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Short Notes

Protective effects of mycorrhizal association in tomato and pepper against *Meloidogyne incognita* infection, and mycorrhizal networks for early mycorrhization of low mycotrophic plants

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Summary. Root knot nematodes are obligate phytoparasites that invade the roots of important crop plants causing severe economic losses. Arbuscular Mycorrhizal Fungi (AMF) are soil borne microorganisms that establish mutualistic associations with the roots of most plants. AMF have been frequently indicated to help their host to attenuate the damage caused by pathogens and predators. In this study, the effects of a commercial inoculum of AMF against *Meloidogyne incognita* on tomato and pepper were evaluated under controlled conditions. Mycorrhizal association decreased *M. incognita* development in pepper, and improved tolerance to nematode infection in tomato plants. Rapid plant mycorrhization is critical for delivering protective effects against biotic stress. A novel mycorrhization technique using AMF from the highly mycotrophic plant sorghum was applied to tomato. More rapid mycorrhization was achieved in tomato plants grown in soil containing mycorrhized roots of sorghum than in plants directly inoculated with the commercial AMF.

Keywords. Crop pests, symbiosis, agricultural management.

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INTRODUCTION

Phytoparasite nematodes are part of the soil microfauna with life cycles that are totally or partially within plants. Root-knot nematodes (RKNs) of the genus *Meloidogyne* are obligate endoparasites affecting a large number of plant species (Sasser and Freckman, 1987). They form characteristic galls in roots and block host plant conductive tissues, causing moisture stress

(Meon *et al*. 1978), poor root development and growth, and significantly reduce crop productivity (Hussey, 1985; Melakeberhan and Webster, 1993).

RKNs are present in most farmlands, and can infect more than 5500 plant species, including vegetables, fruit crops, cereals and ornamentals (Blok *et al*., 2008). Economic losses due to RKN are estimated at tens of billions of euros per year (Jones *et al.,* 2013). For example, more than 40% of economic crops in the southeast of France are affected by *Meloidogyne* spp. (Djian-Caporalino, 2010, 2012). The usual methods for controlling RKNs included use of bromide/chloride/phosphorus-based products which are very concerning for the environment and human health, and therefore have been phased out in the European Union since 2009 (Council of the European Union, 2009). Physical approaches include prophylaxis, steam disinfection and solarisation, which are not always effective. Biological approaches for controlling RKNs are based on resistant plant varieties, nematode parasitic bacteria, toxins from nematicidal plants, biofumigation from plant oil cakes, and fungi that alter nematode life cycles (Djian-Caporalino *et al.,* 2009).

Arbuscular mycorrhizal fungi (AMF) are obligate biotrophs that exclusively colonise plant roots. These fungi form hyphae connections between roots from one or several host species to establish the Common Mycorrhizal Networks (CMNs) (Simard *et al.,* 2012). Plants associated with CMNs have improved assimilation of phosphate, macronutrients such as N, K and Mg, and some micronutrients (Bhatia *et al.,* 1998; Montaño *et al.,* 2007). Colonising AMF receive organic carbon from the host plants (Sanders and Tinker, 1971). The review of Veresoglou and Rilling (2012) indicated that AMF have capacity to decrease losses caused by diverse plant pathogens, with the interaction between AMF and RKNs representing 28% of the listed reports. For example, early mycorrhization by mixtures of AMF species is effective against *Meloidogyne* spp. and *Pratylenchus* spp. (Vos *et al.,* 2012). Sikora and Schönbeck (1975) reported that *Funneliformis mosseae* and *Rhizophagus fasciculatus* decreased *M. incognita* infection on tomato by, respectively, 13% and 50%. In pepper, Peregrin *et al.,* (2012) assessed effects of AMF and *Bacillus megaterium* (simultaneously and individually) on *Meloidogyne incognita*, although the bioprotection conferred by the AMF was not clearly demonstrated.

Tomato and pepper have been frequently reported as mycotrophic plants (Cress *et al.,* 1979; Al-Karaki, 2000; Schroeder and Janos, 2004; Schroeder-Moreno and Janos, 2008; Gashua *et al.,* 2015; Chialva *et al.,* 2019). Nevertheless, tomato plants do not rapidly develop intensive mycorrhization compared to highly mycotrophic species (Schroeder and Janos, 2004; Kubota, 2005; Thougnon Islas *et al.,* 2014). This can be inconvenient for horticultural applications, as any probable benefit from AMF against RKN may only be obtained through early mycorrhization (Jaizme-Vega *et al.,* 1997; Molinari and Leonetti, 2019). Interconnection from mature plants by CMNs could improve establishment and growth of seedlings (van der Heijden and Horton, 2009). Derelle *et al.,* (2012) reported enhanced mycorrhization of *Silene vulgaris* (weakly mycotrophic) by mycorrhizal networks (MNs) previously developed by *Medicago truncatula* (highly mycotrophic) under *in vitro* conditions. Therefore, examining new strategies for tomato mycorrhization involving MNs could provide worthwhile new and practically valuable knowledge.

To test bioprotection of AMF against RKNs, the effect of mycorrhizal colonisation against development of *M. incognita* was examined in tomato and pepper, as two economically important crop plants. Additionally, the potential of MNs for accelerating mycorrhization was demonstrated on tomato plants using MNs previously established by a suitable highly mycotrophic host such as sorghum.

MATERIALS AND METHODS

Plant material

RKN-susceptible seedlings of tomato (*Solanum lycopersicum* 'Saint Pierre') and pepper (*Capsicum annuum* 'Doux long des Landes') were transplanted into 9 cm × 9 cm pots containing sterilised soil, and were inoculated with AEGIS powder from NIXE® (AMF inoculum containing *Rhizophagus irregularis*). Unless otherwise stated, all the plant cultures were in a growth chamber at 25°C (± 1°C) with a 16 h light / 8 h dark illumination cycle. A nutrient solution adapted for AMF development (200 mg L^{-1} $Ca(NO_3)_2$, 300 mg L^{-1} KNO_3, 25 mg L^{-1} KH_2PO_4, 150 mg L^{-1} $MgSO_4$ 7 H_2O, 1.5 mg L^{-1} H_3BO_3, 0.05 mg L^{-1} $(NH_4)_6Mo_7O_{24}$, 1 mg L^{-1} $ZnSO_4$ 7 H_2O, 2 mg L^{-1} $MnSO_4$ H_2O, 0.25 mg L^{-1} $CuSO_4$ 5 H_2O, 225 mg L^{-1} Fe EDTA) was added every 3 d to the plants, at 1 mL per application for the first week of culture, then increased by 1 mL every week from the second to the fifth weeks. After 6 weeks of culture, the root mycorrhization rates were assessed for three plants of each species, and 5000 freshly hatched J2s of *M. incognita* suspended in water were inoculated onto each plant. The number of nematode egg masses was assessed on each plant at 6 weeks after J2 inoculation, by acid eosin staining. The same experiment was performed simultaneously with non-AMF treated plants as experimental controls.

Tomato mycorrhization by mycorrhizal networks consisted of growing an AMF inoculated sorghum sudangrass plant (*Sorghum bicolor* × *Sorghum sudanense* (Piper) Stapf) under equivalent conditions to the seedlings for the RKN experiments. After 6 weeks, the aerial part and roots were shredded and integrated to the pot soil. A tomato seedling was then transplanted into the sorghum/soil mix, and the mycorrhization rate was assessed after 2 and 4 weeks. Tomato plants inoculated directly with the commercial inoculum were used as experimental controls.

Assessment of root mycorrhization rates

Plant roots were bleached with 1% (w/v) KOH solution at 80° C for 1 h, and then incubated in a 5% solution of ink/lactic acid (80%) for 12 h. After rinsing, 1 cm root segments were mounted in glycerol/lactic acid (1/1 v/v) on glass microscope slides. Mycorrhization rates were evaluated by light microscopy, by considering the mycelium frequency inside and outside each root segment, the quantity of colonized root, and the abundance of developed arbuscules/vesicles (Trouvelot *et al.,* 1986).

Evaluation of Meloidogyne incognita *development*

The roots of experimental plants were rinsed thoroughly with water and the *M. incognita* egg masses were stained with an aqueous solution of 5% eosin B and 0.5% acetic acid. The egg masses (red spots on the roots) were quantified.

Statistical analyses

Results from each experiment were analysed by comparing measured parameters for mycorrhized and non-mycorrhized plants. Differences between experimental conditions were tested by Student's t-Test at significant levels ($P < 0.05$) using R Software.

RESULTS

Figure 1 shows effects of inducing AMF root colonisation of tomato from direct inoculation before seedling transplantation, compared to formation of a MN in the

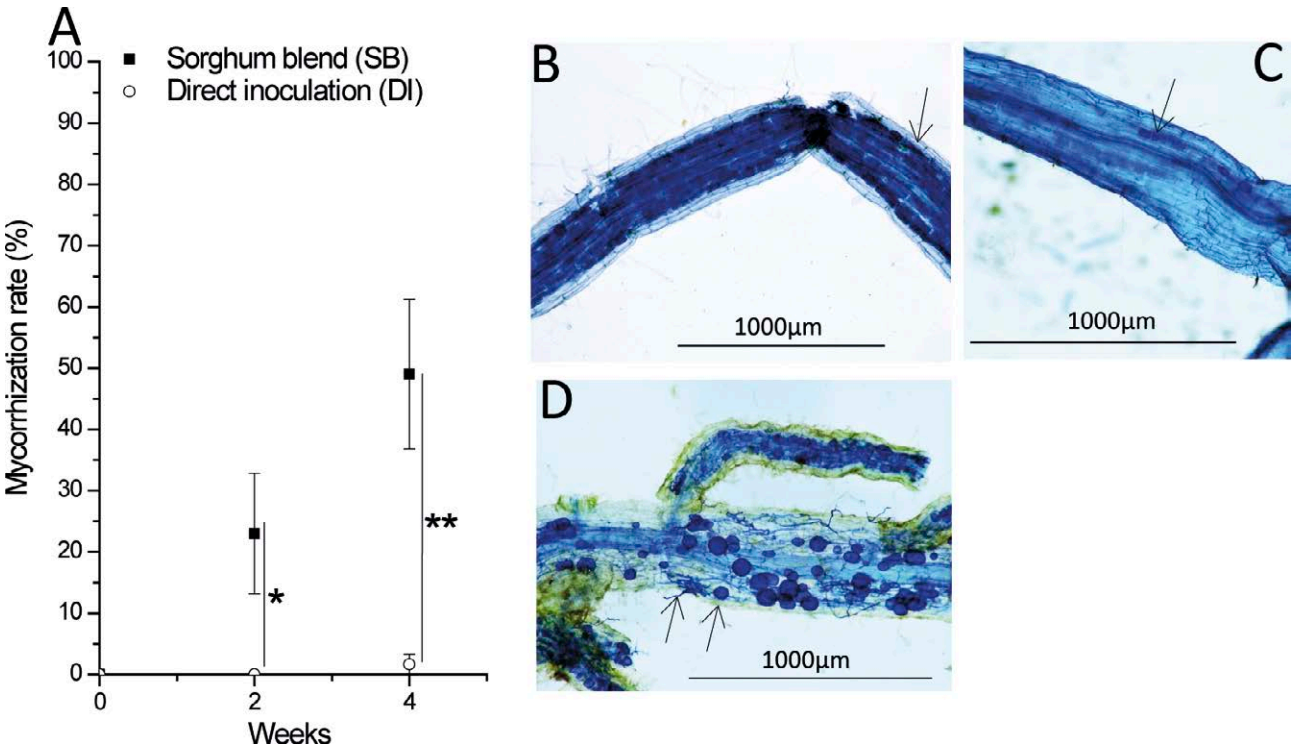

Figure 1. (Graph A) Mean mycorrhization rates (and standard errors: n ≥ 4) in tomato roots resulting from different AMF inoculation procedures at 2 and 4 weeks after inoculation. Before the tomato seedlings were transplanted to pots, a commercial inoculum was applied directly to their roots (direct inoculation: DI), or the soil was blended with leaves and roots of 6-week-old mycorrhized sorghum plants (micrograph D) (sorghum blend: SB). * and **, respectively, indicate differences at $P < 0.05$ and 0.01. Characteristic AMF colonisation of tomato roots grown for 4 weeks after SB (micrograph B) or DI (micrograph C) treatments. Arrows indicate typical AMF structures.

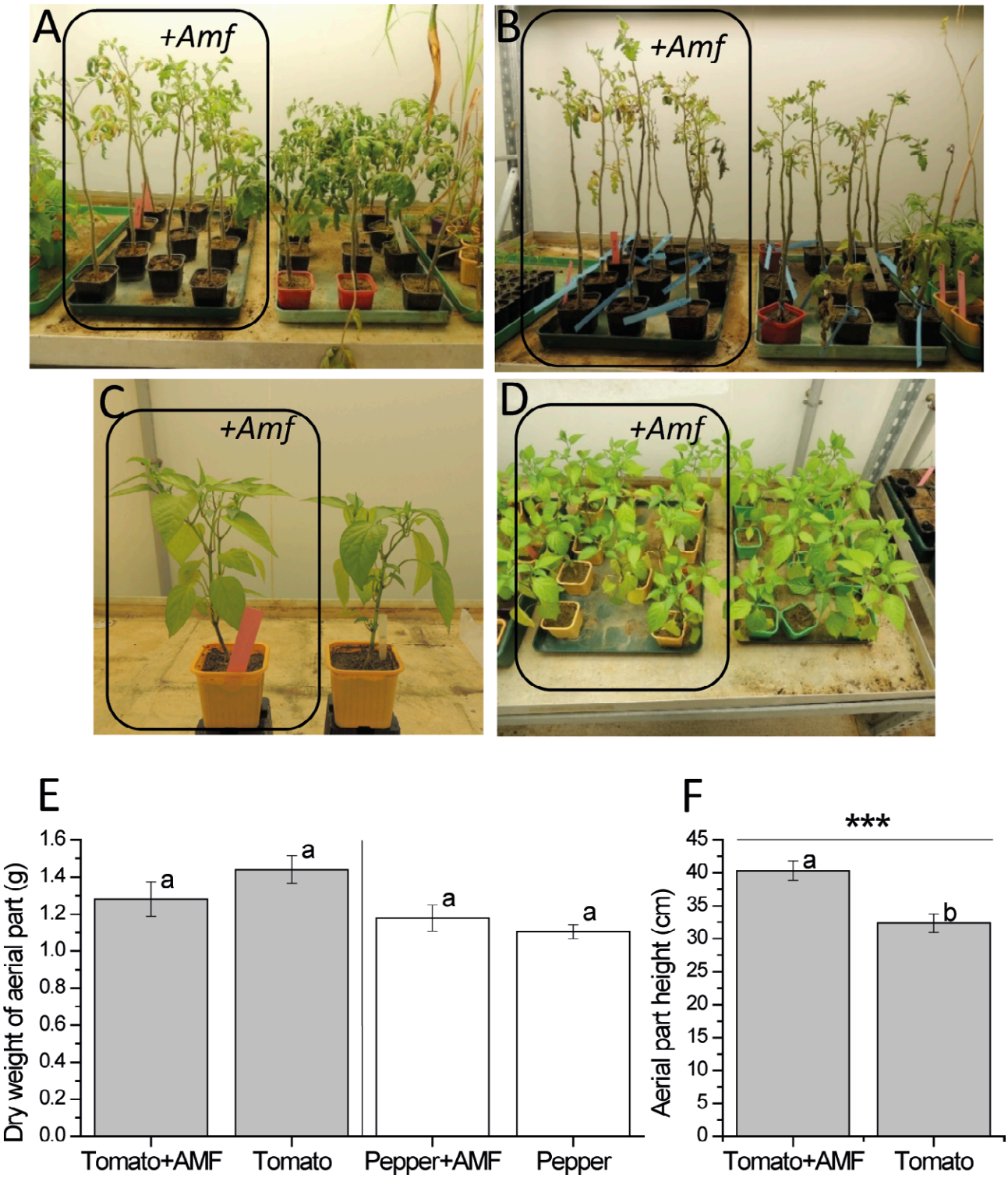

Figure 2. Plants grown in growth chambers for evaluating AMF effects on root knot nematode (RKN) development. Tomato plants at 4 weeks (micrograph A) and 6 weeks (micrograph B) after RKN inoculation. Pepper plants (micrographs C and D) 6 weeks after inoculation with RKN. Means (and standard errors: $n \geq 9$) of shoot dry weights (Graph E) and plant heights (Graph F) for 12-week-old tomato and pepper plants 6 weeks after inoculations with J2s of *Meloidogyne incognita*. Means accompanied by different letters are significantly different ($P < 0.001$ (***), Student's test).

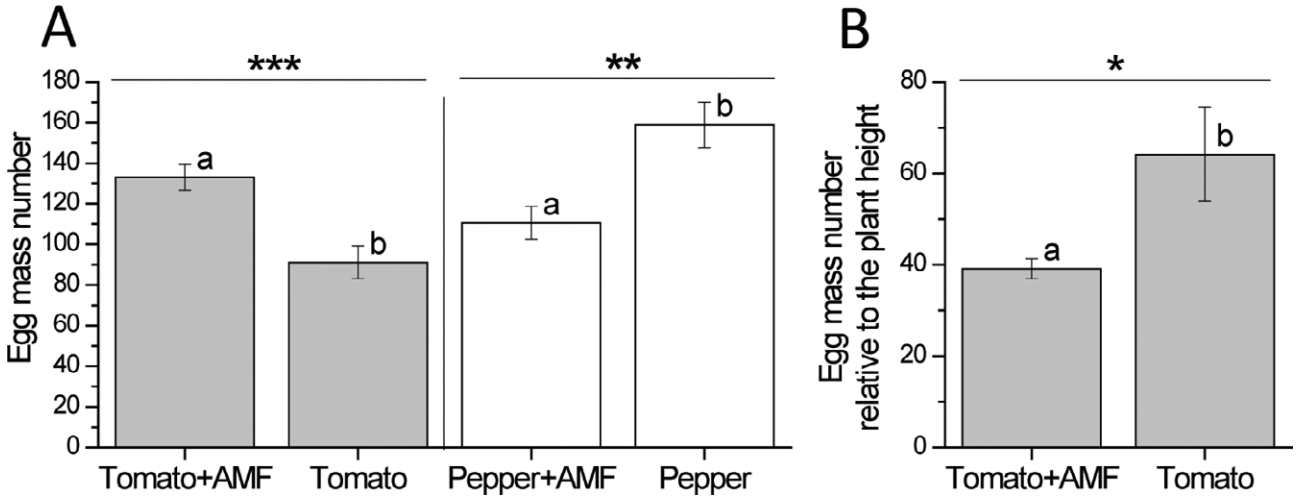

Figure 3. Mean numbers of *Meloidogyne incognita* egg masses in root segments of tomato or pepper plants (Graph A), and mean numbers of egg masses (normalised to plant height) in root segments of tomato plants (Graph B), with or without AMF inoculation treatments, 6 weeks after inoculations with J2 nematodes. Means accompanied by different letters are significantly different ($n \geq 9$: $P < 0.05$ (*), 0.01 (**) or 0.001 (***), Student's test).

soil. Sorghum developed mycorrhization rates of 50–70% within 6 weeks before the tomato seedlings were transplanted. After 2 weeks of culture, tomato roots from the SB treatment had a mean of 22% mycorrhization, whereas the plants from the DI treatment had no mycorrhization. After 4 weeks, roots from the SB treated plants had a mean of 49 % of mycorrhization, while the DI treated plants had very low mycorrhization rates (<5%). The previous formation of a MN in the media accelerated the mycorrhization of tomato roots, which under the growth chamber conditions required 6 weeks for development of mycorrhization of approx. 40%.

To evaluate the protective potential of the AMF under growth cabinet conditions, the effects of conventional mycorrhization against *M. incognita* development were assessed in tomato and pepper plants. Before *M. incognita* inoculation, tomato roots had 40% (± 18% S.D.) mycorrhization and pepper roots had 68% (± 21% S.D.) mycorrhization. At 4 weeks after *M. incognita* inoculation, the AMF treated tomato plants had longer stems and more abundant foliage than the uninoculated plants (Figure 2A). The tomato plants were severely affected during the last 2 weeks of RKN infection. At the end of the experiment, the non-mycorrhized plants had shorter stems and more withered leaves than the mycorrhized tomato (Figure 2B). AMF treatment gave no obvious on shoot dry matter of the plants (Figure 2E), but mycorrhization induced significantly increased plant height (Figure 2F).

The reproduction rates of the nematodes were evaluated by counting the numbers of egg masses produced by *M. incognita* females, which represents the population of nematodes able to complete life cycles within host roots. There was a significant decrease (almost 30%) of egg masses in roots of the AMF treated pepper plants (Figure 3A). Mycorrhized tomato plants had greater numbers of egg masses than pepper plants (Figure 3A). However, the relatively unfavourable state of the non-mycorrhized tomato for RKN infection could also indicate that tomato was a less suitable host than pepper for RKN development. Therefore, the numbers of egg masses were normalised to the shoot height of tomato plants (Figure 3B). The resulting values of mycorrhized tomato plants were on average 40% less than for non-mycorrhized plants.

DISCUSSION

Mycorrhization of tomato plants can be challenging due to their low mycotrophy compared to other species (Schroedder and Janos, 2004). The present study has demonstrated that developing a MN in soil before transplanting of seedlings is a promising procedure for improving tomato mycorrhization. We used sorghum-sudangrass because it has rapid growth, low nutrient demand, high mycotrophy and biofumigant properties, and is a known nematode trap crop. The sorghum variety selected here is currently used as a cover crop for nematode control which can be interplanted with legumes such as soybean (Djian Caporalino *et al.,* 2019; Dover *et al.,* 2004). Therefore, the proliferation of AMF by a

highly mycothrophic host, which is eventually harvested and blended with soil, could be a useful technique for improving plant fitness and for RKN control, if the host also has nematicidal properties, as for the sudangrass cultivar selected. Rapid mycorrhization using CMNs has been previously tested by Derelle *et al*., (2012). These types of experiments under *in vitro* conditions, require barriers between plants to avoid competition and did not use relevant crop plants. In the present study, the MN developed by the sorghum plants could provide increased amounts and viability of AMF compared to more usual AMF inoculum. This approach probably bypasses the low mycotrophy of tomato. Increased activity and intact spores or hyphae could explain the acceleration of AMF colonisation on tomato. However, many aspects addressing the early mycorrhization of tomato by MN remain unclear. For example, a comparative study of the response to the commercial AMF and the MN inoculum to the chemical signalling (i.e. branching factors) from the potential host has not been carried out.

Protection of pepper plants due to AMF has been previously demonstrated for *Fusarium*, *Phytophthora*, and *Rhizoctonia* pathogens (Sahi and Khalid, 2007; Sid Ahmed *et al.,* 2003; Sid Ahmed *et al.,* 1999). In other *Solanaceae*, protection of plants against phytoparasitic nematodes due to host mycorrhization has been evaluated for tobacco, with reductions of 25–35% of *Heterodera solanacearum* cysts (Fox and Spasoff, 1972), eggplant, with mycorrhized roots presenting 87% fewer galls of *M. incognita* than non-mycorrhized roots (Horta, 2015), and mycorrhized tomato, with a 13% reduction of *M. incognita* compared to controls without AMF (Masadeh, 2005). Castillo *et al.,* (2006) also evaluated the protection of olive plants using AMF, against *M. javanica* and *M. incognita* under controlled conditions.

Results from the present study indicate that a 6 week mycorrhization period prior to *M. incognita* infection considerably decreased RKN development in pepper. Host nutrition and root development were specifically restricted in this experiment, which probably explains the abnormal state of the plant shoots. Pepper plant were more tolerant than tomato under the experimental conditions of this study. This research is one of few studies reporting ability of AMF to decrease *M. incognita* development in pepper. In tomato we verified increased tolerance to *M. incognita* infection symptoms. The symptoms of infection by *M. incognita* on tomato were more attenuated when roots were treated with AMF. Even so, egg masses were more abundant in mycorrhized plants, so we considered plant height for adjusting numbers of nematode masses in roots. These indices are extensively used for estimating the whole plant infection, considering RKN proliferation and general plant development (Mateille *et al.,* 2005). The enhanced phenotype of AMF treated tomato shoots was possibly due to acclimation, which could help hosts to resist RKN infections for long periods. Hyphae replacing part of roots damaged by *M. incognita* could cause tomato tolerance to *M. incognita* infections. Additionally, shoot configuration from environmental stress may also be important, as photosynthetic activity and leaf development can be positively affected by the AMF colonisation (Chastain *et al.,* 2016; Chandrasekaran *et al.,* 2019). This means that more *M. incognita* reproductive cycles can occur in mycorrhized hosts, whereas non-mycorrhized plants will not withstand RKN development because roots and shoots grow poorly and the plants will rapidly die due to infections. Economically, AMF treatments may provide enhanced or more consistent production of tomato fruit despite *M. incognita* proliferation. The differences in results between tomato and pepper plants confirm that AMF bioprotection is dependent on host species (Veresoglou and Rillig, 2012).

Revitalisation of indigenous AMF by highly mycotrophic plants with nematicidal properties could be combined with resistant horticultural varieties for crop bioprotection and durable control of RKNs. The results of the present study on tomato also suggest that future research should assess leaf acclimation of mycorrhized plants under RKN biotic stress, using *in vivo* approaches such as monitoring of chlorophyll-a fluorescence.

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