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The influence of plant anatomy on oviposition and reproductive success of the omnivorous bug *Orius insidiosus*

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The mechanisms whereby the reproductive behaviour and success of omnivorous insects are influenced by plant characteristics are poorly understood. We examined how the oviposition behaviour of zoophytophagous *Orius insidiosus* and the subsequent longevity of its progeny are influenced by the physical structure and internal anatomy of five plant species. Female *O. insidiosus* oviposit into plant species with the thinnest layers of epidermal and collenchyma cells, a decision that is significantly correlated with the survival of their offspring. Once a plant species is chosen, the female mainly bases her oviposition decisions on epidermal thickness and the surface density of hair-like appendages on the plants. That females laid more eggs and nymphs survived longer on plants with thinner external tissues suggest that the mechanisms that drive female oviposition decisions have evolved such that optimal plant-based resources are available for the females' progeny. Microscopic examination of plant anatomical features revealed that vascular and cellular tissues are fully accessible to the piercing–sucking mouthparts of the developing insects, suggesting that multiple sources of plant nutrients are available to this omnivore. The ecological implications of plant-based contributions to *O. insidiosus* fitness are discussed.

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The cues and underlying factors that drive maternal reproductive decisions in omnivores are undoubtedly complex and poorly understood. Owing to their often omnivorous feeding habits, the importance of plants to their life histories, and their economic relevance as natural enemies in natural and managed habitats (Alomar & Wiedenmann 1996; Schaefer & Panizzi 2000; Rutledge et al. 2004; Rutledge & O'Neil 2005; Desneux et al. 2006), zoophytophagous bugs in the family Heteroptera are excellent candidates for examining how plant-mediated reproductive decisions in females affect their reproductive success. One case in point, *Orius insidiosus* (Say) (Heteroptera: Anthocoridae) lays its eggs beneath the epidermis of a range of plants (Isenhour & Yeargan 1982; Lundgren & Fergen 2006), and although this species is most appreciated as an entomophagous insect, *O. insidiosus* is phytophagous to some degree during its immature stages (Kiman & Yeargan 1985; Naranjo & Gibson 1996; Cocuzza et al. 1997; Corey et al. 1998). Furthermore, the

reproductive decisions of this species are strongly influenced by both the plant species and variation within a plant (Isenhour & Yeargan 1982; Coll 1996; Lundgren & Fergen 2006). Even so, the factors that render one plant a better oviposition site than another and the implications of the oviposition decision on the fate of the progeny have not been explored.

A number of plant morphological features are known to affect the behaviour and fitness of insects. Trichomes (hair-like appendages) impede insect movement and constitute a physical and sometimes chemical barrier to insect feeding (Powell & Lambert 1993; Panda & Khush 1995; Smith 2005). These structures also can influence the oviposition of zoophytophagous insects, either positively through protection from predation (Benedict et al. 1983; Griffen & Yeargan 2002) or negatively through repellency or toxicity to the females (Bergman & Tingey 1979; Obrycki & Tauber 1984; Simmons & Gurr 2004). Plant surface tissues, typically consisting of an epidermal layer composed of parenchyma cells or an epidermis plus a subtending layer of thick-walled collenchyma cells (Dickison 2000), also present an obstacle to oviposition and feeding by insects (Pollard 1973; Alvarez et al.

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2006). Finally, the depth of the vascular tissues may restrict the range of insects that can extract nutrients from them, particularly for insects with piercing–sucking mouthparts (Pollard 1973; Hoffman & McEvoy 1986).

The current research identifies some plant anatomical characteristics that influence *O. insidiosus* oviposition and feeding by immature stages, and establishes a decision framework for how females select oviposition sites among plant species as well as within a suitable plant. Furthermore, quantitative evidence is presented on the correlation of reproductive decisions of the female and the survival of developing nymphs.

METHODS

Insects and Plants

Orius insidiosus adults were purchased from Koppert Canada Limited (Scarborough, ON, Canada), and maintained in vermiculite substrate on eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) with 2 cm sections of green beans used as a water source. Adults were allowed to acclimate to environmental conditions of 27°C, 14:10 h light:dark cycle for 3 days before the experiments. The plant species used were green bean, *Phaseolus vulgaris* L. cv. Jade (J. W. Jung Seed Co., Randolph, WI, U.S.A.), soybean, *Glycine max* L. var. Surge SD(M)92-1233 (South Dakota State University), velvetleaf, *Abutilon threophrasti* L., redroot pigweed, *Amaranthus retroflexus* L., and ivyleaf morning glory, *Ipomoea hederacea* (L.) Jacq.

Oviposition Preferences

Approximately 100 cm^2 of leaflets with petioles (equivalent to a single leaf of velvetleaf, the largest foliage of the group) from each plant species was cut and placed into a single water pick in the centre of each of 10 cylindrical cages (43 cm tall and 23 cm diameter) covered with mesh (0.33 mm squares). Excess *E. kuehniella* eggs were placed in the bottom of each cage as food. Thirteen mated *O. insidiosus* females were placed into each cage, and allowed to oviposit for 72 h. Climatic conditions were LD 16:8 h, 60–70% relative humidity, and 26.5°C. After 72 h, the plants were refrigerated until the eggs laid upon each could be counted. The number of females recovered from each cage was also recorded. The number of eggs per plant per cage was counted, and the mean numbers of eggs per plant species per female (the number alive at the end of the exposure) was compared using the nonparametric Kruskal–Wallis ANOVA (SYSTAT 2004). Significantly different means were separated using the least significant difference test (LSD test; SYSTAT 2004).

Trichome Densities

Plants of each species ($N = 3$) were caged (as above) separately with 14 *O. insidiosus* adults (nine females and five males), which were allowed to oviposit for 72 h. The plants were then dissected and tissues containing eggs were excised using a razor blade and preserved in formalin–acetic acid–alcohol (FAA) fixative (Jensen 1962) until they could be examined.

Microscopic linear transects at 50× were used to assess the abundance of trichomes on preferred and unpreferred oviposition sites on the petioles of each plant species. Petioles were the most preferred oviposition site for all plants except velvetleaf (petioles: $N = 147$ total eggs for all species; leaf veins: $N = 82$; stems: $N = 34$), and so this tissue was selected to assess the intraspecific influence of trichome densities on *O. insidiosus* oviposition decisions. On each petiole where an egg was laid, the egg was centred in the middle of an ocular micrometer and aligned parallel with the length of the petiole, and the trichomes that intersected with the micrometer within 2 mm on either side of the egg were counted. The petiole was then flipped over, and the number of trichomes per 4 mm was recorded from an unpreferred site. Trichome abundances on the petioles from each plant species near eggs and opposite from the egg were analysed independently with Kruskal–Wallis nonparametric ANOVA.

To determine whether trichome density influenced plant preferences for oviposition, the trichomes were enumerated at oviposition sites on the leaf veins of each plant species. On velvetleaf, *O. insidiosus* females laid their eggs only on the leaf veins, which restricted us to the use of this tissue for interspecific comparisons of trichome densities at preferred oviposition sites. The trichome numbers (per 4 mm) near oviposition sites on the leaf veins for each plant species were square-root transformed and analysed using ANOVA, and the means were separated using the LSD test.

Histological Procedures

Patterns in the internal anatomical characteristics within and among plant species were investigated by examining thin sections of fixed tissues (as per Jensen 1962) of each plant species near oviposition sites. Tissue samples (1 cm long) from each plant species that included *O. insidiosus* eggs or were directly adjacent to the tissues with eggs were excised using a razor blade and placed directly into FAA (formalin–acetic acid–alcohol) (Jensen 1962). Tissue samples were embedded in paraffin, sectioned to a thickness of 15 μm on a microtome, stained with safranin and counterstained with fast green solution (Jensen 1962). Slides were examined microscopically using a Zeiss Axioskop (Carl Zeiss Inc., Oberkochen, Germany) and photos were taken at 40×, 100× and 200× using an ocular-mounted Nikon Coolpix 950 (Nikon, Tokyo, Japan). The images were exported to Microsoft PhotoEditor 3.0.2.3 (Microsoft, Redmond, WA, U.S.A.), the sizes were standardized by pixels, and the images were printed in colour.

Using these images, oviposition was related to the thickness of the external cellular layers of green bean ($N = 11$) and soybean ($N = 10$). The low number of

oviposition sites on sectioned tissues of pigweed ($N = 2$), velvetleaf ($N = 4$) and morning glory ($N = 1$) prevented us from including these data in this set of analyses. For the sections containing the eggs, we measured the thicknesses of the epidermal and collenchyma cellular layers (for soybeans only; green beans had no collenchyma cells) adjacent to where the egg was laid and on the side of the section opposite from the egg. The tissue thicknesses were log-transformed and compared between both sides and the various plants using a two-factor ANOVA, with plant species and opposite–adjacent as grouping variables.

To compare the anatomical features among the plant species, the sample sizes were increased by including sections of tissues from areas neighbouring oviposition sites. Thus, the thicknesses of the epidermis and collenchyma layer (when present) and the minimum distances from the outside of the epidermis to the phloem and xylem were measured in each plant species. Specifically, three measurements of each parameter were taken for each 1 cm portion of tissue, and a composite mean was generated for each tissue portion. Eggs are laid only on the leaf veins of velvetleaf (J. G. L., personal observation), so we also sectioned five pieces of petiole and stems of this species to determine whether the internal anatomy may influence this egg-laying pattern. The final sample size for each plant species was as follows: morning glory ($N = 5$), pigweed ($N = 4$), green bean ($N = 11$), soybean ($N = 18$) and velvetleaf ($N = 5$). We compared the mean thicknesses of the epidermises and the external thicknesses of the different plants using the nonparametric Kruskal–Wallis ANOVA.

O. insidiosus Morphometrics

The morphometrics of head characters in *O. insidiosus* were sampled from egg until adulthood. Although the pathway that stylets of *O. insidiosus* take as they penetrate through plant tissue is unknown, it was presumed for this study that they travel linearly to reach plant tissues of suitable nutrition. The lengths of nymph mouthparts ($N = 12–19$ from each stadium) from the base to the tip were measured using a compound microscope at $100–400\times$. The widths of the head capsules directly behind the eyes were also recorded using a dissecting microscope at $50\times$ for each stadium. The ovipositor lengths of insectary-produced females ($N = 18$) were recorded to determine the potential maximum depth of oviposition.

Nymphal Survival

In general, *O. insidiosus* nymphs are commonly regarded as being primarily entomophagous, but they can consume and even complete their development on certain plant-based foods (Kiman & Yeargan 1985; Corey et al. 1998). We hypothesized that plant-based resources are particularly important for newly hatched nymphs, who have poor dispersal and therefore predation capabilities. *Orius insidiosus* was maintained as a colony on *E. kuehniella* eggs and bee pollen (Y. S. Organic Bee Farms, Sheridan, IL, U.S.A.). Females were allowed to lay eggs in 2.5 cm

sections of green beans, which had been produced in a greenhouse. Daily, the eggs were separated from the females and were monitored for hatching. Newly hatched nymphs (<24 h old) were randomly assigned to treatments involving one of the five plant species. Immediately before the experiment, a leaflet was severed from the stem at the node, and petioles were placed into 1.5 ml microcentrifuge tubes filled with water. Tubes containing similar amounts of foliage were placed individually into 15 cm diameter petri dishes. No other food or water was provided to the nymphs.

We placed 1-day-old nymphs individually into each dish containing plant material, for a total of 15 observations on each plant species. Petri dishes were sealed with Parafilm and kept at $27°C$, 40% relative humidity and LD 16:8 h. We checked dishes daily for survival of *O. insidiosus* and refilled water wicks as needed. We compared the average life span of nymphs between treatments using a Kruskal–Wallis nonparametric ANOVA, followed with an LSD test for means separation. Comparisons of survivorship curves were conducted using stratified survival analyses and the nonparametric Mantel–Haenszel test statistic (SYSTAT 11, SYSTAT 2004).

Correlations of Plant Anatomy with Morphometrics

We used using general linear models (SYSTAT 2004) to compare regressions among nymphal longevity (days) and oviposition preferences for the plant species (number of eggs laid) with trichome densities near the oviposition sites on leaf veins (trichomes/mm) and the thicknesses of the total external covering (mm, log-transformed) and epidermis alone (mm).

RESULTS

Ovipositional Behaviour

We deprived females ($N = 5$) of oviposition substrates for at least 24 h, provided them with 1 cm sections of green beans and observed their oviposition behaviour. The females began foraging by gently poking and wiping their mouthparts on the green bean. This behaviour was often followed by a short feeding bout (less than 5 min), when the mouthparts were slightly inserted into the bean. Females then resumed walking on the bean and eventually inserted the entire length of their ovipositors into the bean tissue. There was no experimental probing with the ovipositor. As it travelled down the ovipositor sheaths into the bean tissue, the egg was visible as a swollen area of the ovipositor. The process of injecting the egg was often accompanied by rapid pulsations of the entire abdomen. Once the egg was fully injected into the tissue, the sheaths were extracted and the female reinitiated foraging.

Ovipositional Preferences for Different Plants

The majority of the *O. insidiosus* recovered from the cages had survived the entire oviposition period. *Orius*

insidiosus preferred to oviposit on morning glory and green bean ($\chi_4^2 = 37.15$, $P < 0.0001$; Fig. 1). Soybean and pigweed were of intermediate acceptability, and no eggs were laid on velvetleaf plants.

Trichome Densities and Oviposition

The number of eggs laid in the petioles and leaf veins varied among the different plant species. For each species the numbers of eggs laid in the leaf veins were 10, 38, 6, 18 and 10 for green bean, morning glory, pigweed, soybean and velvetleaf, respectively. The numbers of eggs laid in the petioles of green bean, morning glory, pigweed, soybean, and velvetleaf were 16, 43, 32, 56 and 0, respectively.

The number of trichomes adjacent to and opposite from the oviposition sites on the petioles were significantly different for all plant species except for pigweed (soybean:
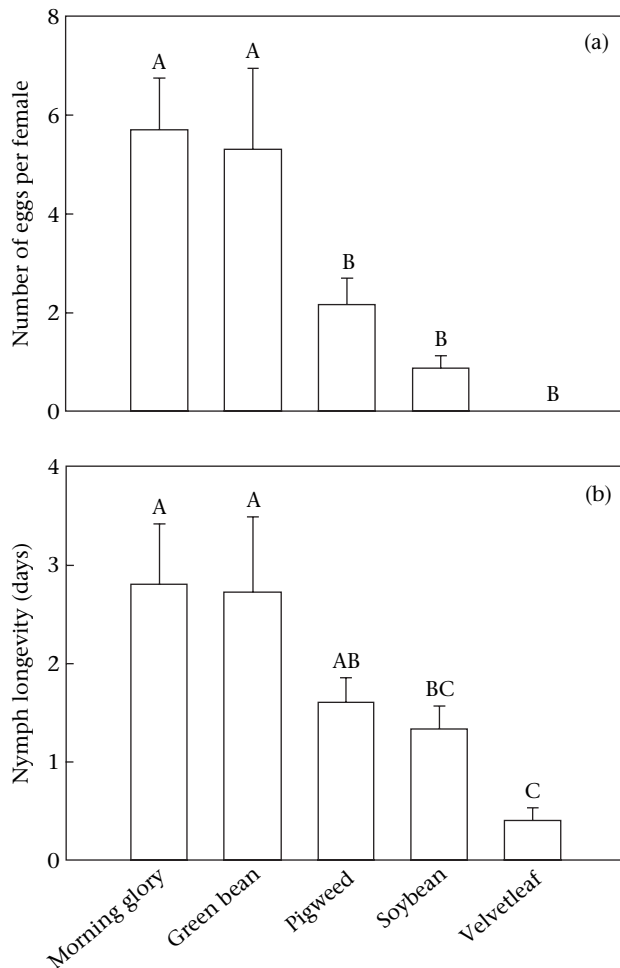
$\chi_1^2 = 27.21$, $P < 0.0001$; green bean: $\chi_1^2 = 14.73$, $P < 0.0001$; morning glory: $\chi_1^2 = 9.24$, $P = 0.002$; pigweed: $\chi_1^2 = 2.39$, $P = 0.12$; Fig. 2). Trichome densities surrounding oviposition sites on the leaf veins varied significantly among plant species (mean $\pm$ SE trichomes per mm for pigweed: 0.63 ± 0.14; morning glory: 2.72 ± 0.29; soybean: 2.78 ± 0.26; green bean: 3.19 ± 0.61; velvetleaf: 9.98 ± 0.70; $F_{4,77} = 33.14$, $P < 0.0001$). Although trichomes were less abundant on pigweed than on the other species, these trichomes were noodle-like and laid down on the leaf veins such that the examined plant tissues were often covered by the trichomes. Velvetleaf had the most trichomes, which were glandular (Sterling et al. 1987) and had multiple hairs arising from each trichome base.

Internal Plant Anatomy and Oviposition

A representative cross section with the pertinent tissues indicated is presented in Fig. 3. In soybeans and green beans, the epidermal coverings where the egg was laid were ca. 50% as thick as on the opposite side of the shoot (adjacent to or opposite from egg: $F_{1,38} = 16.47$, $P < 0.0001$; species: $F_{1,38} = 1.88$, $P = 0.17$; interaction: $F_{1,38} = 0.05$, $P = 0.83$; Fig. 4). Although sample sizes were small for the other three plant species ($N = 1, 2$ and 4 observations for morning glory, pigweed and velvetleaf, respectively), they followed the same general pattern of having thinner epidermises where the egg was laid. The influence of the thickness of the collenchyma layer and epidermis combined (total external covering) on within-plant oviposition patterns was analysed solely for soybeans, since green bean shoots do not have a collenchyma layer. The total external covering of soybeans
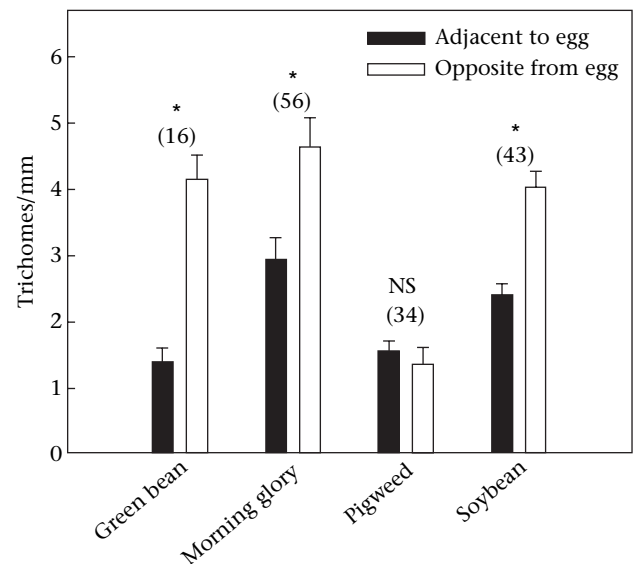

Figure 1. Effects of plant species on (a) oviposition preferences of *Orius insidiosus* females and (b) longevity of nymphs. The preferences of females were tested under choice conditions in the laboratory. Neonate nymphs were reared on the different plants in the absence of prey. Significantly different means ($\alpha = 0.05$; Kruskal–Wallis nonparametric comparison) were separated using LSD tests. All values presented are means $\pm$ SE.

Figure 2. A comparison of the trichome densities on preferred and unpreferred oviposition sites on the petioles of four plant species. The trichome densities adjacent to and opposite from *O. insidiosus* eggs were compared separately for each plant species. *Indicates significant differences ($\alpha = 0.05$, Kruskal–Wallis ANOVA). Sample sizes for each plant species are indicated in parentheses. All values presented are means $\pm$ SE.
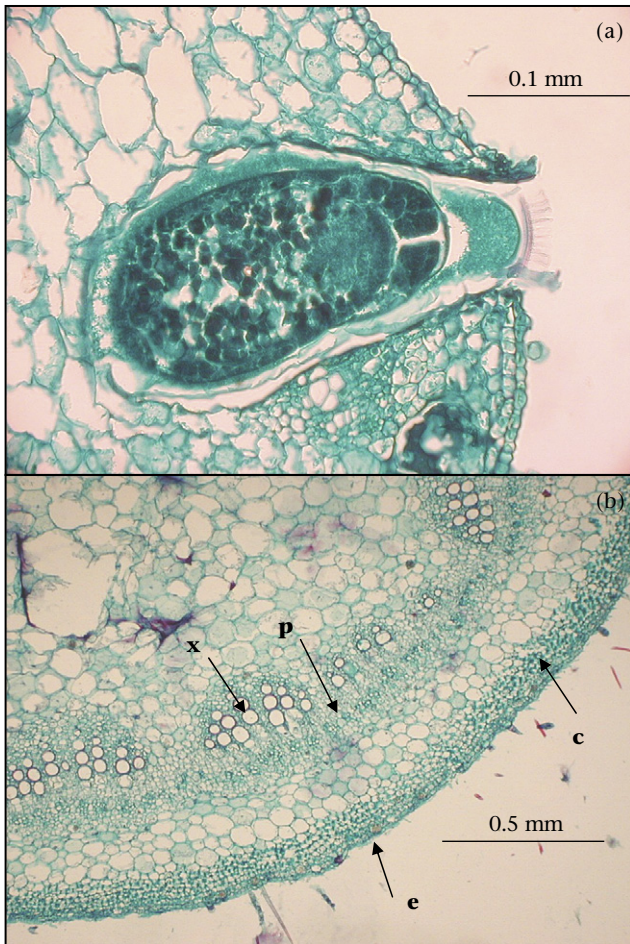
Figure 3. Cross sections of anatomical features. (a) *Orius insidiosus* egg inserted into the petiole of soybean. (b) Stem of velvetleaf with the epidermis, **e**, collenchyma, **c**, phloem, **p**, and xylem, **x**, tissues indicated for reference.
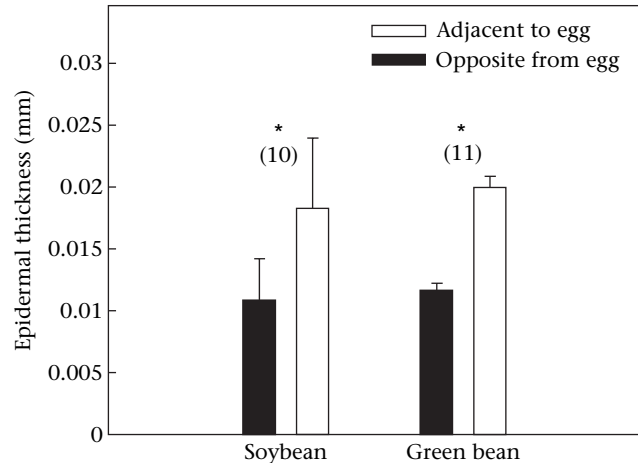

Figure 4. Comparison of the epidermal thicknesses at preferred and unpreferred oviposition sites of *O. insidiosus* on the shoots of two plant species. The epidermal thicknesses adjacent to and opposite from *O. insidiosus* eggs were compared separately for each plant species. *Indicates significant differences ($\alpha = 0.05$, ANOVA). Sample sizes for each plant species are indicated in parentheses. All values presented are means ± SE.

near the egg was similar to the thickness opposite from the egg ($F_{1,18} = 0.31$, $P = 0.58$).

The thickness of the epidermises ($\chi^2_4 = 30.56$, $P < 0.001$) and total coverings ($\chi^2_4 = 46.52$, $P < 0.001$) near eggs differed significantly between plant species. Mean ± SE thicknesses of the epidermises were 0.018 ± 0.001, 0.017 ± 0.001, 0.013 ± 0.0005, 0.014 ± 0.0005 and 0.016 ± 0.001 mm for green bean, morning glory, soybean, pigweed and velvetleaf, respectively. Mean ± SE thicknesses of the epidermis plus the collenchyma tissues were 0.018 ± 0.001, 0.017 ± 0.001, 0.034 ± 0.001, 0.048 ± 0.007 and 0.078 ± 0.005 mm for green bean, morning glory, soybean, pigweed and velvetleaf, respectively.

O. insidiosus Morphometrics

Head capsule widths ($F_{4,29} = 554$, $P < 0.0001$) and proboscis lengths ($F_{4,29} = 1025$, $P < 0.0001$) were distinct for each instar (Table 1). The phloem and xylem on at least some of the measured tissues from each plant species were accessible to the mouthparts of even the youngest nymphs (Tables 1, 2). Mean length of the female ovipositors was 0.52 ± 0.006 mm.

Nymphal Longevity

Maximum nymphal longevity on plant leaves in the absence of prey was 9 days, with none of the nymphs surviving until adulthood. The longevity of *O. insidious* nymphs was significantly affected by plant species ($\chi^2_4 = 19.27$, $P = 0.001$; Fig. 1). Green bean and morning glory both sustained *O. insidiosus* nymphs for a mean of approximately 3 ± 0.7 days, whereas all nymphs reared with velvetleaf died before the second day. Survival analysis showed that nymphal mortality patterns differed significantly between the plant species ($\chi^2_4 = 22.65$, $P < 0.0001$). More than half the nymphs died within 2 days in the soybean and velvetleaf treatments, and survival of a greater proportion of nymphs was prolonged in the other treatments.

Correlations of Plant Anatomy with Life History Traits

Nymphal longevity was strongly correlated with oviposition preference for the different plants ($F_{1,3} = 50.17$, $P = 0.006$). Females laid more eggs and nymphs survived

Table 1. Morphometric representation of head and mouthpart characteristics (mean ± SE; mm) of different life stages of *Orius insidiosus**

Instar (N)	Head capsule width	Rostrum length
1 (19)	0.176 ± 0.002	0.290 ± 0.002
2 (14)	0.224 ± 0.004	0.344 ± 0.003
3 (12)	0.269 ± 0.005	0.415 ± 0.004
4 (13)	0.308 ± 0.003	0.487 ± 0.004
5 (16)	0.354 ± 0.002	0.559 ± 0.005

*Nymphs were produced from insectary-reared individuals. Nymphal morphometrics within columns differed significantly from one another ($P < 0.05$; ANOVA with LSD means separations).

Table 2. Minimum distance (mean ± SE; mm) to the vascular tissues found in different plant species near oviposition sites of *Orius insidiosus**

Species		Sample size	Phloem	Xylem
Green bean	Stem	2	0.414±0.139	0.489±0.149
	Petiole	3	0.149±0.031	0.202±0.033
	Leaflet petiole	2	0.415±0.091	0.457±0.082
	Leaf vein	4	0.276±0.046	0.330±0.050
Morning glory	Leaf vein	5	0.256±0.039	0.256±0.040
Pigweed	Petiole	5	0.244±0.017	0.286±0.020
Soybean	Petiole	2	0.103±0.010	0.159±0.010
	Leaflet petiole	4	0.148±0.023	0.202±0.018
	Leaf vein	12	0.128±0.010	0.170±0.013
Velvetleaf	Stem†	5	0.231±0.015	0.410±0.023
	Petiole†	5	0.226±0.015	0.299±0.020
	Leaf vein	5	0.08±0.005	0.132±0.006

*Each sample represents a composite mean from three measurements randomly collected along a 1 cm portion of tissue.
†No eggs were laid on these tissues, so pieces were randomly selected from the plant to use as general observations.

longer on plants with thinner external tissues (Fig. 5). The epidermal thicknesses alone were not correlated with nymphal longevity ($F_{1,3} = 1.57$, $P = 0.23$) or with oviposition preference ($F_{1,3} = 1.47$, $P = 0.31$). There were also no correlations between the density of trichomes surrounding the oviposition sites on the leaf veins of different plant species and the ovipositional preference for each plant species ($F_{1,3} = 9.31$, $P = 0.41$) or nymphal survival on each plant species ($F_{1,3} = 2.08$, $P = 0.25$).

DISCUSSION

Our results suggest that reproductive females select plants for oviposition based on plant anatomical traits that are strongly correlated with the survival of immature stages. Specifically, females prefer plants as ovipositional hosts that have the thinnest external tissues. Once a plant is chosen, *O. insidiosus* selects sites to lay her eggs based on the relative trichome densities and epidermis thickness of the various plants. The clear relationship between oviposition decisions among plants and reproductive success suggests the importance of plant feeding to this facultatively phytophagous predator during its early developmental stages. Still, the importance of plant preferences by ovipositing females on the demographics of *O. insidiosus* in the field needs to be substantiated.

The current research indicates that females distinguish plants based on the thickness of their external tissues, including the epidermis and collenchyma layers. Our research indicates that the condition of these tissues not only has direct implications for the female, but also for her offspring's ability to use a given plant as a food source. Relative trichome densities on the different plants
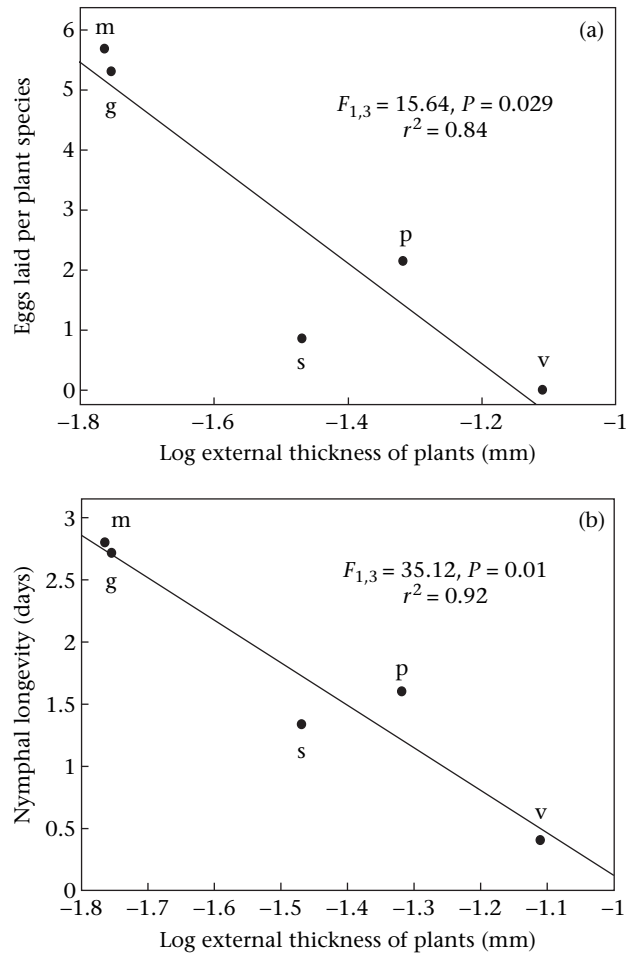

Figure 5. Relationships between the mean thickness of the external coverings of five plant species and (a) mean oviposition preferences for the different plants and (b) the mean nymphal longevity on the different plants in the absence of prey. m = morning glory, g = green bean, p = pigweed, s = soybean, v = velvetleaf.

were not a good predictor of oviposition preferences among plants. It is notable that the linkage between oviposition preference and nymphal survival that we observed for *O. insidiosus* does not necessarily apply to all heteropteran omnivores (Benedict et al. 1983). *Lygus hesperus* (Knight) prefers to oviposit on cotton phenotypes with the highest trichome densities. The *L. hesperus* nymphs that hatched from these hairy varieties were significantly smaller than those from the less preferred glabrous varieties.

Once a plant is selected for oviposition, the females then use trichome density and epidermal thickness to orient to a suitable oviposition site. Females prefer to lay eggs at specific sites within a given plant (Isenhour & Yeargan 1982; Lundgren & Fergen 2006). We found that females were able to distinguish the epidermal thickness and trichome densities on an extremely fine scale; there were mean differences of only 0.08 mm in the epidermal thickness and 1.6 trichomes per mm between where eggs were laid and directly opposite from the oviposition site. Observations suggest that females use their

proboscises, rather than their ovipositors, to assess the quality of different oviposition sites, possibly through chemo- or mechano-sensors located on their mouthparts. Castane & Zalom (1994) found that *O. insidiosus* females cannot insert their ovipositor through paraffin-coated gelatin of more than 0.045 mm thickness, and in their study, most females laid eggs on paraffin whose thickness was 0.030 mm. Our work shows that *O. insidiosus* females may penetrate even deeper than this when ovipositing into plant tissue; specifically, the maximum thickness that *O. insidiosus* penetrated was 0.056 mm on the leaf veins of velvetleaf. Volatile cues do not appear to influence the ability of *O. insidiosus* females to locate perspective oviposition hosts even over short distances (J. G. L., unpublished data). How plant chemistry influences the decision-making process of the females on a more proximal scale merits further attention.

The importance of the plant species to the longevity of *O. insidiosus* nymphs and the resulting implications for plant feeding by this omnivorous bug deserve some discussion. Clearly, our work indicates that prey is important for the complete development of *O. insidiosus*, but the current research also supports the hypothesis that plant nutrients can sustain nymphs for several days in the absence of prey. Although Armer et al. (1998) presented data that nicely shows feeding on the xylem with slight consumption of cellular tissue, they concluded that *O. insidiosus* adults obtained minimal nutrition from soybean plants. Our research shows that neonate *O. insidiosus* survive better on soybean (and many of the other plants) than on water alone, which suggests that these developing nymphs are able to use plant tissue for nutrition. Indeed, the phloem and xylem on soybeans are packaged together in bundles, such that nutritious phloem would undoubtedly be encountered even by xylem-feeding insects. Moreover, the vascular tissues of at least portions of each plant species are at a depth that is fully accessible to the mouthparts of all life stages of *O. insidiosus* (the mouthparts of even the youngest *O. insidiosus* instars are nearly one-third of their total body length). A similar finding was made by Hoffman & McEvoy (1986); histological sections revealed that the xylem was accessible to the mouthparts of even the first instars of *Philaenus spumarius* (L.) (Homoptera: Cercopidae). More work on exactly which plant tissues are being consumed by developing *O. insidiosus* would aid our understanding of their nutritional ecology.

In conclusion, zoophytophagous insects overcome periods of low prey availability during their development by consuming plant material. Still, not all plant resources are equally suitable for insects, and our results suggest that females of *O. insidiosus* are able to assess the structural qualities of plants and select to lay eggs on those species that are nutritionally optimal for their progeny, an interesting trait for an insect most appreciated for their entomophagous nature. How this reproductive behaviour manifests itself in the field in the form of *O. insidiosus* demographics within a habitat has implications for the use of these insects as natural control agents of crop pests.

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