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Predation behaviors of *Franklinothrips orizabensis* (Thysanoptera: Aeolothripidae) towards *Scirtothrips perseae* and *Heliothrips haemorrhoidalis* (Thysanoptera: Thripidae)

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Abstract

The foraging behaviors of predatory female *Franklinothrips orizabensis* Johansen towards *Scirtothrips perseae* Nakahara and *Heliothrips haemorrhoidalis* (Bouché) in avocado leaf arenas were videotaped and analyzed. *F. orizabensis* encountered and attacked more second instar *S. perseae* with 80% ($n = 113$) attacks on this life stage being observed compared to 20% on first instars ($n = 28$) when equal numbers of these prey were presented simultaneously. However, there was no significance difference by life stage for the probability of being attacked after being encountered. Successful attacks by *F. orizabensis* only occurred against propupal *H. haemorrhoidalis* ($n = 6$) that lacked protective fecal droplets, 65% of prey encounters were with this life stage, and 6% of encounters with propupae resulted in attacks. Second instar *H. haemorrhoidalis* larvae bearing protective droplets were encountered less frequently and were not attacked when contacted even though equal numbers of both stages were presented simultaneously. Consequently, the mean proportion of the time spent grooming by *F. orizanbensis* females attacking immature *H. haemorrhoidalis* was four times greater than that for females attacking *S. perseae* larvae even though there was no significant difference in mean time (s) spent in each grooming bout. Significant differences in mean consumption times by *F. orizabensis* existed across life stages and prey species. Consumption times were shortest for first instar *S. perseae* larvae, intermediate for second instars, and longest for *H. haemorrhoidalis* propupae. Mean consumption times for sequentially attacked second instar *S. perseae* declined significantly indicating satiation of predators. Predators would spend on average approximately 7–13 s probing leaves with mouthparts and feeding on fluids; a behavior that on average occupied 2–5% of their time. This result may explain observed mortality of *F. orizabensis* in the laboratory and field when this predator forages on avocado leaves that have been treated with insecticides that exhibit translaminar activity.

Keywords: Avocado; Predatory behavior; Prey preference; Time budget; Ethogram

1. Introduction

Since the establishment of *Scirtothrips perseae* Nakahara in southern California, USA, in 1996, this thrips rapidly became the major pest affecting avocado, *Persea americana* Miller, production in this state (Nakahara, 1997). Recently developed control programs for *S. perseae* are predominantly insecticide-based (Yee et al., 2001a,b). The increased reliance and use of insecticides for *S. perseae* management has seriously disrupted the biologically oriented pest control paradigm for which California avocado production was world-renowned (McMurtry, 1992). The generalist predator thrips, *Franklinothrips orizabensis* Johansen, has been identified as an important natural enemy of *S. perseae* in California avocado orchards (Hoddle et al., 2000). Consequently, this native predator has been considered as a potential biological control agent that could be mass reared for augmentative releases into avocado orchards to bolster resident *F. orizabensis* populations in the spring when *S. perseae* populations begin to increase and cause economic damage to immature fruit (Hoddle et al., 2001a,b).

In addition to attacking *S. perseae*, *F. orizabensis*, and its congener *Franklinothrips vespiformis* Crawford

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also attack another thrips pest of avocados, the greenhouse thrips, *Heliothrips haemorrhoidalis* (Bouchè). This pest has a cosmopolitan distribution and feeds on a variety of agricultural and ornamental plants (Ebeling, 1959; Hoddle et al., 2001a; Hoddle, 2003). The seriousness of *H. haemorrhoidalis* as an avocado pest in California has been reduced, in part, because of the establishment of the parasitoid *Thripobius semiluteus* Boucek (Hymenoptera: Eulophidae), via a classical biological control program against this pest (McMurtry et al., 1991); modified fruit harvesting strategies that eliminate breeding and feeding sites for *H. haemorrhoidalis* (Phillips, 1997); and insecticides that are used to control *S. perseae*.

The developmental biology of *S. perseae* differs from *H. haemorrhoidalis*. Immature and adult *S. perseae* feed on leaves and immature fruit. Late second instar larvae abandon the host plant and drop into the soil where the propupal and pupal stages develop (Hoddle, 2002). *H. haemorrhoidalis* larvae carry fecal droplets on the tips of the abdomen, propupae, pupae, and adults lack droplets, and pupation occurs on the host plant (Ebeling, 1959). In an avocado orchard, foraging *F. orizabensis* would encounter larval and adult *S. perseae* and larval, pupal, and adult stages of *H. haemorrhoidalis*. Both pest species can be found feeding on fruit or leaves.

To effectively use *F. orizabensis* in an augmentative program against *S. perseae* and *H. haemorrhoidalis*, and to assist with the accurate interpretation of results from field trials with this predator, a fundamental understanding of the searching and predatory behaviors of this natural enemy is required. The work presented here quantified in the laboratory the prey life stage preferences exhibited by *F. orizabensis* towards first and second instar *S. perseae*. Behavioral observations were made to determine if fecal droplets carried by *H. haemorrhoidalis* larvae on the tip of the abdomen deterred predator attacks as suggested by McMurtry and Badii (1991). To verify the protective nature of droplets, *F. orizabensis* was presented with *H. haemorrhoidalis* second instar larvae that carried droplets and similarly sized propupae that lacked fecal droplets. The time spent by *F. orizabensis* in various behaviors associated with foraging and processing these two prey species was determined and compared.

2. Materials and methods

2.1. Sources of *S. perseae*, *H. haemorrhoidalis*, and *F. orizabensis*

Scirtothrips perseae larvae were collected from a heavily infested ‘Hass’ avocado orchard in Bonsall, California. Immature avocado leaves with thrips were removed from the orchard, placed in plastic bags, and returned to the laboratory in a cooler. First and second instar larvae were removed from leaves with the aid of a dissecting microscope and fine paintbrush, and placed at pre-determined densities in experimental arenas (see below). A *H. haemorrhoidalis* colony was maintained at 25–27 °C under long days (14:10 [L:D] h) on green lemons at the University of California at Riverside. Second instar larvae with fecal droplets (if droplets were shed during transfer larvae were discarded) and propupae lacking droplets were removed from lemons with the aid of a dissecting microscope and fine paintbrush, and placed at pre-determined densities in experimental arenas (see below). *F. orizabensis* was reared at the University of California following methods outlined by Hoddle et al. (2000), and this colony was the source of predators used for experiments. Predators were harvested from cages as pupae in hollow plastic tubes (Hoddle et al., 2001b) and held individually in glass vials until adults emerged. Unmated and unfed adult female *F. orizabensis* ~24 h of age were used in all behavioral assays.

2.2. Filming *F. orizabensis* searching on artificial arenas

Foraging activities of *F. orizabensis* females searching for prey on an excised avocado leaf arena (5 cm × 5 cm) were videotaped. Leaf arenas were placed on water-saturated foam pads in stainless steel pans. A video camera MTV-7366 (ScienceScope, Chino California, USA) was mounted on a dissecting microscope (Leica MZ12, Wetzler Germany) and used to record foraging activities. Female *F. orizabensis* were individually placed on avocado leaf arenas containing either five first and five second instar *S. perseae* or three second instar (with protective fecal droplets) and three *H. haemorrhoidalis* propupae (lacked droplets). Prey were introduced approximately 1 h ahead of predators and left to settle and select feeding sites. The immature stages of *H. haemorrhoidalis* are substantially larger than *S. perseae*. Consequently, more *S. perseae* were presented in an attempt to approximate the biomass of the larger *H. haemorrhoidalis*. Each life stage consumed was replaced, upon cessation of feeding by the predator, with the same prey species and life stage that was attacked. Twenty and 13 female *F. orizabensis* were videotaped when presented with *S. perseae* or *H. haemorrhoidalis* as prey, respectively. Observations and video recording of predatory behavior began immediately after the introduction of a predator onto the leaf arena containing thrips prey, and foraging *F. orizabensis* were videotaped for a minimum of 45–60 min. If predators were engaged in prey attack at the 45–60 min period, then additional taping ensued until the attack behavior had been completed. Videotaped behaviors were categorized and time in behavior categories was quantified in seconds.

2.3. Behavioral categories, behavioral quantification, and ethogram construction

A combined total of nine behavioral categories were observed for *F. orizabensis*, these being: (1) biting the leaf (female probed leaf with mouthparts and extracted fluids); (2) defecating; (3) drinking (female would imbibe water from water-saturated sponge at the margin of the leaf arena); (4) feeding (female would consume attacked prey); (5) grooming (female would clean her legs, antennae, wings, and abdomen); (6) necrophagy (female would commence feeding on cadavers of previously killed prey that were re-encountered during searching); (7) prey encounter (predator would contact prey and inspect it with antennae and forelegs. This would either result in the prey being attacked, ignored, or the predator being repelled); (8) resting (predator would stand motionless); and (9) searching (predator would walk at various speeds around the arena).

A time budget was constructed from videotaped behaviors using the mean time in seconds engaged in a behavior and the mean proportion of time spent by predators in each behavioral category. Mean time in seconds spent in each behavior for each prey species was compared using Student's *t* tests on log transformed data in SAS (SAS, 1990). Proportion of time spent in observed behaviors was square root arcsine transformed and compared using Student's *t* tests in SAS (SAS, 1990). Behavioral pathways for *F. orizabensis* were constructed by calculating the percentage of behaviors and directional path of each observed behavior in general order of occurrence. Rare behaviors occurring less than 10 times in frequency were omitted from analyses.

2.4. Prey consumption

Prey preference for each instar was determined and mean consumption times of prey life stage across instar and species were compared using ANOVA on log transformed data in SAS and Tukey's Studentized range test for means separation (SAS, 1990). Mean sequential consumption times of second instar *S. perseae* by *F. orizabensis* were tested with regression analysis (SAS, 1990) to determine if feeding times declined as number of prey attacked and eaten increased.

3. Results

3.1. Behavioral quantification

Mean times spent biting leaves ($t = 3.43, \mathrm{df} = 358, P < 0.005$), encountering prey ($t = 6.92, \mathrm{df} = 452, P < 0.005$), and resting ($t = 8.43, \mathrm{df} = 117, P < 0.005$) were all significantly greater for *F. orizabensis* attacking *S. perseae* larvae (Table 1). No significant differences in time spent drinking water ($t = 1.197, \mathrm{df} = 38, P = 0.24$), grooming ($t = 1.11, \mathrm{df} = 540, P = 0.27$), or searching ($t = 1.27, \mathrm{df} = 1425, P = 0.20$) were observed for *F. orizabensis* attacking *S. perseae* and *H. haemorrhoidalis* (Table 1). No significant differences in mean proportion of time spent biting leaves ($t = 1.37, \mathrm{df} = 15, P = 0.19$), drinking ($t = 0.55, \mathrm{df} = 19, P = 0.58$) or searching ($t = 1.93, \mathrm{df} = 14, P = 0.07$) were observed when *S. perseae* and *H. haemorrhoidalis* were presented as prey (Fig. 1). Significant differences in mean proportion time spent feeding ($t = 2.91, \mathrm{df} = 14, P = 0.011$), grooming ($t = 2.47, \mathrm{df} = 12, P = 0.029$), encountering and inspecting prey ($t = 2.88, \mathrm{df} = 31, P = 0.007$), and resting ($t = 3.94, \mathrm{df} = 30, P < 0.005$) were observed (Fig. 1).

3.2. Ethogram construction

A total of 2702 (total time = 119,401 s) and 1494 (total film time = 33,850 s) behavioral events were recorded for female *F. orizabensis* attacking *S. perseae* and *H. haemorrhoidalis*, respectively. Females began their behavioral pathway by searching and when *S. perseae* was presented as prey 17.22% of searching events resulted in prey encounters of which 5.19% resulted in successful attacks on larvae (Fig. 2A). When *H. haemorrhoidalis* was presented as prey, 10.17% of searching events led to prey encounters and of these just 0.33% resulted in successful attacks and 6.58% resulted in predators being repelled by contact with droplets (Fig. 2B). Approximately 1.34% of the time searching would lead to flight attempts by *F. orizabensis* and this was only observed for predators presented with *H. haemorrhoidalis* as prey (Fig. 2B). Searching leading to drinking was approximately the same for *F. orizabensis* attacking either prey species, but searching leading to leaf biting was around two times greater when *H. haemorrhoidalis* was presented as prey in comparison to *S. perseae*.

3.3. Prey consumption

Franklinothrips orizabensis encountered second instar *S. perseae* larvae more frequently than first instars, and 80% ($n = 113$ attacks) of recorded attacks occurred against second instars when compared with 20% ($n = 28$ attacks) for first instars. The probability of being attacked after being encountered did not differ significantly ($\chi^2 = 0.48, \mathrm{df} = 1, P = 0.49$) between first (56% of encounters led to attacks) and second instars (49% of encounters led to attacks). This suggests that first and second instars are consumed by *F. orizabensis* at the same rates but second instars are found four times more often. Mean prey consumption times for first and second instar *S. perseae* and *H. haemorrhoidalis* propupae differed significantly ($F = 54.69, \mathrm{df} = 2, 144, P < 0.0005$) (Table 1). Consumption times were shortest for first instar *S. perseae*, intermediate for second instar

Table 1
Mean time in seconds (±SE) of behaviors of female *F. orizabensis* attacking either *S. perseae* or *H. haemorrhoidalis*, and proportion (Prop.) of predators that engaged in that behavior for each prey species

Behavior	Prey species					
	S. perseae	*n*	Prop.	*H. haemorrhoidalis*	*n*	Prop.
Biting leaf	12.50 ± 2.54a	171	0.90	6.75 ± 0.73b	205	0.85
Defecating	3.24 ± 0.50	12	0.60	—[a]		0.00
Drinking	57.95 ± 13.38a	43	0.55	85.16 ± 18.38a	19	0.69
Feeding on 1st instars	105.79 ± 21.28*i*	28	0.70	—		0.00
Feeding on 2nd instars	547.59 ± 31.13*ii*	113	1.00	—		0.00
Feeding on propupae	—		0.00	1670.50 ± 314.26*iii*	6	0.46
Grooming	17.26 ± 2.14a	458	1.00	25.87 ± 5.70a	240	1.00
Necrophagy	17.45 ± 4.11	168	0.95	—		0.00
Prey encounter	11.56 ± 2.47a	308	0.95	2.32 ± 0.55b	151	0.92
Resting	208.59 ± 40.99a	73	0.95	13.17 ± 1.96b	60	0.69
Searching	25.57 ± 2.44a	1074	1.00	18.68 ± 0.67a	642	1.00

Means followed by the same letters across columns or italicized roman numerals within and across columns for prey consumption times are not significantly different at the 0.05 level. Summary data were prepared from results obtained for 20 and 13 videotaped female *F. orizabensis* foraging for *S. perseae* and *H. haemorrhoidalis*, respectively.

[a] Dash (—) indicates that behavior was not observed or the life stage was not tested.

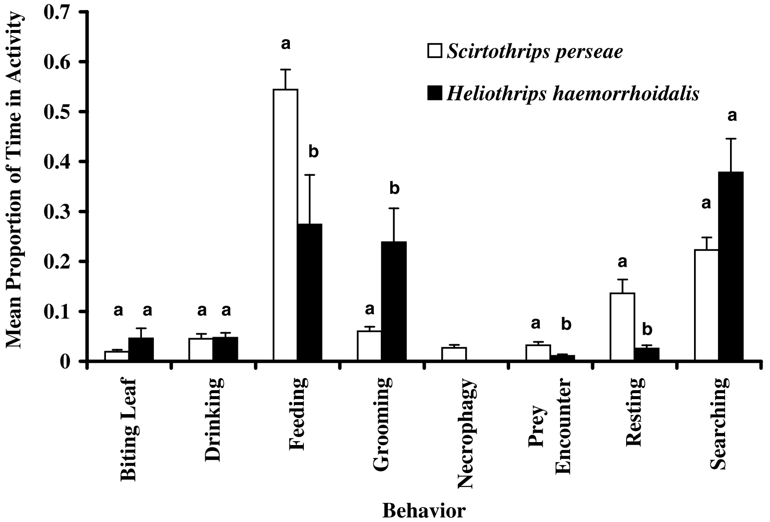

Fig. 1. Mean proportion of time spent in observed behavior by female *F. orizabensis* attacking *S. perseae* or *H. haemorrhoidalis*. Within behavioral categories bars with the same letters are not significantly different at the 0.05 level.

S. perseae, and longest for *H. haemorrhoidalis* propupae (Table 1). Average consumption times by *F. orizabensis* of second instar *S. perseae* were 5.2 times greater than first instars, and average feeding times on *H. haemorrhoidalis* propupae were 3.05 times longer than those for second instar *S. perseae* larvae (Table 1). A significant decline ($F = 8.53, \mathrm{df} = 1, 9, P = 0.017$) in the mean consumption times by *F. orizabensis* of sequentially attacked second instar *S. perseae* larvae was observed with mean consumption times of the twelfth eaten larvae being approximately 57% shorter than mean consumption times for the first eaten second instars (Fig. 3). *F. orizabensis* only attacked and consumed propupal *H. haemorrhoidalis* ($n = 6$). Of prey encounters by *F. orizabensis*, 65% occurred with propupae and just 6% of propupal encounters resulted in successful attacks on this life stage. No successful attacks on second instar larvae bearing protective fecal droplets were observed.

4. Discussion

Franklinothrips orizabensis is a voracious predator of *S. perseae* and can on average consume approximately 20-s instar larvae in a 24-h period. Over the same time period, the average consumption rate is just 2–3 immature *H. haemorrhoidalis* that lack protective droplets (Hoddle, 2003). In this study, *F. orizabensis* encountered and attacked more second instar *S. perseae* larvae although attack rates on first and second instars were not significantly different after an encounter. It is probable that *F. orizabensis* (which appeared to search in experi-

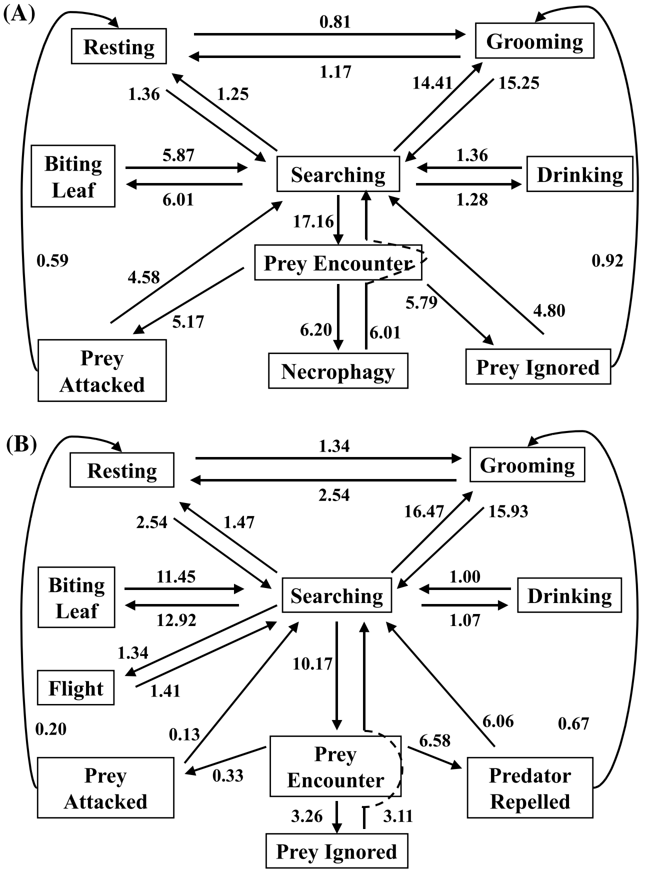

Fig. 2. Ethograms for *F. orizabensis* females attacking (A) *S. perseae* or (B) *H. haemorrhoidalis* in avocado leaf arenas. Numbers indicate percentage of behavioral events calculated from total observed behavioral events.

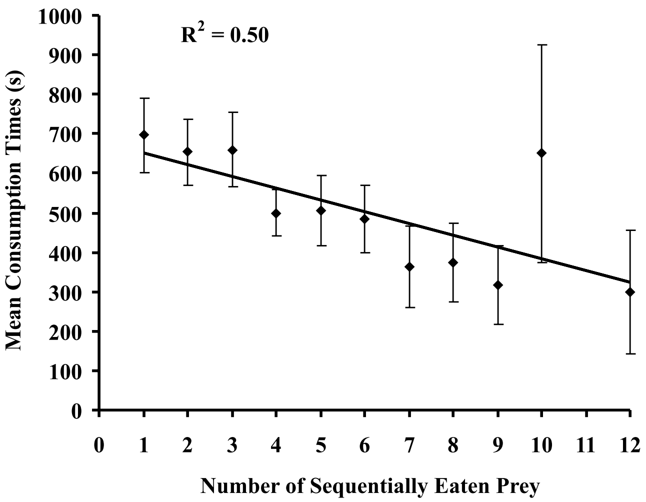

Fig. 3. Mean consumption times of sequentially attacked *S. perseae* larvae by female *F. orizabensis*.

mental arenas randomly) encountered more second instar *S. perseae* because this life stage is larger and cannot conceal itself as effectively along leaf veins in comparison to smaller first instar larvae. When presented with second instar greenhouse thrips larvae with protective fecal droplets carried on the tip of the abdomen or propupae lacking protective droplets, *F. orizabensis* females only attacked and fed on propupae and exhibited avoidance reactions when they contacted protective fecal droplets on second instar larvae. This resulted in unsuccessful attacks by *F. orizabensis* on second instar *H. haemorrhoidalis* larvae. Although no significant differences in mean grooming times by *F. orizabensis* attacking *S. perseae* or *H. haemorrhoidalis* were detected, a significant difference in the mean proportion of time grooming existed. Predators attacking *H. haemorrhoidalis* spent on average four times more time cleaning to remove irritants than those attacking *S. perseae* larvae. This indicates that grooming bouts were of similar duration for each prey species, but grooming occurred more frequently when *H. haemorrhoidalis* was presented as prey.

Additionally, prey encounter times were approximately five times greater for *F. orizabensis* foraging for *S. perseae* larvae in comparison to times spent handling immature *H. haemorrhoidalis*, and a significantly higher proportion of time was spent in prey encounters with *S. perseae*. Protective fecal exudates carried by larval *H. haemorrhoidalis* appear to effectively repel attacks by *F. orizabensis*. Droplets also significantly increased the proportion of time spent grooming by predators after prey contacts, and significantly decreased prey encounter times and proportion of time spent inspecting prey. Also, flight activity by *F. orizabensis* was higher in arenas with *H. haemorrhoidalis*, which further suggests that droplets associated with immature greenhouse thrips are highly irritating to this predator. Analysis of fecal droplets collected from *H. haemorrhoidalis* indicates that they contain a potentially repellant diol that may act as a defensive allomone (J. Millar, unpublished). Work on *H. haemorrhoidalis* fecal droplet chemistry is ongoing.

Franklinothrips orizabensis is being mass-reared by commercial insectaries in California for sale as a natural enemy for augmentative releases against thrips pests in avocado orchards (Hoddle et al., 2001b). The results of this work have demonstrated that first and second instar *S. perseae* are attacked at the same rates after being encountered, and greenhouse thrips are unacceptable prey if they are protected with fecal droplets. Therefore, augmentative releases of *F. orizabensis* need to be targeted at the appropriate thrips species and life stage. It is unlikely that *F. orizabensis* will be a successful biological control agent of greenhouse thrips because it is unable to circumvent protective fecal droplets that are carried by first and second instar larvae. Behavioral studies similar to this one would be required to determine if *F. orizabensis* would be a suitable natural enemy for augmentative releases against larvae of western flower thrips, *F. occidentalis* (Pergande) (Thysanoptera: Thripidae), a serious thrips pest of a variety of greenhouse grown vegetable and ornamental crops that exhibits aggressive defensive behavior towards antagonists (Terry and Dyreson, 1996). *F. occidentalis* produces droplets on the tip of the abdomen when attacked by predators. These droplets may contain defensive allomones (Teerling et al., 1993) that could affect attack success by generalist predators such as *F. orizabensis*.

An unanticipated finding from this behavioral study was leaf biting and feeding on leaf fluids by *F. orizabensis*. Female *F. orizabensis* would spend approximately 7–13 s on average probing avocado leaves with their mouth parts and feeding on plant juice. Leaf biting occupied 2–5% of their time budget, and 85–90% of females exhibited oral leaf probing activity. This result explains findings from previous research that had been difficult to interpret. *F. orizabensis* experiences moderately high mortality rates in the laboratory when placed on leaves with field weathered spinosad and abamectin residues (Silvers, 2000). Both of these insecticides are routinely used for *S. perseae* control in California (Yee et al., 1999). Spinosad and abamectin exhibit translaminar activity when mixed with refined petroleum oils and have very short leaf surface residue times (Yee et al., 1999).

Under field conditions, treatment of avocado trees with spinosad and abamectin can suppress *F. orizabensis* populations for up to 17 days before predator populations recover to densities similar to those seen on unsprayed trees (Yee et al., 1999). Predator mortality on insecticide treated avocado trees may be due to direct contact with insecticides, imbibing of toxins that have moved into leaf tissue, ingestion of poisons while feeding on intoxicated *S. perseae* larvae, or starvation and abandonment of trees due to lack of prey to attack. Consequently, these "safe" insecticides are probably not as harmless to natural enemies as previously thought (Cisneros et al., 2002) and may seriously harm resident populations of predatory thrips.

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