

RESEARCH ARTICLE

Organic farming practices in a desert habitat increased the abundance, richness, and diversity of arbuscular mycorrhizal fungi[#]

Sangeeta Kutty Mullath¹, Janusz Błaszowski², Byju N. Govindan³, Laila Al Dhaheri¹, Sarah Symanczik⁴, Mohamed N. Al-Yahya'ei^{1*}

¹Department of Aridland Agriculture, College of Food and Agriculture, United Arab Emirates University, Al Ain 15551, UAE, ²Department of Plant Protection, West Pomeranian University of Technology, Szczecin Slowackiego 17, PL-71434 Szczecin, Poland, ³Department of Entomology, College of Food Agriculture and Natural Resources, University of Minnesota, Saint Paul, MN 55108, USA, ⁴Department of Soil Sciences, Research Institute of Organic Agriculture (FiBL), Ackerstrasse 113, CH-5070 Frick, Switzerland, ⁵Department of Vegetable Science, College of Horticulture, Kerala Agricultural University, Thrissur, India.680656

[#]This paper was presented at the 3rd Conference on Ecology of Soil Microorganisms, Helsinki, Finland in June 2018.

ABSTRACT

Agricultural practices are known to affect the diversity and efficiency of arbuscular mycorrhizal fungi (AMF) in improving overall plant performance. In the present study we aimed to compare the abundance, richness, and diversity of AMF communities under organic farming of a desert ecosystem in the Arabian Peninsula with those of an adjacent conventional farming system and native vegetation. In total, 12 sites, including six plant species, were sampled from both farming systems and the native site. Spore morphotyping revealed 24 AMF species, with 21 species in the organic farming system, compared to 14 species in the conventional site and none from rhizosphere soil of a native plant (*Tetraena qatarensis*). The AMF spore abundance, species richness, and Shannon–Weaver diversity index were high under organic farming. In both systems, the AMF community composition and abundance associated with different crops followed similar trends, with pomegranates having the highest values followed by limes, grapes, mangoes, and lemons. Our results show that organic farming in such a desert ecosystem promotes AMF diversity. These data imply that AMF might play an important role in the sustainable production of food in resource-limited desert habitats.

Keywords: AMF species; Organic farming; Spore abundance; Species richness; Shannon–Weaver index; Desert ecosystem

INTRODUCTION

Organic agriculture is a holistic system characterized by the strict prohibition of chemical fertilizers, herbicides, and pesticides, and by managing soil through the use of organic supplements and crop rotation (IFOAM, 2006). Hence, the soil fertility, sustainability, and productivity of organic farming systems mostly rely on biological processes carried out by soil microorganisms. These organisms represent key elements in the functionality of agroecosystems, and, therefore, are critical factors for the success of organic agriculture (Gosling et al., 2006).

Arbuscular mycorrhizal fungi (AMF) and plants form perhaps the oldest symbiotic association on earth (Redecker

et al., 2000). It has been estimated that 80–90% of all land plants form associations with AMF (Parniske, 2008). AMF act as a living interface between plant roots and soil in order to acquire water and nutrients for their host plants (Smith and Read, 2008). In addition, AMF were shown to protect their plants against biotic and abiotic stresses (Veresoglou and Rilling, 2012). A role for AMF in the synthesis of secondary plant metabolites has been reported, contributing to the production of safe and high-quality food (Giovannetti et al., 2012).

Organically managed soils were found to harbor higher AMF diversity (Oehl et al., 2003, 2004; Verbruggen et al., 2010; Säle et al., 2015; Gottshall et al., 2017), root-colonization rates (Mäder et al., 2000; Smukler et al., 2008)

*Corresponding author:

Mohamed N. Al-Yahya'ei, Department of Aridland Agriculture, College of Food and Agriculture, United Arab Emirates University, Al Ain 15551, UAE. E-mail: mohamed.yahyaiei@uaeu.ac.ae

Received: 14 June 2019; Accepted: 21 November 2019

and spore abundances (Galvez et al., 2001; Oehl et al., 2003, 2004) compared to conventionally managed soils. These findings suggest that AMF may play an essential functional role in the maintenance of soil biological fertility, to compensate for external inputs such as chemical fertilizers and pesticides (Lekberg and Koide, 2005; Gosling et al., 2006). Variations between AMF species in functions such as colonization rates, growth of extra-radical hyphae, and phosphorus (P) uptake have been investigated (Hart and Reader, 2002; Munkvold et al., 2004; Jansa et al., 2005). It is expected that high AMF diversity is more beneficial for host plants than low AMF diversity (van der Heijden et al., 1998) due to the potential for greater functional complementarity (Fitter, 2005).

High-input agricultural practices, such as monocropping, deep ploughing, chemical fertilization, and pesticide use are known to negatively affect AMF populations in terms of biodiversity (Sasvári et al., 2011) and activity, which is evaluated as the colonization ability (Mozafar et al., 2000; Ryan et al., 2000).

Vegetation growing in the desert ecosystem of the Arabian Peninsula (Fisher and Membery, 1998; Glennie and Singhvi, 2002) must cope with drought, heat, soil salinity, and low fertility, particularly due to low P availability (Al-Yahya'ei et al., 2011). Additionally, sandy soils possess a loose structure with a low water-holding capacity. It is plausible that the symbiosis between plants and AMF plays a key role in helping plants to cope with such harsh environmental conditions. The multiple benefits conveyed by AMF for plant growth and survival under stressful environments are well known (Smith and Read, 2008). Under arid conditions, for example, mycorrhizal plants were found to maintain higher drought tolerance (Augé, 2001) and to have better access to P than non-mycorrhizal plants (Neumann and George, 2004). AMF also enhance the soil aggregate stability, a particularly relevant feature for sandy soils prone to erosion (Rillig and Mummey, 2006).

Morphological and molecular analyses revealed unique communities of AMF in the south Arabian Peninsula (Al-Yahya'ei et al., 2011) that harbor newly reported AMF species (Symanczik et al., 2014a, b). An assembly of AMF species isolated from Arabian deserts has shown complementary abilities in colonizing the root system under different water regimes (Symanczik et al., 2015). These findings suggest that the diversity of AMF in such arid regions may play an important role in the fitness of plants.

However, to our knowledge, limited studies have been conducted to examine the effect of organic agricultural

practices on the diversity of AMF in desert ecosystems. A comparative investigation of such an effect will further the understanding of the behavior of these symbiotic fungi and their roles in providing ecological services in sustainable agriculture.

Our aim was to analyze AMF communities associated with different crops under organic farming in a desert habitat and to compare them with AMF communities from adjacent conventionally farmed systems. Spore morphotyping was used to study the AMF diversity in both agricultural systems. The results showed that organic farming in such a desert habitat enhances AMF abundance, richness, and diversity.

MATERIALS AND METHODS

Study sites and sampling

The study sites are located in a sandy desert in the Emirate of Abu Dhabi of the United Arab Emirates. The area consists of two of Al Rawafed Agriculture Farms. One farm (24° 25' 07 N, 54° 49' 40 E) is organically certified, has an area of 50 hectares, and produces fruits, vegetables, honey, and mushrooms. The other farm (24° 24' 36 N, 54° 49' 44 E) is managed by conventional methods with an area of 60 hectares. Chemical fertilizers (mainly nitrogen, phosphorus and potassium) were added according to recommended fertilizer doses, based on soil test data. The two farms are separated by approximately 150 m within an area that is representative of the surrounding desert region, in terms of soil type and vegetation.

The region has a hot desert climate, with temperatures ranging from a maximum of 51°C in July to a minimum of 5°C in January. The rainfall is infrequent (total annual rainfall of approximately 60 mm). The area is 44 m above sea level with an annual average relative humidity of 50%.

In this study, we selected five crops grown at different locations within each farming system with a maximal distance of 200 m between sampling sites: pomegranate (*Punica granatum*), grape (*Vitis vinifera*), mango (*Mangifera indica*), lime (*Citrus aurantifolia*), and lemon (*Citrus limon*). All crops were simultaneously planted in both farms during the cultivation seasons of 2010 and 2011. In addition to the five individual crop plants, an organically managed pomegranate–cabbage (*Brassica oleracea var. capitata*) intercropped plot was included. Soil samples from the rhizosphere of *Tetraena qatarensis*, the only native plant naturally growing in the uncultivated area between the two farms were also collected. In total, there were twelve sampling sites (six under organic farming system, five under conventional farming system, and one native vegetation site).

Soil samples were collected in January 2016. Five replicate plants in an area of ca. 400 m² were randomly chosen at each site. From the rhizosphere of each plant, three soil samples were collected and pooled using a soil auger with a diameter of 5 cm and a length of 30 cm. Sixty pooled soil samples were obtained from 180 original samples. The soil samples were stored in sealable plastic bags for transportation and air dried before analysis. Soil samples for soil-nutrient analysis were collected from the rhizosphere of five plants of each species, at each site. The five samples from each plant species were pooled to obtain one composite sample per plant per site and further used for soil-nutrient analysis.

Soil-nutrient analysis

Soil samples were passed through a 2-mm sieve and mixed thoroughly to obtain composite samples. Soil macronutrients (P, K, Ca, Mg, Na, and S) and micronutrients (Cu, Fe, Mn, Co, and Zn) were measured with an inductively coupled plasma–optical emission spectrometer (Model: 710-ES, Manufacturer: Varian, USA).

AMF spore isolation and identification

AMF spores were extracted by wet sieving and sucrose density-gradient centrifugation, using a modification of the method of Daniels and Skipper (1982). For each sample, approximately 15 g of air-dried soil was well suspended in 20 mL of water in a 50-mL Falcon tube. Twenty-five ml of sucrose solution (70% v/w) was injected at the bottom of the tube, forming a stepped density gradient, and the tube was centrifuged at 900 × g for 2 min. The supernatant was washed with tap water for 2 min in a 32-μm sieve and transferred to Petri dishes. Spores, spore clusters, and sporocarps were collected from the Petri dish and mounted on slides with polyvinyl-lactic acid-glycerol (Koske and Tessier, 1983) or polyvinyl-lactic acid-glycerol mixed 1: 1 (v/v) with Melzer's reagent (Brundrett *et al.*, 1994) and examined under a light microscope (Zeiss; Primostar) at a magnification of up to ×1000. AMF species identity and abundance were determined for each sample. Spore abundance was assessed by counting the total number of AMF spores extracted from 15 g of field soil, whereas species richness was derived from the total number of AMF species found in the soil samples. The Shannon–Weaver index was used to compare the diversity of AMF communities between farming systems and crops.

Identification was based on original and recent species descriptions and identification manuals (The International Culture Collection of Arbuscular and Vesicular-Arbuscular Endomycorrhizal Fungi, INVAM: <https://invam.wvu.edu/>; Arbuscular Mycorrhizal Fungi (Glomeromycota), Endogone, and Complexipes species deposited in

the Department of Plant Pathology, University of Agriculture in Szczecin, Poland: <http://www.zor.zut.edu.pl/Glomeromycota/>).

Statistical analysis

Analysis of variance (ANOVA) was employed to statistically compare the AMF species richness, spore density, diversity, and similarity index at eleven sites representing the six crops and two farming system combinations.

AMF-abundance data were analyzed after omitting outlier values to ensure that data met the assumptions of normality. The resultant unbalanced dataset was handled using the Kenward and Roger method to approximate the denominator degrees of freedom and to adjust the estimated standard errors for fixed effects (Littell *et al.*, 2006). ANOVA was used to compare species richness across two or more groups, and analysis of similarity (ANOSIM) was conducted to test whether the AMF species composition of different crops and farming system combinations significantly differed from results based on the Bray–Curtis dissimilarity measure. ANOVA was followed by Tukey's honest significant difference test (Tukey's HSD) with a significance level of $\alpha = 0.05$.

The estimation of species richness and diversity indexes was performed using R software, version 3.2 (vegan and anosim package), and ANOVA and Tukey's HSD were performed using SAS software, version 9.4. Graphical visualizations were performed using the ggplot2 package in R, version 3.2 (R Core Team, 2016).

RESULTS

Soil-nutrient analysis

Soil-nutrient analysis of the study sites (Table 1) showed that soil from the conventional farm had significantly higher amounts of Mg, Na, S, Ca, Fe, and Mn than soil from the organic farm ($p < 0.05$). No significant differences were observed between the organic and conventional farms with respect to soil P, Cu, Co, and Zn contents.

AMF spore abundance in crops across farming systems

AMF spore abundances differed significantly when analyzing crops ($F_{5,43} = 45.18$, $p < 0.0001$), the farming system ($F_{1,43} = 188.01$, $p < 0.0001$), and their interaction ($F_{4,43} = 10.1$, $p < 0.0001$). With the organic farming system, the spore abundance was the highest (Fig. 1a) for the pomegranate–cabbage intercrop (123 spores/15g dry soil) and the lowest for lemons (48 spores/15 g dry soil). With the conventional farming system, the highest spore abundance was recorded for pomegranates (72.25 spores/15 g dry soil) and the lowest was recorded for mangoes (33.4 spores/15 g dry soil). For each crop, the

spore abundance under the organic farming system was significantly higher than the corresponding value under the conventional farming system, with the exception that lemons had similar spore abundances under both farming systems. No spores were detected in the case of soil samples from the native site.

Table 1: Soil-nutrient status of conventional and organic farming systems. Mean values of the same element followed by different letters indicate significant differences between the two farming systems

| Soil nutrients | Organic farming | Conventional farming |
|----------------|---------------------|----------------------|
| Phosphorus (%) | 0.032 ^A | 0.025 ^A |
| Potassium (%) | 0.125 ^B | 0.147 ^A |
| Magnesium (%) | 0.596 ^B | 1.050 ^A |
| Sodium (%) | 0.016 ^B | 0.356 ^A |
| Sulphur (%) | 0.033 ^B | 0.075 ^A |
| Calcium (%) | 8.394 ^B | 14.134 ^B |
| Iron (%) | 0.390 ^B | 0.490 ^A |
| Manganese (%) | 0.011 ^B | 0.018 ^A |
| Copper (ppm) | 3.628 ^A | 7.988 ^A |
| Cobalt (ppm) | 2.755 ^A | 3.704 ^A |
| Zinc (ppm) | 15.846 ^A | 27.738 ^A |

AMF species richness in crops across farming systems

AMF species richness differed significantly when analyzing crops ($F_{5,44} = 25.26$, $p < 0.0001$), the farming system ($F_{1,44} = 62.86$, $p < 0.0001$), and their interaction ($F_{4,44} = 11.04$, $p < 0.0001$). With the organic farming system, the species richness was highest (Fig. 1b) for pomegranates (9–12 species) and lowest for lemons (2–3 species). With the conventional system, the highest species richness was also recorded in pomegranates (1–8 species) and the lowest was recorded for mangoes (2–3 species). The Tukey–Kramer pairwise-comparison test indicated that the species richness for pomegranates, limes, and grapes was significantly higher in the organic farm than in the conventional farm. In the case of lemons and mangoes, the species richness was not significantly different under the two farming systems.

AMF diversity (Shannon–Weaver index)

The Shannon–Weaver index (H') was significantly affected by the crop species ($F_{5,44} = 10.9$, $p < 0.0001$), farming system ($F_{1,44} = 20.04$, $p < 0.0001$), and their interaction ($F_{4,44} = 25.26$, $p = 0.043$). Tukey–Kramer multiple-

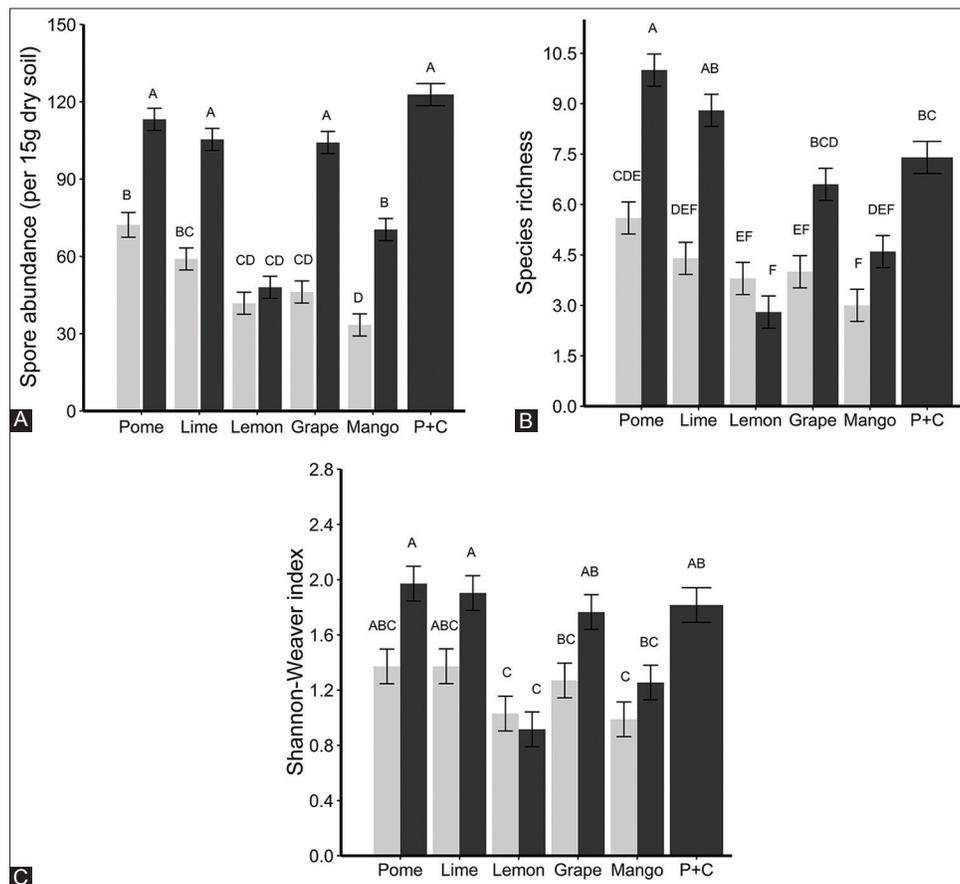


Fig 1. (A) AMF spore abundance (per 15 g dry soil), (B) AMF species richness, and (C) AMF Shannon–Weaver Index in the rhizosphere of pomegranates (Pome), limes, lemons, grapes, mangoes, and the pomegranate–cabbage mixed crop (P + C) grown in conventional (grey bars) or organic (black bars) farming systems. The letters above the bars indicate significant differences according to the Tukey–Kramer pairwise-comparison test with a significance level of $\alpha = 0.05$. The data shown represent the means + SE ($n = 5$).

comparison testing (Fig. 1c) revealed that H' values for pomegranates, limes, grapes, and the pomegranate–cabbage intercrop cultivated under organic farming were significantly different from those of grapes, mangoes, and limes cultivated under conventional farming.

Distribution pattern of the AMF species detected

Twenty-four AMF species were identified in this study, including four previously undescribed species (Table 2, Fig. 2). Among the 11 species shared by both farming systems, *Rhizoglossum* sp. UD-2 and UD-3 (*Ambispora*-like) were present in all crops. The organically grown pomegranates harbored the highest number of species with a relative spore abundance (RSA) of 21.2% of *Rhizoglossum irregularis* spores, followed by a 17.8% RSA for *Rhizoglossum* sp. UD-2. *Acaulospora excavata* and *Entrophospora* spp. contributed an RSA of only 1.2%. In contrast, the rhizosphere of conventionally grown pomegranates was dominated by *Dominikia* sp. UD-1, with an RSA of 78.9%.

The species *A. excavata*, *Funneliformis mosseae*, *Entrophospora* spp., *Glomus* spp., *P. scintillans*, *Septoglossum*

titan, and *Septoglossum constrictum* were only associated with pomegranates; *Glomus pallidum* and *P. franciscana* were only associated with limes; and *Cetraspora pellucida* was only associated with the pomegranate–cabbage mixed cropping system. The remaining species were associated with more than two to four crop plants. For instance, *Rhizoglossum fasciculatum* was associated only with limes and lemons, whereas *Dominikia* sp. UD.1 was only associated with pomegranates, grapes, limes, and the mixed pomegranate–cabbage crop.

Two major groups of AMF species were primarily recognized. Group one consisted of species that were present and generally abundant across most crop and farming-system combinations like *Rhizoglossum* sp. UD.2, UD.3 (*Ambispora*-like), *R. irregularis*, and *F. coronatum*. Group two consisted of species with a more restricted distribution that were mainly abundant in either farming system for a given crop. The abundance of *P. scintillans*, *S. titan*, and *Dominikia* sp. UD.1 was highest in conventionally grown pomegranates, whereas *Claroideoglossum claroideum* and *Cetraspora pellucida* were mainly associated with organically grown grapes and the

Table 2: Relative spore abundance (%) of arbuscular mycorrhizal fungi (AMF) across different crops and farming systems

| Farming system | Organic | | | | | | Conventional | | | | | |
|--|---------|-----------------|------|-------|-------|-------|-------------------|-----------------|------|-------|-------|-------|
| | Crop | Pg [†] | Lime | Lemon | Mango | Grape | Pg-C [‡] | Pg [†] | Lime | Lemon | Mango | Grape |
| AMF species present in organic and conventional farming systems | | | | | | | | | | | | |
| <i>Dominikia</i> sp. [§] UD-1 | - | 19.9 | - | - | - | 9.6 | 19.5 | 78.9 | 12.9 | - | - | - |
| <i>Rhizoglossum</i> sp. UD-2 | 17.8 | 20.9 | 32.1 | 37.5 | 25.3 | 13.7 | 7.6 | 16.9 | 25.8 | 28.1 | 33.8 | |
| UD-3 (<i>Ambispora</i> -like) | 17.5 | 23.9 | 55.4 | 37.8 | 13.6 | 17.9 | 3.8 | 30.8 | 58.4 | 49.1 | 38.1 | |
| <i>Rhizoglossum irregularis</i> | 21.2 | 10.6 | - | 12.5 | 12.5 | 12.2 | 3.6 | 26.8 | 7.2 | 15.6 | 12.1 | |
| <i>Diversispora eburna</i> | - | 2.5 | - | 3.4 | - | - | - | 5.1 | - | - | - | |
| <i>Pacispora scintillans</i> | 3.2 | - | - | - | - | - | 1.1 | - | - | - | - | |
| <i>Rhizoglossum intraradices</i> | - | 2.7 | 12.5 | - | 3.8 | - | - | - | 4.3 | - | - | |
| <i>Funneliformis coronatum</i> | 17.1 | 4 | - | 4.5 | 9 | 6.8 | - | - | 3.3 | 7.2 | - | |
| <i>Glomus</i> sp. | 2.7 | - | - | - | - | - | 0.3 | - | - | - | - | |
| <i>Glomus macrocarpum</i> | 2.8 | 2.7 | - | - | - | - | - | - | - | - | 5.2 | |
| <i>Diversispora spurca</i> | - | - | - | - | 21.7 | 22.6 | 2.2 | - | - | - | 10.8 | |
| AMF species present in the organic farming system | | | | | | | | | | | | |
| <i>Acaulospora excavate</i> | 1.2 | - | - | - | - | - | - | - | - | - | - | |
| <i>Acaulospora scrobiculata</i> | 2.5 | 1.7 | - | 4.3 | - | 2.8 | - | - | - | - | - | |
| <i>Cetraspora pellucida</i> | - | - | - | - | - | 2.3 | - | - | - | - | - | |
| <i>Claroideoglossum claroideum</i> | 1.8 | - | - | - | 4.4 | - | - | - | - | - | - | |
| <i>Entrophospora</i> sp. | 1.2 | - | - | - | - | - | - | - | - | - | - | |
| <i>Glomus pallidum</i> | - | 3.6 | - | - | - | - | - | - | - | - | - | |
| <i>Pacispora franciscana</i> | - | 0.9 | - | - | - | - | - | - | - | - | - | |
| <i>Septoglossum constrictum</i> | 4.6 | - | - | - | - | - | - | - | - | - | - | |
| <i>Trichispora nevadensis</i> | 2.5 | 1.9 | - | - | - | 2.1 | - | - | - | - | - | |
| UD-4 (<i>Ambispora</i> -like) | 3.9 | 4.7 | - | - | - | - | - | - | - | - | - | |
| AMF species present in the conventional farming system | | | | | | | | | | | | |
| <i>Funneliformis mosseae</i> | - | - | - | - | - | - | 1.9 | - | - | - | - | |
| <i>Rhizoglossum fasciculatum</i> | - | - | - | - | - | - | - | 7.5 | 1 | - | - | |
| <i>Septoglossum titan</i> | - | - | - | - | - | - | 0.6 | - | - | - | - | |
| Total number of AMF species | 15 | 12 | 3 | 6 | 8 | 9 | 9 | 7 | 5 | 4 | 5 | |

[†]Pg, pomegranate; [‡]Pg-C, pomegranate–cabbage mixed cropping system; [§]UD, undescribed

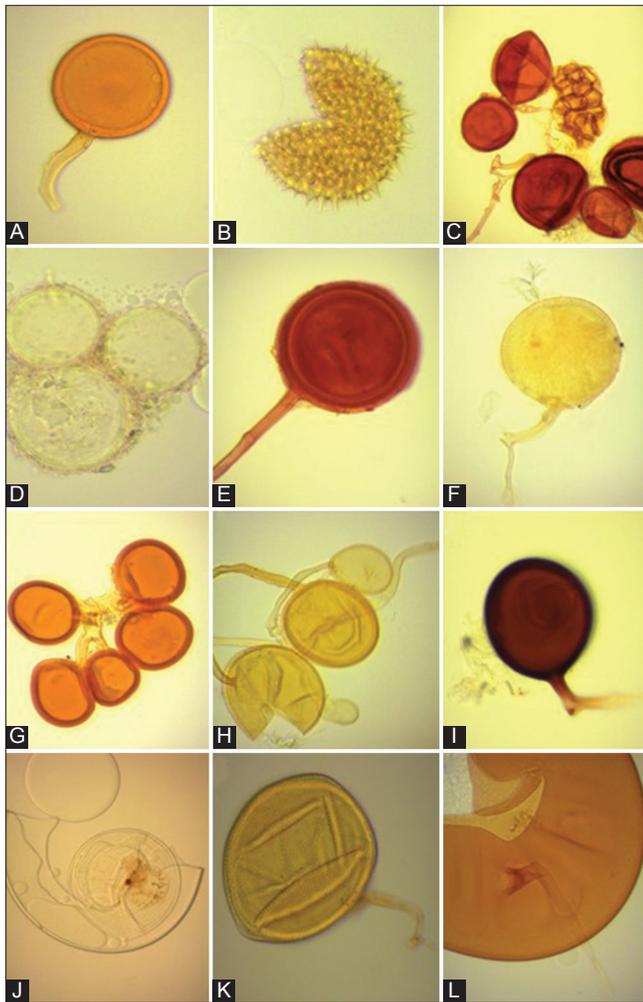


Fig 2. Morphological characteristics of some of the spores detected in this study. (A) *Rhizogloium* sp. UD-2. (B) *Tricispora nevadensis*. (C) *Rhizogloium irregulare*. (D) *Diversispora spurca*. (E) *Glomus macrocarpum*. (F) *Rhizogloium fasciculatum*. (G) *Dominikia* sp. UD-1. (H) *Rhizogloium intraradices*. (I) *Septogloium constrictum*. (J) *Cetraspora pellucida*. (K) *Acaulospora scrobiculata*. (L) *Funneliformis coronatum*.

pomegranate–cabbage mixed cropping system, respectively. In contrast, *D. spurca* was highly abundant in both cropping systems. The remaining AMF species were mainly associated with limes, lemons, and mangoes and were identified with either or both farming systems.

Comparing the RSA across farming systems revealed that UD-3 (*Ambispora*-like) was the most abundant species under organic farming (23.8%) followed by *Rhizogloium* sp. UD-2 (22.6%), while *A. excavata*, *Pacispora franciscana* and *Entrophospora* sp. occurred only rarely 0.2% (Table 3). In the conventional system *Dominikia* sp. UD-1 (45.1%) was the most abundant species followed by UD-3 (*Ambispora*-like) (21.3 %).

AMF families identified in the study

The AMF species identified in this study were grouped within eight families (Table 4). Twelve species were

Table 3: Relative spore abundance (RSA, %) of arbuscular mycorrhizal fungi (AMF) across farming systems

| AMF species | RSA organic | RSA conventional |
|-----------------------------------|-------------|------------------|
| <i>Acaulospora excavata</i> | 0.2 | 0 |
| <i>Acaulospora scrobiculata</i> | 2 | 0 |
| <i>Cetraspora pellucida</i> | 0.5 | 0 |
| <i>Claroideogloium claroideum</i> | 1.2 | 0 |
| <i>Diversispora eburna</i> | 0.9 | 0.75 |
| <i>Diversispora spurca</i> | 8.9 | 2.5 |
| <i>Entrophospora</i> sp. | 0.2 | 0 |
| <i>Funneliformis coronatum</i> | 7.9 | 1 |
| <i>Funneliformis mosseae</i> | 0 | 1.1 |
| <i>Glomus macrocarpon</i> | 1.1 | 0.6 |
| <i>Glomus pallidum</i> | 0.7 | 0 |
| <i>Glomus</i> sp. | 0.5 | 0.2 |
| <i>Pacispora franciscana</i> | 0.2 | 0 |
| <i>Pacispora scintillans</i> | 0.6 | 0.6 |
| <i>Rhizogloium irregularis</i> | 12.8 | 9.4 |
| <i>Rhizogloium fasciculatum</i> | 0 | 1.2 |
| <i>Rhizogloium intraradices</i> | 2.3 | 0.5 |
| <i>Septogloium constrictum</i> | 0.9 | 0 |
| <i>Septogloium titan</i> | 0 | 0.4 |
| <i>Trichispora nevadensis</i> | 1.3 | 0 |
| <i>Dominikia</i> sp. UD-1 | 9.8 | 45.1 |
| <i>Rhizogloium</i> sp. UD-2 | 22.6 | 15.7 |
| UD-3 (<i>Ambispora</i> -like) | 23.8 | 21.3 |
| UD-4 (<i>Ambispora</i> -like) | 1.7 | 0 |

grouped in *Glomeraceae*; three species were grouped in *Diversisporaceae*; two each were grouped in *Acaulosporaceae*, *Pacisporaceae*, and *Ambisporaceae*; and one each was grouped in *Entrophosporaceae*, *Claroideoglomeraceae*, and *Gigasporaceae*.

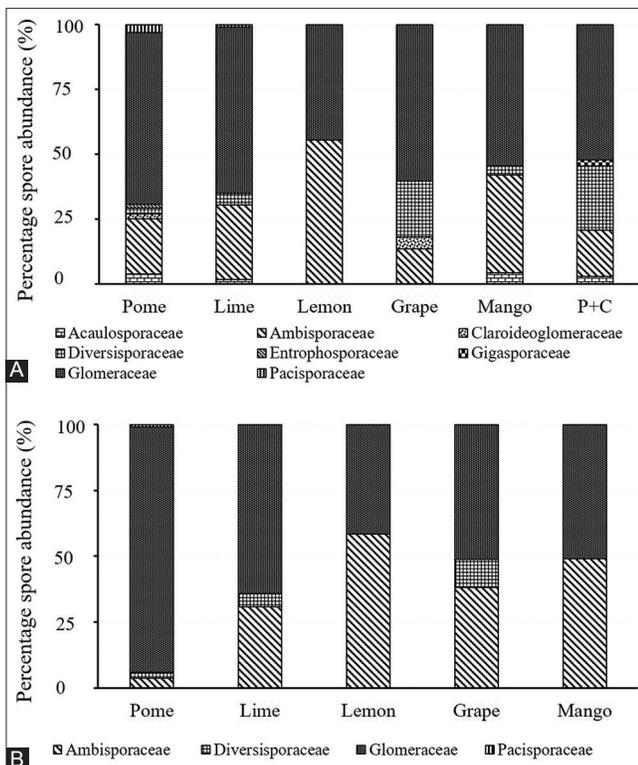
The percentage of spores belonging to different families was calculated separately for each crop and farming system (Fig. 3a, b). Eight and four AMF families were detected in the organic and conventional farming system, respectively. The percentage of spores belonging to *Glomeraceae* was highest in all crops under both farming systems except for lemons, for which the highest percentage of spores belonged to *Ambisporaceae*. Under organic farming, pomegranates were associated with seven AMF families, whereas lemons were only associated with two families. Under conventional farming, the number of AMF families associated with five crops ranged from two to four.

ANOSIM

ANOSIM was employed to assess differences in the AMF community composition across the two farming systems. With respect to the farming system, the value of the ANOSIM was equal to 0.1267 ($p = 0.001$), using data related to the presence or absence of different species. Specifically, neither the species composition between the conventional and organic farming systems, nor within either farming system (across all crops) showed

Table 4 : Species of arbuscular mycorrhizal fungi (AMF) identified within each family

| AMF family | AMF species |
|-----------------------------|---|
| <i>Acaulosporaceae</i> | <i>Acaulospora excavata</i> , <i>Acaulospora scrobiculata</i> |
| <i>Diversisporaceae</i> | <i>Diversispora</i> sp., <i>Diversispora eburne</i> , <i>Diversispora spurca</i> |
| <i>Glomeraceae</i> | <i>Funneliformis coronatum</i> , <i>Funneliformis mosseae</i> , <i>Glomus macrocarpum</i> , <i>Glomus pallidum</i> , <i>Glomus</i> sp., <i>Rhizoglomus irregularis</i> , <i>Rhizoglomus fasciculatum</i> , <i>Rhizoglomus intraradices</i> , <i>Septoglomus constrictum</i> , <i>Septoglomus titan</i> , <i>Rhizoglomus</i> sp. UD-2, <i>Dominikia</i> sp. UD-1 |
| <i>Entrophosporaceae</i> | <i>Entrophospora</i> sp. |
| <i>Pacisporaceae</i> | <i>Pacispora scintillans</i> , <i>Pacispora franciscana</i> |
| <i>Ambisporaceae</i> | UD-4 (<i>Ambispora</i> -like), UD-3 (<i>Ambispora</i> -like) |
| <i>Claroideoglomeraceae</i> | <i>Claroideoglomus claroideum</i> |
| <i>Gigasporaceae</i> | <i>Cetraspora pellucida</i> |

**Fig 3.** Distribution of AMF families (%) in the rhizosphere of different crops grown (A) under organic farming and (B) under conventional farming

marked dissimilarities. ANOSIM for individual crops and either farming system was also performed. The species compositions between the organic and conventional farming groups were more dissimilar than the species

compositions within crops under the same farming system, for pomegranates ($R = 0.684$, $p = 0.005$), limes ($R = 0.854$, $p = 0.011$), and grapes ($R = 0.824$, $p = 0.006$). In contrast, with mangoes ($R = 0.062$, $p = 0.313$) and lemons ($R = 0.18$, $p = 0.157$), an even distribution of high and low ranks of dissimilarity was observed within and between the groups, suggesting that their species compositions between two farming systems and within a farming system (replicates of a given crop) were not dissimilar.

DISCUSSION

Organic versus conventional farming

AMF spore abundance, species richness, and diversity were significantly higher in organically managed soils than in conventional ones. Similarly, positive effects of organic farming on AMF communities have been reported in other ecosystems (Oehl et al., 2004; Lee and Eom, 2009; Verbruggen et al., 2010; Bedini et al., 2013; Säle et al., 2015). An enhancement in AMF species richness under organic farming compared to conventional farming has also been observed in red peppers (Lee et al., 2008) and maize (Bedini et al., 2013). Furthermore, it has been reported that AMF from less intensively managed sites better promote plant biomass production than AMF from sites with higher management intensity (Johnson, 1993; Singh et al., 2008). Hence, this may suggest that AMF-rich communities from organically managed fields contribute more to plant productivity and other ecosystem functions than do those of conventionally managed fields.

The differences observed among the two farming systems might be partially attributed to the quality and quantity of the applied fertilizers. The use of mineral fertilizers can have strong effects on fungal symbionts (Oehl et al., 2004; Bünemann et al., 2006), further implying a net negative effect on plant nutrition and growth (Verbruggen et al., 2010). Indeed, the loss of fungal diversity can disrupt major ecosystem services such as plant biodiversity, ecosystem variability, and productivity (van der Heijden et al., 1998; Wagg et al., 2014). Furthermore, it was observed that AMF taxa might react differentially to external influences. Many of the identified AMF species belonging to the *Acaulospora*, *Entrophospora*, *Cetraspora*, and *Claroideoglomus* genera, appeared to be restricted to plots managed by organic farming. Similar observations were reported previously (Oehl et al., 2004). Wetzal et al. (2014) observed that *S. constrictum* was more abundant under reduced tillage and low-input agriculture, which is in line with observations made in this study. In addition, Oehl et al. (2003) found that *Glomeraceae* species were similarly abundant in all farming systems, whereas *Scutellospora* species were more abundant in organic systems than in conventional systems. These

observations suggest that some taxa are more sensitive to certain agricultural practices like tillage, fertilization, or the use of fungicides than others. Because AMF species are functionally important for natural ecosystems and low-input sustainable farming, their loss under conventional farming may negatively impact environmental and agronomical services, and might affect multiple ecosystem functions.

Effect of host plants on AMF communities under organic and conventional farming systems

AMF species compositions were found to be host plant-dependent in this study. The rhizosphere of pomegranates harbored the highest abundance and richness of AMF species, in contrast to lemons, which had the lowest values. These observations are in agreement with results found in other ecosystems (Vandenkoornhuysen et al., 2002, 2003; Gollotte et al., 2004; Scheublin et al., 2004; Li et al., 2010; Alguacil et al., 2011). Sýkorová et al. (2007) showed that AMF communities differed significantly between the two co-existing host plants *Gentiana verna* and *Gentiana acaulis*, but did not differ within the same host plant at different locations. These observations indicated the strong impact of host plant identity on the AMF community composition and might be explained by differences in the degree of AMF selectivity for certain plant species. While some plants preferentially associate with a broad spectrum of AMF species, others might favor association with only few species, or with more specific and specialized AMF (Oehl et al. 2003; Scheublin et al. 2004). In this study, pomegranates harboring the highest AMF abundance and richness might be considered the best host for promoting the diversity of AMF communities. Similar observations have been made by Deyn et al. (2011). They reported that increased AMF abundance was explained by plant species identity in the case of the grass species *Anthoxanthum odoratum*.

Effect of agriculture on the natural AMF community of native plants

Identifying AMF communities associated with various crops under both farming systems, along with those of native plant species was meant to shed light on the influence of crop introduction on native AMF communities. Any shift in the AMF community composition would be attributed to changes in the land-use pattern because the underlying assumption is that the same AMF community was present in all the three habitats (i.e., organic and conventional farming systems, and undisturbed land with native vegetation). However, no spores were detected within the rhizosphere soil of the native plants. Potentially present AMF species could be recovered by trap culturing (Al-Yahya'ei et al., 2011) or through more intensive sampling efforts and successive trap-culturing techniques (Stutz and Morton 1996; Bever et al. 2001). The relatively

rich AMF communities observed within the two cultivated systems were most likely stimulated by the establishment of crop plants and the application of agricultural inputs and irrigation. Such a trend of increasing AMF abundance and richness upon initiation of agricultural land use is more pronounced in desert ecosystems. In southern Arabia, natural undisturbed habitats are directly exposed to harsh climatic conditions, including pronounced drought (Cui and Nobel 1992) and heat (Bendavid-Val et al. 1997). Only a few plant species can withstand such conditions and, consequently, the landscape is shaped by a scarce vegetation cover. Thus, AMF lacking appropriate host plants fail to propagate and hence, propagule numbers in the soil decrease (Requena et al., 1996). Therefore, introducing agriculture in such habitats represents a drastic change in the environmental conditions, and thus a marked shift in the AMF community is expected. Similar observations of higher AMF diversity in agricultural sites than in adjacent natural sites were reported for other hot and arid ecosystems (Li et al., 2007 and Al-Yahya'ei et al., 2011).

AMF species detected in this study

Among all AMF species identified in this study, three out of four novel species were among the most abundant species. Hence, it can be assumed that those species might be especially adapted to withstand and successfully propagate under such extreme conditions. Adaptations of AMF species to distinct environmental conditions, such as drought or extreme temperatures, were already shown and explained previously (Marulanda et al., 2007; López-Gutiérrez et al., 2008; Lekberg & Koide, 2008; Antunes et al., 2011).

In this study, 24 AMF species were detected in both farming systems. Similar numbers were recorded in previous studies conducted in southern Arabia (Al-Yahya'ei et al., 2011), the arid ecosystem of Rajasthan, India (Verma et al., 2016), and the sand dunes of Morocco (Hibilik et al., 2016). However, the community composition seems to be quite unique, with only one species in common with the AMF community revealed from southern Arabia (Al-Yahya'ei et al. 2011; Symanczik et al., 2014a, b). In this sense, the study significantly contributes towards unfolding the mycorrhizal diversity in the arid habitats of the Arabian Peninsula.

CONCLUSIONS

The present study showed that organic farming in desert ecosystems is a suitable agricultural management strategy with beneficial effects on AMF biodiversity compared to conventional farming. Therefore, our findings should help uncover the role that AMF might play in supporting sustainable agriculture in desert ecosystems.

ACKNOWLEDGMENTS

We thank the supporting team from Al Rawafed Farms. We also thank Mr. Felix Guiabar from United Arab Emirates University for his support in the soil chemical analysis. This work was supported by the United Arab Emirates University Program for Advanced Research [UPAR fund No. 31 F043], which is gratefully acknowledged.

Author's contributions

Mohamed Al-Yahya'ei initiated the project, collected the soil samples and supervised all the technical aspects of the experiments and result interpretations. He revised the final version of the manuscript. Sangeeta Kutty Mullath Sarah Symanczik and Mohamed N. Al-Yahya'ei designed the experiment. Sangeeta Kutty Mullath conducted the experiments, collected and tabulated data and wrote the manuscript. Byju N. Govindan performed the statistical analysis of the data and helped in interpretation. Laila Al Dhaheri assisted in taking observations and editing the manuscript. Janusz Blaszkowski identified the spore morphologies, helped in designing the experiment and revising the manuscript. Sarah Symanczik interpreted the results and revised the manuscript. All authors read and approved the final manuscript.

REFERENCES

- Alguacil, M. M., M. P. Torres, E. Torrecillas, G. Díaz and A. Roldán. 2011. Plant type differently promotes the arbuscular mycorrhizal fungi biodiversity in their rhizospheres after revegetation of a degraded, semiarid land. *Soil Bio. Biochem.* 43: 167-173.
- Al-Yahya'ei, M. N., F. Oehl, M. Vallino, E. Lumini, D. Redecker, A. Wiemken and P. Bonfante. 2011. Unique arbuscular mycorrhizal fungal communities uncovered in date palm plantations and surrounding desert habitats of Southern Arabia. *Mycorrhiza*. 21: 195-209.
- Antunes, P. M., A. M. Koch, K. E. Dunfield, M. M. Hart, A. Downing, M. C. Rillig and J. N. Klironomos. 2008. Influence of commercial inoculation with *Glomus intradices* on the structure and functioning of an AM fungal community from an agricultural site. *Plant Soil*. 317: 257-266.
- Augé, R. M. 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza*. 11: 3-42.
- Bedini, S., L. Avio, C. Sbrana, A. Turrini, P. Migliorini, C. Vazzana and M. Giovannetti. 2013. Mycorrhizal activity and diversity in a long-term organic Mediterranean agroecosystem. *Biol. Fertil. Soils*. 49: 781-790.
- Bendavid-Val, R., H. D. Rabinowitch, J. Katan and Y. Kapulnik. 1997. Viability of VA-mycorrhizal fungi following soil solarization and fumigation. *Plant Soil*. 195: 185-193.
- Bever, J. D., P. A. Schultz, A. Pringle and J. B. Morton. 2001. Arbuscular mycorrhizal fungi: More diverse than meets the eye, and the ecological tale of why. *Bioscience*. 51: 923-931.
- Brundrett, M., L. Melville and L. Peterson. 1994. *Practical Methods in Mycorrhiza Research*. Mycologue Publications, Sydney.
- Bünemann, E. K., G. D. Schwenke and L. Van Zwieten. 2006. Impact of agricultural inputs on soil organisms a review. *Aust. J. Soil Res.* 44: 379-406.
- Cui, M. and P. S. Nobel. 1992. Nutrient status, water uptake and gas exchange for three desert succulents infected with mycorrhizal fungi. *New Phytol.* 122: 643-649.
- Daniels, B. A. and H. D. Skipper. 1982. Methods for the recovery and quantitative estimation of propagules from soil. In: N. C. Schenck (Ed.), *Methods and Principles of Mycorrhizal Research*. The American Phytopathological Society, St. Paul, pp. 29-35.
- De Deyn, G. B., H. Quirk and R. D. Bardgett. 2011. Plant species richness, identity and productivity differentially influence key groups of microbes in grassland soils of contrasting fertility. *Biol. Lett.* 7: 75-78.
- Fisher, M. and D. A. Mobery. 1998. Climate. In: M. Fisher. and D. A. Mobery (Eds.), *Geobotany: Vegetation of the Arabian Peninsula*. Kluwer Academic Publishers, Dordrecht, the Netherlands, pp. 5-38.
- Fitter, A. H. 2005. Darkness visible: Reflections on underground ecology. *J. Ecol.* 93: 231-243.
- Galvez, L., D. D. Jr. Douds, L. E. Drinkwater and P. Wagoner. 2001. Effect of tillage and farming system upon VAM fungus populations and mycorrhizas and nutrient uptake of maize. *Plant Soil*. 118: 299-308.
- Giovannetti, M., L. Avio, R. Barale, N. Ceccarelli, R. Cristofani, A. Iezzi, F. Mignolli, P. Picciarelli, B. Pinto, D. Reali, C. Sbrana and R. Scarpato. 2012. Nutraceutical value and safety of tomato fruits produced by mycorrhizal plants. *Br. J. Nutr.* 107: 242-251.
- Glennie, K. W. and A. K. Singhvi. 2002. Event stratigraphy, paleoenvironment and chronology of SE Arabian deserts. *Quat. Sci. Rev.* 22: 853-869.
- Gollotte, A., D. van Tuinen and D. Atkinson. 2004. Diversity of arbuscular mycorrhizal fungi colonising roots of the grass species *Agrostis capillaris* and *Lolium perenne* in a field experiment. *Mycorrhiza*. 14: 111-117.
- Gosling, P., A. Hodge, G. Goodlass and G. D. Bending. 2006. Arbuscular mycorrhizal fungi and organic farming. *Agric. Ecosyst. Environ.* 113: 17-35.
- Gottshall, C. B., M. Cooper and S. M. Emery. 2017. Activity, diversity and function of arbuscular mycorrhizae vary with changes in agricultural management intensity. *Agric. Ecosyst. Environ.* 241: 142-149.
- Hart, M. and R. Reader. 2002. Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. *New Phytol.* 153: 335-344.
- Hibilik, N., K. Selmaoui, J. Touati, M. Chliyah, A. O. Touhami, R. Benkirane and A. Douira. 2016. Mycorrhizal status of *Eryngium maritimum* in the mobile dune of Mehdiya (Northwest of Morocco). *Int. J. Pure Appl. Biosci.* 4: 35-44.
- IFOAM. 2006. *The IFOAM Basic Standards for Organic Production and Processing*. Version 2005. IFOAM Publications, Germany.
- Jansa, J., A. Mozafar and E. Frossard. 2005. Phosphorus acquisition strategies within arbuscular mycorrhizal fungal community of a single field site. *Plant Soil*. 276: 163-176.
- Johnson, N. C. 1993. Can fertilization of soil select less mutualistic mycorrhizae? *Ecol. Appl.* 3: 749-757.
- Koske, R. E. and B. Tessier. 1983. A convenient permanent slide-mounting medium. *Mycol. Soc. Am. Newsl.* 34: 59.
- Lee, J. E. and A. H. Eom. 2009. Effect of organic farming on spore diversity of arbuscular mycorrhizal fungi and glomalin in soil. *Mycobiology*. 37: 272-276.
- Lee, S. W., E. H. Lee and A. H. Eom. 2008. Effects of organic farming on communities of arbuscular mycorrhizal fungi. *Mycobiology*. 36: 19-23.

- Lekberg, Y. and R. T. Koide. 2005. Is plant performance limited by abundance of arbuscular mycorrhizal fungi? A meta-analysis of studies published between 1988 and 2003. *New Phytol.* 168: 189-204.
- Lekberg, Y. and R. T. Koide. 2008. Effect of soil moisture and temperature during fallow on survival of contrasting isolates of arbuscular mycorrhizal fungi. *Botany.* 86: 1117-1124.
- Li, L., T. Li, Y. Zhang and Z. Zhao. 2010. Molecular diversity of arbuscular mycorrhizal fungi and their distribution patterns related to host-plants and habitats in a hot and arid ecosystem, Southwest China. *FEMS Microbiol. Ecol.* 71: 418-427.
- Li, L. F., T. Li and Z. W. Zhao. 2007. Differences of arbuscular mycorrhizal fungal diversity and community between a cultivated land, an old field, and a never-cultivated field in a hot and arid ecosystem of southwest China. *Mycorrhiza.* 17: 655-665.
- Littell, R. C., G. A. Milliken, W. W. Stroup, R. D. Wolfinger and O. Schabenberger. 2006. SAS for Mixed Models. 2nd ed. SAS Institute Inc., Cary, NC.
- López-Gutiérrez, J., G. Malcolm, R. T. Koide and D. Eissenstat. 2008. Ectomycorrhizal fungi from Alaska and Pennsylvania: Adaptation of mycelial respiratory response to temperature? *New Phytol.* 180: 741-744.
- Mäder, P., S. Edenhofer, T. Boller, A. Wiemken and U. Niggli. 2000. Arbuscular mycorrhizae in a long-term field trial comparing low-input (organic, biological) and high-input (conventional) farming systems in a crop rotation. *Biol. Fertil. Soils.* 31: 150-156.
- Marulanda, A., R. Porcel, J. M. Barea and R. Azcón. 2007. Drought tolerance and antioxidant activities in lavender plants colonized by native drought-tolerant or drought-sensitive *Glomus* species. *Microb. Ecol.* 54: 543-52.
- Mozafar, A., T. Anken, R. Ruh and E. Frossard. 2000. Tillage intensity, mycorrhizal and non- mycorrhizal fungi, and nutrient concentrations in maize, wheat, and canola. *Agron. J.* 92: 1117-1124.
- Munkvold, L., R. Kjølter, M. Vestberg, S. Rosendahl and I. Jakobsen. 2004. High functional diversity within species of arbuscular mycorrhizal fungi. *New Phytol.* 164: 357-364.
- Neumann, E. and E. George. 2004. Colonisation with the arbuscular mycorrhizal fungus *Glomus mosseae* (Nicol. and Gerd.) enhanced phosphorus uptake from dry soil in *Sorghum bicolor* (L.). *Plant Soil.* 261: 245-255.
- Oehl, F., E. Sieverding, K. Ineichen, P. Mäder, T. Boller and A. Wiemken. 2003. Impact of land use intensity on the species diversity of arbuscular mycorrhizal fungi in agroecosystems of central Europe. *Appl. Environ. Microbiol.* 69: 2816-2824.
- Oehl, F., E. Sieverding, P. Mäder, D. Dubois, K. Ineichen, T. Boller and A. Wiemken. 2004. Impact of long-term conventional and organic farming on the diversity of arbuscular mycorrhizal fungi. *Oecologia.* 138: 574-583.
- Parniske, M. 2008. Arbuscular mycorrhiza: The mother of plant root endosymbiosis. *Nat. Rev. Microbiol.* 6: 763-775.
- Redecker, D., J. B. Morton and T. D. Bruns. 2000. Ancestral lineages of arbuscular mycorrhizal fungi (*Glomales*). *Mol. Phylogenet. Evol.* 14: 276-284.
- Requena, N., P. Jeffries and J. M. Barea. 1996. Assessment of natural mycorrhizal potential in a desertified semiarid ecosystem. *Appl. Environ. Microbiol.* 62: 842-847.
- Rillig, M. C. and D. L. Mummey. 2006. Mycorrhizas and soil structure. *New Phytol.* 171: 41-53.
- R Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ryan, M. H., D. R. Small and J. E. Ash. 2000. Phosphorus controls the level of colonisation by arbuscular mycorrhizal fungi in conventional and biodynamic irrigated dairy pastures. *Austr. J. Exp. Agric.* 40: 663-670.
- Säle, V., P. Aguilera, E. Laczko, P. Mäder, A. Berner, U. Zihlmann, M. G. A. van der Heijden and F. Oehl. 2015. Impact of conservation tillage and organic farming on the diversity of arbuscular mycorrhizal fungi. *Soil Biol. Biochem.* 84: 38-52.
- Sasvári, Z., L. Hornok and K. Posta. 2011. The community structure of arbuscular mycorrhizal fungi in roots of maize grown in a 50-year monoculture. *Biol. Fertil. Soils.* 47: 167-176.
- Scheublin, T. R., K. P. Ridgway, J. P. W. Young and M. G. A. van der Heijden. 2004. Nonlegumes, legumes, and root nodules harbor different arbuscular mycorrhizal fungal communities. *Appl. Environ. Microbiol.* 70: 6240-6246.
- Singh, S., A. Pandey and L. M. S. Palni. 2008. Screening of arbuscular mycorrhizal fungal consortia developed from the rhizospheres of natural and cultivated tea plants for growth promotion in tea [*Camellia sinensis* (L.) O. Kuntze]. *Pedobiologia.* 52: 119-125.
- Smith, S. E. and D. J. Read. 2008. Mycorrhizal Symbiosis. Academic Press, London.
- Smukler, S. M., L. E. Jackson, L. Murphree, R. Yokota, S. T. Koike and R. F. Smith. 2008. Transition to large-scale organic vegetable production in the Salinas Valley, California. *Agric. Ecosyst. Environ.* 126: 168-188.
- Stutz, J. C. and J. B. Morton. 1996. Successive pot cultures reveal high species richness of arbuscular endomycorrhizal fungi in arid ecosystems. *Can. J. Bot.* 74: 1883-1889.
- Sýkorová, Z., A. Wiemken and D. Redecker. 2007. Co-occurring *Gentiana verna* and *Gentiana acaulis* and their neighboring plants in two Swiss upper montane meadows harbour distinct arbuscular mycorrhizal fungal communities. *Appl. Environ. Microbiol.* 73: 5426-5434.
- Symanczik, S., J. Błaszowski, G. Chwat, T. Boller, A. Wiemken and M. N. Al-Yahya'ei. 2014a. Three new species of arbuscular mycorrhizal fungi discovered at one location in a desert of Oman: *Diversispora omaniana*, *Septoglomus nakheelum* and *Rhizophagus arabicus*. *Mycologia.* 106: 243-259.
- Symanczik, S., J. Błaszowski, S. Koegel, T. Boller, A. Wiemken and M. N. Al-Yahya'ei. 2014b. Isolation and identification of desert habituated arbuscular mycorrhizal fungi newly reported from the Arabian Peninsula. *J. Arid Land.* 8: 488-497.
- Symanczik, S., P. E. Courty, T. Boller, A. Wiemken and M. N. Al-Yahya'ei. 2015. 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. *Mycorrhiza.* 25: 639-647.
- van der Heijden, M. G. A., J. N. Klironomos, M. Ursic, P. Moutoglis, R. Streitwolf-Engel, T. Boller, A. Wiemken and I. R. Sanders. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature.* 396: 69-72.
- Vandenkoornhuysse, P., R. Husband, T. J. Daniell, I. J. Watson and J. M. Duck. 2002. Arbuscular mycorrhizal community composition associated with two plant species in a grassland ecosystem. *Mol. Ecol.* 11: 1555-1564.
- Vandenkoornhuysse, P., K. Ridgway, I. J. Watson, A. H. Fitter and J. P. W. Young. 2003. Co-existing grass species have distinctive arbuscular mycorrhizal communities. *Mol. Ecol.* 12: 3085-3095.
- Verbruggen, E., W. F. M. Roling, H. A. Gamper, G. A. Kowalchuk, H. A. Verhoef and M. G. A. van der Heijden. 2010. Positive effects of organic farming on below-ground mutualists: Large-scale comparison of mycorrhizal fungal communities in agricultural soils. *New Phytol.* 186: 968-979.

- Veresoglou, S. and M. Rillig. 2012. Suppression of fungal and nematode plant pathogens through arbuscular mycorrhizal fungi. *Biol. Lett.* 8: 214-217.
- Verma, N., J. C. Tarafdar, K. K. Srivastava and B. Sharma. 2016. Arbuscular mycorrhizal (AM) diversity in *Acacia nilotica* subsp. *indica* (Benth.) Brenan under arid agroecosystems of western Rajasthan. *Int. J. Adv. Res. Biol. Sci.* 3: 134-143.
- Wagg, C., S. F. Bender, F. Widmer and M. G. A. van der Heijden. 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proc. Natl. Acad. Sci. U. S. A.* 111: 5266-5270.
- Wetzel, K., G. Silva, U. Matczinski, F. Oehl and T. Fester. 2014. Superior differentiation of arbuscular mycorrhizal fungal communities from till and no-till plots by morphological spore identification when compared to T-RFLP. *Soil Biol. Biochem.* 72: 88-96.