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ORIGINAL ARTICLE

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Occurrence and distribution of arbuscular mycorrhizal fungal species in three types of grassland community of the Tibetan Plateau

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Abstract Arbuscular mycorrhizal (AM) fungal spore communities and distribution patterns were surveyed in montane scrub grassland, alpine steppe, and alpine meadow sites at altitudes ranging from 3,500 to 5,200 m a.s.l. on the Tibetan Plateau. Thirty-two representative soil samples were collected from the root zone of the dominant and common plant species in late May 2004. Twenty-three AM fungal species representing six genera (*Acaulospora*, *Entrophospora*, *Glomus*, *Pacispora*, *Paraglomus*, and *Scutellospora*) were detected and species richness varied from 5.3 ± 0.8 to 10.5 ± 2.5 per site. Some AM fungal species were restricted to one vegetation type and *Glomus mosseae*, *Glomus intraradices*, and *Scutellospora calospora* were detected in all three vegetation types. *Glomus* species were found to be the most frequent and abundant in all three vegetation types. *Acaulospora* occurred mostly in the alpine steppe and alpine meadow. *Scutellospora* occurred mostly in montane scrub grassland. At the species level, *Glomus mosseae* was dominant in the montane scrub, *Acaulospora laevis* and *Pacispora scintillans* were dominant in the alpine steppe, and *Acaulospora laevis*, *Pacispora scintillans*, and *Glomus claroideum* dominated the alpine meadow. It was evident from the distribution pattern of AM fungi in the different vegetation types that the abundance and diversity of AM fungal species were lowest in the montane scrub grassland than the other two plant communities. Climatic conditions, especially temperatures, and intensity of land use may be the most important factors influencing the AM fungal community.

Keywords Arbuscular mycorrhiza · Tibet · Vegetation types · Spore community · Distribution

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Introduction

Arbuscular mycorrhizal (AM) fungi are important components of terrestrial ecosystems (Smith and Read 2008) and are ubiquitous in many herbaceous plant communities (Allen et al. 1995; Kennedy et al. 2005). AM associations are of great interest because of their potential influence on ecosystem processes, their role in determining plant diversity in natural communities, and the capacity of AM fungi to induce a wide variety of growth responses in coexisting plant species. Because the growth responses are not equal among different plant–fungal species combinations, the diversity and species composition of plant communities may also exert a reciprocal influence on associated mycorrhizal fungi (Bever 2002). Host plant species in grassland ecosystems may have an important role in determining the development and sporulation of AM fungi and patterns of fungal species composition and diversity (Eom et al. 2000; Kernaghan 2004).

Tibet is the largest and highest plateau in the world with an average altitude of 4,500 m a.s.l. The terrain ranges from desert to wetland and includes important grassland areas. Under the prevailing extreme environmental conditions, grassland is very important for the Tibetan way of life. Tibet is one of the five most important pastoral areas in China, with 82.1 million ha of grassland representing about 21% of the total natural grassland in the country and 68% of the total land area of Tibet. According to the first national survey of grassland resources, the range of grassland communities in Tibet ranks first among all Chinese provinces and autonomous regions, having 17 of the 18 types of grassland recognized in the country. Of these, alpine steppe is the most important vegetation type on the Qinghai-Tibet Plateau, representing about 35.3% of the total Tibetan grassland area. Alpine meadow is also important, occupying about 16% of the total grassland area of Tibet. Montane scrub grassland occupies about 2% of the total grassland area and is also important in Tibetan agriculture.

There are few reports on AM fungal communities at high altitudes. Most studies have focused on mycorrhizal colonization (Fisher and Fule 2004; Gehring et al. 2006), with few addressing the diversity of AM fungi (Chaurasia et al. 2005). Spore populations have been found belonging to five genera, namely *Acaulospora*, *Glomus*, *Gigaspora*, *Sclerocystis* and *Scutellispora*. The genus *Glomus* was found to be dominant in the rhizosphere soil samples of all the rhododendron species investigated by Chaurasia et al. (2005) in the Kumaun region of the Indian central Himalaya and the most frequent and abundant species was found to be *G. fasciculatum*. Up to now there have been no published reports on the distribution patterns of AM fungi in the grasslands of Tibet. We therefore conducted a survey of the spore distribution of AM fungal species in three typical grassland types occurring at different altitudes in Tibet.

Materials and methods

Study sites

The investigation was conducted in the central grassland of Tibet. Two regions, the plateau lake-basin area in the northeast and the middle reaches of the Brahmaputra River in the south, were included in the study (29°–33°N, 90°–93°E). Three grassland types, montane scrub grassland, alpine steppe, and alpine meadow, which were distributed from south to north (3,500 to 5,200 m a.s.l.) were chosen as the study sites. The climate of the sampling areas varies from a semi-arid type of temperate climate to alpine plateau climate. Information on climatic and soil conditions in the three grassland communities is shown in Table 1.

The montane scrub grassland in this study was located at the middle reaches of the Brahmaputra River at altitudes ranging from 3,500 to 4,100 m a.s.l. The grass canopy height of the plant communities is 30–150 cm (shrubs) and 15–60 cm (herbage). Total vegetation cover of the montane scrub grassland ranges from 30 to 50%. *Sophora moorcroftiana* is the dominant shrub species and *Pennisetum centrasiaticum* is the dominant herbaceous plant species.

The alpine steppe is located on the Qiangtan High Plateau at altitudes ranging from 3,500 to 4,100 m a.s.l. The grass canopy height of the plant communities is 25–30 cm (shrubs) and 10–25 cm (herbage) and total vegetation cover is 15–50%. *Stipa purpurea* and *Carex moorcroftii* are the dominant plant species in the alpine steppe.

The alpine meadow is located in the northeast of Tibet at altitudes ranging from 4,500 to 5,200 m a.s.l. The grass canopy height is 3–8 cm, and total plant cover is 70–90%. Plant communities are composed of perennial herbage, mainly *Kobresia* species, with *Kobresia pygmaea* the dominant plant.

Sample collection

Two to three sampling sites were selected within each vegetation type (Fig. 1). Soil samples were collected from the root zones of the dominant and common plant

Table 1 Description of the sampling sites in the three grassland vegetation types

Vegetation type	Montane scrub grassland	Alpine steppe	Alpine meadow
Location	90°47′–91°76′E 29°18′–29°59′N	91°12′-92°14E 30°41′–32°52N	90°34′–92°03′E 31°35–32°42′N
Number of sampling sites	3	2	3
Elevation (m a.s.l.)	3,500–4,100	4,500–4,900	4,500–5,200
Annual average temperature (°C)	4–12	−4 to 0	−6 to −2
Cumulative temperature ≥ 0°C (°C)	3,000–6,000	< 500	< 1,500
Annual precipitation (mm)	300–500	150–300	400–500
Moisture coefficient *k*	0.25–0.5	0.25–0.5	0.5–1.0
Associated plants	*Agrostis hugoniana, Festuca rubra, Imperata cylindrica, Pennisetum centrasiaticum, Poa annua, Salsola nepalensis, Sophora moorcroftiana*	*Artemisia wellbyi, Carex moorcroftii, Festuca rubra, Kobresia parva, Stipa purpurea, Orinus thoroldii, Poa alpina, Poa pratensis, Poa oreali-tibetica*	*Carex moorcroftii, Cyperus cuspidatus, Kobresia humilis, Kobresia littledalei, Kobresia parva, Kobresia prainii, Kobresia pygmaea, Kobresia tibetica*
Soil pH (in water)	8.1 ± 0.2	8.4 ± 0.2	7.4 ± 0.2
Soil organic matter (g kg^{-1})	4.5 ± 0.9	2.0 ± 0.4	20.2 ± 6.3
Soil olsen-P (mg kg^{-1})	45.9 ± 9.4	11.5 ± 2.3	9.5 ± 1.7

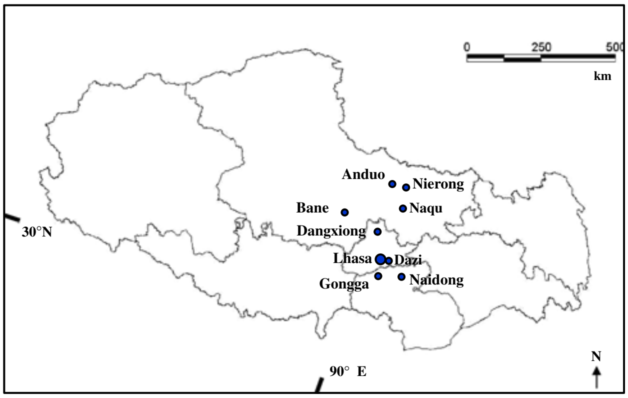

Fig. 1 Map of Tibet showing Lhasa and the sampling zones of the three vegetation types in central Tibet. The montane scrub grassland occurred at Dazi, Gongga, and Naidong counties, the alpine steppe at Bange and Anduo, and the alpine meadow at Dangxiong, Naqu, and Nierong counties

species to a depth of 20 cm at 10 different locations in each sampling area. Soil samples from a particular area were combined and mixed to give a composite sample of about 2 kg. A total of eight composite soil samples were collected from the alpine steppe community, 12 composite soil samples from the montane scrub grassland, and 12 composite soil samples from the alpine meadow in late May 2004. Soil pH (1:2.5 soil/water), available P (Olsen and Sommers 1982) and organic matter content were determined.

Establishment of trap cultures

Trap cultures were established from fresh soil samples mixed with autoclaved sand in a ratio of 2:1. A 2-kg aliquot of the mixture was placed in each pot to produce trap culture from each sample. Clover (*Trifolium repens* L.) and sorghum (*Sorghum vulgare* Pers.) were used as host plants. Trap cultures in 32 pots were grown in a glasshouse for 5 months and then harvested.

AMF spore extraction and identification

Spores and sporocarps were extracted from 100 g air-dried sub-samples of each soil sample in triplicate by wet sieving followed by flotation–centrifugation in 50% sucrose (Dalpé 1993). The finest sieve used was 38 μm. AM fungal spores were counted on a grid-patterned dish under a binocular stereomicroscope.

Spores of AM fungi isolated from the field soil and from trap cultures were mounted on glass slides in polyvinyl-lactoglycerol (PVLG) or PVLG + Melzer's reagent (1:1, v/v). Spores were examined microscopically and identified according to taxonomic criteria (Schenck and Péréz 1990) and using information from the INVAM Web site on the Internet (http//:invam.caf.wvu.edu) and Web page of Arthur Schüßler about glomeromycota phylogeny and taxonomy on the Internet (http://www.lrz-muenchen.de/~schuessler/amphylo/). Data from field soil and trap cultures were combined to determine species composition.

Data analysis

Spore density, richness, frequency, and relative abundance were based on spores recovered directly from the soils. The ecological parameters were calculated as follows. Spore density (SD) was expressed as numbers of AM fungal spores in 100 g dried field soil. Relative abundance (RA) was defined as percentage of number of spores of a given species or genus from the total number of spores produced in the field soil. Frequency (F) was calculated as the percentage of samples from which the particular species or genus was isolated. The dominant species were determined by the importance value (I), which is the average of species frequency and relative abundance of a particular species. Dominance was measured by the Berger and Parker index, which is the total number of individuals of all species divided by the number of individuals in the most common species (Southwood 1968). Species richness (SR) is defined as the number of AM fungal taxa found in a particular site. Species diversity was calculated by the Shannon index (Krebs 1989).

Results

Twenty-three AM fungal species representing six genera were detected across the three vegetation types (Table 2). Three species were from the genus *Acaulospora,* 13 were from *Glomus*, four from *Scutellospora*, one from *Entrophospora*, one from *Paraglomus*, and one from *Pacispora*. One undescribed species could only be identified to the genus level. Seven of the AM fungal species detected (30.4%) formed ornamented spores.

AM fungal species composition differed slightly among the three vegetation types. Ten species were discovered from montane scrub grassland, while 16 species were from alpine steppe and 13 species from alpine meadow. Only *Glomus mosseae*, *Glomus intraradices*, and *Scutellospora calospora* were detected in all three plant communities. Ten species (43.5%) were detected in two of the vegetation types and nine species (39.1%) were restricted to one vegetation type (Table 2). It was evident from the spore density, species richness, and diversity indices of AM fungi that the abundance and diversity of AM fungal species were lowest in the montane scrub grassland (Table 3).

Rhizosphere soil from Tibetan grassland appeared to be dominated by spores of *Glomus,* which occurred most frequently and abundantly in the three vegetation types examined. The genera *Acaulospora* and *Pacispora* were in the second rank (Table 4).

The dominant species also differed among the three vegetation types (Table 5). *Glomus mosseae* was the

Table 2 Occurrence of AM fungal species in the three vegetation types studied in Tibet

Species	Montane scrub grassland	Alpine steppe	Alpine meadow
Acaulospora laevis Gerd. and Trappe	–	+	+
Acaulospora scrobiculata Trappe	+	–	+
Acaulospora spinosa Walker and Trappe	–	–	+
Entrophospora infrequens (Hall) Ames and Schneid	+	–	–
Glomus aggregatum Schenck and Smith	–	+	–
Glomus claroideum Schenck and Smith emend Walker and Vestberg	–	+	+
Glomus convolutum Gerd. and Trappe	–	–	+
Glomus diaphanum Morton and Walker	–	+	–
Glomus etunicatum Becker and Gerd.	+	+	–
Glomus geosporum (Nicolson and Gerd.) Walker	+	+	–
Glomus intraradices Schenck and Smith	+	+	+
Glomus manihotis Howeler, Sieverd. and Schenck	–	+	+
Glomus mosseae (Nicolson and Gerd.) Gerd. and Trappe	+	+	+
Glomus rubiforme (Gerd. and Trappe) Almeida and Schenck	+	–	–
Glomus verruculosum Błaszk.	–	+	+
Glomus versiforme (Karst.) Berch	–	+	–
Glomus sp1	–	+	+
Pacispora scintillans (Błaszk.) Oehl and Sieverd.	–	+	+
Paraglomus occultum (Walker) Morton and Redecker	–	+	+
Scutellospora calospora (Nicolson and Gerd.) Walker and Sanders	+	+	+
Scutellospora pellucida (Nicolson and Schenck) Walker and Sanders	+	–	–
Scutellospora persica (Koske and Walker) Walker and Sanders	+	–	–
Scutellospora verrucosa (Koske and Walker) Walker and Sanders	–	+	–

+, AM fungus found; –, AM fungus not found

Table 3 Species richness and spore density (mean ± SE) and diversity indices of AM fungi in the three vegetation types

Parameter	Montane scrub grassland	Alpine steppe	Alpine meadow
Species richness	5.3 ± 0.8	10.5 ± 2.5	7.7 ± 1.8
Spores per 100 g soil	120.5 ± 36.0	175.5 ± 32.5	259.0 ± 38.5
Shannon index	1.47 ± 0.1	2.10 ± 0.2	2.01 ± 0.1

Table 4 Frequency and relative abundance of spores of genera of AM fungi in the three grassland plant communities in Tibet

AM fungus	Relative abundance (%)	Frequency (%)
Acaulospora	18.7	16.9
Entrophospora	0.9	1.2
Glomus	52.0	61.4
Paraglomus	9.6	3.6
Pacispora	16.7	9.6
Scutellospora	2.2	7.2

Table 5 Importance values of the dominant AM fungal species in the three vegetation types (I ≥ 0.25)

Montane scrub grassland	Alpine steppe	Alpine meadow
Glomus mosseae (0.703)	*Acaulospora laevis* (0.371)	*Pacispora scintillans* (0.269)
	Pacispora scintillans (0.340)	*Acaulospora laevis* (0.259)
		Glomus claroideum (0.256)

most abundant and common species found in the montane scrub grassland. *Acaulospora laevis* and *Pacispora scintillans* were the dominant species in both alpine steppe and alpine meadow and *Glomus claroideum* was another dominant species in the alpine meadow community.

AM fungal species were not evenly distributed among the three different vegetation types. *Glomus* was the dominant genus in all three plant communities. *Acaulospora* occurred at the highest frequency in the alpine meadow and at the lowest frequency in the montane scrub grassland. *Scutellospora* occurred mostly in the montane scrub grassland. *Paraglomus* and *Pacispora* were not found in the montane scrub grassland, while *Entrophospora* was found only in the montane scrub grassland (Fig. 2).

Discussion

Arbuscular mycorrhizae are ubiquitous associations between fungi and plants in natural ecosystems, including arid and alpine areas at high altitude. A total of 23 AM fungal species were detected. Comparing the three plant communities, AM fungal species richness

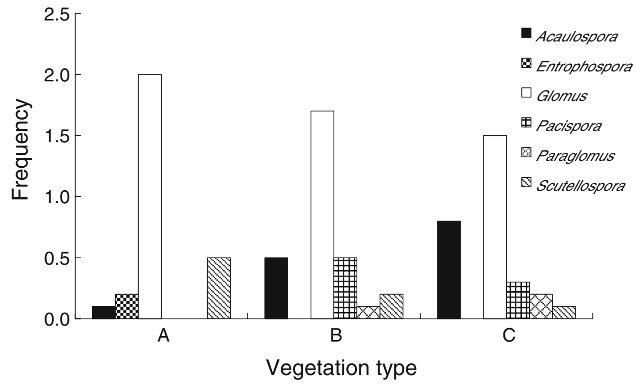

Fig. 2 Frequency of occurrence of spores of AM fungal genera in the three vegetation types (*A*, Montane scrub, *B*, Alpine steppe, *C*, Alpine meadow)

was ten in the mountain scrub grassland, 16 in the alpine steppe, and 13 species in the alpine meadow. Studies on species richness in temperate mountain grasslands have indicated about 10–20 species in Europe and America (Lugo and Cabello 2002; Börstler et al. 2006), a range of values similar to the results for the montane scrub grassland in our study. Most previous studies on alpine habitats have focused on the mycorrhizal colonization of root samples and there has been little investigation of the AM fungal communities (Gardes and Dahlberg 1996). Chaurasia et al. (2005) studied the diversity of AM fungi associated with central Himalayan rhododendrons (1,500 to 4,500 m a.s.l.) and observed 16 spore-forming AM fungal species, a result that was similar to ours.

Species in *Glomus* were dominant in Tibertan grassland communities, indicating adaptability in adjusting patterns of sporulation to environmental conditions as evidenced by its global distribution (INVAM biogeographical database; http//:invam.caf.wvu.edu). However, the genus *Pacispora* seemed to occur primarily at higher altitudes and may be adapted to the extreme alpine climate conditions. Of the seven species described in *Pacispora*, at least five have been found to be abundant in alpine habitats at high altitudes. *P. franciscana*, *P. coralloidae*, and *P. robigina* have been reported to occur frequently at high altitudes in the Swiss Alps (Oehl and Sieverding 2004). In the present study, we found that *P. scintillans* occurred frequently in the alpine steppe and alpine meadow in Tibet. *P. chimonobambusae* has also been found in the Everest region of Tibet (Gai et al. unpubl. data). Spores of *Pacispora* have also been found in Mediterranean and tropical regions, which suggests that this genus is ubiquitous and has adapted to a wide range of environmental conditions (Oehl and Sieverding 2004).

Climatic conditions, especially temperatures, may be the most important factors influencing the AM fungal community (Koske 1987; Heinemeyer and Fitter 2004). The montane scrub grassland had very different communities of AM fungal spores compared to the alpine steppe and alpine meadow. As for the climate, the conditions in the alpine steppe and alpine meadow are somewhat similar with an alpine plateau climate, but the montane scrub grassland has a semi-arid type of temperate plateau climate. It was assumed that effects of temperature included two components, namely a direct effect on the fungi and an indirect effect mediated through the host plants (Koske 1987).

The occurrence and distribution of AM fungi can also be influenced by soil conditions and other environmental conditions (Johnson et al. 1992; Kernaghan 2004). This has been documented in previous studies showing that phosphorus can affect the composition and diversity of AMF communities as well as spore and mycelium densities in temperate and tropical agroecosystems (Jansa et al. 2005; Singh and Adholeya 2004). P-levels in the soil (45.9 mg kg^{-1} in the montane scrub compared to 9.5–11.5 mg kg^{-1} in the alpine communities) may be influencing the number of species in the montane community. There have been few reports of the occurrence of *Scutellospora* at high altitudes above 3,500 m (Mullen and Schmidt 1993). Species in *Scutellospora* were found in all three vegetation types (3,500–5,300 m) in the present study. However, their frequency of occurrence differed, with 0.5, 0.2, and 0.1 in the montane scrub grassland, alpine steppe, and alpine meadow, respectively. There were also some AM fungal genera that were found only in particular vegetation types, presumably due to preferences of the AM fungi for certain environmental conditions. Indeed, it has been suggested that local environmental conditions may select the suite AM fungal species that are available for colonization (Klironomos et al. 2001; Bever et al. 2002).

Species richness, spore density, and the Shannon index of AM fungi were lowest in the montane scrub grassland and one likely explanation is the intensity of land use. The montane scrub grassland is important for agriculture and animal husbandry and these grasslands are severely disturbed. The present study thus agrees with previous reports of lower diversity and abundance of AM fungal spores in disturbed than in natural soils (Jasper et al. 1991; Boddington and Dodd 2000; Gai et al. 2006).

The present study was based on spore counts and on identification of AM fungi by spore morphology. It has been established that spore populations do not directly reflect the AM fungal communities actually colonizing the plant roots (Clapp et al. 1995). It may be possible to obtain a more complete picture of AM fungal communities by using molecular identification tools. However, this approach is currently limited due to the lack of adequate primers to cover the whole range of AM fungi and the difficulties involved in assigning sequences to taxonomic units (Oehl et al. 2005). Therefore, morphological identification of AM fungi is still the only feasible way to assess AMF communities in studies on soil samples taken from the field (Oehl et al. 2003).

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