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Impact of water regimes on an experimental community of four desert arbuscular mycorrhizal fungal (AMF) species, as affected by the introduction of a non-native AMF species

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Abstract Field studies have revealed the impact of changing water regimes on the structure of arbuscular mycorrhizal fungal (AMF) communities, but it is not known what happens to the abundance of individual AMF species within the community when the water conditions in the rhizosphere change. The behavior of four AMF species isolated from the Arabian desert (*Diversispora aurantia*, *Diversispora omaniana*, *Septoglomus africanum*, and an undescribed *Paraglomus* species) was investigated when assembled in microcosms containing *Sorghum bicolor* as host plant, and treated with various water regimes. Furthermore, the impact of invasion of these assemblages by *Rhizophagus irregularis*, an AMF species widely used in commercial inocula, was studied. The abundance of each AMF species in sorghum roots was measured by determining the transcript numbers of their large ribosomal subunit (rLSU) by real-time PCR, using cDNA and species-specific primers. Plant biomass and length of AMF extraradical hyphae were also measured. The abundance of each AMF species within the sorghum roots was influenced by both the water regime and the introduction of *R. irregularis*. Under dry conditions, the introduction of *R. irregularis* reduced the total abundance of all native AMF species in roots and also led to a reduction in the amount of extraradical mycelium, as well as to a partial decrease in plant biomass. The results indicate that both water regime and the introduction of an invasive AMF species can strongly alter the structure of an AMF native assemblage with a consequent impact on the entire symbiotic mycorrhizal relationship.

Keywords Adaptation · Arbuscular mycorrhiza · Competition · Desert · Mycorrhizal community · Water regime

Introduction

Water availability, and hence water regimes, in the soil are strong determinants for the community composition of microorganisms inhabiting the rhizospere. Soil harbors a considerable fraction of global biodiversity (Decaëns 2010), and soil microbial communities support a wide range of key ecosystem functions (Eisenhauer et al. 2012). Studies have demonstrated detrimental effects of drought on soil biota, with a consequent reduction in belowground functioning (Kardol et al. 2010; Blankinship et al. 2011; Landesman et al. 2011). One of the widespread constituents of soil communities are the symbiotic arbuscular mycorrhizal fungi (AMF) which associate in a mutualistic symbiosis with 80 % of all land plants (Parniske 2008). They have been shown to positively influence plant nutrition (Smith and Read 2008), plant productivity (Klironomos et al. 2000), and improve their host plants tolerance to biotic and abiotic stresses (Azcón-Aguilar and Barea

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1996; Augé 2001; Hildebrandt et al. 2007; Pozo et al. 2010; Porcel et al. 2011).

The effect of drought on AMF communities has frequently been studied under field conditions. Changes in the community structure were revealed by assessment of AMF structures inside plant roots (Apple et al. 2005), by quantifying the amount of extraradical mycelium in the soil (Clark et al. 2009), and by molecular approaches (Querejeta et al. 2009; Sánchez-Castro et al. 2012). However, there is a lack in understanding how the soil water regime, as a single factor, affects individual AMF species in AMF communities. This can be studied best in model experiments under controlled conditions, in which the abundance of each AMF species can be traced individually using molecular markers.

Biotic exchange could threaten biodiversity (Sala 2000). The deliberate or accidental introduction of a species to an ecosystem can lead to the displacement or a change in the structure of native species communities. Accidental introductions can happen by a wide range of human activities; they have increased dramatically in the run of globalization (Mooney and Hobbs 2000; Hendrix et al. 2006). Deliberate introductions where an exotic species is set into a new habitat, for example to fight against a pest, have already led to a negative impact on biodiversity (Hall and Mills 2000; Lowe et al. 2000). Further, it has been shown that invasive belowground organisms can greatly alter aboveground and belowground ecosystem properties (Bohlen and Scheu 2004).

Currently, the use of commercial AMF inoculants is growing, and certain AMF species (mainly *Rhizophagus irregularis*) are traded globally as biofertilizers and used in agriculture and revegetation programs (Gianinazzi et al. 2002), even if they are not native at the site of application. The question of how the introduced AMF species would alter the native AMF community is still poorly understood, and it has only been addressed in a few greenhouse studies. Recent studies demonstrated a decrease in the diversity of the native AMF community after inoculation, as revealed by terminal restriction fragment length polymorphism (T-RFLP) techniques (Mummey et al. 2009; Koch et al. 2011). However, no study has evaluated the effect of the worldwide commercially used AMF species *R. irregularis* on the total abundance of AMF species inhabiting roots within native AMF communities.

A controlled experiment was therefore conducted under greenhouse conditions to evaluate the interacting effects of water regime and the presence of the potentially invasive AMF species *R. irregularis* on an assemblage of AMF species previously isolated from natural and agricultural sites in Southern Arabia (Al-Yahya'ei et al. 2011; Symanczik et al. 2014a; Symanczik et al. 2014b). The AMF community colonizing roots of *Sorghum bicolor* was assessed by determining the transcript numbers of large ribosomal subunit (rLSU) genes of each individual fungus, using real-time PCR and species-specific primers. Using transcript numbers is considered more suitable for the comparison of AMF species differing in gene copy numbers, because the total expression of functional genes (the total amount of transcripts) can be expected to be similar between species to maintain their physiological functions (Gamper et al. 2008). The results show that both water regime and the introduction of a non-native AMF species can strongly alter the structure of a native AMF assemblage. These findings highlight the fragility of ecosystems and suggest that both factors can drastically influence the symbiotic mycorrhizal relationship. These changes could have great impacts on whole ecosystem functioning, especially in arid environments where the occurring AMF species are adapted to the environmental conditions.

Materials and methods

Plant growth conditions and experimental setup

Experiments were performed with sorghum (*S. bicolor* (L.) Moench), cv Pant-5. Seeds were surface sterilized (10 min in 2.5 % KClO) then rinsed with sterile water several times and soaked in sterile water overnight. Seeds were germinated in sterile moist sand at 25 °C for 3 days in darkness. The four AMF isolated from a hyper-arid sand plain in Oman (*D. aurantia*, *D. omaniana*, *Septoglomus africanum*, and an undescribed *Paraglomus* sp.) and *R. irregularis* BEG-75 (Botanical Institute, Basel, Switzerland) were propagated as previously described (Symanczik et al. 2014a; Symanczik et al. 2014b). To establish the mycorrhizal symbiosis, three pre-germinated seeds were individually inoculated in 1-L pots filled with 1100 g of an autoclaved (120 °C, 20 min) mixture of sand (quartz sand, 0.125–0.25 mm; Kaltenhouse, Alsace, France), Terragreen (American aluminum oxide, oil-dry US special, type III R, 0.125 mm; Lobbe Umwelttechnik, Iserlohm, Germany), and Loess soil from a local site (8:2:1, *w*/*w*/*w*). Two fungal treatments were applied: the native AMF assemblage (*D. aurantia*, *D. omaniana*, *S. africanum*, and *Paraglomus* sp.) and the *R. irregularis*-invaded assemblage (*D. aurantia*, *D. omaniana*, *S. africanum*, *Paraglomus* sp., and *R. irregularis*). One hundred spores of each AMF species were used to prepare each mix, i.e., a total of 400 spores for the native AMF assemblage and 500 spores for the *R. irregularis*-invaded assemblage. Each pot received 5 ml of filtered washings of AMF inoculum to correct for possible differences in microbial communities (Koide and Elliott 1989). This filtrate was prepared by wet sieving 100 g of each inoculum through a 32-mm sieve and a paper filter (FS 14 1/2; Schleicher & Schuell), yielding a final volume of 1 L.

During 5 weeks, plants were watered twice a week with distilled water. Then, three water regimes were applied, namely "WW" (well-watered condition, 80–100 % field capacity

"FC"), "DS" (drought-stressed condition, 35–55 % FC), and "DC" (drying cycles, 35–100 % FC). Soil water content was monitored and adjusted by weighing the pots periodically twice per week. In addition, the pots received 10 mL of a phosphorus-free Hoagland solution (Gamborg and Wetter 1975) weekly. All plants were grown in the greenhouse under controlled conditions (light 16 h of ≥700 μmol m^{-2} s^{-1} intensity (PPFD); temperature 20–25 °C; relative humidity 65 %). The experiment was set up in a randomized block design where each treatment was replicated six times. *S. bicolor* plants were harvested after 16 weeks of growth. The root system was carefully washed, cut into 1-cm pieces, and thoroughly mixed. Three subsamples of about 100 mg of fresh roots were snap-frozen and stored at −80 °C for further analyses. Above- and belowground biomass were oven dried at 65 °C for 72 h and weighed to determine plant biomass.

Quantification of AMF root colonization by real-time PCR, using species-specific primers for rLSU

The abundance of each fungal species in sorghum roots was measured within the two AMF assemblages by quantitative PCR on cDNA, using primers targeting species-specific motifs in the rLSU genes. RNA extraction, cDNA synthesis, and qPCR analysis were performed as described by Courty et al. (2009), and as specified in Online Resource 1. Selected primers (Microsynth AG, Balgach, Switzerland) were specific and yielded amplification products only with the targeted species, and not with any of the other four species.

Hyphal length density

Hyphal length density (HLD) was determined by the modified grid-line intersection method (Jakobsen et al. 1992), using 10 g of the growth substrate. After sieving successively through a 400- and a 32-μm mesh, the material was collected and transferred into 50 mL of distilled water and homogenized for 10 s at full speed in a blender. The suspension was transferred into a beaker, diluted to 500 mL, and stirred for 1 min before five subsamples were taken every 10 s and loaded onto the filtration apparatus (MF-Membranfilter 1.2 μm; Millipore).

Statistical analyses

Data were analyzed using either one-way ANOVA (to compare transcript numbers of rLSU gene of individual AMF species among water regimes), two-way ANOVA (with the factors AMF assemblage and water regime for HLD and biomass) followed by Tukey's honest difference test with a significance level of α=0.05 or an independent-samples *t* test. Transcript numbers of rLSU genes of the AMF species were ln(x)-transformed before statistical analyses. Correlations were calculated using Pearson's correlation. Analyses were performed using JMP software version 5.0.1 (SAS, North Carolina, USA).

Results

Response of the AMF assemblages to different water regimes

The abundance of the different AMF species within roots, expressed as transcript numbers of rLSU genes per ng RNA, varied strongly when the native AMF assemblage and the *R. irregularis*-invaded assemblage were exposed to the different water regimes (Table 1). No significant difference in transcript numbers was measured for *S. africanum*. Conversely, the abundance of *D. aurantia* ($p<0.001$ for both AMF assemblages), of *D. omaniana*, and of *Paraglomus* sp. ($p<0.01$ and $p<0.001$ for the native AMF and *R. irregularis*-invaded assemblages, respectively) was significantly decreased under DS conditions, DC, or both water regimes. Interestingly, the abundance of *R. irregularis* significantly increased from WW to DS conditions compared to the AMF species from the native AMF assemblage ($p<0.001$). Changing the water regime modified the structure of the native AMF assemblage colonizing the roots (Fig. 1a). Under WW and DC conditions, it was significantly dominated by *D. omaniana* with a relative transcript abundance of 56 and 47 %, respectively, while under DS conditions, *S. africanum* and *Paraglomus* sp. dominated with a relative abundance of 45 and 34 %, respectively.

Introduction of *R. irregularis* into the native AMF assemblage

R. irregularis was clearly the most abundant AMF species colonizing sorghum roots under the three different water regimes, as reflected by a relative transcript abundance of 64 % in WW conditions, and of 90 and 98 % in DC and DS conditions, respectively (Fig. 1b-1). Under DS and DC conditions, the introduction of *R. irregularis* strongly decreased the rLSU transcript numbers of the other species in the native AMF assemblage while no reduction was observed under WW conditions (Fig. 2a). Interestingly, the introduction of *R. irregularis* differentially affected the abundance of the native AMF species colonizing roots (Fig. 2b–e). The abundance of *S. africanum* (Fig. 2b) and of *D. omaniana* (Fig. 2d) was significantly decreased under the three different water regimes, while the abundance of *Paraglomus* sp. (Fig. 2c) was significantly decreased only under the DS condition. In contrast, the abundance of *D. aurantia* (Fig. 2e) was significantly increased under WW conditions. Additionally, the introduction of *R. irregularis* modified the community structure of species from the native AMF assemblage colonizing the roots

Table 1 Transcript numbers of large ribosomal subunit genes (rLSU per ng RNA) of the arbuscular mycorrhizal fungal (AMF) species within the native AMF and *Rhizophagus irregularis*-invaded assemblages exposed to three water regimes

AMF assemblage	Water regime	AMF species abundance									
		Septoglomus africanum		*Diversispora aurantia*		*Diversispora omaniana*		*Paraglomus* sp.		*Rhizophagus irregularis*	
AMF native assemblage	WW	196	a	40	a	714	a	376	a	np	
	DC	163	a	1	b	210	b	58	b	np	
	DS	308	a	4	b	122	b	176	a	np	
	F_{ANOVA}	0.16 ns		22.69***		12.82**		11.3**			
AMF-invaded assemblage	WW	77	a	122	a	225	a	548	a	2747	b
	DC	34	a	2	b	43	a	101	b	1763	b
	DS	79	a	1	c	6	b	56	b	6948	a
	F_{ANOVA}	0.16 ns		121.49***		15.82***		37.06***		13.83***	

The AMF native assemblage includes the species *Septoglomus africanum*, *Diversispora aurantia*, *Diversispora omaniana*, and *Paraglomus* sp., the AMF-invaded assemblage includes the same four species and additionally *Rhizophagus irregularis*. The water regimes analyzed were well-watered (WW), drying cycles (DC), and drought-stressed (DS). Letters following the means of transcript numbers of large ribosomal subunit genes (n=6) indicate significant differences within AMF species between water regimes (p<0.05). Data were analyzed using one-way ANOVA followed by Tukey's honest significant difference test with a significance level of α=0.05; F_{ANOVA} is also given

ns not significant, *np* not present

*p<0.05; **0.001≤p<0.01; ***p<0.001

(Fig. 1b-2). Under WW and DC conditions, *Paraglomus* sp. significantly dominated the assemblage with a relative transcript abundance of 61 and 54 %, respectively. Under DS conditions, *S. africanum* and *Paraglomus* sp. together dominated the assemblage with a relative transcript abundance of 54 and 41 %, respectively.

Hyphal development and plant biomass production

HLD was significantly affected by water regime (p>0.001) and the interaction of water regime*AMF assemblage (p>0.01). Under the DS condition, the fungi from the native AMF assemblage produced significantly more extraradical hyphae than fungi from the *R. irregularis*-invaded assemblage (Fig. 3a). No significant differences in HLD were measured under DC and WW conditions. The HLD of the native AMF assemblage was similar under all three water regimes: 23.1, 26.7, and 28.3 cm g^{-1} soil dry weight for DC, DS, and WW conditions, respectively. In the *R. irregularis*-invaded assemblage, the HLD significantly differed between the water regimes: 17.2, 19.9, and 35.6 cm g^{-1} soil dry weight for DC, DS, and WW conditions, respectively.

Plant biomass correlated with the HLD (p<0.01). The plant biomass was significantly affected by water regime (p<0.001) and the interaction of water regime*AMF assemblage (p<0.05). The three water regimes affected the growth of sorghum differently, depending on the AMF assemblage (Fig. 3b). Dry weight of plants inoculated with the native AMF assemblage was significantly reduced only under the DC condition (3.9 g), compared to DS (5.0 g) and WW conditions (5.2 g). In contrast, the dry weight of plants inoculated with the *R. irregularis*-invaded assemblage was generally reduced under dry conditions (4.4 g for DS conditions and 3.6 g for DC) compared to the WW condition (5.5 g). Overall, drought resistance of the plants was reduced when *R. irregularis* was introduced into the AMF assemblage, as shown by the significant water regime*AMF assemblage interaction.

Discussion

Results from the present greenhouse experiment demonstrate that changes in the water regime can have a strong impact on the abundance of AMF inside a host root, and that AMF species can react differently upon such changes. Data illustrate that, under drought conditions, the introduction of a potentially invasive AMF species can lead to partial displacement of a native, drought-adapted AMF assemblage and to a significant decrease in HLD, which might reduce the plant benefit conferred by the fungi.

Based on rLSU transcript numbers, the four AMF species in the experimental assemblage with sorghum roots were

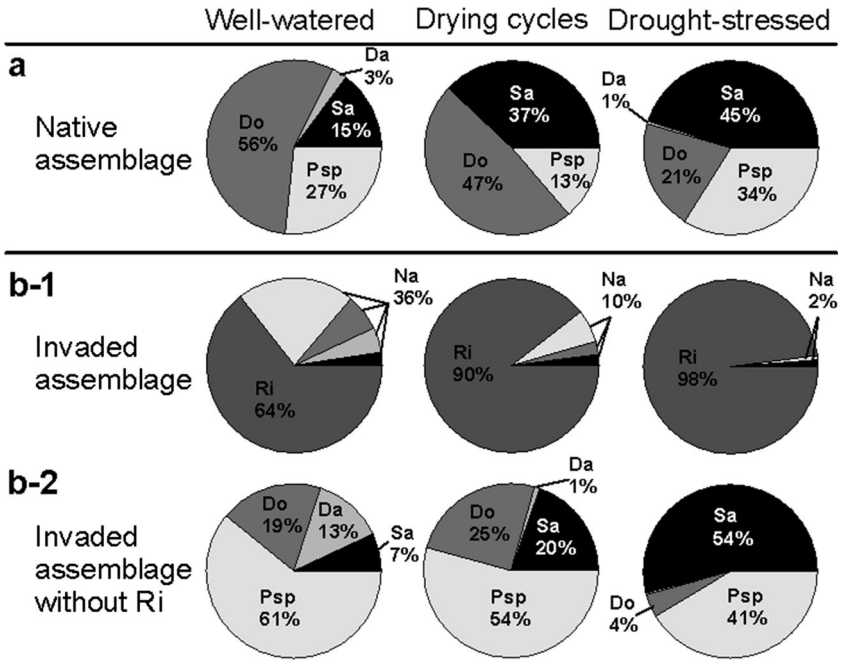

Fig. 1 Relative transcript abundance of large ribosomal subunit (*rLSU*) genes of the different arbuscular mycorrhizal fungal (*AMF*) species within **a** the "native AMF assemblage" (*NA*) containing *Septoglomus africanum* (*Sa*), *Diversispora omaniana* (*Do*), *Diversispora aurantia* (*Da*), and *Paraglomus* sp. (*Psp*), (*b-1*) the "*Rhizophagus irregularis*-invaded assemblage," and (*b-2*) the "*Rhizophagus irregularis*-invaded assemblage minus Ri" (where *Rhizophagus irregularis* (*Ri*) was excluded for calculations), exposed to the three different water regimes: well-watered, drying cycles, and drought-stressed. Each slice represents a mean of six replicates

differentially affected by the different water regimes. The abundance of *D. aurantia*, *D. omaniana*, and *Paraglomus* sp. decreased when exposed to dry conditions, while the abundance of *S. africanum* remained constant. Ruiz-Lozano et al. (1995) previously reported variable changes in root colonization of lettuce plants by AMF under different water

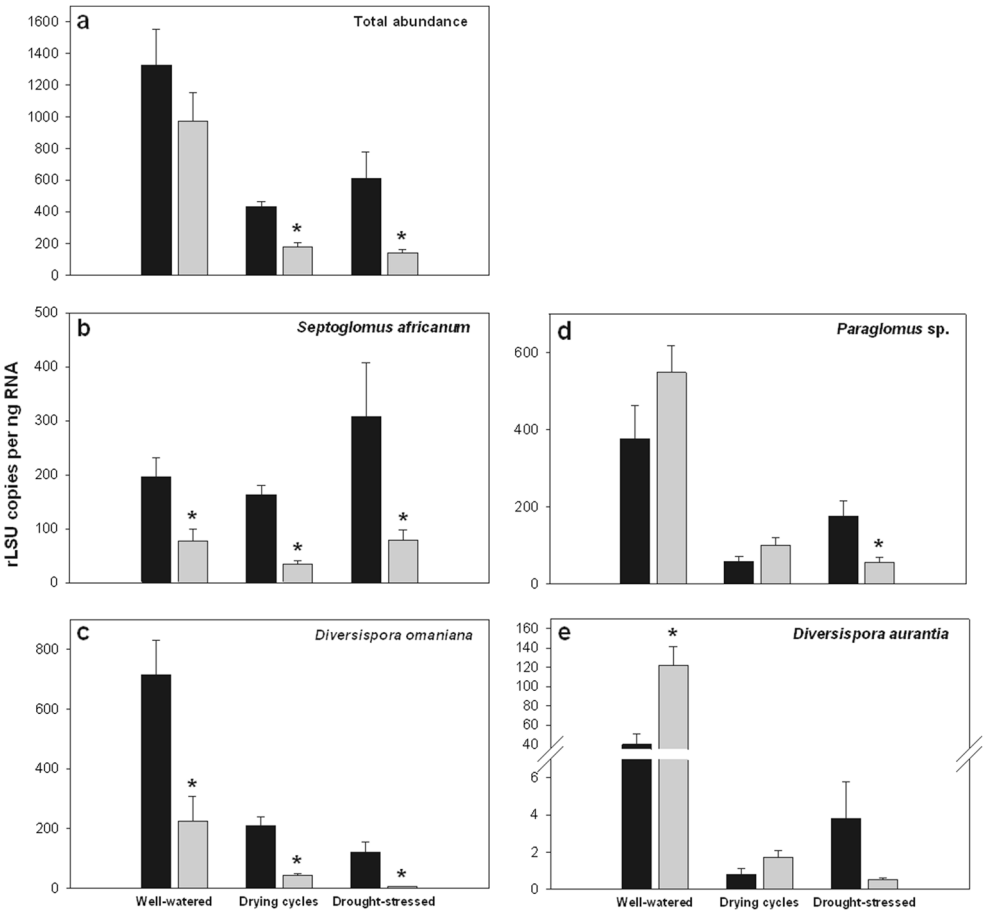

Fig. 2 Comparison of the abundance of the native AMF species, measured by transcript abundance of large ribosomal subunit (*rLSU*) genes, exposed to the three water regimes: well-watered, drying cycles, and drought-stressed. The abundances were measured as **a** total abundance of the four native AMF species, and **b**–**e** separately for each species without (*black bars*) and with (*gray bars*) introduction of *Rhizophagus irregularis*. *Stars* indicate significant differences of rLSU transcript numbers with and without the introduction according to the independent-samples *t* test. Data represent means+SE ($n=6$)

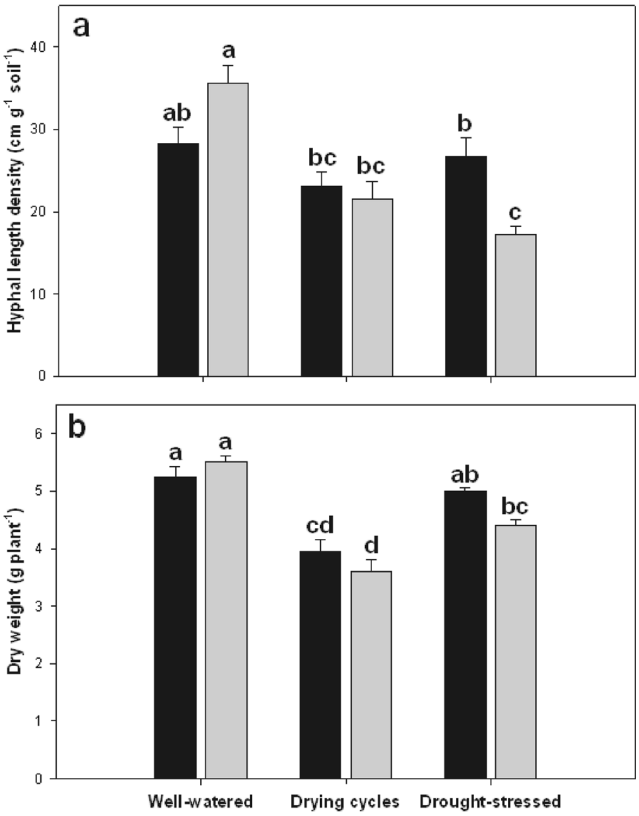

Fig. 3 Impact of the introduction of *Rhizophagus irregularis* on **a** the hyphal length density (*HLD*) in the soil and **b** the combined shoot and root biomass of sorghum plants inoculated with the native AMF assemblage (*black bars*) and the *R. irregularis*-invaded assemblage (*gray bars*), exposed to the three different water regimes: well-watered, drying cycles, and drought-stressed. *Different letters above bars* indicate significant differences according to Tukey's honest significant difference test with a significance level of α=0.05. Data represent means+SE (n=6)

regimes: under dry conditions, the level of colonization decreased in roots inoculated by *Glomus mosseae* or *Glomus occultum* but remained constant when inoculated by *Glomus deserticola* or *Glomus etunicatum*. Differences in root colonization ability might be a result of the physiological and functional characteristics of AMF species (Fitter 2005), and may be influenced by specific adaptations to environmental conditions prevalent at the place where the AMF species originated from (Marulanda et al. 2007; Lekberg and Koide 2008). Due to such adaptations, AMF species or even different strains of a same species might be either restricted or dominant in an ecosystem, leading to distinct AMF communities in different continents and climatic zones (Opik et al. 2006; Opik et al. 2013). Egerton-Warburton et al. (2007) and Querejeta et al. (2009) reported a dominance of *Glomus* species in AMF communities in soils of xeric habitats. Likewise, *S. africanum* and *R. irregularis*, both belonging to the family of Glomaceae, were either not affected or showed an increase in abundance in sorghum roots under DS conditions.

A water regime-dependent shift in the AMF community colonizing sorghum roots was observed under DS conditions; the dominant *D. omaniana* was replaced by *S. africanum* and *Paraglomus sp*. Shifts in AMF community structure due to seasonal changes in precipitation have also been reported under field conditions, and included changes in AMF structures inside host roots (Martínez-García et al. 2012), in the production of extraradical mycelium and glomalin (Clark et al. 2009), or of DGGE- or T-RFLP-band patterns of DNA root extracts (Hawkes et al. 2011). Furthermore, Querejeta et al. (2009) found a shift from Glomaceae to Gigasporaceae dominance in an oak forest between dry and wet years, respectively. Several other studies have revealed the importance of environmental factors in shaping AMF communities, such as host plant identity (Bever et al. 1996; Helgason et al. 1998; Bainard et al. 2014), soil type (Landis et al. 2004; Lekberg et al. 2007), or soil management practices (Jansa et al. 2003; Oehl et al. 2003; Al-Yahya'ei et al. 2011).

R. irregularis was by far the most abundant AMF species in sorghum roots inoculated with the *R. irregularis*-invaded assemblage under all the three water regimes when comparing the relative abundance of rLSU transcript numbers. The formation by *R. irregularis* of intraradical spores, not formed by species of the native AMF assemblage, probably overestimated the abundance of the fungus as spores have a high nucleic acid content (Gamper et al. 2008). It is therefore difficult to draw conclusions about the physical dominance of *R. irregularis* in terms of intraradical hyphal length or number of active exchange sites by comparing transcript abundance with that of the other species in the native AMF assemblage. Nevertheless, the significant reduction in the total abundance of the rLSU transcripts of the native AMF assemblage under DS and DC conditions does suggest their replacement within the root and consequently a dominant physical presence of *R. irregularis*, even though this might be only by the production of intraradical spores. The dominance of *R. irregularis* over other AMF has already been reported. It was shown to be the most abundant AMF when grown in competition with *Glomus aggregatum* (Engelmoer et al. 2013; Werner and Kiers 2014), and to dominate over *G. mosseae* when grown under saline stress, phosphorus stress, or in association with certain host plants (Alkan et al. 2006). In contrast, Jansa et al. (2008) found that *G. mosseae* was a better competitor compared to *R. irregularis* or *Glomus claroideum* under certain agricultural practices. These different observations might be explained, in part, by the fact that different AMF strains were used.

Inoculation with *R. irregularis* differentially affected the AMF species in the native AMF assemblage colonizing sorghum roots. Under WW conditions, the introduction of *R. irregularis* modified the abundance of the other AMF species, repressing *S. africanum* and *D. omaniana*, and stimulating *D. aurantia*. It has similarly been observed that *G. mosseae* can exert a decreasing and increasing effect on the abundance of *R. irregularis* and *G. claroideum*,

respectively (Jansa et al. 2008). In addition, Hart et al. (2012) found that the abundance of *Glomus custos* colonizing *Plantago* roots increased when associated with other AMF species, and that the identity of the co-occurring AMF species determined the root colonization level of *G. custos*. The diverse interactions found between co-occurring AMF species might be attributed to different species-specific colonization patterns (Bever et al. 2009; Verbruggen et al. 2012). For example, Hart and Reader (2002) observed that AMF species from the Glomeraceae invest more in the production of hyphae inside the root whereas species from the Gigasporaceae invest more into the extraradical mycelium. Consequently, they suggested that functional traits may be phylogenetically conserved, as also proposed by Maherali and Klironomos (2007).

Differences in the functional traits of AMF species might also explain the absence of correlation between rLSU transcript abundance inside the sorghum roots and the production of extraradical hyphae. Under the DS condition, extraradical hyphal production and, partially, dry weight accumulation of sorghum plants were reduced when *R. irregularis* was added to the native AMF assemblage, although the rLSU transcript abundance of *R. irregularis* reached its maximum value. This reduction might be explained by the species-specific colonization pattern of *R. irregularis*, and the consequent replacement of AMF species from the native AMF assemblage inside the roots. The fungal species in the native AMF assemblage came from a hyper-arid environment and might, therefore, be better adapted to dry conditions and better proliferate in dry soils. Up to date, only a few studies have investigated the impact of different water regimes on the performance of AMF species in terms of extraradical mycelium production. For example, exotic and native isolates of *G. mosseae* and *R. irregularis* were found to exhibit diverse adaptation to water availability when grown under drought conditions, with the production of extraradical mycelium as measured by glomalin accumulation being highest in soils colonized by the native AMF (Marulanda et al. 2007). Furthermore, other studies investigating the adaptation of AMF species to distinct environmental conditions by assessing differences in plant growth have revealed that mycorrhizal growth promotion was best when the experimental conditions, e.g., water availability or temperature, were closest to the environmental conditions from where the AMF were isolated (Marulanda et al. 2007; Lekberg and Koide 2008; Antunes et al. 2011). Another aspect that might influence the effect of mycorrhizal colonization on the plant is functional complementarity of AMF in the symbiosis. Several studies have shown that AMF species exhibit different functions for the host plant (Smith et al. 2004; Facelli et al. 2010). The present study similarly suggests that a community of native AMF species can buffer against different water regimes, as reflected by the constant production of extraradical mycelium under all water regimes although changes in the fungal community structure were observed. The results from these different investigations implicitly explain the importance of AMF diversity for host plant performance, especially by buffering the system against diverse stresses.

The observed decrease in extraradical hyphal production under dry conditions when the exotic species *R. irregularis* was introduced into the native AMF assemblage has implications regarding the possible consequences of a commercial application of AMF species. Long-term studies and AMF community surveys of field sites, where AMF inoculants have been applied, would shed light on the question about the impact of their application on the native AMF communities. Molecular tracing of introduced AMF has been successfully applied to investigate their long-term persistence under field conditions (Sýkorová et al. 2012). Additionally, some studies have assessed the impact of introducing AMF on native AMF communities, showing contrasting results. Whereas Koch et al. (2011) and Mummey et al. (2009) demonstrated a decrease in the diversity, Antunes et al. (2009) and Alguacil et al. (2011) observed no and even promoting effects on native AMF communities, respectively. Without such knowledge about possible alterations of these communities due to current application practices, there remains a risk of future unwanted consequences (Schwartz et al. 2006). The results reported here should also be considered with respect to revegetation programs, as AMF inocula may help to establish plants, especially in arid and semi-arid ecosystems (Requena et al. 1996; Azcón-Aguilar et al. 2003). These and other studies underline the importance of selecting appropriate fungal ecotypes, preferentially originating from the natural surroundings of the targeted application site, for producing adapted inocula for AMF-assisted revegetation programs (Barea et al. 2011).

In conclusion, changes in soil water availability can have a strong effect on the AMF community structure inside the roots of a host plant. In addition, the introduction of an AMF species widely used in commercial inoculum, such as *R. irregularis*, can lead to a partial displacement of native AMF species with an associated decrease in the extraradical mycelium. Considering the current worldwide spread of droughts, in addition to widespread biotic exchanges in a globalized world, these two factors may interact to hamper plant benefits provided by drought-adapted native AM fungi and, therefore, may affect ecosystem functioning.

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