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Effect of arbuscular mycorrhizal colonization on ecological functional traits of ephemerals in the Gurbantonggut desert

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Abstract

The spring ephemerals are distinct and important flora in the Gurbantonggut desert, in central Asia and northwestern China. In order to understand the role of arbuscular mycorrhizal (AM) fungi on growth of ephemerals, a pot experiment was conducted in greenhouse conditions. Two desert ephemerals, *Erodium oxyrrhynchum* and *Plantago minuta*, were tested for their response to inoculation with two AM fungi, BEG 167 (*Glomus mosseae*) and BEG 141 (*Glomus intraradices*). The results showed that mycorrhizal colonization led to marked improvement in both the reproductive (timing of flowering and number of seeds) and vegetative (dry matter) phase of the two ephemeral plants. Dry weight per plant inoculated with AM fungi was 57 to 67 percent higher than the control in *E. oxyrrhynchum* and 8 to 11 times higher than the control in *P. minuta*. Anthesis was advanced by 14 to 17d in *P. minuta* and 5 to 7d in *E. oxyrrhynchum*, respectively, when both plants were inoculated with AM fungi. Colonization of mycorrhizal fungi significantly increased the total number of seeds or fruits per plant. Water use efficiency and photosynthetic rates were significantly higher in inoculated *E. oxyrrhynchum* plants than those of non-inoculated plants. These results indicate that although the two spring ephemerals were able to finish their life cycle without AM fungi, the fungi might greatly enhance survival and population expansion by advancing the timing of flowering and by increasing seed production in the desert environment in the spring.

Keywords: Spring ephemeral, arbuscular mycorrhizal fungi, Dzungar Basin, Xinjiang, ephemeral, anthesis, reproductive growth

1. Introduction

Ephemeral plants form significant synusiae in arid desert ecosystems with typical characteristics of early germination and rapid development during the vegetative growth stage. Ephemerals are widely distributed in arid desert areas, both in arid woodland and open deserts (Robinson, 2004). We use the term "ephemerals" here to include both annual and perennial species with a very short period of growth aboveground in desert. Such ephemerals are present in the Gurbantonggut desert in western and central Asia (Mao and Zhang, 1994). The plants play a very important role in stabilizing the surface of sand dunes (Wang et al., 2005) and in decreasing the intensity as well as occurrence frequency of sandstorms because the development of ephemeral synusiae coincides with occurrence of sand storms in April to June in the Gurbantonggut desert (Wang et al., 2004).

Plants growing in sandy deserts can survive by various strategies, including specialized morphological and physiological adaptation (Mulroy and Rundel, 1977; Fox, 1989). Many kinds of ephemeral plants are adapted to the desert environment. They remain dormant until a rare rainfall event or snowmelt occurs in early spring, resume rapid growth rates with the help of high resource use efficiency, and flower and produce seeds before the summer dry season. The period of active growth for spring ephemeral plants coincides with the period of high availability of soil water between snow melting in early spring and soil moisture deficits in early summer.

Arbuscular mycorrhizas of desert plants have been the subject of a number of studies in recent years (O'Connor et al., 2001; Titus et al., 2002; Collier et al., 2003; Ferrol et al., 2004); desertification reduces the diversity and inoculum potential of AM fungi (Jasper et al., 1991). Many plant families in arid regions have been found to form AM associations (Trappe, 1981). AM symbiosis contributes to greater P uptake in mycorrhizal plants and better soil aggregate formation in mycorrhizal soil, which is of particular importance in the reclamation of desertified

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ecosystems (Azcón and Barea, 1997; Caravaca et al., 2002; Herrera et al., 1993; Medina et al., 2004; Requena et al., 1996). AM fungi may also stabilize the soil by promoting formation of soil aggregates and enhance plant growth by alleviating drought stress (Carrillo-Garcia et al., 1999; Augé, 2001; Rillig, 2004; Valentine et al., 2006).

Several studies have shown that ephemerals can form arbuscular mycorrhiza (AM). For example, the proportions of root length colonized by AM fungi on the ephemerals *Hyacinthoides non-scripta* and *Erythronium americanum* were up to 65 and 75% in sugar maple forests (DeMars, 1996) and Brundrett and Kendrick (1988) found that the ephemerals *E. americanum* and *Allium tricoccum* can form AM associations, with root colonization rates of 86 and 83%, respectively. However, these studies were carried out in deciduous forests. Recently, Shi et al. (2006) investigated the arbuscular mycorrhizal (AM) status of 73 spring ephemeral plants that grow in Gurbantonggut desert ecosystem, and 89% of those were colonized by AM fungi. However, little information is available on the role of AM fungi in the development and growth of ephemerals in desert ecosystems, and the significance of the interaction between AM fungi and ephemeral plants in desert ecosystems is still less understood.

An earlier study showed that the content of available phosphorus and soil organic matter in Gurbantunggut are only 1.58 mg/kg and 1.2 g/kg. Soil moisture content in topsoil (30 cm) in April is 2% to 5%, while in May it sharply declines to 0.8% to 1.2% (Wang et al., 2004). Why desert ephemeral plant species that finish their life span (even if only aboveground) in such short periods of time sacrifice their valuable carbohydrates to the associated fungi is an interesting question. We hypothesized that formation of a symbiotic association with AM fungi would enhance survival of ephemerals in Gurbantonggut desert by improving functional traits, e.g. acquiring more water and nutrients from desert soil, advancing the time of anthesis and producing more seed. To test this hypothesis, the effect of inoculation with mycorrhizal fungi on the timing of flowering, seed production, photosynthesis, water use efficiency and nutrition uptake of two spring ephemerals, *Plantago minuta* and *Erodium oxyrrhynchum*, were investigated under controlled conditions.

2. Materials and Methods

Pot experiment under controlling condition

The soil used was a typical sandy soil of low nutrient status with the following physico-chemical properties (dry matter basis): pH (in H_2O) 8.19, organic matter 0.35%, Kjeldahl-N 0.02%, Olsen-P (0.5 mol l^{-1} $NaHCO_3$-extractable) 7.75 mg kg^{-1}, and exchangeable K (1 mol l^{-1} NH_4OAc) 39.0 mg kg^{-1}. The soil was sterilized by autoclaving at 120°C for 2 h and then air-dried. 1070 g of soil was placed into a 19×14×16 cm plastic pot.

Two ephemeral plants, *Plantago minuta* and *Erodium oxyrrhynchum*, were used as host plants. Seeds of both plants were collected from the Gurbantonggut desert (N44°32.407' E88°16.779') in Northwestern China in 2004, and dry seeds were stored in a refrigerator at <4°C before being used. The seeds were pre-incubated on moist filter paper for 48 h until the radicles appeared. Ten uniform seeds were sown per pot, and seedlings were thinned to five for of *P. minuta* and two for *E. oxyrrhynchum*, respectively after emergence.

The AM fungi, *Glomus mosseae* (BEG167) and *Glomus intraradices* (BEG 141), were propagated on maize. The mycorrhizal inoculum consisted of spore, mycelium and colonized root segments of both fungal species. Each pot was inoculated with 60 g inoculum for the mycorrhizal treatments or 60 g autoclaved sterilized inoculum with 10 ml filtrates free from mycorrhizal propagules from the inoculum for the non-mycorrhizal treatments. *G. mosseae* was originally isolated from *Allium deserticolum* growing in a saline habitat in the Dzungaria Basin (N42°39' E80°20'), which is close to Gurbantonggut desert. The isolate was selected as an efficient one for improving the growth of plant under salinity stress (Wang et al., 1994; Tian et al., 2004). *G. intraradices* was originally isolated from *Allium cepa* in temperate agricultural biome in France (http://www.kent.ac.uk/bio/beg/englishhomepage.htm).

Experimental design

The experiment was a randomized block factorial design with mycorrhizal colonization (inoculated or uninoculated) and two plant species. Each treatment was replicated eight times. The plants were grown in late January to early May in a glasshouse with 5 hours supplementary light every day in the afternoon and evening. The temperature in January and February was approximately 5–20°C and 10–30°C from March to May. Soil moisture was maintained at 10% by weighing pots daily.

Photosynthetic rate, transpiration rate, stomatal conductance were measured using a portable infrared gas exchange system with a leaf chamber type (Li-6400, USA) in an open-system configuration. The third leaf from the top was used to measure these parameters. Water use efficiency (WUE) was calculated as the ratio between photosynthetic rate and transpiration rate. Photosynthesis was measured in a fine day from 09:00 to 11:00 o'clock when the plant was eight weeks old.

Phenological status of the plants was recorded each day. Plants were harvested when they produced seeds and were senescent. The total number of seed or fruit per plant of *Plantago minuta* and *Erodium oxyrrhynchum* were counted at harvest. Shoots and roots were separated and the oven dried (70°C for 48 h) prior to recording dry weights. Mycorrhizal dependency was calculated using the following formula (Menge et al., 1978):

$$\text{Mycorrhizal dependency (\%)} = \frac{\text{Total biomass of mycorrhizal plant} \times 100}{\text{Total biomass of non-mycorrhizal plant}}$$

Fresh roots (ca. 0.3 g) were washed free of soil and cleared in 10% (w/v) KOH at 90°C in a water bath for 20–30 min and stained with acid fuchsin (0.5% w/v) (Biermann and Linderman, 1981). Thirty root fragments (ca. 1 cm long) were mounted on slides in polyvinyl alcohol-lactic acid-glycerol (Koske and Tessier, 1983) and examined at ×100 to 400 magnifications using an Olympus BX50 microscope equipped with an automatic photomicrographic system for the presence of AM fungal structures. The proportion of root length colonized was calculated according to the method of Trouvelot et al. (1986).

The samples were ground and dry-ashed in a muffle furnace at 300°C for 3 h and at 550°C for 5 h. The ash was dissolved in 2% (v/v) HCl. Phosphorus was determined by inductively coupled plasma-atomic emission spectroscopy (ICP-AES; Perkin Elmer Optima 3300DV).

Data analysis

All data were analyzed by One-way ANOVA using SAS software version 6.12. (Version 6.12; SAS Institute, Cary, NC). Critical differences at the 5% level of significance were tested using (LSD) test.

3. Results

Colonization of different AM fungi on the two ephemeral plants

Microscope assessment confirmed that all plants of the non-inoculation treatment were not colonized by mycorrhizal fungi. *E. oxyrrhynchum* had a mean percentage colonization of 40% and 41% when inoculated with *G. intraradices* and *G. mosseae*, respectively. *P. minuta* inoculated with *G. intraradices* and *G. mosseae* had the percentage colonization of 55% and 60%, respectively (Table 1). There were no significant differences in colonization rates between *G. mosseae* and *G. intraradices* within both plant species (Table 1).

The growth and P uptake of the two ephemeral plants inoculated with or without AM fungi

Inoculation of AM fungi improved the growth of both plants. Shoot biomass of inoculated *P. minuta* plants were 5.18 to 5.25 times higher, and inoculated *E. oxyrrhynchum* were 1.8 to 2.14 times higher than the control plants (Table 1). The seed number per plant was significantly higher in inoculated treatments of both plants than those of control. Mycorrhizal dependency of *P. minuta* was higher than *E. oxyrrhynchum*, but there was no significant difference between the two AM fungi in growth benefit of both plants species (Table 1).

Mycorrhizal colonization improved the P status of *P. minuta* and *E. oxyrrhynchum* (Table 2). Shoot P concentration in mycorrhizal *P. minuta* was 68% higher in *G. mosseae* treatment comparing to non-mycorrhizal plants. The P concentration in shoots of *E. oxyrrhynchum* was increased by 34.48% and 14.94% when it was associated with *G. mosseae* or *G. intraradices*, respectively. The amount of P uptake differed among the treatments: the plants colonized by *G. mosseae* showed significantly higher P uptake than that of the plants colonized by *G. intraradices* (Table 2).

Effects of AM fungi on the timing of flowering of the two ephemerals

AM fungal colonization increased photosynthetic activity and water use-efficiency (WUE) of *E. oxyrrhynchum* (Table 3). Comparing to control, colonization of *G. mosseae* and *G. intraradices* significantly increased water use efficiency (Table 3). Stomatal conductance and transpiration rate were also increased by AM fungi. Comparing with BEG 141, the plants colonized by *G. mosseae* had higher photosynthetic rates (Table 3).

AMF colonization altered the timing of flowering of both ephemerals (Fig. 1). In comparison with non-inoculated *P. minuta* plants, the flowering of plants inoculated with *G. mosseae* and *G. intraradices* took place 17 and 14 days in advance, respectively (Fig. 1). *E. oxyrrhynchum* colonized by *G. mosseae* or *G. intraradices* flowered 7 and 5 days earlier, respectively, than those of non-inoculated plants (Fig. 1). The seed numbers in *E. oxyrrhynchum* or fruits of *P. minuta* were significantly increased by colonization of both AM fungal species (Table 1).

4. Discussion

The most distinct features of desert habitats are drought and nutrient poor soils. It has been reported that desert ephemerals evolve distinct strategies to survive in extreme environments (Robinson, 2004). Gutterman (1993) found that some desert plants form mucilaginous diaspores on the seed surface to absorb water for germination. Lambers and Shane (2006) reported that some plants form cluster or

Table 1. Mean proportion of root length colonized (%), shoot dry weight (g), root dry weight (g), mycorrhiza dependency and seed production per plant of *E. oxyrrhynchum* and *P. minuta* inoculated with or without AM fungi, *G. intraradices* or *G. mosseae*.

	Inoculation treatment	Colonization rate (%)	Shoot dry weight (g pot^{-1})	Root dry weight (g pot^{-1})	Mycorrhiza dependency	No. of seed or fruit per plant*
E. oxyrrhynchum	Control	0 b	1.02 b	0.33 b	0	45 b
	G. mosseae	40 a	2.18 a	0.81 b	222	75 a
	G. intraradices	41 a	1.84 a	0.62 a	182	70 a
P. minuta	Control	0 b	0.28 b	0.17 b	0	1 b
	G. mosseae	60 a	1.45 a	0.97 a	538	12 a
	G. intraradices	55 a	1.47 a	0.88 a	522	9 a

*To show seed production we used seed number per plant for *E. oxyrrhynchum* and fruit number per plant for *P. minuta*. Different letters following the data in one column mean significant difference at the 5% level.

Table 2. P concentration, P uptake and P utilization rate of *E. oxyrrhynchum* and *P. minuta* inoculated with or without AM fungi, *G. mosseae* or *G. intraradices*.

Inoculation treatment	P concentration (mg.g^{-1})				P uptake (mg.pot^{-1})				P utilization rate (g.mg.P^{-1})	
	P. minuta		*E. oxyrrhynchum*		*P. minuta*		*E. oxyrrhynchum*		*P. minuta*	*E. oxyrrhynchum*
	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Shoot
Control	0.66 b	0.82 c	0.87 b	0.48 a	0.18 c	0.14 b	0.89 c	0.16 b	1.52 a	1.15 a
G. mosseae	1.11 a	1.40 a	1.17 a	0.59 a	1.61 a	1.35 a	2.56 a	0.48 a	0.90 c	0.86 b
G. intraradices	0.77 b	1.04 b	1.00 ab	0.66 a	1.13 b	0.92 a	1.80 b	0.39 a	1.30 b	1.0 ab

Different letters following the data in one column mean significant difference at the 5% level.

Table 3. Photosynthetic rate, stomatal conductance, transpiration rate and water use efficiency of *E. oxyrrhynchum* inoculated with or without AM fungi, *G. mosseae* or *G. intraradices*.

Inoculation treatment	Photosynthetic rate (μmol/m^2/s)	Stomatal conductance (mol H_2O/m^2/s)	Transpiration rate (mmol/m^2/s)	Water use efficiency (μmol CO_2/mmol H_2O)
Control	13.88 c	0.20 b	7.46 b	1.93 b
G, mosseae	31.29 a	0.65 a	12.66 a	2.51 a
G. intraradices	24.21 b	0.58 a	10.09 ab	2.42 a

Different letters following the data in one column mean significant difference at the 5% level.

dauciform roots which can release large amounts of carboxylates to mobilize insoluble phosphorus from soil; the ephemerals have high photosynthetic efficiency and grow fast when the environmental conditions are favourable (Li and Tang, 2006).

Several studies have shown that desert ephemerals can form AM association (Brundrett and Kendrick, 1988; Shi et al., 2006). AM fungi play a key role in improving plant survival and maintaining the succession of individual population. Moreover, AM fungi have strong effects on plant diversity and plant community structure (van der Heijden et al., 1998; O'Connor et al., 2002). However, the effects of AM fungi on growth and survival of desert ephemerals are still poorly documented.

As expected, both ephemerals showed a high mycorrhizal dependency in this study, and inoculating with AM fungi enhanced their shoot or root growth and seed productivity (Table 1). The timing of flowering of both

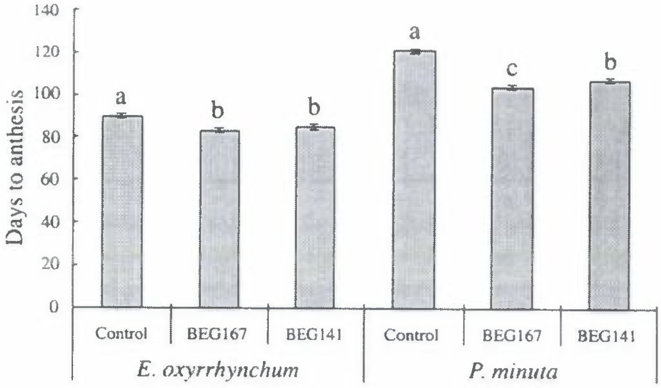

Figure 1. Days from sowing to anthesis of the *E. oxyrrhynchum* and *P. minuta* inoculated with or without AM fungi, *G. mosseae* or *G. intraradices*. Error bars represent ± SD. Different letters indicate significant difference ($p<0.05$) between treatments.

ephemerals was advanced. These may be attributed to improved P content, water efficiency and photosynthetic rate (Tables 2 and 3). Our recent field inoculation trial showed that mycorrhizal colonization of *E. oxyrrhynchum* was significantly increased from 25.84% (non-inoculating plots) to 44.38% (inoculating plots), and aboveground biomass of *E. oxyrrhynchum* in plots inoculated with *G. mosseae* was significantly increased by 163% compared to the control plots (Shi, 2006). These results support our hypothesis that colonization of AM fungi alters functional traits of the desert ephemerals and therefore enhances their survival in the extremely dry and poor edaphic environment.

In desert systems, water is always the most important ecological factor for plant survival. Maintaining high water use efficiency is one of the most important features of plants in deserts. In late May and early June, water content in the top soil in Gurbantonggut desert is only 0.8%–1.2% (Wang et al., 2004). No plant can escape drought stress in such a habitat. It is reported that aquaporins in virtually all living organisms, are membrane intrinsic proteins that form water-permeable complexes (Uehlein et al., 2003). Some studies have demonstrated that enhanced symplastic water transport via the plasma membrane aquaporin NtAQP1 is important for the efficiency of AM symbiosis, at least under drought stress conditions (Siefritz et al., 2002; Porcel, 2005). AM fungi can upregulate gene expression of tonoplast-located aquaporins parsley and in alfalfa (Roussel et al., 1997; Krajinski et al., 2000). Siefritz et al. (2004) reported that increase in transpiration, photosynthetic activity and stomatal conductance of mycorrhizal plants was related to upregulating of NtAQP1. Our present results indicate that mycorrhizas improved water use efficiency, stomatal conductance and transpiration rate of the desert ephemeral, *E. oxyrrhynchum*, which might be connected with the express of AQP. Further research on plant AQP would provide new avenues for the research into ephemerals.

Flowering, the switch from vegetative to reproductive growth, is a key developmental change in the life cycle of plant (Simpson and Dean, 2002). Earlier flowering implies earlier activity in metabolic processes (e.g. leaf expansion, root growth, nutrient uptake etc.) that are important for niche differentiation among coexisting species (Veresoglou and Fitter, 1984; McKane et al., 1990), and will alter competitive interactions between species. Many researches indicate that AM fungi induce advanced flowering and produced significantly greater number of flowers or seeds in seasonal ornamental plants or vegetables, such as *Petunia hybrida*, *Callistephus chinensis*, *Impatiens balsamina* (Gaur, 2000) and *Freesia hybrid* (Scagel, 2003), cucumber (Trimble, 1995; Chen, 1996), *Chamerion angustifolium* (Wolfe, 2005), *Pelargonium hortorum* (Nowak, 2004). In the Gurbantonggut desert, the highest temperature can reach more than 40°C in May, which accelerates drying of soil and sharply reduces moisture to less than 2% in the top 20 cm soil layer (Wang et al., 2004). Therefore earlier maturation may help the plant to reduce the risk from drought, and higher seed production may benefit regeneration. It seems, from our results, that AM fungi play a role as support systems for offspring succession of desert ephemerals by regulating the processes of vegetation growth and reproductive growth.

Flowering is controlled by both environmental and developmental signals. In this study, the mechanisms by which AM fungi stimulated early flowering were probably involved in (1) improving phosphorus state of the ephemerals. Similar results have been found in several species of plants by other researchers (Lu et al., 1994; Gaura, 2000); (2) Promoting the accumulation of carbohydrates in storage organs. It suggested that certain amount of carbohydrate is needed for a plant to transfer from vegetative growth to reproductive growth (Lapointe, 2001). AM fungi enhanced photosynthetic rate of the ephemerals, which would speed up carbohydrate accumulation of plant and further shorten the growing periods.

In summary, our work demonstrates a significant effect of AM fungal colonization on anthesis and seed production of desert ephemerals, a group that is poorly understood. Such symbiotic associations are ecologically crucial in guaranteeing that the ephemerals escape from the quick decline of soil moisture and to help the plant to maximum resource use efficiency and seed production by regulating the processes of vegetative and reproductive growth of the ephemerals. However, further research is needed to determine the mechanisms by which AMF alter plant ecophysiology and hence timing of flowering and water use in the ephemeral plants.

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