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Review

Arbuscular mycorrhizal symbiosis is a key factor to domesticate *Ziziphus mauritiana* Lam. in orchards

Bâ A.M.[1,2*], Guissou T[3]., Thioye B.[4,5], Duponnois R[1], Fall F[1,2] & Sylla S.N.[5,6]

(1) UMR113 LSTM Laboratoire des Symbioses Tropicales et Méditerranéennes IRD/CIRAD/UM2/Sup-AgroM/INRAE, France ; (2) Laboratoire de biologie et physiologie végétales, Université des Antilles, Guadeloupe, France, (3) Laboratoire de Microbiologie, INERA/DPF 03, Ouagadougou 03, Burkina Faso, (4) UniLaSalle-AGHYLE research unit UP 2018.C101, Mont-Saint-Aignan, France (5) Laboratoire Commun de Microbiologie IRD/ISRA/UCAD, Dakar, Sénégal, (6) Département de Biologie végétale, UCAD, Dakar, Sénégal.

(*) Corresponding author, email: amadou.ba@univ-antilles.fr

Abstract:

Ziziphus mauritiana Lam. also named Indian jujube is an important indigenous fruit tree (IFT) to rural people as a source of food and income, whereas it is neglected and underutilized in the West African agroforestry systems. Domestication of *Z. mauritiana* can help to preserve its genetic resources, to cultivate its germplasm and to improve its fruit production in orchards. Controlled mycorrhization and rock phosphate (RP) fertilization are two approaches to domesticate *Ziziphus mauritiana* Lam. by improving its growth, nutritional status and fruit production in the P-deficient soils. Here, we review the following (i) relative mycorrhizal dependency (RMD) of *Z. mauritiana* compared to six *Ziziphus* spp. [*Z. lotus* (L.) Lam., *Z. spina-christi* (L.) Desf., *Z. mucronata* Willd., *Z. amphibia* A. Chev., *Z. abyssinica* A. Rich. and *Z. sphaerocarpa* Tul.] and eleven ITFs [*Adansonia digitata* L, *Aphania senegalensis* Radlk, *Anacardium occidentale* L., *Cordyla pinnata* (Lepr. ex A. Rich.) Milne-Redhead, *Dialium guineensis* Wild., *Landolphia heudelottii* A.DC., *Sclerocarya birrea* (A. Roch.) Hochst., *Saba senegalensis* (A. DC.) Pichon, *Balanites aegyptiaca* (L.) Del., *Parkia biglobosa* (Jacq.), *Tamarindus indica* L.], (ii) response to arbuscular mycorrhizal (AM) inoculation and RP fertilization on *Z. mauritiana* growth and nutrition in nursery, (iii) impact of an introducing exotic AM fungus on already existing AM fungal assemblages in roots of jujube trees after planting, (iv) role of AM fungi and RP fertilizer on growth and fruit production of two *Z. mauritiana* cultivars (Gola from India and Tasset from Senegal) after planting in arid and semi-arid regions of Senegal. *Z. mauritiana* provenances and cultivars (Gola and Tasset) appeared to be higher depend on AM fungi than *Ziziphus* spp. and IFTs. In AM *Z. mauritiana* seedlings inoculated with *Rhizophagus irregularis* IR 27, the highest phosphorus dose of RP applied (250 kg P per ha) produced the best plant growth regardless of the sources of the phosphorus applied. The growth-promoting effects of pre-inoculated jujube with the exotic strain *R. irregularis* IR 27 in nursery was still maintained 18 months after planting, with significant higher rates of survival and an increase of fruit production for inoculated jujube cultivars without disturbance of native AM fungal communities. Inoculated Tasset cultivar gave the highest mean number of fruits (c.a. 300 and per tree), twice the amount of that obtained for Gola, whereas highest mean fresh weight of fruits was obtained for inoculated Gola cultivar (c.a. 670 g per tree). Success and sustained positive effects of pre-inoculation with *R. irregularis* IR27 hold promise for the role that AM fungal inoculum could play within fruit production of other fruit trees cultivated in West African orchards.

Key words: *Ziziphus mauritiana*, Controlled mycorrhization, Rock phosphate fertilization, Metabarcoding, Fruit production.

1. Introduction

African farmers commonly cultivate commercially exotic fruit trees like citrus, papayas, bananas, and mangoes in West Africa region (Ortas 2018). However, indigenous fruit trees (IFTs) such as baobab, African locust bean, desert date, and jujube are often overlooked and underutilized in the region's agroforestry systems. These IFTs are valuable biological resources (Akinnifesi et al. 2008; Bayala et al. 2011; Awodoyin et al. 2015; Leakey and Akinnifesi, 2017) and thrive in drylands where growing exotic fruit species is challenging, especially in rural areas and during drought in Sahelian and Sudanian countries in West Africa region (Stadlmayr et al. 2013). The IFT's natural habitats are being lost due to deforestation caused by drought and human activities, like tree cutting for firewood or charcoal, climate changes and population growth (Cemansky, 2015). Those, along with overexploitation, disrupt ecological balance, degrade natural resources, and affect soil properties and fruit production of IFTs (Requena et al. 2001; Guissé et al. 2013).

Fruit production of IFTs is important to rural people both as a source of food and as a source of income (Tchoundjeu et al. 2008). It provides a range of ecosystem services through high-quality products (e.g. fruits, medicine, fuel, fodder, fibers), food security, health and income-generating values for the farmers during the critical food insecure in dry season (Leakey et al. 2017). *Ziziphus mauritiana* Lam., also known as Indian jujube, is one of the selected tree species within the pan-African Great Green Wall (GGW) project. This initiative aims to combat poverty, soil degradation, and desertification (Cissé and Sarr, 2010; Thioye et al. 2019). The GGW project spans across 11 African countries in the Sahelian region, covering a 15 km wide and 7,600 km long strip of land from Dakar to Djibouti. It promotes the planting of trees and economically valuable drought-tolerant plant species, as well as the construction of water retention ponds, agricultural production systems, income-generating activities, and essential social infrastructure (Cissé and Sarr, 2010; Turner et al. 2022). Furthermore, according to surveys carried out in North-eastern Senegal, the sale of *Z. mauritiana* fruits by farmers, in particular by women, can represent more than 50% of the income derived from the savana by pastoralists located in the Mbiddi drilling area in northern Senegal (ISRA-DRPF Projet ligneux 1997; Diallo et al. 2022). The farmers are mainly interested in the fruit pulp, which is consumed fresh or dry, and also prepared into a juice (Ouédraogo et al. 2006). However, the fruits from local cultivars (e.g. Tasset from Senegal) are small-sized, whereas farmers are more interested by domesticated Indian cultivars (e.g. Gola from India) which produce early, large and tasty fruits. Although jujube cultivars with high potential for fruit production have been identified, little work has been done to bring them into improved management and domestication (Bâ et al. 2003). Domestication of jujube could be achieved through a combination of approaches including selection and multiplication of quality planting material, fertilization, irrigation, pruning, and controlled mycorrhization (Guissou et al. 1998; Bâ et al. 2003; Ouédraogo et al. 2006).

Controlled mycorrhization is a practice that harnesses the vital plant-microbe mutualism between plant roots and arbuscular mycorrhizal (AM) fungi from the phylum *Glomeromycota* (Davison et al. 2015). The AM fungi are known for their ability to improve plant growth and notably to efficiently scavenge for soil phosphorus (P) resources, one of the most limiting factors for the establishment of tree plantations and agricultural crops in West African soils (Bâ et al. 2000). The AM symbioses develop extracellular hyphal networks facilitating the absorption of water and mineral nutrients (mainly P) by the fungus, vesicles where fungus stores C mainly in the form of lipids, and arbuscules which are the sites of exchange between fungus and host plant: fungus provides water and nutrients to the host plant which, in return, provides C to the fungus (Davidson et al. 2015). Many IFTs are depending on AM fungi for their growth and mineral nutrition (Guissou et al. 1998a; Guissou et al. 1998b; Bâ et al. 2000; Bâ et al. 2001; Muok and Ishii, 2006; Guissou et al. 2016; Thioye et al. 2017; Thioye et al. 2018; Ortas 2018; Olayiiwola and Abiodun, 2019; Thioye et al. 2019; Thioye et al. 2020). Nevertheless, there are still few data on the importance of AM fungal inoculation on the fruit production of IFTs (Thioye et al. 2021) where available soil P is often a limiting factor for plant growth in West Africa. Given rock phosphate (RP) is a natural resource readily available in West Africa, it is obviously very important to know under which conditions it may be profitable as an alternative source of P either to replace or complement the conventional sources (Jaitieng et al. 2021). Plants inoculated with AM fungi utilize more soluble P from RP than non-AM plants (Manjunath et al. 1989; Bâ et al. 1996; Bâ et al. 2001; Jaitieng at al. 2021).

Here, we review the following (i) relative mycorrhizal dependency (RMD) of *Z. mauritiana* compared to six *Ziziphus* spp. [*Z. lotus* (L.) Lam., *Z. spina-christi* (L.) Desf., *Z. mucronata* Willd., *Z. amphibia* A. Chev., *Z. abyssinica* A. Rich. and *Z. sphaerocarpa* Tul.] and eleven ITFs [*Adansonia digitata* L, *Aphania senegalensis* Radlk, *Anacardium occidentale* L., *Cordyla pinnata* (Lepr. ex A. Rich.) Milne-Redhead, *Dialium guineensis* Wild., *Landolphia heudelottii* A.DC., *Sclerocarya birrea* (A. Roch.) Hochst., *Saba senegalensis* (A. DC.) Pichon, *Balanites aegyptiaca* (L.) Del., *Parkia biglobosa* (Jacq.), *Tamarindus indica* L.], (ii) response to AM inoculation and RP fertilization on *Z. mauritiana* growth and nutrition in nursery, (iii) impact of an introducing exotic AM fungus on already existing AM fungal assemblages in roots of jujube trees after planting (iv) role of AM fungi and RP fertilizer on growth and fruit production of two *Z. mauritiana* cultivars (Gola from India and Tasset from Senegal) after planting in arid and semi-arid regions of Senegal. Indeed, controlled mycorrhization with AM fungi and fertilization with RP to domesticate IFTs are poorly documented and may present advantages for the management of ITFs in the low-input agroforestry systems of West Africa.

2. Domestication of ITFs

The genus *Ziziphus* in the *Rhamnaceae* could be between 86 and 170 species of deciduous and evergreen shrubs, climbers and trees occurring throughout the tropics, subtropics and warmer temperate regions (Azam-Ali et al. 2006; Cahen et al. 2021). However, the two main domesticated species in agroforestry systems are *Z. mauritiana*, the Indian jujube and *Z. jujuba*, the Chinese jujube (Azam-Ali et al. 2006; Cahen et al. 2021; Paudel et al. 2023). The Indian jujube *Ziziphus mauritiana*, often called ber, was domesticated in India 11,000 years ago (Gupta 2004; Azam-Ali et al. 2006; Cahen et al. 2021). It was naturalized in Africa, Asia, Australia and some pacific and Caribbean Islands. Some cultivars (e.g. Gola, Seb) of *Z. mauritiana* were introduced as scion with success in West Africa, where they have been grafted onto rootstocks of naturalized *Z. mauritiana* (Danthu et al. 2002; Danthu et al. 2004; Koné et al. 2009). The Indian jujube is a versatile tree species used for its edible fruit and medicinal properties. It is commonly planted in traditional parklands in Pakistan as living hedges, but its impact on soil fertility can vary (Sharif et al. 2019). With the growing concern for global climate change, the intercropping of *Z. mauritiana* with *Vigna mungo* in traditional agroforestry systems in India shows potential for increasing carbon stocks through plant biomass (Kumar et al. 2022). However, caution is advised regarding consumption and use in folk medicine due to the cytotoxicity potential of Indian jujube leaf extracts (Owolarafe et al. 2020). In West Africa, *Z. mauritiana* is one the IFTs farmers maintain on their farms (Ouédraogo et al. 2006). Fruits of *Z. mauritiana* are grown for their fruit pulp as food and kernel, which play a major role in the local economy. The dried fruit is its main product, but also the most marketed. Fruit pulp of jujube is very rich in vitamin C (much more than lemon), phosphorus, carotene and calcium and its leaves are also rich in vitamin C and A (Rashwan et al. 2020; Abdel-Sattar et al. 2021). The germplasm of *Z. mauritiana* is rich with more than 100 and 330 accessions in Pakistan and India, respectively (Sharif et al. 2019). Several molecular markers such as amplified fragment length polymorphism (AFLP), random amplified polymorphic DNA (RAPD) and single sequences repeats (SSRs) were developed to characterize genetic relationships and cultivars of Indian jujubes (Singh et al. 2007; Khan et al. 2013; Liang et al. 2019; Chiou et al. 2020). Of these DNA markers, the SSRs offer valuable information on the genetic relationship of Indian jujubes, which is basically in agreement with the genealogy of its breeding history (Chiou et al. 2020). The Indian jujube has been successfully grafted onto the rootstocks of the following *Ziziphus* species: Z. *abyssinica*, *Z. amphibia*, *Z. mauritiana*, *Z. mucronata* and *Z. rotundifolia* (Koné et al. 2009; Sherani et al. 2021). The grafted plants of all cultivars improved with all rootstocks, flowered and fruited with a remarkable precocity reaching 6 months after grafting. However, though salinity stress impaired *Ziziphus* growth, *Z. rotundifolia* used as rootstock and Gola scions budded on *Z. rotundifolia* were much less affected than *Z. spina-christi* and *Z. mauritiana* with or without Gola scions (Singh et al. 2022). The Indian jujube plants, especially the exotic cultivars, also produced fruits 25 times larger than the fruits of the unimproved local individuals (Sherani et al. 2021). Therefore, vegetative propagation and grafting were one of the important steps for these new cultivars from Indian jujube. Another possibility to improve fruit trees productivity of *Z. mauritiana* was to combinate pruning and foliar sprays of nutrients (Saritha et al. 2021). Positive responses of *Z. mauritiana* to AM fungal inoculation and fertilization with P were well documented in phosphorus-deficient soils (Guissou et al. 1998a; Bâ et al. 2000; Sidibé et al. 2012; Thioye et al. 2019). The increase of nutrients (N, P, K and Mg) in the mycorrhizal plants of *Z. mauritiana* compared to non-mycorrhizal plants, was greater in a stress regime than in a normal regime without improving on water use efficiency (Guissou et al. 2001).

It is well established that *Z. mauritiana* contributes significantly to household income and provides an excellent opportunity for small-scale farmers to generate more income and move towards sustainable cropping system (Dawson et al. 2020). They constitute an important food supplement for smallholder farmer in the tropics, particularly in drylands where cultivation of exotic fruit species is often not possible (Awodoyin et al. 2015). *Z. mauritiana* is different to exotic fruits like pineapple, banana or mango, which have been imported from other continents, although they are now naturally growing in many West African countries (Ortas, 2018). Unlike exotic fruit tree species that are planted and therefore come under private property, *Z. mauritiana* is a part of the natural environment and are therefore more accessible to the poor people. Due to their importance to rural communities, cultivation of *Z. mauritiana* is not yet received the expected attention due to the lack of knowledge on their reliable propagation techniques and management (Dawson et al. 2020). *Z. mauritiana* could be lose, as many of them are fast disappearing due to the overexploitation and loss of biodiversity that are the major downsides of the traditional approach that relies on wild harvesting. However, it presents an important food source, neither agricultural research, nor agricultural extension services, nor even national forestry services take sufficient account. Domestication of *Z. mauritiana* can help to preserve biodiversity and genetic resources on-farm. Significant progress has been made on *Z. mauritiana* through the participatory domestication approach, including (i) species priority setting, in which farmers listed their preferred species for domestication; (ii) provenance trials, germplasm resources, seed and fruits of known traits (iii) clonal selection and development of new cultivars, (iv) regeneration and sustainable cultivation of the ITF species including controlled mycorrhization and P fertilization and (v) field management of the IFTs in agroforestry systems. Based on the advances in the domestication process, we can consider *Z. mauritiana* as one of the domesticated ITFs according to the data in the scientific literature (Koné et al. 2009; Sanou et al. 2011; Khan et al. 2013; Munthali et al. 2013; Chiou et al. 2020; Danthu et al. 2004; Diawara et al. 2020; Rashwan et al. 2020; Abdel-Sattar et al. 2021; Cahen et al. 2021; Sherani et al. 2021) (Table 1).

Table 1: Advances in domestication of some IFTs in the tropics

Genus, species	Plant family	Natural distribution	Main use	Advance in domestication	Reference
Adansonia digitata	Bombacaceae	Tropical Africa	Fruit, medicine	Semi-domesticated	Chládová et al. 2019
Anacardium occidentale	Anacardiaceae	Tropical America, Africa, Asia	Fruit, firewood	Undomesticated	Medney et al. 2001
Aphania senegalensis	Sapindaceae	West Africa	Fruit, medicine	Undomesticated	Fall et al. 2017
Balanites aegyptiaca	Balanitaceae	Africa, Asia, India	Fruit, medicine	Undomesticated	Yadav et al. 2010
Cordyla pinnata	Fabaceae	West Africa	Fruit, timber	Undomesticated	Dieng et al. 2016
Dialium guineensis	Fabaceae	West Africa	Fruit, medicine	Undomesticated	Besong et al. 2016
Landolphia heudelottii	Apocynaceae	West Africa	Fruit, medicine	Undomesticated	Mireku et al. 2016
Parkia biglobosa	Fabaceae	West Africa	Fruit, medicine	Semi-domesticated	Houndonougbo et al. 2020
Saba senegalensis	Apocynaceae	Tropical Africa	Fruit, medicine	Undomesticated	Diawara et al. 2020
Sclerocarya birrea	Anacardiaceae	Africa	Fruit, food industry	Undomesticated	Haro et al. 2021
Tamarindus indica	Fabaceae	Tropical Africa, Asia, India	Fruit, medicine	Semi-domesticated	Buba et al. 2020
Ziziphus abyssinica	Rhamnaceae	Africa	Fruit, medicine	Undomesticated	Ahmed and Sati, 2018
Z. amphibia	Rhamnaceae	Tropical Africa	Fruit, medicine	Undomesticated	Thioye et al. 2018
Z. lotus	Rhamnaceae	Africa, Asia, Europe	Fruit, medicine	Undomesticated	Abdoul-Azize, 2016
Z. mauritiana	Rhamnaceae	India, Africa, Asia	Fruit, forage	Domesticated	Sharif et al. 2019
Z. mucronata	Rhamnaceae	Tropical Africa	Fruit, medicine	Undomesticated	Mokgolodi et al. 2011
Z. sphaerocarpa synonym to *Z. spina-christi*	Rhamnaceae	Tropical Africa	Fruit, timber	Undomesticated	Mokgolodi et al. 2011
Z. spina-christi	Rhamnaceae	Arabic, Tropical Africa	Fruit, timber	Undomesticated	Saied et al. 2008

3. Controlled mycorrhization

Controlled mycorrhization consists in identifying, isolating, selecting, large-scale of inoculum producing, applying inoculants and tracking of the mycorrhizal fungi in the field (Hart et al. 2017; Corsini et al. 2022). The success of controlled mycorrhization depends on host response to inoculation, fungal provenance (native or exotic), inoculation timing, soil structure, organic matter content and fertility (mainly P), and site disturbance (Hart et al. 2017; Epelde et al. 2020; Martignoni et al. 2020). For example, pre-inoculation with ECM fungi can help seagrape plants to mitigate salt stress by improving Na exclusion and storage, plant K nutrition and water status (Bullain Galardis et al. 2022). Native AM fungal species must to be preferentially choosen *vs* commercial strain due to their competitiveness and adaptation to soil and climate conditions (Solomon et al. 2022). However, the majority of field inoculation studies have successfully been conducted in degraded soils of post mining or soils with very low inoculum potential in conventional agriculture or desertified areas (Hart et al. 2017). There is also increasing evidence that priority effects of AM fungal pre-inoculation are important for AM fungi establishment but not always (Mummey et al. 2009). Another important factor determining the success of inoculation is the host responses that can vary following their relative mycorrhizal dependency (RMD) (Hart et al. 2017; Epelde et al. 2020; Martignoni et al. 2020).

Consideration of RMD of plants is an important factor determining the magnitude of benefits from improved management of AM fungi (Plenchette et al. 1983; Bâ et al. 2000; Tawaraya, 2003; Hoeksema et al. 2010). The RMD is defined as the degree to which a plant responds to mycorrhizal inoculation under given environmental conditions (Plenchette et al. 1983). The RMD is often related to the morphological properties of plant roots and regulated by the effectiveness of AM fungi, soil AM potential and P availability (Schweiger et al. 1995). It can vary greatly from one plant species to another and even between provenances or cultivars within a single species (Ceballos et al. 2013; Thioye et al. 2019; Thioye et al. 2021). It is therefore useful to determine whether a plant derives or not benefits from AM symbiosis and to know how to manage it accordingly. The RMD differed between IFT species and was significantly influenced by AM fungal species (Guissou et al. 1998a; Table 2). However, *Z. mauritiana* in symbiosis with *A. spinosa, R. irregularis* IR27 or *G. manihotis* showed the highest RMD values compared with other plant-fungus combinations. *P. biglobosa* and *T. indica* had comparable RMD values which were never higher than 36%. Irrespective of plant-fungus combinations, the RMD of plant species decreased in the following order: *Z.*

mauritiana, P. biglobosa and *T. indica* (Guissou et al. 1998a; Table 2). However, the absence of a significant correlation between density and length of root hairs and RMD did not support Baylis's hypothesis (Baylis, 1970). Therefore, density and length of root hairs of non-AM fruit trees may not necessarily be "an alternative mean of by passing the phosphate depletion zone around the root" as proposed by Schweiger et al. (1995). This study was extended to other important ITF species because their AM status is often unknown and may have particular importance for establishment in degraded soils of arid and semi-arid areas, particularly during their first phase of growth in nutrient-deficient soils (Bâ et al. 2000). Therefore, we tested the RMD of thirteen ITFs from arid and semi-arid lands with two AM fungal species under conditions of P deficiency (Bâ et al. 2000). The RMD values ranged from 0% to 77% and were most clearly demonstrated with *R. irregularis* IR27. Based on these data, we proposed a ranking of ITFs according to the RMD categories defined by Habte and Manajunath (1991): *Z. mauritiana* was considered very highly dependent (RMD > 75%), *T. indica* was highly dependent (50–75% RMD), *D. guineensis*, *P. biglobosa* and *C. pinnata* were moderately dependent (25–50% RMD), *A. occidentale*, *A. senegalensis*, *S. birrea* and *A. digitata* were marginally dependent (0–25% RMD), and *L. heudolottii*, *S. senegalensis* and *B. aegyptiaca* were found not to be dependent on mycorrhizas (Table 2) (Guissou et al. 1998a ; Bâ et al. 2000). This last category includes species that are not hosts to AM fungi and those that did not respond positively to AM fungal colonization. Similar results in terms of RMD were obtained on *T. indica* (Reena and Bagyaraj, 1989), *S. birrea* (Muok and Ishii, 2006; Haro et al. 2021) and *Z. mauritiana* (Mathur and Vyas, 1997; Guissou, 2009). Altogether, *Z. mauritiana* was found to be the ITF species responding better to AM fungal inoculation, regardless of the inoculated AM fungal species (Table 2).

Table 2. Relative mycorrhizal dependency (RMD) on *Z. mauritiana* compared to eleven IFT species

Plant species	AM fungal species	Growth period (month)	Soil P (ppm)	Colonization rate (%)	RMD (%)	Reference
Adansonia digitata	*Rhizophagus irregularis*[1]	3	6.6	64	10	Bâ et al. 2000
	Rhizoglomus intraradices[2]	3	6.6	63	3	Bâ et al. 2000
Anacardium occidentale	*Rhizophagus irregularis*[1]	3	6.6	73	24	Bâ et al. 2000
	Rhizoglomus intraradices[2]	3	6.6	55	8	Bâ et al. 2000
Aphania senegalensis	*Rhizophagus irregularis*[1]	3	6.6	38	23	Bâ et al. 2000

	Rhizoglomus intraradices[2]	3	6.6	25	-	Bâ et al. 2000
Balanites aegyptiaca	*Rhizophagus irregularis*[1]	3	6.6	53	-	Bâ et al. 2000
	Rhizoglomus intraradices[2]	3	6.6	8	3	Bâ et al. 2000
Cordyla pinnata	*Rhizophagus irregularis*[1]	3	6.6	25	28	Bâ et al. 2000
	Rhizoglomus intraradices[2]	3	6.6	22	15	Bâ et al. 2000
Dialium guineensis	*Rhizophagus irregularis*[1]	3	6.6	48	46	Bâ et al. 2000
	Rhizoglomus intraradices[2]	3	6.6	15	-	Bâ et al. 2000
Landolphia heudelottii	*Rhizophagus irregularis*[1]	3	6.6	0	-	Bâ et al. 2000
	Rhizoglomus intraradices[2]	3	6.6	0	-	Bâ et al. 2000
Parkia biglobosa	*Acaulospora spinosa*[3]	2	3.8	91	24	Guissou et al. 1998a
	Rhizophagus irregularis[1]	2	3.8	93	36	Guissou et al. 1998a
	Glomus manihotis[4]	2	3.8	90	31	Guissou et al. 1998a
	Rhizoglomus intraradices[2]	2	3.8	90	12	Guissou et al. 1998a
Parkia biglobosa	*Funeliformis mosseae*[5]	2	3.8	17	4	Guissou et al. 1998a
Parkia biglobosa	*Rhizophagus irregularis*[1]	3	6.6	68	33	Bâ et al. 2000
	Rhizoglomus intraradices[2]	3	6.6	42	-	Bâ et al. 2000
Parkia biglobosa	*Glomus mosseae*	4	19	nd	-	Olayiwola and Abiodun, 2019
Saba senegalensis	*Rhizophagus irregularis*[1]	3	6.6	0	-	Bâ et al. 2000
	Rhizoglomus intraradices[2]	3	6.6	0	-	Bâ et al. 2000
Sclerocarya birrea	*Rhizophagus irregularis*[1]	3	6.6	76	18	Bâ et al. 2000
	Rhizoglomus intraradices[2]	3	6.6	65	2	Bâ et al. 2000
S. birrea subsp. *multifoliolata*	*Gigaspora margarita*	3	nd	39	7	Muok and Ishii, 2006
S. birrea subsp. *birrea*	*Gigaspora margarita*	3	nd	41	33	Muok and Ishii, 2006
S. birrea subsp. *caffra*	*Gigaspora margarita*	3	nd	42	21	Muok and Ishii, 2006
S. birrea	*Gigaspora margarita*	3	nd	37	23	Muok et al. 2009
S. birrea	Mixed inoculum	9	1.74	28	39	Haro et al. 2021
	Glomus aggregatum	9	1.74	23	37	Haro et al. 2021
	Rhizophagus irregularis[1]	9	1.74	18	28	Haro et al. 2021

Tamarindus indica	*Gigaspora margarita*	6	2.4	90	26	Reena and Bagyaraj, 1989
	Glomus fasciculatum	6	2.4	86	22	Reena and Bagyaraj, 1989
T. indica	*Acaulospora spinosa*[3]	2	3.8	94	33	Guissou et al. 1998a
	Rhizophagus irregularis[1]	2	3.8	96	33	Guissou et al. 1998a
	Glomus manihotis[4]	2	3.8	96	21	Guissou et al. 1998a
	Rhizoglomus intraradices[2]	2	3.8	88	14	Guissou et al. 1998a
	Funeliformis. mosseae[5]	2	3.8	39	9	Guissou et al. 1998a
T. indica	*Rhizophagus irregularis*[1]	3	6.6	89	54	Bâ et al. 2000
	Rhizoglomus intraradices[2]	3	6.6	25	23	Bâ et al. 2000
T. indica	*Rhizophagus irregularis*[1]	4	2.2	78	70	Guissou, 2009
Z. mauritiana	*Acaulospora spinosa*[3]	2	3.8	91	78	Guissou et al. 1998a
	Rhizophagus irregularis[1]	2	3.8	95	70	Guissou et al. 1998a
	Glomus manihotis[4]	2	3.8	88	74	Guissou et al. 1998a
	Rhizoglomus intraradices[2]	2	3.8	86	58	Guissou et al. 1998a
	Funeliformis. mosseae[5]	2	3.8	48	48	Guissou et al. 1998a
Z. mauritiana	*Glomus constrictum*	4	nd	83	46	Mathur and Vyas, 1995
Z. mauritiana	*Rhizophagus irregularis*[1]	3	6.6	98	78	Bâ et al. 2000
	Rhizoglomus intraradices[2]	3	6.6	97	73	Bâ et al. 2000
Z. mauritiana	*Rhizophagus irregularis*[1]	6	2.2	90	80	Guissou, 2009

[1] Fungal isolate IR27; [2] Fungal isolate 89-30-14; [3] Fungal isolate FL257-2; [4] Fungal isolate IR15; [5] Fungal isolate 92-07-21; (-) no dependence; (nd) not determined.

The inoculation by AM fungi significantly improved growth and mineral nutrition of *Ziziphus* spp., particularly the P nutrition (Table 3) (Thioye et al. 2017). The RMD differed between plant species according to the AM fungi (Thioye et al. 2017). Irrespective of plant-fungus combinations, *Z. sphaerocarpa* showed the highest RMD values when inoculated with *R. irregularis* IR27. These RMD values ranged from 68.81 to 78.65%. *Ziziphus amphibia* in symbiosis with *F. mosseae* showed the lowest RMD values of 30.5%. However, the RMD values of *Ziziphus* spp. declined with AM fungi in the following order: *R. irregularis* (69.51%), *R. intraradices* (63.58%) and *F. mosseae* (52.45%). There was a significant positive correlation between RMD and hyphal length (r = 0.902, $P < 0.0001$), and RMD and mycorrhizal infection (r = 0.908, $P < 0.0001$) (Thioye et al. 2017). Consequently, the highest levels of mycorrhizal colonization have fostered the highest values of RMD on *Ziziphus* spp. Indeed, RMD on *Ziziphus* spp. with *F. mosseae* was 52.45%, whereas the highest RMD values with *R. irregularis* and *R. intraradices* reached 69.51% and 63.58%, respectively. The differences of RMD 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 (Tawaraya, 2003; Thioye et al. 2017a).

Table 3. Relative mycorrhizal dependency (RMD) on eight *Ziziphus* species.

Ziziphus species	AM fungal species	Growth period (month)	Soil P (ppm)	Colonization rate (%)	RMD (%)	Reference
Z. mauritiana	*Rhizophagus irregularis*[1]	4	2.1	78	71	Thioye et al. 2017
	Rhizoglomus intraradices[2]	4	2.1	73	70	Thioye et al. 2017
	Funeliformis mosseae[5]	4	2.1	46	68	Thioye et al. 2017
Z. lotus	*Rhizophagus irregularis*[1]	4	2.1	67	45	Thioye et al. 2017
	R. intraradices[2]	4	2.1	53	55	Thioye et al. 2017
	Funeliformis mosseae[5]	4	2.1	49	68	Thioye et al. 2017
Z. spina-christi	*Rhizophagus irregularis*[1]	4	2.1	85	69	Thioye et al. 2017
	R. intraradices[2]	4	2.1	84	46	Thioye et al. 2017
	Funeliformis mosseae[5]	4	2.1	73	57	Thioye et al. 2017
	Mixed inoculum of *Glomus mosseae* and *Glomus monosporum*	3	nd	68	37	Al-Qarawi and Alshahrani, 2010
Z. mucronata	*Rhizophagus irregularis*[1]	4	2.1	77	69	Thioye et al. 2017
	R. intraradices[2]	4	2.1	74	46	Thioye et al. 2017
	Funeliformis mosseae[5]	4	2.1	51	57	Thioye et al. 2017
Z. nummularia	*Glomus deserticola*	6	nd	86	66	Mathur & Vyas, 1995
	Mixed inoculum of *Glomus mosseae* and *Glomus monosporum*	3	nd	51	56	Al-Qarawi and Alshahrani, 2010
Z. amphibia	*Rhizophagus irregularis*[1]	4	2.1	79	74	Thioye et al. 2017

	R. intraradices[2]	4	2.1	46	67	Thioye et al. 2017
	Funeliformis mosseae[5]	4	2.1	44	30	Thioye et al. 2017
Z. abyssinica	*Rhizophagus irregularis*[1]	4	2.1	67	70	Thioye et al. 2017
	R. intraradices[2]	4	2.1	56	68	Thioye et al. 2017
	Funeliformis mosseae[5]	4	2.1	43	44	Thioye et al. 2017
Z. sphaerocarpa	*Rhizophagus irregularis*[1]	4	2.1	67	78	Thioye et al. 2017
	R. intraradices[2]	4	2.1	62	74	Thioye et al. 2017
	Funeliformis mosseae[5]	4	2.1	64	69	Thioye et al. 2017

[1]Fungal isolate IR27; [2]Fungal isolate 89-30-14; [5]Fungal isolate 92-07-21.

Six West African provenances (Tasset, Ségou, Atar, Dori, Sadoré and Sangalkam) of jujube seedlings showed the highest RMD values when inoculated with *R. irregularis* IR27 (Table 4) (Thioye et al. 2018). The RMD of these provenances of jujube plants with *R. irregularis* IR27 ranged from 63% to 74%, while the RMD with *R. irregularis* DAOM197198 and *F. mosseae* was far below around 50% to 68% and 34% to 56%, respectively (Thioye et al. 2018). The differences of RMD among the tested *Z. mauritiana* provenances could be due to differences in the development of hyphal length in the soil and in P uptake by the external hyphae (Thioye et al. 2018). Indeed, there were significant correlations between RMD and hyphal length (r = 0.617, $P < 0.0001$) and between RMD and mycorrhizal infection (r = 0.831, $P < 0.0001$) (Thioye et al. 2018). In contrast, five provenances (Bandia, Colomba, Darha, Gonsé and Léri) of jujube seedlings have a high and comparable mycorrhizal root colonization levels with *R. irregularis* IR27, whereas their RMD values were low ranging from 18% to 30% (Guissou et al. 2016). This suggests that the level of AM root colonization remains a weak indicator of plant growth benefits (Cavender et al. 2006; Nunes et al. 2008) because it was not always consistent with the impact AM symbiosis has on plant growth yields.

Table 4. Relative mycorrhizal dependency (RMD) on eleven *Z. mauritiana* provenances.

Provenances of *Ziziphus mauritiana*	AM fungal species	Growth period (month)	Soil P (ppm)	Colonization rate (%)	RMD (%)	Reference
Senegal (Tasset)	*Rhizophagus irregularis* [1]	4	2.1	76	54	Thioye et al. 2018
	Rhizoglomus intraradices[2]	4	2.1	64	50	Thioye et al. 2018
	Funeliformis mosseae[5]	4	2.1	57	47	Thioye et al. 2018

Senegal (Gola)	*Rhizophagus irregularis* ^{1}	4	2.1	80	64	Thioye et al. 2018
	Rhizoglomus intraradices^{2}	4	2.1	69	40	Thioye et al. 2018
	Funeliformis mosseae^{5}	4	2.1	65	46	Thioye et al. 2018
Senegal (Bandia)	*Rhizophagus irregularis* ^{1}	6	2.2	90	30	Guissou et al. 2016
Senegal (Colomba)	*Rhizophagus irregularis* ^{1}	6	2.2	91	30	Guissou et al. 2016
Senegal (Darha)	*Rhizophagus irregularis* ^{1}	6	2.2	91	27	Guissou et al. 2016
Mali (Ségou)	*Rhizophagus irregularis* ^{1}	4	2.1	65	61	Thioye et al. 2018
	Rhizoglomus intraradices^{2}	4	2.1	55	39	Thioye et al. 2018
	Funeliformis mosseae^{5}	4	2.1	55	36	Thioye et al. 2018
Mauritania (Atar)	*Rhizophagus irregularis* ^{1}	4	2.1	76	50	Thioye et al. 2018
	Rhizoglomus intraradices^{2}	4	2.1	68	22	Thioye et al. 2018
	Funeliformis mosseae^{5}	4	2.1	58	36	Thioye et al. 2018
Burkina Faso (Dori)	*Rhizophagus irregularis* ^{1}	4	2.1	68	68	Thioye et al. 2018
	Rhizoglomus intraradices^{2}	4	2.1	70	57	Thioye et al. 2018
	Funeliformis mosseae^{5}	4	2.1	55	42	Thioye et al. 2018
Burkina Faso (Gonsé)	*Rhizophagus irregularis* ^{1}	6	2.2	90	18	Guissou et al. 2016
Burkina Faso (Léri)	*Rhizophagus irregularis* ^{1}	6	2.2	91	32	Guissou et al. 2016
Niger (Sadoré)	*Rhizophagus irregularis* ^{1}	4	2.1	55	49	Thioye et al. 2018
	Rhizoglomus intraradices^{2}	4	2.1	51	14	Thioye et al. 2018
	Funeliformis mosseae^{5}	4	2.1	44	39	Thioye et al. 2018

^{1}Fungal isolate IR27; ^{2}Fungal isolate 89-30-14; ^{5}Fungal isolate 92-07-21.

Overall, results make it possible to confirm the choice of *Z. mauritiana* used as a plant model among the ITF species tested in the study of interactions between ITFs and AM fungi involved in the phosphorus cycle. Furthermore, *R. irregularis* IR27 constitutes a promising biological tool for the production of higher quality nursery stock with expected improved performance of *Z. mauritiana* in terms of growth and fruit production within West African orchards. The AM fungus *R. irregularis* IR27, originally isolated and identified as *Glomus* *aggregatum* (Bâ et al. 1996) in the rhizosphere soil of *Acacia holosericea* growing in semi-arid area of Burkina Faso (West Africa), is considered exotic since it was introduced into others West African countries (Thioye et al. 2021).

4. Rock phosphate fertilization of mycorrhizal jujube seedlings

Phosphorus deficiency in soils is one of the limiting factors for the establishment of tree plantations and agricultural crops within subtropics and tropics (Kobae, 2019; Hou et al. 2021; Jaitieng at al. 2021). The available P contents are low in most subtropical and tropical soils due to their high P retention capacity. Regarding the low mobility of available P in the soil, its absorption leads to the formation of depletion zones around the roots and rapidly limits its further uptake by plants (Jaitieng et al. 2021). To overcome this, organic matter sources, soluble P and rock phosphate (RP) fertilizers can be applied to increase the available phosphorus content of soils depleted of this element (Hou et al. 2021). However, the quantity of available organic matter recycled back to the soil is low, and soluble P fertilizers are too expensive for agriculture in developing countries (Nye and Kirk, 1987). Organic P could be mineralized by AM fungi thanks to cohort of P-solubilizing bacteria growing on the surface of hyphae (Jiang et al. 2021).

In West Africa where RP is a natural resource readily available, it is obviously very important to know under which conditions it may be profitable as an alternative source of P either to replace or complement the conventional sources (Jaitieng at al. 2021). Investigations with RP, originating from the semi-arid zone of West Africa, have mainly centered on their agronomic and forestry potential (Bâ et al. 1996; Guissou et al. 1998b). The application of RP originating from other regions (e.g. Morocco, Tunisia) is also well documented in these areas (Islam et al. 1980). However, the fertilizer effectiveness of RP depends on factors relating to RP itself (minerology, chemical reactivity and rate of application), soil factors (pH acid, phosphate and calcium status) and the mycorrhizal status of plants. RP solubilizes at pH acid and its reactivity depends on the percentage of P_2O_5. Plants inoculated with AM fungi utilize more soluble P from RP than non-AM plants (Manjunath et al. 1989; Bâ et al. 1996; Bâ et al. 2001; Jaitieng at al. 2021). Furthermore, available P from soil and RP increased with the levels of RP doses (Guissou et al. 1998b). As consequence, AM jujube seedlings absorb P from soil and RP more efficiently than unfertilized AM jujube (Guissou et al. 1998b). The simplest explanation is that AM fungi develop an extramatrical mycelium, which increases the volume of soil explored by roots and therefore the number of sites available for root P absorption, as proposed by Bolan (1991). The effectiveness of three RPs from West Africa depends on their P_2O_5 (%) content and can be ranked in ascending order as follows: Mali (Tilemsi phosphate with 15% total phosphorus), Burkina Faso (Kodjari phosphate with 12.5% total phosphorus), and Senegal (Taiba phosphate with 12.2% total phosphorus). These RPs were compared to triple superphosphate (TSP with 23% soluble phosphate), which served as the reference fertilizer (Table 5). It appeared that, in the absence of AM fungus, growth and P nutrition of jujube seedlings were low whatever the RP used. The jujube seedlings were therefore confirmed to be highly dependent on mycorrhizae for their P nutrition. Indeed, when they were mycorrhizal, jujube seedlings absorbed better the P provided by the different sources of P. These results agree with those of Bâ and Guissou (1996) that showed AM *Faidherbia albida* seedlings with *Glomus manihotis* or *R. irregularis* IR27 improved plant growth and increased P contents at any RP application rate. Similarly, Jaitieng at al. 2021 showed that RP fertilizer application at 400 g per plant promoted root colonization density, available P in soil, and total P in leaves of robusta coffee plants. According to Table 5, the results show that RP from Mali was the sole RP that increased the overall biomass of AM jujube when compared to AM jujube without P supply. However, when P levels were raised through TSP supply, both RMD and AM colonization exhibited a decrease. This implies that jujube seedlings used available P rather than forming mycorrhizal associations because they represent an energy cost for the plants. These results are consistent with those of Ayedemi et al. (2021) showed a negative correlation between AM growth response in soybean cultivars and soil P availability. Apart from a few exceptions depending on the interaction between plant and fungal genotypes, high P levels reduce AM fungal community and growth, root colonization and benefits in plant growth (Verbruggen et al. 2013; Peña Venegas et al. 2021).

Table 5. Effect of phosphate fertilization and fungal inoculation with *Rhizophagus irregularis* IR27 on growth and P nutrition of jujube seedlings in pot after 3 months in a greenhouse experiment. Relative mycorrhizal dependency (RMD); rock phosphate (RP) at 250 kg phosphorus × ha^{-1}; triple superphosphate (TSP) at 25 kg phosphorus × ha^{-1} (Bâ et al. 2001).

Status of jujube	Origin of P	Total biomass (g)	RMD (%)	P in leave and shoot (%)	Mycorrhizal colonization (%)
Uninoculated	Control	0.38 a	-	0.05 a	0.00 a
	RP from Mali	0.57 a	-	0.05 a	0.00 a
	RP from Senegal	0.29 a	-	0.05 a	0.00 a

	RP from Burkina Faso	0.32 a	-	0.04 a	0.00 a
	TSP	1.80 d	-	0.20 e	0.00 a
Inoculated	Control	1.50 bc	75 ab	0.14 b	78.47 bc
	RP from Mali	1.87 d	69 b	0.16 c	95.39 d
	RP from Senegal	1.30 bc	77 a	0.17 cd	66.00 b
	RP from Burkina Faso	1.25 b	74 ab	0.18 de	87.13 cd
	TSP	2.70 e	33 c	0.19 e	63.60 b

In each column, means followed by the same letter are not significantly different according to Newman and Keuls at the 5% level. Each value represents the mean over twelve plants.

The effectiveness of RP from Mali on growth of AM jujube justified its use at different levels compared with TSP fertilizer (Table 6). In AM jujube seedlings, the highest level of P (125 kg P × ha–1) provoked the best plant growth, regardless of the origin of the applied phosphorus. Furthermore, AM fungal colonization was comparable regardless of the level of RP used, while it significantly decreased with increasing levels of TSP. Since environmental and economic cost of fertilizers, it may be recommended to fertilize AM jujube seedlings in nursery with RP from Mali rather than with TSP, although the latter fertilizer has also positive effects with or without inoculation (Bâ et al. 2001). Our results agree with those of Jaitieng at al. (2021) who found that RP application promoted growth and P nutrition of AM coffee plants.

Table 6. Effect of phosphate fertilization levels and fungal inoculation with *Rhizophagus irregularis* IR27 on growth and P nutrition of jujube seedlings in pot after 3 months in a greenhouse experiment. Relative mycorrhizal dependency (RMD); triple superphosphate (TSP); rock phosphate (RP) (Bâ et al. 2001).

Status of jujube	Origin of P	Level of P (kg Pxha^{-1})	Total biomass (g)	RMD (%)	P in leave and shoot (%)	Mycorrhizal colonization (%)
Uninoculated	Control	0	0.27 a	-	0.09 ab	0.00 e
	RP from Mali	25	0.21 a	-	0.10 ab	0.00 e
		50	0.30 a	-	0.07 a	0.00 e
		75	0.28 a	-	0.06 a	0.00 e
		100	0.28 a	-	0.12 b	0.00 e
		125	0.30 a	-	0.11 ab	0.00 e
	TSP	25	1.86 bc	-	0.20 ef	0.00 e
		50	2.41 cde	-	0.18 c	0.00 e
		75	2.37 bcde	-	0.25 f	0.00 e
		100	3.49 fg	-	0.25 f	0.00 e
		125	2.87 ef	-	0.31 gh	0.00 e
Inoculated	Control	0	1.67 bc	84 a	0.24 ef	74.80 ab
	RP from Mali	25	2.12 bcd	90 a	0.23 def	64.44 b
		50	2.44 cde	88 a	0.19 cde	67,98 ab
		75	2.11 bcd	87 a	0.19 cde	57.38 bc
		100	1.82 bc	85 a	0.23 def	86.29 a

	125	3.06 efg	90 a	0.19 cde	73.64 ab
TSP	25	2.88 ef	35 b	0.22 cdef	57.15 bc
	50	2.41 cde	-	0.26 f	76.46 ab
	75	2.65 de	10 b	0.25 f	46.02 c
	100	2.67 de	-	0.31 gf	48.82 c
	125	3.59 g	20 b	0.27 fg	30.74 d

In each column, means followed by the same letter are not significantly different according to Newman and Keuls at the 5% level. Each value represents the mean over twelve plants. (-) no dependence

5. Pre-inoculation effect on root colonization and native AM fungal communities of jujube trees

5.1. Pre-inoculation effect on root colonization

Pre-inoculation of seedlings with AM fungal inoculants at early stage is a common practice in horticultural and sylvicultural crops (Al-Karaki, 2006; Mummey et al. 2009; Klinsukon et al. 2021; Thioye et al. 2021). Beneficial interactions between a pre-inoculated mix of two exotic AM fungi *Glomus* sp. and *G. intraradices* and the native AM fungal community have been suggested for field trials with *Olea europaea* in arid and semi-arid degraded lands (Dag et al. 2009). The introduction of AM fungal inoculants at the nursery stage is especially beneficial as it provides the plants with an established and tailored AM fungal symbiosis before they are transplanted in the land reclamation (Ceballos et al. 2013; Hart et al. 2017). However, the establishment success of exotic AM fungi in part depends on they ability to outcompete the native AM fungal community, given AM fungi already established in the field may be competitively superior due to a potential priority effect compared with the introduced ones (Ceballos et al. 2013; Verbruggen et al. 2013). Indeed, the native AM community is often one the crucial biotic soil factors limiting the success of the introduction of AM fungal inoculants (Mummey et al. 2009; Ceballos et al. 2013; Renaut et al. 2019; Epelde et al. 2020; Martignoni et al. 2020). Martignoni et al. (2020) propose a model with some criteria to assess the risks and benefits of the introduction of AM fungal inoculants and to determine their spreading speed in the field. The model predicts that the introduction of AM fungal inoculants has little or no effect on plant growth when in the presence of a well-established native fungal community in terms of root colonization and viable AM fungal propagules in the soil (Martignoni et al. 2020). Possible changes in native AM fungal communities, resulting from the potential invasion of inoculant strains, should be taken into account when assessing the risks and benefits of unintended consequences in the future (Schwartz et al. 2006). It is worth noting that pre-inoculation with exotic strains can lead to complete or partial changes in native AM fungal communities (Rodriguez and Sanders; Hart et al. 2017).

Some factors such as high levels of available P, culturing of non-host plants and low levels of organic matter, can also reduce the root colonization and viable AM fungal propagules belonging to the native AM fungal communities (Martignoni et al. 2020; Jiang et al. 2021). Furthermore, it is thought that field soil at a low level of native AM fungal propagules and soil available P, can facilitate the establishment of the exotic AM fungi (Verbruggen et al. 2013; Solomon et al. 2022). In this respect, we specifically tested whether two pre-inoculated cultivars (Gola from India and Tasset from Senegal) of jujube trees with the exotic *R. irregularis* IR27 and fertilized with RP can establish in two contrasted orchards located in arid (100-200 mm rainfall, 6 ppm P-Bray 1) and semi-arid (100-400 mm rainfall, 26 ppm P-Bray 1) areas of Senegal (Thioye et al. 2019; Thioye et al. 2020; Thioye et al. 2021).

We showed number of infective propagules of *R. irregularis* IR27 applied in nursery was superior to those of both orchard soils ones (Thioye et al. 2019; Thioye et al. 2021). This could indicate that large doses of inoculum used have been a requirement for successful establishment of the exotic *R. irregularis* (Thioye et al. 2021). It is established that high density of propagules of the exotic AM fungi may lead to increase their competitiveness among native AM fungi and a trade-off with their ability to colonize and promote plant productivity. By instance, a two year-long field monitoring previously demonstrated the link between increasing colonization rate and yield increases to *Medicago sativa* (Pellegrino et al. 2012). A meta-analysis based on inoculation surveys between 1998 and 2003 confirmed this relationship for 23 % of studied sites (Lekberg and Koide, 2005). However, the number of viable AM fungal propagules is a key ecological aspect to consider when introducing AM fungi into soils (Janouskovά et al. 2013). Furthermore, the levels of colonization of both jujube cultivars ranged from 64% to 70% before transplanting (Thioye et al. 2021), whereas the minimum level of root pre-colonization necessary for successful establishment of mycorrhizal jujube plants to the field is not known in our experiments. Al Karazi (2006) had considered a level of colonization rate of 13% with AM fungi was adequate for successful establishment of mycorrhizal tomatoes after transplanting. Similarly, Bierman and Linderman (1983) reported that low levels of colonization (<10%) in nursery spread rapidly to new roots after transplanting. Furthermore, the differences in terms of root colonization between pre-inoculated and non-pre-inoculated jujube seedlings in greenhouse remained 18 months after planting despite the competition between *R. irregularis* and native AM fungal isolates in the field (Thioye et al. 2021). Potential priority effect due to the pre-colonization of jujube roots with *R. irregularis* IR27 in the nursery and a higher competitiveness of this AM fungus compared to native AM fungi may explain why there was a higher colonization of *R. irregularis* IR27 compared to the native AM fungal communities. However, tracking and quantification of *R. irregularis* populations by using *RPB1* gene in *Z. mauritiana* roots at 18 months after planting, showed this hypothesis was not consistent with the low persistence of *R. irregularis* IR27 estimated approximately at 15% of *R. irregularis* populations (Thioye et al. 2020). A second hypothesis suggests inoculant may interact positively with the native AM fungal community colonization as demonstrated by Alguacil et al. (2011) which showed beneficial interactions between a mix of two exotic AM fungal *Glomus* sp. and *G. intraradices* with the native AM fungal community on *Olea europaea* root colonization growing in field trials (Alguacil et al. 2011). Indeed, pre-inoculation of *O. europaea* with *Glomus* spp. greatly restricted numbers of other native AM fungal ribotypes able to subsequently colonize roots after exposure to *Glomeraceae*-dominated field soil. This suggests that phylogenetic relatedness and life history strategies may play a role in AM fungal community assembly as suggested by Mummey et al. (2009). A third hypothesis suggests within species of the *Rhizophagus* genus, AM fungal strains can anastomose, which could lead to both an under-estimation of *R. irregularis* IR27 and a gradual dilution of its effects (Rodriguez and Sanders, 2015). In this regard, there is a potential risk that introduction of *R. irregularis* IR27 can cause genetic exchange with native AM fungi and as consequence increase or decrease mutualistic quality (Colard et al. 2011; Hart et al. 2017).

5.2. Pre-inoculation effect on native AM fungal communities

There are three levels of ecological impact of introducing exotic AM fungi on already existing AM fungal assemblages: (i) alteration of composition and structure of native AM fungal population and/or community, (ii) exchange of genetic material with native AM fungal population and/or community, and (iii) persistence and/or spread of AM fungal inoculants, increasing consequently the first two impacts (Rodriguez and Sanders 2015). The controlled mycorrhization in nurseries has provided valuable insights into the impact of the exotic *R. irregularis* IR27 strain on the growth and nutrition of jujube trees (Thioye et al., 2017). However, the extent of disturbance caused by the pre-inoculation of jujube trees with the exotic fungus *R. irregularis* IR27 on the native AM fungal community varied across different forest sites (Thioye et al., 2019; Thioye et al., 2021). In both field experiments, the majority of OTUs belonged to the family of Glomeraceae in Gola and Tasset cultivars (Figure 1a) (Thioye et al. 2019; Thioye et al. 2021). Overall, the dominance of Glomeraceae and its high frequency in the native AM fungal community of jujube trees in orchards (Thioye et al. 2019;

Thioye et al. 2021), confirms the worldwide trend described by Davison et al. (2015). As consequence, ruderal life strategy of Glomeraceae *i.e.*, early production of spores, high fungal growth rates, higher intraradical host colonization, is particularly adapted for early re-colonization of host plants in degraded environments as the ones encountered on the route of the GGW (Chagnon and Bainard, 2014; Thioye et al. 2019). Of the native AM fungal community associated with jujube trees, *Rhizophagus* constituted the most dominant genera in Glomeraceae (Figure 1b). This is consistent with several studies showed that *Rhizophagus* is one the most dominant genera in Glomeraceae in semiarid environments (Yamato et al. 2009; Alguacil et al. 2011; Torrecillas et al. 2012). At the species level, the impact of mycorrhizal inoculation observed on *Rhizophagus* was mainly due to a strong decrease of *Rhizophagus fascilitus* in Tasset cultivar and *R. manihotis* in Gola cultivar (Figure 1b). Overall, in the orchard located in semi-arid region, no significant impact of AM fungal inoculation or the type of cultivar was observed on AM fungal community richness and diversity (Table 7), whereas in orchard under arid region AM fungal richness had a significant impact by only inoculation treatment, leading to a negative effect on abundance of few AM fungal OTUs (not shown) (Thioye et al. 2019). This discrepancy in terms of impact of *R. irregularis* IR27 on AM fungal richness between both orchards may be due to less harsh conditions in the semi-arid compared to arid areas (Thioye et al. 2019). At present, there is no information whether there are environmental factors that influence a given assemblage in a given locality (Rodriguez and Sanders, 2015).

Figure 1. Taxonomic distribution of AM fungal (a) genera and (b) species associated with non-inoculated and inoculated jujube cultivars (Tasset and Gola) 18 months under field conditions (Thioye et al. 2021).

Table 7. Effect of jujube cultivar and mycorrhizal pre-inoculation on richness and diversity of the jujube root-associated AM fungal community 18 months under field conditions (Thioye et al. 2021).

Treatment	Number of OTUs (Richness)	Chao (Richness)	Shannon (Diversity)	Invsimpson (Diversity)
Gola	178 ± 15	255.6 ± 28	1.9 ± 0.3	4.2 ± 1.2
Gola + Ri	153 ± 17	235.7 ± 19	1.7 ± 0.4	4.5 ± 1.3

Tasset	160 ± 16	224.2 ± 26	1.9 ± 0.4	4.5 ± 1.9
Tasset + Ri	168 ± 12	229.6 ± 24	1.9 ± 0.2	4.4 ± 1.6
Factors				
Cultivar (C)	ns	ns	ns	ns
Inoculation (I)	ns	ns	ns	ns
C × I	ns	ns	ns	ns

The values represent means of each treatment using ANOVA test (n=10); Ri: *Rhizophagus irregularis*; ns: not significant.

6. Pre-inoculation effect on plant growth and fruit production

The lack of understanding on how AM fungal pre-inoculants interact directly or indirectly with native AM fungal communities makes it difficult to disentangle mechanisms behind the plant growth and fruit production of jujube trees in both orchards (Thioye et al. 2021). Given AM fungal inoculation is costly and time-consumed, only increases in crop yield and fungal persistence among native AM fungal community, may justify inoculation of jujube trees with the exotic *R. irregularis* IR27. Pre-inoculated seedlings of jujube with the exotic *R. irregularis* IR27 showed a significant growth and P nutrition increase *versus* non-pre-inoculated seedlings at the nursery stage (Thioye et al. 2019; Thioye et al. 2021). These differences remained after 4, 8, 12 and 18 months after planting of both jujube cultivars in terms of growth, survival and fruit production in both orchards, suggesting that *R. irregularis* IR27 was an efficient and persistent AM fungus despite the presence of native AM fungal communities (Thioye et al. 2019; Thioye et al. 2021). Our results showed large differences between the both cultivars with or without the AM fungus (Figures 2 and 3). After two years plantation, Gola cultivar had produced lesser number of fruits (385 *versus* 258) than Tasset ones, whereas it was more productive in terms fresh weight (467 g *versus* 278 g) and diameter (3.5 cm *versus* 1.3 cm) of fruits, irrespective of AM inoculation. Moreover, pre-inoculated jujube trees with inoculant were superior to controls except to the number of fruits, whatever cultivar. At this end, pre-inoculated Gola and Tasset cultivars had produced similar number of fruits (556 *versus* 317), whereas pre-inoculated Gola more productive than Tasset in terms of fresh weight (1044 g *versus* 434 g) and diameter (3.6 cm *versus* 1.8 cm) of fruits (Thioye et al. 2021). However, the degree of responsiveness to pre-inoculation depended on jujube genotypes. Similarly, the obtained results on cassava demonstrate that maximizing the inoculation responsiveness is above all dependent on genotypes of this root vegetable (Peña Venegas et al. 2021). The increased fruit production may be due to the fact orchard soil was found to be poor in terms of soil available P and AM fungal propagules, and pre-inoculation may be, in this context, an important factor contributing fruit production of jujube trees. Increase of fruit production of jujube trees could be due to the improving of absorption of nutrients thanks to AM inoculation. Similarly, pre-transplanting inoculation with *R. irregularis* contributed to improve significantly fruit production of melon and vine and to prevent the severity of the disease (Pia Aleandri et al. 2015). We don't know, however, whether AM fungal inoculation that results in improved of fruit production of jujube trees is due to a direct effect of the introduced *R. irregularis* on the plant or indirectly through a change in the local AMF community.

Application of *R. irregularis* is also currently a way of increasing cassava yields (Ceballos et al. 2013; Peña Venegas et al. 2021). Our results are also match with those of Köhl et al. (2016) who found that the exotic *R. irregulare* (named also *R. irregularis*) isolate BEG21 can improve growth of clover irrespective of initial soil P availability and AM fungal propagules abundance. Overall, *R. irregularis* was reported as a ubiquitous AM fungus occurred in a wide range of environment and considered as a good competitor (Badri et al. 2016; Kölh et al. 2016; Hijri, 2016; Renaut et al. 2019; Pellegrino et al. 2020). Some other exotic AM fungi can also play similar role. For instance, Pellegrino et al. (2012) showed that field inoculation with two exotic *Funneliformis mosseae* isolates IMAI and AZ225C increased biomass production of *Medicago sativa*. Some factors (*i.e.* pruning, fertilization, irrigation) can also increase fruit production irrespective with AM fungal status of jujube trees. At this end, Ouédraogo et al. (2006) reported that jujube trees responded positively to irrigation and fertilization with rock phosphate in P-deficient soil by displaying the highest fruit production with Gola cultivar compared to the local cultivar. Similarly, a combination of pruning or irrigation with foliar sprays of potassium increased significantly growth and fruit production of *Z. mauritiana* (Pengrui et al. 2021; Saritha et al. 2021). In any case, increasing of fruit production due to AM fungal inoculation were rarely observed on fruit trees, whereas they were widely occurred on vegetables such as cassava (Sery et al. 2016; De Bauw et al. 2021; Peña Venegas et al. 2021), sweet pepper (Nurzynska-Wierdak et al. 2021), cucumber (Ortas, 2010) and tomato (Al-Karaki, 2006; Huang et al. 2013; Hijri, 2016) as well as fruit berries like strawberry (Bona et al. 2015) and raspberry (Chen et al. 2022).

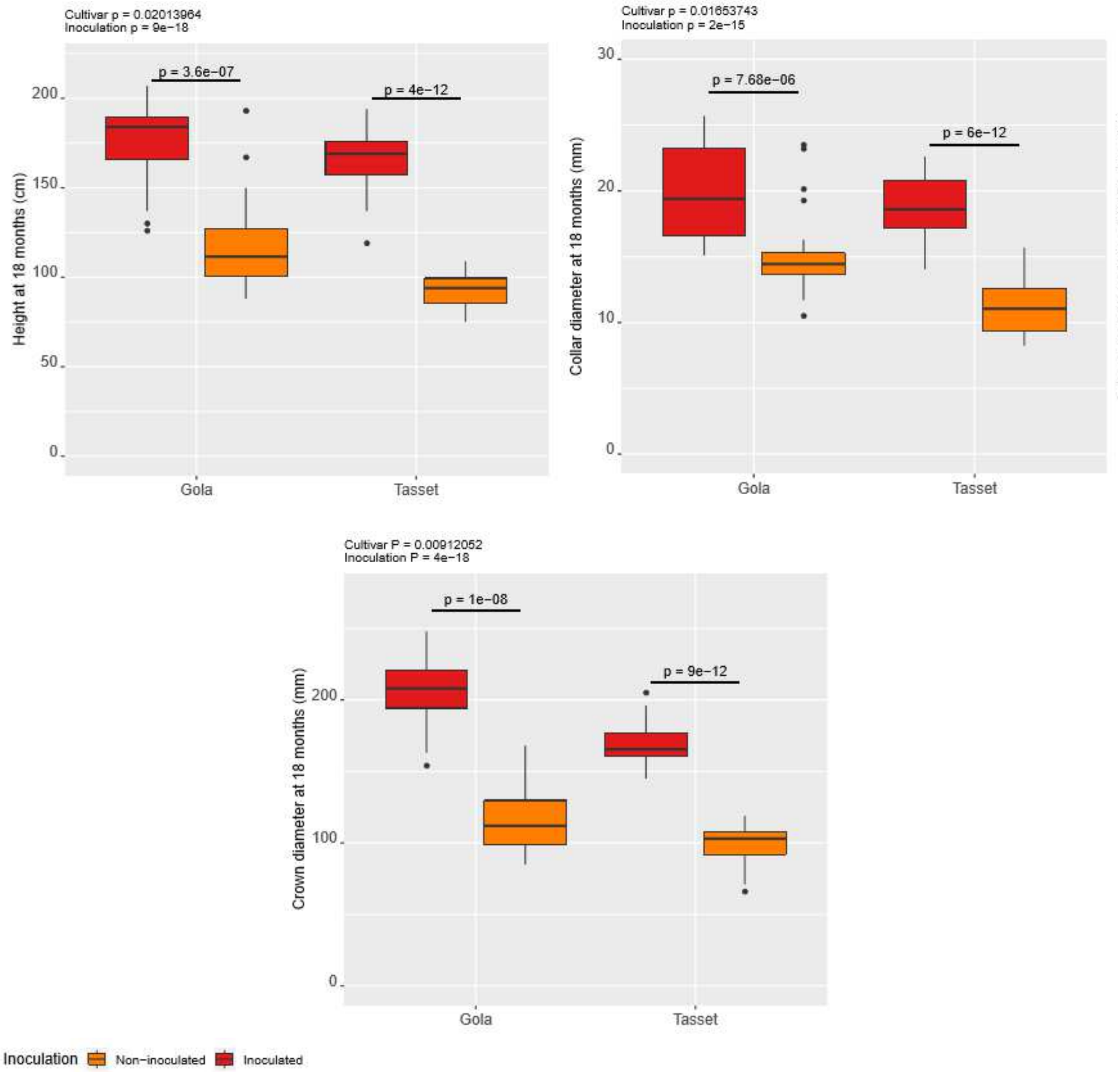

Figure 2. Effect of inoculation with *Rhizophagus irregularis* IR27 on growth parameters (height, collar and crown diameter) of *Z. mauritiana* cultivars 18 months under field conditions. The boxplot with p-values represent means of each treatment using Kruskal-Wallis test (n=10); significant levels: $P<0.05$. (Thioye et al. 2021).

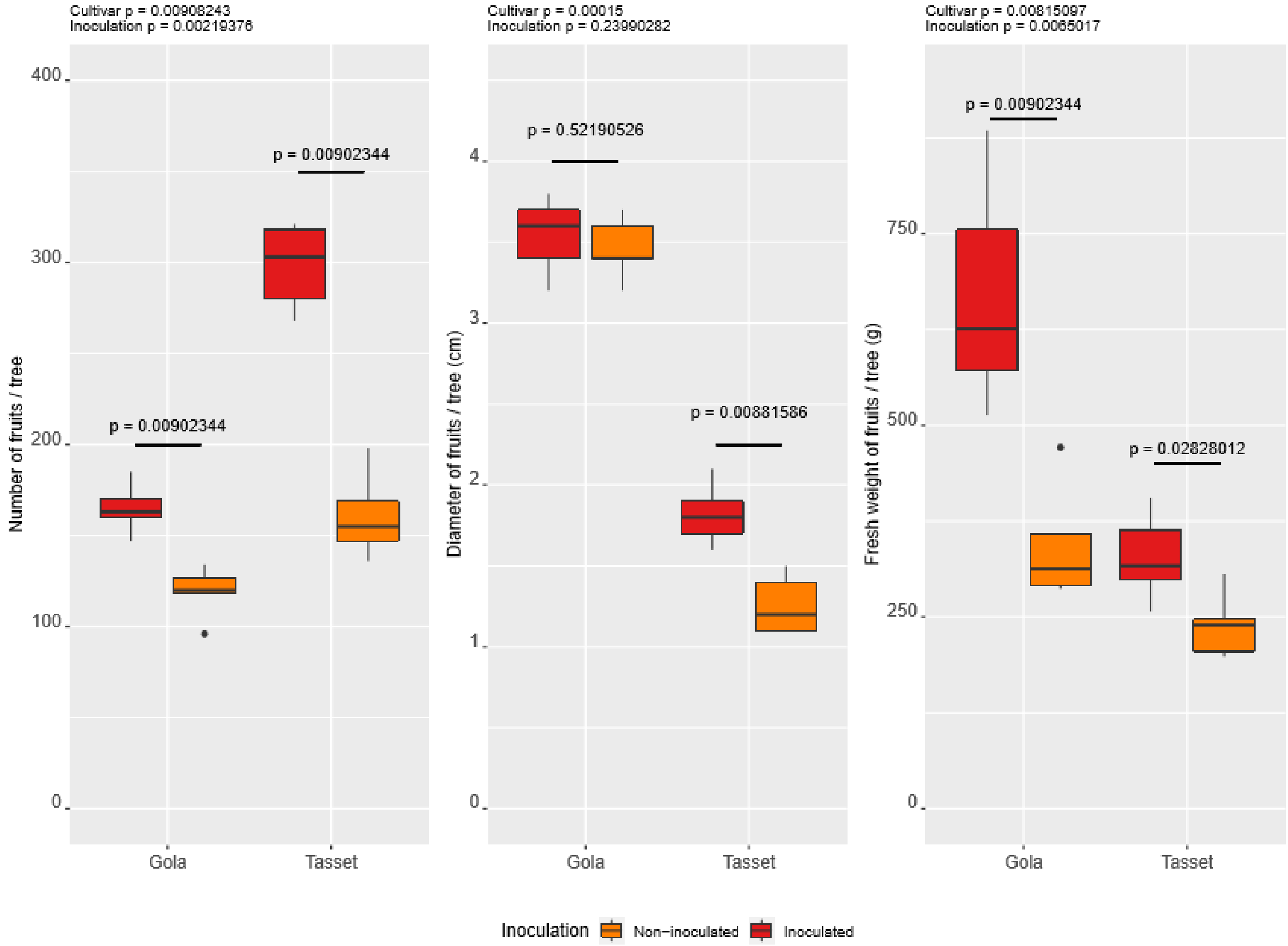

Figure 3. Effect of inoculation with *Rhizophagus irregularis* IR27 on fruit parameters (number, diameter and fresh of fruits) and mycorrhizal colonization of *Z. mauritiana* cultivars 18 months after transplanting. The boxplot with p-values represent means of each treatment using Kruskal-Wallis test (n=10); significant levels: *P*<0.05 (Thioye et al. 2021).

7. Conclusion and future directions

To reap the benefits of mycorrhization, it is suggested that the consideration of RMD categories should be the first level of screening for ITF to determine whether they derive or not benefits from AM symbiosis and to know how to manage it in agroforestry systems accordingly. Our data indicate that *Z. mauritiana* cultivars and provenances differ in their response to AM fungal inoculation during the first phase of growth and that AM fungi also improve growth, nutrient content and fruit production of jujube trees. The obtained results demonstrate that maximizing the inoculation responsiveness of *Z. mauritiana* is dependent on provenances and cultivars and fungal genotypes. The current results also highlight the major benefits of mycorrhizal pre-inoculation on jujube trees, extending beyond the evaluation of fruit production, which is a goal that is rarely achieved. The substantial increase in fruit production has the potential to significantly improve income for farmers, particularly during the critical period of food insecure. Overall, results make it possible to confirm the choice of *Z. mauritiana* used as a plant model among the ITF species tested in the study of interactions between ITFs and AM fungi involved in agroforestry systems. They provide also important insights to develop and improve the ecological management of jujube orchards, strengthening the importance of using *R. irregularis* IR27 as a sustainable inoculant for increased food security. At this end, *R. irregularis* IR27 constitutes a promising biological tool for the production of higher quality nursery stock with expected improved performance of *Z. mauritiana* in terms of growth and fruit production within agroforestry systems. Given the environmental and economic costs linked to the utilization of soluble fertilizers, it is recommended to contemplate fertilizing AM jujube seedlings in the nursery with RP from Mali instead of TSP. Nonetheless, it is worth noting that TSP also exhibits beneficial effects on plant growth, both with and without inoculation, particularly in phosphorus-deficient soils. Furthermore, since AM inoculation is also costly, only increases in crop yield and fungal persistence among native AM fungal community, could justify inoculation of jujube trees with the exotic *R. irregularis* IR27. The significant increase of AM colonization of both inoculated jujube cultivars compared to controls suggests that the inoculant can stimulate AM fungal colonization by native AM fungi without change *a priori* the native AM fungal community. If invasive, the inoculant may pose a threat to native microbiota community and plant biodiversity. Of the mechanisms, the possible effects of genetic exchange between inoculant and native strain constitute a major challenge rarely investigated and remain a research priority on mutualistic quality. Understanding how inoculants interact and coexist with the native microbiota community and whether this interaction directly leads to changes in plant productivity remains a challenge in promoting the use of inoculants in agroforestry systems, especially in arid and semi-arid areas where sustainable plant productivity is crucial. When native strains demonstrate a comparable effect on plant growth to exotic strains, it is advisable to prioritize their use. Additionally, further efforts should be made to domesticate important IFTs that exhibit high mycorrhizal dependence (such as *T. indica*), moderate dependence (such as *D. guineensis*, *P. biglobosa*, and *C. pinnata*), or marginal dependence (such as *A. occidentale*, *A. senegalensis*, *S. birrea*, and *A. digitata*).

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