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Diversity of arbuscular mycorrhizal fungi associated with desert ephemerals growing under and beyond the canopies of Tamarisk shrubs

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Abstract The arbuscular mycorrhizal (AM) fungal status of the four most common ephemeral plant species, *Chorispora tenella* (Pall.) DC., *Cerato-cephalus testiculatus* (Crantz) Bess., *Eremopyrum orientale* (L.) Jaub et. Spash and *Veronica campy-lopoda* Boiss growing in an area dominated by Tamarisk shrubs (*Tamarix* spp.) was investigated. Samples of the four ephemerals and their rhizosphere soils were collected from underneath and beyond the canopies of the Tamarisk shrubs. Plant mycorrhizal status and soil AM fungal spore densities and community structures were analyzed and compared under and beyond the shrub canopies. The mycorrhizal colonization rates of the ephemerals and spore densities in their corresponding rhizosphere soils were significantly lower under the shrub canopies than beyond. The number of AM fungal species under the shrubs (12) was also lower than beyond the canopies (19). When soil properties in the rhizospheres of the four ephemerals were examined, available N and P and total P, organic matter content, total salt content and electrical conductivity (EC) were all higher under the canopies than beyond. In contrast, soil available K and pH showed no such trend. A total of 21 AM fungal species were isolated from rhizosphere soils of the four ephemerals. Five belonged to *Acaulospora,* one to *Archaeospora*, thirteen to *Glomus* and two to *Paraglomus*. We

conclude that the canopies of *Tamarix* spp. exerted some influence on the AM status of the ephemerals and on the AM fungal communities and some of the properties of their rhizosphere soils.

Shrubs in arid ecosystems typically grow in patchy distributions with low plant cover and the vegetation patches commonly constitute 'fertility islands'[1], or 'resource islands'[2,3], where facilitation among plants may be strongly fostered[4,5]. Fertility islands may differ from areas outside plant canopies (interspatial soils) in numerous ways including the occurrence of high concentrations of soil nitrogen and other nutrients[6], reduced solar radiation and lower soil temperatures[7−10]. He *et al*. (2002)[11] showed that shrubs influenced AM fungal diversity. Arbuscular mycorrhizal (AM) fungi are soil microorganisms known to establish a universally distributed mutualistic association with the majority of higher plant species. Arbuscular mycorrhizas are widespread among terrestrial plants, with mycorrhizas occurring in 83% of the dicotyledonous and 79% of the monocotyledonous species observed so far[12,13]. It is well known that AM fungi promote plant establishment by increasing resistance to environmental stresses, increasing plant nutrient acquisition and enhancing soil quality. As a result, AM fungi can increase plant diversity and productivity and succession in plant communities[14,15]. There is considerable evidence that mycorrhizal associations play a significant role in the stability and productivity of natural ecosystems. Because of the key ecological functions of AM associations, loss or diminution of mycorrhizal potential in degraded areas may limit the successful reestablishment of the native plants[16,17]. Investigations of AM fungal diversity may therefore help us to understand the developmental trends and productivity of plant communities.

There have been several studies on arbuscular mycorrhizal fungi in the fertility islands of shrubs[18−22]. However, most studies have concentrated on the arbuscular mycorrhizal status of the shrubs themselves and the AM fungal diversity in their rhizosphere soils. We hypothesize that shrubs can influence the arbuscular mycorrhizas of neighbouring herbaceous plant species growing under their canopies and AM fungal diversity in their rhizosphere soils. In the present study we selected four ephemeral plant species growing under and beyond the canopies of *Tamarix* spp. Ephemer-

als are specially adapted desert plants that remain dormant until rare rainfall events occur. They then spring to life and grow and flower quickly before the desert dries up again. It is a particular trait of desert plants in variable areas that they can take advantage of water resources and temperature conditions in the spring to complete their life cycle in only about two months[23,24]. Ephemerals include two types of plants, annuals that develop from seed and perennials with a very short epigeous period during which shoots are present aboveground that germinate from corms or seeds each year[25]. As an important and unique component of China's desert flora, ephemerals can form significant synusia from late March to mid June, a season witnessing the strongest wind forces in the desert regions of north Xinjiang Autonomous Region. They are also one of the zonal indicators of botanic geography in the arid zone of Eurasia. Furthermore, ephemerals can stabilize sand dunes and are pioneer species during the rehabilitation of degraded desert areas[26] and they can lower the frequency of occurrence and intensity of sandstorms. In addition, ephemerals are a valuable resource providing flowers, grazing and medicinal materials in early spring in desert ecosystems. Accordingly, these plants have attracted the interest of ecologists and botanists[25,27−30]. However, to our knowledge there have been no studies on AM associations of ephemeral plants. The objectives of the present survey were to investigate and compare the AM fungal colonization and developmental status of ephemerals and AM fungal communities in the rhizosphere soils under and beyond the canopies of Tamarisk shrubs, to understand the characteristics of 'fertility islands' and to explain the process of desertification.

1 Materials and methods

1.1 Study sites

The study was carried out at the Tamarisk shrublands (44°7.487′N, 87°49.099′E) located 50 km from Urumqi in the southern Junggar Basin of the northern Tianshan Mountains, northern Xinjiang Autonomous Region, northwestern China. The area lies in the climatic zone of continental aridity, with an annual mean temperature of 5.7℃, hot and dry summers (highest monthly mean temperature 23.5℃ in July), and cold winters (lowest monthly mean temperature −15.4℃ in January). The annual average precipitation is about 200 mm and the annual latent evaporation is about 2500 mm. However,

about 45% of the precipitation occurs during spring. The average altitude is 518 m above sea level. The soil type is aridisol according to the USDA soil classification system. Over ten species of *Tamarix* occur naturally over the area and form a dominant component of the plant cover. They are very difficult to identify to species level and their distribution is closely related to soil moisture conditions. Among the associated herbaceous plant species, ephemerals develop in spring before the Tamarisk shrubs sprout and they are the dominant plant species. In particular, *Chorispora tenella* (Pall.) DC., *Ceratocephalus testiculatus* (Crantz) Bess., *Eremopyrum orientale* (L.) Jaub et. Spash and *Veronica campylopoda* Boiss are the most common species both under and beyond the Tamarisk canopies. Other plant species present include other ephemerals such as *Lepidium perfoliatum* (Cruciferae), *Tulipa illiensis* (Liliaceae) and the annual or perennial species *Phragmites australis* subsp. Australis (Gramineae), *Aeluropus* sp. (Gramineae), *Suaeda acuminate* (Chenopodiaceae), *Halostachys caspica* (Chenopodiaceae), and *Camphorosma monspeliaca* (Chenopodiaceae). When the plant species associated with the Tamarisk shrubs were examined no differences in plant species richness or density were observed under the shrub canopies compared with plants beyond the canopies.

1.2 Collection of soil and root samples

The four commonest ephemerals, *Chorispora tenella* (Pall.) DC., *Ceratocephalus testiculatus* (Crantz) Bess., *Eremopyrum orientale* (L.) Jaub et. Spash and *Veronica campylopoda* Boiss were surveyed. Samples of roots and soils were collected from the rhizospheres of four plants of the same species randomly distributed under and beyond Tamarisk shrub canopies during April and May 2004 according to the procedures described by Liu and Li[31]. Ten shrub canopies and locations between canopies were investigated. Care was taken during the collection of individual plants that the roots could be positively identified as belonging to a particular individual plant. The root samples of the ephemerals were dug out together with plants to ensure that the roots were connected to those particular plants. Samples were taken to the laboratory for determination of AM root colonization. The soil samples had a sandy texture and were then air-dried in the shade at ambient laboratory temperature for spore extraction, counting and identification. Soil physicochemical properties were measured according to the methods described by Lu[32].

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1.3 Measurement of AM colonization

Fine and fibrous roots were selected to obtain sub-samples of the fresh root samples. After thorough washing to remove all soil particules, roots were placed in plastic cassettes used in medicine for processing biopsy tissues. The roots were cleared with 10% (w/v) KOH by heating to 90℃ in a water bath for 20－30 min, the exact time depending on the degree of lignification of the roots and their pigmentation. The cooled root samples were washed 4－5 times with water, cut into 0.5- to 1.0-cm-long segments, and immersed in 2% (v/v) HCl for 15－20 min and stained with 0.05% (w/v) acid fuchsin[33]. To determine the proportion of root length colonized by AM fungi, thirty cleared and stained root segments were mounted on slides (10 per slide) and the colonized root tissue was evaluated according to the method of Trouvelot et al.[34]. The AM fungal structures present were also recorded.

1.4 Enumeration and isolation of AM fungal spores

AM fungal spores were isolated from 20-mL sub-samples of air-dried soil by the wet sieving and decanting method followed by sucrose centrifugation[35]. After centrifugation, each supernatant was poured through a 50-μm mesh and quickly rinsed with tap water. Turgid spores (suggesting viability) were grouped under a dissecting microscope at 40× magnification according to their morphological characteristics. All spores that were intact, i.e. non-collapsed, with cytoplasmic contents and free from parasitic attack, were counted. Sporocarps and spore clusters were considered as one unit. Diagnostic permanent slides were prepared for each different spore morphotype using either poly-vinyl-lactoglycerol (PVLG) or PVLG+Melzer's (1∶1) reagent. After confirming the uniformity of the morphological groups under the optical microscope, the different morphotypes were identified to genus and species. Spore identification was based mainly on spore size, colour, wall structure and hyphal attachment[36]. Spore identification was corroborated by comparison with the descriptions of the reference cultures in INVAM (http://invam.cag.wvu.edu) and IBG (International Bank of the Glomales). AM fungal spores were classified according to the taxonomic system devised by Morton and Redecker[37].

1.5 Statistical analysis

One-way analysis of variance (ANOVA) was used to compare AM fungal colonization and spore density in the rhizosphere of the four ephemerals under the Tamarisk canopies with those beyond. The SPSS software package version 11.0 was used.

2 Results

2.1 Soil properties

Soil properties under the canopies were: total salt content 1.57 g/kg, pH 8.24, organic matter content 16.5 g/kg, available N 65.4 mg/kg, available P 44.5 mg/kg, available K 217 mg/kg, total P 0.64 g/kg, and electrical conductivity 0.40 mS/cm. Values beyond the canopies were: total salt content 0.81 g/kg, pH 8.38, organic matter content 14.5 g/kg, available N 32.3 mg/kg, available P 33.85 mg/kg, available K 344 mg/kg, total P 0.63 g/kg, and electrical conductivity 0.18 mS/cm. All soil parameters except for pH and available K had higher values under the canopies than beyond.

2.2 Comparison of AM fungal colonization status

The AM fungal colonization status of the four ephemerals under and beyond the shrub canopies is shown in Fig. 1. No AM fungal colonization was observed in roots of Chorispora tenella (Pall.) DC. either under the shrub canopies or beyond. The other three species were colonized by AM fungi, with the proportion of root length colonized ranging from 0.9% to 18.8%. The extent of root colonization on all three mycorrhizal ephemerals was affected significantly by the shrub canopies, with higher colonization under the canopies than beyond ($p<0.01$). Ceratocephalus testiculatus showed the highest colonization rates both under (7.3%) and (18.0%) shrub canopies.
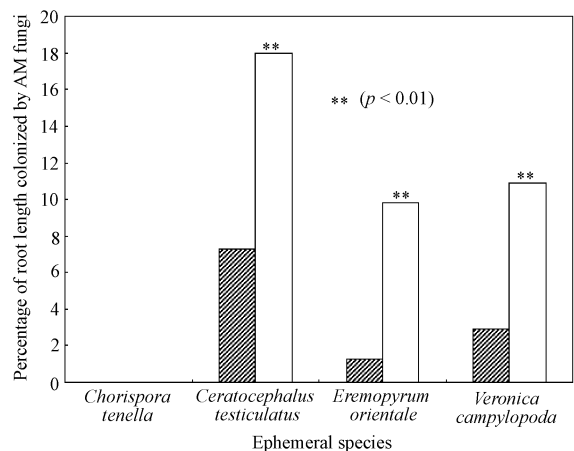

Fig. 1. Mean arbuscular mycorrhizal colonization rate of ephemerals under (hatched bars) and beyond (open bars) the Tamarisk canopies.

2.3 AM structures under and beyond Tamarisk canopies

AM structures of ephemerals collected under and beyond shrub canopies are shown in Table 1. No AM structures were observed in *Chorispora tenella* either under or beyond the shrub canopies. Vesicles, intra-radical non-septate hyphae and extra radical non-septate hyphae were observed in root samples of *Ceratocephalus testiculatus*, *Eremopyrum orientale* and *Veronica campylopoda*. Arbuscules were observed in two out of the four plant species growing beyond the canopies. No arbucules were found in any root samples collected from under the shrub canopies.

2.4 AM fungal spore densities

The spore densities in 20 mL rhizosphere soil of four ephemeral species growing under and beyond the shrub canopies are presented in Fig. 2. The spore densities under the canopies were significantly lower than those beyond. The sequence of the four ephemerals in terms of AM spore density differed under and beyond the canopies as follows: *Eremopyrum orientale* (31), *Ve-*
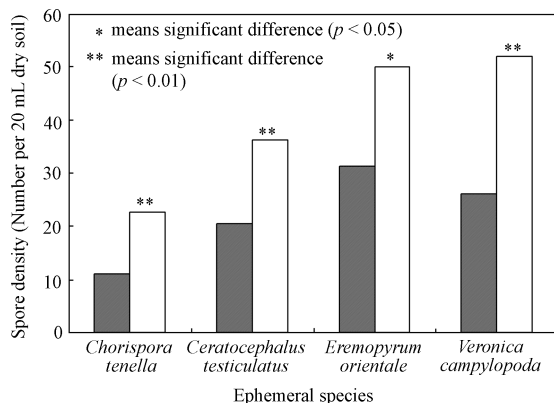

Fig. 2. Mean AM fungal spore densities in rhizospheres of ephemerals under (hatched bars) and beyond (open bars) the Tamarisk canopies.

ronica campylopoda (26), *Ceratocephalus testiculatus* (21), and *Chorispora tenella* (11) under the canopies, and *Veronica campylopoda* (52), *Eremopyrum orientale* (50), *Ceratocephalus testiculatus* (36), and *Chorispora tenella* (23) beyond the canopies.

2.5 AM fungal species identified

Twenty-one AM fungal species belonging to four genera, with one species in *Archaeospora*, five in *Acaulospora,* thirteen in *Glomus* and two in *Paraglomus*, were isolated and identified in the rhizosphere of the four ephemeral species under and beyond the shrub canopies (Table 2). Twelve species representing 3 genera of AM fungi were present in the rhizospheres of the ephemerals growing under the shrub canopies. Among the 12 species, 2 belonged to *Acaulospora,* 8 to *Glomus* and 2 to *Paraglomus,* with no *Archaeospora* spp. present. Except for *G. mosseae* and *P. occltum*, all AM fungal species were isolated and identified in the rhizospheres of ephemerals beyond the shrub canopies. All four ephemeral species showed higher numbers of AM fungal species in the rhizosphere soil beyond the shrub canopies than under the canopies.

3 Discussion

Studies on the interactions among plants, microorganisms and the environment are necessary prerequisites for understanding the course of desertification[38−40]. Numerous studies have shown that AM fungi can enhance the P nutrition of host plants, increase the diversity and stability of plant communities, and enhance the resistance of host plants to abiotic stresses such as drought and salt stress[16,41−43]. Until now, few studies have been carried out on the mycorrhizal status of ephemeral plants that play an important role in the stability of desert ecosystems. In the

Table 1 Typical arbuscular mycorrhizal structures in ephemerals under and beyond the Tamarisk canopies

Host plant species	Arbuscules[b]	Vesicles	Intra-radical non-septate hyphae	Extra-radical non-septate hyphae
Chorispora tenella (Pall.) DC.[a]	−	−	−	−
Chorispora tenella (Pall.) DC.	−	−	−	−
Ceratocephalus testiculatus (Crantz) Bess.[a]	−	+	++	+
Ceratocephalus testiculatus (Crantz) Bess.	+	++	++	++
Eremopyrum orientale (L) Jaub et Spash[a]	−	(+)	+	+
Eremopyrum orientale (L) Jaub et Spash	−	+	++	+
Veronica campylopoda Boiss.[a]	−	+	+	+
Veronica campylopoda Boiss.	+	+	++	++

a) Samples were collected under canopies of *Tamarix ramosissima* Lebedour. b) ++, always present in significant numbers; +, always present; (+), very rare, only present in cortical colonization; −, not detected.

Table 2   AM fungal communities in the rhizosphere soils of ephemerals growing under and beyond Tamarisk canopies

AM fungus \ Ephemeral species	*Chorispora tenella*[a]	*C. tenella*	*Ceratocephalus testiculatus*[a]	*C. testiculatus*	*Eremopyrum orientale*[a]	*E. orientale*	*Veronica campylopoda*[a]	*V. campylopoda*
Acaulospora								
A. appendicula Spain, Sieverding & Schenck				+[b]			+	
A. elegans Trappe & Gerdemann						+		+
A. excavate Ingleby & Walker	+	+			+	+		+
A. mellea Spain & Schenck						+		
A. rehmii Sieverding & Toro				+			+	
Archaeospora								
Ar. leptoticha (Schenck & Smith) Morton et R.						+		
Glomus								
G. aggregatum Schenck & Smith emend. Koske			+	+	+	+		
G. australe (Berk.) Berch	+		+	+				
G. claroideum Schenck & Smith		+	+	+	+	+	+	+
G. clarum Nicolson & Schenk	+	+		+			+	
G. deserticola Trappe, Bloss & Menge			+		+			+
G. etunicatum Becker & Gerd.			+	+		+	+	
G. geosporum (Nicol. & Gerd.) Walker	+	+	+			+		+
G. globiferum Koske & Walker							+	
G. macrocarpum Gerd. & Trappe	+	+	+	+			+	+
G. microcarpum Tul. & Tul.		+					+	
G. mosseae (Nicol. & Gerd.) Gerd. & Trappe			+					
G. multicaule Gerdemann & Bakshi								+
G. reticulatum Bhattacharjee & Mukerji				+				+
Paraglomus								
P. brasilianum (Spain et Miranda) Morton et. Redecker	+	+						+
P. occultum (Walker) Morton et. Redecker					+			

a) Samples were collected under Tamarisk canopies; b) +, AM fungi were present in samples.

present study, 21 AM fungal species belonging to 4 genera were isolated from the rhizospheres of 4 common ephemerals growing under and beyond Tamarisk shrub canopies and demonstrated that AM fungi were a notable component of the Tamarisk desert ecosystem.

van der Heijden[16] showed that mycorrhizal fungal diversity determines plant biodiversity and ecosystem variability and productivity. AM fungi colonize root tissues biotrophically and form an extensive network of extra-radical mycelium, providing a direct physical link between the soil and plant roots[44]. The arbuscular mycorrhizal (AM) fungal status of the four most common ephemerals, *Chorispora tenella* (Pall.) DC., *Ceratocephalus testiculatus* (*Crantz*) Bess., *Eremopyrum orientale* (L.) Jaub et. Spash and *Veronica campylopoda* Boiss growing in Tamarisk shrublands were investigated. Their mycorrhizal status, AMF spore densities and community structures were analyzed, and the differences under and beyond the shrub canopies were compared. All four ephemeral species formed AM associations except for *Chorispora tenella*. The shrub canopies decreased the AM colonization rate of ephemerals and the AM fungal diversity in the rhizosphere soils of three mycorrhizal ephemeral species. The root colonization rate and occurrence of AM fungal structures were lower under the canopies than beyond. Possible explanations are higher nutrients restraining colonization and spore reproduction under the canopies because AM fungal infection levels are generally inversely correlated with nutrient availability (especially phosphorus and nitrogen) and soil moisture[45,46]. In addition, He *et al*.[47] showed that AM fungal spore densities were negatively correlated with soil available N under halophyte canopies in the Negev Desert. In our study site all soil nutrition concentrations measured were higher under the canopies than beyond, except for available K. The relatively high soil nutrient concentrations under the canopies may have led to a decrease in the mycorrhizal dependence of the ephemerals compared with those growing beyond the canopies. This result supports the conclusion of Dhillion and Zak[48] that when plants have high nutrient availability, a negative response of AM fungi and low infection levels may be expected. Another possible explanation is that the higher water and nutrient contents increased root development under the canopies, resulting in lower mycorrhizal colonization rates under the canopies than beyond.

Although AM structures were not observed in the

ephemeral species *Chorispora tenella*, AM fungal spores were isolated from its rhizosphere soils. This may be due to the intermingling of plant roots of different species in the field sample so that mycorrhizal plants may have influenced sporulation in the rhizosphere soils of non-mycorrhizal plants.

Twenty-one AM fungal species were isolated from the rhizosphere soils of the ephemerals and identified. The number of AM fungal species extracted was higher than in some previous investigations in desert ecosystems. For example, 15 AM fungal species associated with *Sporobolus wrightii* were found in riparian habitats in arid south-western North America[49]. Far fewer AM fungi (5 species) were isolated in shrub-associated resource islands from a semiarid Mediterranean ecosystem threatened by desertification[22]. It is unlikely that the desertification was serious in our sampling sites because the soil total salt content was relatively low (1.57 g/kg). Other possible explanations are differences in ecological factors or species of shrub, and further studies are required to elucidate these factors in detail. In addition, we still do not understand how AM fungi associated with ephemerals complete their life cycle after the death of the ephemeral host plants and this question requires intensive study.

The spore densities of AM fungi in rhizosphere soils of ephemerals were relatively high (mean of 31 per 20 mL air-dried soil). Kennedy and Smith[50] showed that land degradation tended to reduce microbial diversity and/or activity belowground. Mycorrhizal associations and fungal propagules usually suffer from degradative processes[51−53]. It has been clearly demonstrated that mycorrhizal activity, among other biological processes within the soil–plant system, is diminished by desertification in Mediterranean ecosystems[54]. Thus, spore densities were lower than in tropical ecosystems where mean spore densities were up to 476 per 100 mL soil[55]. The differences in spore density under and beyond shrub canopies are contradictory to the report of Carrillo-Garcia *et al*.[19] in which spore densities were higher in soils beneath shrubs than in interspatial positions. In other studies, shrub fertile islands contained the largest amounts of mycorrhizal inocula[18−20]. The explanation is that previous studies concentrated on the AM status of the shrubs themselves with absorbing roots deeply distributed within the soil. However, our study focused on herbaceous ephemerals with relatively shallow absorbing roots. The environments and shrub

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species were different in our study and in previous studies. Another possible explanation is that mycorrhizal inocula consist largely of hyphal fragments rather than spores, a conclusion that was drawn by Bashan *et al.* (2000) in their Sonoran Desert studies[56].

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