

# Within plant interspecific competition does not limit the highly invasive thrips, *Frankliniella occidentalis* in Florida

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**Abstract.** 1. Species invasions are often linked to reductions in biodiversity, and competitive superiority is often cited as the main reason for the success of an invasive species. Although invaded ecosystems are often examined, few have studied areas in which an invasive species has failed to successfully invade.

2. The western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), is a damaging pest and tospovirus vector that has invaded most of the world, and competitive superiority is considered one of the main reasons for this species' success.

3. However, a recent study demonstrated that competition between larval *F. occidentalis* and a native thrips species may be limiting *F. occidentalis* abundance in much of the eastern United States. *Frankliniella occidentalis* also has a limited abundance in central and southern Florida, which is dominated by the endemic *F. bispinosa* (Morgan). The potential for interspecific competition to limit *F. occidentalis* abundance in Florida was assessed.

4. The effects of competition between *F. occidentalis* and *F. bispinosa* on adult reproduction on a common host (*Capsicum annuum* L.) were quantified, using a response surface experimental design and a combination of linear and non-linear competition models.

5. Evidence of symmetric competition between these thrips species was found, but contrary to expectations, *F. occidentalis* reproduced more in dense interspecific populations than *F. bispinosa*. These results suggest that, unlike most of the eastern US, interspecific competition is not important in limiting *F. occidentalis* abundance in central and southern Florida.

**Key words.** Biotic resistance, invasive species, response surface design.

## Introduction

Reduced species richness and evenness can lead to detrimental effects on resource assimilation and biomass production by ecological communities (Cardinale *et al.*, 2006; Crowder *et al.*, 2010). Because species richness and native species are often degraded by interactions with invasive species (Mooney & Cleland, 2001; Sakai *et al.*, 2001), reducing the effects of invasive species may be an important part of preserving the

important ecosystem functions provided by diverse ecological communities. Interspecific competition is one component of the biotic resistance of the ecosystem that invaders must overcome to successfully establish. Although the impact of invasive species may be reduced through competitive interactions with native species that an invader encounters when entering a new environment (Levine *et al.*, 2004), superior competitive ability has often been cited as a major reason for the success of invasive species (Sakai *et al.*, 2001; Reitz & Trumble, 2002; Vila & Weiner, 2004). These examples comprise systems in which an invasive species has successfully invaded, however, and little is known of systems in which a highly invasive species has failed to invade and dominate (though

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see O'Connor, 1986; Baltz & Moyle, 1993; Lounibos *et al.*, 2003; Paini *et al.*, 2008). Direct studies of competition between endemic species and potentially invasive species that have yet to invade the region are vital in understanding the importance of this form of biotic resistance in affecting the invasive success of non-native species.

Since the 1970s the western flower thrips *Frankliniella occidentalis* (Pergande) has invaded much of the world, becoming dominant in most of the areas where it has been introduced (Kirk & Terry, 2003; Morse & Hoddle, 2006). *Frankliniella occidentalis* has replaced *Thrips tabaci* Lindeman as the dominant species in European greenhouses, for example, where its success has been attributed to competitive superiority rather than a higher reproductive rate (van Rijn *et al.*, 1995). *Frankliniella occidentalis* has also been implicated in the displacement of *F. intonsa* (Trybom) in Turkey (Atakan & Uygun, 2005) and the displacement of *F. gemina* Bagnall in Argentina (de Borbon *et al.*, 2006).

In the eastern United States, however, *F. occidentalis* has failed to establish as the dominant species (Salguero Navas *et al.*, 1991; Eckel *et al.*, 1995; Reitz, 2002; Reitz *et al.*, 2003; Paini *et al.*, 2007; Northfield *et al.*, 2008) despite repeated accidental introductions (Kirk & Terry, 2003). Paini *et al.* (2008) demonstrated that *F. occidentalis* larvae are, in fact, competitively inferior to the congeneric *F. tritici* (Fitch), a species endemic to most of the eastern United States. The authors concluded that interspecific larval competition between *F. occidentalis* and *F. tritici* probably contributes to biotic resistance of this region, limiting the spread of *F. occidentalis* into much of the eastern United States.

*Frankliniella occidentalis* has also failed to become dominant in central and southern Florida, U.S.A., where the congeneric *F. bispinosa* (Morgan), rather than *F. tritici*, dominates (Childers *et al.*, 1990; Kirk, 2002; Hansen *et al.*, 2003; Frantz & Mellinger, 2009). *Frankliniella occidentalis* and *F. bispinosa* are often found together on cultivated (Reitz, 2002; Reitz *et al.*, 2003) and uncultivated host plants (Paini *et al.*, 2007; Northfield *et al.*, 2008), so it is a reasonable assumption that they compete for resources. Both species transmit *Tomato spotted wilt virus*, a very damaging plant disease (Prins & Goldbach, 1998), but *F. occidentalis* is a more effective vector and therefore has the potential to be a more damaging pest than *F. bispinosa* in central and southern Florida (Avila *et al.*, 2006). This system therefore presents an opportunity to test whether or not interspecific competition has led to the failure of a potentially invasive species to dominate herbivore communities in a new environment. We tested the effects of interspecific competition between *F. occidentalis* and *F. bispinosa* on adult reproductive success to evaluate the hypothesis that this competitive interaction is contributing to biotic resistance in Florida.

## Materials and methods

### Study organisms

Adults and larvae of *F. bispinosa* and *F. occidentalis* tend to aggregate within flowers when these are available

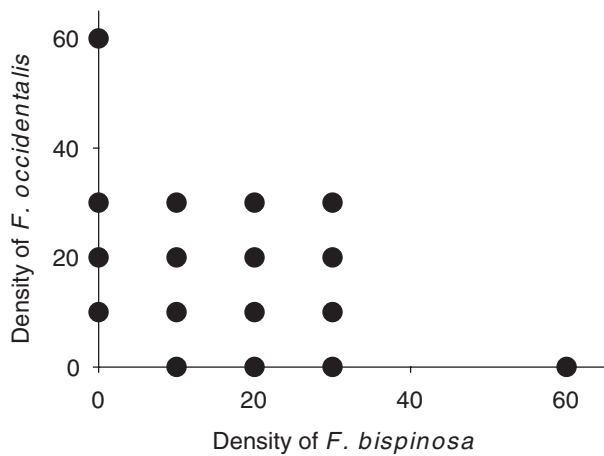
(Hansen *et al.*, 2003). Because adults are capable of interplant movement, but larvae are largely restricted to their natal, host oviposition site selection greatly influences reproductive success. *Frankliniella* spp. thrips are generally considered *r*-selected (Reitz, 2009). Females deposit eggs individually into the epidermis of plant material with a saw-like ovipositor (Hansen *et al.*, 2003; Reitz, 2009). However, females are capable of ovipositing up to 7 eggs per day and producing over 200 eggs during their lifetime, generating the potential to produce large thrips populations in very little time (Robb & Parrella, 1991). Furthermore, females do not need to mate to reproduce, as unfertilised eggs develop into haploid males and fertilised eggs develop into diploid females (Moritz, 1997). We studied the effects of interspecific competition on the reproduction of *F. bispinosa* and *F. occidentalis* females in flowering pepper (*Capsicum annuum* L.) plants, which is a reproductive host for both species.

Female *F. bispinosa* were taken directly from perennial peanuts (*Arachis glabrata* Benth) in Gainesville, FL. Female *F. occidentalis* were collected from a colony initiated each spring and reared on green bean pods and supplemented with wild individuals from various plant hosts, depending on host phenology, every 1–2 weeks. During summer months, *F. occidentalis* were generally collected from crape myrtle (*Lagerstroemia indica* L.). No *F. occidentalis* or *F. bispinosa* were collected from pepper plants. Colonies were maintained at 21–23 °C and 50–80% relative humidity with 14 : 10 photophase: scotophase days to replicate spring conditions in Florida. Experiments were conducted using flowering pepper plants. Pepper plants were grown in a greenhouse with no insecticides and were checked regularly for insects, which were killed manually.

### Experimental design

To test the hypothesis that interspecific competition limits thrips reproduction, we used a response surface-designed experiment (Inouye, 1999, 2001; Young, 2004; Paini *et al.*, 2008) and a combination of linear and non-linear modelling to compare the effects of intra- and interspecific competition on the reproduction of *F. occidentalis* and *F. bispinosa*. Competition studies on animals have often used an additive or substitutive design (e.g., Connell, 1961; Moran & Whitham, 1990; Forseth *et al.*, 2003). However, the additive design does not specifically compare the effects of interspecific competition and intraspecific competition, and the substitutive design does not allow a specific statistical test for either form of competition (Snaydon, 1991; Damgaard, 1998; Inouye, 2001; Young, 2004). By varying the densities of each species independently we were able to specifically quantify intra- and interspecific competition between the two thrips species.

Densities of *F. bispinosa* and *F. occidentalis* comprised a bivariate factorial arrangement from 0 to 30 females per plant in increments of 10, with additional single species treatments of 60 (Fig. 1), reflecting densities previously recorded in the field (Ramachandran *et al.*, 2001). Each treatment was replicated five times. The experiment was conducted on flowering pepper



**Fig. 1.** Experimental densities of *Frankliniella bispinosa* and *F. occidentalis* used to measure the effects of intra- and interspecific competition on the number of larvae produced per female of each species.

plants (Funderburk *et al.*, 2000; Ramachandran *et al.*, 2001; Hansen *et al.*, 2003). For each thrips density treatment, thrips were released onto a single whole pepper plant that had been trimmed slightly so that each plant had two flowers. The 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-proof screen (Green-Tek, Inc., Janesville, Wisconsin), and the bottom was inserted into the soil to prevent escape. Each cage had two holes, each 2-cm in diameter, covered with thrips-proof screen to increase ventilation. The experiment was conducted in a climate-controlled room set at 23 °C and a 14 : 10 photophase: scotophase day.

Female thrips were introduced to the pepper plants and allowed to feed and oviposit for 10 days, after which plants were destructively sampled, and all larvae were removed. Eggs typically develop to adult in approximately 12 days at optimal temperatures (28 °C, 5° greater than the experimental conditions) (Reitz, 2008), and after 10 days only larvae were present on plants. Because the larvae of these two species cannot be distinguished, larvae from each replicate were placed in a 30-ml container with green beans and excessive bee pollen (to minimise larval competition in rearing cages) and raised to adults for species identification. To account for differential mortality in the larval rearing process, we estimated the larval species ratio at the end of the experiment by dividing the number of surviving larvae of each species by the mean survivorship rate in the single species treatments (14.2% for *F. bispinosa* and 32.7% for *F. occidentalis*). These single species survival rates were calculated by determining the mean per cent larval survival to adult in single species treatments after larvae were transferred to rearing containers for each species. For each treatment we multiplied this estimated final larval species ratio by the total number of thrips larvae produced in the treatment to estimate the number of larvae produced per female per species in the treatment. To test for competition between larvae in rearing cages we conducted a logistic regression using proc logistic in SAS version 9.2 (SAS

Institute, 2008) to evaluate the effects of total larval density on total larval survivorship across all treatments (combined species density and survivorship).

#### Competition analysis

To evaluate the effects of interspecific competition on the reproduction of each species, we fitted a model describing the effects of inter- and intraspecific competition. There are many candidate models that could be derived to include each type of competition. We tested the five candidate competition models reviewed by Inouye (2001) and no model fitted better (all AIC for other candidate models were greater than the presented model for each focal species, or the difference was less than one) than the following model predicting reproduction by species *X*:

$$R_X = \lambda/[1 + c(X + \beta_{XY}Y)] + \varepsilon \quad (\text{Law \& Watkinson, 1987}),$$

where  $R_X$  is the number of larvae produced per female of species *X* during the 10-day experiment and *X* and *Y* represent the adult female densities of species *X* and *Y*, respectively. The parameter  $\lambda$  estimates the maximum number of larvae per female of species *X* produced at very low intra- and interspecific densities. The parameter  $c$  describes the effect of overall competition on species *X*. The parameter  $\beta_{XY}$  is the competition coefficient, which compares the effects of interspecific competition from females of species *Y* to that of intraspecific competition on species *X*, which is scaled to one by the  $c$  parameter. Finally, the parameter  $\varepsilon$  is the error term, assumed to be normally distributed with mean zero and variance proportional to the expected thrips reproduction at given densities of each thrips species,  $\sigma^2 R_X$ . In other words, we fit the model with non-linear weighted regression with weights  $1/R_X$  for each thrips species. Non-linear model fits were calculated for each species separately using R version 2.8.0 (R Core Development Team, 2008). We selected this error structure empirically to homogenize variances; this error structure could be generated by several processes, including sampling error and demographic stochasticity. For each thrips species we next fitted a model with equal effects of inter- and intraspecific competition by setting  $\beta_{XY} = 1$ . For each thrips species, we then evaluated differences between inter- and intraspecific competition using a likelihood ratio test to compare the fits of the model with different effects of each competition, to the model with equal effects ( $\beta_{XY} = 1$ ) (Judge *et al.*, 1985; Bolker, 2008). Under the null hypothesis that the two types of competition are equal, twice the likelihood ratio will have a  $\chi^2$  distribution with 1 [to account for the one parameter ( $\beta_{XY}$ ) removed from the full model] degree of freedom.

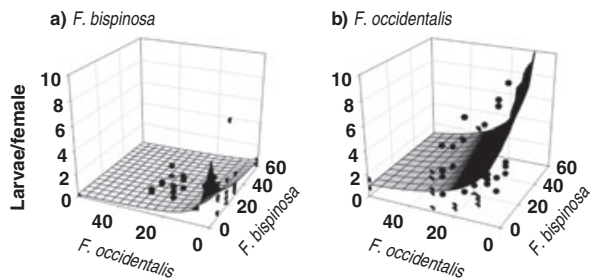
#### Results

There was no effect of larval density on survivorship to adult in the larval rearing containers (likelihood ratio  $\chi^2(1) = 2.30$ ,  $P = 0.1291$ ), suggesting that little larval competition occurred

**Table 1.** Model parameters and confidence intervals measuring effects of competition on the number of larvae produced per *Frankliniella bispinosa* female after 10 days on pepper plants (see text for model).

Focal species	Variable	Estimate
<i>F. bispinosa</i>	$c$	0.13
	$\beta$	3.89
	$\lambda$	5.44
<i>F. occidentalis</i>	$c$	0.096
	$\beta$	-0.20
	$\lambda$	6.58

The parameter  $c$  is the overall value of competition,  $\beta$  is the competition coefficient, and  $\lambda$  is the predicted number of larvae produced per female in the absence of competition. The parameter  $\beta$  for *F. bispinosa* was significantly greater than 1 [ $\chi^2(1) = 14.55$ ,  $P < 0.001$ ], suggesting that the effects of interspecific competition on reproduction was significantly greater than the effects of intraspecific competition. The parameter  $\beta$  for *F. occidentalis* was significantly less than 1 [ $\chi^2(1) = 10.50$ ,  $P = 0.001$ ], suggesting that the effects of interspecific competition on reproduction was significantly less than the effects of intraspecific competition.



**Fig. 2.** (a) Larvae produced per *Frankliniella bispinosa* and (b) *F. occidentalis* females across various levels of intra- and interspecific densities. Data are presented by closed circles, and planes represent linear competition models fit through weighted non-linear regression. Darker shades in model planes represent increased thrips reproduction. Gridlines and opaque planes are presented to better demonstrate surface shape.

in the rearing containers and that our method of estimating original larval species ratios was appropriate.

The value and confidence intervals for  $\beta_{XY}$  indicated that the per-capita effect of interspecific competition on *F. bispinosa* reproduction was 3.89 times greater than the per-capita effect of intraspecific competition (Table 1; Fig. 2a). Furthermore, this interspecific competition was significantly greater than intraspecific competition [ $\chi^2(1) = 14.55$ ,  $P < 0.0001$ ]. In contrast, the effect of interspecific competition on *F. occidentalis* reproduction ( $\beta_{XY}$ ) was significantly weaker than the effect of intraspecific competition [ $\chi^2(1) = 10.50$ ,  $P = 0.0012$ ; Table 1; Fig. 2b].

## Discussion

The results of this study indicate that strong asymmetrical competition occurs between *F. occidentalis* and *F. bispinosa*.

Increasing densities of females of both *F. occidentalis* and *F. bispinosa* decreased the average reproductive success of *F. bispinosa* females (Table 1, Fig. 2a). However, increasing densities of female *F. bispinosa* did not negatively affect the reproductive success of *F. occidentalis* females (Table 1, Fig. 2b). These results suggest that interspecific competition from *F. bispinosa* should not limit the invasion of *F. occidentalis* in central and southern Florida, where *F. bispinosa* has been the predominant flower thrips species. However, *F. bispinosa* continues to be the predominant flower thrips in this region, except in situations with intense synthetic insecticide use (Frantz *et al.*, 1995; Hansen *et al.*, 2003; Frantz & Mellinger, 2009). Unlike most of the eastern US (Paini *et al.*, 2008), competition from an abundant native species does not appear to be a factor contributing to the biotic resistance to *F. occidentalis* in central and southern Florida.

The mechanisms that lead to the competitive superiority of *F. occidentalis* over *F. bispinosa* are unclear. Paini *et al.* (2008) found that when starting with cohorts of neonate larvae, survivorship of *F. occidentalis* decreased with increasing densities of *F. tritici*. Their results indicate that direct interactions among larvae have a greater impact on the survivorship of *F. occidentalis* than on *F. tritici*. Our experimental system allowed for interactions to occur among and within different life stages, which mimics field conditions where eggs, larvae, and adults are found within the same flowers. Therefore, interference or scramble type competitive interactions could have occurred between larvae of *F. occidentalis* and *F. bispinosa* while on pepper plants in our experimental system. Other interactions could also have occurred among adults, which could have reduced oviposition by *F. bispinosa* to a greater extent than for *F. occidentalis*. The negative competition coefficient ( $\beta_{XY}$ ) in the model measuring the effect of *F. bispinosa* on *F. occidentalis* (Table 1) suggests that *F. occidentalis* reproduction increased in the presence of *F. bispinosa*. This benefit could be because of some level of intraguild predation by *F. occidentalis* on *F. bispinosa*. *Frankliniella occidentalis* is a facultative predator of arthropod eggs (Faraji *et al.*, 2002), and it may increase its reproductive output and reduce *F. bispinosa* densities through supplemental consumption of *F. bispinosa* eggs or larvae (Trichilo & Leigh, 1988). Such intraguild predation may facilitate the spread and increase the abundance of *F. occidentalis*, but future research is necessary to determine if such predation does occur.

Behavioural differences between the two species may also affect the outcome of interspecific interactions. In particular, *F. bispinosa* adults move between flowers more often than *F. occidentalis* (Ramachandran *et al.*, 2001) and can thus colonise newly available host plant resources more rapidly than *F. occidentalis* (Ramachandran *et al.*, 2001; Reitz *et al.*, 2006). If *F. bispinosa* becomes established on hosts before *F. occidentalis*, it may gain a numerical advantage and not be as subject to competitive effects from *F. occidentalis*. In Florida, *F. bispinosa* populations are more abundant than *F. occidentalis* on some common, uncultivated hosts (Frantz *et al.*, 1996; Paini *et al.*, 2007; Northfield *et al.*, 2008), and this could further enable *F. bispinosa* to invade crop plants from surrounding vegetation before *F. occidentalis*.

Evaluating the spatiotemporal dynamics of *F. occidentalis* and *F. bispinosa* at larger spatial scales may help explain why *F. occidentalis* has not become the predominant thrips species in peninsular Florida. Kerr *et al.* (2002), using a combination of model simulations and experimental communities of the bacteria *Escherichia coli* (Migula), demonstrated that at local scales an inferior competitor can persist in the presence of superior competitors by rapidly colonising unoccupied habitats. This type of coexistence may occur quite often in cases where resources are ephemeral and habitats are patchy (Kneitel & Chase, 2004), such as those occupied by thrips (Mound, 2005).

Although this type of interaction may help explain the coexistence of the two species, it does not explain the dominance of *F. bispinosa* in Florida. Climatic conditions have been shown to affect the role of competitive interactions on species coexistence (Park, 1954; Grover, 1988), and there may be differences between experimental and field conditions that enable *F. bispinosa* to establish dominance over *F. occidentalis* in Florida. Similarly, *F. bispinosa* and *F. occidentalis* may also differ in other life history characteristics, such as generation time, that favour *F. bispinosa* dominance.

Another factor often cited as determining the success of an invader is escape from natural enemies (Strong *et al.*, 1984; Mack *et al.*, 2000; Morse & Hoddle, 2006). In Florida, however, a key native predator *Orius insidiosus* (Say) (Hemiptera: Anthocoridae) is able to suppress flower thrips populations (Funderburk *et al.*, 2000; Reitz *et al.*, 2003). Importantly, in mixed populations, *F. occidentalis* is subject to greater predation from *O. insidiosus* than is *F. bispinosa* (Reitz *et al.*, 2003, 2006). Further, in contrast to most of the eastern US, *O. insidiosus* actively feeds on thrips throughout the winter in central and southern Florida (Bottenberg *et al.*, 1999; Hansen *et al.*, 2003) and this continual predation pressure from *O. insidiosus* may limit *F. occidentalis* numbers in central and southern Florida.

Despite the presence of *F. occidentalis* in Florida for many years, *F. bispinosa* continues to be the most abundant thrips species in central and southern Florida (Childers *et al.*, 1990; Kirk, 2002; Hansen *et al.*, 2003). An exception to this pattern has been in certain agricultural fields where intense insecticide use typically eliminates *F. bispinosa* and *O. insidiosus*, which are more susceptible to insecticides than *F. occidentalis* (Hansen *et al.*, 2003; Reitz *et al.*, 2003). In such situations, the relative and absolute abundance of *F. occidentalis* increases (Frantz & Mellinger, 2009; Funderburk, 2009). These shifts in relative abundances suggest that the combination of native species such as *F. bispinosa* and *O. insidiosus* provide biotic resistance to *F. occidentalis*. Predator preferences may commonly determine the dominance of exotic species (Settle & Wilson, 1990; White *et al.*, 2006). Although it is often assumed that competitive ability of invasive species leads to their success, predator-mediated apparent competition or other complex interactions may provide biotic resistance of ecosystems against an otherwise highly successful invasive species. Therefore, it is important to evaluate different aspects of an invasive species, as a wide range of biotic and abiotic factors affect species distributions (Sakai *et al.*, 2001), and

sources of biotic resistance to a particular invasive species may vary by geographic location and community.

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