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Foreign exploration for *Scirtothrips perseae* Nakahara (Thysanoptera: Thripidae) and associated natural enemies on avocado (*Persea americana* Miller)

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Abstract

Scirtothrips perseae Nakahara was discovered attacking avocados in California, USA, in 1996. Host plant surveys in California indicated that *S. perseae* has a highly restricted host range with larvae being found only on avocados, while adults were collected from 11 different plant species. As part of a management program for this pest, a “classical” biological control program was initiated and foreign exploration was conducted to delineate the home range of *S. perseae*, to survey for associated natural enemies and inventory other species of phytophagous thrips on avocados grown in Mexico, Guatemala, Costa Rica, the Dominican Republic, Trinidad, and Brazil. Foreign exploration efforts indicate that *S. perseae* occurs on avocados grown at high altitudes (>1500 m) from Uruapan in Mexico south to areas around Guatemala City in Guatemala. In Costa Rica, *S. perseae* is replaced by an undescribed congener as the dominant phytophagous thrips on avocados grown at high altitudes (>1300 m). No species of *Scirtothrips* were found on avocados in the Dominican Republic, Trinidad, or Brazil. In total, 2136 phytophagous thrips were collected and identified, representing over 47 identified species from at least 19 genera. The significance of these species records is discussed. Of collected material ~4% were potential thrips biological control agents. Natural enemies were dominated by six genera of predatory thrips (*Aeolothrips*, *Aleurodothrips*, *Franklinothrips*, *Leptothrips*, *Scolothrips*, and *Karnyothrips*). One genus each of parasitoid (*Ceraninus*) and predatory mite (*Balaustium*) were found. Based on the results of our sampling techniques, prospects for the importation of thrips natural enemies for use in a “classical” biological control program in California against *S. perseae* are not promising. © 2002 Elsevier Science (USA). All rights reserved.

Keywords: *Aeolothrips*; *Ceraninus*; *Frankliniella*; *Franklinothrips*; *Neohydatothrips*; *Pseudanaphothrips*; *Scolothrips*; *Selenothrips*; *Thrips*

1. Introduction

Scirtothrips perseae Nakahara (Thysanoptera: Thripidae) is a new pest of major economic significance in California avocado orchards. This insect was first discovered in June 1996 damaging fruit and foliage in Saticoy and Oxnard, Ventura County, CA, USA. By July 1997, infestations of *S. perseae* were north of the initial discovery area in San Luis Obispo County and south into San Diego County. Heavily infested orchards in Ventura County experienced 50–80% crop damage in

1997 and fruit that suffered feeding damage was either unmarketable or downgraded in packinghouses (Hoddle and Morse, 1997, 1998). Crop losses in 1998 were estimated at \$7.6–\$13.4 million (US) from the combined effects of losses in quality and increased production costs associated with *S. perseae* management (Jetter, 1999). By May 1998, *S. perseae* infested 80% of California avocado acreage (Hoddle et al., 1998) and currently ~95% of fruit-bearing acreage have this pest.

Feeding damage by high densities of *S. perseae* larvae and adults on young leaves through the late fall to the end of spring can result in defoliation. However, the main source of economic loss attributable to *S. perseae* is scarring of immature fruit in spring by feeding thrips. Although scarring can be severe enough to render the

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entire fruit surface brown with a characteristic “alligator skin” appearance, these fruits can mature and flesh within damaged fruit is healthy, although the oil content may be reduced (Hoddle et al., 1998, 1999). Scarring to 5% of the fruit surface results in economic losses to growers (Phillips, 1997).

When initially discovered in California, *S. perseae* was an undescribed species that was new to science and its country of origin was unknown. Subsequent taxonomic work based on morphological comparisons determined that *S. perseae* was similar to *Scirtothrips* species endemic to Mexico and Central America rather than the known *Scirtothrips* species (e.g., citrus thrips, *Scirtothrips citri* [Moulton]) in North America (Nakahara, 1997).

Inoculative or “classical” biological control programs targeting pests of exotic origin involve prospecting for natural enemies within the pest’s native range. Suitable natural enemies associated with the pest in its country of origin that clear quarantine and meet regulatory requirements after importation are eligible for release against the target pest in its new home range (Bellows and Legner, 1993; Rose and DeBach, 1990; Rosen and DeBach, 1992; Van Driesche and Bellows, 1996). The California avocado industry has had a long history of dependence on biological control as a cornerstone for pest management (Fleschner, 1954; Fleschner et al., 1955; McMurtry, 1992). Consequently, concern over crop damage caused by *S. perseae* prompted funding of a “classical” biological control program by the California Avocado Commission. Because *S. perseae* was an unknown entity when discovered in California, the first step in this biological control initiative was to locate and delineate the home range of *S. perseae* and to simultaneously prospect for natural enemies associated with this pest.

Five separate lines of evidence justified initial exploration for *S. perseae* in Mexico and Central America: (1) *S. perseae* is morphologically more similar to congeners from Mexico and Central America than North America and other areas of the world (Nakahara, 1997). (2) In 1971, two undescribed specimens of *Scirtothrips* were found on leaves of avocado plants intercepted from Oaxaca, Mexico, by APHIS-PPQ at the Port of San Diego, California. One damaged specimen examined initially varied slightly from *S. perseae*, but subsequent re-examination by S. Nakahara indicated that it was within the acceptable range of morphological variation for this species. Later, a second thrips specimen from the same interception was located and both specimens are now considered to be the first known record of *S. perseae*. (3) Host plant surveys in California avocado orchards have found immature stages of *S. perseae* feeding only on avocados (see below for host plant survey results) and this was the only *Scirtothrips* species causing economic damage to avocados. (4) In California, *S.*

perseae outbreaks occur during cool spring weather when avocados are developing young leaves and fruit. Immature leaves and fruit are used for feeding and oviposition by *S. perseae* and population outbreaks are closely synchronized with plant phenology induced by cool weather (Hoddle, 2002a). Furthermore, laboratory-generated demographic growth statistics are highest for *S. perseae* reared on avocado leaves at low temperatures ($\leq 20^\circ\text{C}$), suggesting that this pest may have evolved closely with avocado to exploit nutritive and oviposition resources induced by low temperatures (Hoddle, 2002b). (5) Three geographic races of avocados are recognized; *Persea americana* var. *drymifolia* (Mexican race), *P. americana* var. *guatemalensis* (Guatemalan race), and *P. americana* var. *americana* (West Indian race). The Mexican and Guatemalan races evolved in high altitude regions of central Mexico and Guatemala, respectively. West Indian varieties are thought to have developed in humid lowland Pacific Ocean areas from Guatemala through Costa Rica. Humans transported avocados from these areas of origin, probably as seeds, into other areas of the Americas and elsewhere (Kopp, 1966; Mhameed et al., 1997; Popenoe, 1915; Scora and Bergh, 1990; Storey et al., 1986; Williams, 1977).

Laboratory and field studies in California have indicated that *S. perseae* may be closely adapted to avocado phenology. Host plant surveys showed a highly restricted host range (i.e., can complete entire life cycle only on avocado), suggesting that this pest may have evolved with *P. americana* somewhere in the natural range of this plant. This study provides the results of foreign exploration efforts for *S. perseae*, collection records for other species of phytophagous thrips and associated thrips natural enemies found on avocados in Mexico, Central America, the Caribbean, and South America.

2. Materials and methods

2.1. Collecting and mounting techniques

Plants were sampled for thrips and natural enemies by beating branches bearing young foliage or flowers, onto white plastic trays (18 cm \times 30 cm \times 1.2 cm). Adult and larval thrips (phytophages and predators), predatory mites, and parasitic Hymenoptera were removed from collecting trays with fine paint brushes and placed in labeled 2-ml plastic vials (Nalgene cryogenic vials 5000-0020, Nalge Company, Rochester, NY) containing a preservative (60% ethanol (10 parts), glycerine (1 part), and glacial acetic acid (1 part) (Lewis, 1973).

Avocado trees were sampled in private residences, non-commercial and commercial orchards, botanic gardens, and along roadsides. Date and locality data were recorded along with GPS (Magellan Pioneer,

Table 1

Collection records for *Scirtothrips perseae* and other thrips species collected from potential host plants growing in three avocado orchards in Southern California that were heavily infested with *S. perseae* in 1999

Potential host plant	<i>S. perseae</i> adults present?	<i>S. perseae</i> larvae present?	Thrips species collected
<i>Acca sellowiana</i>	Yes	No	<i>Scirtothrips perseae</i>
<i>Annona cherimola</i>	Yes	No	<i>Scirtothrips perseae</i> <i>Thrips tabaci</i> Lindeman
<i>Carica papaya</i>	No	No	–
<i>Chenopodium album</i>	No	No	<i>Frankliniella occidentalis</i> (Pergande) <i>Pseudanaphothrips achaetus</i> <i>Aeolothrips kuwanaii</i> Moulton
<i>Citrus</i> spp.	No	No	<i>Frankliniella gossypiana</i> Hood <i>Frankliniella occidentalis</i> <i>Thrips tabaci</i>
<i>Coffea</i> sp.	No	No	–
<i>Cucurbita</i> spp.	Yes	No	<i>Frankliniella occidentalis</i> <i>Scirtothrips perseae</i> <i>Thrips tabaci</i>
<i>Cyphomandra betacea</i>	No	No	<i>Frankliniella gossypiana</i> <i>Frankliniella occidentalis</i>
<i>Eriobotrya japonica</i>	No	No	–
<i>Eucalyptus</i> spp.	No	No	–
<i>Ficus carica</i>	No	No	–
<i>Lycopersicon lycopersicum</i>	Yes	No	<i>Frankliniella occidentalis</i> <i>Scirtothrips perseae</i>
<i>Macadamia</i> sp.	No	No	<i>Frankliniella occidentalis</i> <i>Scirtothrips inermis</i> Priesner
<i>Malus</i> sp.	No	No	–
<i>Malva purviflora</i>	No	No	<i>Frankliniella occidentalis</i> <i>Franklinothrips orizabensis</i>
<i>Mangifera indica</i>	Yes	No	<i>Scirtothrips inermis</i> <i>Scirtothrips perseae</i>
<i>Musa acuminata</i>	Yes	No	<i>Frankliniella occidentalis</i> <i>Scirtothrips perseae</i>
<i>Olea europaea</i>	No	No	–
<i>Nerium oleander</i>	No	No	<i>Frankliniella occidentalis</i>
<i>Nicotiana</i> sp.	No	No	<i>Caliothrips fasciatus</i> (Pergande) <i>Frankliniella occidentalis</i> <i>Thrips tabaci</i>
<i>Passiflora edulis</i>	No	No	<i>Frankliniella occidentalis</i>
<i>Persea americana</i>	Yes	Yes	<i>Scirtothrips perseae</i> <i>Franklinothrips orizabensis</i>
<i>Persea indica</i>	No	No	–
<i>Prunus persica</i>	Yes	No	<i>Frankliniella occidentalis</i> <i>Scirtothrips perseae</i>
<i>Psidium</i> sp.	Yes	No	<i>Scirtothrips perseae</i>
<i>Punica granatum</i>	Yes	No	<i>Frankliniella occidentalis</i> <i>Scirtothrips perseae</i>
<i>Rubus</i> sp.	No	No	<i>Frankliniella gossypiana</i> <i>Frankliniella occidentalis</i> <i>Thrips tabaci</i>
<i>Sambucus caerulea</i>	No	No	<i>Frankliniella occidentalis</i> <i>Thrips australis</i> (Bagnall) <i>Aeolothrips collaris</i> Priesner <i>Aeolothrips kuwanaii</i> Moulton
<i>Sonchus</i> sp.	No	No	<i>Frankliniella occidentalis</i>

Table 1 (continued).

Potential host plant	<i>S. perseae</i> adults present?	<i>S. perseae</i> larvae present?	Thrips species collected
			<i>Aeolothrips collaris</i>
<i>Urtica dioica</i>	No	No	–
<i>Vaccinium corymbosum</i>	No	No	–
<i>Vitis</i> sp.	Yes	No	<i>Frankliniella occidentalis</i> <i>Scirtothrips perseae</i>

Table 2

Phytophagous and predatory thrips found on avocados in Mexico

Town or city	State	Elevation (m)	GPS coordinates	Thrips species found
Atlixco	Puebla	2100	–	<i>Frankliniella</i> sp. nr. <i>aureus</i> Moulton <i>Scirtothrips perseae</i>
Ayutla	Oaxaca	1897	17°01.89N 96°0.4.56W	<i>Aeolothrips mexicanus</i> Priesner <i>Frankliniella chamulae</i> <i>Frankliniella occidentalis</i> <i>Frankliniella</i> sp. nr. <i>occidentalis</i> <i>Leptothrips mcconnelli</i> <i>Neohydatothrips burungae</i> <i>Scirtothrips aceri</i> Moulton <i>Scirtothrips perseae</i>
Chilapa de Diaz	Oaxaca	1592	17°34.94N 97°38.07W	<i>Caliothrips phaseoli</i> (Hood) <i>Frankliniella</i> sp. nr. <i>bruneri</i> Watson <i>Frankliniella cubensis</i> Hood <i>Frankliniella</i> sp. nr. <i>cubensis</i> <i>Frankliniella occidentalis</i> <i>Frankliniella</i> sp. <i>runneri</i> group (Morgan) <i>Franklinothrips vespiformis</i> <i>Leptothrips mcconnelli</i> <i>Leucothrips furcatus</i> Hood <i>Neohydatothrips burungae</i> <i>Scirtothrips perseae</i> <i>Scirtothrips</i> sp. <i>Scolothrips pallidus</i> (Beach)
Coatepec-Harinas	Mexico	2000	–	<i>Aeolothrips major</i> Bailey <i>Frankliniella cubensis</i> <i>Neohydatothrips burungae</i> <i>Scirtothrips perseae</i>
Oaxaca	Oaxaca	1635	17°03.63N 96°39.78W	<i>Frankliniella cubensis</i> <i>Frankliniella fallaciosa</i> Priesner <i>Franklinothrips vespiformis</i> <i>Leptothrips mcconnelli</i> <i>Neohydatothrips burungae</i>
Piste	Yucatan	25	20°41.79N 88°35.13W	<i>Stephanothrips occidentalis</i> Hood & Williams <i>Pseudophilothrips</i> sp. nr. <i>perseae</i>
San Andres Huayapan	Oaxaca	1587	17°06.29N 96°39.93W	<i>Frankliniella cephalica</i> (Crawford) <i>Frankliniella cubensis</i> <i>Frankliniella</i> sp. nr. <i>exigua</i> Hood <i>Frankliniella gossypiana</i> Hood <i>Frankliniella occidentalis</i> <i>Frankliniella</i> sp. nr. <i>occidentalis</i> <i>Frankliniella</i> sp. <i>runneri</i> <i>Franklinothrips vespiformis</i> <i>Leptothrips mcconnelli</i> <i>Neohydatothrips burungae</i> <i>Scirtothrips aceri</i> <i>Scirtothrips citri</i> <i>Scirtothrips perseae</i> <i>Scirtothrips</i> sp. <i>Scolothrips pallidus</i>

Table 2 (continued).

Town or city	State	Elevation (m)	GPS coordinates	Thrips species found
San Francisco la Chigolio	Oaxaca	1644	17°01.72N 96°35.96W	<i>Frankliniella cephalica</i> <i>Neohydatothrips burungae</i> <i>Scirtothrips aceri</i> <i>Scirtothrips citri</i> (Moulton) <i>Scirtothrips</i> sp.
Tlalixtac	Oaxaca	1580	17°03.63N 96°39.78W	<i>Frankliniella chamulae</i> <i>Frankliniella</i> sp. nr. <i>bruneri</i> <i>Frankliniella cubensis</i> <i>Frankliniella</i> sp. <i>runneri</i> group <i>Franklinothrips vespiformis</i> <i>Karyothrips flavipes</i> (Jones) <i>Neohydatothrips burungae</i> <i>Scirtothrips perseae</i> <i>Scirtothrips</i> sp. <i>Scirtothrips</i> sp. nr. <i>citri</i>
Uruapan	Michoacan	2010	19°25.83N 102°04.51W	<i>Caliothrips fasciatus</i> (Pergande) <i>Frankliniella brunnea</i> Priesner <i>Frankliniella</i> sp. nr. <i>bruneri</i> <i>Frankliniella cubensis</i> <i>Frankliniella fallaciosa</i> <i>Frankliniella insularis</i> (Franklin) <i>Frankliniella occidentalis</i> <i>Frankliniella</i> sp. nr. <i>bruneri</i> <i>Frankliniella chamulae</i> <i>Frankliniella</i> sp. <i>fulvipennis</i> Moulton group <i>Franklinothrips orizabensis</i> Johansen <i>Franklinothrips vespiformis</i> <i>Haplothrips gowdeyi</i> (Franklin) <i>Neohydatothrips burungae</i> <i>Neohydatothrips tibialis</i> Priesner <i>Scirtothrips perseae</i>
Valladolid	Yucatan	30	20°41.82N 88°35.13W	<i>Pseudophilothrips</i> sp. nr. <i>perseae</i>
Xoxocotlan	Oaxaca	1504	17°01.21N 96°39.93W	<i>Frankliniella cephalica</i> <i>Frankliniella cubensis</i> <i>Frankliniella</i> sp. nr. <i>cubensis</i> <i>Neohydatothrips burungae</i>

Magellan, San Dimas California) derived coordinates and elevation for trees or orchards that yielded samples. Adult and larval thrips, mites, and micro-parasitoids were slide mounted in Hoyers and identified to species where possible. Keys used for thrips identifications were Mound and Marullo (1996), Sakimura and O'Neil (1979), and Wilson (1975).

2.2. Host plant surveys in California, USA

Potential host plants including avocados were sampled (May–June 1999) in three heavily infested California avocado orchards to determine if *S. perseae* was utilizing these plants for development. Plants sampled for *S. perseae* were: apple (*Malus* sp.), avocado (*P. americana*), banana (*Musa acuminata* Colla), blackberry (*Rubus* sp.), blueberry (*Vaccinium corymbosum* L.), blue

elderberry (*Sambucus caerulea* Raf.), Buddha's hand, key lime, mandarin, and tangelo (all *Citrus* spp.), cheeseweed (*Malva* sp.), cherimoya (*Annona cherimola* Mill.), coffee (*Coffea* sp.), eucalyptus (*Eucalyptus* spp.), grape (*Vitis* sp.), feijoa (*Acca sellowiana* [O. Berg.] Burret), fig (*Ficus carica* L.), guava (*Psidium* sp.), lambsquarters (*Chenopodium album* L.), loquat (*Eriobotrya japonica* Thunb.), macadamia (*Macadamia* sp.), mango (*Mangifera indica* L.), oleander (*Nerium oleander* L.), olive (*Olea europaea* L.), papaya (*Carica papaya* L.), passion fruit (*Passiflora edulis* Sims), peach (*Prunus persica* (L.) Batsch), *Persea indica* (L.) K. Spreng, pomegranate (*Punica granatum* L.), sow thistle (*Sonchus* sp.), squash (*Cucurbita* spp.), stinging nettle (*Urtica dioica* L.), tamarillo (*Cyphomandra betacea* [Cav.] Sendtn.) tomato (*Lycopersicon lycopersicum* [L.] Karsten ex. Farwell), and wild tobacco (*Nicotiana glauca* Graham).

2.3. Foreign exploration for *S. perseae* and associated natural enemies

In chronological order, foreign exploration for *S. perseae* was conducted in Mexico, Guatemala, Costa Rica, Dominican Republic, Trinidad, and Brazil. Only avocados were beat tray sampled for *S. perseae* and potential natural enemies.

Mexico. Avocados were sampled in Atlixco (state of Puebla, 11–12 October 1997), Coatepec-Harinas (state of Mexico, 10 October 1997), Ayutla, Chilapa de Diaz, San Francisco la Chigolio, San Andres Huayapan, Tlalixtac, Oaxaca, and Xoxocotlan (state of Oaxaca, 12–16 April 1998), Uruapan (state of Michoacan, 18–12 October 1999), Piste and Valladolid (state of Yucatan, 26–28 October 2000), and Coba, Tulum, and Muyil, (state of Quintana Roo, 28 October–3 November 2000).

Guatemala. Avocados were sampled in Sacatepequez, Antigua, and Altas (state of Guatemala, 26–29 October 1998) and Tal Petate (state of Santa Rosa 30 October, 1998).

Costa Rica. Avocados were sampled in Alajuela, Zarcero (state of Alajuela), Heredia (state of Heredia), and San Marcos de Tarrazu (state of San José). Sampling was conducted over 27–29 October 1999.

Dominican Republic. Avocados were sampled in El Cujulito, San Cristobal, Bani, San José de Ocoa, Piedra Blanca, Bonao, and Rio San Juan (18–22 April 2000).

Trinidad. Avocados were sampled in Tunapuna (district of Tacarigua, 25 April 2000), St. Ann's (district of St. Ann's, 25 April 2000), Arima (district of Arima, 25 April 2000), Valencia (district of Valencia, 26 April 2000), Sangre Grande and Manzanilla (district of Manzanilla, 26 April 2000), St. Joseph (district of Guayaquayare, 26 April 2000), Rio Claro (district of Cocal, 26 April 2000), Poole (district of Charuma, 26 April 2000), and Princes Town (district of Savana Grande, 26 April 2000).

Brazil. Avocados were sampled in Piracicaba, Araquara, and Jaboticaba (state of São Paulo, 28–30 August 2000).

3. Results

3.1. Host plant surveys for *S. perseae* in California, USA

Of the 32 species of plants surveyed for *S. perseae*, adult thrips were detected on 34% of species examined, indicating that adult *S. perseae* adults are vagile and will land in detectable numbers on a variety of non-avocado host plants when pest densities in avocado orchards are high (Table 1). Larval *S. perseae* were only detected on avocados, suggesting that this insect may have a highly restricted host range in California (Table 1). Detection

of *Pseudanaphothrips achaetus* (Bagnall) (Thysanoptera: Thripidae), from flowering weeds in a Bonsall (California) avocado orchard, was a new USA record for this species, which was previously known only from Australia and New Zealand (Table 1).

3.2. *Scirtothrips perseae* survey results from Mexico, Central and South America, and the Caribbean

Mexico. *S. perseae* was found on avocados in all locations that were sampled except for the Yucatan Peninsula (Table 2). Of the 801 slide mounted specimens identified from Mexico, 42% were *S. perseae* and 35% were *Neohydatothrips burungae* Hood (Thysanoptera: Thripidae) (Fig. 1A). Few natural enemies associated with thrips on avocados were detected with the beat tray sampling method ($n = 46$). The most common natural enemy found with *S. perseae* was a predatory thrips,

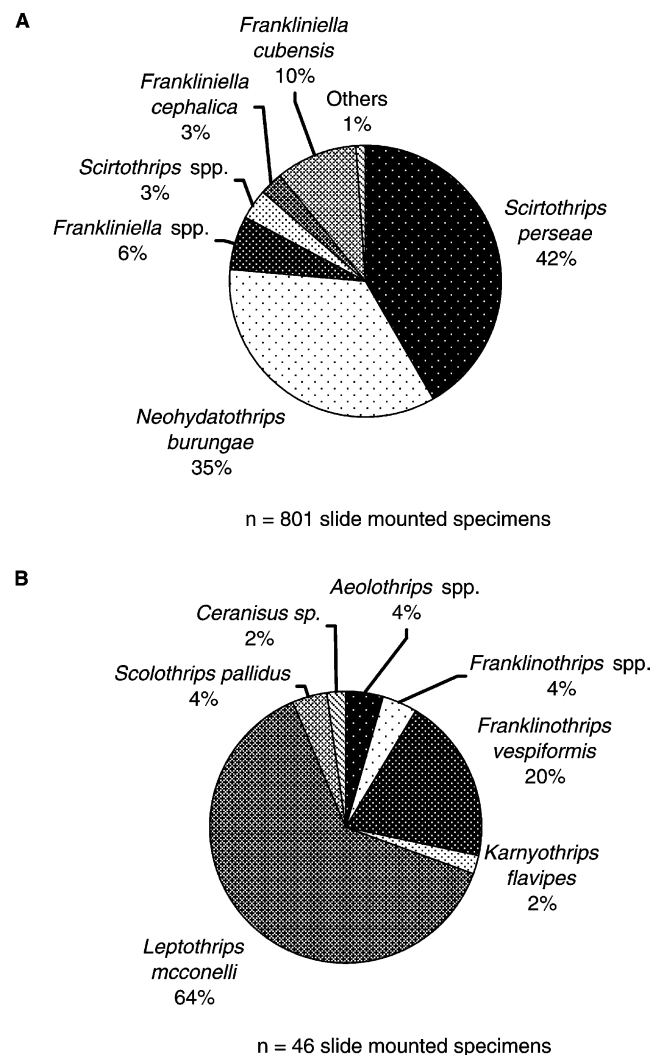


Fig. 1. Percentage composition of phytophagous thrips (A) and natural enemies (B) collected from avocados in Mexico.

Leptothrips mcconnelli Crawford (Thysanoptera: Phlaeothripidae), (Fig. 1B) and it was only recovered from sites sampled in Oaxaca (Table 1). A single larval thrips endoparasitoid, an undescribed male *Ceraninus* (Hymenoptera: Eulophidae), was found in Chilapa de Diaz in the state of Oaxaca (Fig. 1B).

Guatemala. *S. perseae* was recovered at all sites sampled, except for the lowland coastal area of Tal Pete (state of Santa Rosa) (Table 3), and was the dominant thrips species recovered from avocados in Guatemala (Fig. 2A). Beat tray sampling recovered few thrips natural enemies ($n = 12$), and predatory *Aeolothrips* spp. (Thysanoptera: Aeolothripidae) dominated ($n = 6$) the natural enemy fauna (Fig. 2B). Two male *Ceraninus* sp. were found in Sorsoya in the state of Guatemala (Fig. 1B). Four adult predatory mites in the genus *Balaustium* (Acari: Erythraeidae) were recovered from Milpas Altas (state of Guatemala) (Fig. 1B).

Costa Rica. Avocados sampled in the states of Alajuela, San José, and Heredia in October 1999 did not result in collection of *S. perseae*. An undescribed congener, *Scirtothrips* n. sp., constituted 58% of collected specimens and dominated the thrips fauna (Fig. 3) in

75% of sampled sites (Table 4). No thrips natural enemies were found during surveys.

Dominican Republic. No specimens of *Scirtothrips* were found on avocados in the Dominican Republic (Table 5). *Frankliniella* spp., in particular *Frankliniella cubensis* Hood (Thysanoptera: Thripidae), were the dominant thrips species recovered (Fig. 4A). *Frankliniella vespiformis* Crawford (Aeolothripidae) was the dominant predator found along with *Ceraninus* sp. collected in San José de Ocoa (Fig. 4B).

Trinidad. No specimens of *Scirtothrips* were found on avocados in Trinidad (Table 6). *Frankliniella* spp., in particular the undescribed *Frankliniella* sp. 1, were the dominant thrips species recovered (Fig. 5A). *Dolichothrips indicus* Hood (Phlaeothripidae), an invasive thrips from India was collected at five sites (Table 6). Three species of predatory Phlaeothripine thrips were recovered (Fig. 4B). *Aleurodothrips fasciapennis* (Franklin) is a whitefly and scale predator, and *Karnyothrips* spp. are assumed to be predatory, but the biology of this genus is poorly understood (Mound and Marullo, 1996). Two specimens of a *Ceraninus* sp. were collected in Tunapuna (Fig. 5B).

Table 3
Phytophagous and predatory thrips found on avocados in Guatemala

Town or city	State	Elevation (m)	GPS coordinates	Thrips species found
Antigua	Guatemala	2103	14°34.67N 90°37.85W	<i>Pseudophilothrips perseae</i> <i>Neohydatothrips</i> sp. <i>Scirtothrips perseae</i>
Chylla	Guatemala	2136	14°37.95N 90°41.51W	<i>Frankliniella williamsi</i> Hood <i>Frankliniella</i> sp. <i>Neohydatothrips</i> sp. <i>Pseudophilothrips perseae</i> <i>Scirtothrips aceri</i> <i>Scirtothrips perseae</i>
Milpas Altas	Guatemala	2317	14°35.64N 90°39.98W	<i>Aeolothrips</i> sp. <i>Frankliniella</i> sp. nr. <i>bruneri</i> <i>Frankliniella cubensis</i> <i>Frankliniella gardeniae</i> Moulton <i>Scirtothrips perseae</i> <i>Scirtothrips</i> sp.
Sorsoya	Guatemala	2051	14°35.01N 90°39.01W	<i>Aeolothrips mexicanus</i> <i>Aeolothrips</i> sp. nr. <i>mexicanus</i> <i>Aeolothrips vittipennis</i> Hood <i>Bravotherips kraussi</i> (Crawford) <i>Bravotherips</i> sp. nr. <i>kraussi</i> <i>Dinurothrips vezenyii</i> (Bagnall) <i>Frankliniella cubensis</i> <i>Frankliniella gossypiana</i> <i>Frankliniella williamsi</i> <i>Frankliniella</i> sp. <i>minuta</i> Moulton group <i>Neohydatothrips burungae</i> <i>Scirtothrips aceri</i> <i>Scirtothrips perseae</i> <i>Selenothrips rubrocinctus</i> (Giard)
Tal Petate	Santa Rosa	21	14°00.14N 90°27.95W	<i>Frankliniella gardeniae</i> <i>Karnyothrips merrilli</i> (Watson)

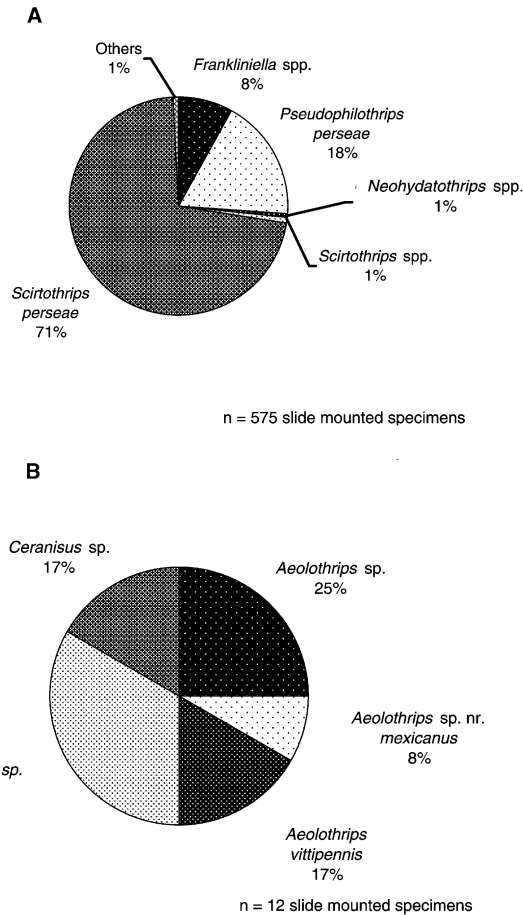


Fig. 2. Percentage composition of phytophagous thrips (A) and natural enemies (B) collected from avocados in Guatemala.

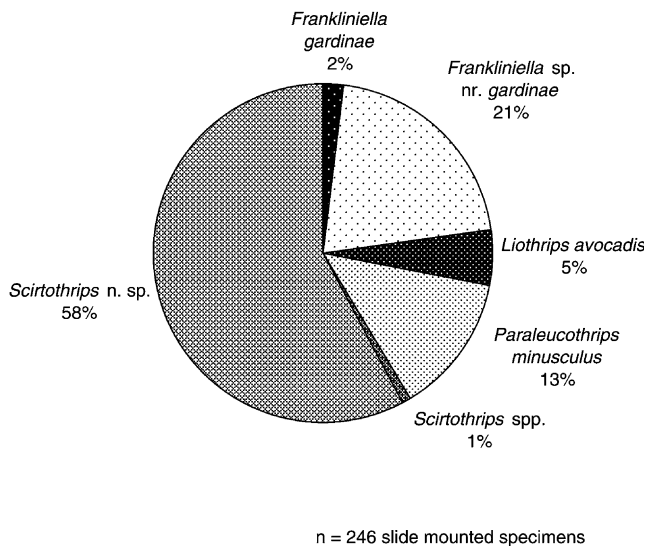


Fig. 3. Percentage composition of phytophagous thrips collected from avocados in Costa Rica.

Brazil. No specimens of *Scirtothrips* were collected from avocados in São Paulo, Brazil (Table 7). Two undescribed species of *Frankliniella* (*Frankliniella* sp. 5

and *Frankliniella* sp. 6) dominated the collected thrips fauna (Fig. 6). No natural enemy species were found during surveys.

4. Discussion

Exploration for *S. perseae* in Mexico, Central and South America, and the Caribbean delineated a home range for this pest that extends from high altitude areas (>1500 m above sea level) in central (Michoacan, Coatepec-Harinas, and Atlixco) and southern (Oaxaca) Mexico to similar high elevation areas around Guatemala City and Antigua in Guatemala. In Costa Rica, *S. perseae* was replaced as the dominant phytophagous thrips on avocados by an undescribed congener on avocados grown at high altitudes (>1300 m above sea level). *Scirtothrips perseae* was not found on avocados grown in lowland areas of Mexico (i.e., the Yucatan Peninsula) and Guatemala (i.e., Tel Petate) (both areas <30 m above sea level) (Fig. 7). In the Caribbean, no members of the genus *Scirtothrips* were found on avocados, and in South America, avocado sampling yielded negative results for this genus in Brazil (this study) and Chile (L.A. Mound, personal communication 2001). *S. perseae* is found in California avocado orchards at elevations <300 m where cool sea breezes moderate summer temperatures. *S. perseae* persists at very low non-economic densities in hotter interior orchards where cool marine breezes do not reach (Hoddle, 2002a). The marine influence in coastal California avocado orchards may produce yearly temperature regimens similar to those under which *S. perseae* evolved at high altitudes in Mexico and Guatemala thereby facilitating the establishment of this pre-adapted pest in California.

The natural enemy fauna associated with *S. perseae* and other phytophagous thrips on avocados in nearly all areas surveyed was not abundant and comprised just 4.26% of collected material. A total of 95 natural enemies from six genera with known predatory thrips (*Aeolothrips*, *Aleurodothrips* [whitefly and scale specialists], *Frankliniella*, *Leptothrips*, *Scolothrips* [mite specialists], and *Karnyothrips*), one genus of hymenopterous parasitoid (*Ceraninus*) and a predatory mite (*Balaustium*) were found. *Ceraninus* sp. adults ($n = 7$) were most abundant in the Dominican Republic in association with relatively large numbers of *F. vespiformis* ($n = 24$), which were feeding on immature *Pseudacysta perseae* (Heidemann) (Hemiptera: Tingidae). This parasitoid may have been using larval *F. vespiformis* as hosts, although neither this thrips nor any other member of the Aeolothripidae are known hosts for *Ceraninus* (Loomans et al., 1997).

The prospects for importation of an effective thrips natural enemy associated with *S. perseae* for use in a classical biological control program in California are not

Table 4
Phytophagous thrips found on avocados in Costa Rica

Town or city	State	Elevation (m)	GPS coordinates	Thrips species found
Carrizal	Alajuela	1558	10°06.04N 84°09.75W	<i>Scirtothrips aceri</i> <i>Scirtothrips</i> n. sp. <i>Paraleucothrips minusculus</i> Johansen <i>Frankliniella gardeniae</i> <i>Liothrips avocadis</i> Hood
San Marcos de Tarrazú	San José	1717	09°40.22N 83°59.63W	<i>Frankliniella</i> sp. nr. <i>gardeniae</i> <i>Liothrips avocadis</i> <i>Scirtothrips lumarius</i> Mound & Marullo
Santa Barbara	Heredia	1316	10°03.48N 84°08.29W	<i>Liothrips avocadis</i> <i>Paraleucothrips minusculus</i> <i>Scirtothrips</i> n. sp.
Zacero	Alajuela	1548	10°10.16N 84°22.90W	<i>Scirtothrips</i> n. sp.

Table 5
Phytophagous and predatory thrips found on avocados in the Dominican Republic

Town or city	State	Elevation (m)	GPS coordinates	Thrips species found
Bani	–	30	18°15.90N 70°20.65W	<i>Chaetanaphothrips leeuweni</i> (Karny) <i>Frankliniella cubensis</i> <i>Frankliniothrips vespiformis</i>
Banoa	–	251	18°58.64N 70°25.58W	<i>Frankliniothrips vespiformis</i> <i>Selenothrips rubrocinctus</i> <i>Leucothrips piercei</i> (Morgan)
El Cujuilito	–	61	18°15.65N 70°22.69W	<i>Frankliniella cubensis</i> <i>Frankliniothrips vespiformis</i>
San Cristobal	–	131	18°25.91N 70°03.05W	<i>Frankliniella bruneri</i> <i>Frankliniella cubensis</i> <i>Frankliniothrips vespiformis</i>
San José de Ocoa	–	693	18°41.54N 70°26.72W	<i>Frankliniella bruneri</i> <i>Frankliniella cubensis</i> <i>Frankliniella insularis</i> <i>Frankliniothrips vespiformis</i> <i>Haplothrips gowdeyi</i> <i>Heliothrips haemorrhoidalis</i> <i>Selenothrips rubrocinctus</i>

encouraging as attested by the low populations of natural enemies and limited diversity of species relative to the abundance of this pest in Mexico and Guatemala. However, two caveats that should be noted are related to the sampling protocol employed and the time of year samples were taken. First, beat tray sampling may not be an effective method for sampling thrips natural enemies. Winged predatory hemipterans and parasitic Hymenoptera may have flown away without detection during the beat tray sampling process while less vagile species were captured. Second, the phenology of *S. perseae* in its home range is unstudied. In California, *S. perseae* population densities vary significantly throughout the year as does the generalist natural enemy fauna responding to population outbreaks (Hoddle, 2002a). Consequently,

time of year that foreign exploration was conducted for *S. perseae* could have a significant impact on natural enemy species detected and their relative abundance. Manipulative field studies have revealed that native thrips species can be regulated by indigenous generalist natural enemies that respond in a density-dependent manner to population outbreaks (Funderburk et al., 2000). Therefore a multi-year study of *S. perseae* and associated natural enemies on avocados in the pest's home range will be necessary to fully understand its population dynamics, to identify the full suite of biological control agents, and to determine the efficacy of the natural enemy guild associated with *S. perseae*.

There are no well-documented "classical" biological control programs where an imported natural enemy

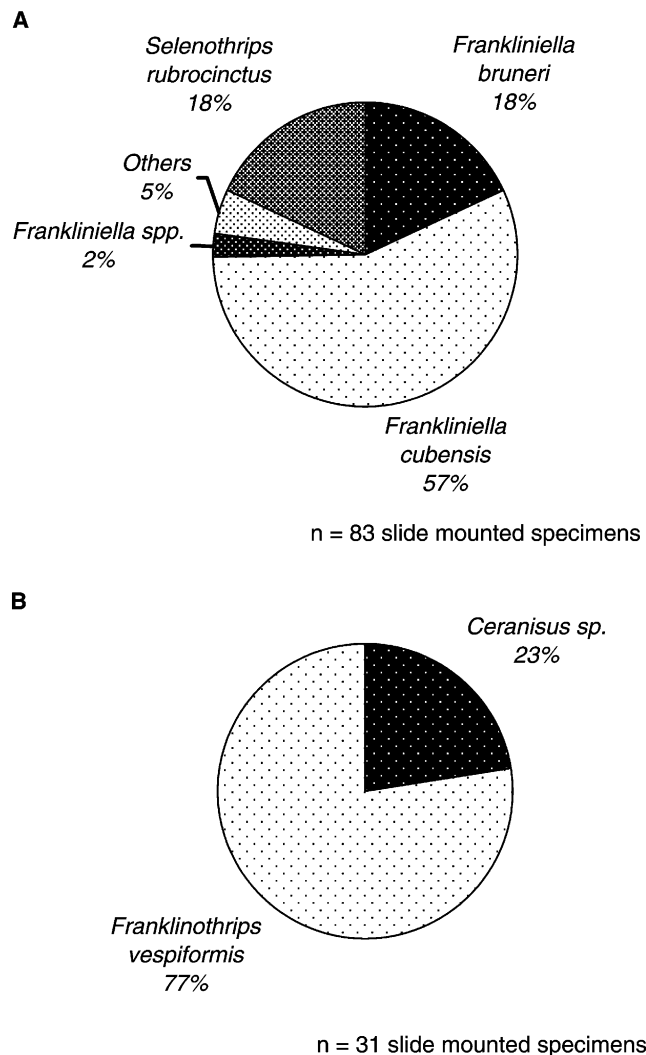


Fig. 4. Percentage composition of phytophagous thrips (A) and natural enemies (B) collected from avocados in the Dominican Republic.

has been effective against an exotic thrips pest. *Thripobius semiluteus* Boucek (Hymenoptera: Eulophidae) was imported into California from Australia and Brazil during 1986–1988 to control *Heliothrips haemorrhoidalis* (Bouché), a serious pest of avocado fruit. This parasitoid has been established in California and reportedly provided control of *H. haemorrhoidalis* (McMurtry et al., 1991). However, there have been no rigorous evaluation and quantification of the impact of *T. semiluteus* on *H. haemorrhoidalis* in California (e.g., life table studies) and successful suppression of this pest may have occurred through the adoption of new fruit harvesting strategies (Phillips, 1997) or the use of new insecticides like abamectin and spinosad that have been registered for use in California against *S. perseae*. *Thripobius semiluteus* was recently released in New Zealand for biological control of *H. haemorrhoidalis* in avocados (P. Stevens, personal communication 2001).

Apart from locating natural enemies and delineating the geographic distribution of *S. perseae*, foreign exploration allowed the compilation of a list of other phytophagous thrips species unknown in California which could be serious avocado pests should they become established. One species, *Neohydatothrips burungae*, was as common as *S. perseae* on avocados in Mexico and is not known to be present in California. Given the common occurrence of *S. perseae* on avocados in Mexico and its pestiferous nature in California, *N. burungae* could also pose a threat to California grown avocados.

The threat of new avocado pests of exotic origin establishing in California has increased substantially with the recent legalization of avocado imports from Mexico into the USA, a trade practice that had been banned since 1914 to prevent the unwanted introduction of arthropods, especially *Anastrepha* sp. (Diptera: Tephritidae) that infest fruit (Morse et al., 1995).

The three most recent avocado pests to establish in California are *Tetraleurodes perseae* Nakahara (Homoptera: Aleyrodidae), *Oligonychus perseae* Tuttle, Baker, and Abbatiello (Acari: Tetranychidae), and *S. perseae* and were found in 1982, 1990, and 1996, respectively. *Tetraleurodes perseae* and *S. perseae* were new to science at the time of their initial discovery in California (Nakahara, 1995, 1997; Rose and Woolley, 1984). *Oligonychus perseae* was first described from specimens intercepted at a border inspection station in El Paso, Texas, USA (Tuttle et al., 1976) and both *T. perseae* and *S. perseae* had been previously intercepted at border ports of entry before detection in California. These facts highlight three important points.

First, there are probably additional serious avocado pests in Central America that are unknown entities that may be able to establish in California and inflict severe damage to commercially grown avocados. Foreign exploration for *S. perseae* and its natural enemies has revealed at least four new species of *Frankliniella* from Costa Rica, the Caribbean, and South America. In addition, there is at least one new species of *Scirtothrips* from Costa Rica, which dominates the thrips fauna on avocados in that country. Furthermore, only three species of thrips (*Frankliniella cephalica* [Crawford], *Heliothrips haemorrhoidalis* [already present in California], and *Pseudophilothrips perseae* [Watson]) from Mexico are listed as potential pests by USDA-APHIS (Firko, 1995). All three species have been collected during the exploration efforts reported here. However, from examination of 2136 slide mounted specimens in this study, over 47 species of phytophagous thrips in at least 19 genera have been recorded from avocados in areas outside of California. Of collected specimens, it is unknown how many species were collected as incidental visitors that originated from other host plants. A total of 38 phytophagous thrips species have been collected from

Table 6
Phytophagous and predatory thrips found on avocados in Trinidad

Town or city	District	Elevation (m)	GPS coordinates	Thrips species found
Arima	Arima	74	10°38.69N 61°17.35W	<i>Dolichothrips indicus</i> (Hood)
Arouca	Tacarigua	73	10°37.98N 61°19.60W	<i>Dolichothrips indicus</i> <i>Frankliniella insularis</i>
Barataria	St. Ann's	52	10°38.80N 61°21.67W	<i>Dolichothrips indicus</i> <i>Frankliniella</i> sp. 1 <i>Frankliniella</i> sp. 2* <i>Frankliniella</i> sp. 3 <i>Frankliniella insularis</i> <i>Frankliniella parvula</i> Hood <i>Rhamphothrips pandens</i> Sakimura <i>Selenothrips rubrocinctus</i>
Manzanilla	Manzanilla	29	10°30.90N 61°02.85W	<i>Frankliniella</i> sp. 1 <i>Frankliniella insularis</i> <i>Frankliniella</i> sp. nr. <i>kelliae</i> Sakimura <i>Frankliniella parvula</i> Hood
Maraval	Diego Martin	96	10°39.99N 61°29.60W	<i>Frankliniella</i> sp. 1 <i>Neohydatothrips geminus</i> (Hood) <i>Rhamphothrips pandens</i>
Maturita	Arima	116	10°38.52N 61°16.29W	<i>Dolichothrips indicus</i> <i>Frankliniella</i> sp. 1
Poole	Charuma	77	10°17.94N 61°13.45W	<i>Frankliniella</i> sp. 1 <i>Selenothrips rubrocinctus</i>
Princes Town	Savana Grande	60	10°16.17N 61°22.71W	<i>Frankliniella</i> sp. 1 <i>Frankliniella</i> sp. nr. <i>kelliae</i> <i>Frankliniella parvula</i> <i>Karnyothrips merrilli</i>
Rio Claro	Cocal	72	10°18.38N 61°10.05W	<i>Frankliniella</i> sp. 1 <i>Karnyothrips longiceps</i> Hood
Sangre Grande	Manzanilla	59	10°35.18N 61°07.62W	<i>Frankliniella</i> sp. 1 <i>Frankliniella insularis</i> <i>Frankliniella</i> sp. nr. <i>kelliae</i> <i>Frankliniella parvula</i> <i>Microcephalothrips abdominalis</i> (Crawford)
St. Joseph	Guayaguayare	9	10°18.44N 61°00.14W	<i>Frankliniella</i> sp. 1 <i>Heliothrips haemorrhoidalis</i>
Tunapuna	Tacarigua	159	10°39.56N 61°23.57W	<i>Anisoplothrips venustulus</i> (Priesner) <i>Dolichothrips indicus</i> <i>Frankliniella</i> sp. 1 <i>Frankliniella insularis</i> <i>Frankliniella</i> sp. nr. <i>kelliae</i> <i>Heliothrips haemorrhoidalis</i> <i>Neohydatothrips geminus</i> (Hood) <i>Rhamphothrips pandens</i>
Valencia	Valencia	81	10°38.87N 61°12.50W	<i>Aleurodothrips fasciapennis</i> (Franklin) <i>Frankliniella</i> sp. 1 <i>Frankliniella insularis</i> <i>Frankliniella parvula</i> <i>Heliothrips haemorrhoidalis</i>

*New species near *cephalica*.

avocados in Mexico by Johansen et al. (1999), but only seven species, *Frankliniella bruneri* Priesner, *F. chamulae* Johansen, *Heliothrips haemorrhoidalis*, *Pseudophilothr-*

ips perseae, *Scirtothrips aguacatae* Johansen and Mojica-Guzmán, *Scirtothrips kupandae* Johansen and Mojica-Guzmán, and *S. perseae* were considered pests

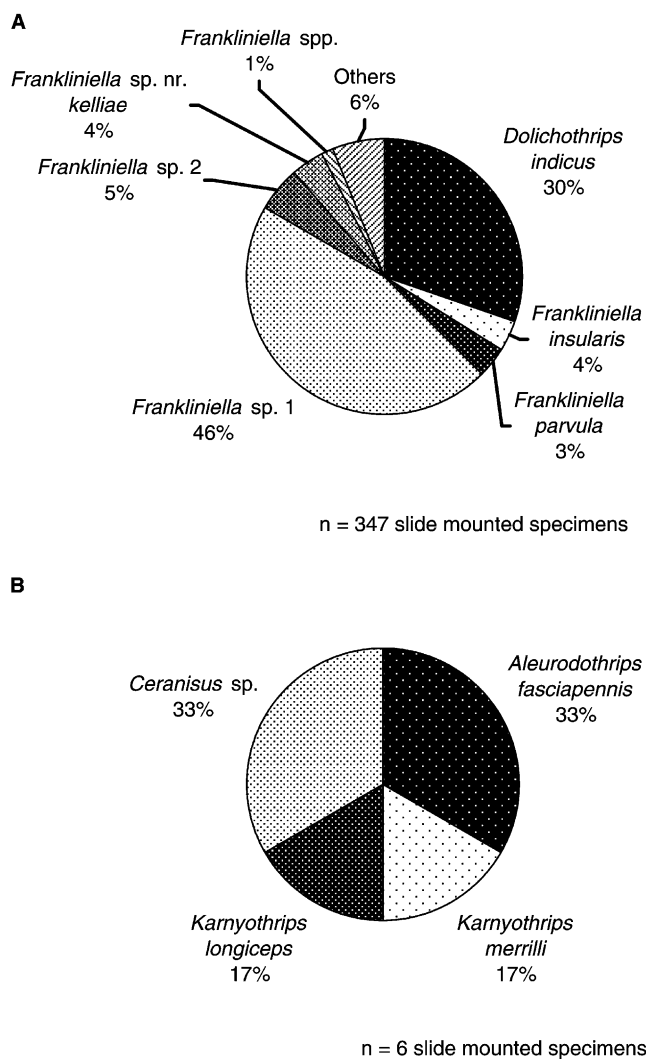


Fig. 5. Percentage composition of phytophagous thrips (A) and natural enemies (B) collected from avocados in Trinidad.

(Hernández et al., 2000). The validity of new *Scirtothrips* species collected from avocados in Mexico and described in a recent taxonomic review (Johansen and Mojica-Guzmán, 1998) has been questioned as species designations were made according to morphological characters that exhibit high variation amongst individuals of the same species (Mound and zur Strassen, 2001).

Broad spectrum pesticide use in commercial Mexican avocado orchards for suppression of serious pests (e.g., tephritids [*Anastrepha* spp.] and curculionids [*Heilipus* and *Conotrachelus* spp.]) may inadvertently control thrips that would be problematic in the absence of sprays. This scenario most likely explains the relatively unimportant status of *S. perseae* as a pest in commercial Mexican orchards, while in non-commercial, unsprayed orchards *S. perseae* densities reach levels that cause leaf and fruit damage similar to that in California (MSH, personal observations in Coatepec-Harinas). Consequently, deficits in knowledge on the taxonomy, ecology, and biology of the arthropod fauna on commercially grown avocados in exporting countries may render any mitigation of accidental pest importation practices ineffectual.

Second, APHIS-PPQ at Mexican border ports of entry intercepted both *O. perseae* (Tuttle et al., 1976) and *S. perseae* on avocados from Mexico before either pest became established in California. This strongly suggests that interception and exclusion policies are extremely valuable in preventing exotic avocado pests from Central America entering and establishing in California. The biology of potentially serious pests, like thrips for example, makes detection very difficult. Thrips eggs are extremely small and are usually laid within the tissue of leaves or skin of fruit. The numbers of eggs laid within individual leaves and fruit in orchards infested

Table 7
Phytophagous thrips found on avocados in Brazil

Town or city	State	Elevation (m)	GPS coordinates	Thrips species found
Araraquara	São Paulo	634	22°42.27S 47°37.17W	<i>Frankliniella</i> sp. 5 <i>Frankliniella</i> sp. 6 <i>Frankliniella condei</i> John <i>Frankliniella rodeos</i> Moulton <i>Frankliniella schultzei</i> (Trybom) <i>Haplothrips gowdeyi</i>
Jaboticaba	São Paulo	562	21°16.59S 48°17.58W	<i>Frankliniella</i> sp. 5 <i>Frankliniella</i> sp. 6 <i>Frankliniella condei</i> <i>Haplothrips gowdeyi</i>
Piracicaba	São Paulo	327	22°42.27S 47°37.17W	<i>Frankliniella</i> sp. 5 <i>Frankliniella</i> sp. 6 <i>Frankliniella condei</i> <i>Frankliniella gemina</i> Bagnall <i>Frankliniella rodeos</i> <i>Heliothrips haemorrhoidalis</i>

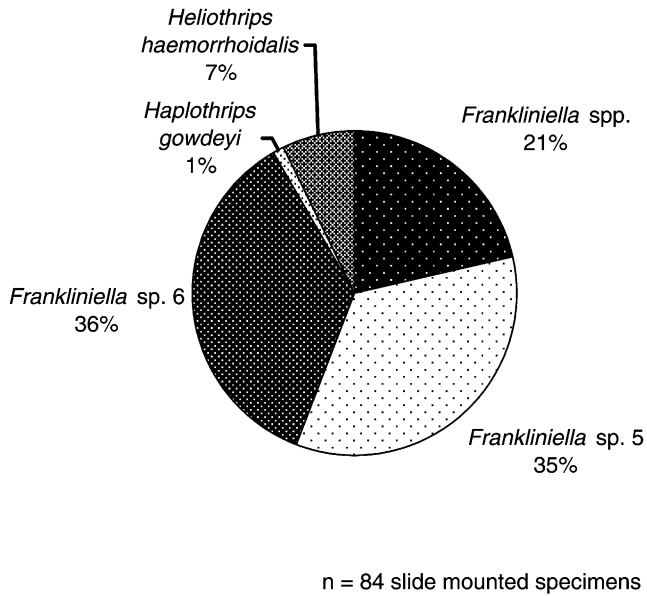


Fig. 6. Percentage composition of phytophagous thrips collected from avocados in Brazil.

with *S. perseae* in California can easily exceed 20 (Hoddle, 2002c). Plant material entering the USA (either legally or illegally) with this number of viable eggs provides a good-sized cohort that could establish a reproducing population in a permissive environment (i.e., abundant food, mild climate, lack of natural enemies).

Third, the small numbers of pests intercepted at border inspection stations on avocado plants that are moved into the USA suggest that founding populations of pests may often be very small. Work on *Sericothrips*

staphylinus Haliday (Thysanoptera: Thripidae) used for the biological control of *Ulex europaeus* (L.), a noxious weed in New Zealand, has demonstrated that 33% of carefully managed releases of just 10 adult thrips into a permissive environment can result in establishment and proliferation (Mommott et al., 1998). The greater the frequency of small introductions, the higher the likelihood of establishment in comparison with fewer introductions of larger numbers of thrips which might go extinct due to adverse chance effects (Mommott et al., 1998). This scenario from biological control of weeds may apply to the establishment of new thrips pests outside of their home range, that is, frequent introductions of small numbers of pests may ultimately lead to establishment when founding populations encounter a permissive environment.

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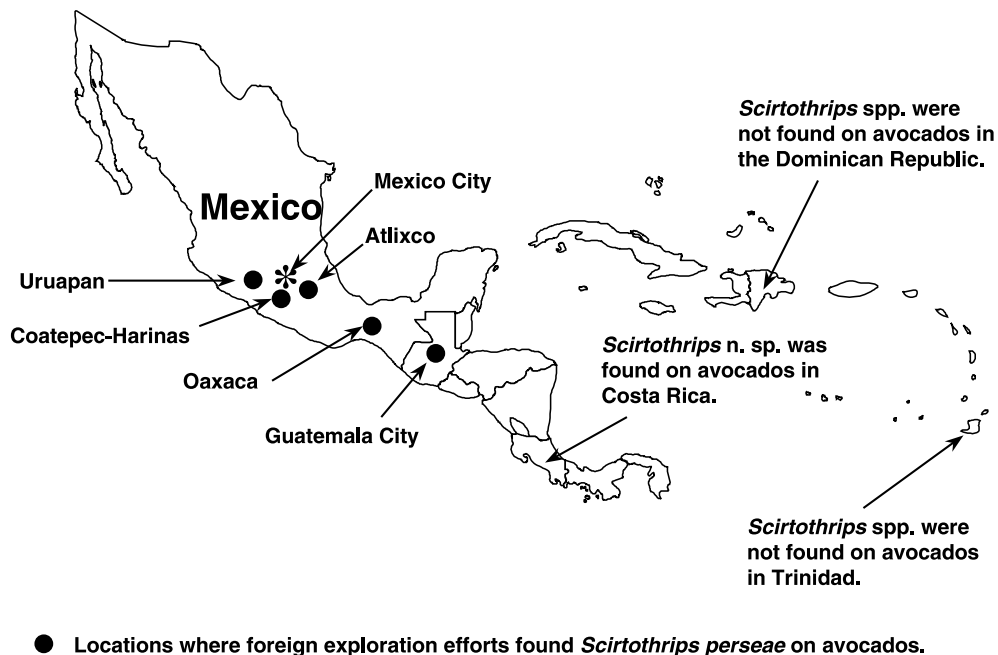


Fig. 7. Geographic distribution of *Scirtothrips perseae* in Mexico and Central America.

Harinas), Guatemala (Wilmar Méndez Mérida of Profruta, Amilcar Casasola of BioAgroservices), Costa Rica (Paul Hansen, University of Costa Rica), the Dominican Republic (Alejandro Bencosme and Manuel Castillo, AgroForestry Macapai), Trinidad (Moses Kairo, CABI), and Brazil (Jão Lopes, University of São Paulo).

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