THRIPS COMPETITION AND SPATIOTEMPORAL DYNAMICS ON REPRODUCTIVE HOSTS

By

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A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2005

This document is dedicated to my wife, Kirsten for all of her support and understanding throughout this process. It is also dedicated to my parents for their guidance and support.

ACKNOWLEDGMENTS

I would like to thank my major professor, Dr. Joe Funderburk, for the guidance and assistance in designing and conducting my experiments, and for helping me develop as a scientist. I would also like to thank Dr. Dean Paini, a committee member, who also spent a great deal of time advising and assisting me whenever possible. My other committee members, Drs. Stuart Reitz and Russ Mizell, were a tremendous source of assistance and knowledge, for which I am grateful. Dr. Michelle Stuckey proofread drafts and assisted in the experimental procedure, as well as offered good advice. I would like to thank Dr. Brian Inouye for his assistance in interpreting the models, and the model-fitting process. I appreciated Dr. Ben Bolker's patience and instruction on the modeling process and using R to fit the models. Marcus Griswold helped in providing an R code to work with. Dr. Todd Jackson also lent assistance and insight in developing my experiments. Rebecca Riddle also assisted in the experimental procedure, for which I am grateful.

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of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Master of Science

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August, 2005

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Frankliniella spp. thrips feed and reproduce on crops, causing a silvering of plant tissue, and spread plant diseases such as *Tomato spotted wilt virus* into crops. However, little is known about the factors affecting *Frankliniella* spp. thrips abundance and distribution. Thrips often migrate into cropping systems from surrounding vegetation, but few of these uncultivated plant sources have been studied to determine cycles of thrips abundance to evaluate sources of thrips migration. Furthermore, no research has been conducted on the population effects of competition in thrips to better understand thrips distribution. This study was composed of a field work portion, which focused on evaluating uncultivated plant host use, and a laboratory portion, which focused on competitive interactions between *Frankliniella occidentalis* and *F. bispinosa*.

For the field work study, samples were collected from *Raphanus raphanistrum, Rubus trivialis, Rubus cuneifolius, Trifolium repens, Vicia sativa, Solidago canadensis*, and *Chenopodium ambrosioides*, and thrips spatiotemporal dynamics were determined

for each. Thrips preferred flowers to leaves on every plant species sampled. *Frankliniella* spp. thrips were most abundant on *R. raphanistrum, T. repens*, and *R. cuneifolius* in spring months and *S. canadensis* in the fall. The most abundant thrips species collected were *F. tritici* and *F. bispinosa*. These plants may serve as important sources of *Frankliniella* spp. thrips, and reducing abundance of the available hosts may decrease thrips populations migrating into cropping systems.

For the laboratory study, interspecific competition was evaluated between the world-wide crop pest *F. occidentalis,* and *F. bispinosa*, a species native to Florida. In addition, intraspecific competition for each species was assessed. Larvae per female of *F. bispinosa* and *F. occidentalis* were counted at varying densities of each species, using a factorial response surface design. A competition model was fit to the data for each species to evaluate effects of interspecific and intraspecific competition on the number of larvae per female produced. Significant interspecific and intraspecific competition affected *F. bispinosa*, and the effect of interspecific competition from *F. occidentalis* was over four times greater than the effect from intraspecific competition. Interspecific competition did not affect *F. occidentalis*, but statistically significant intraspecific competition occurred. Furthermore, intraspecific competition had a greater effect on *F. bispinosa* than on *F. occidentalis*. This superior competitive ability may enhance the spread of *F. occidentalis,* and competition between *F. occidentalis* and native species must be assessed when considering the world-wide spread of *F. occidentalis*.

CHAPTER 1
LITERATURE REVIEW

Introduction

Debate over the factors that affect thrips population dynamics have persisted for more than 50 years, since Davidson and Andrewartha (1948a, b) first claimed there were no density dependent factors affecting populations. Several researchers subsequently refuted their conclusions (Smith 1961, Orians 1962), and more recently both density dependent and density independent factors have been shown to influence thrips population dynamics. These factors include host defenses (deJager et al. 1996), plant selection and nutrition (Brodbeck et al. 2002), climate (Brødsgaard 1993), predation (Baez et al. 2004), and parasitism (Funderburk et al. 2002). Despite these studies, little is known of the temporal and spatial dynamics of thrips, particularly outside cropping systems. The purpose of this chapter is to discuss recent research on density dependent and independent factors that affect thrips spatial and temporal dynamics.

The population dynamics of thrips are strongly influenced by their small body size (0.5-5.0 mm in length), which confers both advantages and disadvantages. Such disadvantages include large fluctuations in body temperature and water loss, due to a high surface area to volume ratio (Kirk 1997a). Conversely, thrips' small size permits escape from predators to small, secure areas on the host (Sabelis and Van Rijn 1997), and also may result in extensive wind dispersal as gusts of wind can disrupt thrips' flight patterns (Pearsall and Myers 2001).

Diversity

An appreciation of the natural history and diversity within the Thysanoptera order can reveal similarities in the population characteristics between phylogenetically related species, thereby enhancing the current understanding of thrips population dynamics. The diversity of the thrips order is exemplified by the diversity in feeding habits, which have evolved from that of a fungus feeding ancestor related to Hemiptera, Psocoptera, and Pthiraptera (Mound 1997, Moritz et al. 2001) to species that have adapted to feed on leaves, flowers and small arthropods (see Kirk 1997b for review).

The order Thysanoptera is divided into two sub-orders, the Tubulifera and Terebrantia. The Tubulifera consists of a single family, the Phlaeothripidae, which consists of over three thousand species, mostly living on fungus in wet tropics (Moritz et al. 2001). Tubulifera use a U-shaped ovipositor, rather than a straight ovipositor like the Terebrantia. The U-shaped ovipositor is used to deposit eggs on the surface of, rather than into the host tissue, as the fungus provides adequate protection for the eggs (Terry 1997).

In contrast to the predominantly fungivorous Tubulifera, the sub-order Terebrantia includes eight families of thrips that display a wide variety of food preferences and use a saw-like ovipositor to insert one egg at a time into the host tissue (Terry 1997). The largest and most diverse family of Terebrantia is the Thripidae, which are represented by over 1,750 species in 260 genera. Species of Thripidae range from Greenland to the sub-Antarctic islands (Moritz et al. 2001). One sub-family of Thripidae, the leaf-feeding Pancheatothripinae, comprising 120 species in 35 genera, is found throughout the tropics and sub-tropics, and includes some crop pests. Thripinae, a more diverse sub-family of Thripidae, consists of approximately 1,400 species in over 200 genera. Many feed and

oviposit in leaves, and some of the more recently evolved species feed and oviposit in flowers. This group exhibits a wide variety of feeding habits and includes thrips species that are predaceous, anthophagous, phytophagous, or even associated with mosses (Mound 1997). The wide variety of food preferences of many Thripinae species includes commercial crops, and some of these species can cause direct damage to crops by feeding and oviposition as well by vectoring plant viruses (Mound 1997, Moritz et al. 2001).

Population Attributes

Thysanoptera are opportunistic and r-selected, utilizing a high reproductive rate and short generation time to enhance population growth rates under favorable conditions (Mound 1997) and the exploitation of ephemeral resources (Mound and Tuelon 1995). Parthenogenesis, a form of asexual reproduction, is a strategy used to enhance reproduction, and in combination with F_1 back-crossing, can result in a single female forming an entirely new population (Mound and Tuelon 1995). Furthermore, parthenogenesis and back-crossing of an insecticide-resistant female can lead to rapid growth of an insecticide-resistant population, further aiding in adaptation. Vagility enhances the opportunistic, r-selected strategy, improving location and exploitation of new environments and food resources (Mound and Tuelon 1995). A moderately broad food tolerance enhances vagility by enabling invasive thrips to survive in new environments of limited host diversity and increases population stability during seasonal decline of preferred host availability (Mound 1997).

The extent of vagility and opportunism in thrips varies by feeding group (Mound and Tuelon 1995). Polyphagous thrips are more vagile than monophagous thrips, which often develop periodicity with the cycle of food availability. Anthophagous thrips include many polyphagous, vagile species that can exploit ephemeral resources.

Alternatively, foliage-feeding thrips include few polyphagous, vagile species, as many develop a cyclic lifestyle in line with the host. The most damaging and opportunistic crop pests are those that feed on both flowers and leaves, and move to new food sources as hosts become inadequate or unavailable without developing host-correlated periodicity.

Predaceous thrips are also opportunistic, due to the opportunistic nature of their prey, but few fungal spore or hyphae feeders are vagile or opportunistic because their food source is stable (Mound and Tuelon 1995). Exceptions include those in the tropics, where dry fungi hanging in trees are preferred, and thrips must feed before the fungi falls to the ground. Gall-forming thrips are monophagous, and feed in a stable environment, and are therefore less opportunistic than other thrips species.

Plant Defenses

A generalist strategy allows phytophagous thrips to feed on a number of hosts and gain access to a variety of available nutrients (Mound and Tuelon 1995). However, a generalist strategy usually includes constraints in plant defense adaptation. Theoretically, a generalist cannot coevolve with a range of hosts as well as a specialist can with a single host plant, due to evolutionary constraints (Ananthakrishnan and Gopichandran 1993). Although the vagility and opportunistic nature of phytophagous thrips enhances adaptability, plant defenses may cause one host to be less suitable than others.

Morphological plant defenses, such as dense trichomes, limit phytophagous thrips host suitability. For example, nectarines and peaches are the same species (*Prunus persica* (L.) Batsch), but *Frankliniella occidentalis* prefer nectarine hosts due to the smoother tissue of the developing fruit (Felland et al. 1995). Other examples include surface wax and epidermal cell wall thickness, which reduce leaf host quality (Zeier and

Wright 1995), and pollen stickiness, which contributes to a plant's defense due to extra handling and grooming time (Kirk 1985).

Plant chemical defenses, or allelochemicals, reduce thrips' host preference as well (deJager et al. 1995a, deJager et al. 1995b, Kumar et al. 1995). Allelochemical precursors may include acetyl coenzyme A, mevalonic acid, and shikimic acid and are grouped into quantitative or qualitative defenses (Lowman and Morrow 1998). The effect of quantitative defenses, or digestive reducers, varies by concentration. These immobile, carbon-based chemicals accumulate with tissue age, and passively or actively decrease thrips nutrition. Qualitative defenses are mobile chemicals that affect essential functions, such as respiration or DNA repair, in small chemical concentrations and degrade quickly. Resistance to thrips may be caused by a single chemical present in the plant tissue or by a synergistic effect from a number of chemicals (deJager et al. 1996). These chemicals may be found in a number of plant parts, including leaves or flowers; however constitutive (continuously present) defenses may be more concentrated in flower tissue than in leaves (Strauss et al. 2004).

Host Selection and Nutrition

Thrips feeding and oviposition choices may be due in part to thrips host location cues. Host location cues may include visual cues such as the colors blue, white and yellow (Frey et al. 1994, Cho et al. 1995a, Childers and Brecht 1996, deKogel and Koschier 2002). Olfactory host location cues may also be important, but the level of importance is unclear. In choice tests, *F. occidentalis* individuals were attracted to volatile chemicals extracted from chrysanthemum flowers, but could not locate whole flowers without visual cues (Koschier et al. 2000, deKogel and Koschier 2002). Flower type also affects host selection in plant species that exhibit more than one flower type. In

chrysanthemums, *F. occidentalis* prefer cultivars with disc florets over spider-type flowers that do not include disc florets (Broadbent and Allen 1995, deJager et al. 1995a).

Another important factor in thrips host selection is the nutritional quality of the plant (deJager et al. 1995b, Mollema and Cole 1996), though little is known about thrips nutritional ecology (Brodbeck et al. 2002). Mass determinations for growth rate and tissue samples for nutrient retention are difficult to obtain due to thrips' small size, and short development time and non-feeding prepupae and pupae make the organism difficult to observe. Therefore, population experiments are often easier to conduct than individual tests.

Past population experiments have shown that population growth is correlated with nitrogen concentration. Because immature thrips molt four times in a short time span, and only eat in two instar stages, they must consume large amounts of amino acids to build new proteins to support the rapid growth (Kirk 1995, Brodbeck et al. 2001). Thrips may therefore prefer hosts with essential amino acids, especially those most rarely found in plants: tryptophan, phenylalanine, and methionine (Ananthakrishnan and Gopichandran 1993). Recent studies have shown a strong correlation between thrips crop damage and concentration of aromatic amino acids, especially phenylalanine, which enhances cuticle production and hardening, reducing the occurrence of dessication or entomopathogenic fungal infection (Mollema and Cole 1996). Glutamine, which can be converted to other essential amino acids, may also stimulate thrips feeding (Andersen et al. 1992).

In addition, carbohydrates are important to thrips nutrition and may stimulate feeding. There has been some success in adding sugars to insecticide to increase

insecticide consumption (Parrella 1995) and plant carbohydrate concentration increases *F. occidentalis* feeding rates, though not as strongly as plant protein concentration (Scott Brown et al. 2002).

Within Plant Distribution

Thrips' small size enables access to recessed areas of a plant, which provide small microclimates that inhibit the desiccation or freezing of thrips (Kirk 1997a). These crevices also enhance protection from predation and being washed off the plant by rain.

Vertical distribution of thrips within a plant appears to vary by host plant. In tomatoes most adult thrips feed in the upper portions of the plant, especially in the spring, while larvae are found in the lower portions (Navas et al. 1994, Reitz 2002). In cucumbers, *F. occidentalis* prefer higher, younger leaves for oviposition, and in a non-choice experiment, oviposition on younger cucumber leaves produced more offspring than on older leaves (deKogel et al. 1997b). In British Columbia nectarine orchards, *F. occidentalis* adults are more common in the lower portions of the trees, possibly due to a preference of low lying plant hosts (Pearsall 2002).

Within plant distribution and movement also varies with season and thrips species. For example, *F. occidentalis* fly higher in the summer than in the spring in nectarine orchards (Pearsall and Myers 2001). In addition, *F. tritici* and *F. bispinosa* are more locally mobile than *F. occidentalis* (Ramachandran et al. 2001, Hansen et al. 2003), and *F. fusca* is generally considered more of a foliage feeder than *F. occidentalis* (Chellemi et al. 1994, Pearsall and Myers 2000).

Seasonal Dynamics

Low temperatures can reduce host availability, making overwintering difficult for thrips (Kirk 1997a). *F. occidentalis* have a developmental threshold of 10°C (Robb

1989, Cho et al. 1995b), and can survive at -5°C for approximately 56-63 hours (Brødsgaard 1993). *Frankliniella* species either overwinter actively or are dormant in soil, while some species are capable of both, depending on environmental conditions. For example, in higher latitudes, such as British Columbia, Canada, *F. occidentalis* overwinter as dormant, mated females in soil (Pearsall and Myers 2000), while in lower latitudes such as North Carolina, *F. occidentalis* survive winters actively on hosts (Cho et al. 1995b). Soil type and host plant species also influence thrips overwintering, as larvae burrow further into lighter soil than heavier soil (MacGill 1929, 1930) and do not burrow into sand (Bailey 1933). Furthermore, thrips with cold resistant hosts may be less likely to overwinter in soil than those without (Kirk 1997a).

Thrips populations increase dramatically in early spring, in the presence of increased temperatures and host bloom (Childers et al. 1990, Chellemi et al. 1994, Pearsall and Myers 2000, 2001). This rapid increase varies temporally with latitude. For example, in South Florida *F. bispinosa* increases in March (Childers et al. 1990), whereas in North Florida *F. bispinosa* displays greatest increase in April and May (Chellemi et al. 1994). Similarly, in North Florida *F. occidentalis* population densities rapidly increase in early spring (Chellemi et al. 1994), but show greatest increase in late April and May in British Columbia, Canada (Pearsall and Myers 2000, 2001).

Summer usually includes a significant decrease in thrips populations (Childers et al. 1990, Chellemi et al. 1994, Reitz 2002, Nault et al. 2003). Reasons for this population decrease are unclear, as it does not appear due to temperature levels increasing above thrips range. In North Florida, Reitz (2002) found a decrease in *F. occidentalis* in May, although the temperatures never rose above *F. occidentalis'* optimal temperature range

(29-31°C) throughout the experiment (van Rijn et al. 1995, Florida Automated Weather Network UF/IFAS 2003).

One possible reason for the summer decline in thrips populations is the presence of natural enemies. *Orius insidiosus* (Say), a natural predator of *F. occidentalis*, is most abundant in May and June and may decrease thrips densities in summer months (Ramachandran et al. 2001, Reitz et al. 2003).

Increased host resistance may also influence thrips summer decline. DeKogel *et al*. (1997a) found a negative correlation between thrips damage and solar radiation. The authors suggested that summer plant hosts might be more resistant to thrips, increasing thrips population decline.

Populations increase slightly in the fall, possibly due to additional host bloom and/or reduced predation by natural enemies (Cho et al. 1995b, Reitz 2002, Groves et al. 2003). Although *O. insidiosus* is present during the fall, it is less abundant than during early summer months, and this decline may enable thrips populations to increase again (Ramachandran et al. 2001).

Biotic Factors

Predation by *O. insidiosus* affects thrips population size, and may affect spatial and temporal dynamics (Funderburk et al. 2000). Thrips populations may migrate to alternative hosts in the presence of *O. insidiosus* (Funderburk 2002) causing less preferred hosts to gain higher populations in the presence of predators. Predation from *O. insidiosus* may also affect thrips species ratios by predating one thrips species preferentially (Baez et al. 2004).

Thrips spatial and temporal dynamics are also affected by parasitism and possibly competition. Nematodes (*Thripinema* spp.) infect thrips, leaving females sterile and reducing population growth (Funderburk et al. 2002). In addition, competition may affect population dynamics. No research has been published on thrips competition, but distribution, fecundity and mortality appear density-dependent in greenhouse thrips (Puche and Funderburk 1992, Kirk 1994 as cited by Kirk 1997a). Competition may be a cause of the density dependent distribution and decreased fecundity and survivorship.

North Florida Thrips

Three native thrips species *Frankliniella bispinosa, F. fusca* and *F. tritici,* and an introduced species, *F. occidentalis* damage crops in North Florida. Feeding and reproduction of these pests causes chlorosis, deformation of leaves and leaflets, stunting of plants, reduction of photosynthesis, and induction of air pockets in cells, causing fruit malformation and scarring (Chamberlin et al. 1992, Funderburk et al. 1998, Fung et al. 2002, Hao et al. 2002). In addition, *F. bispinosa* causes premature cellular evacuation, cellular collapse, necrosis and plasmolysis, leading to premature fruit drop (Childers et al. 1994).

Species that vector tospoviruses such as *Tomato spotted wilt viru*s can also indirectly reduce crop yields. Tomato spotted wilt causes plant wilt and fruit malformation, greatly reducing crop yield (see Prins and Goldbach 1998 for review). Vectors of tomato spotted wilt in North Florida include *F. occidentalis*, *F. fusca*, and *F. bispinosa* (Sakimura 1962, 1963, Webb et al. 1997). *Thrips tabaci*, and *Frankliniella schultzei* also vector tomato spotted wilt (Sakimura 1963, Cho et al. 1988), but are not common in the area. Although *F. tritici* is a common crop pest, this species does not vector tomato spotted wilt (Sakimura 1953, 1962, de Assis Filho et al. 2004).

Only larvae acquire transferable virus, when the salivary glands are adjacent to the midgut and movement of the virus from the midgut to the salivary glands is possible (Moritz et al. 2004). The virus replicates in the salivary glands as the thrips matures and is eventually transferred to other plants via the saliva (Ullman et al. 1993). Because only larvae acquire the virus, only those plant species that are reproductive hosts can serve as sources for the virus.

Reproductive Hosts

Little is known of the range of thrips' reproductive hosts. Although reproductive hosts can be identified as those plants with larvae present, there is no key for *Frankliniella* larvae, so identifying the larvae is difficult. Most publications list adult feeding hosts, or include reproductive hosts, but do not specify the reproducing species, due to the inability to identify larvae (though see Childers et al. 1990, Chamberlin et al. 1992, Childers et al. 1994, Cho et al. 1995b, Groves et al. 2002). Rearing thrips larvae to determine species is often difficult due to high mortality in lab rearing, especially when thrips are reared on an alternative host. However, a molecular technique has been developed to determine *Frankliniella* larval species, aiding in future experiments (Moritz et al. 2002).

Frankliniella fusca, F. occidentalis, F. tritici, and *F. bispinosa* reproduce on a range of dicots and some monocots. Although knowledge is limited, there are some known taxonomic groups that thrips prefer. For example, *F. occidentalis* reproductive hosts include three or more host species each in Asteraceae, Fabaceae, Rosaceae, and Solanaceae (Table 1-1), and *F. fusca* reproduces mostly on Asteraceae, Fabaceae and Poaceae plants (Table 1-2). Little research has been focused on *F. tritici* and *F. bispinosa* due to *F. tritici's* inability to vector TSWV, and the geographically limited range of *F.*

bispinosa (Childers et al. 1990, Childers et al. 1994, Tsai et al. 1996). At present, there are no apparent trends in *F. tritici* and *F. bispinosa* reproductive hosts (Tables 1-3 and 1-4).

Conclusion

There are several density dependent and independent factors affecting thrips population dynamics. However, most of these factors are poorly understood. More research is needed to understand aspects of thrips ecology such as competition, predation, parasitism, and utilization of uncultivated hosts. Understanding these factors will allow a more complete knowledge of thrips population dynamics, enabling development of better pest management programs. This thesis will present research conducted on utilization of uncultivated plant hosts and competition between thrips species.

Table 1-1. *F. occidentalis* Reproductive Hosts.

F. occidentalis Reproductive Host	Common Name	Family	Source
Arctium lappa	Burdock	Asteraceae	Bautista et al. 1995
Chrysanthemum morifolium	Florist's Daisy	Asteraceae	Monteiro 2002
Lactuca serriola	Prickly Lettuce	Asteraceae	Stewart et al. 1989
Lactuca sativa var. longifolia	Romaine Lettuce	Asteraceae	Bautista et al. 1995
Verbesina encelioides	Crownbeard	Asteraceae	Stewart, et al. 1989, Mitchell and Smith 1996
Impatiens walleriana	Buzzy Lizzy	Balsaminaceae	Chen et al. 2004
*Raphanus raphanistrum**	Wild Radish	Brassicaceae	Buntin and Beshear 1995
Cucumis sativus	Cucumber	Cucurbitaceae	deKogel et al. 1997b
*Trifolium vesiculosum**	Arrowleaf Clover	Fabaceae	Chamberlin et al. 1992
Medicago polymorpha	Bur Clover	Fabaceae	Stewart et al. 1989
*Medicago sativa**	Alfalfa	Fabaceae	Monteiro 2002
Trifolium repens	White Clover	Fabaceae	Heagle 2003
*Trifolium vesiculosum**	Arrowleaf Clover	Fabaceae	Chamberlin et al. 1992
Vicia villosa	Hairy Vetch	Fabaceae	Toapanta et al.. 1996
Saintpaulia ionantha	African Violet	Gesneriaceae	Monteiro 2002
Alstroemeria sp.	Allstroemeria	Liliaceae	Monteiro 2002
Rosa sp.	Rose	Rosaceae	Chamberlin et al. 1992, Monteiro 2002
Prunus persica	Peach	Rosaceae	Monteiro 2002
Prunus Persica var. nucipersica	Nectarines	Rosaceae	Monteiro 2002
*Prunus Serotina**	Black Cherry	Rosaceae	Chamberlin et al. 1992
Capsicum annuum	Pepper	Solanaceae	Scott Brown et al. 2002, Reitz et al. 2003
Datura stramonium	Jimson Weed	Solanaceae	Bautista et al. 1995
Lycopersicon esculentum	Tomato	Solanaceae	Navas et al. 1994
Solanum niagrum	Amer. Black Nightshade	Solanaceae	Stewart et al. 1989

*Not confirmed, assumed due to high abundance of adults in the presence of larvae

Table 1-2. *F.fusca* Reproductive Hosts.

F. fusca Reproductive Host	Common Name	Family	Source
Emilia sonchifolia	Lilac Tasselflower	Asteraceae	Stumpf and Kennedy 2005
*Gnaphalium obtusifolium**	Rabbit Tobacco	Astaraceae	Cho et al. 1995b
Gnaphalium purpureum	Spoonleaf Purple Ever.	Asteraceae	Groves et al. 2002
Hypochaeris radicata	Hairy Catsear	Asteraceae	Groves et al. 2002
Lactuca scariola	Prickly Lettcuce	Asteraceae	Groves et al. 2002
Lactuca floridana	Woodland lettuce	Asteraceae	Johnson et al. 1995
Sonchus asper	Spiny Sowthistle	Asteraceae	Johnson et al. 1995, Groves et al. 2002
Taraxacum officinale	Dandelion	Asteraceae	Cho et al. 1995b, Groves et al. 2002
Verbesina encelioides	Crownbeard	Astaraceae	Mitchell and Smith 1996
Raphanus raphanistrum	Wild Radish	Brassicaceae	Cho et al. 1995b, Groves et al. 2002
*Cerastium vulgatum**	Mouseear Chickweed	Caryophyllaceae	Cho et al. 1995b
Scleranthus annuus	German knotgrass	Caryophyllaceae	Groves et al. 2002
Stellaria media	Common Chickweed	Caryophyllaceae	Groves et al. 2002
Arachis hypogaea	Florunner Peanut	Fabaceae	Funderburk et al. 1998, Tipping et al. 1998
Arachis hypogaea	Volunteer Peanut	Fabaceae	Chamberlin et al. 1992
Trifolium campestre	Field Clover	Fabaceae	Groves et al. 2002
Geranium carolinianum*	Carolina Geranium	Geraniaceae	Cho et al. 1995b
*Allium vineale**	Wild Garlic	Lilliaceae	Cho et al. 1995b
Lamium amplexicaule	Henbit Deadnettle	Lamiaceae	Groves et al. 2002
Plantago rugeli	Blackseed Plantain	Plantaginaceae	Groves et al. 2002
*Plantago lanceolate**	Buckhorn Plantain	Plantaginaceae	Cho et al. 1995b
*Agropyron repens**	Quackgrass	Poaceae	Cho et al. 1995b
Secale cereale	Winter Rye	Poaceae	Buntin and Beshear 1995
Triticum aestivum	Winter Wheat	Poaceae	Buntin and Beshear 1995
Ranunculus sardous	Hairy Buttercup	Ranunculaceae	Johnson et al. 1995, Groves et al. 2002
Capsicum annuum var. camelot	Cheyenne Pepper	Solanaceae	Toapanta et al. 1996, Reitz et al. 2003
Datura stramonium	Jimsonweed	Solanaceae	Stumpf and Kennedy 2005

* Not confirmed, assumed due to high abundance of adults in the presence of larvae

Table 1-3. *F. tritici* Reproductive Hosts.

F. tritici Reproductive Host	Common Name	Family	Source
Raphanus raphanistrum*	Wild Radish	Brassicaceae	Buntin and Beshear 1995
Trifolium vesiculosum*	Arrowleaf Clover	Fabaceae	Chamberlin et al. 1992
Vicia villosa	Hairy Vetch	Fabaceae	Toapanta et al. 1996
Ranunculus sardous	Hairy Buttercup	Ranunculaceae	Johnson 1995
Capsicum annuum var. camelot	Cheyenne Pepper	Solanaceae	Reitz et al. 2003

* Not confirmed, assumed due to high abundance of adults in the presence of larvae

Table 1-4. A list of plants *F. bispinosa* Reproductive Hosts.

F. bispinosa Reproductive Host	Common Name	Family	Source
Alocasia cucullata^	Chinese taro	Araceae	Tsai et al. 1996
Bidens pinosa^	Spanish needle	Asteraceae	Tsai et al. 1996
Phoenix roebelenii^	Pygmy date palm	Arecaceae	Tsai et al. 1996
*Raphanus raphanistrum**	Wild Radish	Brassicaceae	Eger et al. 1998
Capsicum annuum	Cheyenne Pepper	Solanaceae	Childers et al. 1994, Reitz et al. 2003
*Pinus elliottii**		Pinaceae	Childers et al. 1994
var. densa^		Pinaceae	Tsai et al. 1996
*Pinus taeda**	Loblolly Pine Carolina	Pinaceae	Childers et al. 1994
*Prunus Caroliniana**	Laurelcherry	Rosaceae	Childers et al. 1994
*Citrus paradisi**	Grapefruit	Rutaceae	Childers et al. 1990
Citrus sinensis var. navel*	Navel Oranges	Rutaceae	Childers et al. 1990
Citrus sinensis var. valencia*	Valencia Oranges	Rutaceae	Childers et al. 1990
*Salix caroliniana**	Coastal Plain Willow	Salicaceae	Childers et al. 1994
Typha domingensis^	Cattail	Typhaceae	Tsai et al. 1996

* Not confirmed, assumed due to high abundance of adults in the presence of larvae
^Reproduced on lab Pollen

CHAPTER 2
SPATIOTEMPORAL DYNAMICS ON REPRODUCTIVE HOSTS

Introduction

Frankliniella spp. thrips cause extensive economic damage to many types of crops through feeding and oviposition (Kirk 2002). Damage is either direct, from feeding that causes a silvering of plant tissue, or indirect, via the transmission of tospoviruses, including *Tomato spotted wilt virus*, one of the most damaging worldwide plant viruses (Prins and Goldbach 1998). The most researched of the *Frankliniella* thrips is *Frankliniella occidentalis* (Pergande) (see Kirk and Terry 2003 for review). This worldwide crop pest, native to California (Kirk and Terry 2003), has a broad host range and feeds on many types of crops, including many present in North Florida (Buntin and Beshear 1995, Puche et al. 1995, Funderburk et al. 2000, Funderburk et al. 2002). Other *Frankliniella* species occurring in North Florida are *F. fusca* (Hinds), *F. bispinosa* (Morgan) and *F. tritici* (Fitch), all three of which are native to the southeastern United States. *Tomato spotted wilt virus* vectors include *F. occidentalis, F. fusca,* and *F. bispinosa*, but not *F. tritici* (Sakimura 1953 as cited by Sakimura 1962, Sakimura 1962, 1963, Webb et al. 1997, de Assis Filho et al. 2004).

In order to make better predictions of thrips population abundance, it is necessary to study cycles of thrips abundance (Funderburk 2002). These cycles have been studied extensively in crops such as tomatoes (Reitz 2002, Nault et al. 2003), citrus (Childers et al. 1990), nectarines (Felland et al. 1995, Pearsall and Myers 2000), and small grains (Buntin and Beshear 1995), but little research has been conducted in uncultivated plant

hosts (though see Chamberlin et al. 1992, Chellemi et al. 1994, Cho et al. 1995, Toapanta et al. 1996). Furthermore, past studies either did not monitor thrips populations over the entire year (Chamberlin et al. 1992, Cho et al. 1995, Toapanta et al. 1996), or did not present thrips numbers for each plant host (Chellemi et al. 1994). Thrips often migrate from uncultivated hosts into cropping systems (Pearsall and Myers 2001), so cycles of abundance on uncultivated hosts must be understood to locate potential sources of thrips populations and *Tomato spotted wilt virus*.

Often adult thrips feed on a host, but do not reproduce on the plant (Chamberlin et al. 1992), so a distinction must be made between feeding hosts and reproductive hosts. Reproductive hosts have a more direct connection to population growth than feeding hosts, and are the only sources of *Tomato spotted wilt virus*, since a transferable virus can only be acquired by a larva (Ullman et al. 1993, Wijkamp et al. 1993). Therefore, it is important to focus on reproductive hosts rather than plants where only adults occur (i.e. feeding hosts). The objective of this study was to determine the cycles of abundance of *Frankliniella* species on several species of potential reproductive plant hosts growing in field margins. The leaves, fruits and flowers of each plant were sampled to compare plant parts inhabited by the larvae and adults.

Materials and Methods

Sampling Procedure

The study was conducted at the North Florida Research and Education Center in Quincy, Gadsden County. The plants sampled were *Solidago canadensis* L., *Chenopodium ambrosioides* L., *Rubus trivialis* Michx., *R. cuneifolius* Pursh., *Raphanus raphanistrum* L., *Trifolium repens* L., and *Vicia sativa* L. These species were selected based on the work of Chamberlin et al. (1992), Cho et al. (1995), Groves et al. (2002),

Heagle (2003) and Dean Paini (Personal Communication). Each species was sampled biweekly, when available, between November 19, 2003 and November 5, 2004

On each sample date, 10 different sites were selected, and one plant was sampled from each site. For each plant, 20 leaves, 20 flowers, 20 fruits, and 20 racemes were placed, as appropriate for each plant species, in vials containing 70-95% ethanol. For clover, only four racemes were sampled per plant due to the low number and large size of the racemes. For *V. sativa*, which has prominent terminal buds, four buds were sampled per plant, in addition to the flowers, fruits and leaves. The total numbers of flowers, fruits and leaves per plant were also estimated. Because thrips were highly aggregated in the flowers, the number of each thrips species per flower and the number of flowers per plant were used to estimate the total number of each thrips species per plant on dates when thrips were common on the plant host. In the laboratory, the contents of each vial were placed in a Petri dish, and the plant parts were dissected to extract thrips. Adult thrips were identified under a microscope using 6.5-40x magnification. Larvae were counted, but not identified, because no morphological keys were available.

Data Analysis

Repeated measures ANOVA analyses and Tukey's tests were used to determine the effect of plant part and date on combined thrips densities for data collected when all plant parts were present. A one-way ANOVA was conducted to analyze plant part means of *R. cuneifolius*, as all three parts were only present on one sample date.

Separate repeated measures ANOVA analyses were conducted on the number of *Frankliniella* spp. thrips per flower on each sample date, and the interaction of *Frankliniella* species by date was used to compare the patterns of abundance of the different thrips species (Littell et al. 1996). An unidentified non-*Frankliniella* species

was abundant on *C. ambrosioides*, so it was included in the analysis. Effects were considered significant when $p \leq 0.05$. In order to compare the patterns of abundance of the two most abundant species present, contrast procedures were conducted on the interaction between date and species. Specificially, contrast procedures were conducted on the interaction between date and the means of *F. tritici* and *F. bispinosa* on each host: *R. raphanistrum*, *R. cuneifolius* and *T. repens*. Contrast procedures were conducted on the interaction between date and the means of *F. tritici* and *F. fusca* on each host: *R. trivialis*, and *V. sativa*. For *S. canadensis*, no contrast procedure was conducted due to the low numbers of *F. fusca*, *F. bispinosa*, and *F. occidentalis*. For *C. ambrosioides*, a contrast procedure was conducted on the interaction between date and the means of *F. tritici* and the non-*Frankliniella* species. Data were only analyzed when thrips were present. For *R. raphanistrum* these dates were April 14 through July 20, 2004. For *R. trivialis*, these dates were March 29 through April 29, 2004. For *R. cuneifolius*, these dates were March 29 through April 29, 2004. For *V. sativa*, these dates were March 29 to April 14, 2004. For *T. repens*, these dates were April 14 to May 24, 2004. For *S. canadensis*, these dates were September 9 to October 21, 2004. For *C. ambrosioides*, these dates were August 19 to October 21, 2004.

All analyses were conducted using SAS (SAS Institute 2000). A Cochran's test for homogeneity showed there was significant heterogeneity in the data, so the data were log-transformed using the formula log(x+1) to increase homogeneity. There was still significant heterogeneity in the data for comparing abundances of different thrips species, but the F- tests were considered robust enough to remain unaffected due to the number of treatments and sample size (Underwood 1999).

Results

There were 8,112 thrips extracted from 2,068 samples of the seven hosts, and 62% were adults. The adult thrips collected were 75.9% *F. tritici*, 14.7% *F. bispinosa*, 3.5% *F. fusca*, 1.1% *F. occidentalis,* and 4.8% non-*Frankliniella* spp. thrips.

Raphanus raphanistrum flowered from December 5, 2003 to July 20, 2004. Thrips were most abundant from April 14 to July 20 (Tables 2-1 through 2-3). There was a significant interaction between plant part and date ($F = 4.44$; $df = 18, 184$; $p<0.0001$). There was a significant difference between thrips densities on plant parts ($F = 183.01$; $df = 2, 34$; $p<0.0001$), with more thrips on flowers than on leaves or fruits (Tukey's $p<0.0001$). The most abundant thrips species were *F. tritici* and *F. bispinosa,* comprising 74.5% and 19.9% of adults, respectively. There was a significant difference between the densities of thrips species ($F = 65.97$; $df = 3, 36$; $p<0.0001$), and a significant date effect ($F = 25.76$; $df = 6, 184$; $p<0.0001$) and interaction between species and date ($F = 7.29$; $df = 18, 184$; $p<0.0001$). There was a significant interaction between date and the means of *F. tritici* and *F. bispinosa* ($F = 7.17$; $df = 6, 184$; $p<0.0001$). Both species were abundant from April 14 to July 20, and there were more *F. tritici* than *F. bispinosa* collected on all dates. However, there were low abundances of both species on June 9, and since *F. tritici* was more abundant on the previous date than *F. bispinosa*, there was a greater relative decrease in *F. tritici* than in *F. bispinosa,* causing a difference in the patterns of abundance. Larvae consisted of 34.6% of total thrips present and were most abundant from April 14 to July 20.

Rubus trivialis flowered from March 2 to April 29, 2004 and thrips were most abundant March 29 through April 14 (Tables 2-4 through 2-6). There was a significant interaction between plant part and date ($F = 3.13$; $df = 4, 35$; $p<0.05$). There was a

significant difference in thrips densities on plant parts ($F = 16.41$; $df = 2, 38$; $p<0.0001$) from March 29 to April 29, with significantly more thrips on flowers than fruits or leaves (Tukey's $p<0.0001$). The most abundant thrips species were *F. tritici* and *F. fusca*, comprising 54.0% and 14.7% of adults, respectively. There was a significant difference in densities of thrips species ($F = 2.70$; $df = 3, 36$; $p<0.005$), and a significant interaction between species and date ($F = 2.70$; $df = 6, 48$; $p<0.05$), but no significant date effect ($F = 2.60$; $df = 2, 95$). There was a significant interaction between date and means of *F. tritici* and *F. fusca* ($F = 5.58$; $df = 2, 48$; $p<0.01$). *F. tritici* was abundant on *R. trivialis* from March 17 through April 29, but *F. fusca* was not abundant until April 29. Larvae consisted of 33.9% of thrips collected and were most abundant from March 29 to April 29.

Rubus cuneifolius flowered from March 29 to May 12, 2004, and thrips densities were most abundant on April 29 (Tables 2-7 through 2-9). There was a significant difference in thrips densities on plant parts ($F = 67.64$; $df = 2, 14$; $p<0.0001$), with significantly more thrips on flowers than on fruits or leaves (Tukey's $p<0.05$) on April 29. The most abundant species were *F. tritici* and *F. bispinosa,* comprising 87.5% and 7.3% of adults, respectively. There was a significant difference in densities of thrips species ($F = 33.52$; $df = 3, 36$; $p<0.0001$), and a significant date effect ($F = 19.06$; $df = 2, 68$; $p<0.0001$) and interaction between date and species ($F = 6.91$; $df = 6, 68$, $p<0.0001$). There was a significant interaction between date and the means of *F. tritici* and *F. bispinosa* ($F = 5.78$; $df = 2, 68$; $p<0.005$). *F. tritici* were abundant from April 14 to April 29, but *F. bispinosa* were not present until April 29. Larvae were most abundant on *R. cuneifolius* on April 29, and consisted of 27.5% of thrips collected.

Vicia sativa flowered from December 5 to April 14, and thrips were collected from March 29 to April 14 (Tables 2-10 through 2-13). There was a significant interaction between date and plant part ($F = 4.01$; $df = 6, 52$; $p<0.005$), and a significant difference in thrips densities on plant parts ($F = 6.43$, $df = 3, 40$; $p<0.005$). There were significantly more thrips on flowers than on the leaves or fruits (Tukey's $p<0.05$), but not buds (Tukey's $p>0.05$). The most abundant species were *F. tritici*, and *F. fusca*, comprising 81.9% and 15.3% of adults, respectively. There was no significant difference in densities of thrips species ($F = 1.77$; $df = 3, 36$), or significant difference in thrips densities on March 29 and April 14 ($F = 0.00$; $df = 1, 8$). There was no significant interaction between date and species ($F = 0.00$; $df = 1, 8$), indicating that there was no difference in the patterns of abundance of any thrips species. Larvae consisted of 47.1% of thrips collected and were present from March 29 to April 14.

Trifolium repens flowered from December 12, 2003 to July 7, 2004, and thrips were most abundant April 29 through May 24 (Tables 2-14 and 2-17). There was a significant interaction between date and plant part ($F = 6.32$; $df = 5, 88$; $p<0.0001$), and there were significantly more thrips on racemes than leaves ($F = 337.44$; $df = 1, 18$; $p<0.0001$). The most abundant thrips species were *F. tritici* and *F. bispinosa*, comprising 79.4% and 12.0% of adults, respectively. There was a significant difference in densities of thrips species ($F = 52.49$; $df = 3, 36$; $p<0.0001$), and a significant date effect ($F = 9.36$; $df = 3, 108$; $p<0.0001$) and interaction between date and species ($F = 4.61$; $df = 9, 108$; $p<0.0001$). There was no significant interaction between date and the means of *F. tritici* and *F. bispinosa* ($F = 1.97$; $df = 3, 108$), indicating that there was no difference in the

patterns of abundance of the two species. Larvae consisted of 27.4% of thrips collected, and were abundant from April 14 to May 12.

Solidago canadensis flowered from August 19 to November 5, 2004. Thrips were present on *S. canadensis* from September 24 to October 21, although 82% of thrips were observed on October 21 (Tables 2-16 and 2-17). There was a significant interaction between plant part and date ($F = 9.16$; $df = 2, 22$; $p<0.005$), and significantly more thrips on racemes than leaves ($F = 84.63$; $df = 1, 27$; $p<0.0001$). Of the adults collected, 81.5% were *F. tritici* and 17.7% were a combination of non-*Frankliniella* species. There was a significant difference in thrips species ($F = 19.72$; $df = 3, 36$; $p<0.0001$), and a significant date effect ($F = 6.50$; $df = 3, 72$; $p<0.001$) and interaction between date and species ($F = 6.23$; $df = 9, 72$; $p<0.0001$). This interaction was due to the absence of *F. bispinosa, F. fusca,* and *F. occidentalis* during *F. tritici* abundance on October 21, 2004. Larvae consisted of 68.5% of thrips collected, and were most abundant on October 21.

Chenopodium ambrosioides flowered from November 19 to December 5, 2003 and from June 24 to November 5, 2004. Thrips were collected on November 19, 2003 and from August 2 to October 21, 2004 (Tables 2-18 and 2-19). There was a significant interaction between date and plant part ($F = 3.27$, $df = 5, 66$; $p<0.05$), and there were significantly more thrips on racemes than leaves ($F = 79.45$; $df = 1, 20$; $p<0.0001$). The most abundant species were an unidentified non-*Frankliniella* sp. and *F. tritici*, comprising 68.0% and 14.6% of adults, respectively. There was a significant difference in densities of thrips species ($F = 13.92$; $df = 4, 45$; $p<0.0001$), and a significant interaction between date and species ($F = 1.97$; $df = 16, 170$; $p<0.05$), but no significant difference in the means of different sample dates ($F = 0.60$; $df = 4, 170$). There was a

significant interaction between date and the means of *F. tritici* and non-*Frankliniella* sp. ($F = 6.98$, $df = 4, 170$; $p<0.0001$). *F. tritici* were only abundant on August 19, while non-*Frankliniella* sp. were abundant from September 2 through November 5, 2004. Larvae consisted of 67.3% of thrips collected, and were abundant from August 19 to November 5.

There were 332 adult thrips and 116 larvae per *R. raphanistrum* plant from May 12 to June 24, 2004 (Table 2-20). There were 7 adult thrips and 8 larvae per *R. trivialis* plant from March 29 to April 14, 2004 (Table 2-20). There were 43 adult thrips and 11 larvae per *R. cuneifolius* plant on April 29, 2004 (Table 2-20). There were 3 adult thrips and 3 larvae per *V. sativa* plant on April 14, 2004 (Table 2-20). There were 142 adult thrips and 49 larvae per *T. repens* plant from April 29 to May 24, 2004 (Table 2-20). There were 574 adult thrips and 2,142 larvae per *S. canadensis* plant on October 21, 2004 (Table 2-20). There were 378 adult thrips and 765 larvae per *C. ambrosioides* plant from August 19 to October 21, 2004.

Discussion

More thrips were found on the flowers than leaves or fruits of all sampled plants, suggesting there is a nutritional or morphological preference for flowers. Thrips may prefer flowers to leaves because of the higher nitrogen content of pollen (Brodbeck *et al*. 2002), or for the microclimates flowers provide, that reduce desiccation, freezing, and access by predators (see Kirk 1997 for review). The statistically significant interaction between date and plant part on all plants was not considered biologically significant, because thrips were so highly aggregated in the flowers when flowers were present. The abundance of larvae on *R. cuneifolius* fruits when fruits were first present was probably

due to the inability of larvae to move to new flowers quickly, as there were very few adults collected from fruits on the same date.

There were 2.2 larvae per female collected on *S. canadensis*, and *F. tritici* was the only *Frankliniella* sp. collected, suggesting that *S. canadensis* is a good reproductive host for *F. tritici*. The high number of larvae per plant, and the abundance of plants throughout the country (USDA, NRCS 2004) suggest that *S. canadensis* may be an important source of *F. tritici* larvae that migrate into fall crops as adults. In addition, *S. canadensis* could be a source of larvae that overwinter as pupae in the soil. When temperatures rise, these developing adults may initiate the build up in thrips population numbers in early spring. If *S. canadensis* were not available to thrips, there may be a reduction in fall thrips populations and a delay in the spring population growth of thrips.

There were many *F. tritici* and *F. bispinosa* collected from *R. raphanistrum*, suggesting that *R. raphanistrum* is a good feeding host for both species. There were only 0.53 larvae per female collected, suggesting that it was not as good a reproductive host as *S. canadensis*. However, the mean numbers of *F. tritici* and *F. bispinosa* per plant were high for *R. raphanistrum*, indicating that utilization of *R. raphanistrum* as a feeding and reproductive host may still be an important part of each species' ecology. Furthermore, *R. raphanistrum* is a host for *Tomato spotted wilt virus* and may therefore be a source of virus infection in thrips populations (Parrella et al. 2003). *R. raphanistrum* is common in most of the United States (USDA, NRCS 2004) and may be an important factor in thrips ecology throughout the country.

The most common thrips species on *R. cuneifolius* and *T. repens* were *F. tritici* and *F. bispinosa*. There were 0.39 larvae per female collected from each plant species,

suggesting that neither species is a preferred host. Fewer thrips per plant were collected from *T. repens* and *R. cuneifolius* than from *S. canadensis* and *R. raphanistrum*. Reduced abundance per plant may be partially due to a lower number of flowers per plant during thrips abundance and the frequent mowing of *T. repens* during spring and summer.

There were high numbers of thrips per plant on *C. ambrosioides*, but a majority of adults were not *Frankliniella* species, indicating that it may not support as many crop pests as other plants sampled. Low numbers of thrips per plant were collected from *R. trivialis* and *V. sativa*, suggesting that neither is a preferred feeding or reproductive host.

Reasons for high *Frankliniella* species abundance on *S. canadensis, R. raphanistrum, R. cuneifolius,* and *T. repens* are unclear, since they are all from different taxonomic families (Asteraceae, Brassicaceae, Fabaceae and Rosaceae). Flowering time does not appear to be a major factor, since all plants were flowering when thrips were abundant. Nutritional differences among the plant species may cause thrips to prefer *R. raphanistrum, R. cuneifolius, T. repens* and *S. canadensis*. Thrips are known to prefer aromatic amino acids, which enhance cuticle production and hardening, and these amino acids may be more common in the more suitable hosts (Mollema and Cole 1996, Brodbeck et al. 2002). Furthermore, there may be a difference in chemical or morphological defenses, such as primary or secondary metabolites and trichomes that cause some plant species to be more attractive than others (Felland et al. 1995, deJager et al. 1996). More research must be conducted on the physical and chemical characteristics of plant hosts to understand why there were more *Frankliniella* spp. thrips on *R. raphanistrum, R. cuneifolius*, and *S. canadensis* than other plants surveyed.

In addition to plant host charachterisitics, there may be competitive interactions between thrips species on *R. trivialis*, *R. cuneifolius,* and *C. ambrosioides* that affect species abundance. In *R. trivialis*, *F. fusca* was only abundant on April 29, when *F. tritici* was reduced. However, only one plant flowered on April 29, so this difference in patterns of abundance may be due to sampling error and the low abundance of *F. fusca* on most sample dates. In *R. cuneifolius*, *F. tritici* may benefit from an early abundance, allowing a competitive advantage over *F. bispinosa.* If interspecific competition is occurring, *F. bispinosa* may find the plant host less desirable if there are established interspecific competitors present.

There may be climatic or plant physiological changes altering the species ratios on *C. ambrosioides*. For example, the cooler fall temperatures may benefit non-*Frankliniella* sp. populations more than *F. tritici,* or the plant may accumulate defenses to which only non-*Frankliniella* sp. have adapted. In addition, competitive displacement may have occurred locally, limiting abundance of *F. tritici* in the presence of non-*Frankliniella* sp.

Reasons for the low abundance of thrips on *R. raphanistrum* on June 9, that caused the interaction between *F. tritici* and *F. bispinosa,* are unclear. Populations of *F. tritici* on *T. repens* were also reduced on that date, indicating that reduced thrips abundances were not limited to *R. raphanistrum*. Climatic effects, such as heavy rain or wind, prior to the sample date may have reduced thrips densities on *R. raphanistrum*.

Although *R. raphanistrum* flowered from December 5 to August 2, there were no thrips collected from the flowers until April 14. The reasons for the delay in abundance of thrips on *R. raphanistrum* are unclear. Highest numbers of thrips were not found in *R.*

raphanistrum until after *R. cuneifolius* finished flowering on May 24 and larvae to adult ratios were low, suggesting that *R. raphanistrum* may not be a preferred host, and is only utilized when alternative hosts are not available. *Raphanus raphanistrum* could also be utilized as an enemy-free niche as there was only one *Orius insidiosus,* an important thrips predator, collected from this host and thrips presence on this host corresponds to the seasonal increase of *O. insidiosus* in crops, as presented in past studies. For example, Reitz et al. (2003) collected most *O. insidiosus* during May and June in peppers, reaching abundances of one individual per 1.4 flowers during the same season as peak thrips densities on *R. raphanistrum* in my study.

Reasons for the delay in abundance of larvae on *R. raphanistrum* are also unclear. The slight delay in abundance from April 29 to May 24 could be due to naturally occurring oviposition and incubation times. However, it is unclear why there were much higher larvae per female numbers from June 24 to July 20 than from April 29 to May 24. There may be a physiological change occurring in the plant during this time that makes the host more suitable for reproduction. Conversely, thrips may choose to oviposit in *R. raphanistrum* during these dates due to an abundance of *O. insidiosus* in cropping systems (Reitz et al. 2003). *O. insidiosus* preferentially feeds on larvae (Baez et al. 2004), and there may be selective pressure to reproduce in areas with less predation during this time of high predator abundance.

Fewer *F. occidentalis* were collected than were collected previously in North Florida tomatoes and peppers (Funderburk et al. 2000, Reitz et al. 2003), and fewer *F. fusca* than were collected from North Florida peanuts (Funderburk et al. 2002). *Frankliniella fusca* and *F. occidentalis* may have different nutritional requirements to

those of *F. tritici,* and this may partially explain their general absence from these hosts. Furthermore, there may be competitive interactions occurring on uncultivated hosts that are different from those in crops. Although *F. occidentalis* are excellent competitors on fertilized pepper plants (see chapter 3), they may not be able to compete as well on unfertilized wild hosts.

More *F. occidentalis* per flower were found in *R. raphanistrum* in Georgia than in Florida (Buntin and Beshear 1995). Reasons for the reduced densities of *F. occidentalis* in Florida are unclear. Because of their abundance on cultivated crops in past studies, climate does not appear to be the only factor limiting *F. occidentalis* densities on *R. raphanistrum*. However, there may be an interaction between climate and availability of other reproductive hosts. An increase in alternative host species in Georgia would increase the overall population and may increase the number of thrips migrating into *R. raphanistrum*. The difference in densities may also be due to an interaction between climate and interspecific competition. Although conditions in Georgia and Florida are similar, the slight change may affect competition in *F. occidentalis*, decreasing their competitive ability on *R. raphanistrum* under Florida conditions compared with those in Georgia.

Conclusion

Seven uncultivated reproductive hosts were sampled to determine the seasonal abundance of *Frankliniella tritici*, *F. bispinosa*, *F. fusca*, and *F. occidentalis* populations on each plant host. The abundant thrips species on *Raphanus raphanistrum, Rubus cuneifolius,* and *Trifolium repens* were *F. tritici* and *F. bispinosa*. The abundant thrips species on *Rubus trivialis* and *Vicia sativa* were *F. tritici* and *F. fusca*. The abundant

thrips species on *Solidago canadensis* was *F. tritici*. The abundant thrips species on *Chenopodium ambrosioides* were *F. tritici* and an unidentified non-*Frankliniella* sp. Thrips were highly aggregated in the flowers, rather than leaves or fruits, of every plant species. The spring hosts that supported the largest *Frankliniella* spp. thrips populations included *R. raphanistrum, T. repens,* and *R. cuneifolius*, and the fall host that supported the largest *Frankliniella* spp. populations was *S. canadensis*. Reducing the occurrence of these uncultivated hosts in areas surrounding crops may decrease the number of thrips migrating into cropping systems, leading to a reduction in crop damage.

Table 2-1. Mean number (SEM) of adult *Frankliniella tritici,* adult *F. fusca,* adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 20 flowers of *Raphanus raphanistrum* collected biweekly on 17 dates from December 12, 2003 to August 2, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
2003					
12-Dec	0	0	0	0	0
5-Dec	0.7(0.4)	0	0	0	0
2004					
2-Jan	0.9(0.3)	0	0	0	0
15-Jan	0.6(0.3)	0	0	0	0
29-Jan	0.1(0.1)	0	0	0	0
17-Feb	0.3(0.2)	0.1(0.1)	0	0	0
2-Mar	0.3(0.2)	0	0	0	0
17-Mar	0.3(0.2)	0	0	0	0
29-Mar	0.2(0.1)	0.1(0.1)	0	0	0
14-Apr	5.3(2.0)	0.6(0.3)	0.2(0.2)	0	0.1(0.1)
29-Apr	21.3(11.2)	1.7(1.6)	4.1(2.1)	0.3(0.2)	6.3(4.0)
12-May	100.3(19.9)	6.1(3.1)	25.6(13.5)	2.7(1.1)	26.9(11.5)
24-May	60.8(14.9)	0.5(0.4)	15.3(2.8)	0.7(0.3)	37.4(11.4)
9-Jun	11.4(3.1)	0.9(0.3)	5(1.4)	0.2(0.1)	7.1(1.5)
7-Jul	19.0(4.9)	0.2(0.2)	10.2(3.0)	1.0(0.6)	72(0.2)
20-Jul	13.8(2.7)	0.3(0.2)	4.6(1.9)	0	27.4(5.6)
2-Aug	2.3(0.9)	0	0.5(0.5)	0	8.5(5.3)

Table 2-2. Mean number (SEM) of adult *Frankliniella tritici,* adult *F. fusca,* adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 20 leaves of *Raphanus raphanistrum* collected biweekly on 17 dates from December 12, 2003 to August 2, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
2003					
12-Dec	0	0	0	0	0
5-Dec	0	0	0	0	0
2004					
2-Jan	0	0	0	0	0
15-Jan	0	0	0	0	0
29-Jan	0	0	0	0	0
17-Feb	0	0	0	0	0
2-Mar	0	0	0	0	0
17-Mar	0	0	0	0	0
29-Mar	0	0	0	0	0
14-Apr	0	0	0	0	0.2(0.2)
29-Apr	0.3(0.3)	0.3(0.3)	0.4(0.4)	0	0.4(0.3)
12-May	1.8(1.0)	0.4(0.2)	0	0.1(0.1)	3.5(1.2)
24-May	1.7(0.7)	0.3(0.2)	0.9(0.4)	0.1(0.1)	4.6(1.5)
9-Jun	0.1(0.1)	0	0	0	1.3(1.7)
7-Jul	0.2(0.2)	0	0	0	0.2(0.2)
20-Jul	0.3(0.2)	0.2(0.1)	0	0	0.5(0.2)
2-Aug	0	0	0	0	0

Table 2-3. Mean number (SEM) of adult *Frankliniella tritici,* adult *F. fusca,* adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 20 fruits of *Raphanus raphanistrum* collected biweekly on 17 dates from December 12, 2003 to August 2, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
2003					
12-Dec	0	0	0	0	0
5-Dec	0.1(0.1)	0	0	0	0
2004					
2-Jan	0	0	0	0	0
15-Jan	0	0	0	0	0
29-Jan	0	0	0	0	0
17-Feb	0	0	0	0	0
2-Mar	0	0	0	0	0
17-Mar	0	0	0	0	0
29-Mar	0	0	0	0	0
14-Apr	0.1(0.1)	0	0	0	0
29-Apr	0	0.1(0.1)	0.1(0.1)	0	0.1(0.1)
12-May	0.6(0.3)	0	0	0	3.9(1.7)
24-May	0.8(0.4)	0	0.2(0.1)	0	3.3(1.2)
9-Jun	0.3(0.2)	0	0	0	0.1(0.1)
7-Jul	0	0	0	0	0
20-Jul	0.3(0.2)	0	0	0	0.1(0.1)
2-Aug	0	0	0	0	0

Table 2-4. Mean number (SEM) of adult *Franklniella tritici*, adult *F. fusca*, adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 20 flowers of *Rubus trivialis* collected biweekly on 5 dates from March 2 to April 29, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
2-Mar	0	0	0	0	0.3(0.6)
17-Mar	0.5(0.3)	0.2(0.1)	0	0	0.1(0.1)
29-Mar	2.3(1.0)	0.3(0.2)	0	0.2(0.1)	1.1(0.4)
14-Apr	10.0(0.5)	0	0	0	3.5(0.1)
29-Apr*	8	5	0	2	2

*n=1 (Only one plant flowering)

Table 2-5. Mean number (SEM) of adult *Frankliniella tritici,* adult *F. fusca,* adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 20 leaves of *Rubus trivialis* collected biweekly on 5 dates from March 2 to April 29, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
2-Mar	0	0	0	0	0.1(0.1)
17-Mar	0	0	0	0	0
29-Mar	0	0	0	0	0
14-Apr	0	0	0	0	0
29-Apr	0	0.1(0.1)	0	0	0

Table 2-6. Mean number (SEM) of adult *Frankliniella tritici,* adult *F. fusca,* adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 20 fruits of *Rubus trivialis* collected biweekly on 3 dates from March 29 to April 29, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
29-Mar	0	0	0	0	0.2(0.2)
14-Apr	0	0.1(0.1)	0	0.1(0.1)	1.4(0.5)
29-Apr	0	0.1(0.1)	0	0	0.2(0.1)

Table 2-7. Mean number (SEM) of adult *Frankliniella tritici,* adult *F. fusca,* adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 20 flowers of *Rubus cuneifolius* collected biweekly on 4 dates from March 29 to May 12, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
29-Mar	0.2(0.1)	0.1(0.1)	0	0	0
14-Apr	23.0(17.3)	0.1(0.1)	0.4(0.3)	0.1(0.1)	0.8(0.3)
29-Apr	49.6(18.0)	0.2(0.1)	5.5(2.0)	0.3(0.2)	11.0(3.9)
12-May	0	0	0	0	0

Table 2-8. Mean number (SEM) of adult *Frankliniella tritici,* adult *F. fusca,* adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 20 leaves of *Rubus cuneifolius* collected biweekly on 4 dates from March 29 to May 12, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
29-Mar	0	0	0	0	0
14-Apr	0	0	0	0	0.4(0.3)
29-Apr	0.1(0.1)	0.1(0.1)	0	0	0
12-May	0	0.1(0.1)	0	0	0.2(0.1)

Table 2-9. Mean number (SEM) of adult *Frankliniella tritici,* adult *F. fusca,* adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 20 fruits of *Rubus cuneifolius* collected biweekly on 2 dates from April 29 to May 12, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
29-Apr	1.7(0.7)	0.2(0.2)	0.2(0.2)	0	20.8(4.3)
12-May	0	0.1(0.1)	0	0	0.7(0.4)

Table 2-10. Mean number (SEM) of adult *Frankliniella tritici,* adult *F. fusca,* adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 20 flowers of *Vicia sativa* collected biweekly on 6 dates from January 29 to April 14, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
29-Jan	0	0	0	0	0
17-Feb	0.1(0.1)	0	0	0	0.1(0.1)
2-Mar	0	0	0	0	0
17-Mar	0	0	0	0	0
29-Mar	0.1(0.1)	0	0	0	0.7(0.6)
14-Apr	3.7(2.7)	0.5(0.3)	0.2(0.2)	0	3.2(1.4)

Table 2-11. Mean number (SEM) of adult *Frankliniella tritici,* adult *F. fusca,* adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 20 leaves of *Vicia sativa* collected biweekly on 6 dates from January 29 to April 14, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
29-Jan	0	0	0	0	0.1(0.1)
17-Feb	0	0	0	0	0
2-Mar	0	0	0	0	0
17-Mar	0	0	0	0	0
29-Mar	0	0	0	0	0
14-Apr	0.1(0.1)	0	0	0	0

Table 2-12. Mean number (SEM) of adult *Frankliniella tritici,* adult *F. fusca,* adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 20 leaves of *Vicia sativa* collected biweekly on 3 dates from March 17 to April 14, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
17-Mar	0	0	0	0	0
29-Mar	0	0.2(0.2)	0	0	0.1(0.1)
14-Apr	0.1(0.1)	0.1(0.1)	0	0	0.3(0.2)

Table 2-13. Mean number (SEM) of adult *Frankliniella tritici,* adult *F. fusca,* adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 4 buds of *Vicia sativa* collected biweekly on 6 dates from January 29 to April 14, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
29-Jan	0	0	0	0	0.2(0.2)
17-Feb	0	0	0	0	0
2-Mar	0	0	0	0	0.2(0.2)
17-Mar	0	0	0	0	0
29-Mar	0	0	0	0	0
14-Apr	1.4(1.0)	0.1(0.1)	0	0	0.9(0.4)

Table 2-14. Mean number (SEM) of adult *Frankliniella tritici*, adult *F. fusca*, adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 4 racemes of *Trifolium repens* collected biweekly on 14 dates from December 12, 2003 to July 7, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
2003					
12-Dec	0.2(0.2)	0	0	0	0.1(0.1)
2004					
2-Jan	0	0	0	0	0
15-Jan	0.8(0.6)	0	0	0	0
29-Jan	0.1(0.1)	0	0	0	0.2(0.1)
17-Feb	0.1(0.1)	0	0	0	0.2(0.1)
2-Mar	0	0	0	0	0.1(0.1)
17-Mar	0.1(0.1)	0	0	0	0
29-Mar	0.2(0.1)	0	0.2(0.1)	0	0.2(0.1)
14-Apr	1.7(0.7)	0.1(0.1)	0.2(0.1)	0	3.1(1.4)
29-Apr	9.0(4.1)	0.6(0.3)	1.5(0.7)	0.2(0.1)	4.4(0.9)
12-May	5.9(2.2)	1.5(0.7)	0.8(0.4)	0.1(0.1)	10.8(6.1)
24-May	21.5(7.6)	0.1(0.1)	3.5(1.3)	0	0.4(0.2)
9-Jun	1.0(0.4)	0.0(0.0)	0.1(0.1)	0	0.6(0.3)
7-Jul	1.9(0.5)	0.1(0.1)	0.1(0.1)	0.1(0.1)	0.1(0.1)

Table 2-15. Mean number (SEM) of adult *Frankliniella tritici*, adult *F. fusca*, adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 20 leaves of *Trifolium repens* collected biweekly on 14 dates from December 12, 2003 to July 7, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
2003					
12-Dec	0	0	0	0	0
2004					
2-Jan	0	0	0	0	0
15-Jan	0	0	0	0	0.1(0.1)
29-Jan	0	0	0	0	0
17-Feb	0	0	0	0	0
2-Mar	0	0	0	0	0
17-Mar	0	0	0	0	0
29-Mar	0.1(0.1)	0	0	0	0
14-Apr	0	0.3(0.2)	0	0	0
29-Apr	0.1(0.1)	0	0.1(0.1)	0	0.2(0.1)
12-May	0	0.1(0.1)	0.1(0.1)	0	0.1(0.1)
24-May	0	0.1(0.1)	0	0	0.1(0.1)
9-Jun	0.1(0.1)	0	0	0	0
7-Jul	0	0	0	0	0

Table 2-16. Mean number (SEM) of adult *Frankliniella tritici,* adult *F. fusca,* adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 20 racemes of *Solidago canadensis* collected biweekly on 5 dates from September 2 to November 5, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
2-Sep	0	0	0	0	0.5(0.3)
24-Sep	5.7(2.7)	0	0.1(0.1)	0	0.4(0.4)
7-Oct	3.2(0.9)	0	0	0	3.2(1.2)
21-Oct	23.8(8.9)	0	0	0.2(0.2)	89.5(44.1)
5-Nov	0	0	0	0	0

Table 2-17. Mean number (SEM) of adult *Frankliniella tritici,* adult *F. fusca,* adult *F. bispinosa*, adult *F. occidentalis* and *Frankliniella* species larvae from samples of 20 leaves of *Solidago canadensis* collected biweekly on 5 dates from September 2 to November 5, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	*Frankliniella* spp. Larvae
2-Sep	0	0	0	0	0
24-Sep	0	0	0	0	0
7-Oct	0	0	0	0	0
21-Oct	0.2(0.2)	0	0	0	0
5-Nov	0	0	0	0	0

Table 2-18. Mean number (SEM) of adult *Frankliniella tritici,* adult *F. fusca,* adult *F. bispinosa*, adult *F. occidentalis*, adult non-*Frankliniella* species, and larvae from samples of 20 racemes of *Chenopodium ambrosioides* collected biweekly on 2 dates from November 19 to December 5, 2003 and 6 dates from August 19 to November 5, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	Adult non-*Frankliniella* sp.	Larvae
2003						
19-Nov	0	0	0	0	0	0.4(0.3)
5-Dec	0	0	0	0	0	0
2004						
19-Aug	1.1(0.5)	0	0	0	0.1(0.1)	4.4(0.1)
2-Sep	0.1(0.1)	0	0	0	1.7(1.1)	2.2(0.9)
24-Sep	0.2(0.2)	0	0	0	1.6(0.7)	5.1(2.0)
7-Oct	0.1(0.1)	0	0	0	1.5(0.6)	1.8(0.6)
21-Oct	0.3(0.3)	0	0	0	2.0(1.6)	5.3(1.7)
5-Nov	0	0	0	0	1.6(0.7)	7.4(2.8)

Table 2-19. Mean number (SEM) of adult *Frankliniella tritici,* adult *F. fusca,* adult *F. bispinosa*, adult *F. occidentalis,* adult non-*Frankliniella* species, and larvae from samples of 20 leaves of *Chenopodium ambrosioides* collected biweekly on 2 dates from November 19 to December 5, 2003 and 6 dates from August 19 to November 5, 2004 in Gadsden County, Florida.

Date	Adult *F. tritici*	Adult *F. fusca*	Adult *F. bispinosa*	Adult *F. occidentalis*	Adult non-*Frankliniella* sp.	Larvae
2003						
19-Nov	0.1(0.1)	0	0	0	0	0.1(0.1)
5-Dec	0	0	0	0	0	0
2004						
19-Aug	0	0	0	0	0	0.1(0.1)
2-Sep	0	0	0	0	0	0.1(0.1)
24-Sep	0	0	0	0	0	0
7-Oct	0	0	0	0	0	0
21-Oct	0	0	0	0	0	0
5-Nov	0	0	0	0	0	0

Table 2-20. Mean number of adult *Frankliniella tritici, F. fusca, F. bispinosa, F. occidentalis*, larvae and non-*Frankliniella* sp. per plant for seven plant species on selected dates.

Plant Species	Dates	Adult *F. tritici* per Plant	Adult *F. fusca* per Plant	Adult *F. bispinosa* per Plant	Adult *F. occidentalis* per plant	Larvae per Plant	Adult non-*Frankliniella* spp. per plant
R. raphanistrum	12-May to 24-Jun	244.30	11.37	71.51	5.04	115.80	0
R. trivialis	29-Mar to 14-Apr	6.66	0.09	0	0.47	8.13	0
R. cuneifolius	29-Apr	40.79	0.08	1.97	0.12	11.41	0
V. sativa	14-Apr	2.62	0.57	0.12	0.00	2.74	0
T. repens	29-Apr to 24-May	115.17	6.96	18.35	0.95	49.36	0
S. canadensis	21-Oct	570.41	0	0	3.99	2142.03	0
C. ambrosioides	19-Aug to 21-Oct	70.22	0	0	0	764.60	307.90

CHAPTER 3
INTRASPECIFIC AND INTERSPECIFIC COMPETITION IN THRIPS ON FLOWERING PEPPER PLANTS

Introduction

Competition can be an important factor in determining population size, structure and interactions (Inouye 1999a, b, Hansen et al. 2003, Young 2004). Interspecific competition may be particularly important when assessing the impact of invasive species, which are often good competitors (Mooney and Cleland 2001). Competitive ability enhances invasive species' capabilities to increase rapidly and become pests in new environments (Gurnell 1996, Petren and Case 1996, Holway et al. 1998, Callaway and Aschehoug 2000).

There have been several examples of invasive species out-competing native species and becoming pests. The Argentine ant *Linepithema humile* has outcompeted several native species, and become a pest in the southern United States, and many other areas of the world (Holway et al. 1998, Holway and Suarez 2004). Competitive superiority of the invasive fire ant *Solenopsis invicta* over the native ant *Forelius mccooki* has enhanced the spread of *S. invicta*, allowing the species to reach pest status in the southeastern United States (Mehdiabadi et al. 2004). Competitive superiority of the invasive mosquito *Aedes albopictus* over several native species also appears to have aided in the spread of this invasive pest (Griswold and Lounibos 2005, Juliano and Lounibos 2005). Competition has therefore been an important factor assisting the spread of invasive species and should be considered when assessing any invasive species'

success. Once the factors affecting the spread of the invasive organism are understood, invasions can be predicted, and pest management programs can be improved (Strong and Pemberton 2000, Yasuda et al. 2004).

Interspecific competition studies on animals have often used an additive or substitutive design (e.g. Connell 1961, Moran and Whitham 1990, Forseth et al. 2003). Additive design experiments maintain one species at a constant density, while varying the density of the other (Figure 3-1). Using this design does not distinguish the effect of interspecific competition from intraspecific competition due to the varying number of overall individuals (Damgaard 1998, Inouye 2001, Young 2004). Substitutive designs vary the frequency of the two competing species while maintaining a constant combined density (Figure 3-2), and are therefore useful in comparing interspecific and intraspecific competition. Because the treatments are conducted at the same overall density, interspecific and intraspecific competition can only be measured in relation to each other. The statistical significance of either form of competition can not be determined (Snaydon 1991, Inouye 2001).

A third type of design, the response surface design, varies the densities of each species independently and competition models can be used to generate a quantitative value of competition (Inouye 2001). By so doing, empirical data can be fit to a theoretical model, providing a connection between empirical and theoretical approaches that is not possible using an additive or substitutive design experiment (Damgaard 1998, Inouye 2001). Response surface designs have often been used in plant intserspecific competition studies (Law and Watkinson 1987, Rees et al. 1996, Damgaard 1998), but

have been rarely used in animal interspecific competition experiments (though see Inouye 1999a, Young 2004).

Frankliniella occidentalis is an invasive crop pest that causes damage to flowers and developing fruits through feeding and ovipositing, as well as by spreading *Tomato spotted wilt virus* (Sakimura 1962), one of the most damaging worldwide plant viruses (Prins and Goldbach 1998). This species has spread from its native western North America to every continent except Antarctica in the last 30 years (Kirk and Terry 2003). Research has been conducted on some of the factors contributing to the spread of *F. occidentalis*, including host range (Chellemi et al. 1994), climate (Brødsgaard 1993, Wang and Shipp 2001) and predation (Baez et al. 2004), but no research has been conducted on the population effects of thrips competition. Determining whether or not competition between *F. occidentalis* and native species occurs may partially explain the spread of this worldwide crop pest. I used a response surface design to test for competition between *F. occidentalis* (Pergande) and *F. bispinosa* (Morgan), a native Florida species. A competition model was fit to the data to generate quantitative values measuring the effects of intraspecific and interspecific competition, and make qualitative (presence or absence) determinations of each type of competition.

Materials and Methods

Experimental Design

Female *F. bispinosa* were collected from perennial peanuts (*Arachis glabrata*) in Gainesville, FL. Female *F. occidentalis* were taken from a colony maintained at 21-23˚C and 50-80% relative humidity, with a 14:10 photophase: scotophase, and regularly supplemented with wild individuals. The experiment was conducted on flowering pepper plants (*Capsicum annuum*), a known reproductive host for both species (Funderburk et al.

2000, Ramachandran et al. 2001, Hansen et al. 2003). Pepper plants were grown in a greenhouse with no insecticides and were checked regularly for insects, which were killed manually. For the experiment, each pepper plant was enclosed in a plexiglass cylindrical cage 15.5-cm in diameter and 36.5-cm in height. The top of each cage was covered with thrips screen (Green-Tek, Inc., WI), and the bottom was inserted into the soil to prevent thrips escape. Each cage had two 2-cm diameter holes covered with thrips screen to increase ventilation. The experiment was conducted in a climate-controlled room set at 23˚C with greater than 95% relative humidity within the cages.

The densities of female *F. bispinosa* and *F. occidentalis* were arranged in a bivariate factorial arrangement from 0 to 30 per plant in increments of ten, with additional single species treatments of 60 (Figure 3-3). These densities reflect those previously recorded in the field (Ramachandran et al. 2001). The single species treatments of 60 were added to increase the chance of including the population carrying capacity in the treatment range, since the carrying capacity was unknown. Each treatment was replicated five times.

Female thrips were introduced to the pepper plants and allowed to feed and oviposit. After ten days, plants were destructively sampled, and all larvae were removed. The larvae from each treatment were placed in 30-ml containers with green beans and bee pollen, and the species of each was determined after development to adult. The species ratio of emerged adults was assumed to be the species ratio of larvae produced for the treatment. The larval species ratio and the overall number of larvae produced were multiplied together to estimate the number of larvae produced by each species. Then the number of larvae produced per species for each treatment was divided by the number of

adult females in the treatment to estimate the number of larvae per female of each species. The number of larvae produced per female of each species at the various densities was used to evaluate the effect of competition on female oviposition.

Model Fitting

Larvae per female of each species were used as the response variable to obtain a measurement of oviposition. The model was fit using maximum log-likelihood estimation, assuming a Poisson error distribution. This method uses the data to estimate the probability of occurrence for each possible value of each parameter. The log of each likelihood (probability) value is then calculated. Then the value for each parameter that had the highest log-likelihood (probability of occurring) was selected. Confidence intervals were determined using log-likelihood ratios. This technique used the χ^2 distribution of the log-likelihood of each parameter to determine the confidence intervals with the other parameters fixed at the best fit values. All calculations were completed using R (R Development Core Team 2005). Several models were tested, and the best-fit model was the following:

$$R_X = \frac{\lambda}{1 + c(X + \beta_{XY} Y)}$$ (Law and Watkinson 1987)

Where R_X is the number of larvae produced per female of species X after ten days, and λ is generated by the model to predict the larvae per female of species X produced at low densities, in the absence of competition. The parameter c measures intraspecific competition. The parameter β_{XY} is the competition coefficient, which measures the relative effect of species Y on the reproduction of species X. This competition coefficient compares the effects of interspecific competition with that of intraspecific competition, which is set at one. For example, if the competition coefficient were estimated as 3, it

would indicate that each interspecific competitor would have 3 times the effect of a conspecific on reproduction. The competition model was fit for both focal species. Model simulation of intraspecific competition was conducted by graphing the models for each species with the number of interspecific competitors set at zero.

Results

The mean number of larvae per female from the different treatment densities of adult female F. occidentalis and F. bispinosa are presented in Table 3-1. In treatments with only one species present, there were more F. occidentalis larvae produced per female than F. bispinosa. The larvae per *F. bispinosa* female averaged over all treatments was 0.58 (SE ± 0.13), and the larvae per *F. occidentalis* female averaged over all treatments was 2.6 (SE ± 0.28).

The model parameters and confidence intervals measuring effects of competition on the number of larvae produced per *F. bispinosa* female are presented in Table 3-2. Statistically significant intraspecific competition affected *F. bispinosa*, as indicated by the confidence interval for *c*, which did not include zero. The maximum likelihood estimation for β_{XY} indicated that the effect of interspecific competition from *F. occidentalis* was 4.62 times greater than intraspecific competition on *F. bispinosa* reproduction. The 95% confidence intervals for β_{XY} did not include one, proving that interspecific competition from *F. occidentalis* had a significantly greater effect on the number of *F. bispinosa* larvae produced per female than intraspecific competition.

The model parameters and confidence intervals measuring effects of competition on the number of larvae produced per *F. occidentalis* female are presented in Table 3-3. Statistically significant intraspecific competition affected *F. occidentalis*, as indicated by the confidence interval for *c*, which did not include zero. The estimated value for β_{XY} for

F. occidentalis was negative, suggesting that *F. occidentalis* benefited slightly from the presence of *F. bispinosa*.

Intraspecific competition had a greater effect on *F. bispinosa* than on *F. occidentalis*, as indicated by the 95% confidence intervals for *c* (Tables 3-3 and 3-4), which did not overlap. Model simulation of intraspecific competition also indicated that *F. bispinosa* were more affected by intraspecific competition than *F. occidentalis* as the number of larvae per female decreased more rapidly with increased intraspecific competition for *F. bispinosa* than for *F. occidentalis* (Figure 3-4). However, the values for λ were similar, indicating that in the absence of competition, both species would produce similar numbers of larvae per female.

Discussion

These results indicate that *F. occidentalis* is competitively superior to *F. bispinosa* on pepper plants. Being a superior competitor may enhance the spread and abundance of *F. occidentalis*.

The competitive mechanism that occurred between the two species is not clear, although the behavior of these two species indicate that interference occurred. *F. bispinosa* are more mobile than *F. occidentalis* in pepper flowers and are more likely to flee in the presence of a predator (Reitz et al. 2002). *F. bispinosa* may also be more inclined than *F. occidentalis* to move to another feeding or oviposition site when in the presence of a competitor. This extra time spent locating feeding or oviposition sites would decrease time allotted for feeding and reproducing, reducing fecundity in the presence of intraspecific and interspecific competition.

The negative competition coefficient measuring the effect of *F. bispinosa* on *F. occidentalis* suggests that F. occidentalis benefited from the presence of F. bispinosa.

This benefit may be due to two effects. First, there may have been intraguild predation, with *F. occidentalis* increasing fecundity by feeding on *F. bispinosa,* as *F. occidentalis* are facultative predators (Faraji et al. 2002). If intraguild predation is occurring, it may increase the spread of *F. occidentalis*. In addition, there was a higher mortality rate for *F. bispinosa* than *F. occidentalis* in the single species larval growth chambers. This differential mortality may have slightly altered the species ratios in interspecific treatments, causing an apparent increase of *F. occidentalis* due to the misidentification of *F. bispinosa* larvae. However, if superior larval survivorship is occurring, there may be further characteristics in the relationship between the two species that would increase the spread of *F. occidentalis*.

Effects of Competition on *F. occidentalis* Population Abundance in Florida

Currently *F. occidentalis* populations are abundant in North America. However, *F. occidentalis* are much more abundant in North Florida than Central and Southern Florida, while *F. bispinosa* is the most abundant thrips species in Central and Southern Florida and its range extends to North Florida (Childers et al. 1990, Kirk 2002, Hansen et al. 2003). High effects of interspecific competition on *F. bispinosa*, and no effects of interspecific competition on *F. occidentalis* should influence the abundance of *F. occidentalis* in Central and Southern Florida. If there were no extrinsic factors, *F. occidentalis* would be able to out-compete *F. bispinosa* in pepper flowers throughout Florida. Furthermore, there is an abundance of pepper plants available to support populations of *F. occidentalis* in southern Florida (Kokalis-Burelle et al. 2002, Hansen et al. 2003), and the species has existed in North Florida and Georgia long enough to invade the southern portions of Florida (Beshear 1983). However, *F. occidentalis* is not common in central and southern pepper plants, indicating some additional factors affect

the abundance of *F. occidentalis* in Florida. Differential predation may be one of the factors maintaining higher *F. bispinosa* abundance in central and southern Florida.

Differential predation benefits native mosquitoes and ants by limiting population densities of invasive species (Mehdiabadi et al. 2004, Griswold and Lounibos 2005). Similarly, *F. bispinosa* may be the most abundant species in southern Florida due to a reduction in *F. occidentalis* from differential predation by *Orius insidiosus*, a predator of both species (Reitz et al. 2002). Although *O. insidiosus* is abundant in the eastern United States, it is only able to actively overwinter in central and southern Florida (Bottenberg et al. 1999 as cited by Hansen et al. 2003). This winter predation may limit *F. occidentalis* numbers in central and southern Florida. Climate may also limit *F. occidentalis* populations in central and southern Florida, as the species is considered a temperate to subtropical pest (Kirk and Terry 2003). In addition, *F. occidentalis* may be limited by alternative host availability.

Effects of Competition on World-Wide *F. occidentalis* Spread

F. occidentalis has spread to six continents, all of which have native thrips inhabiting the local flora (Moritz et al. 2001, Kirk and Terry 2003). If *F. occidentalis* is capable of out-competing the native species, as was shown in this study, it will increase the invasive threat of this economically-damaging crop pest. A better understanding of the competitive interactions between *F. occidentalis* and native species may lead to new methods of controlling the world-wide spread of *F. occidentalis* by adjusting environmental or ecological conditions to decrease the competitive advantage of *F. occidentalis* when it is competing against less damaging species.

Table 3-1 The mean number (SEM) of larvae per female 10 days after different treatment densities of adult female *F. occidentalis* and *F. bispinosa* were introduced in cages containing a pepper plant.

Number of Adult Females per Pepper Plant		Mean number of larvae per female (SEM)	
F. occidentalis	*F. bispinosa*	*F. occidentalis*	*F. bispinosa*
0	10		1.48(0.51)
0	20		2.16(1.26)
0	30		0.81(0.28)
0	60		0.42(0.09)
10	0	3.18(1.41)	
10	10	3.15(0.29)	0.03(0.03)
10	20	5.10(1.41)	0.37(0.20)
10	30	4.48(1.28)	0.25(0.14)
20	0	0.72(0.12)	
20	10	3.57(1.39)	0.44(0.18)
20	20	1.33(0.56)	0.68(0.36)
20	30	3.11(1.23)	0.03(0.03)
30	0	1.93(0.54)	
30	10	2.60(0.66)	0.17(0.11)
30	20	2.32(0.41)	0.13(0.08)
30	30	1.69(0.76)	0.55(0.27)
60	0	1.03(0.18)	

Table 3-2. Model parameters and confidence intervals measuring effects of competition on the number of larvae produced per *F. bispinosa* female after 10 days on a pepper plant (see text for model). Where c is the value of intraspecific competition, β is the competition coefficient, and λ is the larvae per female produced in the absence of competition.

Parameter	Value	95% Confidence Interval
c	0.266	0.111 to 4.86
β	4.62	3.58 to 5.97
λ	8.46	4.11 to 134.82

Table 3-3. Model parameters and confidence intervals measuring effects of competition on the number of larvae produced per *F. occidentalis* female after 10 days on a pepper plant (see text for model). Where c is the value of intraspecific competition, β is the competition coefficient, and λ is the larvae per female produced in the absence of competition.

Parameter	Value	95% Confidence Interval
c	0.0741	0.0543 to 0.104
β	-0.161	-0.274 to -0.0574
λ	6.16	4.98 to 7.93

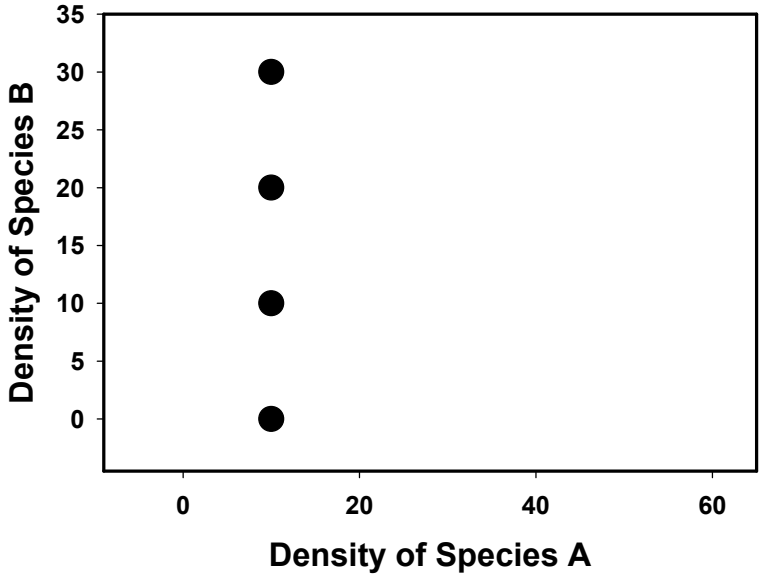

Figure 3-1. Example of an additive design. Each point represents a density treatment, which includes a combination of densities of species A and B per unit area.

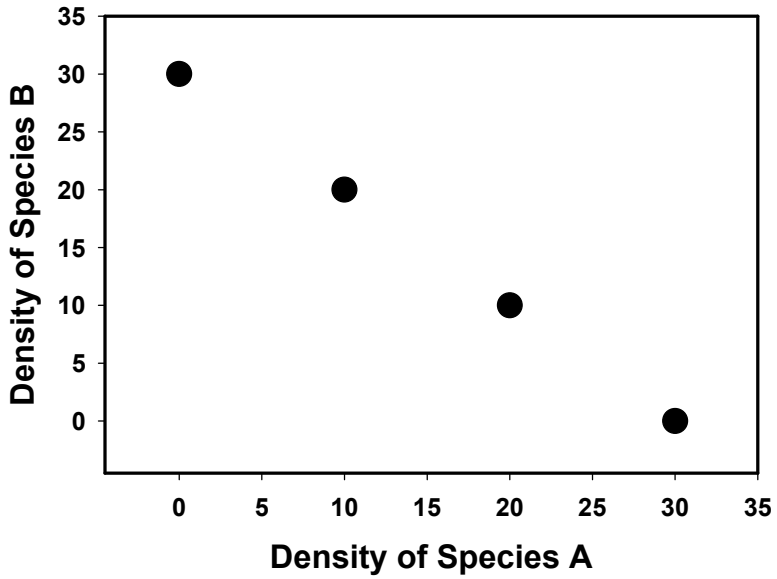

Figure 3-2. Example of a substitutive design. Each point represents a density treatment, which includes a combination of densities of species A and B per unit area.

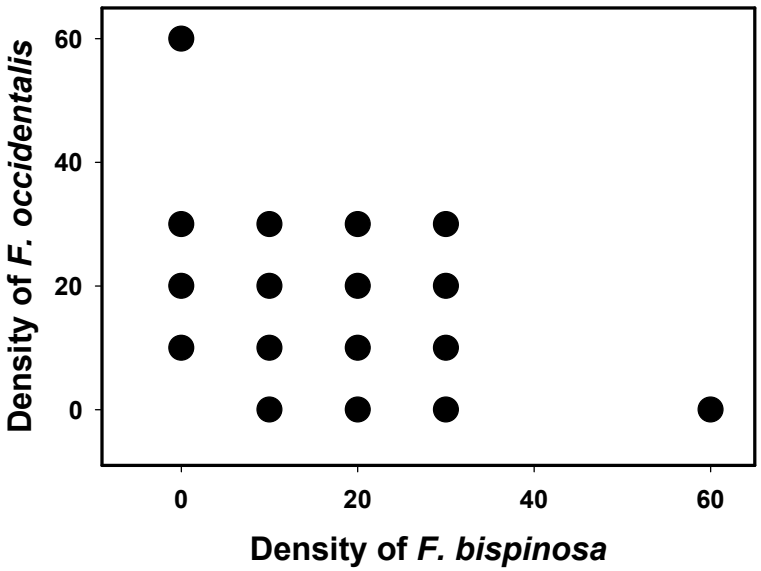

Figure 3-3. Treatments of varying *F. bispinosa* and *F. occidentalis* densities to measure the larvae produced per female at different levels of competition.

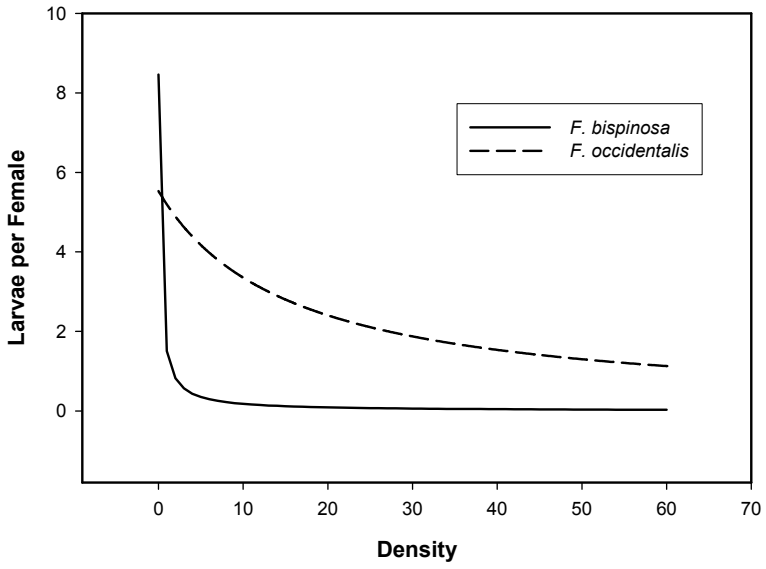

Figure 3-4. Simulation of intraspecific competition of *F. bispinosa* and *F. occidentalis* based on the competition model (refer text) predicting the number of larvae per female produced after 10 days on pepper plants.

CHAPTER 4
CONCLUSION

Developing a better understanding of the factors affecting thrips abundances in cropping systems may lead to new methods of limiting damage from thrips feeding and the vectoring of *Tomato Spotted Wilt Virus* (TSWV). Known elements affecting population dynamics include host suitability, migrations from alternative hosts, predation, parasitism, and competition.

Migration from uncultivated hosts into crops is known to occur in thrips populations (Pearsall and Myers 2001), but little research has been conducted on the sources of thrips migration (though see Chamberlin *et al.* 1992, Chellemi *et al.* 1994, Cho *et al.* 1995, and Toapanta *et al.* 1996). My research documents several sources, from which thrips may migrate into cropping systems. The most important of these thrips hosts included *R. raphanistrum* in the spring and *S. canadensis* in the fall. *Raphanus raphanistrum* may serve as a predator free niche, as well as a source of TSWV (Parrella *et al.* 2003). *Solidago canadensis* may be an important source of thrips feeding on fall crops. Furthermore, larvae developing on *S. canadensis* may overwinter as pupae that initiate the establishment of thrips populations in the early spring. *Solidago canadensis* may also be a TSWV host (Parrella *et al.* 2003), indicating that it could also be a source of viral infection in fall and spring crops. Plant nutrition and defense influence thrips dynamics, and may influence thrips abundance on these and other reproductive hosts. Furthermore, effects such as predation, parasitism, and competition may be affecting the abundance and distribution on reproductive hosts.

Past research has demonstrated effects from predation (Funderberk *et al.* 2000, Reitz *et al.* 2003, Baez *et al.* 2004), and parasitism (Funderberk *et al.* 2000, 2002), but my study is the first to give evidence of competition occurring in thrips populations. *Frankliniella occidentalis* is a better competitor than *F. bispinosa* on peppers in Florida conditions, demonstrating that competitive superiority may be a reason for the invasive ability of this worldwide pest.

More research must be conducted on the interactions between the host quality, migration, predation, parasitism and competition. For example, predation by *Orius insidiosus* may preferentially be feeding on *F. occidentalis*, limiting the abundance of *F. occidentalis* in Florida. In addition, research must be conducted on the effect of host plant variation on competition, as host plant quality may influence competition if the thrips species have different nutritional requirements. Conversely, niche displacement and host utilization may be caused by competition or predation. Research on the complex interactions between host quality, migration, predation, parasitism and competition will enable a better understanding of thrips population dynamics, enabling the development of more efficient pest management programs.

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BIOGRAPHICAL SKETCH

Tobin Northfield was born and raised in Enumclaw, WA, where he attended school at Enumclaw High School. He then attended Pacific Lutheran University in Tacoma, WA, where he first decided to pursue a career in entomology during a general entomology course. He earned a Bachelor of Science degree in biology at Pacific Lutheran University. Tobin plans to continue working on insects, and eventually earn a Ph.D. in a related field.