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ORIGINAL PAPER

Tomato belowground–aboveground interactions: *Rhizophagus irregularis* affects foraging behavior and life history traits of the predator *Macrolophus pygmaeus* (Hemiptera: Miridae)

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Abstract In recent years, studies on arbuscular mycorrhizal fungi (AMF) have been revealing that the belowground symbiosis can influence the performance of aboveground herbivores and their natural enemies through its effects on the host plant. In this study, we tested whether the colonization of tomato plants by the arbuscular mycorrhizal fungus *Rhizophagus irregularis* (Syn. *Glomus intraradices* Schenk and Smith) (Glomeromycota: Glomeraceae) affects the performance of the zoophytophagous mirid bug *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae). Mycorrhizal colonization in tomato plants positively influenced the predator host-plant acceptance for feeding and oviposition, as well as nymphal survival and female weight. We hypothesize that AMF can modify mirid bug foraging behavior and performance.

Keywords Arbuscular mycorrhizal fungi · Host selection · Mirid bug · Performance · *Solanum lycopersicum* · Zoophytophagy

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Introduction

Arbuscular mycorrhizal fungi (AMF) are soil-borne fungi establishing symbiosis with more than 80 % of terrestrial plants including important crop species. This mutualistic interaction is known to promote plant growth and helps plants to cope with biotic and abiotic stress (Smith and Read 2008). For this reason, AMF have been broadly used in agriculture as plant growth-promoting fungi and as plant protection agents against plant pathogens (Azcón-Aguilar and Barea 1997). Besides improving plant nutrition and competition, experimental evidence supports a major role of plant defenses in plant protection mediated by AMF (Nogales et al. 2009; Pozo et al. 2015). During mycorrhiza establishment, modulation of plant defense responses occurs and a mild, but effective activation of the plant immune responses seems to occur, not only locally but also systemically (Pozo et al. 2002). This activation leads to a primed state of the plant that allows a more efficient activation of defense mechanisms in response to attack by potential enemies (herbivore insects and/or phytopathogens) (Jung et al. 2012).

AMF are also recognized by their ability to mediate below- and aboveground plant-arthropod interactions in natural and agricultural ecosystems, influencing herbivores, their natural enemies and pollinators in a positive or in a negative way (Wolfe et al. 2005; Gehring and Bennett 2009). AMF effects on aboveground organisms vary with the specific fungal isolate, the host plant cultivar, environmental AMF growing conditions and insects feeding habits (Goverde et al. 2000; Leitner et al. 2010; Estaún et al. 2010). Concerning those feeding habits, certain patterns have been reported: Leaf-chewing and leaf-mining herbivores would be adversely affected by AMF colonization of their host plants, whereas those that are phloem

feeders and cell feeders (e.g., aphids and spider mites) would be positively or not influenced by the symbiosis. These contrasting effects are associated with a higher nutrient availability and growth of the mycorrhizal plant and/or based on the activation of the plant defense system (Vannette and Hunter 2009). A better plant quality is commonly related with the enhanced performance of phloem feeders (Gange et al. 1999). By contrast, AMF improvement in the plant nutrient uptake allows plants to increase the production of diverse chemical defense metabolites, thereby increasing plant resistance principally to leaf chewer herbivores (Roger et al. 2013).

In relation to benefits, as a general pattern, the positive roles of arthropods on plants are favored in mycorrhizal plants. For example, AMF positively influence visitation rates of pollinating insects (Wolfe et al. 2005). Similarly, changes in the volatile profile of mycorrhizal plants under attack by herbivores result in a higher attraction of parasitoids and predators that may help the plant to control the pest (Hempel et al. 2009; Hoffmann et al. 2011a, b; Schausberger et al. 2012; Babikova et al. 2013). Concerning tomato, the only investigation reported on this matter was published by Guerrieri et al. (2004), who showed that *Glomus mosseae* Nicol and Gerd (Gerdemann and Trappe) enhances the attractiveness of the aphid parasitoid wasp *Aphidius ervi* Haliday (Hymenoptera: Braconidae) toward tomato plants colonized by this mycorrhizal fungus.

The polyphagous predator *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae) is one of the most effective biocontrol agents for the protection of greenhouse and field tomato crops in Europe (Alomar et al. 2002; Castañé et al. 2004; Perdikis et al. 2008; Arnó et al. 2009). As other predatory mirids, *M. pygmaeus* has zoophytophagous habits and is strongly linked to the host plant both for feeding and oviposition. Plants provide water, that is needed to sustain its physiological status and for prey consumption, but also plants contribute with nutrients to support predator development and reproduction, especially in periods of prey scarcity or even in the total absence of prey (Gillespie and McGregor 2000; Ingegno et al. 2011; Maselou et al. 2014). When feeding, mirids pierce prey or plant tissue with their stylets and macerate it with digestive enzymes that they inject from their salivary glands (Cohen 1995). This type of feeding habit may injure plant tissues that under certain circumstances related with the scarcity of prey can produce crop damage (Castañé et al. 2011). The feeding lesions produced resemble those of cell feeders as spider mites or thrips. Mirid bugs also need plants for oviposition since they lay their eggs inside the plant tissues, mainly in the veins or in the stems (Wheeler 2001). Hence, plant physiological traits can affect *M. pygmaeus* performance and behavior. This phytophagous behavior of

the predator can also influence plant resistance against some pests, as shown by Pappas et al. (2015) on tomato with spider mites. In a previous study, Battaglia et al. (2013) have shown that the root-associated biocontrol fungus *Trichoderma longibrachiatum* strain MK1 on tomatoes produced quantitative differences in the release of specific volatile organic compounds, a better aphid (*Macrosiphum euphorbiae*) population growth indices, a higher attractiveness toward the aphid parasitoid *A. ervi* and the polyphagous predator *M. pygmaeus*, and a quicker development of the aphid predator. In the present study, we wanted to test whether the AMF *Rhizophagus irregularis* (Syn. *Glomus intraradices* Schenk and Smith) could also have an impact in the performance of the polyphagous predator *M. pygmaeus*. *R. irregularis* has been used as inoculant in many host plants, including tomato and a wide range of other horticultural and woody crops (Smith and Read 2008) although the application of mycorrhizal inocula to commercial tomato production is still rather limited. Our hypothesis was that early inoculation of tomato plants with *R. irregularis* would cause a positive effect in predator performance since its feeding habits resemble those of cell feeders. To test this hypothesis, we evaluated whether mycorrhizal colonization of tomato plants had an effect on adult plant preferences for feeding and oviposition, on predator immature development and in the first generation female progeny.

Materials and methods

Plant material, mycorrhizal inoculum and insect colonies

The AMF used in the experiments was an isolate of *R. irregularis* registered as BEG 72 in the European Bank for the Glomeromycota. It was obtained from a *Citrus* nursery in the Northeastern Spanish coastline (Camprubi and Calvet 1996) and has proved to be effective at promoting plant growth and tolerance against biotic and abiotic stress in many agricultural crops (Calvet et al. 2001; Estaún et al. 2003; Camprubi et al. 2008). The mycorrhizal inoculum was produced in pot cultures using leek (*Allium porrum* L.) as a host plant, calcined clay (Terragreen®) as growing substrate and included root fragments, spores (at least 1000 spores in 10 ml) and hyphae of *R. irregularis*.

Tomato seeds (*Solanum lycopersicum* L. variety San Marzano Nano) were germinated and grown in a mixture of commercial potting soil and perlite (Stender® Propagating substrate A 240) for 3 weeks under greenhouse conditions (15 ± 2 °C, 14 h daylight, 70–77 % r.h.). Tomato seedlings were transplanted into plastic pots (10 cm deep-12 cm diameter) containing an autoclaved sand, quartz

silicate and peat mixture (3:2:1 v/v). At transplant, half of the pots ($N = 85$ of 170 in total) received 10 ml of *R. irregularis* inoculum. The inoculum was placed below the roots in the planting hole. Inoculated and non-inoculated plants were maintained in a heated glasshouse (15–25 °C, 14 h daylight, 70–77 % r.h). Plants were watered two times a week and were fertilized every 8 days with 50 ml of Hoagland nutrient solution without P (Hoagland and Arnon 1950). All plants were 18 weeks old when used in the bioassays, and growth parameters were measured: Shoot dry weight was achieved by ten plants per treatment (inoculated and non-inoculated with *R. irregularis*) and total shoot length by twenty plants per treatment.

To determine the mycorrhizal status of tomato seedlings inoculated with *R. irregularis,* root samples of 10 plants taken at random were examined. Roots were washed with water to remove the substrate and cleared in 10 % KOH before staining with trypan blue dye, following the methodological procedure of Koske and Gemma (1989). To establish the percentage of mycorrhizal colonization on tomato plants, the gridline intersect method described by Giovannetti and Mosse (1980) was used. The percentage of positive observations for mycorrhizal colonization (presence of arbuscules, vesicles and hyphae) was noted and quantified as the percentage of mycorrhizal colonization on each tomato plant sample. Root samples of 10 non-inoculated plants were also taken, cleared and stained to check their mycorrhizal-free status.

All insect colonies were maintained under environmental controlled conditions (25 ± 1 °C, 16L: 8D h and 70–10 % r.h.). *Bemisia tabaci* (Gennadius) (Hemiptera: Aleurodidae) biotype B was reared on seedlings of cabbage. This biotype was initially collected from Murcia (Spain) in 1992. *M. pygmaeus* was reared as described in Agustí and Gabarra (2009a, b), that is, on tobacco plants with eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), a common factitious prey used in the rearing of many insect predators. This colony was established, and it is yearly renewed with individuals collected from commercial tomato crops in the coastal area of Barcelona (Spain).

Experimental design

To test whether mycorrhizal inoculation affects *M. pygmaeus* performance, three different experiments were conducted:

Experiment 1

A host selection experiment was designed under controlled conditions (25 ± 1 °C, 16L: 8D h, 70–10 % r.h.). Four detached tomato leaves were simultaneously offered to *M.*

pygmaeus adults: Two leaves were taken from mycorrhizal tomato plants colonized by *R. irregularis* (M) and the other two from non-mycorrhizal plants (NM). Each leaf was placed in a corner of a rectangular acrylic glass box (44 cm width × 67 cm length) with the two leaves from mycorrhizal tomato plants placed between the non-colonized control ones. Each leaf was kept in a vertical position with the petiole inserted in a plastic container filled with water and a nutrient solution (50 ml), to prevent leaf desiccation. *Ephestia kuehniella* eggs, the standard rearing prey, were offered glued to a 1 × 1 cm of post-it paper that was attached to the lower leaf surface. Eight mated *M. pygmaeus* (4 females and 4 males) 7–10 days old were released in the center of the box, and the number of adults on each leaf was counted after 3 days. Leaves were then isolated in ventilated clear plastic cages (21 cm height × 12 cm width), and the number of young nymphs emerged were counted 11 days later. Thirteen cage replicates were surveyed along the experiment.

Experiment 2

Immature survival and the weight of emerged adults were evaluated in a second experiment set in a glasshouse (23–28 °C, 14 h daylight, 68–70 % r.h.). The six upper leaves from 18-week-old M and NM tomato plants were covered with a muslin net bag (1 mm diameter of the hole in the mesh). Twenty-one instar nymphs of *M. pygmaeus* collected from our stock colony with a mouth aspirator were introduced in each bag, and 3 weeks later adult emergence was monitored every 2 days, until all nymphs molted to adults. All emerged adults were sexed, individually introduced in a gelatin capsule and weighed in a precision scale (readability 0.001 g). One week before introducing predatory nymphs in the bags, *B. tabaci* adults (≈ 180) were initially introduced to serve as prey for the predators, and more adults (≈ 50 s) were periodically supplied until predatory nymphs reached the adult stage. Ten replicates per treatment (M and NM plants) were used.

Experiment 3

The fertility of females developed on M and NM tomato plants was assessed under controlled conditions (25 ± 1 °C, 16L: 8D h, 70–10 % r.h.). Females and males emerged from experiment 2 were kept together on two tomato plants (one for insects developed in each of the treatments: M and NM) for 7 days to allow them to mate and to mature their eggs. *Bemisia tabaci* adults and eggs of *E. kuehniella* were supplied as prey. Afterward, pairs of a female and a male were isolated during 4 days in plastic cages (21 cm height × 12 cm width) containing a detached leaf of NM tomato plants. As previously, leaves

had the petiole inserted in a plastic container (50 ml) filled with water in order to avoid desiccation. Eggs of *E. kuehniella* were supplied as food. After 11 days passed for egg maturation, the number of newly emerged nymphs was recorded on the leaves. Fifteen cage replicates per treatment were used.

Statistical analyses

To analyze data of host plant selection by adults, a mixed-model ANOVA was performed with sex and plant treatment (NM and M plants) as fixed effects and leaf offered to the predator nested within sex and plant treatment, after checking for normality of the data. The female progeny, or the number of nymphs emerged on the leaves after eggs hatched, was instead analyzed by nested-ANOVA with plant treatment (NM and M plants) as main factor and leaf nested within plant treatment.

Student's *t* tests were performed to determine differences on predator immature survival, adult weight and female progeny between predators developed as immatures on NM and M tomato plants and differences in plant growth parameters (shoot dry weight and total shoot length) between NM and M plants.

All statistical analyses were performed using R. 3.2.3 software for windows (R Development Core Team 2015) library "base".

Results

Experiment 1

Eighteen weeks after inoculating tomato San Marzano Nano plants, there were no significant differences in plant growth between M and NM plants (Shoot length: $t_{38} = -0.437$, $P = 0.665$; shoot dry weight: $t_{18} = 1.289$, $P = 0.2161$) despite the root colonization achieved by *R. irregularis* in inoculated plants (32.37 ± 4.05 %). Shoot length data (in cm) and shoot dry weight data (in g) obtained were 95.53 ± 21.22 and 5.61 ± 1.32 for M plants and 93.25 ± 9.68 and 4.96 ± 0.86 for NM plants.

Figure 1 shows the mean number (±SE) of recaptured *M. pygmaeus* adults (males and females) on two leaves from NM and two leaves from M tomato plants in the host plant selection experiment. Females and males showed a statistically significant preference for leaves of the M plants in comparison with the NM ones ($F_{1,96} = 5.35$, $P < 0.05$, Fig. 1). No significant differences were detected between sexes ($F_{1,96} = 0.911$, $P = 0.76$) nor between leaves nested within plant treatment and sex ($F_{4,96} = 1.487$, $P = 0.212$). Additionally, significant differences were assessed in the number of *M. pygmaeus*
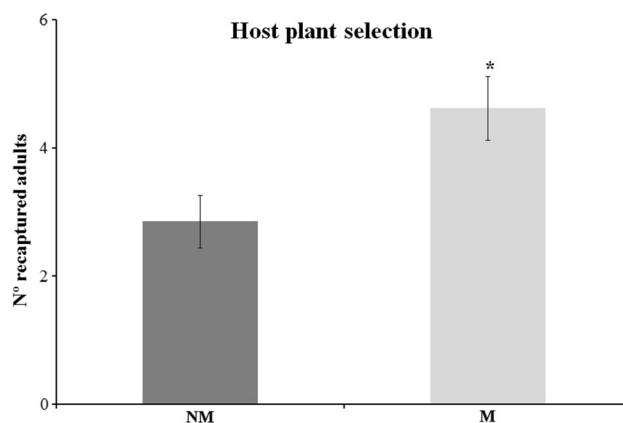

Fig. 1 Number (mean ± SE) of *M. pygmaeus* adults (males and females) recaptured on detached leaves from non-mycorrhizal (NM) and mycorrhizal (M) tomato plants inoculated with *R. irregularis* 72 h after their release in the cage. Two leaves per treatment were offered in each cage, *n* = 13. Significant differences (*asterisk*) were detected between plant treatments but not between sexes ($P < 0.05$)

emerged nymphs on leaves from NM and M plants ($F_{1,48} = 4.74$, $P < 0.05$). The mean number of newborn nymphs of *M. pygmaeus* was higher on leaves of mycorrhizal tomato plants (Fig. 2).

Experiment 2

When the survival of immatures was analyzed, the numbers of both females and males emerged from M plants were higher than those in NM ones ($t_{38} = -4.2516$, $P < 0.001$) (Fig. 3). A similar proportion of females developed in both treatments (0.5 for Control and 0.49 for AMF treatments). A significant increase in the weight of females reared on M tomato plants was observed in comparison with the control
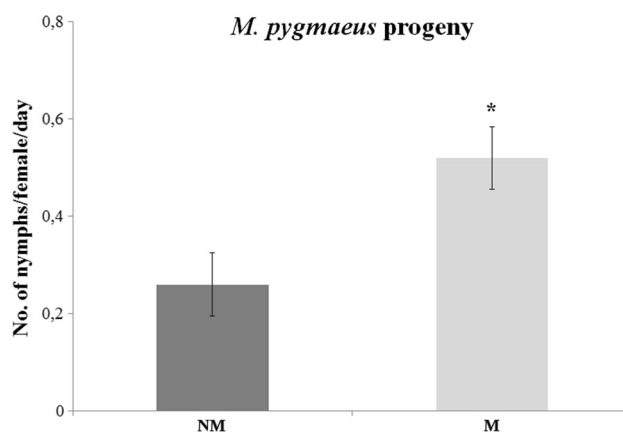

Fig. 2 Number (mean ± SE) of *M. pygmaeus* newly born nymphs from detached leaves of non-mycorrhizal (NM) and mycorrhizal (M) tomato plants inoculated with *Rhizophagus irregularis*, 11 days after the end of the host-plant selection assay (*n* = 26). Significant differences (*asterisk*) were detected between plant treatments ($P < 0.05$)
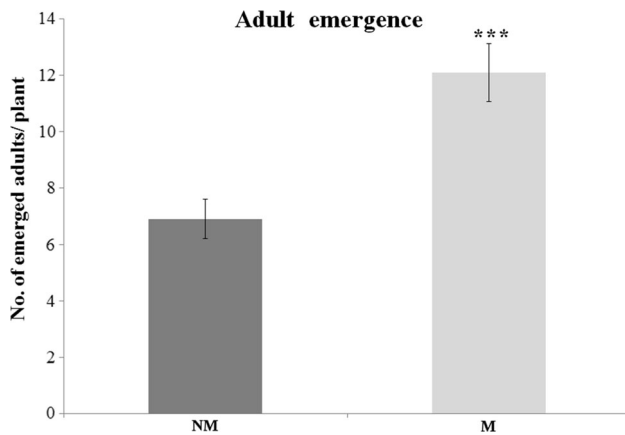
Fig. 3 Number (mean ± SE) of *M. pygmaeus* adults (females and males) developed on non-mycorrhizal and mycorrhizal tomato plants inoculated with *R. irregularis* after introducing 20 first instar nymphs in muslin bags that enclosed the six upper leaves of the plants. *Bemisia tabaci* adults were offered as prey. Significant differences (*asterisk*) were detected between plant treatments but not between sexes ($P < 0.001$), $n = 10$

ones (Table 1), while no significant differences were found in the weight between males reared on NM and M plants (Table 1).

Experiment 3

When examining fertility of females developed as immatures on tomato plants, either M or NM plants, and offered a NM tomato plant as an oviposition substrate together with *E. kuehniella* eggs as prey, no statistically significant differences were found in the mean number of newborn nymphs ($t_{28} = 0.2795$, $P = 0.7819$).

Discussion

The isolate BEG 72 of *R. irregularis* had successfully colonized tomato plants 18 weeks after inoculation, but plants from both treatments (M and NM) showed no significant differences yet in plant growth parameters when leaves were extracted to be used in the experiments. Despite the lack of plant growth stimulation due to the symbiosis, both females and males of *M. pygmaeus* showed

higher attractiveness to leaves from *R. irregularis*-colonized tomato plants than from NM plants, proving that the AMF *R. irregularis* influenced *M. pygmaeus* preferences in tomato San Marzano Nano. This preferential choice was made despite the supplemental high-quality prey (*E. kuehniella* eggs) that was also offered in both treatments. Regardless of plant growth responses, AM symbiosis triggers changes in the quality composition of diverse host plant species by altering the balance of C and N, the phosphorous and zinc plant tissues concentration and the content of different types of micronutrients (George et al. 1995; Smith and Smith 2011). Studies on the effect of plant-prey-provided nutrients on insect biology indicate that P and N are limiting factors for insect performance because P and N are key elements for the growth of both herbivores and their predators via amino acid requirements (Awmack and Leather 2002; Denno and Fagan 2003). Roger et al. (2013) showed that 8 weeks after inoculation, AMF-mediated effects on herbivore performance can already be detected.

Detached leaves from mycorrhizal plants were in addition preferred by reproductive females for egg oviposition. This result was confirmed by the higher number of newborn nymphs recorded on leaves from M tomato plants compared to NM plants. It is important to highlight that *R. irregularis* positive effect on the quality of the tomato plant as a resource and/or oviposition substrate lasts even when we offered to *M. pygmaeus* single leaves detached from *R. irregularis*-colonized tomato plants artificially maintained during 3 days after their cut. Our results with detached leaves are in line with those of Hoffman et al. (2009, 2011a, b). *M. pygmaeus* preferences toward leaves of *R. irregularis*-colonized tomato plants would be mediated by quantitative or/and qualitative changes in the blend of volatile organic compounds (VOCs thereafter) released by tomato plants associated with this AMF. Allocation of plant resources to indirect plant defenses based on the production of VOCs has already been demonstrated on diverse plant species colonized by different AMF species (Fontana et al. 2009; Leitner et al. 2010). For instance, it has been shown that VOCs produced by AMF tomato plants attract the aphid parasitoid *Aphidius ervi*, even in the absence of aphids (Guerrieri et al. 2004), and VOCs

Table 1 Weight (mean number ± SE in grams) of *M. pygmaeus* females and males emerged on non-mycorrhizal (NM) and mycorrhizal (M) tomato plants inoculated with *Rhizophagus irregularis*

M. pygmaeus	Treatment					Statistics	
	n	NM	*n*	M	df	*t*	*P* value
Female	26	0.696 ± 0.03	48	0.8 ± 0.02	72	−2.3807	0.01993[*]
Male	27	0.425 ± 0.02	50	0.402 ± 0.01	75	0.7915	0.4312

[*] $P < 0.05$

produced by AMF bean plants attract the predatory mite *Phytoseiulus persimilis* (Schausberger et al. 2012). Our results are also in line with those reported by Battaglia et al. (2013) showing that tomato plants colonized by the plant growth-promoting fungi *T. longibrachiatum* increases the attractiveness of *M. pygmaeus*. Even if AMF and *Trichoderma* sp. have different mechanisms of colonization and induction of biochemical, physiological and molecular responses on the host plant (Strack et al. 2003; Smith and Smith 2011; Hermosa et al. 2012), both of these plant growth-promoting fungi produced changes in the blend of VOCs (Battaglia et al. 2013; Fontana et al. 2009; Schausberger et al. 2012) and increase plant nutrient uptake (Harman et al. 2004; Smith and Smith 2011).

Our data concerning the effect of mycorrhizal inoculation on the predator immature development showed that, compared with NM tomato plants, those associated with *R. irregularis* increased *M. pygmaeus* nymph survival and female weight at emergence. These results might be directly mediated by an enrichment of the nutritional quality of tomato leaves and/or stems derived from the mycorrhizal fungus capacity to mobilize and increase plant uptake of water and micro- and macronutrients (George et al. 1995; Smith and Smith 2011; Augé et al. 2015; Chitarra et al. 2016; He et al. 2016) and/or with changes in the plant metabolite profile (Fiorilli et al. 2009; León-Morcillo et al. 2012; Song et al. 2013). Better performance (female's weight and fecundity) of sucking–piercing feeders has been demonstrated when aphids were reared on plants colonized by *G. intraradices* (Gange et al. 1999), and better performance (net reproductive rate) of cell feeders has been demonstrated when spider mites were reared plants colonized by *G. mosseae* (Hoffmann et al. 2009).

In our experiments, improvement in nymphal survival and female's weight might also be related to an improvement in the prey quality (*B. tabaci*). AMF ability to alter the nutrient composition of the host plant can cascade up to the next trophic level by changing the nutritional quality of the prey. Hoffmann et al. (2011b) found that foraging and oviposition behaviors of the predator mite *Phytoseilus persimilis* (Phytoseiidae) are affected by its capacity to recognize *G. mosseae*-enhanced quality of its prey-mite via prey-related cues. Finally, the absence of differences in the fertility of the heavier females reared on M tomato plants in comparison with NM plants can be related with its reproductive physiology. *M. pygmaeus* is a synovigenic insect that develops its ovaries in the adult stage and fully forms its eggs in relation with the availability of nutrients (Castañé et al. 2007). Therefore, when we offered them the same NM plant and the same prey during the period when maturing their eggs, differences among females of the two origins may disappear.

In conclusion, in the present study, we found that *R. irregularis* symbiotic association with the *S. lycopersicum* variety San Marzano Nano positively modulates the interaction of this plant species with *M. pygmaeus*, to the benefit of the mirid bug. Fitness gains achieved by the predator are an enhanced adult host-plant acceptance for feeding and oviposition and a higher nymphal survival and female weight. Further research could show more specifically whether the nutritional quality of different prey present in tomato crops is affected by *R. irregularis*. From a practical point of view, the results of this study indicate that *R. irregularis* root colonization on tomato plants could potentially contribute to the successful establishment of the predator in the crop by increasing its attractiveness toward tomato plants. This is important at the beginning of the tomato growing season, when mirid bugs are frequently introduced and prey are scarce (Arnó et al. 2009). Moreover, better biological traits attained by *M. pygmaeus* on *R. irregularis*-colonized tomato plants (e.g., higher production of offspring and female weight) could facilitate the maintenance of the predator population for longer time and would indirectly modulate its effectiveness as biocontrol agent.

References

Agustí N, Gabarra R (2009a) Puesta a punto de una cría masiva del depredador polífago *Dicyphus tamaninii* Wagner (Heteroptera: Miridae). Bol Sanid Veg Plagas 35:205–218

Agustí N, Gabarra R (2009b) Effect of adult age and insect density of *Dicyphus tamaninii* Wagner (Heteroptera: Miridae) on progeny. J Pest Sci 82:241–246

Alomar O, Goula M, Albajes R (2002) Colonization of tomato fields by predatory mirid bugs (Hemiptera: Heteroptera) in northern Spain. Agric Ecosyst Environ 89:105–115

Arnó J, Gabarra R, Estopà M, Gorman K, Petershmitt M, Bonato O, Vosman B, Hommes M, Albajes R (2009) Implementation of IPM programs in European greenhouse tomato production areas, tools and constraints. Edicions i Publicacions de la UdL, Lleida, Spain

Augé RM, Toler HD, Saxton AM (2015) Arbuscular mycorrhizal symbiosis alters stomatal conductance of host plants more under drought than under amply watered conditions: a meta-analysis. Mycorrhiza 25:13–24

Awmack CS, Leather SR (2002) Host plant quality and fecundity in herbivorous insects. Annu Rev Entomol 47:817–844

Azcón-Aguilar C, Barea JM (1997) Arbuscular mycorrhizas and biological control of plant pathogens: an overview of the mechanisms involved. Mycorrhiza 6:457–464

Babikova Z, Gilbert L, Bruce TJA, Birkett M, Caulfield JC, Woodcock C, Pickett JA, Johnson D (2013) Underground signals carried through common mycelial networks warn neighboring plants of aphid attack. Ecol Lett 16:835–843

Battaglia D, Bossi S, Cascone P, Digilio MC, Duran JP, Guerrieri E, Iodice L, Lingua G, Lorito M, Maffei ME, Massa N, Ruocco M, Sasso R, Trotta V (2013) Tomato belowground-aboveground interactions: *Trichoderma longibrachiatum* affects the performance of *Macrosiphum euphorbiae* and its natural antagonists. Mol Plant Microbe Interact 26:1249–1256

Calvet C, Pinochet J, Hernández-Dorrego A, Estaún V, Camprubí A (2001) Field microplot performance of the peach-almond hybrid GF-677 after inoculation with arbuscular mycorrhizal fungi in a replant soil infested with root-knot nematodes. Mycorrhiza 10:295–300

Camprubi A, Calvet C (1996) Isolation and screening of mycorrhizal fungi from citrus nurseries and orchards and studies of greenhouse inoculation systems. HortScience 31:366–369

Camprubi A, Estaun V, Nogales A, Garcia-Figueres F, Pitet M, Calvet C (2008) Response of grapevine rootstock Richter 110 to inoculation with native and selected arbuscular mycorrhizal fungi and growth performance in a replant vineyard. Mycorrhiza 18:211–216

Castañé C, Alomar O, Goula M, Gabarra R (2004) Colonization of tomato greenhouses by the predatory mirid bugs *Macrolophus caliginosus* and *Dicyphus tamaninii*. Biol Control 30:591–597

Castañé C, Alomar O, Riudavets J, Gemeno C (2007) Reproductive biology of the predator *Macrolophus caliginosus*: effect of age on sexual maturation and mating. Biol Control 43:278–286

Castañé C, Arnó J, Rosa G, Alomar O (2011) Plant damage to vegetable crops by zoophytophagous mirid predators. Biol Control 59:22–29

Chitarra W, Pagliarani C, Maserti B, Lumini E, Siciliano I, Cascone P, Schubert A, Gambino G, Balestrini R, Guerrieri E (2016) Insights on the impact of arbuscular mycorrhizal symbiosis on tomato tolerance to water stress. Plant Physiol 171:1009–1023

Cohen AC (1995) Extraoral digestion in predaceous terrestrial arthropoda. Annu Rev Entomol 40:85–103

Denno RF, Fagan WF (2003) Might nitrogen limitation promote omnivory among carnivorous arthropods? Ecology 84:2522–2531

Estaún V, Camprubi A, Calvet C, Pinochet J (2003) Nursery and field response of olive trees inoculated with two arbuscular mycorrhizal fungi, *Glomus intraradices* and *Glomus mosseae*. J Am Soc Horticult Sci 28:767–775

Estaún V, Calvet C, Camprubi A (2010) Effect of differences among crop species and cultivars on the arbuscular mycorrhizal simbiosis. In: Koltai H, Kalpulnik Y (eds) Arbuscular mycorrhizas: physiology and function. Springer, New York, pp 279–295

Fiorilli V, Catoni M, Miozzi L, Novero M, Acotto GP, Lanfranco L (2009) Global and cell-type gene expression profiles in tomato plants colonized by an arbuscular mycorrhizal fungus. New Phytol 184:975–987

Fontana A, Reichelt M, Hempel S, Gershenzon J, Unsicker SB (2009) The effects of arbuscular mycorrhizal fungi on direct and indirect defense metabolites of *Plantago lanceolata* L. J Chem Ecol 35:833–843

Gange AC, Bower E, Brown VK (1999) Positive effects of an arbuscular mycorrhizal fungus on aphid life history traits. Oecologia 120:123–131

Gehring C, Bennett A (2009) Mycorrhizal fungal–plant–insect interactions: the importance of a community approach. Environ Entomol 38:93–102

George E, Marschner H, Jakobsen I (1995) Role of arbuscular mycorrhizal fungi in uptake of phosphorus and nitrogen from soil. Crit Rev Biotechnol 15:257–270

Gillespie DR, McGregor RR (2000) The functions of plant feeding in the omnivorous predator *Dyphus hesperus*: water places limits on predation. Ecol Entomol 25:380–386

Giovannetti M, Mosse B (1980) An evaluation of techniques for measuring vasicular-arbuscular mycorrhizal infection in roots. New Phytol 84:489–500

Goverde M, van der Heijden MGA, Wiemken A, Sanders IR, Erhardt A (2000) Arbuscular mycorrhizal fungi influence life history traits of a lepidopteran herbivore. Oecologia 125:362–369

Guerrieri E, Lingua G, Digilio MC, Massa N, Berta G (2004) Do interactions between plant roots and the rhizosphere affect parasitoid behaviour? Ecol Entomol 29:753–756

Harman GE, Howell CR, Viterbo A, Chet I, Lorito M (2004) *Trichoderma* species-opportunistic, avirulent, plant symbionts. Nat Rev Microbiol 2:43–56

He F, Zhang H, Ming T (2016) Aquaporin gene expression and physiological responses of *Robinia pseudoacacia* L. to the mycorrhizal fungus *Rhizophagus irregularis* and drought stress. Mycorrhiza 26:311–323

Hempel S, Stein C, Unsicker SB, Renker C, Auge H, Weisser WW, Buscot F (2009) Specific bottom–up effects of arbuscular mycorrhizal fungi across a plant–herbivore–parasitoid system. Oecologia 160:267–277

Hermosa R, Viterbo A, Ilan Chet, Monte E (2012) Plant-beneficial effects of *Trichoderma* and of its genes. Microbiology 158:17–25

Hoagland D, Arnon DI (1950) The water culture method for growing plants without soil. California agricultural experimental Station, circular no 347. University of California, Berkeley

Hoffmann D, Vierheilig H, Riegler P, Schausberger P (2009) Arbuscular mycorrhizal symbiosis increases host plant acceptance and population growth rates of the two-spotted spider mite *Tetranychus urticae*. Oecologia 158:663–671

Hoffmann D, Vierheilig H, Peneder S, Schausberger P (2011a) Mycorrhiza modulates aboveground tritrophic interactions to the fitness benefit of its host plant. Ecol Entomol 36:574–581

Hoffmann D, Vierheilig H, Schausberger P (2011b) Arbuscular mycorrhiza enhances preference of ovipositing predatory mites for direct prey-related cues. Physiol Entomol 36:90–95

Ingegno BL, Pansa MG, Tavella L (2011) Plant preference in the zoophytophagous generalist predator *Macrolophus pygmaeus* (Heteroptera: Miridae). Biol Control 58:174–181

Jung SC, Martínez-Medina A, López-Raez JA, Pozo MJ (2012) Mycorrhiza-induced resistance and priming of plant defenses. J Chem Ecol 38:651–664

Koske RE, Gemma JN (1989) A modified procedure for staining roots to detect V-A mycorrhizas. Mycol Res 92:486–488

Leitner M, Kaiser R, Hause B, Boland W, Mithöfer A (2010) Does mycorrhization influence herbivore-induced volatile emission in *Medicago truncatula*? Mycorrhiza 20:89–101

León-Morcillo RJ, Martin-Rodríguez JA, Vierheilig H, Ocampo JA, García-Garrido JM (2012) Late activation of the 9-oxylipin pathway during arbuscular mycorrhiza formation in tomato and its regulation by jasmonate signaling. J Exp Bot 63:3545–3558

Maselou DA, Perdikis DCh, Sabelis MW, Fantinou AA (2014) Use of plant resources by an omnivorous predator and the consequences for effective predation. Biol Control 79:92–100

Nogales A, Aguirreolea J, Santa Maria E, Camprubí A, Calvet C (2009) Response of mycorrhizal grapevine to *Armillaria mellea* inoculation: disease development and polyamines. Plant Soil 317:177–187

Pappas ML, Steppuhn A, Geuss D, Topalidou N, Zografou A, Sabelis MW et al (2015) Beyond predation: the zoophytophagous predator *Macrolophus pygmaeus* induces tomato resistance against spider mites. PLoS ONE 10(5):e0127251. doi:10.1371/journal.pone.0127251

Perdikis DCh, Kapaxidi E, Papadoulis G (2008) Biological control of insect and mite pests in greenhouse solanaceous crops. Eur J Plant Sci Biotechnol 2:125–144

Pozo MJ, Cordier C, Dumas-Gaudot E, Gianinazzi S, Barea JM, Azcón-Aguilar C (2002) Localized versus systemic effect of arbuscular mycorrhizal fungi on defense responses to *Phytophthora* infection in tomato plants. J Exp Bot 53:525–534

Pozo MJ, López-Raez JA, Azcón-Aguilar C, García-Garrido JM (2015) Phytohormones as integrators of environmental signals in the regulation of mycorrhizal symbioses. New Phytol 205:1431–1436

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/

Roger A, Gétaz M, Rasmann S, Sanders I (2013) Identity and combinations of arbuscular mycorrhizal fungal isolates influence plant resistance and insect preference. Ecol Entomol 38:330–338

Schausberger P, Peneder S, Jurschik S, Hoffman D (2012) Mycorrhiza changes plant volatiles to attract spider mite enemies. Funct Ecol 26:441–449

Smith SE, Read DJ (2008) Mycorrhizal Symbiosis. Elsevier, London

Smith SE, Smith FA (2011) Roles of arbuscular mycorrhizas in plant nutrition and growth: new paradigms from celular to ecosystem scales. Annu Rev Plant Biol 62:227–250

Song YY, Ye M, Li CY, Wang RL, Wei XC, Luo SM, Zeng RS (2013) Priming of anti-herbivore defense in tomato by arbuscular mycorrhizal fungus and involvement of the jasmonate pathway. J Chem Ecol 39:1036–1044

Strack D, Fester T, Hause B, Schliemann W, Walter MH (2003) Arbuscular mycorrhiza: biological, chemical, and molecular aspects. J Chem Ecol 29:1955–1979

Vannette RL, Hunter M (2009) Mycorrhizal fungi as mediators of defence against insect pests in agricultural systems. Agric Forest Entomol 11:351–358

Wheeler AG Jr (2001) Biology of the plant bugs (Hemiptera: Miridae): pests, predators, opportunists. Cornell University Press, Comstock Publishing Associates, New York

Wolfe BE, Husband BC, Klironomos JN (2005) Effects of a belowground mutualism on an aboveground mutualism. Ecol Lett 8:218–223