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Original article

Growth response of different species of *Ziziphus* to inoculation with arbuscular mycorrhizal fungi

B. Thioye[1,2,3,6,a], S. Mania[4], A. Kane[1,2], C. Ndiaye[2], A. Ould Soule[7], D. Fall[5], R. Duponnois[3], S.N. Sylla[1,2] and A.M. Bâ[3,6]

[1] Département de Biologie Végétale, Université Cheikh Anta Diop, BP 5005, Dakar, Senegal
[2] Laboratoire Commun de Microbiologie IRD/ISRA/UCAD, BP 1386, Bel-Air Dakar, Senegal
[3] Laboratoire des Symbioses Tropicales et Méditerranéennes, UMR113 INRA/AGRO-M/CIRAD/IRD/UM2-TA10/J, Campus International de Baillarguet, 34398 Montpellier, France
[4] Embrapa Agrobiologia, Km 7 BR 465 Seropédica, Rio de Janeiro, Cep 23891 000, Brazil
[5] Centre National de Recherches Forestières (CNRF), BP 2312, Dakar-Hann, Senegal
[6] Laboratoire de Biologie et Physiologie Végétales, Faculté des Sciences Exactes et Naturelles, Université des Antilles, BP 592, 97159 Pointe-à-Pitre, Guadeloupe, France
[7] Ecole Normale Supérieure de Nouakchott, BP 990, Mauritania

Summary

Introduction – **Many of species of *Ziziphus* are underutilized crops despite their potential interests in agroforestry systems. Except for *Ziziphus mauritiana*, the effectiveness of arbuscular mycorrhizal fungi (AMF) on growth and mineral nutrition of *Ziziphus* spp. is not known. The aim of our study was to evaluate the mycorrhizal dependency (MD) of *Ziziphus* spp. in greenhouse conditions.** *Materials and methods* – **Three isolates of AMF were used: *Rhizophagus irregularis* isolate IR27, *Funneliformis mosseae* isolate DAOM227131 and *Rhizoglomus intraradices* isolate DAOM197198, on seven species of *Ziziphus*: *Z. mauritiana*, *Z. lotus*, *Z. spina-christi*, *Z. mucronata*, *Z. amphibia*, *Z. abyssinica* and *Z. sphaerocarpa*. Plants were grown in nursery receiving 20 g portions of a crude inoculum of AMF. The experiment was set up as a 4 × 7 factorial design consisting of three AMF, one control (disinfected soil without inoculum) and seven *Ziziphus* spp.** *Results and discussion* – **Inoculation by AMF significantly improved growth and mineral nutrition of *Ziziphus* spp., particularly the P nutrition. Mycorrhizal dependency values of *Ziziphus* spp. declined with AMF in the following order: *R. irregularis* (69.51%), *R. intraradices* (63.58%) and *F. mosseae* (52.45%). Total length of AMF hyphae in soil samples from inoculated treatments was significantly higher in all *Ziziphus* spp. with *R. intraradices* combinations. The differences of MD among the tested *Ziziphus* spp. seem to be due to differences in the development of hyphal length in the soil and in P uptake by the external hyphae.** *Conclusion* – ***Rhizophagus irregularis* constitutes a promising tool for the production of higher quality nursery stock with expected improved performance of *Ziziphus* spp. in agroforestry systems.**

Keywords
Senegal, jujube, *Ziziphus* spp., mycorrhizal dependency, tree nursery, mineral nutrition, hyphal length, agroforestry system

[a] Corresponding author: babacarthioye@yahoo.fr.

Significance of this study

What is already known on this subject?

- The effectiveness of arbuscular mycorrhizal fungi (AMF) is well and widely known for the growth and mineral nutrition of *Z. mauritiana* seedlings.

What are the new findings?

- Mycorrhiza inoculation, particularly with *R. irregularis* isolate IR27, promoted seven species of *Ziziphus* (including *Z. mauritiana*) growth by enhancing significantly biomass production and nutrient uptake under greenhouse conditions.

What is the expected impact on horticulture?

- *Rhizophagus irregularis* isolate IR27 constitutes a promising tool for the production of higher quality nursery stock with potential improved field performance of species of *Ziziphus* in agroforestry systems.

Résumé

Réponse à l'inoculation de différentes espèces de *Ziziphus* avec des champignons mycorhiziens à arbuscules.

Introduction – **Plusieurs espèces de *Ziziphus* sont sous-utilisées malgré leur intérêt potentiel dans les systèmes agroforestiers. L'efficacité des champignons mycorhiziens à arbuscules (CMA) sur la croissance et la nutrition minérale de *Ziziphus* spp. n'est pas connue à l'exception de *Ziziphus mauritiana*. L'objectif de notre étude était d'évaluer la dépendance mycorhizienne (DM) de *Ziziphus* spp. en serre.** *Matériel et méthodes* – **Trois souches de CMA ont été utilisées: *Rhizophagus irregularis* isolat IR27, *Funneliformis mosseae* isolat DAOM227131 et *Rhizoglomus intraradices* isolat DAOM197198, sur sept espèces de *Ziziphus*: *Z. mauritiana*, *Z. lotus*, *Z. spina-christi*, *Z. mucronata*, *Z. amphibia*, *Z. abyssinica* et *Z. sphaerocarpa*. Les plants cultivés en pépinière ont reçu une portion de 20 g d'inoculum de CMA. L'expérience a été mise en place suivant un dispositif de type factoriel 4 × 7**

composé de trois CMA, un témoin non inoculé et sept *Ziziphus* spp. *Résultats et discussion* **– L'inoculation avec les CMA a considérablement amélioré la croissance et la nutrition minérale (en particulier le phosphore) des espèces de *Ziziphus*. Les valeurs de la dépendance mycorhizienne des espèces de *Ziziphus* ont diminué suivant l'ordre : *R. irregularis* (69,51%), *R. intraradices* (63,58%) et *F. mosseae* (52,45%). La longueur totale des hyphes de CMA dans les échantillons de sol était significativement plus élevée dans les traitements inoculés avec *R. intraradices*. Les différences de DM entre *Ziziphus* spp. semblent être dues à des différences au niveau du développement et de la longueur des hyphes dans le sol et de l'absorption de P par les hyphes extramatricielles.** *Conclusion* **– *Rhizophagus irregularis* constitue un outil prometteur pour la production de qualité supérieure de plants en pépinière avec des performances améliorées des espèces de *Ziziphus* dans les systèmes agroforestiers.**

Mots-clés
Sénégal, jujubier, *Ziziphus* spp., dépendance mycorhizienne, pépinière, nutrition minérale, longueur d'hyphes, système agroforestier

Introduction

Domestication of fruit trees could be achieved through a combination of approaches including selection and multiplication of quality planting material, fertilization, irrigation, pruning, and controlled mycorrhization (Bâ *et al*., 2003). One of the promising approaches that can be used in the domestication of indigenous fruit trees is the arbuscular mycorrhizal (AM) inoculation, since it is established that many of these fruit trees benefit in terms of growth and mineral nutrition from this symbiotic association (Guissou *et al*., 1998, 2016; Bâ *et al*., 2000, 2001; Mathur and Vyas, 2000; Sidibé *et al*., 2012). The AM symbioses are associations between roots of terrestrial plants and members of the fungal phylum *Glomeromycota* (Schüßler *et al*., 2001). These are the most common and widespread symbioses, involving 80% of land plants and at least 250 morphologically defined arbuscular mycorrhizal fungi (AMF) (Davison *et al*., 2015). The AMF receive plant-synthetized carbon and increase capacity of plants for nutrient capture through its network of external hyphae (Smith and Read, 2008). The AMF are promoted as biofertilizers for sustainable agriculture (Verbruggen *et al*., 2013; Hart *et al*., 2015). Nevertheless, they are poorly investigated, particularly with the indigenous fruit trees from the Sahelian and Sudanian zones of West Africa.

Ziziphus mauritiana Lam., commonly named jujube, is one of the indigenous fruit tree species farmers maintain on their farms as a source of food and income in West Africa (Ouédraogo *et al*., 2006). Jujube is a multipurpose tree providing mainly fruits and fodder. It also planted to reforest degraded soils and as hedgerows to protect crops. Nearly every part of *Ziziphus* plants can be utilized. Due to the high dry weight protein content, leaves are an important source of protein for cattle (Arndt and Kayser, 2001; Ngwa *et al*., 2000). Responses of *Z. mauritiana* to AM inoculation differ with respect to functional compatibility, measured as mycorrhizal formation, root colonization, nutrient absorption and morphological properties of the root (Guissou *et al*., 1998; Bâ *et al*., 2000, 2001; Mathur and Vyas, 2000; Sidibé *et al*., 2012). Guissou *et al*. (1998) showed that *Rhizophagus irregularis*, isolate IR27 (syn. *Glomus aggregatum* IR27; [Bâ *et al*., 1996]), was one of the AMF providing high growth and mineral nutrition benefits for *Z. mauritiana* seedlings. Mycorrhizal dependency (MD) of *Z. mauritiana* as defined by Plenchette *et al*. (1983), can reach a maximum of 78%. Similar results were found by Guissou *et al*. (2001) and Sidibé *et al*. (2012). Bâ *et al*. (2001, 2003) concluded that the absence of AM inoculation on *Z. mauritiana* seedlings in nursery could lead to higher mortality of outplanted jujube trees in the field. It is also well known that responses of AM inoculation vary greatly from one plant species to another and even between origin and cultivars within a single species (Smith *et al*., 2009). Guissou *et al*. (2016) highlighted the importance of considering seed provenance of *Z. mauritiana* when performing pre-selection of mycotrophic plant candidates prior to large-scale fruit tree propagation in orchards and agroforestry systems.

The complex taxonomy in the genus *Ziziphus* is subjected to debates and could be between 86 and 170 species (Azam-Ali *et al*., 2006). However, the two major cultivated species in agroforestry systems are *Z. mauritiana*, the Indian jujube or ber, and *Z. jujuba* Mill. the Chinese jujube (Azam-Ali *et al*., 2006). Many of other species of *Ziziphus* are underutilized crops despite their potential interests in agroforestry systems as fruits, firewood, fodder, medicines and live hedge (Soule, 2011). Except for *Z. mauritiana*, the effectiveness of AMF on growth and mineral nutrition of *Ziziphus* spp. is not known. Arbuscular mycorrhizae may have a particular importance for these multipurpose fruit trees because P is often the limiting nutrient in agroforestry systems. The objective of this work was to investigate the effects of three AMF (*Rhizophagus irregularis* isolate IR27, *Funneliformis mosseae* isolate DAOM227131 and *Rhizoglomus intraradices* isolate DAOM197198) on mycorrhizal dependency (MD) and mineral nutrition of seven species of *Ziziphus* (*Z. mauritiana*, *Z. lotus*, *Z. spina-christi*, *Z. mucronata*, *Z. amphibia*, *Z. abyssinica* and *Z. sphaerocarpa*) in greenhouse conditions.

Materials and methods

Soil preparation

The soil used in the experiment was collected from Sangalkam (14°46'N, 17°13'W), Senegal. It was a sandy soil with 88.8% sand, 5.8% silt, 5.4% clay, 0.6% organic matter, 0.3% total C, 0.02% total N, ratio C/N = 14, 333.5 ppm total K, 41.4 ppm total P, 2.1 ppm P-Bray 1, 1.03 ppm Ca, 0.3 ppm Mg, pH = 6.0 of a soil/water mixture (ratio 1:2, v/v) and pH = 4.6 of a soil/KCl mixture (ratio 1:2, v/v). The soil was passed through a 2 mm sieve, sterilized for 4 h in an autoclave oven system at 180 °C to eliminate native AMF, and transferred into plastic bags (1.5 kg soil per plastic bag).

Fungal inocula and inoculation

Three isolates of AMF were used: *Rhizophagus irregularis* isolate IR27 (syn. *Glomus aggregatum* IR27) (Bâ *et al*., 1996), *Funneliformis mosseae* (T.H. Nicolson and Gerd.) C. Walker and A. Schüssler (Redecker *et al*., 2013) and *Rhizoglomus intraradices* (N.C. Schenck and G.S. Sm.) Sieverd, G.A. Silva and Oehl (Sieverding *et al*., 2014). The AMF were provided by the LCM laboratory (IRD, Dakar, Senegal, certified ISO 9001, version 2000). They were propagated on maize (*Zea mays* L.) for 3 months on sterilized sandy soil in greenhouse conditions. Mycorrhizal inoculation of the soil was achieved by placing 20 g portions of a crude inoculum of AMF consisting of sand,

spores, fragments of hyphae and maize root segments below the seeds during transplanting. The inoculum density of *R. irregularis* IR27, *F. mosseae* and *R. irregularis* was calibrated by the most probable number method (Adelman and Morton, 1986) as 1,635, 1,023 and 1,347 infective propagules per 20 g of inoculum, respectively. Controls also received 20 g of autoclaved crude inoculum of AMF.

Plant materials

Seeds of seven species of *Ziziphus* (*Z. mauritiana* Lam., *Z. lotus* (L.) Lam., *Z. spina-christi* (L.) Desf., *Z. mucronata* Willd., *Z. amphibia* A. Chev., *Z. abyssinica* A. Rich. and *Z. sphaerocarpa* Tul.) (Table 1) were surface-sterilized with 1% NaOCl for 15 min, washed several times and soaked in sterile distilled water for 30 min before being planted in the soil as three per plastic bag (24 cm × 7.5 cm). Plants were grown in the nursery at ISRA/IRD Research Center, Dakar – Bel Air, Senegal (14°44'N, 17°30'W) under natural sunlight (35 °C day, 27 °C night, relative humidity 75% and 14 h photoperiod). After emergence, the seedlings were thinned to one plant per plastic bag. The experiment was set up as a 4 × 7 factorial design consisting of three AMF and control and seven *Ziziphus* spp. Experiment was arranged in a completely randomized design with 15 replicates per treatment combination.

Quantitative evaluation

Four months after sowing, plants were harvested to measure height, dry weight of shoots and roots (48 h at 70 °C). The MD of each plant of *Ziziphus* spp. was calculated using the formula:

$$MD\ (\%) = 100 \times \frac{(TDWM - TDWNM)}{TDWM}$$

where TDW_M and TDW_{NM} are total dry weight of mycorrhizal and non-mycorrhizal plants, respectively (Plenchette *et al*., 1983).

For mycorrhizal root infection measurement, a part of fresh fine roots was collected from the root system of each seedling. Root were gently washed under tap water, bleached (KOH, 10%) at 80 °C during 30 min, and stained in 0.05% trypan blue at 80 °C during 35 min following the method of Phillips and Hayman (1970). Percentage of root length colonized by AMF was assessed at ×40 magnification using 100 fragments of lateral roots (approximately 1 cm length) on microscopic slides. Mycorrhizal root colonization was evaluated by using the method of Trouvelot *et al*. (1986). After drying, leaf tissues of each plant were ground, mineralized through heating at 500 °C, digested in 2 mL HCl (6N) and 10 mL HNO_3. Total K content was determined by the atomic absorbance and total P content was determined by colorimetry through a spectrophotometer at 660 nm. Analyses were performed in the Agricultural Chemistry Laboratory of Embrapa, Rio de Janeiro, Brazil.

To measure the length of hyphae of each AMF, 2 g of soil samples from each treatment (three replicates per treatment) were blended with 500 mL distilled water, and 30 mL aliquots of this were filtered and stained with trypan blue on gridded membrane filters (1.2 µm) according to the method described by Jakobsen and Rosendahl (1990). The gridded membrane filters were mounted on slides and hyphae were viewed at 100× by using an optical microscope (Olympus BH4). Many of hyphae occurring on the membranes presented a morphology similar to those produced by members of the *Glomeromycota* and were attached to spores and auxiliary cells. All intersections between hyphae and a gridded membrane filter were counted in 20 fields of view. We used the method of Newman (1966) to calculate hyphal length (H):

$$H = \frac{\pi N A}{2 L}$$

where N is intersections between the hyphae and the gridded lines, A is the total area of the filter and L is the total line length of the gridded lines.

Data analysis

Mycorrhizal infection percentages were arcsine transformed to normalize the distribution of data before statistical analysis. Two-way analysis of variance (ANOVA) was performed on all data. Mean values were compared using Tukey test (Honestly significant differences, HSD) at the significance level ($P < 0.05$) with XLSTAT (version 2010, Addinsoft) software. Pearson's correlation coefficient between dependent variables was performed using the same software.

Results and discussion

Root colonization

The two factors (AMF and plant species) had a significant effect ($P < 0.05$) on all parameters studied (Table 2). No AM colonizations were observed in the non-inoculated controls (Table 2). Mycorrhizal infection varied with plant species and AMF. *R. irregularis* had colonized better *Z. lotus*, *Z. amphibia* and *Z. abyssinica* than the other AMF. Mycorrhizal colonization was significantly higher with *R. irregularis* and *R. intraradices* in roots seedlings of *Z. spina-christi*, *Z. mucronata, Z. mauritiana* and *Z. sphaerocarpa* than with *F. mosseae*. Overall, *F. mosseae* showed the lowest AM colonization compared to the other AMF (Table 3).

The extent of root colonization found in the inoculated *Z. mauritiana* by *R. irregularis* was 78.20%. These values are

Table 1. Geographical data and characteristics of seed provenance locations and main uses of the seven *Ziziphus* spp.

Ziziphus spp.	Country of seed provenance	Seed collection site	Longitude	Latitude	Main uses
Z. mauritiana	Mauritania	Bouguedra	08°97'W	32°25'N	Fruit, forage
Z. lotus	Mauritania	Atar	13°05'W	20°50'N	Fruit, live hedge
Z. spina-christi	Mauritania	Maghama	12°85'W	15°54'N	Fruit, timber
Z. mucronata	Mauritania	Maghama	12°85'W	15°54'N	Forage, firewood
Z. amphibia	Mauritania	Bouguedra	08°97'W	32°25'N	Fruit, medicine
Z. abyssinica	Burkina Faso	Dindéresso	04°25'W	11°13'N	Fruit, medicine
Z. sphaerocarpa	France (Guadeloupe)	Bois Jolan	61°36'W	16°23'N	Fruit

Table 2. Significance level obtained from two-way ANOVA testing the effects of AMF and *Ziziphus* spp. level on growth parameters, mycorrhizal dependency, hyphal length and mycorrhizal infection after four months under greenhouse conditions.

Factors tested	Height (cm)	SDW (g)	RDW (g)	Root/shoot ratios	Total dry biomass (g)	Mycorrhizal dependency (%)	Hyphal length (cm g^{-1})	Mycorrhizal infection (%)
AMF	***	***	***	**	***	***	***	***
Ziziphus spp.	***	**	*	*	**	***	***	**
AMF × *Ziziphus* spp.	***	***	**	NS	***	***	***	***

Significant values are indicated: *P < 0.05; **P < 0.01; ***P < 0.001; NS: not significant to Tukey's HSD; RDW: root dry weight; SDW: shoot dry weight.

similar to those presented by other authors as being good indicators of the effectiveness of inoculation (Guissou *et al*., 1998, 2016; Bâ *et al*., 2000, 2001; Sidibé *et al*., 2012; Guissou, 2009). Moreover, Bâ *et al*. (2000), Guissou (2009) and Sidibé *et al*. (2012) found that the absence of the AM inoculation could have a detrimental effect on the growth of *Z. mauritiana* in unsterile nursery soils. Here, we have extended these findings by reporting for the first time, the effectiveness of three AMF (*R. irregularis*, *R. intraradices* and *F. mosseae*) on seven *Ziziphus* spp. (including *Z. mauritiana*) in greenhouse conditions. All analyzed seedlings of *Ziziphus* spp. were colonized better with *R. irregularis* (67.10%) and *R. intraradices* (65.30%) than *F. mosseae* (59.96%).

Hyphal length

There were some variations in the production of external hyphae by AMF (Table 3). The total length of hyphae in the rhizospheric soil samples from inoculated treatments was significantly higher in *Ziziphus* spp. associated with *R. intraradices* than *R. irregularis* and *F. mosseae*, except for *Z. abyssinica* (Table 3). Irrespective of *Ziziphus* spp., the production of external hyphae increased in the following order: *F. mosseae, R. irregularis* and *R. intraradices* (Table 3).

In our study, the production of hyphal length significantly increased according to fungal species in the following order: *R. intraradices*, *R. irregularis* and *F. mosseae*. Hence, there was a significant positive correlation (r = 0.902, P < 0.0001) between development of external hyphae and MD. The results of the present study are in agreement with those of Yao *et al*. (2001) who found that the MD of three *Triticum aestivum* cultivars was determined by hyphal development. The mycorrhizal inoculation induced a significant decrease of the root/shoot ratios particularly for the *Z. sphaerocarpa* and *Z. spina-christi* compared with non-mycorrhizal plants. Moreover, there were negative correlations between root/shoot ratios and hyphal length (r = -0.300, P < 0.014), mycorrhizal colonization (r = -0.236, P < 0.184) and MD (r = -0.236, P < 0.184). These results already occurred with argan tree (Nouaim and Chaussod, 1994), and can be explained by the higher efficiency of a mycorrhizal root system due to the development of external hyphae. The production of external hyphae could play a key role for uptake and transport of P (Jakobsen *et al*., 1992). Our findings indicate that total length of hyphae in soil samples from inoculated treatments was significantly higher in the association with *R. intraradices*.

There was a significant positive correlation between MD and hyphal length (r = 0.822, P < 0.0001). Our measurements of hyphal length clearly showed that the effectiveness of one fungus depended on the associated *Ziziphus* spp. The hyphal length differed between AMF in previous studies (Jakobsen *et al*., 1992; Pearson and Jakobsen, 1993) and in the present study. The underground hyphal networks formed by AMF can influence plant growth, nutrient acquisition as well as plant-plant interactions (Smith and Read, 2008). In our study, the production of hyphal length significantly decreased according to species in the following order: *R. intraradices*, *R. irregularis* and *F. mosseae*. *R. intraradices* who produced the highest hyphal length also mobilized more P than the other AMF. Hence, there was a significant positive correlation (r = 0.908, P < 0.0001) between hyphal length and P concentrations in shoots of *Ziziphus* spp. Our results are in accordance with works of Smith *et al*. (2000) who found that *Medicago trunculata* with *Scutellospora calospora* grew better than plants growing with *Gigaspora caledonium*. This was due to the development of external hyphae.

Plant growth

The growth advantages resulting from inoculation with AMF isolates were not the same for each *Ziziphus* spp. in the P-deficient soil (Table 3). Non-inoculated *Ziziphus* spp. displayed the lowest growth compared to the inoculated plants. Inoculation with AMF enhanced significantly height of *Ziziphus* spp. as compared with non-inoculated controls, except for *Z. lotus*. There was a positive effect of *R. irregularis* in the production of biomass of *Ziziphus* spp. when compared to the non-inoculated controls, except in the case of *Z. mucronata*. *Rhizophagus intraradices* increased biomass production only on *Z. mauritiana*, *Z. amphibia* and *Z. sphaerocarpa* in comparison to non-inoculated ones. With respect to biomass production, *F. mosseae* showed higher values only on *Z. mauritiana*, *Z. mucronata*, *Z. amphibia*, and *Z. sphaerocarpa* as compared with non-inoculated plants. The lowest effect of AMF inoculation on biomass production of *Ziziphus* spp. was observed with *F. mosseae* except for *Z. mucronata-R. irregularis* (Table 3). *Ziziphus sphaerocarpa* showed the highest SDW values when inoculated with *R. irregularis* irrespective of plant-fungus combinations. RDW varied with plant species and AMF and its highest values were observed in *Z. abyssinica-R. irregularis* combination (Table 3). The root/shoot ratios of inoculated and non-inoculated *Ziziphus* spp. were similar, except in the cases of *Z. spina-christi* and *Z. sphaerocarpa*. There was a significant increase in this ratio only in *Z. amphibia* inoculated with *R. irregularis* and *F. mosseae* (Table 3). This could probably be explained by the fact that *R. irregularis* positively influence RDW and SDW production of *Z. amphibia*. Similar trends were found by Guissou *et al.* (1998) and with *Acaulospora spinosa*, *Glomus manihotis* and *Glomus aggregatum*.

Of the AMF tested, only *R. irregularis* and *R. intraradices* led to increase all parameters measured. Our findings confirm previous studies indicating that *Z. mauritiana* seedlings give the best responses in terms of biomass production particularly with *R. irregularis* (Guissou *et al*., 1998, 2009, 2016; Bâ *et al*., 2000, 2001; Sidibé *et al*., 2012).

The mycorrhizal dependency (MD) differed between plant species according to the AMF (Table 3). Irrespective

Table 3. Effect of inoculation with arbuscular mycorrhizal fungi (AMF) on growth parameters, mycorrhizal dependency, hyphal length and mycorrhizal infection after four months under greenhouse conditions. Data values represent means ± standard errors (n = 15).

Ziziphus spp. with or without AMF	Height (cm)	SDW (g)	RDW (g)	Root/shoot ratios	Total dry biomass (g)	Mycorrhizal dependency (%)	Hyphal length (cm g^{-1})	Mycorrhizal infection (%)
Z. mauritiana								
R. irregularis	31.66±3.34 a	0.58±0.03 b-e	1.06±0.31 a-d	1.85±0.72 b-f	1.64±0.31 abc	71.73±1.07 bcd	46.62±0.77 ef	78.20±16.29 ab
F. mosseae	26.11±4.63 a-e	0.57±0.06 b-f	0.91±0.19 b-f	1.59±0.29 d-g	1.48±0.24 bcd	69.33±0.66 de	34.10±1.51 i	46.09±14.46 ghi
R. intraradices	28.00±4.06 a-d	0.55±0.08 c-g	1.01±0.10 a-e	1.85±0.38 b-f	1.56±0.14 a-d	70.30±1.22 de	63.14±1.94 a	73.78±18.15 bc
Control	13.33±1.13 hi	0.14±0.02 lm	0.31±0.14 ijk	2.24±0.62 a-d	0.45±0.16 h-k	-	-	-
Z. lotus								
R. irregularis	12.44±1.50 hi	0.33±0.14 h-l	0.38±0.12 h-k	1.18±0.26 e-j	0.71±0.25 g-j	45.29±1.80 g	41.94±1.79 g	67.05±15.26 cd
F. mosseae	13.55±1.13 hi	0.31±0.13 i-l	0.15±0.04 k	0.50±0.32 j	0.46±0.15 h-k	68.22±1.58 de	40.38±2.70 hi	49.12±9.67 fghi
R. intraradices	14.00±1.87 hi	0.43±0.20 e-j	0.30±0.08 ijk	0.67±0.41 h-j	0.73±0.24 g-j	55.74±1.46 f	55.46±1.06 bc	53.40±8.96 fg
Control	11.00±1.22 i	0.08±0.01 m	0.13±0.03 k	1.61±0.31 c-g	0.21±0.03 k	-	-	-
Z. spina-christi								
R. irregularis	24.11±6.16 b-f	0.57±0.15 b-f	1.06±0.26 a-d	1.85±0.29 b-f	1.64±0.40 abc	69.66±1.06 de	40.38±3.29 hi	85.49±8.52 a
F. mosseae	25.00±4.10 b-f	0.42±0.08 e-j	0.83±0.17 b-g	1.96±0.67 b-e	1.25±0.54 c-f	57.52±1.38 f	42.54±0.49 fg	73.55±2.42 bc
R. intraradices	23.66±4.49 c-g	0.44±0.07 e-j	0.68±0.22 e-h	1.57±0.40 d-g	1.12±0.24 d-g	46.14±1.55 g	61.80±1.25 a	84.96±4.87 a
Control	11.55±1.93 i	0.21±0.03 klm	0.63±0.03 f-i	2.98±0.45 a	0.85±0.06 e-h	-	-	-
Z. mucronata								
R. irregularis	18.11±2.52 gh	0.17±0.02 klm	0.11±0.03 k	1.62±0.18 c-g	0.29±0.04 jk	68.88±1.43 de	52.78±0.47 bc	76.95±4.50 b
F. mosseae	23.00±4.59 d-g	0.56±0.05 c-g	0.28±0.05 jk	0.50±0.07 j	0.84±0.09 e-i	45.40±0.90 g	44.25±1.14 efg	51.67±5.47 fgh
R. intraradices	20.66±4.55 efg	0.36±0.07 g-k	0.26±0.15 jk	0.85±0.45 g-j	0.63±0.17 h-k	55.02±1.43 f	61.37±1.13 a	74.37±6.02 bc
Control	11.77±1.39 i	0.08±0.01 m	0.11±0.01 k	1.39±0.21 e-i	0.20±0.03 k	-	-	-
Z. amphibia								
R. irregularis	29.22±3.10 abc	0.71±0.09 bcd	1.16±0.06 ab	1.63±0.13 c-g	1.87±0.15 ab	74.57±2.65 abc	32.81±2.05 i	79.84±14.45 ab
F. mosseae	24.22±3.64 b-f	0.54±0.14 c-g	0.76±0.15 d-g	1.40±0.30 e-h	1.30±0.23 cde	30.50±0.75 h	40.38±0.59 gh	44.02±3.76 hi
R. intraradices	28.00±4.18 a-d	0.70±0.10 bcd	0.84±0.03 b-g	1.20±0.14 e-j	1.55±0.12 a-d	67.21±2.16 e	54.28±0.74 bc	46.93±11.86 ghi
Control	11.44±1.81 i	0.25±0.02 j-m	0.12±0.03 k	0.48±0.13 j	0.37±0.04 ijk	-	-	-
Z. abyssinica								
R. irregularis	20.22±3.52 fg	0.53±0.03 d-h	1.31±0.30 a	2.46±0.80 ab	1.84±0.31 ab	70.55±1.30 cde	56.83±0.65 b	67.46±6.96 cd
F. mosseae	20.33±2.29 efg	0.37±0.10 f-k	1.05±0.36 a-d	2.83±0.40 a	1.42±0.44 bcd	44.14±1.26 g	40.38±1.09 i	43.69±8.63 i
R. intraradices	20.33±3.04 efg	0.46±0.08 e-i	1.12±0.21 abc	2.43±0.65 ab	1.58±0.21 a-d	68.15±2.25 de	52.29±1.92 c	56.20±4.94 ef
Control	12.88±1.76 hi	0.36±0.11 g-k	0.84±0.29 b-g	2.33±0.40 a-d	1.20±0.38 c-f	-	-	-
Z. sphaerocarpa								
R. irregularis	29.66±1.58 ab	0.99±0.19 a	1.00±0.20 a-e	1.01±0.41 f-j	1.99±0.33 a	78.65±1.65 a	51.40±1.54 cd	66.89±10.31 cd
F. mosseae	24.55±3.53 b-f	0.74±0.07 bc	0.78±0.15 c-g	1.05±0.23 f-j	1.53±0.14 a-d	68.81±1.66 de	47.55±0.90 de	64.33±9.90 d
R. intraradices	29.22±3.52 abc	0.77±0.15 b	1.02±0.20 a-e	1.32±0.27 e-i	1.79±0.32 ab	74.96±1.99 ab	53.60±2.31 bc	62.50±8.60 de
Control	13.88±2.80 hi	0.27±0.03 i-m	0.55±0.20 g-j	2.37±1.10 a-d	0.82±0.45 f-i	-	-	-

Means in the same column followed by the same letter are not significantly different (P < 0.05) according to Tukey's HSD; RDW: root dry weight; SDW: shoot dry weight.

of plant-fungus combinations, *Z. sphaerocarpa* showed the highest MD values when inoculated with *R. irregularis*. These MD values ranged from 68.81 to 78.65%. *Z. amphibia* in symbiosis with *F. mosseae* showed the lowest MD values of 30.5%. However, MD values of *Ziziphus* spp. declined according to AMF in the following order: *R. irregularis*, *R. intraradices* and *F. mosseae* (Table 3). There was a significant positive correlation between MD and hyphal length (r = 0.902, $P < 0.0001$), and MD and mycorrhizal infection (r = 0.908, $P < 0.0001$) (Table 6). Consequently, the highest levels of mycorrhizal colonization have fostered the highest values of MD on *Ziziphus* spp. Indeed, MD on *Ziziphus* spp. with *F. mosseae* was 52.45%, whereas the highest MD values with *R. irregularis* and *R. intraradices* reached 69.51% and 63.58%, respectively. However, there was a significant positive correlation between MD and mycorrhizal infection (r = 0.908, $P < 0.0001$). The MD of the plant species also was different among AMF (Tawaraya, 2003). These differences in MD could be due to differences in the development of hyphal length. MD is often attributed to increased P uptake by AMF in P-deficient soils (Tawaraya, 2003; Smith and Smith, 2012). It is well known that MD values of different plants decreased with the increase in the soil P level (Tawaraya, 2003). At a soil P level, the values of MD also vary with host plants and AMF (Bâ *et al.*, 2001). When the soil P was low, MD of fruit trees differed markedly with AMF (Guissou *et al.*, 1998, 2016; Bâ *et al.*, 2000). *Ziziphus mauritiana* inoculated with *R. irregularis* showed the highest MD values reaching 74%. In the present study, these features may well have contributed to enhancing the availability of nutrients in the *Ziziphus* spp. and as consequence increase biomass production. In this respect, there was not a significant correlation between MD and K (r = 0.166, $P < 0.132$), suggesting that this nutrient contributed little to the biomass production of *Ziziphus* spp.

Nutrient concentrations in shoots

The analysis of variance revealed that P and K concentrations varied with *Ziziphus* spp. and AMF (Table 4). Three plant-fungus combinations such as *Z. sphaerocarpa* – *R. irregularis*, *Z. abyssinica* – *R. irregularis* and *Z. abyssinica* – *R. intraradices* had higher K concentrations in the shoots than the other plant-fungus combinations (Table 5). The plant-fungus combinations *Z. abyssinica* – *R. irregularis* and *Z. lotus* – *R. intraradices* showed the highest P concentrations in shoots compared with the other plant-fungus combinations. In all, *R. irregularis* and *R. intraradices* provided more K and P in shoots of *Ziziphus* spp., respectively, than *F. mosseae* (Table 5). Shoot P concentrations had significant positive correlations with hyphal length (r = 0.908, $P < 0.0001$), mycorrhizal infection (r = 0.841, $P < 0.0001$) and MD (r = 0.822, $P < 0.0001$), whereas K concentrations did not (Table 6).

Nutrition acquisition of nutrient ions is considered to be a major factor associated with improved seedling growth of different plants in P-deficient soils (Tawaraya, 2003; Mathur and Vyas, 1999; Klironomos, 2003). In our case, inoculation with AMF increased significantly P and K contents of *Ziziphus* spp. Nutrient uptake in mycorrhizal *Ziziphus* spp was higher as compared with non-mycorrhizal ones. Hence, improved total dry biomass of *Ziziphus* spp. could be attributed to improved nutrient uptake by AMF. *Ziziphus* spp. differed in their ability to uptake K and P depending on AMF. *Z. sphaerocarpa* and *Z. abyssinica* in symbiosis with *R. irregularis* accumulated more K and P than the other plant-fungus combinations. The enhanced nutritional status of *Ziziphus* spp. was marked with *R. irregularis* and *R. intraradices*, since they showed the

Table 4. Significance level obtained from two-way ANOVA testing the effects of AMF and *Ziziphus* spp. level on shoot phosphorus (P) and potassium (K) contents after four months under greenhouse conditions.

Factors tested	K (%)	P (%)
AMF	***	***
Ziziphus spp.	**	***
AMF × *Ziziphus* spp.	***	***

Significant values are indicated: **$P < 0.01$; ***$P < 0.001$ to Tukey's HSD.

Table 5. Effect of inoculation with arbuscular mycorrhizal fungi (AMF) on shoot phosphorus (P) and potassium (K) contents after four months under greenhouse conditions. Data values represent means ± standard errors ($n = 15$).

Ziziphus spp. with or without AMF	K (%)	P (%)
Z. mauritiana		
R. irregularis	08.11±0.15 klm	2.64±0.04 cd
F. mosseae	07.33±0.32 lmn	1.93±0.04 i
R. intraradices	06.52±0.15 no	2.54±0.12 cde
Control	05.48±0.02 o	0.70±0.03 k
Z. lotus		
R. irregularis	10.97±0.17 fgh	1.95±0.03 hi
F. mosseae	11.34±0.66 fg	2.32±0.09 efg
R. intraradices	12.15±0.43 ef	2.96±0.12 ab
Control	08.48±0.02 j-m	0.83±0.03 k
Z. spina-christi		
R. irregularis	08.61±0.12 jkl	2.32±0.05 efg
F. mosseae	07.96±0.02 klm	2.12±0.03 f-i
R. intraradices	09.73±0.45 hij	2.38±0.04 def
Control	07.14±0.36 mn	0.84±0.04 k
Z. mucronata		
R. irregularis	12.71±0.20 de	2.62±0.10 cd
F. mosseae	10.89±0.22 fgh	2.15±0.11 f-i
R. intraradices	12.94±0.14 cde	2.23±0.13 fgh
Control	10.48±0.02 gh	0.64±0.04 k
Z. amphibia		
R. irregularis	09.73±0.30 hij	2.21±0.10 f-i
F. mosseae	11.15±0.27 fg	2.17±0.09 f-i
R. intraradices	08.61±0.54 jkl	2.15±0.15 f-i
Control	08.81±0.56 ijk	0.68±0.04 k
Z. abyssinica		
R. irregularis	15.18±0.21 ab	3.18±0.03 a
F. mosseae	13.75±0.83 cd	2.04±0.04 ghi
R. intraradices	15.36±0.45 ab	2.29±0.08 efg
Control	10.51±0.40 gh	0.86±0.02 k
Z. sphaerocarpa		
R. irregularis	16.28±0.12 a	2.77±0.10 bc
F. mosseae	13.73±0.24 cd	2.80±0.03 bc
R. intraradices	14.15±0.37 bc	2.54±0.03 cde
Control	10.12±0.07 ghi	1.30±0.07 j

Means in the same column followed by the same letter are not significantly different ($P < 0.05$) according to Tukey's HSD.

Table 6. Correlation coefficients between hyphal length, mycorrhizal infection, mycorrhizal dependency, root/shoot ratio and nutritional parameters of *Ziziphus* spp. seedlings.

	K	P	HL	MI	MD	Root/shoot ratios
K	1					
P	0.365 NS	1				
HL	0.268 NS	0.908*	1			
MI	0.145 NS	0.841*	0.938*	1		
MD	0.166 NS	0.822*	0.902*	0.908*	1	
Root/shoot ratios	-0.051 NS	-0.256 NS	-0.300 NS	-0.236 NS	-0.236 NS	1

HL: hyphal length; MI: mycorrhizal infection; MD: mycorrhizal dependency; NS: not significant; *$P < 0.0001$ using Pearson's correlation coefficients.

highest mycorrhizal colonization with the both AMF, and it accumulated more P and K with *R. intraradices* and *R. irregularis*, respectively. P absorption probably contributed to this more than the absorption of K (Guissou *et al*., 1998). Our results supported the findings of Koide and Mosse (2004) who found that there is an evident relationship between the degree to which a root system of a plant is colonized by AM fungi and the potential for the plant to benefit significantly from the symbiosis. P is critical for plant growth and makes up about 0.2% of dry weight, but it is one of the most difficult nutrients for plants to acquire (Smith *et al*., 2011).

Conclusion

The present study clearly showed that AM inoculation promoted *Ziziphus* spp. growth by enhancing significantly biomass production and nutrient uptake, particularly P uptake. The differences of MD among the various *Ziziphus* spp. tested seem to be due to differences in the development of hyphal length in the soil and in the P uptake by the external hyphae. Moreover, *Rhizophagus irregularis* seems to be an efficient fungus for all the *Ziziphus* spp. tested. From a practical point of view, this AMF constitutes a promising tool for the production of higher quality nursery stock with potential improved field performance of *Ziziphus* spp. in agroforestry systems.

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