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RESEARCH ARTICLE

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Mycorrhizal and dark septate endophytic fungi under the canopies of desert plants in Mu Us Sandy Land of China

Abstract Biodiversity of arbuscular mycorrhizal colonization and spore density was investigated in 20 desert plants (dominant or common species) collected from different locations of Mu Us Sandy Land of China. We observed three mycorrhizal types including Arum-type, Paris-type, and an intermediate type among the plants. Another type of potentially beneficial fungi associated with roots of all species was also observed, namely, dark septate endophytic fungi (DSEF). Of the 20 sample plants examined, all species were coinfected by the two target fungi (Arbuscular mycorrhizal fungi (AMF) colonization of *Salix psammophila* and DSEF colonization of *Periploca sepium* were as low as 4%). Based on this investigation, we speculated that the DSEF are ubiquitous in desert ecosystems and can co-occur with AMF in desert plants, functioning much like mycorrhizal fungi. Further studies will be required to elucidate interactional mechanisms with AMF and the mechanisms operating in desert ecosystem.

Keywords Arbuscular mycorrhizal fungi, mycorrhiza type, root endophytic fungi, desert plants

1 Introduction

Arbuscular mycorrhizal (AM) associations are ubiquitous in desert ecosystems and may play an important role in plant establishment and growth by bridging between plant and soil (Allen, 1983; Skujins and Allen, 1986; Dhillion and Zak, 1993). Mycorrhizal plants have a greater ability to absorb nutrients and soil water and increase plant fitness, both of which may lead to better survival under stressed environmental conditions (Auge and Stodola, 1990; Sylvia and Williams, 1992). AMF, especially, can form enormous hypha network systems in the rhizosphere, which can enhance the stability of soil aggregates, fix dune, and improve the physical and chemical conditions of the soil (Bearden and Petersen, 1999). Therefore, AMF can play an important role in ecological system protection, restoration, and reconstruction. In addition, root endophytes such as dark septate endophytes (DSE) are abundant in many plant genera and many habitats worldwide (Jumpponen and Trappe, 1998), may be as ubiquitous as or even more than AMF, especially under harsh climatic conditions (Barrow, 2003; Olsson and Tyler, 2004; Addy et al., 2005), and have been reported to confer a positive effect on plant growth (Read and Haselwandter, 1981). The DSE are less well known, but are potentially beneficial to their host plants (Postma et al., 2007). As far as we know, little work has been done concerning the relationships between desert plants and DSE in arid and semi-arid area of northwestern China. Therefore, we examined the diversity of AMF structures and also observed the colonization of the DSE and AMF under the canopy of desert plants.

Mu Us Sandy Land of China is located between 107°20′E to 111°30′E and 37°27′N to 39°22′N, with an area of about 40 thousand km^2, including portions of the Inner Mongolia Autonomous Region, Shaanxi Province, and the Ningxia Hui Autonomous Region (Department of Geography of Peking University et al., 1983). This area has a typical continental semi-arid climate. Annual precipitation ranges from 440 mm in the southeast to 250 mm in the northwest, of which 60%–80% is concentrated in the period from June to August. The annual mean temperature is about 6.0–8.5°C, with monthly mean temperatures of 22°C in July and – 11°C in January. This area is the biggest mobile sand land in the dry and nutrient-poor grasslands of China. With shortage of water, wind exposure, sand texture, and fluctuations in soil, the moisture and

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temperature make the ecological condition very fragile and sensitive.

The target plants belong to eight families of Salicaceae (*Salix psammophila*), Tamaricaceae (*Tamarix chinensis*), Leguminosae (*Caragana intermedia*, *Caragana microphylla*, *Caragana korshinskii*, *Ammopiptanthus mongolicus*, *Oxytropis aciphylla*, *Hedysarum scoparium*, *Hedysarum fruticosum*, *Astragalus adsurgens*, and *Glycyrriza uralensis*), Zygophyllaceae (*Sarcozygium xanthoxylum*), Asclepiadaceae (*Periploca sepium*), Compositae (*Artemisia ordosica*, *Artemisia sphaerocephala*, *Artemisia scoparia*), Gramineae (*Stipa capillata*, *Psamrrmchloa villosa*, *Phragmites australis*), and Liliaceae (*Allium mongolicum*). Among these species, *H. fruticosum*, *C. korshinskii*, *A. sphaerocephala*, and *A. ordosica* are four dominant psammophyte species in Mu Us Sandy Land. Due to its rapid growth and vegetative propagation characteristics, *H. fruticosum* has been widely used in the desertified land. *C. korshinskii* belongs to Leguminosae (*Caragana* Fabr.), uptaking fixed nitrogen in the air and improving soil fertility in the biological sand fixation. *A. sphaerocephala* was the advantages of the Ordos Plateau species, *A. ordosica*, as a key, for mobile dune to semifixed and fixed dunes succession process. *A. mongolicus* is the oldest sand Tertiary relict species, unique in Alashan Desert plant construction group, and others are common in Mu Us Sandy Land.

2 Materials and methods

2.1 Sites description and sampling

Twenty species of desert plants were collected from Mu Us Sandy Land mainly from the Ordos Sandy Land Ecological Station of the Institute of Botany, the Chinese Academy of Sciences (OSES), Shaanxi Yulin Rare Sandy-plants Conversation Field (RSCF), Ningxia Shapotou (SPT), Yanchi (YC), and Alaskan desert (ALS) in October, 2007. For widely distributed species, samples were collected from more than one habitat. Detailed information about the sampling species and sites is described in Table 1.

Soil samples and root samples were collected in four replicates from the rhizosphere of each plant. The rhizosphere soil at 0–30 cm layer from each replicate was placed in an individual plastic bag and transported to the laboratory. Air-dried soil samples were sieved (2 mm mesh size) for each sample. The subsamples of soil from each replicate were used to determine spore density.

2.2 Assessment of AM and DSE colonization

Fresh roots were cut into 0.5 to 1.0 cm long segments and processed by washing them free of soil and clearing in 10% (w/v) KOH at 90°C in a water bath for 15–30 min,

Table 1 Description of site and plant sampling

plant sample						site description		
family	species	life form	root type	nature	locatio	long. (E)	lat. (N)	altitude/m
Salicaceae	*S. psammophila*	shrub	tap root	no	YC	107°10′054″	37°54′333″	1460
Tamaricaceae	*T. chinensis*	shrub	tap root	no	YC	107°10′054″	37°54′333″	1460
Leguminosae	*C. intermedia*	shrub	tap root	no	YC	107°10′054″	37°54′333″	1460
	C. microphylla	shrub	tap root	no	YC	109°57′733″	40°13′175″	1206
	C. korshinskii	shrub	tap root	no	YC	105°4′293″	37°31′418″	1255
	A. mongolicus	shrub	tap root	yes	ALS	104°58′099″	37°54′333″	1460
	O. aciphylla	shrub	tap root	yes	SPT	104°48′406″	37°26′799″	1592
	H. scoparium	shrub	tap root	yes	SPT	104°56′075″	37°26′372″	1360
	H. fruticosum	perennial herb	tap root	no	OSES	110°11′226″	39°29′401″	1280
	A. adsurgens	perennial herb	tap root	yes	YC	107°10′054″	37°54′333″	1460
	G. uralensis	perennial herb	tap root	yes	YC	107°10′054″	37°54′333″	1460
Zygophyllaceae	*S. xanthoxylum*	shrub	tap root	no	YC	107°10′054″	37°54′333″	1460
Asclepiadaceae	*P. sepium*	shrub	fibrous root	yes	ALS	104°58′099″	37°43′573″	1357
Compositae	*A. ordosica*	semi-shrub	tap root	yes	YC	107°10′054″	37°54′333″	1460
	A. sphaerocephala	semi-shrub	tap root	yes	RSCF	109°42′541″	38°20′072″	1100
	A. scoparia	perennial herb	tap root	yes	RSCF	109°42′541″	38°20′072″	1100
Gramineae	*S. capillata*	perennial herb	fibrous root	yes	SPT	107°3′674″	37°59′129″	1415
	P. villosa	perennial herb	fibrous root	yes	SPT	104°56′075″	37°26′372″	1360
	P. australis	perennial herb	fibrous root	yes	SPT	105°03′853″	37°31′883″	1242
Liliaceae	*A . mongolicum*	biennial herb	fibrous root	yes	SPT	104°48′406″	37°26′799″	1592

Note: Ordos Sandy Land Ecological Station of the Institute of Botany, the Chinese Academy of Scienses (OSES), Shaanxi Yulin Rare Sandy-plants Comversation Field (RSCF), Ningxia Shapotou (SPT), Yanchi (YC) and Alaskan desert (ALS) depending on the degree of lignification of the roots. The root subsamples were cooled, washed, and stained with 0.5% (w/v) acid fuchsin. Thirty root fragments were examined at 100–400 times magnification using a Nikon YS100 microscope with an automatic photomicrographic system for the presence of AMF structures. Total AM, hyphal, vesicular, and arbuscular colonization were expressed as the percentage of root segments colonized for each root sample.

Mycorrhizal types were designated according to Smith and Smith (1997), and DSEF tissues were named according to Jumpponen and Trappe (1998). The hyphae and microsclerotium (MS) of DSEF colonization was calculated as the ratio of the number of infected sections to the total number of sections examined.

2.3 Extraction of AMF spores

Spores or sporocarps were extracted from 20 g air-dried soil of each soil sample by wet sieving followed by flotation centrifugation in 50% sucrose (Dalpe, 1993). The spores were collected on a filter paper, washed several times with distilled water, and counted using a dissecting microscope at 75 times magnification. A sporocarp was counted as one unit.

3 Results

Among the 20 plants in this experiment, we found different plant species formed different mycorrhizal morphology, consisting of mainly three AM types of Arum type, Paris type, and intermediate type. The Arum type formed extensive intercellular hyphae. The Paris type was characterized by the absence of intercellular hyphae and replaced by extensive intracellular hyphal coils (Fig. 1 (a)). Moreover, if two morphological structures were represented in the same root system, then it was termed as intermediate type (Fig. 1 (b)). The mycorrhizal types of the target plants are described in Table 2.

All the species were colonized by AMF, although *A. mongolicus* and *A. mongolicum* were not observed to have hyphae and vesicles, respectively, and the colonization of *S. psammophila* was low. The morphology of AMF hyphae (Figs. 1 (a), (b) and Fig. 2 (b)) and vesicles (Figs. 2 (d), (e), (g)) was various. Most of the studied species had no arbuscular colonization, with only low arbuscular colonization of *A. ordosica*, *C. intermedia*, *C. microphylla*, and *C. korshinskii* (Fig. 2 (f)). The spore density (expressed as per 1 g dry soil) under the canopy differed greatly among plants, ranging from 2.45 to 83.60 (Table 2).

In this investigation, plant species belonging to a same or different families formed different AM morphology, suggesting that the morphology of AM was depended on the genotype of host plant (Ahulu et al., 2007).

Coexistence of DSEF and AMF was detected in all investigated plants (Fig. 1 (c) and Fig. 2 (a)), although some species had lower colonization, such as DSE in *P. sepium* and AM in *S. psammophila*. All 20 species had DSE and formed microsclerotium (Fig. 2 (h)); the colonization of microsclerotium in *C. intermedia* was especially high, reaching about 50%. The results indicated the dominant and constructive plants could commonly form AM and DSEF tissues.

Correlation analyses (Table 3) demonstrated that the total percentage of highly significant colonization was positively correlated with hyphal ($P < 0.01$) and vesicular ($P < 0.01$) colonization, whereas the hyphal colonization had a significantly negative correlation ($P < 0.05$) with DSE tissues. Moreover, the microsclerotium colonization was positively correlated with vesicular and arbuscular colonization.

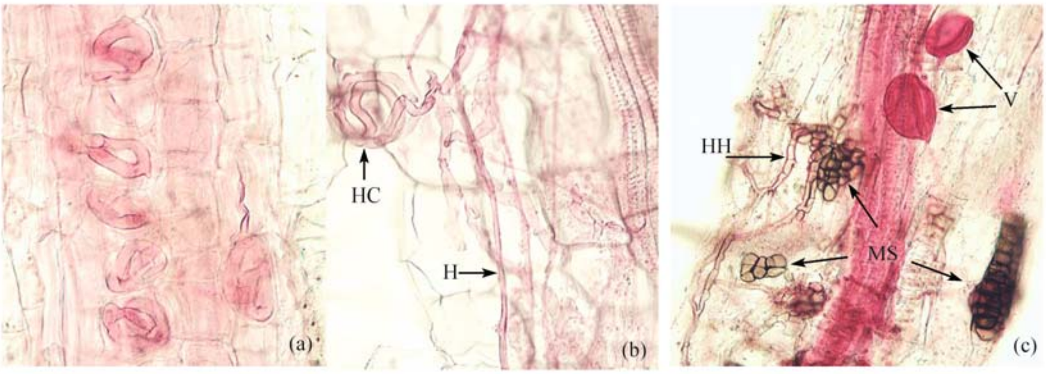

Fig. 1 Mycorrhizal types

Note: (a), (b) and (c) represent Paris-type of *S. capillata*, intermediate type of *C. korshinskii*, and coexistence of AMF and DSEF in *C. korshinskii,* respectively. H, HC, V, HH and MS represent hyphae of AMF, hyphal coils of AMF, vesicles of AMF, hyaline hypha of DSEF and microsclerotium, respectively.

Table 2 Status of different structures and spore density of AMF and DSEF tissues in the arid plots

plant species		mycorrhiza types	hyphae /%	vesicle /%	arbuscule /%	total AM & DSE/%	DSE /%	MS /%	total AM /%	spore density/(spore number·g^{-1} dry soil)
Salicaceae	*S. psammophila*	I	4	4	0	4	100	12	4	34.75
Tamaricaceae	*T. chinensis*	A	68	28	0	24	24	8	68	33.00
Leguminosae	*C. intermedia*	I	87	97	10	67	53	50	100	63.25
	C. microphylla	I	95	67	2	52	47	13	100	5.36
	C. korshinskii.	I	91	60	2	54	40	22	91	8.94
	A. mongolicum	P	88	0	0	24	18	6	88	16.50
	O. aciphylla	P	58	92	0	58	58	42	92	33.45
	H. scoparium	I	85	65	0	75	75	30	85	11.20
	H. fruticosum	A	80	83	0	93	97	7	97	7.50
	A. adsurgens	P	80	40	0	10	20	0	80	26.50
	G. uralensis	P	10	20	0	27	100	30	20	10.85
Zygophyllaceae	*S. xanthoxylum*	A	60	67	0	40	33	20	67	56.00
Asclepiadaceae	*P. sepium*	I	96	20	0	8	4	4	100	8.20
Compositae	*A. ordosica*	P	56	32	4	40	48	12	64	74.60
	A. sphaerocephala	P	83	33	0	33	33	0	83	12.40
	A. scoparia	A	30	40	0	10	25	0	50	39.25
Gramineae	*S. capillata*	P	85	90	0	70	70	10	100	83.60
	P. villosa	P	23	43	0	43	97	20	46	2.80
	P. australis	A	28	28	0	28	33	28	33	2.45
Liliaceae	*A. mongolicum*	I	0	67	0	67	73	27	67	16.05

Table 3 Correlations of different AM structures and DSE tissues

item	vesicle	arbuscular	total AM	spore density	DSE	microsclerotium
hyphae	0.293	0.257	0.869**	0.076	−0.491*	−0.192
vesicle	–	0.360	0.578**	0.307	0.233	0.491*
arbuscule	–	–	0.270	0.418	−0.035	0.488*
total AM	–	–	–	0.103	−0.376	−0.025
spore density	–	–	–	–	−0.054	0.068
DSE	–	–	–	–	–	0.363

Note: ** means the correlation is significant at $P < 0.01$; * means the correlation is significant at $P < 0.05$.

4 Discussion

AMF plays an important role in plant survival and community stability of vegetation in natural ecosystems (Gange et al., 1993; Francis and Read, 1994; Hartnett and Wilson, 2002; Moraes et al., 2004). It is well known that AMF can improve plant nutrient uptake (Tarafdar and Praveen-Kumar, 1996), water use efficiency (Auge and Stodola, 1990), and resistance to abiotic stress under certain conditions (Brundrett, 1991). The present study indicated that AMF was formed in the roots of various plants in Mu Us Sand Land, which demonstrated that these associations might be one of the valid countermeasures of acclimatizing plants to the arid and infertile environments. Plant community structure and AMF distribution and colonization status might be used to monitor desertification and soil degradation. Several studies on AMF have been conducted in recent years in desert ecosystems (Collier et al., 2003; Ferrol et al., 2004; Alarcón and Cuenca, 2005).

The variation in spore density and colonization of AMF associated with different host plant species may be generated by a variety of potential mechanisms, including biological characteristics of rhizosphere under host species, variation in host species, mycorrhizal dependency, host plant-mediated alteration of the soil microenvironment, or other unknown host plant traits, as described by Lorgio et al. (1999) and Eom et al. (2000). In our present study, no significant correlation was observed between mycelial colonization and spore density. However, some researchers found a positive relationship between AM

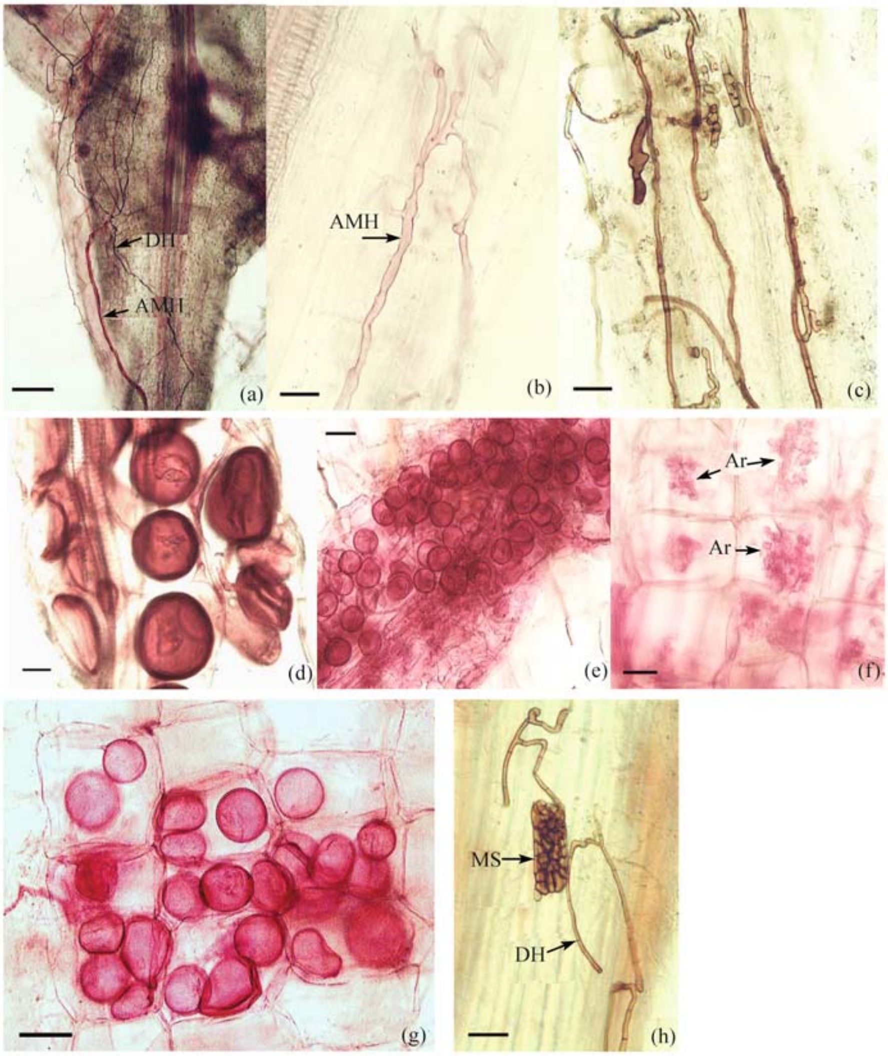

Fig. 2 Colonization by AMF and DSEF in tissues

Note: (a) represents superficial hyphae of AMF (AMH) and DSE (DH) on lateral roots of *H. fruticosum*. (b) represents hyhae of AMF (AMH) through the cell wall in the roots of *A. mongolicum*. (c) represents superficial hyphae of DSE on roots of *G. uralensis*. (d) represents vesicles of AMF in the roots of *O. aciphylla*. (e) represents vesicles of AMF in the roots of *C. korshinskii*. (f) represents arbuscule (Ar) of AMF in the roots of *C. korshinskii*. (g) represents vesicles of AMF in the roots of *C. korshinskii*. (h) represents superficial hyphae of DSE and microsclerotia (MS) on the roots of *P. villosa* ((a), bar = 100 μm ; (b), (c), (d), (e), (f), (g) and (h), bar = 25 μm).

colonization and spore density (Ebbers et al., 1987; Sigüenza et al., 1996), whereas others found a negative relationship (Fontenla et al., 1998).

We found that DSE infected all tested plants and cooccurred with AMF in the plant roots, although the colonization of some species was lower, including *P. sepium* and *S. psammophila*. The results indicated that the common and beneficial species of desert plants could easily form AM and DSEF tissues. Mandyam and Jumpponen (2005) speculated that DSE fungi would be prevalent in various habitats and colonize a substantial proportion of the species present in mixed plant communities. This group of fungi cannot be overlooked while assessing the fungal communities of any ecosystem, as their abundance may equal or even exceed that of the AM fungi. Although different opinions exist regarding whether DSEF should be treated as mycorrhizal fungi or not, there seems to be an agreement that some members play an important role in soil ecosystems in some cases, with DSEF functioning much like mycorrhizal fungi (Jumpponen and Trappe, 1998; Jumpponen, 2001).

In the present study, correlation analysis demonstrated that total colonization was significantly and positively correlated with hyphal and vesicular colonization. This result is due to the mycelium and vesicles, which are the primary structures existing for months or years. Generally, arbuscules begin to form approximately two days after root penetration and begin to collapse after a few days

(Smith, 1995), and the sampling in October lead us to observe only low colonization of arbuscular in *A. ordosica*, *C. intermedia*, *C. microphylla*, and *C. korshinskii*.

The hyphal colonization negatively correlated with the DSE tissue may be AMF competing with DSEF for the econiche. The microsclerotium was positively correlated with vesicular and arbuscular colonization. The microsclerotia of some species of DSE had some special storage substances and may function as propagules (Yu et al., 2001). Therefore, we suggest that the function and growth characteristics of microsclerotium may be similar to the vesicular and arbuscular. In general, the DSEF function and the interaction on AMF are less well known. Our study indicates that the plants in Mu Us Sandy Land may establish a good symbiosis with DSEF, and the symbionts may depend on each other for survival in these extreme environments. Moreover, further studies will be required to elucidate the interactional mechanisms with AMF and the operating mechanisms in desert ecosystems.

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References

Addy H D, Piercey M M, Currah R S (2005). Microfungal endophytes in roots. Can J Bot, 83: 1–13

Ahulu E M, Andoh H, Nonaka M (2007). Host-related variability in arbuscular mycorrhizal fungal structures in roots of *Hedera rhombea*, *Rubus parvifollus* , and *Rosa multiflora* under controlled conditions. Mycorrhiza, 17: 93–101

Alarcón C, Cuenca G (2005). Arbuscular mycorrhizas in coastal sand dunes of the Paraguaná Peninsula, Venezuela. Mycorrhiza, 16(1): 1–9

Allen M F (1983). Formation of vesicular-mycorrhizae in *Atriplex gardneri* (Chenopodiaceae): Seasonal response in a cold desert. Mycologia, 75: 773–776

Auge R M, Stodola A J W (1990). An apparent increase in symplastic water contributes to greater turgor in mycorrhizal roots of droughted Rosa plants. New Phytol, 115: 285–295

Barrow J R (2003). Atypical morphology of dark septate fungal root endophytes of *Bouteloua* in arid southwestern USA rangelands. Mycorrhiza, 13: 239–247

Bearden B N, Petersen L (1999). Influence of arbuscular mycorrhizal fungi on soil structure and aggregate stability of a vertisol. Plant and Soil, 218: 173–183

Brundrett M (1991). Mycorrhizas in natural ecosystems. Advances in Ecological Research, 21: 171–313

Collier S C, Yarnes C T, Herman R P (2003). Mycorrhizal dependency of Chihuahuan Desert plants is influenced by life history strategy and root morphology. Journal of Arid Environments, 55: 223–229

Dalpe Y (1993). Vesicular-arbuscular mycorrhiza. In: Carter M R, ed. Soil Sampling and Methods of Analysis. Raton: Lewis Publishers, 287–301

Department of Geography of Peking University, Commission for Integrated Survey of Natural Resources of Chinese Academy of Sciences, Lanzhou Institute of Desert Research of Chinese Academy of Sciences, Lanzhou Institute of Glacier, Frozen Soil of Chinese Academy of Sciences (1983). Natural Conditions and Its Improvement and Utilization in the Mu Us Sandland. Beijing: Science Press (in Chinese)

Dhillion S S, Zak J C (1993). Microbial dynamics in arid ecosystems: Desertification and the potential role of mycorrhizas. Revista Chilena de Historia Natural, 66: 253–270

Ebbers B C, Anderson R C, Liberta A E (1987). Aspects of the mycorrhizal ecology of prairie dropseed, Sporobolus heterolepis (Poaceae). American Journal of Botany, 74: 564–573

Eom A H, Hartnett D C, Wilson G W T (2000). Host plant species effects on arbuscular mycorrhizal fungal communities in tallgrass prairie. Oecologia, 122: 435–444

Ferrol N, Calvente R, Cano C, Barea J M, Concepción A A (2004). Analysing arbuscular mycorrhizal fungal diversity in shrub-associated resource islands from a desertification threatened semiarid Mediterranean ecosystem. Applied Soil Ecology, 25: 123–133

Fontenla S, Godoy R, Rosso P, Havrylenko M (1998). Root associations in Austrocedrus forests and seasonal dynamics of arbuscular mycorrhizas. Mycorrhiza, 8: 29–33

Francis R, Read D J (1994). The contributions of mycorrhizal fungi to the determination of plant community structure. Plant and Soil, 159: 11–25

Gange A C, Brown V K, Sinclair G S (1993). Vesicular-arbuscular mycorrhizal fungi: a determinantion of plant community structure in early succession. Funct Ecol, 7: 616–622

Hartnett D C, Wilson G W T (2002). The role of mycorrhizas in plant community structure and dynamics: lessons from grasslands. Plant and Soil, 244: 319–331

Jumpponen A, Trappe J M (1998). Dark septate endophytes: a review of facultative biotrophic root-colonizing fungi. New Phytol, 140: 295–310

Jumpponen A (2001). Dark septate endophytes—are they mycorrhizal? Mycorrhiza, 11: 207–211

Lorgio E A, Julio R G, Peter L M (1999). Variation in soil microorganisms and nutrients underneath and outside the canopy of *Adesimia bedwellii* (Papilionaceae) shrubs in arid coastal Chile following drought and above average rainfall. Journal of Arid Environments, 42: 61–70

Mandyam K, Jumpponen A (2005). Seeking the elusive function of the root-colonising dark septate endophytic fungi. Studies in Mycology, 53: 173–189

Moraes R M, Andrade D Z, Bedir E, Dayan F E, Lata H, Khan I (2004). Arbuscular mycorrhiza improves acclimatization and increases lignan content of micropropagated mayapple (*Podophyllum peltatum* L.). Plant Science, 166: 23–29

Olsson P A, Tyler G (2004). Occurrence of non-mycorrhizal plant species in south Swedish rocky habitats is related to exchangeable soil phosphate. Journal of Ecology, 92: 808–815

Postma J W M, Olsson P, Falkengren-Grerup U (2007). Root colonization by arbuscular mycorrhizal, fine endophytic and dark septate fungi across a pH gradient in acid beech forests. Soil Biology & Biochemistry, 39: 400–408

Read D J, Haselwandter K (1981). Observations on the mycorrhizal status of some alpine plant communities. New Phytol, 88: 341–352

Sigüenza C, Espejel I, Allen E B (1996). Seasonality of mycorrhizae in coastal sand dunes of Baja California. Mycorrhiza, 6: 151–157

Skujins J, Allen M F (1986). Use of mycorrhizae for land rehabilitation. Mircen J Appl Microbiol Biotechnol, 2: 161–176

Smith F A, Smith S E (1997). Structural diversity in vesicular-arbuscular mycorrhizal symbioses. New Phytol, 137: 373–388

Smith S E (1995). Discoveries, discussions and directions in research on mycorrhizae. In: Varma A, Hock B, eds. Mycorrhiza, Structure, Function, Molecular Biology and Biotechnology. Berlin: Springer-Verlag, 324

Sylvia D M, Williams S E (1992). Vesicular arbuscular mycorrhizae and environmental stress. ASA Special Publication, 54: 101–124

Tarafdar J C, Praveen-Kumar (1996). The role of vesicular arbuscular mycorrhizal fungi on crop, tree and grasses grown in an arid environment. Journal of Arid Environments, 34: 197–203

Yu T, Nassuth A, Peterson R L (2001). Characterization of the interaction between the dark septate fungus *Phialocephala fortinii* and *Asparagus officinalis* roots. Can J Microbiol, 47: 741–753