Phenology of *Scirtothrips perseae* Nakahara (Thysanoptera:Thripidae) and Associated Natural Enemies in Southern California Avocado Orchards

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Abstract

The phenology of Scirtothrips perseae, an exotic avocado pest, was monitored every 1-2 weeks in three avocado orchards in two distinct climate zones in southern California (CA), USA for 52-95 weeks over 1998-2000. Survey results indicated that mean weekly temperatures over a 24-32 week period that averaged 15° C [range $8.74-24.97^{\circ}$ C]) were significantly correlated with population increases of this pest. Conversely, population declines were strongly correlated with the onset of moderately warm weather where mean weekly temperatures over a 17-21 week period averaged >20°C [range $12.79-27.08^{\circ}$ C]). These field observations confirm results from laboratory studies that *S. perseae* population growth is greatest at low temperatures ($15-20^{\circ}$ C). Low temperatures over winter and spring in CA promote leaf flush and fruit development in avocados that this pest uses for feeding and oviposition. Analysis of results from a grower survey requesting information on severity of *S. perseae* infestations and distance of avocado orchards from the coast indicated a significant relationship; *S. perseae* is most problematic in orchards that are within 24 kms of the coast suggesting that cool ocean breezes produce temperature regimens highly favorable for this insect.

The key natural enemies associated with *S. perseae* in southern CA avocado orchards were the predatory thrips *Franklinothrips orizabensis* Johansen and *Aeolothrips kuwanaii* Moulton (both Thysanoptera: Aeolothripidae).

Introduction

Scirtothrips perseae was an undescribed species when it was first discovered damaging avocado fruit and leaves (*Persea americana* Mill. [Lauraceae]) in California (CA), USA, in June 1996 (Nakahara 1997). Subsequent foreign exploration efforts have revealed that this insect is an exotic invader in CA and is native to Mexico and Guatemala, and only occurs on avocados growing at elevations > 1300 m (Hoddle *et al.*, 2002a). Host plant surveys in CA indicate *S. perseae* may be monophagous, as this pest has only been found feeding on avocados (Hoddle *et al.*, 2002a).

Scirtothrips perseae currently infests -95% of avocado acreage in CA. Female thrips preferentially oviposit into the undersides of immature leaves and small fruit that are 25-54 mm in length (Hoddle, 2002a). In the laboratory, population demographic estimates (i.e., net reproductive rates, longevity, and fecundity) are significantly influenced by temperature. Low temperatures (15-20°C) favor rapid population growth of this pest by promoting higher fecundity, female biased sex ratios of offspring, and higher larval-adult survivorship rates (Hoddle, 2002b).

In southern CA, *S. perseae* builds to high densities on immature avocado foliage and fruit in late winter and spring, and cumulative feeding damage by larvae and adults can induce premature defoliation. Second instar larvae drop from trees to pupate in leaf duff below trees before emerging as alate adults (Hoddle & Morse, 1997; Hoddle *et al*, 1998; Yee *et al.*, 2001a). Feeding by *S. perseae* larvae and adults on immature fruit causes brown scarring and damaged fruit is either unmarketable or downgraded in packinghouses. Crop losses due to downgraded fruit and increased production costs due to insecticide use for control of *S. perseae* have been estimated to cost the CA avocado industry approximately \$7.714.3 million (US) per annum (Hoddle *et al.*, 2003). Control measures rely almost exclusively on insecticides for pest suppression (Yee *et al.*, 2001b, c; Hoddle *et al.*, 2002b).

At the time this work was conducted, relatively little was known about the phenology of *S. perseae* and indigenous natural enemies associated with this pest in avocado orchards in southern CA. Consequently, the phenology of *S. perseae* and associated natural enemies was studied in three avocado orchards in two distinct climatic zones in southern CA. The purpose of this survey was to document the seasonality of population trends of *S. perseae*, inventory associated indigenous natural enemies occurring with *S. perseae*, and to determine the influence of temperature on *S. perseae* population dynamics.

Materials and Methods

Study sites

Three commercial avocado orchards planted with the avocado cultivar 'Hass' (85% of fruit production in California is 'Hass') were selected for the following studies.

Site 1 (33° 19.61N, 117° 08.80W, elevation 214 m) Site one was located in plant climate zone 2S (southern coastal valley [Kimball and Brooks 1959]), Fallbrook San Diego County, CA, USA. A 0.60 ha site on a west facing 18° slope consisting of top-worked trees (i.e., mature trees that had been stumped to promote vigorous re-growth and increased fruit yields) that were flushing heavily with young leaves were selected in a 40 ha orchard. Survey work in Fallbrook ran from 4 March, 1998 to 31 January, 2000.

Site 2 (33° 16.45N, 117° 13.09W, elevation 124 m) This site was also located in plant climate zone 2S (southern coastal valley [Kimball and Brooks, 1959]), in Bonsall, San Diego County, CA, USA. *Scirtothrips perseae* and natural enemy populations on a south facing site with an 11° slope comprised of 105 top-worked trees were monitored. Surveys at this site ran from 18 November, 1998 to 12 January, 2000, when trees were removed for housing.

Site 3 (33° 46.01N, 117° 13.09W, elevation 287 m) Plant climate zone 4S (southern interior valley [Kimball and Brooks, 1959]), Corona, Riverside County, CA, USA. Top-worked trees randomly dispersed in a flat 30 ha orchard were sampled. Surveys were conducted from 22 January, 1999 to 21 January, 2000 when trees were felled to commence a housing development.

Scirtothrips perseae and natural enemy sampling protocols, and data analysis

Every 1-2 weeks, ten trees were randomly selected at each study site and ten expanded leaves (field observations had indicated that this category of immature leaf was most highly infested by *S. perseae* adults and larvae) on each tree were randomly selected and numbers of *S. perseae* adults and larvae on the underside of each leaf were recorded, and the mean

number of thrips counted per leaf was calculated. After *S. perseae* counts were made, each selected tree was divided into four quadrants and 1-2 branches were hit onto a beating tray 3-4 times and the number of larval and adult *Franklinothrips orizabensis, Aeolothrips kuwanaii* (both predatory thrips), *Stethorus* sp. (Coleoptera: Coccinellidae), and *Balaustium* sp. (Acari: Erythraeidae) were recorded. The total number of each natural enemy species counted at each site per sampling period was calculated. Additionally, 4-8 white sticky cards (GemplersTM, Belleville MI, USA [20 cm x 16 cm]) facing in each cardinal direction were hung in trees at each site. Cards were removed at each sampling interval, placed in clear plastic bags and numbers of adult *S. perseae* and *F. orizabensis* trapped on cards was recorded. The mean number of thrips caught per day per card for each site was calculated to standardize for unequal sampling intervals with sticky cards.

To determine the effect of mean weekly temperature (see below) on population increases and declines of *S. perseae*, temperature estimates over the periods of increasing or decreasing *S. perseae* densities were analyzed with Pearson correlation in SAS (SAS, 1990) to determine the intensity of the relationship between these two concurrent trends.

Temperature and relative humidity records

Temperature and percentage relative humidity were recorded at 30 min. intervals in an exposed area in the center of each study plot. Data loggers (Onset®, Bourne, Massachusetts, USA) were attached to wooden stakes 1.5-1.75 m above the ground. Monthly and weekly average temperatures and humidity were calculated for each site.

Orchard location and severity of Scirtothrips perseae infestations

In October 2001, 2,500 surveys were sent to CA avocado growers asking them to rank the infestation severity of *S. perseae* in their orchards.

Growers could choose one of three scores to rank their *S. perseae* infestation: A score of one indicated that thrips were either absent, or if present, densities never reached levels that warranted control; a score of two indicated a moderate thrips infestation that required treatment with insecticides once a season, but sprays were not necessary every year. A score of three meant *S. perseae* caused economic damage to fruit every season and one or more insecticide applications were regularly needed for control. Growers were also asked to indicate the distance of their orchard from the coast, the altitude of the orchard, and the county it was located in. Pest severity scores were allocated to one of seven categories based on distance (kms) from coast and scores were averaged within categories. Linear regression analysis in SAS (SAS, 1990) was performed to determine if pest severity declined with increasing orchard distance from the coast.

Results

Phenology of Scirtothrips perseae

Leaf counts at site 1 (Fallbrook)

Abundance of *S. perseae* larvae and adults on immature avocado leaves showed two distinct intervals of very low density over the periods August-November, 1998 and August-December, 1999 (Fig. 1 A). Population declines over April-August, 1998 (21 weeks) was significantly correlated (r_{20} = -0.80, *P* < 0.005) with increasing mean weekly temperatures that averaged 20°C ± 0.86 (± SE) (range 14.36-27.08°C) over this time period (Fig. 1A). Similarly,

population declines over the period April August, 1999 (19 weeks) was significantly correlated ($r_{18} = -0.62$, P < 0.005) with increasing mean weekly temperatures that averaged 19.06°C±0.71 (range 13.06-24.41°C) over this time period (Fig. 1A).

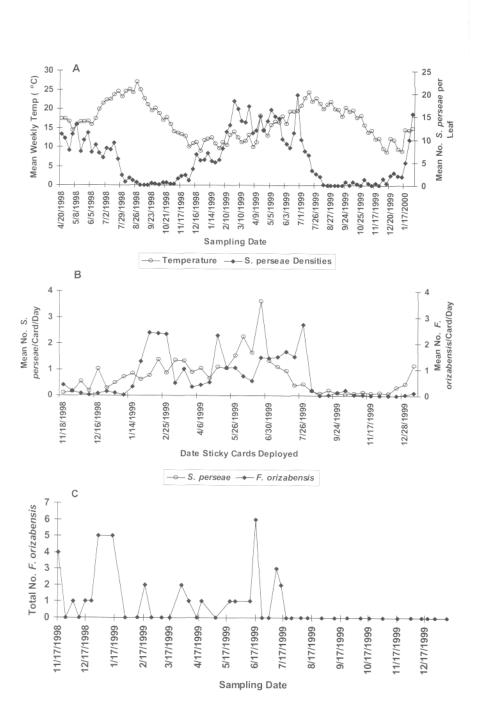


Fig. 1. (A) Temperature and *Scirtothrips perseae* trends, (B) sticky card capture rates for *S. perseae* and *Franklinothrips orizabensis*, and (C) beat tray counts for *F. orizabensis* at site 1, Fallbrook California.

Scirtothrips perseae population densities were highest over March-July, 1998 and mid-

December-July, 1999. Population increase at this site over September 1998 -April, 1999 (32 weeks) was significantly correlated ($r_{31} = -0.52$, P < 0.005) with mean weekly temperatures that were decreasing and averaged 14.01°C ± 0.73 (range 8.98-24.97°C) over this time period (Fig. 1 A). Population growth over the period late August, 1999 to the end of January, 2000 (24 weeks) was significantly correlated ($r_{23} = -0.46$, P = 0.03) with decreasing mean weekly temperatures that averaged 15.38°C ± 0.85 (range 8.74-21.89°C) over this time period (Fig. 1A).

Young leaves suitable for feeding and oviposition by *S. perseae* were abundant at this site for the entire study period including periods of low *S. perseae* densities.

Leaf counts at site 2 (Bonsall).

Larval and adult *S. perseae* densities on immature avocado leaves showed two distinct peaks between November 1998 and August 1999, and a third in January, 2000 when sampling at this site ended (Fig. 2A). Population increase at this site over November 1998 March 1999 was significantly correlated ($r_{16} = -0.57$, P < 0.05) with mean weekly temperatures that were decreasing and averaged 12.79°C ± 0.35 (range 10.49-15.69°C) over this time period (Fig. 1 A). Population declines between March-May 1999 were due, in part, to premature leaf hardening and defoliation caused by *S. perseae* feeding. This resulted in a lack of leaves suitable for oviposition and feeding over this time period. Leaf re-growth over June permitted *S. perseae* populations to recover before mean weekly temperatures around 20°C (range 19.28-22.62°C) in July 1999 were associated with population declines after which *S. perseae* adults and larvae were almost undetectable for three months. Pest populations began rapidly increasing in density by the end of November 1999 January 2000 (13 weeks) when mean weekly temperatures were averaging ~15°C (range 12.29-21.60°C) (Fig. 2A). The correlation between increasing thrips numbers and temperature was not significant ($r_{12} = -0.20$, P = 0.51) over this time period.

Leaf counts at site 3 (Corona)

Low density populations of *S. perseae* were detected irregularly on leaves in this orchard (Fig. 3A). Thrips densities at this site had not been high enough to warrant insecticide applications the preceding year, and similar low densities of *S. perseae* were observed over the course of this study.

Sticky card counts for Scirtothrips perseae and Franklinothrips orizabensis

Site 1 (Fallbrook)

Sticky cards were deployed at this site seven months after leaf monitoring studies commenced. *Scirtothrips perseae* adults were caught on cards over the entire sampling

period and were most common over January July, 1999. *Franklinothrips orizabensis* were frequently captured on cards after mid-January 1999 and declined with decreasing *S. perseae* capture rates in August 1999 to undetectable levels by November 1999 (Fig. 1B).

Site 2 (Bonsall)

Adult *S. perseae* were captured on cards more frequently over November 1998 February 1999 than *F. orizabensis*, and peak capture rates of *F. orizabensis* occurred over May July 1999, approximately three months after *S. perseae* densities had declined (Fig. 2B).

Franklinothrips orizabensis and S. perseae captures declined to very low levels by August 1999 and remained there until the cessation of the trial in January, 2000 (Fig. 2B).

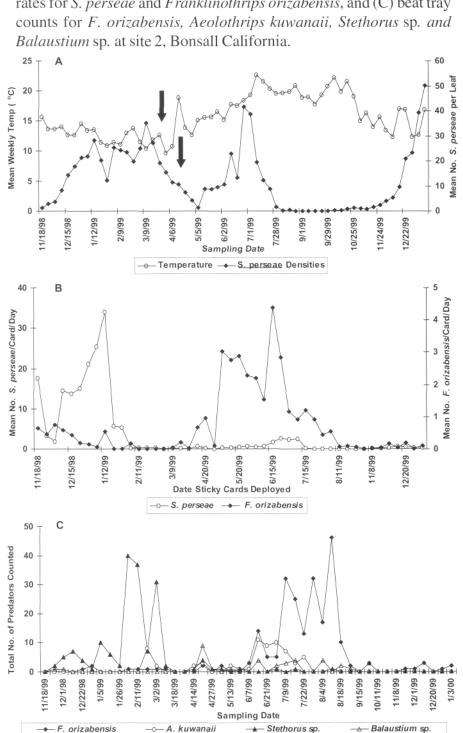
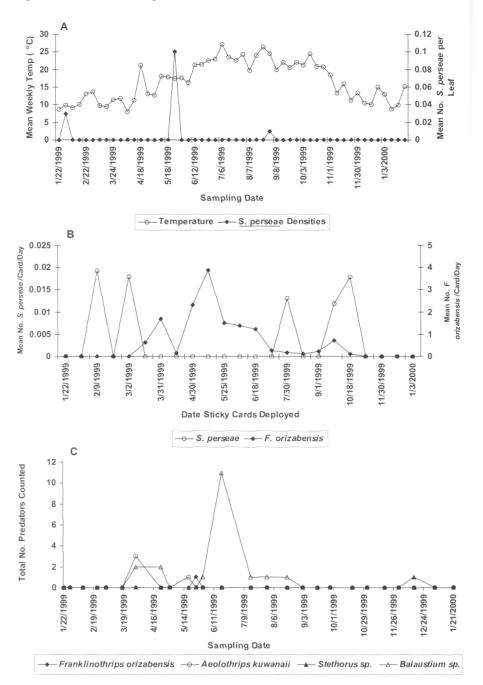


Fig. 2. (A) Temperature and Scirtothrips perseae trends (arrows indicate periods of thrips induced defoliation), (B) sticky card capture rates for S. perseae and Franklinothrips orizabensis, and (C) beat tray

Site 3 (Corona)

Franklinothrips orizabensis was consistently trapped at this site from March October, 1999 with peak densities occurring in early May. *Scirtothrips perseae* adults were detected on sticky cards irregularly at low densities (Fig. 3B).

Fig. 3. (A) Temperature and *Scirtothrips perseae* trends, (B) sticky card capture rates for *S. perseae* and *Franklinothrips orizabensis*, and (C) beat tray counts for *F. orizabensis*, *Aeolothrips kuwanaii*, *Stethorus* sp. and *Balaustium* sp. at site 3, Corona California.



Natural enemy counts from beat tray sampling

Site 1 (Fallbrook)

Beat tray counts of total numbers of *F. orizabensis* indicate this predator was present on avocados from November July, 1999 before declining to undetectable levels with this sampling method in late July (Fig. 1C). These sampling results indicate that adult and larval *F. orizabensis* were on experimental trees at the same time adults were being caught on sticky cards. *Stethorus* sp. and *Balaustium* sp. were detected irregularly at low densities, and *A. kuwanaii* was not detected at all with beat tray sampling (data for these natural enemies are not shown).

Site 2 (Bonsall)

Aeolothrips kuwanaii was first detected around March April 1999 and by late June this predator had declined in abundance and was replaced by *F. orizabensis* that in turn decreased in numbers after August, 1999 (Fig. 2C). *Stethorus* sp. was most prevalent from December 1998 March, 1999 (Fig. 2C). *Balaustium* sp. was most common from March through September, 1999 (Fig. 2C)

Site 3 (Corona)

Balaustium sp. was the most common natural enemy recovered in beat tray sampling. Low numbers of *F. orizabensis* and A. *kuwanaii* were found March through May, 1999 (Fig. 3C).

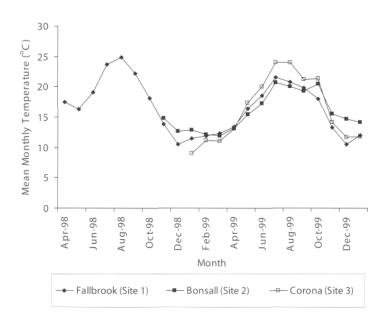


Fig. 4. Mean monthly temperatures at each of the three study sites where phenological studies of cirtothrips perseaewere conducted.

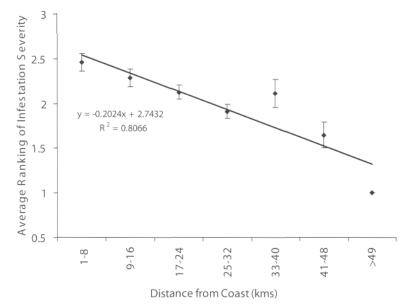
Temperature comparisons across sites

Concurrent estimations of mean monthly temperatures across sites 1 (Fallbrook) and 2 (Bonsall) (both southern coastal valley [Kimball and Brooks, 1959]) were similar over the duration of this study (Fig. 4). Mean monthly temperatures at site 3 (Corona, southern interior valley [Kimball and Brooks, 1959]) were consistently 2-4°C higher than sites 1 and 2 over May October, 1999 (Fig. 4).

Infestation severity of Scirtothrips perseae

Of growers surveyed, approximately 10% returned completed questionnaires. As orchard distance from the coast increased, thrips severity (and presumably density) significantly declined ($F_{1,5} = 18.46$, P = 0.007). *Scirtothrips perseae* infestations were most severe when orchards were located within 24 kms of the coast (Fig. 5).

Fig. 5. Severity of Scirtothrips perseaeinfestations (a score of 1 indicates no pest problem; a score of 3 indicates a severe problem requiring insecticide treatments every season) in avocado orchards in California and the distance of orchards from the coast.



Discussion

Ten species of Scirtothrips are formally recognized as economic pests (Mound & Palmer, 1981). Of these, S. citri (Moulton), a pest of citrus and mango in CA, S. aurantii Faure, a pest of citrus and mango in South Africa, and S. dorsalis Hood, a pest of tea and chillies in India and grapes in Japan are the most studied (Mound & Teulon, 1995; Mound, 1997). Scirtothrips citri, S. aurantii, and S. dorsalis all inflict economic damage to crops over summer when temperatures are high (Bedford, 1943; Faure, 1929; Horton, 1918; Shibaoetal., 1993; Shibao, 1996), and S. citri is typically most damaging to citrus grown in hot arid interior valleys of CA (Tanigoshi, 1981). The thermophilic nature of S. citri is described by phenological models that predict that minimum threshold temperatures for development are high and lie between 14.6°C-18.3°C (Tanigoshi et al., 1980; Rhodes et al., 1989). Furthermore, the recommended rearing temperature for laboratory colonies of S. citri is 31°C (Munger, 1942a) and 95.5% of hatched larvae reach the pupal stage at this temperature (Munger, 1942b). In comparison, the developmental threshold temperature for S. perseae is 6.9°C, and laboratory generated demographic estimates for population growth are highest when thrips are reared and maintained at constant temperatures of 15°C and 20°C (Hoddle, 2002b).

The results of phenology studies for *S. perseae* in southern CA avocado orchards indicate that population outbreaks of this pest were strongly correlated with low temperatures (mean

weekly temperatures over 24-32 week period averaged 15°C [range 8.74-24.97°C]) while density declines were strongly correlated with the onset of moderately warm weather (mean weekly temperatures over a 17-21 week period averaged >20°C [range 12.79-27.08°C]). Declines of high density *S. perseae* populations at sites 1 and 2 occurred with increasing temperatures over July-August even though abundant oviposition and nutritional resources were available in the form of immature leaves on top-worked avocado trees which produced prolific flush growth over the course of these surveys. This result indicates that food was not a limiting factor for pest population growth, natural enemy activity did not appear sufficient to cause *S. perseae* population declines, and the only abiotic factor that appeared responsible for reducing *S. perseae* densities was temperature.

Significant populations of *S. perseae* did not develop at site 3 (interior valley zone) which had mean monthly summer temperatures 2-4°C higher than sites 1 and 2, which probably prevented a large residual pest population from surviving and developing to economically damaging levels in winter and spring. Yee et al., (2001a) reported that *S. perseae* populations declined following warm temperatures in Ventura County (CA, USA) and pest densities in hotter inland areas do not reach the high densities observed in orchards closer to the coast that have more moderate temperatures because of the marine influence. Results of the grower survey indicated that avocado orchards located within 24 kms of the coast were more likely to have *S. perseae* populations occur near the coast because these orchards in this climate zone are subjected to cool ocean breezes that moderate high temperatures that preclude *S. perseae* population growth further inland.

Laboratory studies on the developmental and reproductive biology of *S. perseae* indicate that survivorship and reproductive output is optimal at a constant 20°C. Above this temperature fecundity declines significantly, the sex ratio of offspring is strongly male biased, and developmental rates of pre-imaginal stages significantly increase (Hoddle 2002b). Consequently, population declines of *S. perseae* in CA occur when temperatures increase over summer because immature stages develop more rapidly, female fecundity is reduced, and progeny sex ratios are male biased, which when combined, prevents population increase.

Cool weather conditions over late winter through spring promote leaf flushing, and flower and fruit production of avocados in CA (Liu et al., 1999). Temperatures that drive these developmental events in avocados favor population increases of S. perseae suggesting that the seasonal phenology of this pest is strongly linked to environmental conditions that promote growth of suitable feeding and oviposition substrates (i.e., immature leaves and fruit) in avocados. Phenological and host plant preference data indicate that S. perseae is probably a specialist phytophage of avocados that evolved with this host plant at high altitudes (> 1300 m) in Mexico and Guatemala, which lie within the area of origin for avocados (Scora and Bergh, 1990). Consequently, the phenological data presented here, combined with laboratory-based developmental and reproductive studies (Hoddle, 2002b) strongly support foreign exploration efforts for natural enemies of S. perseae for possible importation into CA from the home range of *P. americana* (Hoddle et al., 2002a). Specialist natural enemies of S. perseae must be able to respond to increasing pest densities during cool weather and survive in orchards over summer when thrips densities are very low. Under these conditions augmentative releases of mass reared natural enemies, in particular, the indigenous F. orizabensis, may be the most efficacious use of biological control agents (Hoddle et al., 2000;

2001a,b).

Sticky card monitoring and beat tray sampling methods were effective tools for monitoring predators associated with *S. perseae* in avocado orchards. These techniques probably provided more accurate data on natural enemy densities and phenology than leaf count techniques which may under estimate natural enemy densities because of substrate abandonment due to turning and handling of individual leaves, and less foliage is sampled within a given time period with leaf turning. Analysis of leaf turn counts for estimating predator densities associated with *S. perseae* resulted in a weak association of one predator, *F. orizabensis*, with increasing thrips densities in Ventura County CA (Yee *et al.,* 2001a). In work presented here, comparison of leaf counts for *S. perseae* and beat counts for *F. orizabensis* show a strong delayed density dependent response by this predator to increasing pest densities at sites 1 and 2. Typically *F. orizabensis* densities peaked 4-9 weeks after peak *S. perseae* densities at these sites.

At site 2, beat tray counts indicted that *A. kuwanaii* responded to *S. perseae* population increases earlier than *F. orizabensis* and this predator was most common over March-July after which *F. orizabensis* became the dominant predator observed at this site. It is unknown whether *A. kuwanaii* population declines were in response to decreasing *S. perseae* densities or whether this predator was competitively displaced by *F. orizabensis* (i.e., out competed for food and oviposition sites) or density reduction was due to high levels of intraguild predation by *F. orizabensis*. Further work investigating competition between these two species of predatory thrips may be warranted.

Stethorus sp. and Balaustium species did not appear to be associated with *S. perseae* population increases. *Stethorus* sp., a specialist tetranychid predator was observed feeding on *Oligonychus punicae* (Hirst) (Acari: Tetranychidae) over November-March, while *Balaustium* sp. was frequently observed attacking adult *Tetraleurodes perseae* Nakahara (Homoptera: Aleyrodidae) from March-October.

Sticky card monitoring detected aerially dispersing *S. perseae* at very low population densities when leaf counts were yielding negative results (e.g., site 3 [Corona]). White sticky cards at site 3 also detected significant numbers of *F. orizabensis* even though this predator was not found regularly with beat tray sampling of avocados. *Franklinothrips orizabensis* may have been responding to increasing prey densities (e.g., *S. citri*) in blocks of citrus that bordered site 3 and predators may have migrated into the immediately adjacent avocado blocks. For sites 1 and 2, sticky card capture rates and leaf counts of *S. perseae* showed that as densities of thrips on leaves increased so did capture rates of adult thrips on sticky cards. Subsequent work has shown significant differences between *S. perseae* and *F. orizabensis* in their preferences towards sticky cards of different colors. White sticky cards are most attractive to airborne *F. orizabensis* while *S. perseae* orients preferentially to yellow (Hoddle et al., 2002c). Consequently, *S. perseae* densities may have been under estimated with white sticky cards deployed at sites 1-3.

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