The arbuscular mycorrhizal symbiosis and its role in date palm production and sustainability

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ABSTRACT

The arbuscular mycorrhizal association is an essential symbiosis between a unique group of soil fungi and a majority of plant species worldwide. The fungi produce an extensive hyphal network that mines soil for unavailable phosphorus and the plants benefit through improved nutrition. Date palms are shown experimentally to be highly dependent on this association, showing increased trunk and leaf biomass even with applied fertilizers and greater tolerance to saline conditions. This dependency is attributed to a coarse root system with a paucity of root hairs, a high P requirement to support growth of a large plant biomass, and a field environment that further limits P mobility in soil. The fungi require plants to grow yet they have a wide host range, so diverse species can associate with date palms. Many fungal species have considerable genetic plasticity and they are pandemic because of ancient origin and coevolution with their hosts. Experiments show that some nonnative fungal strains can benefit plants as well or better than native strains. Therefore, ecological tolerance permits selection of inoculants that benefit palms in a wide range of environments including those with high salinity. Transport of plants between countries necessitates palm production in soilless media, and use of a light weight mineral-based material supplemented with peat for water-holding capacity will provide an optimum compatibility for the mycorrhizal symbiosis. Many questions remain to be answered, but symbiotic interactions clearly are important in both the production phase and for sustainability after outplanting of date palms to the field.

Key Words: fungi, mycorrhizae, Glomeromycota, mycorrhizal dependency, INVAM

INTRODUCTION

The arbuscular mycorrhizal symbiosis is a critical component to the survival and longevity of a vast number of plant species, including all crop plants (Smith and Read, 1997). A survey of the plant kingdom within the framework of their evolution suggests that all of the earliest land plants formed an arbuscular mycorrhizal association (Trappe, 1987) and that over the intervening eons some plants either evolved different kinds of mycorrhizal associations (of which there are six other types – Smith and Read, 1997) or they lost the symbiosis completely. The latter groups of plants (e.g., Brassiceae, Cruciferae, Chenopodiaceae) tend to be fast growing pioneer species in arid and semi-arid environments that contain few native AMF (Brundrett, 2009). Some of the plant species selected for plant revegetation in desert regions belong to these families and are able to grow in soils lacking these fungi. Other plant species are completely dependent on the mycorrhizal association. In discussing the arbuscular mycorrhizal symbiosis and its potential benefit to date palm production, consideration must be given to the biological and ecological properties of the fungi, the phenology and dependency of plant species serving as host for those fungi, and the environment surrounding both partners. Each of these variables will be considered separately and then applied to date palms.

The fungi

Arbuscular mycorrhizal fungi (AMF) evolved four hundred million years ago at about the same time plants appeared on land. Since those early land plants did not have a true root system for absorption of nutrients, the presence of AMF is hypothesized to have been crucial to evolution of plants on land (Morton, 1990; Pirozynski and Malloch, 1975). AMF can obtain carbon for growth and reproduction only through specialized structures called "arbuscules" that form at a close interface between plant and fungus in root cortical cells (Fig. 1A). As a result, these fungi cannot grow apart from a host plant. Each arbuscule appears to fill a cell, but it resides between the wall and membrane to functionally exchange nutrients between host and fungus. Phosphorus tightly bound to soil particles is absorbed by an extensive network of finely branched hyphae that fills the rhizosphere and it is from these hyphae that asexual spores are formed for widespread dispersal (Fig 1B).

Because this association is an obligate one, the fungi have evolved only with their plant hosts since they appeared on land. For that reason, AMF are unique amongst all fungal groups and this is reflected in their classification as a separate phylum (Schüßler *et al.,* 2001). Co-evolution of AMF with their plant hosts has resulted in some important biological and ecological properties.

Evidence indicates AMF are strictly asexual (Pawlowska, 2005). Spores are produced in soil and roots for dispersal, they germinate, infect the host, grow, and produce more spores. They also are isolated from each other, so that hyphae rarely are able to fuse and exchange cytoplasm and nuclei. Total reliance on asexual reproduction generally is a negative trait because harmful mutations can accumulate, but AMF compensate by possessing many nuclei (Fig. 1C) that move and sort independently throughout the hyphae and into spores (VanKuren *et al.,* 2013). This genetic heterogeneity gives the fungi considerable flexibility and longevity.

AMF species show little evidence of host specificity. This means that any fungal strain can colonize the roots any host plant that is able to form an AM association. Because of this property, a large and diverse international culture collection such as INVAM (Morton *et al.,* 1993; http://invam.wvu.edu) can grow more than 1100 strains of 103 species (44% of total known diversity on one plant host: the highly dependent small grain species, *Sorghum sudanense* (sorghum).

Host specificity and host compatibility must be carefully differentiated, because these terms have been used interchangeably. The former relates to the ability of any fungus to colonize roots and establish a symbiosis. The latter reflects the quality of the symbiosis and plant responses after the association has been established. An unpublished study in INVAM designed to identify the ideal host plants for culturing AMF will serve as an example. Two AMF species with broad ecological tolerance, *Claroideoglomus etunicatum* and *Rhizophagus intraradices*, both were able to colonize apple seedling roots, but only the latter species produced extensive root colonization, sporulated, and caused a strong growth response. When present together, only *R. intraradices* was detected in tree roots after three months of growth. This species was compatible with any plant tested, but *C. etunicatum* was most compatible only with herbaceous plants.

AMF species representing all of the major clades in the phylum Glomeromycota are globally distributed, suggesting that a majority of species are pandemic. This conclusion can be inferred only from phylogenetic patterns, because vast regions of the globe have not been sampled enough. The explanation for such remarkable widespread distribution rests with a combination of evolutionary timing and inherent properties. The fungi are hypothesized to have speciated at a time with the earth's land masses were joined into the supercontinent, Pangea (Morton, 1990). During the next 100 million years, as the continents began to separate, there was ample time and opportunity for asexual fungal spores to disperse and colonize almost any plant growing at the time because of a broad host range. The likelihood of pandemism is important to humans because it means that movement of fungal strains across countries or continents for academic or commercial purposes is safe and not likely to impact on most anthropogenic activities.

Widespread dispersal of species coupled with broad host range results in a high level of species diversity within the root system of even a single plant. From more than 3000 cultures grown at INVAM to trap native AMF species, none consisted of only one species. From more than 3000 cultures grown at INVAM to trap native AMF species, none consisted of only one species. The median number of species was three, 82% were in the range of 2-6 species, and 18% were between 7-12 species. Also, species occupying a root system can represent a broad range of evolutionary clades in Glomeromycota. This range of diversity suggests some AMF fungi have broad ecological compatibility and can occupy many niches comfortably.

Ample evidence exists that AMF species differ in how they benefit plants and the magnitude of that benefit (Brundrett, 1991; Smith and Read, 1997). In some cases, particular matches of AMF and plant species may be needed (Streitwolf-Engel *et al.,* 1997; van der Heijden *et al.,* 1998). A study by Kelly et al. (2005) exemplifies the extent of differential responses among strains of a species as well as between species. Different strains of several AMF species sampled from a range of habitats were compared on a highly dependent warm season grass (broomsedge) in soils containing low to toxic levels of aluminum. All

five strains of one species (*Rhizophagus clarus*) grew well and conferred aluminum tolerance at all Al levels, regardless of the habitat from which they were collected. All five strains of another species (*Acaulospora morrowiae*) failed to grow well, regardless of origin. In contrast, compatibility of *Scutellospora heterogama* varied greatly between strains but those differences didn't correlated with habitat of origin. The broad environmental tolerance of *R. clarus* was revealed as well in the ability of a strain from the Senoran desert in Arizona to grow as well or better in a wetland environment (Fig. 2). Anecdotal data from culturing AMF at different soil P levels in INVAM indicate that *R. clarus* and two other species in *Rhizophagus* (*R. intraradices* and *R. diaphanus*) are able to grow well in plant roots when most other AMF are inhibited completely. It is no surprise, then that *R. intraradices* is one of the most widely and effectively used AMF species in commercial inoculants. *Rhizophagus* species all sporulate prolifically inside plant roots and may be unique in being able to undergo anastomosis, which is the fusion of hyphae to allow exchange of nuclei and cytoplasm (Croll *et al.,* 2009; Purin and Morton, 2013). These properties collectively favor dispersal, longevity, and genetic heterogeneity, making them preferred candidates for broad application as inocula.

The Plant Host

The benefits conferred by AMF to their plant hosts are diverse and governed largely by interactions that optimize mineral nutrition for growth and reproductive potential (or yield in agronomic terms) of the plant host species under consideration. In general, the magnitude of the plant response to the symbiosis is a measure of "mycorrhizal dependency" (Tawaraya, 2011). Fig. 3 illustrates a phosphorus response curve of a perennial cool-season grass that has low dependency and a fruit tree that exhibits complete dependency. The meadow fescue (*Festuca arundinacea*) forms a large biomass of finely branched roots that can exploit immobile P in soil and it does not have a high P requirement for photosynthesis. Fescue is highly dependent on the mycorrhizal symbiosis only when soil P level is extremely low. In contrast, apple (*Malus domestica*) has a very coarse root system and never exploits P availability no matter how high it becomes. Apple fails to respond to any fertility level except when AMF are present. Some plant species with root biomass and architecture similar to that of fescue still are highly dependent on the mycorrhizal association. Warm season grasses have a very high requirement for P because of C4 photosynthesis (Brejda *et al.,* 1993), and a large root system alone cannot compensate.

A typical plant response is an increase in shoot and root biomass, and it is expressed mostly by perennial plant species with strong apical dominance in shoot growth (Brundrett, 1991). However, phenology of the plant also is a major determining factor in the type of response expressed. For example, bulbed plants like bluebells show no top growth response when mycorrhizal, yet they cannot survive in nature without the symbiosis. AMF promote P uptake as expected, but the P is sequestered in the bulbs so that shoot emergence from deep within the soil profile is vigorous (Merryweather and Fitter, 1995).

The Growth Medium

The medium in which any plant is grown determines its nutrition status and its growth potential. When AMF are present, properties and environment of that growth medium can greatly impact on mycorrhizal interactions and the magnitude of any benefit. Many types of media are in use. At INVAM, the standard culture medium for culturing all AMF is a coarse sand and loamy soil mix (3:1 v/v) that is steamed twice to remove native microbes. Sand is used because it is completely inert and increases air spaces for root infiltration. This medium has been used by INVAM for 26 years to culture AMF from all continents and a wide range of habitats, so there is strong evidence for broad compatibility. This mixture is well suited to AMF cultures, but it is not the best option for growing plants commercially that must cross borders between states, countries, or continents.

With the increased emphasis on minimizing movement of pathogens or exotic microbes associated with transport of plant material, soilless media is the only option. Sphagnum peat moss is widely used because of its availability, reasonable cost, light weight, and high water-holding capacity. AMF generally are compatible in peat and peat mixes, despite acidity of the medium.

Expanded volcanic rock material, such as perlite or pumice, are light weight and promote aeration and water retention. Vermiculite has similar properties, but it tends to compress over time and reduce aeration. Expanded calcine clays have gained acceptance in recent years, but pH and nutrient content (especially calcium) varies greatly with where the material was mined and with fertilization regimes. All of these materials provide environments within which AMF are compatible as long as pH stays below 6.2-6.4. One of the key variables, other than pH, is particle size. Ridgeway et al. (2006) show that larger particles promote both root infiltration and mycorrhizal colonization.

Results are most inconsistent with the inclusion of composted pine or hardwood barks. Some studies indicate that AMF tolerate bark media, but tests in INVAM show varying levels of inhibition. For example, two mixes with similar proportions of bark (45%), and peat (55%) produced opposite results. One mix completely inhibited AMF colonization whereas mycorrhizae achieved 46-57% in the other mix. In another test (Fig. 4), two different peat-

hardwood bark formulations were equally inhibitory to mycorrhization, especially in relation to a sand-soil mix. Of the three AMF species examined, one never colonized the corn assay host more than 6% and two other species slowly adapted and colonized at levels as high as 40%. The adaptability and tolerance of the two *Rhizophagus* species corroborate the conclusion reached above that strains of species in this genus have wide ecological tolerance.

Application of AMF to Date Palm Production

Date palm (*Phoenix dactylifera* L.) is naturally colonized by mycorrhizal fungi, based on studies from Iraq (Khudairi, 1969), Saudi Arabia (Khaliel and Abou-Hailah, 1985) and Morocco (Bouamri *et al.,* 2006). The native AMF species present in the rhizosphere can be diverse (Al-Yahya 2008), but at levels similar those in a range of other habitats (Morton *et al.,* 2004).

The dependency of date palm on the mycorrhizal symbiosis is expected to be similar to that of apple (Fig. 3) and other fruit tree species. All are long-lived perennial species with a high demand for nutrients to sustain a large above-ground biomass and fruit production. Moreover, the root systems are coarse with a low degree of branching and root hair formation (Fig. 5). The arid habitat in which date palms are grown contributes even more to mycorrhizal dependency. Phosphorus is mostly immobile and relies on diffusion through a water film from soil particles to root surfaces. In an arid climate, this condition occurs infrequently without human intervention (irrigation).

Few studies have been conducted with the intent of evaluating mycorrhizal dependency of date palm to the mycorrhizal symbiosis. Ghulam Shabbi, Ewald Sieverding and coworkers conducted a year-long experiment to measure mycorrhizal responses in pots of the variety Khaneizi watered with a standard and one-third strength fertilizer and at three salinity levels. While this study did not measure a P response curve for date palm to provide a direct measurement of mycorrhizal dependency, results were dramatic and clearly verified a strong reliance of the mycorrhizal symbiosis (Fig. 6). Predictably, the greatest growth benefit occurred with lower fertility and application of fresh water (Fig. 6A). Most notable, however, was that this benefit occurred even with the standard fertilizer regimen and at increasing salt levels. Amelioration of salt stress by AMF may not be that uncommon, as it has been measured in other plants as well (Al-Karaki, 2000). Fig. 6B shows plant phenotypes of mycorrhizal plants with increasing salinity, and reductions in plant growth are not dramatic.

There are several caveats to this study that accentuate the benefit attributable to the mycorrhizal symbiosis. First, the nonmycorrhizal treatment must have contained a low density of native AMF, as evidenced by fairly extensive colonization after a year's growth in pots. The marked growth benefit that occurred with a symbiosis in all pots indicates that rate of colonization is crucial to the final growth response. Inoculation with *R. intraradices* likely led to rapid mycorrhization and an early growth spurt that became magnified over time, whereas slow AMF colonization in nonmycorrhizal pots took much longer to express a growth benefit. If the nonmycorrhizal treatment lacked any AMF colonization, the differences likely would have been much greater. This result dramatically shows the benefit of inoculation in native environments where AMF may be present but in low density. Second, this experiment was conducted in pots. Roots were constrained over time, thus slowing above-ground biomass in the fastest growing plants. Nutrient levels were more homogeneous and more plant-available (no matter how much was added), so that diffusion of P in the fertilizer would be enhanced by sustained moisture in the pot contents. There was no growth depression (as seen with fescue in Fig. 3) under higher fertility and mycorrhizal colonization in the inoculated pots was reduced, but not appreciably. In nature, none of these conditions would be met, so that P availability would be low no matter how much fertilizer was applied and so mycorrhizal colonization likely would not be inhibited. Collectively, these results suggest that inocula of AMF can improve the production of date palms throughout the Middle East and North Africa and improve crop sustainability after outplanting to the field.

With increased demand and the need for movement of plants across national borders, date palms are increasingly being started from tissue culture and then transplanted into soilless media (Awad 2008). The type of medium used in date palm production, therefore, is of major importance. Based on the discussion above, a recommended medium would consist of mineral component such as expanded rock other than calcined clay (such as a pumice-like material) to keep pH below 7.0 amended with a small amount of peat to optimize water-holding capacity. Barks should be avoided because organic components have a high probability of inhibiting mycorrhization. Other organic material such as compost may be less toxic, but results are likely to be unpredictable. Keep in mind that these fungi evolved in high mineral soils and therefore will be most compatible with their plant host in this environment.

Of the more than 230 AMF species currently known (http://invam.wvu.edu), choice of species and strains of AMF that can serve as the "best" inoculant is dictated primarily by breadth of tolerance to a range of environmental variables. As discussed above, the most likely AMF candidates are in the genus *Rhizophagus*. Because of the pandemic distribution of this and other *Rhizophagus* species (in particular *R. clarus*), their introduction into any field or nursery setting is not

likely to be harmful. Assumptions that native species are the best adapted are not always true. Certain AMF species, such as those in *Rhizophagus*, behave similarly in very divergent environments (e.g. desert, wetland, high P soil, high organic matter, root organ culture, high heavy metals, etc.) and could outperform native strains (see Fig. 2).

The central issue in date palm production is whether inoculation is necessary or not. Results chronicled above provide a strong indication that introducing a quality inoculum into a soilless medium for nursery stock is a necessity for vigorous and sustainable plant growth. This benefit is likely to continue in the field setting. While evidence indicates date palms in the field are mycorrhizal and the fungi are taxonomically diverse, little is known about the density and infectivity of these native AMF communities. Important questions that have yet to answered include the following: What is the inoculum potential of native fungi in the field at the time of date palm outplanting? How much does inoculum potential differ with variation in edaphic conditions (temperature, pH, frequency of rainfall, duration of solarization, etc.), the composition and density of pre-existing plant communities, geographic location, and previous anthropogenic practices or disturbances? How does inoculum potential change with age of date palm groves, especially after onset of fruit production? What is the sustainability of an introduced AMF species (the inoculant) over time as it competes with native AMF? These questions indicate that much has yet to be learned to fully understand and predict the relationship between AMF and date palm, especially after transplanting to the field.

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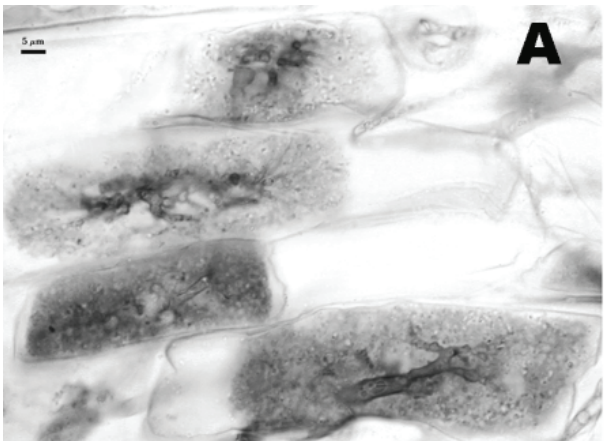
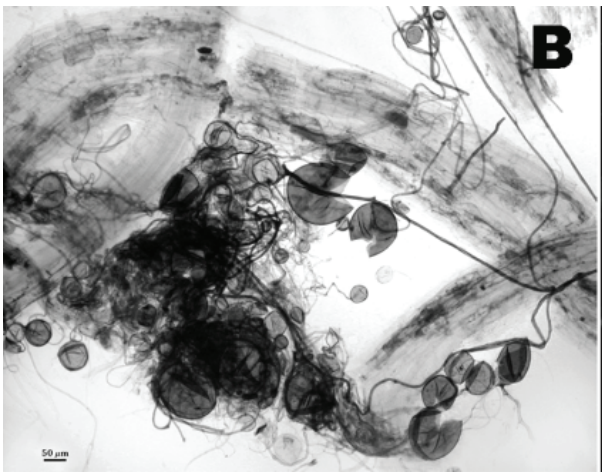
Figures





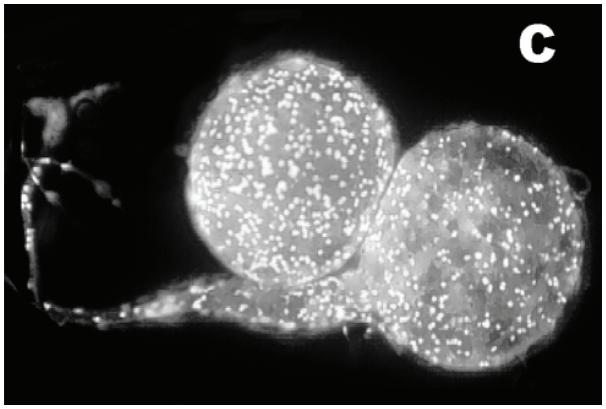


Fig. 1. Basic features of arbuscular mycorrhizal fungi. A. Arbuscules present within the cortical cells of a corn root. B. Mycorrhizal colonization of roots, with external hyphae and asexual spores. C. Multinucleate contents of developing spore and attached hypha.

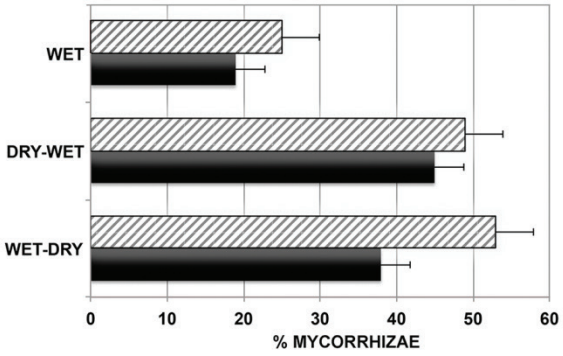


Fig. 2. Mycorrhizal colonization of *Spartina patens* in an artificial wetland by native (black) and non-native strain (hatched) of *Rhizophagus clarus* from the Senoran Desert. Wet = flooded always, dry-wet = mostly dry with short flooded periods, wet-dry = mostly flooded with short dry periods

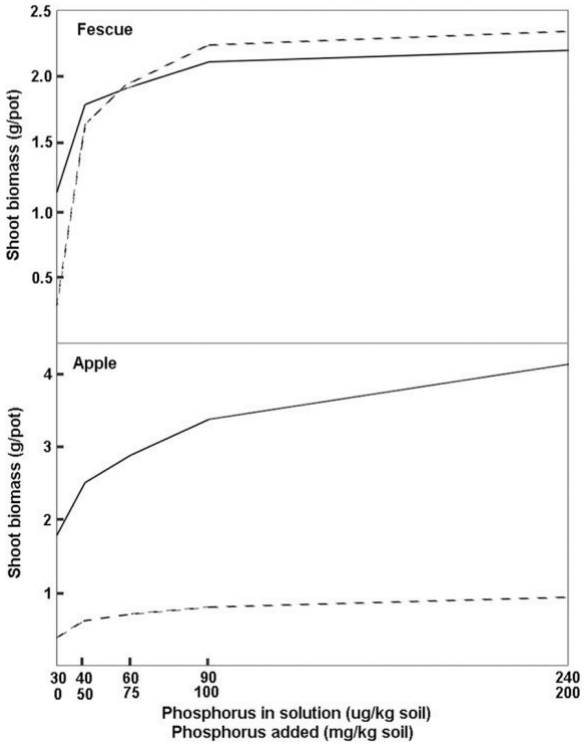


Fig. 3. Mycorrhizal dependency of fescue (*Festuca arundinacea*) and apple (*Malus domestica*) based on phosphorus response curves after 72 days of growth in soil with added P. Solution P was determined by carbon tetrachloride displacement. Dotted line = nonmycorrhizal, solid line = mycorrhizal plants.

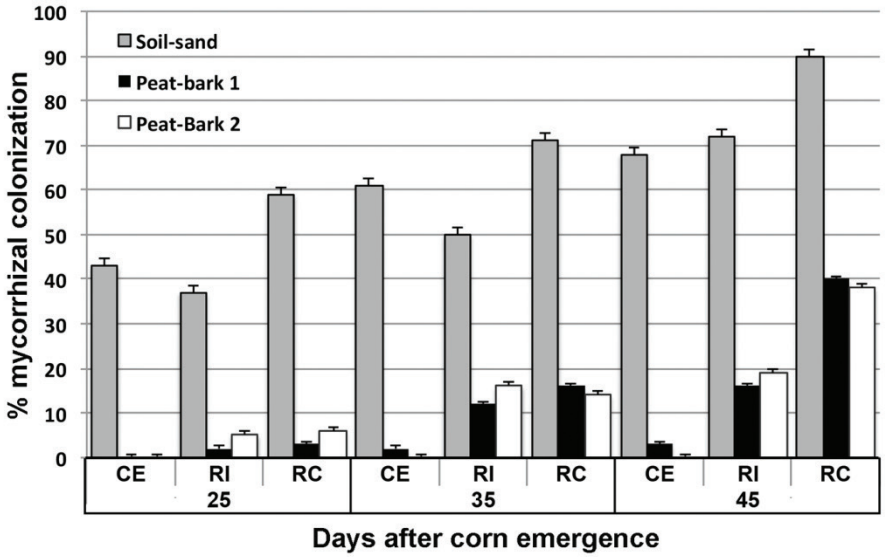


Fig. 4. Variation in amount of mycorrhizal colonization by strains of three AMF species grown on sorghum for 25, 35 and 45 days after emergence. Soil-sand = 1:3 v/v), both peat-barks contained a mix of 40% peat, 45% bark, 15% perlite. CE = *Claroideoglomus etunicatum*, RI = *Rhizophagus intraradices*, RC = *Rhizophagus clarus*,

Fig. 5. Root mass and architecture of mycorrhizal and nonmycorrhizal date palm, variety Khaneizi.

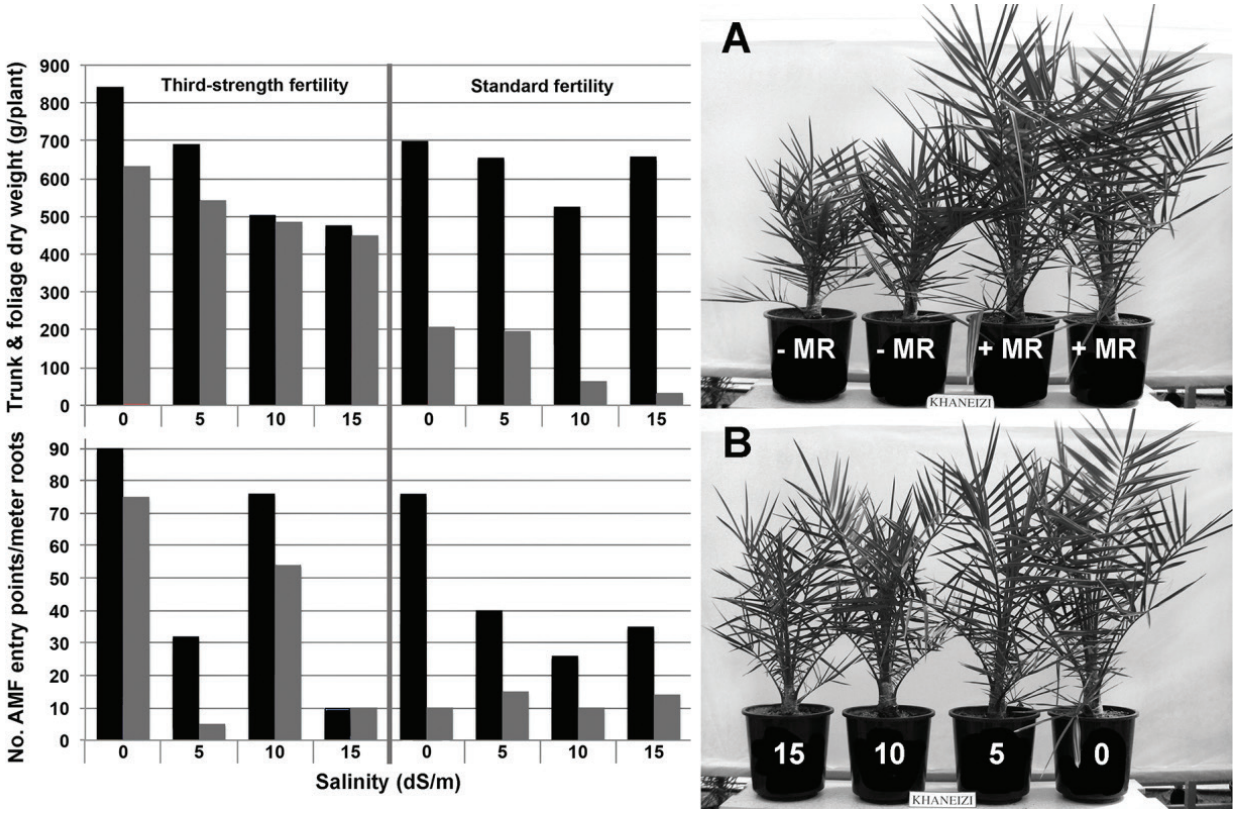


Fig. 6. Reponses by one-year-old date palms, cultivar Khaneizi, to inoculation with *Rhizophagus intraradices* and watered at varying levels of salinity (0-15 dS/m). Plants were grown in a medium consisting of native soil 1.5 m below root zones and a mix of peat and perlite (2:1 v/v). In the chart, blue bars represent mycorrhizal plants and the red bar indicates nonmycorrhizal plants. MR = mycorrhiza. A = paired plants at one-third strength fertility with or without AMF added. B = Plants at standard strength fertility inoculated with AMF and watered at three salt concentrations.