Association of Pepper with Arbuscular Mycorrhizal Fungi Influences Populations of the Herbivore *Frankliniella occidentalis* (Thysanoptera: Thripidae)[1]

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Abstract The symbiosis of plants with arbuscular mycorrhizal fungi can improve crop growth by enhancing nutrient uptake and by increasing plant tolerance to certain pests. Pest populations also can be affected, but the effects of mycorrhizal colonization of plant hosts on species of thrips are unknown. We inoculated 2-week-old bell pepper seedling roots with a commercial mycorrhizal mixture of *Glomus* species (Glomales: Zygomycotina) and evaluated the effects 8 wks later on the bell pepper pest, western flower thrips (*Frankliniella occidentalis* (Pergande)). Females that were 10-days-old after adult emergence significantly preferred plants inoculated with arbuscular mycorrhizae compared with noninoculated plants in a laboratory choice experiment. Their numbers were greater on inoculated plants 48 h after release into cages containing inoculated and noninoculated plants. A no-choice laboratory experiment compared performance of *F. occidentalis* on noninoculated and inoculated bell pepper plants. Females that were 10-days-old after adult emergence were released into cages containing individual plants, and there were significantly greater total thrips (larvae, pupae, and adults) on treated plants. Further testing over a range of plant host fertility levels is needed to evaluate the potential for increased pest damage from *F. occidentalis* on crops growing in mutualistic symbiosis with arbuscular mycorrhizal fungi. Additional interactions with other microorganisms and natural enemies are possible under field conditions.

Key Words *Frankliniella occidentalis*, arbuscular mycorrhizal fungi, *Capsicum annuum*, trophic interactions

Arbuscular mycorrhizal (AM) fungi (Glomales: Zygomycotina) are found in mutualistic symbiosis with plants (Koide and Mosse 2004, Schüssler et al. 2001, Wang and Qiu 2006). The relationship has been shown to enhance the plant's ability to absorb nutrients, although the increased uptake was often only apparent in plants growing in nutrient-poor soil (Borowicz 1997, Gange et al. 1999, Pineda et al. 2010). These fungi improved the ability of plants to survive droughts, excessive salinity, and excessive heavy metals (Auge et al. 1994, Kaya et al. 2009). Increased nutrient uptake due to AM fungal colonization increased foliar biomass (Gange and Smith 2005, Hempel et al. 2009); plant stature (Gange et al. 2005); flower number, petal number, and flower size

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(Gange and Smith 2005, Gange et al. 2005); and seed size, abundance, and viability (Gange and Smith 2005).

In addition to the enhanced nutrient uptake and growth provided to plants, AM fungal colonization sometimes increased the plant's resistance to pests (Gange and West 1994, Pineda et al. 2010). Enhanced nutrient and water uptake led to improved nutrition and greater tolerance of the plant to pest injury (Pineda et al. 2010). Symbiosis with AM fungi enhanced the ability of the plant to regrow tissue after herbivory, and the fungi primed the plant's defense genes to react to attack, enhancing the induced systemic resistance (Pineda et al. 2010). Carbon-based defense compounds such as aucubin and catalpol were increased (Gange and West 1994). The carbon-to-nitrogen ratio was increased (Goverde et al. 2000). Increased abundance of iridoid glycosides increased defense against immediate threats (Bennett et al. 2009). Despite these various enhanced defenses against herbivory, the responses of herbivores to plants with these relationships were varied. Additionally, different species and combinations of species of these fungi had different effects on each species of plant and insect involved in the multitrophic interaction suggesting it was not just the presence, but the identity of the fungus present, which determined the resulting effect and whether it was positive or negative (Goverde et al. 2000, Gange et al. 2005, Pineda et al. 2010).

Mycorrhizal colonization of plants tended to have a negative effect on the performance of generalist chewing insects and a positive effect on the performance of specialist chewing and sap-sucking insects (Gange and West 1994, Gange et al. 2005, Pineda et al. 2010). The larvae of the lepidopteran *Arctia caja* (L.) fed less and had decreased growth on *Plantago lanceolata* L. grown with colonies of AM fungi; whereas, the aphids *Myzus persicae* (Sulzer) and *M. ascalonicus* Doncaster experienced greater teneral adult weight, greater fecundity, and a greater number of mature embryos when reared on the same plants grown with AM fungi (Gange and West 1994, Gange et al. 1999). The larvae of the lepidopteran *Polyommatus icarus* (Rottemburg) had higher survival and greater weights when reared on plants grown with AM fungi versus control plants (Goverde et al. 2000). The coleopteran *Epilachna varivestis* Mulsant experienced greater fitness (pupation rate, mass, and survival) feeding on plants grown with AM fungi (Borowicz 1997), and a few species of leaf-mining and seed-feeding flies reached greater infestation levels on mycorrhizal plants (Gange et al. 2005). An increase in the sugar content and secretion rate of nectar on mycorrhizal plants attracted more pollinators, specifically from the orders Diptera and Hymenoptera (Gange and Smith 2005).

Interactions of other organisms and varying nutrient levels can affect the population biology of herbivores feeding on mycorrhizal plants. The development of *M. persicae* was delayed when reared on mycorrhizal plants or nonmycorrhizal plants growing in soil with earthworms; however, aphids experienced accelerated development when feeding on mycorrhizal plants growing in soil with earthworms (Wurst et al. 2004). Mycorrhizal fungal colonization of the plant host enhanced population reduction of the aphid *Rhopalosiphum padi* (L.) by the braconid *Aphidius rhopalosiphi* De Stefani Peres by increasing eclosion rate and decreasing developmental time of the parasitoid (Hempel et al. 2009). Mycorrhizal colonization of the plant host had a positive effect on the life history traits of *M. persicae* and *E. varivestis*, but this effect was seen only at low and medium levels of phosphorous (Borowicz 1997, Gange et al. 1999).

The effects on Thysanoptera of the symbiosis of plants with AM fungi are not much studied. One study focused on management efforts for *Megalurothrips sjostedti*

(Trybom) on *Vigna unguiculata* L. (Walp.) using combinations of AM fungi, the fungal biocontrol agent *Metarhizium anisopliae* (Metchnikoff), and rhizobia (Ngakou et al. 2008). This combination was effective in reducing the numbers of adult and larval thrips in a field setting (Ngakou et al. 2008). The study did not test the effect on thrips numbers of mycorrhizal versus nonmycorrhizal plants.

The western flower thrips, *Frankliniella occidentalis* (Pergande), spread from the southwestern United States to become a cosmopolitan pest (Kirk and Terry 2003). Damage can result from feeding and oviposition injuries and through transmission of tospoviruses to plants. It is the major vector worldwide of *Tomato spotted wilt virus* as well as numerous other tospoviruses (Pappu et al. 2009, Webster et al. 2011). In addition to being notoriously difficult to control with pesticides due to many factors (Demirozer et al. 2012), *F. occidentalis* prefers and more offspring are produced on plants that are fertilized with greater than the recommended amount of nitrogen (Brodbeck et al. 2001, Baez et al. 2011). We conducted laboratory experiments to evaluate the effects on *F. occidentalis* of pepper (*Capsicum annuum* L.) inoculated with a commercial formulation of AM fungi. A choice experiment was conducted to determine the preferences of adult females for inoculated and noninoculated bell pepper. A no-choice experiment was conducted to determine the effects of inoculating the pepper host on fecundity/survival of *F. occidentalis*.

Materials and Method

Plant Propagation. Bell peppers 'Aristotle' were germinated in seedling trays containing a commercial growing mixture (The Scotts Miracle-Gro® Growing Mix, The Scott's Miracle-Grow Company, Marysville, OH) at 25 ± 1°C, 50 - 80% relative humidity, and 16: 8 [L: D] photophase to scotophase day. Two-week-old seedling peppers were transplanted into 11.5-cm-high by 11.5-cm-diameter pots containing 430 g of growing medium comprised of 2 parts *Pinus* species bark (Graco Fertilizer Co., Cairo, GA), one part peat moss (Lambert Peat Moss, Inc., Riviere-Ouelle, Quebec, Canada), and 1 part sand. Fertilizers added to the growing medium included P (Royster-Clark Triple Super Phosphate, 0 - 46 - 0, Agrium Inc., Alberto, Canada) at 350ppm and K (uriate of potash, 0 - 0-60, Agrium, Inc.) at 250 ppm. Micronutrients were added by applying Micromax® Micronutrients (The Scott's Miracle-Grow Company) at 0.9 g/m^3 of growing media. In the choice experiment to evaluate preference, 150, 175, or 200 ppm N (ammonium nitrate, 34 - 0-0, Agri-AFC, LLC, Decatur, AL) were added, as appropriate to low, medium, and high N pots, respectively. All pots in the no-choice experiment to determine performance received 175 ppm N.

A mixture of AM fungi (MycoApply® Ultrafine Endo, Mycorrhizal Applications, Inc., Grants Pass, OR) comprised of *Glomus intraradices, G. mosseae, G. aggregatum,* and *G. etunicatum*, each at 55 propagules per g, were used in these experiments. For each plant in treatments receiving AM fungi, 2 g of the fungus mixture was applied directly to the roots just prior to transplanting into pots.

***Frankliniella occidentalis* colony.** Thrips for the colony were collected in March 2011 from *Allium cepa* L. growing at the North Florida Research and Education Center, University of Florida in Quincy (N30°32'30" W84°35'30"). Rugman-Jones et al. (2010) found that 2 sympatric cryptic species of *F. occidentalis* occur in California and in other parts of the world where they are invasive. Our population was tested in the above-mentioned study, and they reported it as the 'greenhouse' species. Thrips were kept in containers that were 14 cm on each side and 3 cm high. Containers were supplied with *Phaseolus vulgaris* L. pods and *Typha latifolia* L. pollen. Colonies were maintained at 25 ± 1°C, 50 - 80% RH, and 16: 8 [L: D] photophase to scotophase day (Tsai et al. 1996). New containers were established weekly for about 9 months to provide sufficient adults for the colony and the experiments.

Choice experiment to evaluate preference. The experimental design was a randomized complete block. Treatments were plants inoculated with AM fungi and noninoculated plants. Each experimental unit consisted of 3 pots of low (150 ppm), medium (175 ppm), and high (200 ppm) N. Individual cages served as blocks. An experimental unit of each treatment (1 pot each of low, medium, and high N) was evenly spaced along the long side of a 52-cm × 30-cm wide × 45-cm high Plexiglas rectangular cage. Each cage had three 15-cm-diameter holes covered with thrips-proof screen (Green-Tek, Inc., Janesville, WI) to prevent thrips escape. Twenty five, 10-day-old adult female thrips that were denied food for 1 h were released into each cage containing the 6 plants. Cages were kept in a climate-controlled room at 25 ± 1°C, 50 - 80% RH, and 16: 8 photophase to scotophase day. There were 16 replications (blocks).

After 48 h, flowers from each plant were placed into a vial containing 70% ethyl alcohol. Stems and leaves were rinsed in a 1% soap solution that was poured through a sieve. The thrips were rinsed from the sieve into a Petri dish with 70% ethyl alcohol. Thrips from all samples were counted at 40X magnification.

Analysis of variance was used to evaluate the main effects of AM fungi treatment and block on the log10-transformed (x + 0.5) number of thrips per plant (PROC ANOVA option, SAS Institute 2004). Data were pooled over nitrogen level in this analysis. The treatment x block interaction was used as the error term.

No-Choice experiment to determine performance. Treatments were AM fungi-inoculated and noninoculated 10-week-old pepper plants. Individual plants were covered with a 15.5-cm-diameter × 36.5-cm-high Plexiglas cylinder that was covered at the top with thrips-proof screen, and each cylinder had two 2-cm-diameter ventilation holes covered with thrips-proof screen. Experimental design was completely random. There were 33 replications of each treatment.

Five, 10-day-old female thrips were released into each cage. Cages were kept in a climate-controlled room at 25 ± 1°C, 50 - 80% RH, and 16: 8 scotophase to photophase day. At this temperature, thrips develop from egg to adult in about 12 days (Reitz 2008). Therefore, plants after 12 days were destructively sampled as previously described, and the number of adults, pupae, and larvae determined at 40X magnification.

The effects of treatment on log10-transformed (x + 0.5) males, females, larvae, pupae, and total of these life stages were analyzed using *t*-tests (PROC TTEST option, SAS Institute 2004).

Results

The number of recaptured thrips in the choice experiment after 48 h was about 80%. These recaptured adult females significantly preferred pepper plants inoculated with AM fungi ($F = 9.0$; df = 1, 15; $P = 0.004$) with no significant effect of block in the analysis of variance ($F = 0.5$; df = 15, 15; $P = 0.94$). There were 1.72 times more thrips found on plants inoculated with AM fungi than on noninoculated plants (Fig. 1).

Twelve days is sufficient for the thrips to develop from egg to adult, and there were male and female adults recovered in the no-choice experiment to evaluate AM fungi inoculation of pepper on *F. occidentalis* performance (Fig. 2). It is possible that some

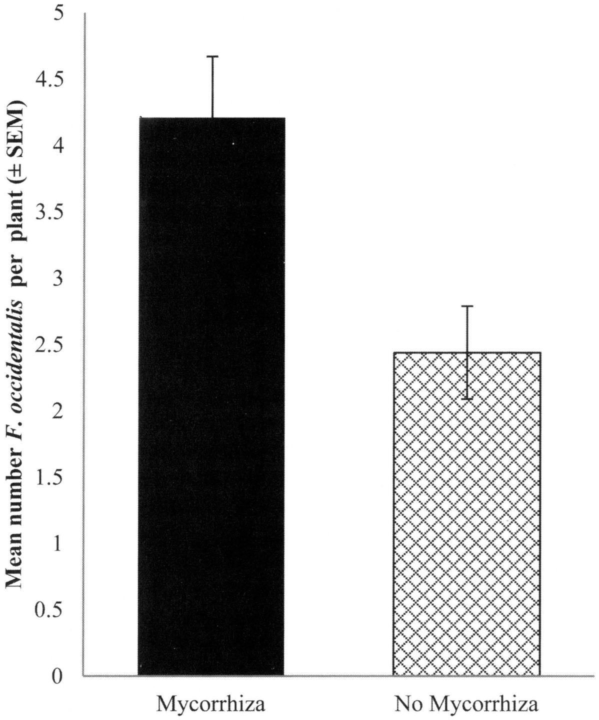

Fig. 1. The mean number (± SEM) of female *Frankliniella occidentalis* per pepper plant after 48 h in a choice test in which 25 10-day-old adults were released into individual cages containing one experimental unit of plants inoculated with arbuscular mycorrhizae and one experimental unit of noninoculated plants. Each experimental unit consisted of 3 pepper plants grown at low, medium, and high nitrogen. Data was pooled across the 3 plants of each experimental unit and analyzed using analysis of variance for a randomized complete block with each cage (n = 16) serving as a block, and means are significantly different at P = 0.004.

of the adults were the original 10-day-old females released into the cages. Reitz (2008) reported a mortality of about 50% for 22-day-old *F. occidentalis* females. Assuming 50% mortality in the no-choice experiment, about 28% of the recovered females were originally released. There were no significant differences in the number of females recovered in inoculated and noninoculated pepper (t = 0.62, df = 64, P = 0.54). Females do not need to mate to reproduce, as unfertilized eggs develop into haploid males and fertilized eggs develop into diploid females (Moritz 1997). About 23% of the recovered adults were male. Significantly more males were recovered in inoculated versus noninoculated pepper (t = 2.79, df = 62, P = 0.007).

About 73% of the thrips recovered in the no-choice experiment were larvae (Fig. 2). Significantly more larvae were recovered in AM fungi-inoculated versus noninoculated pepper plants (t = 2.0, df = 62, P = 0.05). There were no significant differences

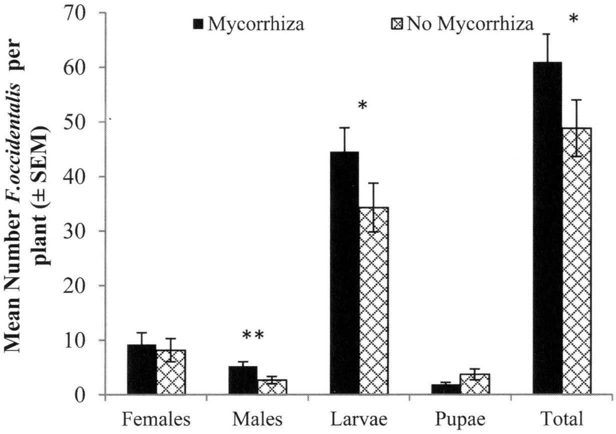

Fig. 2. The mean number (± SEM) of adult female, adult male, larvae, pupae, and total *Frankliniella occidentalis* per pepper plant in the no-choice experiment 12 days after 5, 10-d-old adult females were released into cages containing individual pepper plants grown without or with arbuscular mycorrhizae ($n = 33$). * and ** represent significant differences according to *t*-tests of $P < 0.05$ and 0.01, respectively.

in the number of pupae in inoculated and noninoculated pepper ($t = -1.1$, df = 62, $P = 0.26$). Overall, there were 1.25 times more thrips of all stages recovered from AM fungi-inoculated pepper plants, and the difference versus noninoculated pepper was significant ($t = 2.0$, df = 62, $P = 0.05$).

Discussion

More thrips were found on plants inoculated with AM fungi than on noninoculated plants in both the choice and no-choice experiments. Whether the choice was based on visual or chemical cues is unknown, but it may have been a combination of both as the thrips had 2 d to assess the plants visually and chemically for suitability to feeding and ovipositing. Previous studies using different methods found similar results of attraction to plants growing in symbiosis with AM fungi including increased damage by leafminers, increased attack rates by seed-feeding insects, and increased visits by pollinators (Gange et al. 2005, Gange and Smith 2005).

Terry (1997) reviewed the scientific literature concerning host selection and acceptance by *F. occidentalis*. *Frankliniella occidentalis* adults locate hosts using color, shape, size, and volatiles. Prealighting adults of both sexes are attracted to green-yellow wavelengths for long-range orientation, and they use color contrasts within plants to find flowers, such as the white flowers of pepper. Once a potential host is contacted, odor, tactile, and gustatory cues predominate in postalighting host acceptance. Females are able to choose oviposition sites that optimize reproductive success (Terry and Kelly 1993, Rhainds et al. 2005), avoiding plants with defensive compounds or nutritional levels detrimental to the development of their offspring. Plant chemistry and morphology parameters were not quantified in the choice experiment;

however, the plants inoculated with AM fungi were visibly taller and leaves displayed a darker green color than noninoculated plants of the same nitrogen level. Changes in plant morphology including increases in plant biomass, flower size, and flower numbers are typical for plants growing in symbiosis with mycorrhizae (Gange and West 1994, Gange and Smith 2005, Gange et al. 2005, Hempel et al. 2009).

Plants growing in mutualistic symbiosis with AM fungi frequently have increased nutrient uptake (Gange et al. 1999, Goverde et al. 2000, Wurst et al. 2004, Gange et al. 2005). Increased nitrogen uptake can increase the aromatic amino acid concentrations in plants, and *F. occidentalis* females are known to prefer plants with high aromatic amino acid concentrations (Brodbeck et al. 2001). Arbuscular mycorrhizal fungi also enhance the uptake of phosphorous in pepper plants (Kaya et al. 2009), and *F. occidentalis* populations have been found to increase with increasing levels of phosphorous in *Impatiens walleriana* (Chen et al. 2004).

Increased numbers of *F. occidentalis* as a result of increased nitrogen fertilization were reported for several crop species including pepper (Schuch et al. 1998, Brodbeck et al. 2001, Davies et al. 2005, Baez et al. 2011), although one study showed no influence of nitrogen on densities in tomato (Reitz 2002). The experimental unit in the choice experiment consisted of 3 pepper plants grown at 3 different nitrogen rates from low to high. This unit was chosen to mitigate any potential interactions between AM fungi, nitrogen, and thrips. Herbivores may be most attracted to moderately stressed plants (English-Loeb 1989). Highly stressed plants may be unattractive to herbivores either because of low nutrient levels or due to high levels of defense by carbon-based compounds (Bryant et al. 1983). Alternately, unstressed plants may be defended by nitrogen-based compounds, or they may contain complex proteins that are not easily metabolized by the herbivores (Mattson and Haack 1987), although total nitrogen content can actually decrease at high nitrogen fertility levels (Whitehead 1995). Moderately stressed plants may allocate nutrients to maintenance rather than defense (Bazzaz et al. 1987).

The no-choice experiment showed that there was a physiological benefit to feeding and reproducing on pepper plants inoculated with AM fungi. The greater numbers of *F. occidentalis* on AM treated plants was the result of higher fecundity, higher survival, or both higher fecundity and higher survival. The symbiosis of plant hosts and AM fungi has been shown to increase the survival and fecundity of some insect herbivores (Gange and West 1994, Borowicz 1997, Gange et al. 1999, Goverde et al. 2000, Wurst et al. 2004). Symbiosis with AM fungi has been shown to increase nutrient uptake of pepper (Kaya et al. 2009), and the AM fungi-inoculated pepper may have been more nutritious. Correlations with essential amino acids strongly suggest a role for the compounds in explaining fertilization effects (Schuch et al. 1998, Brodbeck et al. 2001, Davies et al. 2005, Baez et al. 2011), but other factors such as flower number and total flower nitrogen may be important. Plants growing in symbiosis with AM fungi can have larger flowers, more flowers, more pollen, and enhanced nectar quality (Gange et al. 2005, Gange and Smith 2005). Pollen enhances fecundity, development rate, and higher population growth in *F. occidentalis* (Trichilo and Leigh 1988, de Jager et al. 1993, Gerin et al. 1999, Hulshof et al. 2003, Zhi et al. 2005).

Other studies have found that plant hosts growing in symbiosis with AM fungi have negative effects on survival and fecundity of insect herbivores that was attributed to increased defensive compounds and plant resistance (Gange and West 1994, Wamberg et al. 2003, Ngakou et al. 2008). There was no indication in the no-choice experiment that inoculation with AM fungi increased defensive compounds that in turn negatively affected *F. occidentalis*. The mechanisms for enhanced performance could have been the result of greater nutrition, fewer defensive compounds, or both.

Frankliniella occidentalis population attributes of rapid colonization, high fecundity, and a short generation time results in a high potential for damage in pepper and other crops (Reitz 2008, Demirozer et al. 2012). Our results suggest that the damage potential may be increased for plants growing in symbiosis with AM fungi. However, additional research is needed to understand the mechanisms by which an association of plants with AM fungi affects thrips populations. The enhanced preference of *F. occidentalis* females for pepper inoculated with AM fungi and the greater fecundity and/or survival of *F. occidentalis* on these plants could be mediated by interactions with fertility level of the plants (e.g., Borowicz 1997, Gange et al. 1999), and such potential effects on plant nutrition and defense need to be understood. Our results also suggest that damage due to thrips-vectored tospoviruses may be increased for plants growing in symbiosis with AM fungi. Incidences of plants infected with *Tomato spotted wilt virus* previously were increased as a result of increased nitrogen fertility (Stavisky et al. 2002). Interactions with other organisms and natural enemies (e.g., Wurst et al. 2004, Hempel et al. 2009) as has been shown for other insect species also are possible, thereby influencing the effects of symbiosis of plants with AM fungi on preference and performance of *F. occidentalis* populations under field conditions.

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