=1.99$ ,  $P<0.12$ ,  $df=4$ ; Petiole:  $t=7.15$ ,  $P<0.01$ ,  $df=4$ ; Rest of plant:  $t=3.06$ ,  $P=0.04$ ,  $df=4$ ) (Table 1).

### Oviposition choice

*Orius insidiosus* females altered their oviposition decisions based on the physiological status of the bean plants. The water-stressed plants had less surface area ( $60.79 \pm 5.15$  cm<sup>2</sup>) than the unstressed plants ( $137.98 \pm 7.05$  cm<sup>2</sup>) ( $t=8.55$ ,  $P<0.01$ ,  $df=24$ ). Although a similar number of eggs were laid per plant in the two treatments ( $t=1.14$ ,  $P=0.27$ ,  $df=24$ ), there were significantly more eggs laid per unit surface area in the water-stressed plants ( $t=2.02$ ,  $P=0.05$ ,  $df=24$ ). Females laid  $0.17 \pm 0.02$  and  $0.10 \pm 0.01$  eggs per cm<sup>2</sup> on the stressed and unstressed plants, respectively. The proportion of eggs laid on the three plant part categories in the water-stressed plants was different than the proportions on the unstressed plants ( $\chi^2=831.03$ ,  $P<0.01$ ,  $df=2$ ) (Fig. 1). Fewer eggs were laid in the petioles of unstressed plants than other plant tissues (Leaf-Petiole:  $S=121$ ,  $P<0.01$ ,  $df=24$ ; Leaf-Stem:  $S=22$ ,  $P=0.54$ ,  $df=24$ ; Stem-Petiole:  $S=123.5$ ,  $P<0.01$ ,  $df=24$ ) (Fig. 1). In contrast, equal numbers of eggs were laid on the petioles and leaves of water-stressed plants (Leaf-Petiole:  $S=41$ ,  $P=0.16$ ,  $df=24$ ; Leaf-Stem:  $S=37$ ,  $P=0.29$ ,  $df=24$ ), but fewer eggs were laid in the petiole than in the stem ( $S=67.5$ ;  $P<0.01$ ,  $df=24$ ) (Fig. 1).

### Nymphal survival

Approximately half of the nymphs placed were never recovered. Those that were successfully recovered lived for  $1.14 \pm 0.26$  and  $1.55 \pm 0.40$  d on unstressed and water-stressed plants, respectively. The water-stressed treatment had no effect on nymph lifespan ( $\chi^2=0.12$ ,  $P=0.73$ ,  $df=1$ ).

## Discussion

Water-stress and its associated physiological changes resulted in plants more suitable for *O. insidiosus* oviposition. Water stress resulted in physically and physiologically

**Table 1** Physiological characteristics of unstressed and water-stressed *Phaseolus vulgaris* L.

Treatment	Total dry weight (mg)	<sup>a</sup> Leaf dry weight (mg)	Stem dry weight (mg)	<sup>b</sup> Petiole dry weight (mg)	Leaf amino-N (mg g <sup>-1</sup> dry wt)	Petiole amino-N (mg g <sup>-1</sup> dry wt)	Stem amino-N (mg g <sup>-1</sup> dry wt)	Leaf RWC <sup>c</sup> (%)	Petiole RWC (%)	Leaf solute conc. (mmol/kg)	Petiole solute conc. (mmol/kg)
unstressed	388.18±7.39a	306.24±4.68a	71.47±3.05a	10.47±0.42a	2.16±0.11a	1.41±0.03a	2.57±0.12a	93.09±0.70a	82.69±0.76a	302.43±15.73b	371.57±10.76b
Water-stressed	310.18±10.30b	239.47±7.58b	62.09±2.92b	8.62±0.30b	2.43±0.09b	2.40±0.14b	3.06±0.11b	73.87±1.99b	72.57±0.75b	465.28±34.38a	480.28±18.33a

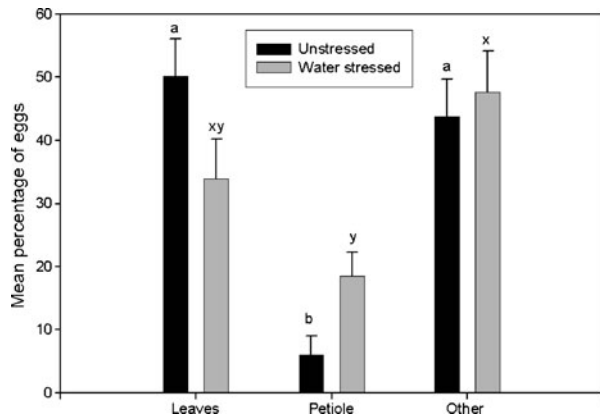
Column means followed with the same letter are not significantly different (Student's *t* test;  $\alpha=0.05$ )

<sup>a</sup> Unifoliate leaves

<sup>b</sup> Petiole was from the unifoliate leaves

<sup>c</sup> Denotes relative water content

**Fig. 1** Distribution of *Orius insidiosus* eggs laid on unstressed and water-stressed *Phaseolus vulgaris* in choice test ( $n=24$ ). Values represent the mean+SEM. Means within treatment with the same letter are not significantly different (Wilcoxon sign test,  $\alpha=0.05$ )



different *P. vulgaris*, compared to unstressed plants. In choice tests, *O. insidiosus* preferred to oviposit on the water-stressed plants. Not only were more eggs laid per unit of surface area but the placement of eggs shifted away from the leaves and toward the petioles, which had elevated levels of amino-N compared to their unstressed counterparts. Because we observed that nymphs failed to perform better on water-stressed plants, we hypothesize that differences in oviposition were driven by female preference based on plant turgidity and other physical properties.

In addition to the anticipated reduction in RWC, water-stressed bean plants also had decreased mass and surface area, greater solute concentrations in sap expressed from unifoliolate leaves and petioles, and increased amino-N concentration in unifoliolate leaf petioles and main stems/trifoliolate leaves. This corresponds to previous reports that water-stress reduces turgor pressure, RWC and plant growth (Hsiao 1973, Price 1991, Inbar et al. 2001). Water stress affects protein metabolism by reducing amino acid synthesis, increasing protein hydrolysis and increasing free amino acid concentrations (Hsiao 1973; Brodbeck and Strong 1987). Water stress in legumes results in accumulation of soluble sugars that persist at elevated levels even when stress is alleviated (Souza et al. 2004). Specific nitrogenous compounds, such as the amino acid proline, which accumulate in response to drought stress, also can serve as osmoprotectants (Aspinall and Paleg 1981). Overall, our results illustrate specific physiological changes in drought-stressed *P. vulgaris*, and these physiological differences in *P. vulgaris* affected the ovipositional behavior of *O. insidiosus*.

The shift in *O. insidiosus* reproductive behavior could have been caused by either turgor-derived resistance to the physical act of oviposition, or by the relative nutritional quality of the plants. *Orius insidiosus* and other anthocorids preferentially oviposit in the leaf veins and petioles of various plant species including *P. vulgaris* (Iglinsky and Rainwater 1950; Askari and Stern 1972; Isenhour and Yeargan 1981; Richards and Schmidt 1996; Groenteman et al. 2006; Lundgren and Fergen 2006). Several authors have speculated that *O. insidiosus* females place eggs at sites that are less prone to desiccation (Iglinsky and Rainwater 1950; Richards and Schmidt 1996). We observed that egg deposition on water-stressed plants was shifted away from the leaves (the plant organ most affected by water-stress) to the petioles (a more drought-resistant structure). The petioles of water-stressed plants also had increased levels of amino-N compared to unstressed plants, while the amino-N content of



leaves was similar in the two treatments. Amino acid availability affects feeding site selection by xylem feeders (Horsfield 1977; Brodbeck et al. 1990), and *O. insidiosus* possibly decided to oviposit near their preferred feeding locations (i.e. petioles), which were altered in the water-stressed bean plants. Lundgren et al. (2008) observed that ovipositing *O. insidiosus* assesses the quality of an oviposition site by probing it with her mouthparts.

Our research does not directly support previous work that has shown that *O. insidiosus* oviposition preference for certain plant species is linked to increased offspring performance (i.e., nymphal lifespan) (Lundgren et al. 2008, 2009). Manipulating water stress resulted in an ovipositional preference in *O. insidiosus*, but we were unable to demonstrate a corresponding increase in nymphal survival, which suggests that the oviposition pattern we saw was not due to the plant's suitability for *O. insidiosus* progeny. Likewise, Groenteman et al. (2006) found no difference in *O. albidipennis* adult survival on cotton plants grown under different N fertilization regimes (although the predators had access to prey in this experiment). However, Lundgren et al. (2008) contend that after a plant species has been deemed suitable for oviposition by *O. insidiosus*, a series of morphological characteristics of the plant dictate the final location of the oviposition site. Specifically, *O. insidiosus* rely upon physical traits such as substrate thickness, trichome density, and shape when selecting an oviposition site (Shapiro and Ferkovich 2006; Lundgren et al. 2008). Thus, it could be that *P. vulgaris* is a very suitable plant for oviposition whether or not it is water-stressed, and females selected the water-stressed plants in our study because these plants presented the best micro-environment for oviposition.

Information on reproductive behaviors of omnivorous predators is important for designing cropping systems that optimize biological control, proper sampling plans that incorporate natural enemies, and mass rearing techniques. Plant diversity in or surrounding cultivated crops increases *O. insidiosus* and other anthorcid populations (Balduf 1923; Shelton and Edwards 1983; Shaltiel and Coll 2004; Lundgren et al. 2009). In some instances this population increase is directly related to the availability of preferred oviposition plants (Lundgren et al. 2009) and these preferences can be useful in explaining the habitat distribution of predaceous heteropterans (Pfannenstiel and Yeargan 1998a, b). There are several scenarios that could produce plants under different degrees of water-stress under natural conditions. In field crop situations, the crop and non-crop vegetation at the field margins often do not receive irrigation. Irrigation in horticultural settings is often directed only to the root zone of the cultivated crop (i.e., drip irrigation under plasticulture), and this scenario might produce non-crop vegetation in the rows that are water-stressed. Crop fields are not homogenous in their elevation or water holding capacity, which could create a gradient of water-stress in dry land crops. Stressed plants could be created to concentrate immature stages of *O. insidiosus* in operations that have fine control over watering. Additionally if these stressed plants were non-crop vegetation they may also provide alternative prey that would perform well on stressed plants. Of course if plants are stressed enough they would likely become less acceptable for oviposition (Evans 1976). Even if these applications are not implemented, the information on *O. insidiosus* reproductive behavior builds upon the knowledge that will allow for the future design of cropping systems with more ecosystem services.

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