

Compatibility of *Orius insidiosus* (Hemiptera: Anthocoridae) with *Amblyseius (Iphiseius) degenerans* (Acari: Phytoseiidae) for control of *Frankliniella occidentalis* (Thysanoptera: Thripidae) on greenhouse roses

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Abstract

The compatibility of two commercially-marketed natural enemies of *Frankliniella occidentalis* (Pergande), an anthocorid bug, *Orius insidiosus* (Say), and a phytoseiid mite, *Amblyseius (=Iphiseius) degenerans* Berlese, was tested on cut roses, *Rosa hybrida* L. cv. ‘Tropicana’. Our goal was to determine the extent to which intraguild predation could affect suppression of *F. occidentalis* by this predator complex. We conducted laboratory experiments to examine: (1) effects of prey densities, prey composition, and crop structure on predation by adult *O. insidiosus*, (2) prey switching behavior in *O. insidiosus*, and (3) effects of *Orius* gender on prey preference. We found that *Orius insidiosus* will switch to the more abundant prey if presented with variable ratios of adult *A. degenerans* and immature or adult *F. occidentalis* on flowers or foliage. If presented with prey in equal numbers, *O. insidiosus* preyed more on *A. degenerans* than adult *F. occidentalis* but equally on *A. degenerans* and immature *F. occidentalis*. Males and females of *O. insidiosus* showed similar patterns of predation, but females killed more prey than males. In greenhouse trials simulating thrips infestations of cut rose crops, we compared control of *F. occidentalis* on roses with releases of both *O. insidiosus* and *A. degenerans* or only *O. insidiosus*. Roses with or without predators produced similar numbers of harvestable flowers, but roses with predators had fewer thrips than roses without predators. Releases of both predators did not enhance thrips control because roses with both predators had similar numbers of thrips as roses with only *O. insidiosus*.

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Keywords: *Orius insidiosus*; *Amblyseius degenerans*; *Frankliniella occidentalis*; *Rosa hybrida*; Biological control; Intraguild predation; Prey switching; Preference; Anthocoridae; Predatory mite; Western flower thrips

1. Introduction

A growing trend among biological control programs is to use two or more species of natural enemies to suppress populations of insect pests. Augmentation biological control programs in protected culture often use combinations of predators, parasitoids, or pathogens against whiteflies (Hoddle, 2004; Avilla et al., 2004), aphids (Chau and Heinz, 2004; Blümel, 2004), thrips (Brødsgaard, 2004; Shipp and Ramakers, 2004) and agromyzid leafminers

(Chow and Heinz, 2004; van der Linden, 2004). As a result, intraguild predation has become a prevalent topic in the biological control literature. One of the more common examples of intraguild predation is when two predator species compete for the same prey and one of them also feeds upon its competitor (Rosenheim et al., 1995). For practitioners of biological control, an important question is: what effects will the presence of intraguild predators have on the ability of the entire community of natural enemies to suppress populations of pests?

Studies on conservation biological control programs have shown intraguild predation to severely limit the impact of predators on agricultural insect pests (Müller and Brodeur, 2002; Prasad and Snyder, 2006). However,

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others have proposed for augmentative biological control programs the use of generalist predator assemblages to quickly and effectively suppress populations of native or introduced insect pests (Symondson et al., 2002). Similarly, Brodeur et al. (2002) argued that disruption of biological control by higher-order predators (generalist predators of herbivores that also attack other predators) interfering with other beneficial agents is less likely to be important in greenhouse systems than in other types of agroecosystems. They provided two reasons supportive of their argument: (1) higher-order predators are likely to disappear from agroecosystems once pest populations are reduced and (2) biological control is restorable, if adversely affected by intraguild predation, through periodic inoculative releases of the beneficial agents. Brodeur et al. (2002) concluded negative effects of intraguild predation could enhance pest suppression if higher-order predators increased in number by feeding on the other agents. In particular, they noted *Orius* (Hemiptera: Anthocoridae) species as examples of higher-order predators that can complement the suppressive actions of predatory mites with minimal disruption of biological control of western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), in greenhouse-grown cucumbers.

Two major groups of commercially available generalist predators, anthocorid flower bugs of the genus *Orius* and phytoseiid mites of the genus *Amblyseius* (Acari: Phytoseiidae), are commonly used in augmentation biological control programs for *F. occidentalis* in greenhouse-grown crops in North America and Europe (Brødsgaard, 2004; Shipp and Ramakers, 2004). Many *Orius* species prey on both larvae and adult thrips and can be effective predators of *F. occidentalis* (Sabelis and van Rijn, 1997). Several species of *Orius* have been used to suppress *F. occidentalis* on greenhouse sweet pepper, cucumber, and eggplants (Gilkeson et al., 1990 [*Orius tristicolor* (White)]; van den Meiracker and Ramakers, 1991 [*Orius insidiosus* (Say)]; Chambers et al., 1993 [*Orius laevigatus* (Fieber)]; Bolckmans and Tetteroo, 2002 [*O. laevigatus*]). Although *Amblyseius* species feed only on 1st-instar thrips, they have been shown to suppress infestations of *F. occidentalis* on cucumber, pepper, and tomato (Gillespie, 1989 [*Amblyseius* (= *Neoseiulus*) *cucumeris* (Oudemans)]; van Houten and van Stratum, 1995 [*Amblyseius* (= *Iphiseius*) *degenerans* Berlese]; Shipp and Wang, 2003 [*A. cucumeris*]; Messelink et al., 2006 [*Amblyseius* (= *Typhlodromips*) *swirskii* (Athias-Henriot)]).

Biological control practitioners have released both predatory mites and anthocorid bugs against *F. occidentalis* in greenhouses (Bolckmans and Tetteroo, 2002; Skirvin et al., 2006), but resulting benefits for pest suppression were not quantitatively validated. Several laboratory studies have investigated the compatibility of *Orius* and *Amblyseius* species for control of thrips. Some studies support the premise of compatibility (Gillespie and Quiring, 1992 [*O. tristicolor* and *A. cucumeris*]; Wittmann and Leather, 1997 [*O. laevigatus* and *A. degenerans*]; Brødsgaard and

Enkegaard, 2005 [*Orius majusculus* (Reuter) and *A. degenerans*]), but others do not (Wittmann and Leather, 1997 [*O. laevigatus* and *A. cucumeris*]; Magalhães et al., 2004 [*O. laevigatus* and *A. cucumeris*]; Sanderson et al., 2005 [*O. insidiosus* and *A. cucumeris*]). However, most of these investigators based their recommendations on the relative preference of the *Orius* species for *F. occidentalis* and the *Amblyseius* species in simple environments such as leaf discs or small vials with no plant material. Still needed is a better understanding of how *F. occidentalis* and different combinations of *Orius* and *Amblyseius* species will interact in more complex plant environments and most importantly what impact these interactions will have for suppression of thrips on greenhouse crops.

We examined compatibility of *O. insidiosus* with *A. degenerans* for control of *F. occidentalis* on greenhouse cut roses. Our goal was to determine the extent to which intraguild predation within this predator complex affects suppression of *F. occidentalis* on this crop. Our three objectives were to: (1) determine the effects of prey densities and composition on predation by *O. insidiosus*, (2) examine prey switching behavior in *O. insidiosus*, and (3) evaluate control of *F. occidentalis* with *O. insidiosus* and *A. degenerans*.

First, we present the results of small cage experiments that tested the effects of prey density, prey composition, and crop-plant structure (flowers versus foliage) on *O. insidiosus* predation and prey switching behavior. Prey switching refers to the proportion killed of a particular prey by a predator changing from less than expected to more than expected as the relative abundance of that prey increases in relation to the alternative prey (Murdoch, 1969). With these laboratory experiments, we showed that total and relative predation of thrips and/or mites by *O. insidiosus* depended on the types of prey available. However, whether foraging on rose flowers or foliage, *O. insidiosus* tended to switch to the most abundant type of prey. Second, we present the results of greenhouse trials that compared control of *F. occidentalis* on cut roses with releases of both *O. insidiosus* and *A. degenerans* or only *O. insidiosus*. With these greenhouse trials we showed that roses with predators had fewer thrips than roses without predators, but roses with both predators had similar numbers of thrips as roses with only *O. insidiosus*.

2. Materials and methods

2.1. Experimental insects and plants

Colonies of *F. occidentalis* were established from individuals collected from a variety of plants growing in Brazos County, TX, USA, and were subsequently reared in the laboratory for at least one year before being used for experiments. The protocol described by Arthurs and Heinz (2002) was used to maintain colonies of *F. occidentalis* and obtain uniform cohorts of larvae and adults under a L14:D10 photoperiod at 26 °C. Colony thrips were pro-

vided with leaves of kidney bean, *Phaseolus vulgaris* L., as a food and oviposition substrate. Bean leaves were streaked with honey and bee pollen (Spring Valley®, Rexall Sun Down Inc., Boca Raton, FL, USA) was added to the leaves as a dietary supplement.

Adult *O. insidiosus* and adult *A. degenerans* were obtained from Koppert Biological Systems Inc. (Romulus, MI, USA). For our experiments, we reduced variation among males or females of the same species by selecting adults of similar size within each gender from commercial shipments approximately 24–48 h after shipping. After selection, *Orius* adults were held individually in 1.5 ml micro-centrifuge tubes (USA Scientific, Ocala, FL, USA) without prey for 24 h before use in assays. We preconditioned *O. insidiosus* and conducted all laboratory experiments in environmental chambers under a L14:D10 photoperiod at 24 °C.

Rose plants were grown from bare-root rose stock (*Rosa hybrida* L. cv. ‘Tropicana’ grafted onto ‘Dr. Huey’ rootstock) individually planted in 14-L, plastic nursery-containers (Poly-tainer®, Nursery Supplies Inc., Orange, CA, USA) with soilless potting mix (Sunshine Mix no.1, Sun Gro Horticulture Canada Ltd., Bellevue, WA, USA), pine bark mulch, and sand (3:1:1, by volume). The plants were cultivated in greenhouses on the Texas A&M University, College Station campus as a cut flower crop following conventional guidelines (Langhans, 1987).

2.2. Effects of different densities of *F. occidentalis* or *A. degenerans* on predation by *O. insidiosus*

2.2.1. Second-instar thrips

A prerequisite to studying predator switching behavior is to avoid an abundance of each prey type. To determine the suitable range of prey densities to use in the switching studies, we first evaluated predation of 2nd-instar *F. occidentalis* by *O. insidiosus*. Cages were constructed from plastic, Petri dishes (15.5 cm diameter × 4.0 cm height) with lids. Each dish had a single opening cut in the side to permit insertion of a flower stem. For each replicate, the stem of a partially-open rose was inserted through the cage opening into a small water-filled cup as the cage sat vertically on the cup’s rim. Non-toxic putty (Plast-i-clay®, American Art Clay Company Inc., Indianapolis, IN, USA) sealed the opening around the stem. Second-instar *F. occidentalis* (6–7 days old) were transferred onto the flower with a fine paint brush. To prevent escape of thrips from the cages, we covered the opening of each cage with clear polyethylene wrap (Glad® Cling Wrap, The Glad Products Company, USA) and then sealed each cage with its lid.

We tested three densities of thrips: 5, 10, and 20 thrips per cage, with both male and female *O. insidiosus*. A single, adult *O. insidiosus* was released onto the flower approximately 1 h after the introduction of the thrips. Twenty-four hours after the introduction of the anthocorid bug, we destructively sampled the flower to determine the numbers

of petals and dead thrips. We also examined the interior surfaces of the cage for dead thrips. Petal number was used to estimate flower size and numbers of dead thrips to estimate predation. Only *Orius* adults that were alive at the end of each treatment were counted as treatment replicates. We completed ten replicates for each treatment combination of *Orius* gender and prey density (total = 60 bugs). Prey mortality, due to handling, was estimated from 10 replicates with 10 thrips per cage but without *Orius*.

2.2.2. Adult thrips or adult mites

To determine the effect of different types of prey on the functional response of *O. insidiosus*, we used the same protocol as the first experiment and evaluated predation of adult *F. occidentalis* (15–17 days old) or adult *A. degenerans* by female *O. insidiosus*. One set of females was confined with only adult *F. occidentalis* and the second set was confined with only adult *A. degenerans*. We tested three densities of 5, 10, and 20 prey per cage, using either thrips or mites as prey. A single, female *O. insidiosus* was released onto the flower approximately 1 h after the introduction of the prey. Twenty-four hours after the introduction of the anthocorid bug, we destructively sampled the flower to determine the numbers of petals and dead prey. Ten replicates were completed for each treatment combination of prey type and prey densities (total = 60 bugs). Prey mortality, due to handling, was estimated from 10 replicates for each type of prey using 10 prey per cage but without *Orius*.

2.3. Prey switching by *O. insidiosus*

We evaluated prey switching by female *O. insidiosus* offered two prey combinations: adult *F. occidentalis* and *A. degenerans*, 2nd-instar *F. occidentalis* and *A. degenerans*. In four assays, we tested for prey switching using different *F. occidentalis*:*A. degenerans* ratios. For each assay, we used a protocol similar to experiment 2 and exposed individual *Orius* females for 24 h to the following prey ratios: 5 *F. occidentalis* and 15 *A. degenerans* (1:3 ratio), 10 *F. occidentalis* and 10 *A. degenerans* (1:1 ratio), 15 *F. occidentalis* and 5 *A. degenerans* (3:1 ratio). We first transferred the required number of thrips and then mites to each rose stem. Thrips were permitted to acclimate for approximately 1 h before the mites were introduced. An *O. insidiosus* female was released onto each stem approximately 1 h after the introduction of the mites. Twenty-four hours after the introduction of the anthocorid bug, we destructively sampled each stem to determine the numbers of dead prey. The interior surfaces of each cage was also examined for dead prey.

We first tested the switching response of *Orius* females offered adult *F. occidentalis* and *A. degenerans* on stems with a single partially-open flower using the same cage setup for experiments 1 and 2. We then repeated the first assay but used stems with only foliage (no flower). Each stem was trimmed back to three or four mature compound leaves (15–20 leaflets) to standardize canopy size. For the

third and fourth assays, we repeated the first and second assays using 2nd-instar *F. occidentalis* and *A. degenerans*. We completed 21 replicates per set for adult *F. occidentalis* and *A. degenerans* on flowers ($n = 63$ bugs) and 10 replicates per set on foliage ($n = 30$ bugs). We also completed 15 replicates per set for 2nd-instar *F. occidentalis* and *A. degenerans* on flowers ($n = 45$ bugs) and 10 replicates per set on foliage ($n = 30$ bugs). Controls consisted of 10 *F. occidentalis* with 10 *A. degenerans* on either flowers or foliage but without *Orius* females. We completed controls for adult *F. occidentalis* with *A. degenerans* on flowers ($n = 21$) or foliage ($n = 10$) and also 2nd-instar *F. occidentalis* with *A. degenerans* on flowers ($n = 15$) or foliage ($n = 10$).

According to Murdoch (1969), the Null or ‘no switch’ model for a system consisting of two prey species is:

$$P_1 = C * F_1 / (1 - F_1 + [C * F_1]) \quad (1)$$

where F_1 is the proportion of prey species 1 in the environment, P_1 is the proportion of prey species 1 among all prey killed by predator, and C is a measure of predator preference for prey species 1 given by:

$$C = (N_1/N_2) : (H_1/H_2) \quad (2)$$

where H_1 and H_2 are, respectively, the numbers of prey species 1 and 2 present in the environment and N_1 and N_2 are the numbers actually killed. In the absence of switching, C is constant and can be estimated at any ratio of H_1/H_2 . If predator preference is not constant but varies with prey availability or encounter rates, C is expected to increase as H_1/H_2 decreases. Thus, if switching occurs, the observed proportion of prey species 1 among all prey killed will be higher than expected when that species is abundant and correspondingly lower when rare.

It is convenient to estimate C when both prey classes are equally available, $H_1 = H_2$. For each replication of the set of 1:1 assays, we estimated a value of P_1 by substituting C in Eq. (1). These estimates were used to calculate the expected numbers of prey species 1 among all the dead prey in each replication of the sets of 3:1 and 1:3 assays. Following the statistical procedure described in Chow and Mackauer (1991), we estimated values for P_1 and compared observed numbers of dead *F. occidentalis* to predicted numbers generated by the Null or ‘no switch’ model.

2.4. Effects of *O. insidiosus* gender on predation of *A. degenerans* and 2nd-instar *F. occidentalis*

Commercial shipments of *O. insidiosus* often have sex ratios around 0.50 (A. Chow unpublished). The degree to which predation of *A. degenerans* by *O. insidiosus* detracts from control of *F. occidentalis* might vary with *Orius* gender. We examined the extent to which predation of both *F. occidentalis* and *A. degenerans* differs between male or female *O. insidiosus*. If male and female *O. insidiosus* show similar preference for prey, the results from our evaluation of prey switching in females should also apply to males.

Using a protocol similar to the prey switching experiment, we tested a prey combination of 10 2nd-instars of *F. occidentalis* and 10 adults of *A. degenerans* on flowers with both male and female *O. insidiosus*. We completed 20 replicates for each sex (total = 40 bugs). To estimate prey mortality due to handling, we also completed 10 replicates without *Orius*.

2.5. Control of *F. occidentalis* with *O. insidiosus* and *A. degenerans* on greenhouse roses

We compared control of *F. occidentalis* on cut roses by *O. insidiosus* and *A. degenerans* under conditions simulating greenhouse production in Texas. Roses were exposed to only *F. occidentalis*, *F. occidentalis* and *O. insidiosus*, or *F. occidentalis* with both *O. insidiosus* and *A. degenerans*. The number of replications was three per treatment and the three treatments were equally distributed within a randomised block design, using position within the greenhouse as the blocking factor.

Each replicate consisted of eight potted plants spaced 5 cm apart and arranged in a 4×2 grid on a greenhouse bench enclosed by a PVC frame (305 cm length \times 152 cm width \times 122 cm height) sheathed with Econet S[®] insect screen (Gintec Shade Technologies Inc., Windham Centre, Ont., Canada). We released five, adult females of *F. occidentalis* twice a week near each plant over seven consecutive weeks (total = 560 thrips over 14 releases per replicate) to simulate a thrips infestation. Release rates of *O. insidiosus* and *A. degenerans* were based on a consensus of recommendations from commercial insectaries. Beginning two weeks after the first release of thrips, an adult *O. insidiosus* of each sex was released near each plant in all replicates assigned only predatory bugs during the third, fifth, and sixth week of the study (total = 48 bugs over three releases per replicate). In addition, 10 adults of *A. degenerans* were released onto each plant with *O. insidiosus* in replicates assigned both predatory bugs and predatory mites (total = 240 mites over three releases per replicate).

The experiment was conducted in a greenhouse from November 2005 to January 2006. Daily temperature was monitored at 4-h intervals inside the enclosed benches with HOBO[®] H8 Pro Series data loggers (Onset Computer Corporation, Bourne, MA, USA). We counted all closed flower buds and fully opened flowers in each replicate once a week for eight consecutive weeks. Starting the same week that predators were released (week 3), we harvested three quarters of the shoots with flowers that opened recently (before pollen release). The remaining quarter of the flowering shoots, consisting of unmarketable or marginal flowers, was left in the crop to provide *O. insidiosus* and *A. degenerans* with pollen. Both predators do better on crops with pollen (see Coll and Guershon, 2002; van Rijn and Sabelis, 2005 for reviews). For each cage, flowers were cut from harvested shoots and individually sealed within plastic containers (33 cm length \times 9 cm width \times 11 cm height). The remaining stems and foliage were also sealed

in different plastic containers. Using a standard protocol developed by Chau et al. (2005), we extracted and counted *F. occidentalis* and predators from the flowers and foliage harvested from each cage. Flower shoots were harvested during the third to eighth weeks of the crop. Flower shoots left for pollen provision were cut the following week, but neither thrips nor predators were extracted because the flowers had senesced. Instead, we inspected pollen providing flowers for both thrips and predators around 2–4 days after each harvest.

2.6. Statistical analyses

All counts and proportions were checked for normality by the Shapiro–Wilk’s test and homogeneity of variance (homoscedasticity) by the Levene test. For ANOVA, we transformed counts to their square root values and proportions to their arcsine values if assumptions of normality and homogeneity were not met. For experiments with different densities of *F. occidentalis* or *A. degenerans*, we used two-way ANOVA with ‘*Orius* gender and thrips density’ or ‘prey type and prey density’ as factors to compare numbers of dead prey and flower size among treatments. One-way ANOVA was used to compare numbers of dead thrips and mites recovered from controls. For the prey switching experiment using only *Orius* females and the choice experiment with both *Orius* genders, we used one-way ANOVA to compare flower size among treatments, and Wilcoxon matched-pairs signed-rank test to compare observed numbers of dead *F. occidentalis* to predicted numbers generated by the ‘no switch’ model, and numbers of dead *F. occidentalis* to numbers of dead *A. degenerans* recovered from treatment cages or controls. For the choice experiment with both *Orius* genders, we used one-way ANOVA to detect significant differences in total dead prey and proportion of *F. occidentalis* among all dead prey recovered among treatments. For the greenhouse study, repeated measures ANOVA was used to compare weekly counts of buds, flowers, thrips, and predators. We also used repeated measures ANOVA to compare the proportions of adult *F. occidentalis* among all thrips extracted from the weekly harvests of flowers. When required, the Greenhouse-Geisser adjustment was used to correct for sphericity in repeated measures tests (Hand and Crowder, 1996). Tukey’s honestly significant difference test (HSD) was used to determine significant differences between pairs of mean values following parametric tests (Sokal and Rohlf, 2000).

3. Results

3.1. Effects of different densities of *F. occidentalis* or *A. degenerans* on predation by *O. insidiosus*

3.1.1. Second-instar thrips

Thrips density (two-way ANOVA: $F_{2,54} = 67.15$, $P < 0.001$) had a significant effect on predation of 2nd-instar *F. occidentalis* on flowers. Predation increased with thrips den-

sity in treatments with either male or female *Orius* (Fig. 1). There was a significant interaction between *Orius* gender and thrips density (two-way ANOVA: $F_{2,54} = 4.70$, $P = 0.013$). Male and female *Orius* killed similar numbers of 2nd-instar *F. occidentalis* at densities below 20 thrips per flower, but females killed nearly 30% more thrips than males when confined with 20 thrips per flower. Flower size could affect encounter rates between *O. insidiosus* and *F. occidentalis*, but there were no significant differences among the size of flowers (mean \pm SEM = 15.03 ± 0.30 petals, $n = 30$) used for treatments with female or male *Orius* (two-way ANOVA: $F_{1,54} = 1.22$, $P = 0.305$) or the three thrips densities (two-way ANOVA: $F_{2,54} = 0.20$, $P = 0.656$). Thrips mortality was very low in the control cages. The numbers of dead 2nd-instars of *F. occidentalis* recovered from controls (mean \pm SEM = 0.60 ± 0.22 , $n = 10$) was, on average, 1/7th of the numbers from treatments with *Orius* and 10 thrips per cage. All dead thrips recovered from treatment or control cages were found on the petals, sepals, or anthers of flowers.

3.1.2. Adult thrips or adult mites

Prey type (two-way ANOVA: $F_{1,54} = 6.18$, $P = 0.016$) and prey density (two-way ANOVA: $F_{2,54} = 65.51$, $P < 0.001$) had significant effects on predation, but there was no significant interaction between prey type and density (two-way ANOVA: $F_{2,54} = 2.98$, $P = 0.059$). Female *Orius* killed more prey as prey density increased and killed, on average, 30–40% more *A. degenerans* than adult *F. occidentalis* when confined with 10 or 20 prey on flowers (Fig. 2). Numbers of dead prey recovered from controls did not vary significantly with prey type (mean = 0.32, 95% CI = 0.10–0.58, one-way ANOVA: $F_{1,18} = 2.35$, $P = 0.143$) and was less than 4% of available prey. There were no significant differences among the size of flowers (mean \pm SEM = 16.98 ± 0.29 petals, $n = 80$) used for either prey type (two-way ANOVA: $F_{1,72} = 0.19$, $P = 0.663$) or among the three prey densities and controls (two-way ANOVA: $F_{3,72} = 0.52$, $P = 0.671$).

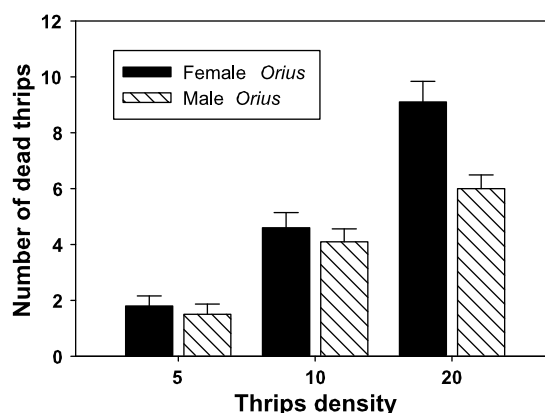


Fig. 1. Mean numbers of 2nd-instar *Frankliniella occidentalis* (+SEM) killed by a single *Orius insidiosus* female or male exposed to 5, 10, or 20 thrips ($n = 10$ per density and *Orius* gender) on a flowering rose stem.

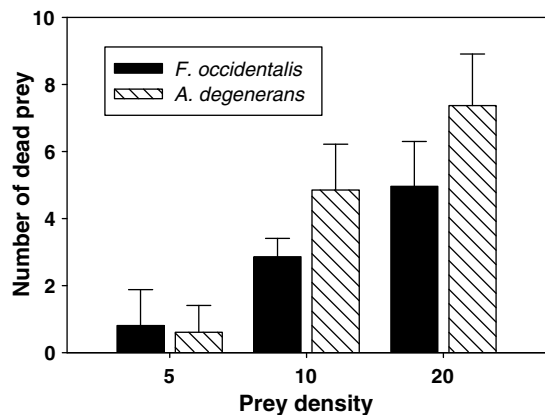


Fig. 2. Mean numbers of *Amblyseius degenerans* or adult *Frankliniella occidentalis* (+SEM) killed by a single *Orius insidiosus* female exposed to 5, 10, or 20 prey of each type ($n = 10$ per density) on a flowering rose stem. Back-transformed means and 95% confidence intervals are presented here.

3.2. Prey switching by *O. insidiosus*

Orius females generally ‘switched’ to the most abundant prey type (Table 1) and their patterns of prey switching were consistent among adult or 2nd-instar *F. occidentalis*. When adult or 2nd-instar *F. occidentalis* were the more abundant prey on either flowers or foliage, *Orius* females killed 2–3 times as many thrips than predicted by the ‘no switch’ model (Table 1). Similarly, when adult or 2nd-instar *F. occidentalis* were the less abundant prey, *Orius*

Table 1
Observed and expected numbers of dead adult or dead 2nd-instar *Frankliniella occidentalis* (WFT) recovered after 24 h of exposure to individual *Orius insidiosus* females on rose flowers or foliage at different ratios of *F. occidentalis* and *Amblyseius degenerans* (AD)

Treatment	Prey ratio (WFT:AD)	No. dead WFT (mean \pm SEM)		Probability ^a
		Observed	Expected	
Adult WFT & AD On flowers $n = 21$	15:5	3.48 \pm 0.41	1.42 \pm 0.12	<0.01
	10:10 5:15	2.19 \pm 0.43 1.10 \pm 0.25	2.38 \pm 0.15	<0.01
Adult WFT & AD On foliage $n = 10$	15:5	2.00 \pm 0.26	0.73 \pm 0.08	<0.01
	10:10 5:15	1.10 \pm 0.23 0.70 \pm 0.21	1.60 \pm 0.21	<0.01
Second-instar WFT & AD On flowers $n = 15$	15:5	7.07 \pm 0.69	2.77 \pm 0.29	<0.01
	10:10 5:15	2.33 \pm 0.49 1.53 \pm 0.22	2.34 \pm 0.22	<0.01
Second-instar WFT & AD On foliage $n = 10$	15:5	3.70 \pm 0.67	1.98 \pm 0.25	<0.05
	10:10 5:15	2.30 \pm 0.33 1.10 \pm 0.31	2.67 \pm 0.30	<0.01

^a Differences between observed and expected values within rows compared by the Wilcoxon match-pairs signed-rank test; probabilities are two-tailed.

females killed 35–50% fewer thrips than predicted by the ‘no switch’ model (Table 1).

Predation by *O. insidiosus* varied with prey type and plant part (Fig. 3). When *A. degenerans* and adult *F. occidentalis* were available in equal numbers, *Orius* females killed twice as many mites as thrips on flowers and almost four times as many mites as thrips on foliage (Fig. 3). However, when *A. degenerans* and 2nd-instar *F. occidentalis* were available in equal numbers, *Orius* females killed similar numbers of thrips and mites on either flowers or foliage (Fig. 3). Interestingly, when 2nd-instar thrips were more abundant than mites, *Orius* females killed twice as many thrips on flowers than on foliage but the numbers of mites killed did not vary with plant part.

Prey mortality in the controls did not differ with prey type or prey combination. The numbers of dead *A. degenerans* and dead adults or dead 2nd-instars of *F. occidentalis* recovered from controls for each of the prey combinations were not statistically different and mean prey mortality ranged from 3% to 7% of available prey. Flower size was uniform among all treatment and controls for experiments using *A. degenerans* and adult *F. occidentalis* (mean \pm SEM = 17.69 \pm 0.25 petals, one-way ANOVA: $F_{3,80} = 1.87$; $P = 0.141$) or *A. degenerans* and 2nd-instar *F. occidentalis* (mean \pm SEM = 17.58 \pm 0.34 petals, one-way ANOVA: $F_{3,56} = 0.37$; $P = 0.778$).

3.3. Effects of *O. insidiosus* gender on predation of *A. degenerans* and 2nd-instar *F. occidentalis*

Female *Orius* killed significantly greater numbers of prey than male *Orius* (one-way ANOVA: $F_{1,38} = 6.17$, $P = 0.018$) when both prey types were offered in equal numbers within rose flowers (Fig. 4); however, the proportions of 2nd-instar *F. occidentalis* among all prey killed by female or male *Orius* were not statistically different (mean = 0.345, 95% CI = 0.244–0.454, one-way ANOVA: $F_{1,38} = 0.07$, $P = 0.849$). Total numbers of prey killed by female *Orius* were, on average, about 40% greater than those killed by male *Orius*. Mortality of *A. degenerans* or 2nd-instar *F. occidentalis* was very low in the control cages. Numbers of dead *A. degenerans* and dead 2nd-instars of *F. occidentalis* recovered from controls were not significantly different (mean \pm SEM = 0.95 \pm 0.21, $n = 20$) (Wilcoxon signed-rank test: $n = 10$; $Z = -0.18$, $P = 0.855$) and less than 10% of each prey type. The size of flowers used for controls and treatments with female or male *Orius* were not significantly different (mean \pm SEM = 16.86 \pm 0.35 petals, one-way ANOVA: $F_{2,47} = 0.45$, $P = 0.642$). No dead thrips and less than 5% of the dead mites recovered from treatment or control cages were found off flowers.

3.4. Control of *F. occidentalis* with *O. insidiosus* and *A. degenerans* on greenhouse roses

Daily temperatures inside the enclosed benches ranged from 18 to 32 °C during November, gradually declined to

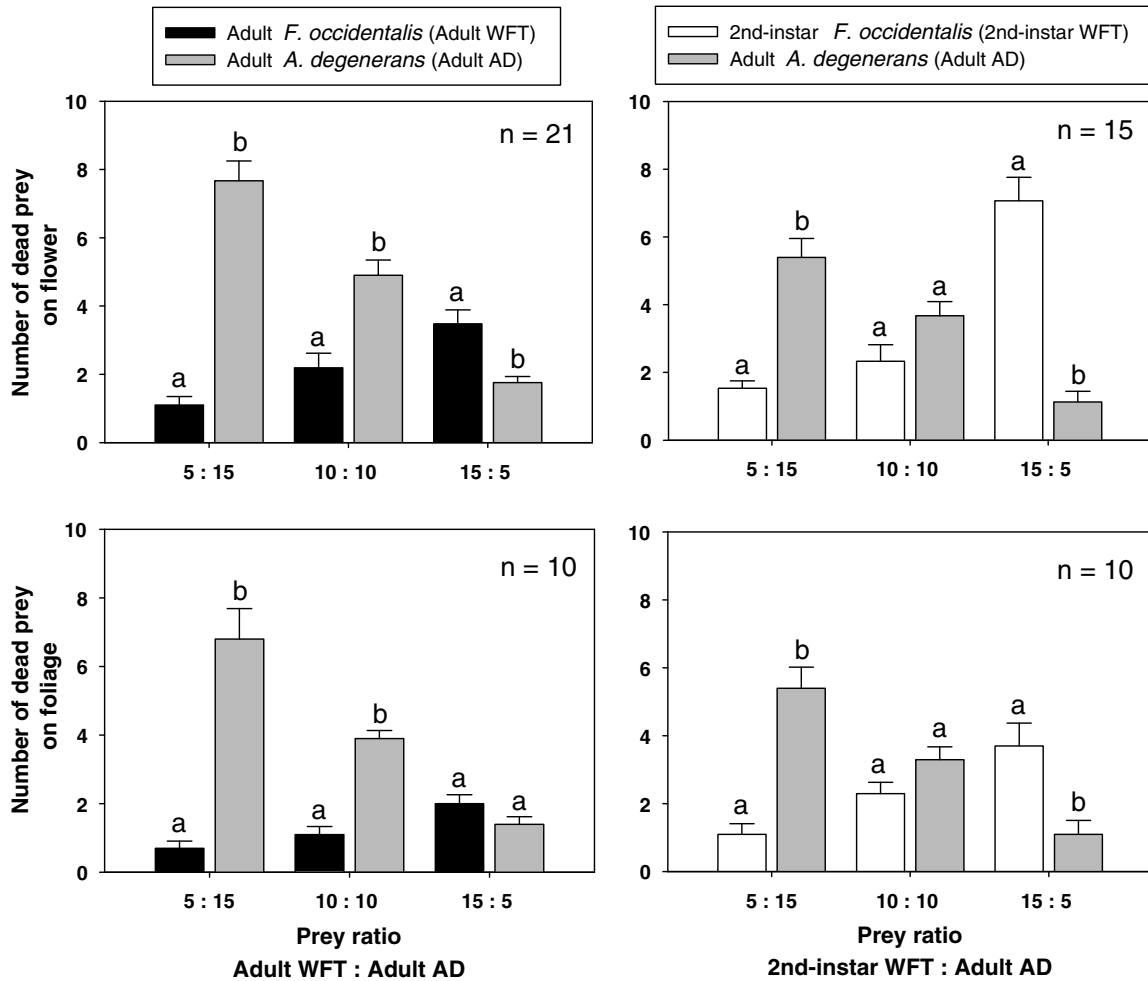


Fig. 3. Mean numbers of *Amblyseius degenerans* and adult or 2nd-instar *Frankliniella occidentalis* (+SEM) killed by a single *Orius insidiosus* female exposed to different ratios of prey on rose flowers or foliage. For each prey ratio, different letters above bars indicate significant differences ($P < 0.05$) determined by Wilcoxon match-pairs signed-rank test.

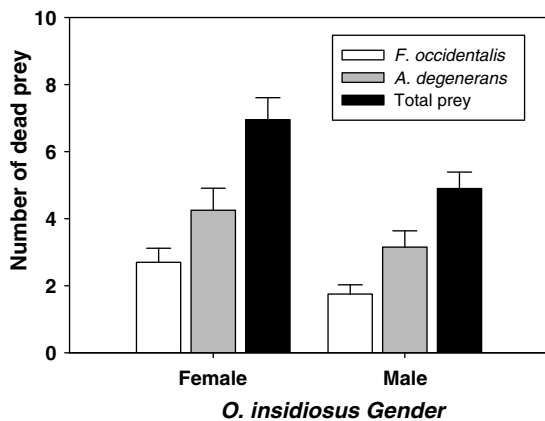


Fig. 4. Mean numbers of *Amblyseius degenerans* and 2nd-instar *Frankliniella occidentalis* (+SEM) killed by a single *Orius insidiosus* female or male exposed to 10 prey of each type together on a flowering rose stem ($n = 20$ per *Orius* gender).

13–25 °C during December, and were within published ranges for survival and activity of our insects and mites (Malais and Ravensberg, 2003). Plants with predators

and plants without predators produced similar numbers of open flowers each week (one-way repeated measures ANOVA: $F_{2,6} = 0.51$; $P = 0.623$). Mean flower counts were 4.53 (95% CI = 4.00–5.09, $n = 9$) in the first week, increased to 9.54 (95% CI = 7.84–11.41, $n = 9$) by the third week, and declined to 4.25 (95% CI = 2.90–5.86, $n = 9$) by the eighth week. The numbers of flowers left to provide pollen within the crop ranged from 1 to 3 per week, but were similar for plants with or without predators (one-way repeated measures ANOVA: $F_{2,6} = 1.40$; $P = 0.318$). We found no significant differences between counts of closed flower buds on plants with predators and plants without predators (one-way repeated measures ANOVA: $F_{2,6} = 0.20$; $P = 0.823$). Mean bud counts started at 10.81 (95% CI = 9.32–12.40, $n = 9$) in the first week and gradually declined to 4.38 (95% CI = 3.09–5.91, $n = 9$) by the eighth week.

Thrips populations grew rapidly during the weeks when the size of the harvestable flower crop increased but quickly declined as the number of flowers decreased. Counts of *F. occidentalis* for flowers harvested from plants without

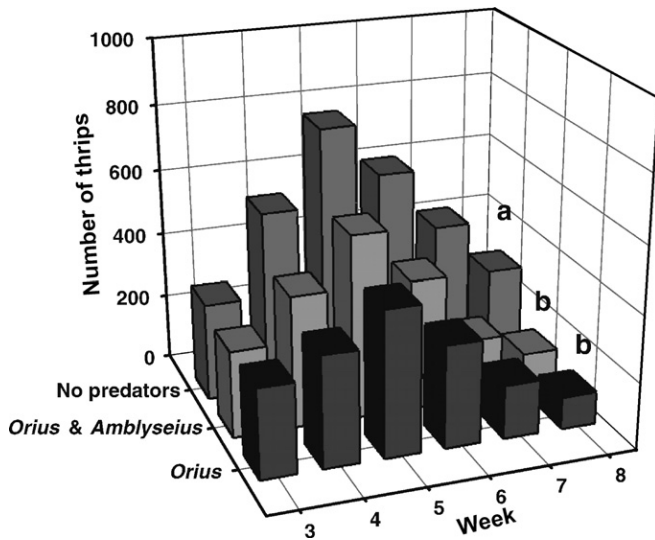


Fig. 5. Mean numbers of adult *Frankliniella occidentalis* (WFT) from weekly counts for cut rose crops exposed to 'no predators' (□) or *Orius insidiosus* (▒) or both *Orius insidiosus* and *Amblyseius degenerans* (■), $n = 3$ per treatment, eight plants per replicate. Different letters above the bars indicate significant differences ($P \leq 0.05$) determined by Tukey's HDS (one-way repeated measures ANOVA: $F_{2,6} = 5.58$; $P = 0.043$). Releases of WFT began on the first week and finished in the seventh week. Releases of predators began on the third week and finished in the sixth week. WFT were counted once every week during the third to eighth weeks of the crop.

predators or plants with predators increased during weeks 3–6 and declined during weeks 6–8 of the crop (Fig. 5). We found significant differences between thrips counts for flowers harvested from plants without predators or plants with predators (repeated measures one-way ANOVA: $F_{2,6} = 5.58$; $P = 0.043$) (Fig. 5), but there was no significant interaction between week and treatment (repeated measures two-way ANOVA: $F_{10,30} = 0.46$; $P = 0.903$). When pooled across weeks, thrips counts were 40–50% higher for flowers from plants without predators (back-transformed mean = 463.38) than for flowers from plants with *O. insidiosus* (back-transformed mean = 251.11) or both *O. insidiosus* and *A. degenerans* (back-transformed mean = 288.04). Although the degree of population growth and decline for *F. occidentalis* was affected by the presence or absence of predators, the trajectory for the population dynamics of the pest was apparently set by the flowering cycle of the crop. *Frankliniella occidentalis* thrive on the flowers of 'Tropicana' roses but generally do less well on the leaves (Chow, unpublished).

Suppression of *F. occidentalis* was not significantly affected by the number of predator species released (Fig. 5). Thrips counts throughout the crop cycle were similar among flowers from plants with only *O. insidiosus* or both *O. insidiosus* and *A. degenerans*. The presence or absence of predators did not affect the proportion of adults among thrips from flowers (one-way repeated measures ANOVA: $F_{2,6} = 4.37$; $P = 0.067$). On average, only 10% of *F. occidentalis* recovered from flowers were adults from

weeks 3–7; however, this proportion increased slightly to 14% by week 8. In our study, almost all the thrips were recovered from flowers. We rarely recovered immature or adult *F. occidentalis* from foliage (1–8 thrips per cage each week) and found no significant differences between the numbers of thrips recovered from the foliage of plants with predators or plants without predators (one-way repeated measures ANOVA: $F_{2,6} = 1.77$; $P = 0.248$).

No predatory bugs or predatory mites were recovered from the foliage of plants with predators and the low numbers of *O. insidiosus* recovered from the flowers of plants with only predatory bugs or both predatory bugs and predatory mites were not statistically different (one-way repeated measures ANOVA: $F_{1,4} = 0.18$; $P = 0.693$). Recovery of *O. insidiosus* from plants with predators started at 1.25 bugs per cage (95% CI = 0.57–2.16, $n = 6$) in week 4 and slowly increased to 1.86 bugs per cage (95% CI = 0.88–3.21, $n = 6$) by week 8. We recovered only adult *O. insidiosus* during weeks 4–6 but both adults and nymphs during weeks 7–8 of the crop. The distribution of *A. degenerans* within the crop was even more limited than that of *O. insidiosus*. Within 2–4 days after releases of *A. degenerans* on the crop, we frequently found predatory mites during visual inspections of open flowers left on plants with both predators. However, we did not recover *A. degenerans* from the harvested flowers of plants. Adult and immature stages of *F. occidentalis* or *O. insidiosus* were often observed with *A. degenerans* within open flowers left on plants with both predators.

4. Discussion

Releases of multiple predator species have been encouraged, in part, as a strategy to improve biological control of pest complexes in greenhouse agroecosystems (Brodeur et al., 2002). With this strategy, advocates add two or more predator species to a pest–crop system and ask which combination does the greatest damage against the pest population. More effective combinations of natural enemies would ideally reduce the total numbers required for effective and timely pest suppression and save clientele money. Quantifying multi-predator interactions and understanding their consequences on target pest populations is needed for optimal implementation of this strategy. Although not always stated, an important aspect is to avoid or minimize intraguild predation. A better understanding of predation patterns among anthocorids would enhance the implementation of these higher-order predators with other beneficial agents in biological control programs for greenhouses.

The causes and modalities of switching have been well investigated among insect predators and to a lesser extent among insect parasitoids (see Lawton et al., 1974; Sherratt and Harvey, 1993; and Elliott, 2006 for reviews). Cornell (1976) proposed that switching would be most likely in mobile predators which forage among many patches where prey species occur in different proportions. Such conditions are well met in *Orius* species which are good fliers, active

foragers and polyphagous predators (Malais and Ravensberg, 2003).

Albajes and Alomar (1999) stated that for *Orius* species there was no evidence in the literature of switching prey preference with prey abundance in the field. Despite the implications of switching behavior for intraguild interactions involving *Orius* species and phytoseiid species used for biological control of *F. occidentalis*, there are few studies addressing this topic. In two studies, the investigators compare *Orius* predation of the *Amblyseius* species and *F. occidentalis* using one fixed number for each type of prey in the single prey treatments and then combined the two numbers for the mixed prey treatments (Brødsgaard and Enkegaard, 2005; Sanderson et al., 2005). Two other studies varied the relative proportion of *F. occidentalis* to the *Amblyseius* species by holding the number of one prey constant and varying the number of the other prey (Gillespie and Quiring, 1992; Wittmann and Leather, 1997). Although these four studies provide useful information on prey preference and the effects of differing densities of thrips and phytoseiid mites on predation by different *Orius* species, their experimental designs prevent the testing of prey switching because the total density of prey vary. We have tested prey switching in *O. insidiosus* and found that this anthocorid always switches to the most abundant prey whether foraging on flowers or foliage.

Preference of anthocorid bugs for phytoseiid mites and *F. occidentalis* has been examined among different combinations of species and prey sizes (age). Both *O. laevigatus* (Wittmann and Leather, 1997) and *O. majusculus* (Brødsgaard and Enkegaard, 2005) show clear preference for thrips when given a choice between *F. occidentalis* larvae and *A. degenerans*. Interestingly, Sanderson et al. (2005) found that *O. insidiosus* strongly prefers *A. cucumeris* when adult *F. occidentalis* is the alternative prey, but *O. majusculus* shows no preference for these two types of prey. Wittmann and Leather (1997) also found that *O. laevigatus* generally shows no preference when offered both *A. cucumeris* and immature or adult *F. occidentalis*. In contrast, Gillespie and Quiring (1992) found that *O. tristicolor* always preferentially attacks *F. occidentalis* when *A. cucumeris* is also available. In choice tests with equal numbers of thrips and predatory mites, we found that *O. insidiosus* preyed upon more *A. degenerans* than thrips if adult *F. occidentalis* was the alternative prey but predation of 2nd-instar *F. occidentalis* and *A. degenerans* was similar. Based on this limited sampling, it appears that intraguild interactions among *Orius* and *Amblyseius* species cannot be generalized. As a result, compatibility of anthocorids and phytoseiid mites for control of *F. occidentalis* should always be assessed for each possible combination of species.

Generalist predators often attack a variety of prey which differs in energetic value and both capture and handling costs. Optimal foraging theory predicts that predators should utilize large prey to maximize energy gain; however, prey of intermediate size may represent the best trade-off in terms of predation costs and rate of energy gain (Stephens

and Krebs, 1986). In an interesting study, Roger et al. (2000) showed that the costs associated with utilization of small or large lepidopterous prey by *Coleomegilla maculata* are higher than for prey of intermediate size. Although *C. maculata* showed the highest level of predation on small prey, the prey-weight-consumption rate was highest for prey of intermediate size. In cages with rose flowers or foliage, we found that levels of predation by *O. insidiosus* was lowest on large prey, adult *F. occidentalis*, but similar for intermediate-sized prey, 2nd-instar *F. occidentalis*, and small prey, adult *A. degenerans*. We have observed that *O. insidiosus* has little difficulty handling adult *A. degenerans* but adult thrips were especially difficult to capture and kill (Chow, unpublished). Additional information on biomass and energetic values for *F. occidentalis* and *A. degenerans* of different size (age) would provide a better understanding of differential utilization of prey by *O. insidiosus*.

Studies that quantify the benefits of combining *Orius* and *Amblyseius* species for control of *F. occidentalis* are few. Extrapolation of our laboratory studies with *O. insidiosus* and *A. degenerans* suggested that these two predators may show some degree of incompatibility if used for control of *F. occidentalis* on cut roses. Results from our greenhouse trial supported our assessment because releases of only *O. insidiosus* or combined releases of both predators provided similar suppression of thrips populations. Interestingly, results vary considerably among three other studies that quantified the effects of combining *Orius* and *Amblyseius* species for suppression of *F. occidentalis* populations on greenhouse crops. In greenhouse cage experiments, Skirvin et al. (2006) released 2nd-instar nymphs of *O. laevigatus* and *A. cucumeris* on potted chrysanthemum for control of *F. occidentalis*. They found that releases of *A. cucumeris* alone was the least effective for reducing thrips numbers but found no differences between releases of only *O. laevigatus* or both predator species. In contrast, Sörensson and Nedstam (1993) claimed that combined releases of *O. insidiosus* and *A. cucumeris* provided better reduction of *F. occidentalis* numbers on four different flowering ornamental crops (sainpaulia, impatiens, gerbera and *Brachyscome* [Brachycome] *multifida*) than releases of each predator alone. In the third study, Ramakers (1993) released both *O. insidiosus* and *A. cucumeris* for control of *F. occidentalis* on greenhouse sweet peppers and found that *A. cucumeris* levels were reduced during the part of the crop season when the two predators coexisted. However, both predatory mite and thrips numbers reached high densities temporarily when anthocorid levels decreased.

The diverse and often contrasting results from both laboratory and field studies on anthocorids, phytoseiid mites and *F. occidentalis* could be due to plant characteristics or distinct behavioral interactions among the predators or between predators and prey. Wittmann and Leather (1997) proposed that the difference in preference of *O. laevigatus* for *A. cucumeris* and *A. degenerans* could be explained by behavioral differences between the two phy-

toseiid mites. They suggested that *A. degenerans* was more mobile than *A. cucumeris* and that *O. laevigatus* may have greater success capturing the less active species. However, Magalhães et al. (2004) found that *A. cucumeris* reduced their activity level when they detected *O. laevigatus* and proposed that this behavior was adaptive because it enabled the phytoseiid mite to avoid detection by the anthocorid. In Petri-dish arenas without plant material, we observed that *O. insidiosus* had the lowest capture success with adult thrips and capture success of 2nd-instar *F. occidentalis* was lower than for adult *A. degenerans* (Chow, unpublished). Large 2nd-instar thrips and adult thrips are reportedly not attacked by phytoseiid mites (Bakker and Sabelis, 1989) and we also did not observe predation of adult or 2nd-instar *F. occidentalis* by *A. degenerans* within Petri-dish arenas (Chow, unpublished). Therefore, mortality of thrips in our laboratory studies was due exclusively to predation by *Orius* bugs.

Plant structure and other crop characteristics may also influence interactions between anthocorids and phytoseiid mites (Shipp and Whitfield, 1991) or anthocorids and thrips (Coll and Ridgway, 1995; Atakan et al., 1996; Coll et al., 1997; Coll and Izraylevich, 1997). We found that predation of *F. occidentalis*, particularly 2nd-instar thrips, by *O. insidiosus* was generally higher on rose flowers than foliage. Partially or fully open rose flowers are relatively confined structures when compared to leaves and anthocorids may have higher capture success for highly mobile prey within flowers. Interestingly, Brødsgaard and Enkegaard (2005) found that predation by *O. majusculus* on larvae of *F. occidentalis* was lower on flowers than leaves of chrysanthemum but predation of *A. degenerans* did not vary with plant location. Differences in the structure of rose and chrysanthemum flowers might provide refuges for thrips but not for phytoseiid mites. Thrips might find refuge within the dense tubular structure of chrysanthemum ray flowers, but not within the simple flowers of roses. In our study, there was little evidence for prey refuges in rose flowers because we frequently recovered *O. insidiosus* and dead thrips or dead mites among all parts of the flowers. It is evident that further studies are necessary to determine the mechanisms responsible for the different predation of *F. occidentalis* and *A. degenerans* by anthocorids on plants.

Plant provided food, such as pollen or nectar, could also influence predator–prey interactions in the crop (see van Rijn and Sabelis, 2005 for review). Skirvin et al. (2007) found that the presence of pollen as a supplemental food for predators of thrips in chrysanthemum crops led to a 55% reduction in thrips predation by *A. cucumeris*. Pollen is also a good food source for *A. degenerans* (van Rijn and Tanigoshi, 1999) but it can reduce their predation of *F. occidentalis* on cucumber plants (van Rijn et al., 2002). In our greenhouse study, the provision of pollen by rose flowers left in the crop may have contributed to the lack of improvement in thrips suppression when both *O. insidiosus* and *A. degen-*

erans were released. Benefits of supplemental pollen for *A. degenerans* include enhanced development and reproduction (van Rijn and Tanigoshi, 1999), but its impact on thrips control for cut rose crops requires further investigation.

In summary, the research results demonstrate the need for caution when combining *Orius* and *Amblyseius* species for control of *F. occidentalis*. We have shown that *O. insidiosus* is an intraguild predator with the capacity to switch between certain stages of *F. occidentalis* and *A. degenerans*. Moreover, we found that thrips control on cut roses was not enhanced by releases of predatory mites in addition to predatory bugs. *Amblyseius degenerans* is expensive to purchase from commercial insectaries, with US clientele paying up to \$137 US for 1000 mites, while *O. insidiosus* costs only \$48 US for 500 bugs (2006 pricing, Koppert Biological Systems Inc.). Although *O. insidiosus* alone may not provide sufficient control of *F. occidentalis* on greenhouse roses, we would advise careful investigation before using concurrent releases of *O. insidiosus* and *A. degenerans* to improve control.

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