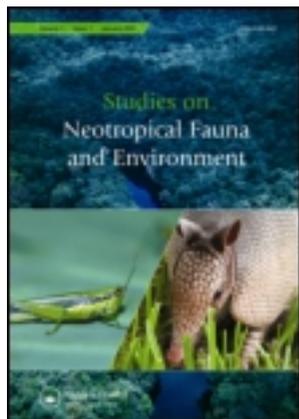


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### Flower stage and host plant preference by floral herbivore thrips (Insecta: Thysanoptera: Frankliniella) in a Brazilian savanna

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## ORIGINAL ARTICLE

### Flower stage and host plant preference by floral herbivore thrips (Insecta: Thysanoptera: *Frankliniella*) in a Brazilian savanna

Estevão Alves-Silva<sup>a</sup>, Pietro Kiyoshi Maruyama<sup>a</sup>, Adriano Cavalleri<sup>b</sup> & Kleber Del-Claro<sup>a\*</sup>

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This study shows that three *Frankliniella* (Thysanoptera) species have species-specific associations with their hosts: *F. varipes*–*Faramea cyanea* (Rubiaceae); *F. musaeperta*–*Hancornia speciosa* (Apocynaceae) and *F. fulvipes*–*Solanum lycocarpum* (Solanaceae). All thrips species had a marked preference for flowers in anthesis, as in this stage flowers provide food and protection from environment. *Frankliniella musaeperta* and *F. varipes* populations were female-biased while *F. fulvipes* was male-biased. Since many species of *Frankliniella* have economic importance, studies on the ecology of these species are essential, given the possibility of invasion of agricultural systems in the future.

**Keywords:** *Frankliniella*; *Faramea cyanea*; *Hancornia speciosa*; *Solanum lycocarpum*; plant–animal interactions; Brazil

#### Introduction

Plant–animal interactions are ubiquitous relationships in terrestrial ecosystems, and the studies of these interactions permit not only the understanding of ecological systems, but also their management and conservation (Bronstein et al. 2006; Del-Claro & Torezan-Silingardi 2009). Due to their evolutionary history, insects are the most common organisms interacting with angiosperms in a wide array of interactions that vary from total antagonistic (e.g. herbivory; Marquis et al. 2001) up to true mutualism (e.g. species-specific pollination; Moog et al. 2002). Recently, ecologists and evolutionary biologists have pointed out that plant–animal interactions occur in a community context of complex ecological interactive networks and that the understanding of who interacts with whom in these systems is key to drawing valid conclusions about evolutionary processes in community ecology (Blüthgen 2010, 2012). Because of their abundance, quick reproduction, diversity and wide distribution, insects are good models for studying plant–animal interactions (Vázquez et al. 2009; Del-Claro & Torezan-Silingardi 2012).

Thrips (Thysanoptera) are considered important insect herbivores (and agricultural pests) in the world (Kirk & Terry 2003). Generally, thrips attack young plant structures such as shoots and fresh leaves as these possess soft tissues and more free nitrogen (see

Kawai 1990; Paine 1992). There are many examples of thrips living and feeding on young leaves (Mound & Zapater 2003; De Borbón & Cardello 2006; Zamar et al. 2007; Alves-Silva 2011), but florivorous thrips are poorly examined, especially in the Neotropics (Carrizo & Klasman 2001).

Thrips are ubiquitous in flowers and inflorescences of a large number of plant species but the knowledge about their preference for different flower stages (buds, anthesis or senescent flowers), as well as thrips life stages occurring in each flower phase is very limited (Mound & Marullo 1996). In general, herbivores can feed on a variety of floral and reproductive tissues, at any period of flower maturation (McCall & Irwin 2006; Cascante-Marin et al. 2009), and thrips, due to their notable feeding flexibility (Morse & Hoddle 2006), are not an exception (see Del-Claro et al. 1997; Sakai 2001). Herbivory during flower maturation is of considerable interest for plant reproductive rates, since bud herbivory is negatively related to fruit production (Oguro & Sakai 2009).

Thrips populations are often sex-biased. Females are predominant because they live longer than males (see Ananthkrishnan 1993; Murai 2001). In addition thrips are haplodiploid (Crespi 1991), favoring a higher abundance of females (Mound & Marullo 1996). According to Milne & Walter (2000), female diet determines fecundity, thus, researchers should

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focus on both females and larvae as their abundances may be important indicators of a thrips species' success on a given host. For flower dwelling thrips this approach is very important. As food quality is related to the floral phase (open flowers possess pollen and soft tissues whereas senescent flowers do not), thrips samplings covering different flower phases may provide a reliable estimation of the quality of hosts in supporting thrips populations.

Thrips host plants are defined as the places in which they feed, lay eggs and develop (Mound & Marullo 1996). Nonetheless studies of interactions between thrips and host plants often do not consider all the life stages of thrips. Published host plant records for Thysanoptera are sometimes based only on winged adults (Tekşam & Tunç 2009; Tillekaratne et al. 2011). According to Mound & Marullo (1996), plants on which only adult thrips are found should be referred to as “finding places” given that recognition of true “host plants” requires concomitant collecting of different thrips instars together with identification of the larval stages (Monteiro 2002; see also Milne & Walter 2000; Aliakbarpour et al. 2010).

In field surveys in Brazilian savanna (*cerrado* biome), we recorded large populations of thrips in three common plants: *Hancornia speciosa* Gomez (Apocynaceae), *Faramea cyanea* Müll. Arg. (Rubiaceae) and *Solanum lycocarpum* St. Hil. (Solanaceae). The choice of representative plants such as these is preferable for the study of thrips since they may sustain different populations and facilitate comparative studies about host preference between distinct sites of the same ecosystem. Hence the aims of this study were: (1) to classify these three plants as true hosts for thrips; (2) to quantify thrips populations on different flower stages of each plant species, in order to investigate the postulation that thrips have a preference for flowers in anthesis, due to

the assumption that at this stage flowers offer more resources and protection from environment (see Sakai 2001).

## Materials and methods

### Plant species

*Hancornia speciosa* is a tree (<3 m) native to Brazil and found in abundance in *cerrado* vegetation. The tree produces latex and fleshy edible fruits known as “mangaba.” The sphingid pollinated flowers are white with a long corolla tube with apical platform, and produce a sweet scent and nectar (Darrault & Schlindwein 2005). Flowers last about five days before senescence and are  $28.8 \pm 4.1$  mm in size. Corolla diameter is  $27.7 \pm 1.9$  mm and the corolla opening measures  $1.3 \pm 0.2$  mm (mean  $\pm$  1 SD,  $n = 20$  flowers; Figure 1A). Thrips sampling in *H. speciosa* was conducted from August to November 2006, during its flowering season.

*Solanum lycocarpum*, known also as “lobeira” or “wolf fruit,” is one of the most common shrubs in pastures and disturbed areas in *cerrado*. The species is andromonoecious, with regular production of hermaphrodite and male flowers. Flowering occurs all year round. Flowers are  $20.1 \pm 1.4$  mm in size and the corolla is  $43.8 \pm 1.1$  in diameter (mean  $\pm$  1 SD,  $n = 50$  flowers; Figure 1B). Flowers have blue petals, yellow anthers, and slight odor and last about five days before senescence. The nectarless flowers offer pollen as the only reward for pollinating bees (Oliveira-Filho & Oliveira 1988). *Solanum lycocarpum* was studied during the blooming period in September 2008, at the beginning of the rainy season.

*Faramea cyanea* is a distylous tree species with reproductive individuals ranging from six to 12 m high. *Faramea cyanea* presents white, tubular actinomorphic flowers, generally tetramerous and with

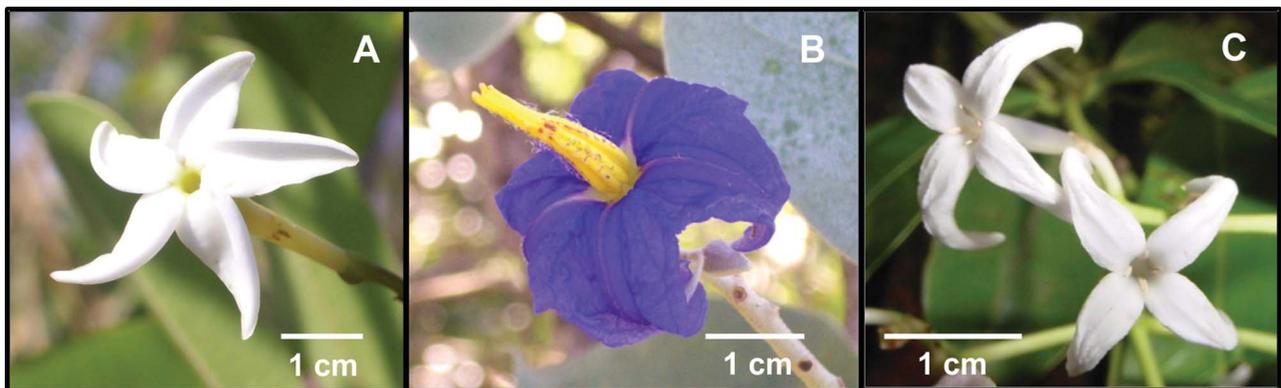


Figure 1. (Color online) Flowers of thrips host plants in a Brazilian savanna: A. *Hancornia speciosa* (Apocynaceae). B. *Solanum lycocarpum* (Solanaceae). C. *Faramea cyanea* (Rubiaceae).

sweet scent, and produces nectar for its pollinators (Figure 1C). The flowers in anthesis last only one day before falling (Maruyama et al. 2010). Flowers are  $10.6 \pm 0.2$  mm in size, the corolla is  $14 \pm 0.1$  mm in diameter and the corolla aperture is  $2.4 \pm 0.2$  mm (mean  $\pm 1$  SD,  $n = 100$  flowers). *Faramea cyanea* was studied during the flowering season in November 2006.

*Hancornia speciosa* and *S. lycocarpum* were studied at the Ecological Reserve of Clube de Caça e Pesca Itororó de Uberlândia (640 ha,  $18^{\circ}97'$  S– $48^{\circ}29'$  W; 863 m asl) in Uberlândia city, Brazil. *Faramea cyanea* is abundant in *cerrado* gallery forest associated with the Panga Ecological Station stream (400 ha,  $19^{\circ}09'$  S– $48^{\circ}23'$  W; 800 m asl), an area 30 km away from Uberlândia city. Both areas are characterized by tropical climate with well-defined dry (April to September) and wet (October to March) seasons, typical of *cerrado*.

### Samplings

The floral stage sampling for the above cited plant species was considered as follows.

- (1) Buds: the pre-anthesis stage, i.e. the period in which flowers are not open. Flower buds ranged from small buds with undeveloped petals to large buds with developed, but closed corolla, and were sampled two to three days before flower anthesis.
- (2) Open flowers: the anthesis stage, when flowers are open, mature, fresh and functional to pollinators.
- (3) Senescent: the post-anthesis phase in which flowers cease pollen and scent production (usually nectar too), pollinators are absent and flowers are dry and flaccid.

For *H. speciosa* 20 individuals were randomly chosen and open flowers were collected every seven days until a total of 20 flowers per individual were obtained ( $n = 400$  flowers in anthesis). In field and laboratory observations no thrips in buds ( $n = 112$ ) and senescent flowers ( $n = 96$ ) were noticed, so we discarded these structures in order to save time and fieldwork effort. Therefore, in *H. speciosa* only flowers in anthesis were examined. For *S. lycocarpum* 18 individuals were sampled and from each one, five flowers of each floral stage were collected, totaling 270 flowers, 90 per stage. For *Fa. cyanea* we collected 10 buds, 10 fresh flowers, and 10 recently fallen flowers (that were still whitish) from each of 20 individuals, totaling 600 flowers, 200 per stage.

Prior to samplings, flowers were placed in a plastic sack to avoid the escape of the thrips. During the study, behavioral observations of thrips on the flowers were made. In addition we dissected 23 fresh and open flowers of *H. speciosa* in the laboratory in order to examine thrips feeding behavior and whether the interior of flowers presented signs of herbivory, such as necrosis spots which indicate thrips feeding. In the laboratory, thrips from all plant species were identified, quantified and classified in relation to the developmental stage and sex.

### Statistical analyses

In all results the number of thrips per flower phase (buds, open, senescent) is presented as mean  $\pm 1$  SE. Sex ratio was tested for departures from 1:1 ratio using one sample Student's *t*-test with mean equal to one. In *Fa. cyanea* we compared the number of adult and immature thrips using a non-parametric goodness of fit chi-square test because of the small amount of individuals found and also because in many plants the presence of thrips was zero. In *H. speciosa* and *S. lycocarpum* the number of adult and immature thrips was compared using the Mann–Whitney *U* test. In *Fa. cyanea*, thrips abundance in open and senescent flowers was compared using the Mann–Whitney *U* test. In this plant the number of thrips found in buds was negligible so these data were excluded from the analysis. The Mann–Whitney *U* test was also used for *S. lycocarpum* thrips, since no thrips were found in buds. In *H. speciosa*, a comparison between flower stages was impracticable as thrips were found only in open flowers. The choice of using non-parametric statistics was based on previous Lilliefors tests ( $<0.05$  in all cases). All statistical procedures were made following Zar (1984).

### Results

#### *Faramea cyanea*

A total of 475 individuals of *Frankliniella varipes* Moulton 1933 (Figure 2A) were collected from *Fa. cyanea* flowers (Table 1). Only 11% ( $n = 48$ ) of the thrips were adults. Females were more abundant than males but sex ratio was not statistically different from 1 (Table 2). Males were smaller and paler than females, which presented dark brown color. Larvae were found together with adults, inside the corolla feeding on flower tissues, but not pollen or nectar. Pupae and prepupal stages were not found in flowers in any phase. Mating behavior was observed once (Figure 2B). After an initial and frontal antennae contact between thrips, the male approached the female

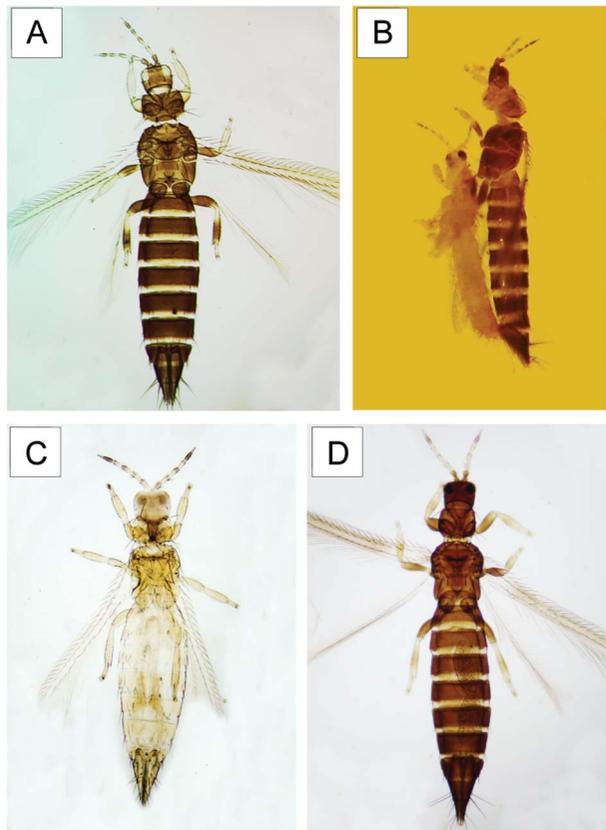


Figure 2. (Color online) Species of *Frankliniella* sampled in a Brazilian savanna: A. *Frankliniella varipes*. B. *F. varipes* in copula, the pale male being under the brownish and larger female. C. *Frankliniella musaeperda*. D. *Frankliniella fulvipes*.

Table 1. Mean abundance (individuals per flower;  $n$  = number of individuals) of thrips in flowers of their host plants in a Brazilian savanna.

Thrips species	Mean $\pm$ ISE ( $n$ )	Statistics
<i>Frankliniella varipes</i> in <i>Fareamea cyanea</i>		
Adults	0.08 $\pm$ 0.02 (48)	$\chi^2 = 302.4$
Immatures	0.72 $\pm$ 0.06 (427)	$p < 0.0001$
<i>Frankliniella musaeperda</i> in <i>Hancornia speciosa</i>		
Adults	1.46 $\pm$ 0.09 (584)	$U = 61189.0$
Immatures	0.73 $\pm$ 0.05 (293)	$p < 0.0001$
<i>Frankliniella fulvipes</i> in <i>Solanum lycocarpum</i>		
Adults	2.83 $\pm$ 0.28 (763)	$U = 23395.0$
Immatures	0.60 $\pm$ 0.07 (161)	$p < 0.0001$

Note: Sample sizes: *F. cyanea*:  $n = 600$  flowers (200 buds, 200 open flowers, 200 senescent flowers); *H. speciosa*:  $n = 400$  (open flowers); *S. lycocarpum*:  $n = 270$  (90 buds, 90 open flowers, 90 senescent flowers).

and curved his abdomen under the female's abdomen. Both thrips remained still and side by side, their bodies forming a V-shape. After approximately five minutes of mating they separated and walked away from each other. Both larvae and adults of *F. varipes*

Table 2. Mean abundance (individuals per flower;  $n$  = number of individuals) of males and females of each thrips species and their sex ratio analysis.

Thrips species	Mean $\pm$ ISE ( $n$ )	Sex ratio
<i>Frankliniella varipes</i>		
Males	0.03 $\pm$ 0.01 (17)	$t = -1.198$
Females	0.05 $\pm$ 0.01 (31)	$p = 0.1241$
<i>Frankliniella musaeperda</i>		
Males	0.65 $\pm$ 0.05 (261)	$t = 2.682$
Females	0.81 $\pm$ 0.06 (323)	$p < 0.01$
<i>Frankliniella fulvipes</i>		
Males	1.57 $\pm$ 0.16 (423)	$t = -16.8732$
Females	1.26 $\pm$ 0.15 (340)	$p < 0.0001$

Notes: In *F. varipes*, there was no statistical difference in the number of males and females. *F. musaeperda* population was biased towards females and *F. fulvipes* was biased towards males.

presented high mobility, since they were observed entering and leaving the interior of the corolla several times. This occurred frequently when the flowers fell to the ground. Then, immatures usually abandoned the flowers and went to the leaf litter whereas adults flew away. *Frankliniella varipes* was found mainly in open flowers ( $1.41 \pm 0.12$ ,  $n = 281$ ) followed by senescent flowers ( $0.92 \pm 0.11$ ,  $n = 184$ ). Thrips occurrence in buds was small ( $n = 10$  thrips in 200 buds;  $0.05 \pm 0.03$ ); therefore these data were excluded from the subsequent analyses. The Mann–Whitney  $U$  test revealed that *F. varipes* was significantly more abundant in open flowers ( $U_{200,200} = 16,450$ ;  $p < 0.001$ ).

### *Hancornia speciosa*

In *H. speciosa* we found 877 ( $2.19 \pm 0.11$  thrips per flower) individuals of *F. musaeperda* Hood 1952 (Figure 2C), comprising 323 females, 261 males and 293 larvae (Tables 1 and 2), all of them in open flowers only. The Mann–Whitey  $U$  test showed a significant difference in the number of adults and larvae (Table 1). We also recorded statistical differences in the sex ratios with approximately 1.23 females per male of *F. musaeperda* (Table 2). Neither pupae nor prepupae were found, only larvae. *Frankliniella musaeperda* individuals were very mobile and were observed flying and migrating from flowers all day long. Thrips were very susceptible to perturbations and, at the least disturbance, leaped from flowers, flew away or entered the corolla. Flowers dissected in the laboratory did not show any damage by herbivory inside of the corolla, where thrips were observed to insert their stylets to feed on flower tissues. Feeding behavior was characterized by up-and-down movements of the head. We also observed thrips sucking up minute droplets which might be nectar or rain drops. The thrips did not feed on pollen or nectar.

### *Solanum lycocarpum*

In *S. lycocarpum* we found the species *F. fulvipes* Bagnall 1919 (Figure 2D) in open ( $8.22 \pm 0.72$ ;  $n = 740$  individuals in 90 open flowers) and senescent flowers ( $2.04 \pm 0.14$ ;  $n = 184$  individuals in 90 senescent flowers) and the Mann–Whitney *U* test revealed that thrips were significantly more frequent in open flowers ( $U_{90,90} = 764.5$ ;  $p < 0.0001$ ) where they fed on pollen. No thrips were found in *S. lycocarpum* flower buds. The 924 individuals comprised 423 males, 340 females and 161 immatures (Tables 1 and 2). Most of the time thrips stayed concealed at the base of the anthers and managed to gain access to the inside of the pollen sacs through holes made by beetles on anthers. *Frankliniella fulvipes* males are pale yellow while females are dark brown. The Mann–Whitney *U* test revealed significantly more adults than immatures (Table 1). Sex ratio showed 1.49 males per female (Table 2). Similarly to *Fa. cyanea* and *H. speciosa*, no pupae or prepupae were found.

### Discussion

According to the criteria of Mound & Marullo (1996), our results classify *Fa. cyanea* as a host plant for *F. varipes*, *H. speciosa* as a host for *F. musaeparda* and *S. lycocarpum* as a host for *F. fulvipes*, since adult thrips were found together with immatures in the same microhabitat (see also Milne & Walter 2000). These are the first records of *Frankliniella* species inhabiting the above-mentioned host plants.

### Thrips sex ratios

The larger number of *F. musaeparda* females found in this study is not uncommon as many natural thrips populations predominantly consist of females (Mound & Terry 2001; Reitz 2002). Higgins (1992) observed that sex ratio was influenced by population density, where females were most common in high densities. On the other hand Crespi (1988) showed that female or male production depended on low and high food availability, respectively. Thus, there appears to be a density-dependent mechanism determining thrips sex ratios, presumably intermingled with the availability of food resources (see Rosenheim et al. 1990). In our study the only flowers which presented food resources even in senescence were those of *S. lycocarpum* (i.e. pollen) and this might explain why the sex ratio of its associated thrips, *F. fulvipes*, was biased toward males. The other thrips species did not feed on pollen but rather on flower tissues, and as their host flowers became dry and wilted, thrips were no longer observed feeding on the flower, suggesting that in *H. speciosa* and *Fa. cyanea* food availability is limited

to the period of anthesis. The presumed relationship between food resources and sex ratios is a promising approach that needs to be examined carefully in upcoming studies, taking into account not only food quality, but also plant chemistry and abiotic factors that are supposed to influence thrips performance, host choices and oviposition sites (Ananthakrishnan 1993; Reitz 2002; Morse & Hoddle 2006).

### Thrips and open flowers

Thrips preference for flowers in anthesis was evident in the three plant species, indicating that the other flower stages were not suitable for thrips maintenance, probably because of the lack of food resources and the changes in flower structure and physiology. These changes include a clear loss of vigor in senescent flowers as well as the end of scent liberation. Many studies showed the role of odor volatiles, particularly sweet scented, in attracting thrips (Jürgens et al. 2000; Koschier et al. 2000). In this sense we may assume that one factor accounting for thrips abandoning flowers was the lack of scent. The other factor most likely was the unavailability of pollen (in *S. lycocarpum*) and edible flower tissues (in *H. speciosa* and *Fa. cyanea*), which are main resources for flower-feeding thrips (see Momose et al. 1998; Sakai 2001).

Besides supplying food resources, flowers also provide protection from harsh environmental conditions, e.g. heavy rains and temperatures above 30°C, which are frequent in the Brazilian savanna during the wet season. The cuticula of thrips is very thin and desiccation may impose a serious problem for species living at high temperatures. In this context, tubular flowers like *Fa. cyanea* and *H. speciosa* or those bearing chambers appear to be better suited for the thrips' survival (Del-Claro et al. 1997). In the open flowers of *S. lycocarpum*, protection is achieved by thrips living among the anthers and at the base of the flowers. This behavior was also observed in thrips living in the Australian Cycad, *Macrozamia macdonnellii* (F. Muell.) A. DC. (Cycadales), where they moved into the center of the cones to avoid the heat and intense solar radiation of the day (Mound & Terry 2001).

The high numbers of larvae recorded on the three plant species indicate that these hosts are important resources for thrips reproduction. *Solanum lycocarpum* blooms the whole year round, providing a permanent and predictable microhabitat for *F. fulvipes*. In contrast, the relationships of thrips with *Fa. cyanea* and *H. speciosa* show reproductive behavior associated with the flowering period of these plants at the beginning of the cerrado rainy season, in October. The lack of pupae and prepupae in all flower stages and plant species is likely explained by the short time span of flowers on the trees. In *Fa. cyanea*, for instance, flowers drop

after just one day, so there is not enough time for the development of thrips to the subsequent stages. That could also explain why neither pupae nor prepupae were found in fallen flowers, as would be expected if thrips used these flowers to pupate. As the flowers fall to the ground, the mobile larvae move to the soil where they complete their development. This is a widespread behavior amongst flower-feeding Thysanoptera, where pupae are often not found together with larvae and adults in flowers, but complete their metamorphosis in the soil (Mound & Marullo 1996). Similar to our findings in *Fa. cyanea*, large numbers of adult thrips were found in the fallen flowers of Bignoniaceae in Neotropical forests. The adult thrips flew back into the tree canopy to oviposit later in the day (Mound 2002).

According to Mound (2005), neither *Fa. cyanea* nor *H. speciosa* flowers present ideal conditions for thrips occurrence or reproduction, because their flowers also attract a wide range of visitors, e.g. bees, butterflies and moths (Darrault & Schlindwein 2005; Maruyama et al. 2010) which compete with the thrips for floral resources. Despite that, we found a great abundance of thrips in these flowers, but no apparent damage due to herbivory was noticed on flowers, especially in *H. speciosa* where a large population of thrips fed on flower tissues. So their presence in flowers is not likely to influence visually guided pollinators (see Malo et al. 2001; Oguro & Sakai 2009).

Natural hosts of *Frankliniella* are seldom examined, despite their importance in serving as natural reservoirs for pest species (Carrizo 2002). In Brazilian savanna this situation deserves attention, since large areas are being converted to crop plantations (Silva & Bates 2002; Klink & Machado 2005). These crops are usually surrounded by a matrix of natural vegetation bearing many natural thrips hosts (see Alves-Silva & Del-Claro 2010). According to Carrizo (2002) thrips find physical refuge and breeding sites on plants growing around crops, allowing for high invasions whenever crop season starts. The migration of thrips from natural hosts to crops and vice versa has been a major issue in studies of *Frankliniella*, which are crop pests (see Chellemi et al. 1994; Carrizo 1998). However, it is still unknown whether thrips have preferences for natural hosts over crops. If so, this could be an alternative to the use of pesticides on plantations, since surrounding vegetation would suffice to decrease thrips population in crops.

Since many species of *Frankliniella* have economic importance, studies on the ecology of these species are essential, given the possibility of invasion of agricultural systems in the future. Studies regarding thrips ecology, biology and relationships with host plants and environment have increased substantially in the past few years, principally in the Neotropics

(Del-Claro & Mound 1996; Cavalleri et al. 2010; Alves-Silva & Del-Claro 2011). Further studies will aim at identifying thrips interactions with other plants and verifying how these insects use different plant species throughout the year.

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