



Mycorrhizal colonization and spore density in *Citrus sinensis*-weed interaction

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Abstract

Arbuscular mycorrhizal fungi (AMF) are microorganisms that establish symbiotic associations with the roots of most crops, enhancing water and nutrient uptake, thus improving growth and yield. However, limited attention has been given to the interactions between crops, weeds and AMF. This study investigates AMF root colonization and spore density in *Citrus sinensis* (L.) cv. Thompson Navel and dominant weed species within a Mediterranean orchard in El-Tarf Province, Algeria. Different sections of the orchard were characterized by varying dominant weed species: *Oxalis pes-caprae* in the western area (S1), *Medicago polymorpha* in the center (S2), *Poa trivialis* in the east (S3), and minimal weed presence at the edge (S4). Root colonization levels indicated low mycorrhizal intensity (M%) in both *C. sinensis* and dominant weeds, ranging from 3.72% to 15%. Spore density in S1, S2, and S3 varied between 178 and 432 spores per 50 g of soil, whereas S4 had a significantly higher density of 897 spores (a 404% increase in comparison to S1). *C. sinensis* and co-occurring weeds had low mycorrhizal colonization, while the highest spore density was observed in the section without dominating weeds, highlighting the influence of weed identity on AMF dynamics and the detrimental effects of conventional agricultural practices.

Keywords Arbuscular mycorrhizal fungi · Root colonization · *Citrus sinensis* · *Medicago polymorpha* · *Poa trivialis* · *Oxalis pes-caprae*

1 Introduction

Most terrestrial plants form symbiotic relationships with a diverse range of soil microorganisms, including arbuscular mycorrhizal fungi (AMF). Through a mutually beneficial exchange, AMF enhance plant uptake of water, available phosphorus and other immobile soil nutrients (Smith and Read 2008), protect against pathogens (Meddad-Hamza et al. 2023), and contribute to shaping and maintaining soil structure and dynamics (Rillig and Mummey 2006; Frey 2019). Recent studies confirmed that AMF are integral components of plant-associated microbiomes, influencing microbial consortia in the rhizosphere (Frey-Klett et al. 2011). A strong association with AMF can stimulate plant growth responses, potentially influencing ecosystem diversity and productivity (van der Heijden et al. 2008). Therefore, assessing the role of

mycorrhizal symbiosis in the field requires evaluating root colonization potential and presence in the soil.

Algeria's Citrus orchards cover approximately 80,000 ha, with oranges occupying around 54,000 ha. National Citrus production augmented from 1.1 M t in 2011 to 1.5 M t in 2021, reaching about 1.8 M t by 2024, with oranges (particularly Thomson Navel) being the predominant cultivar. These orchards play an essential role in meeting the demand for Citrus fruits and significantly contribute to Algeria's agricultural economy (Source: <https://www.agrialgerie.com/la-filiere-agrume-se-porte-bien-en-2023-2024-avec-une-production-estimee-a-18-million-de-tonnes>; accessed 17th June 2025). However, Citrus cultivation faces multiple challenges, including diseases, pests, and competition from weeds, which can reduce yields and disrupt beneficial plant–microbe interactions (Horowitz 2015).

Citrus plants have limited root surface area and short hairs, which reduces their ability to efficiently absorb water and nutrients. Consequently, AMF colonization becomes essential to improving water and nutrient acquisition in these plants (Wu and Xia 2006; Ortas 2012).

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On the other hand, weeds coexisting with Citrus may also form symbioses with AMF, potentially acting as reservoirs or competitors in the mycorrhizal network (Reinhart and Callaway 2006). While positive weed-AMF interactions may enhance AMF inoculum in the soil, certain species can also disrupt symbiosis by altering root exudate profiles or competing for fungal partners (El Omari and Ghachtouli 2021; Brundrett and Tedersoo 2018).

Despite increasing interest in AMF ecology, studies on weed-crop-AMF interactions remain limited in Mediterranean orchards, especially in North African agroecosystems.

The present study investigates the arbuscular mycorrhizal symbiosis between *Citrus sinensis* and dominant weed species in a Mediterranean orchard located in Chihani (El Tarf province, Algeria). Mycorrhizal root colonization levels, spore density and soil physicochemical properties were evaluated. It was hypothesized that the presence of dominant weed species could enhance AMF colonization and spore density in *C. sinensis* roots by acting as complementary hosts and contributing to a more diverse and abundant fungal network.

2 Material and methods

2.1 Study site

The orange orchard is located in Chihani (36°38'38.8"N, 7°47'39.2"E), El Tarf province, Algeria. El Tarf has a Mediterranean climate, characterized by hot, arid summers and mild, rainy winters. In 2021, the recorded mean annual temperature was 18.3 °C, with total annual precipitation reaching 694 mm. Established in the 1960s, the orchard covers an area of 6 hectares and is cultivated with the Thompson Navel variety on clay loam soil.

Agricultural practices include the application in December of nitrogen (80 kg/ha), phosphorus (120 kg/ha), and potassium (120 kg/ha). Irrigation was carried out by sprinkling. In May or June, insecticides were applied at a dosage of 200–300 g per 100 L/ha to control spider mites and flies.

2.2 Inventory of weeds in the orange orchard

During spring of 2021 (March), an inventory of weeds competing with *Citrus sinensis* was conducted according to a systematic sampling approach, followed by the determination of the cover-abundance levels. A floristic survey was carried out based on the minimum area method (Braun-Blanquet 1932). To identify the most dominant weeds in the orchard, the modified cover-abundance method of Braun-Blanquet, as described by Wikum and Shanholtzer (1978), was followed. This method determines species coverage within the minimum area. The

cover-abundance range include: + (Very low coverage), 1 (Low coverage < 5%), 2 (5 to 25%), 3 (25 to 50%), 4 (50 to 75%) and 5 (more than 75% of the surface).

A total of 15 weed taxa from nine botanical families were recorded. The identified species included: *Oxalis pes-caprae* L., *Medicago polymorpha* L., *Poa trivialis* L., *Lathyrus ochrus* L., *Cerastium glomeratum* Thuil., *Stellaria media* L., *Helminthotheca echinoides* L., *Matricaria chamomilla* L., *Ranunculus muricatus* L., *Smyrniololium olusatrum* L., *Lolium perenne* L., *Brassica rapa* L., *Sonchus oleraceus* L., *Arum italicum* Mill., *Picris hieracioides* L.

For the biogeographical origins, five taxa belonged to the Mediterranean element in the broad sense, while ten taxa were part of the continuous intercontinental group (Eurasian, Circumboreal, and various cosmopolitan species). The only exotic species was *O. pes-caprae*, native to South Africa.

2.3 Division of the orchard according to coverage levels

As a preliminary observation, *Oxalis pes-caprae* dominated the western area of the orchard, *Medicago polymorpha* was predominantly found in the central area, and *Poa trivialis* was most abundant in the eastern part, covering approximately 20%, 20%, and 30% of the total area, respectively. In contrast, weed presence was minimal along the orchard edges. Based on this distribution, the orchard was artificially divided into four sections according to the dominant weed species: (i) S1 with *O. pes-caprae*, (ii) S2 with *M. polymorpha*, (iii) S3 with *P. trivialis*, and (iv) a control section (S4).

Furthermore, the Braun-Blanquet cover-abundance assessment (Table 1) indicated that *O. pes-caprae*, *M. polymorpha*, and *P. trivialis* were each assigned a level 4 on the scale, while other weeds exhibited lower coverage levels.

Table 1 Determination of coverage levels of the dominant weeds (*Oxalis pes-caprae*, *Medicago polymorpha* and *Poa trivialis*) and other weeds in the sections from the *Citrus sinensis* orchard

Weeds	Coverage levels of weeds in the sections of the orchard (%)			
	S1	S2	S3	S4
<i>Oxalis pes-caprae</i>	50—75	5—25	5—25	< 5
<i>Medicago polymorpha</i>	5—25	50—75	5—25	+
<i>Poa trivialis</i>	5—25	5—25	50—75	< 5
Other weeds	< 5	< 5	< 5	< 5

S1, section dominated by *O. pes-caprae*; S2, section dominated by *M. polymorpha*; S3, section dominated by *P. trivialis*; S4, control section

2.4 Collection of root and soil samples

On March 25, 2021, root samples were collected from orange trees and the dominant weed species in each section of the orchard. Five plants of each species were randomly selected as representatives of their respective sections.

Roots of *O. pes-caprae*, *M. polymorpha*, and *P. trivialis* were harvested from a soil depth of 10–20 cm. *C. sinensis* roots were sampled from a depth of 30–40 cm.

Rhizospheric soil was sampled simultaneously from the same plants. For each plant, soil was collected from three points near the root zone. These samples were then homogenized to create a single representative sample for each section.

2.5 Soil physicochemical properties

Soil analysis was conducted for each section using standard methods. Phosphorus availability (P_2O_5 , Olsen method), total nitrogen (N, Kjeldahl method), soil organic matter (SOM, Anne method), and pH (H_2O) were analyzed at the agronomic laboratory of the FERTIAL company in Annaba province, Algeria.

2.6 Estimation of root colonization levels

To assess AMF root colonization levels in *C. sinensis*, *O. pes-caprae*, *M. polymorpha* and *P. trivialis*, fine roots were stained following the method of Phillips and Hayman (1970) using lactic acid. Root samples were first immersed in a 10% KOH solution and heated to 90 °C for 30 min. After rinsing, the roots were stained with a 0.05% trypan blue solution and heated to 120 °C for 20 min, followed by a final rinse with distilled water.

Next, the roots were divided into segments measuring 1 cm in length and positioned between a slide and coverslip in a glycerol droplet. Microscopic observation was carried out at a magnification of $\times 400$ to examine AMF colonization levels in the stained root fragments.

Mycorrhizal colonization was assessed and quantified following Trouvelot et al.'s (1986) method using the

MYCOCALC software (www.dijon.inra.fr/mychintec/Mycocalc-prg/download.html). The software facilitated the calculation of three colonization parameters. F % represents the frequency of mycorrhizal colonization and is expressed as the percentage of colonized roots. This shows the distribution and occurrence of mycorrhizal colonization points in roots. M % is the mycorrhizal intensity of root cortex. It indicates the ratio of colonized cortex in comparison to the whole root system. This parameter reflects the overall extent of mycorrhizal colonization in the root system. The arbuscular colonization content (A%) represents the proportion of arbuscular colonization relative to the entire root system. It indicates the percentage of the root system that contains arbuscules.

2.7 Isolation and quantification of AMF spores

Following the wet sieving technique (Gerdemann and Nicolson 1963), AMF spores were meticulously separated from soil samples. Each fraction of soil, post-sieving, was subjected to examination under a binocular microscope. Spore counts were taken for every 50 g of soil, repeated three times.

2.8 Statistical analysis

A one-way ANOVA was performed for soil physicochemical parameters, root colonization levels and spore density. Means were separated by Tukey Honestly Significant Difference (HSD) test at $P < 0.05$ level. Statistical analysis of the results was computed in R 4.3.1.

3 Results

3.1 Physicochemical properties of the soil

In this orange orchard, soil physicochemical analysis showed that in the sections dominated by *Oxalis pes-caprae* (S1), *Medicago polymorpha* (S2) and *Poa trivialis* (S3) (Table 2), the soil was neutral to weakly alkaline, with pH values

Table 2 Soil physicochemical parameters of each section in the *Citrus sinensis* orchard

Soil physicochemical parameters	Sections of the orange orchard				Significance
	S1	S2	S3	S4	
N (%)	0.083 $\pm$ 0.013 (a)	0.059 $\pm$ 0.008 (ab)	0.037 $\pm$ 0.007 (b)	0.057 $\pm$ 0.01 (b)	P=0.002
P_2O_5 (mg/L)	6.66 $\pm$ 0.35 (a)	3.22 $\pm$ 0.05 (c)	1.91 $\pm$ 0.09 (d)	3.9 $\pm$ 0.10 (b)	P<0.01
pH (H_2O)	7.2 $\pm$ 0.10 (c)	7.35 $\pm$ 0.05 (ab)	7.31 $\pm$ 0.08 (bc)	7.45 $\pm$ 0.05 (a)	P=0.002
SOM (%)	1.00 $\pm$ 0.05 (a)	1.01 $\pm$ 0.07 (a)	1.09 $\pm$ 0.2 (a)	1.10 $\pm$ 0.1 (a)	P=0.392

Means followed by different letters are significantly different at $P < 0.05$

ranging from 7.20 to 7.45. S1 had the lowest pH, which was significantly different from the other sections.

Available phosphorus (P_2O_5) levels were extremely low across all sections. S1 had the highest concentration at 6.66 mg/L, followed by the control (S4) with 3.9 mg/L. In contrast, S3 had the lowest phosphorus level at 1.91 mg/L.

Total nitrogen content ranged from 0.037% to 0.083%, with S1 showing the highest significant value. Additionally, all sections had very low soil organic matter content, ranging from 1.01% to 1.1%.

3.2 AMF root colonization levels

In *C. sinensis*, the frequency of colonization (F%) ranged from 38.71% to 48.77%, with a mean of 44.51% (Fig. 1). Weed species exhibited a broader F% range, from 29.28% to 91.42%, with *Medicago polymorpha* in S2 showing the highest significant value. Except for section S2, the difference in colonization levels between *C. sinensis* and the weeds was not statistically significant (Fig. 1).

Mycorrhizal intensity (M%) was generally low in all sections (Fig. 2). In *C. sinensis*, M% ranged from 5.03% to 14.20%, with a significant difference observed between *C. sinensis* in S1 and S2. The dominant weed species had M% values ranging from 3.72% to 15%. The lowest significant M% was recorded in *P. trivialis* (S3) at 3.72%, while the highest value was observed in *M. polymorpha* (S2) (Fig. 2).

Generally, differences in M% between *C. sinensis* and the dominant weeds were not significant within each section,

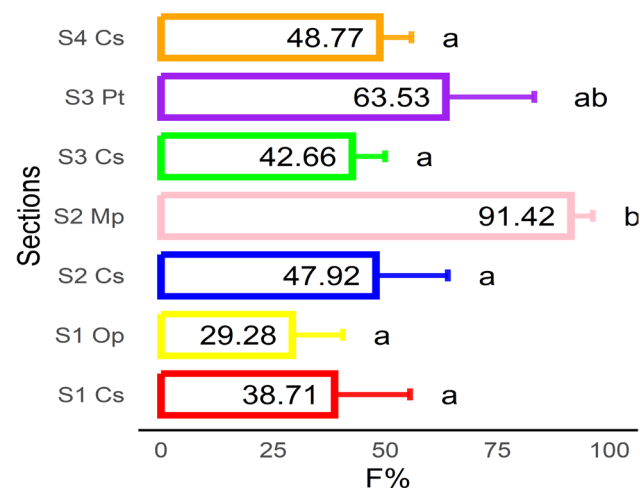


Fig. 1 Frequency of mycorrhizal colonization (F%) of *Citrus sinensis* and dominant weeds *Oxalis pes-caprae*, *Medicago polymorpha* or *Poa trivialis*. (S1 Cs, *C. sinensis* in S1; S1 Op, *O. pes-caprae* in S1; S2 Cs, *C. sinensis* in S2; S2 Mp, *M. polymorpha* in S2; S3 Cs, *C. sinensis* in S3; S3 Pt, *P. trivialis* in S3 and S4 Cs, *C. sinensis* in control S4). Different letters between columns indicate significant differences according to Tukey's HSD test ($P < 0.05$)

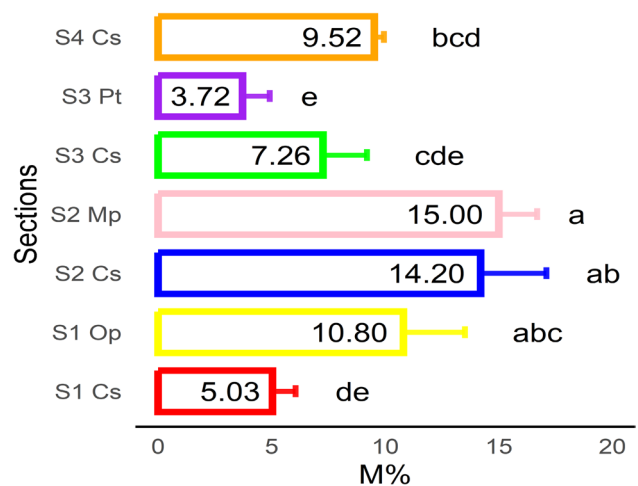


Fig. 2 Mycorrhizal intensity of colonization (M%) of *Citrus sinensis* and dominant weeds *Oxalis pes-caprae*, *Medicago polymorpha* or *Poa trivialis*. (S1 Cs, *C. sinensis* in S1; S1 Op, *O. pes-caprae* in S1; S2 Cs, *C. sinensis* in S2; S2 Mp, *M. polymorpha* in S2; S3 Cs, *C. sinensis* in S3; S3 Pt, *P. trivialis* in S3 and S4 Cs, *C. sinensis* in control S4). Different letters between columns indicate significant differences according to Tukey's HSD test ($P < 0.05$)

except in S1, where *O. pes-caprae* showed a significantly higher M% compared to *C. sinensis* (Fig. 2).

Arbuscular content (A%) in the entire root system ranged from 3.32% to 6.70% in *C. sinensis* across all sections (Fig. 3). The highest percentages were recorded in *C. sinensis* from S1 (6.70%) and S4 (5.97%).

In weed species, A% varied from 2.64% to 8.08%, with *P. trivialis* in S3 showing the lowest significant value.

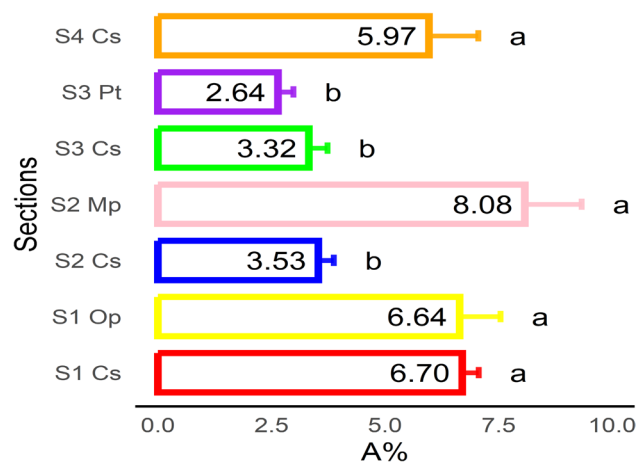


Fig. 3 Mycorrhizal arbuscular content (A%) of *Citrus sinensis* and dominant weeds *Oxalis pes-caprae*, *Medicago polymorpha* or *Poa trivialis*. (S1 Cs, *C. sinensis* in S1; S1 Op, *O. pes-caprae* in S1; S2 Cs, *C. sinensis* in S2; S2 Mp, *M. polymorpha* in S2; S3 Cs, *C. sinensis* in S3; S3 Pt, *P. trivialis* in S3 and S4 Cs, *C. sinensis* in control S4). Different letters between columns indicate significant differences according to Tukey's HSD test ($P < 0.05$)

Moreover, *M. polymorpha* in S2 had a significantly higher A% compared to *C. sinensis* in the same section (Fig. 3).

3.3 AMF spore density

Spore density in S1, S2, and S3 ranged from 178 to 432 spores per 50 g of soil (Fig. 4). However, S4 exhibited a significantly higher spore count, with 897 spores, representing an increase of 404%, 221.5%, and 107.63% compared to S1, S2, and S3, respectively.

4 Discussion

The results revealed that the section dominated by *Oxalis pes-caprae* (S1) had a low soil pH when compared to other sections. This can be attributed to the exudation or decomposition of oxalic acid, which is a potent organic acid, abundant in *O. pes-caprae* tissues (Lane 1984). The elevated available phosphorus (P) levels observed in this section could also be linked to oxalate compounds, which act as phosphorus-chelating agents and thus enhance P availability in the

rhizosphere (Cannon et al. 1995). These results suggest that *O. pes-caprae* may not compete directly with *Citrus sinensis* for phosphorus, however, it could facilitate its bioavailability, benefiting neighbouring crops. On the other hand, lower P concentrations in sections dominated by *Medicago polymorpha* (S2) and *Poa trivialis* (S3) show interspecific competition for soil nutrients.

Despite *O. pes-caprae* being a short-lived species, the higher nitrogen and soil organic matter content in S1 contradicts previous studies reporting negligible impact of this species on nitrogen and carbon cycling (Vilà et al. 2006).

Root mycorrhizal frequency (F%) was moderate to high in both *C. sinensis* and weeds, consistent with Chen et al.'s (2004) observation of AMF colonization in the majority of weeds within a Citrus orchard, confirming AMF's role in agroecosystems. Graham and Syvertsen (1985) stated that mycorrhizal dependency among Citrus trees can be significantly variable.

Mycorrhizal intensity (M%) in *C. sinensis* was generally low, aligning with observations by Wang et al. (2019), who reported colonization rates below 20% in citrus roots. These low colonization levels may result from

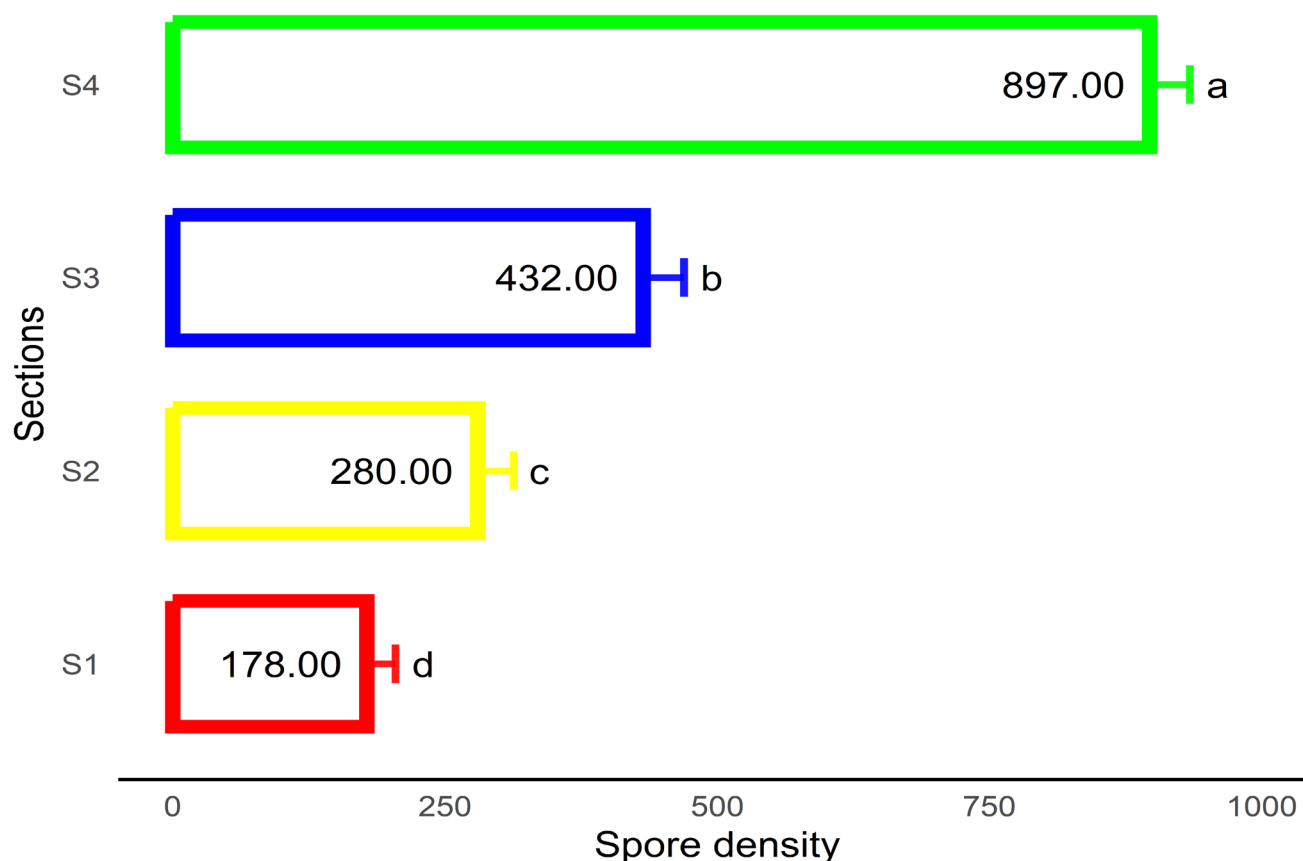


Fig. 4 AMF spore density in sections dominated by *Oxalis pes-caprae*, *Medicago polymorpha* or *Poa trivialis* in a *Citrus sinensis* orchard. (S1, dominated by *O. pes-caprae*; S2, dominated by *M. poly-*

morpha; S3, dominated by *P. trivialis*; S4, control). Different letters between columns indicate significant differences according to Tukey's HSD test ($P < 0.05$)

a combination of environmental factors, suboptimal soil texture and the genetic background of the host plant. Additionally, the physiological age of the trees and a reduced capacity of native AMF propagules to establish symbiosis probably reduced colonization. Furthermore, specific morphological and physiological traits of citrus roots, as noted by Wu and Xia (2006), may restrict AMF penetration and development.

Despite low soil phosphorus levels, *C. sinensis* had low M%, contrary to studies indicating that phosphorus limitation enhances AMF association (Wang et al. 2013). This could be explained by orchard management practices such as pesticide use and tillage which hinder AMF propagation, root colonization, and hyphal spread (Gryndler et al. 2006; Bowles et al. 2017). Pesticides can interfere with the pre-symbiotic phase of AMF by inhibiting spore germination and hyphal growth (Malfatti et al. 2021), thus decreasing colonization in roots.

Among the weed species, *M. polymorpha* had the highest M%, corroborating previous observations reporting 70.2% infection in citrus orchards (Ishii et al. 1998). In contrast, *P. trivialis* had the lowest colonization rates, confirming results by Shahzad et al. (2015) (M% not exceeding 4.56%).

Interestingly, M% in *O. pes-caprae* and *M. polymorpha* was comparable to or higher than in *C. sinensis*, indicating that these weeds probably acquire functional benefits from AMF symbiosis and potentially contribute to maintaining AMF inoculum potential in the soil.

Overall, arbuscular content (A%) was low in *C. sinensis*, possibly due to their short lifespan or seasonal phenology. Additionally, factors such as pesticides use during the AMF pre-symbiotic phase can hinder the initiation of colonization by affecting spore germination and mycelial proliferation (Malfatti et al. 2021), diminishing the symbiotic relationship.

The highest AMF spore density was found in the control section (S4), where no dominant weeds were present. This result suggests that in this orchard, the presence of certain weeds may not enhance, and probably reduce AMF sporulation. Competition for fungal partners, root exudate-mediated suppression, or differences in fungal taxa preference could explain the decreased spore production in sections dominated by *O. pes-caprae*, *M. polymorpha*, and *P. trivialis* (Reinhart et al. 2003; Hodge and Fitter 2013). This could also be attributed to reduced agricultural management at the orchard's edge, which may have created favorable conditions for AMF spore development, since conventional cultivation practices impact negatively AMF spore density (Oehl et al. 2004).

The high spore density in S3 is probably due to the ability of gramineous species such as *P. trivialis* to enhance AMF propagules and influence AMF community structure (Ishii et al. 2007; Malicka et al. 2020).

Although AMF spore densities were moderate to high in weed-dominated sections, root colonization in both *C. sinensis* and associated weeds remained comparatively low. This disconnect between spore abundance and root infection has been noted in previous studies, where spore numbers did not predict colonization intensity or functionality of the symbiosis (Smith and Read 2008; Youpensuk et al. 2009; Smith and Smith 2011). This can be explained by the fact that many AMF spores in the soil may remain dormant, non-viable, or belong to species with sporulation strategies not directly linked to efficient colonization (Brundrett et al. 1996; Hart and Reader 2002). This may also result from a combination of biotic and abiotic stresses, seasonal dynamics, AMF community composition, and the physiological status of host plants (Smith and Smith 2011). In particular, environmental factors such as soil moisture, temperature fluctuations, and pH can strongly influence spore germination and hyphal growth, thereby delaying colonization despite abundant propagules (Han et al. 2019; Johnson et al. 2013).

On the other hand, plant species differ in their degree of compatibility with AMF taxa, with some selecting for fungal partners that sporulate abundantly, however, with a less effective colonization (Helgason et al. 2002; Vandenkoornhuyse et al. 2003). In citrus, root structural traits such as thickened epidermal layers and reduced cortical cell numbers can further restrict AMF entry (Wu and Xia 2006). At the community level, interactions with soil microbiota, including competitive fungi and rhizosphere bacteria, may suppress AMF colonization even when propagules are abundant (Artursson et al. 2006; Verbruggen et al. 2013).

5 Conclusion

This study demonstrates that *Citrus sinensis* and weeds had generally low mycorrhizal intensity, while spore density being superior in the section without dominant weeds. This highlights the role of weed identity in shaping AMF communities, suggesting that not all weedy species are beneficial for AMF preservation in the soil. Moreover, orchard management practices such as tillage and pesticide application negatively affect AMF propagules viability and colonization, despite low soil phosphorus levels.

It is recommended to reduce soil disturbance such as tillage, limit pesticide application particularly during critical AMF development stages, and incorporate cover crops compatible with AMF. Such strategies promote sustainable citrus production and the long-term resilience of the agroecosystem.

Authors contributions HZ: Conception, field and lab manipulations, data processing.

HK: data processing.
 AMH: data processing.
 YB: field and lab manipulations.
 WN: lab manipulations.

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Data availability The data will be made available on request.

Declarations

Consent for publication The authors consent to publication.

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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