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Grassland Degradation Decrease the Diversity of Arbuscular Mycorrhizal Fungi Species in Tibet Plateau

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Abstract

Arbuscular mycorrhizal (AM) fungi play a vital role in restoration of an ecosystem. Grassland degradation in alpine steppe is severe, but the influence of grassland degradation on AM fungi composition in Tibetan Plateau is still not well understood. This research studied the diversity of arbuscular mycorrhizal fungi in degraded alpine steppe, dominated by *Stipa purpurea*. The results showed that the species richness and abundance of AM fungi in degraded grasslands significantly decreased. In different typical grasslands species, diversity of AM fungi genus *Glomus* was much higher than other genera (*Acaulospora* and *Scutellospora*). Compared with normal grassland, the AM fungal species diversity in moderately degraded grassland decreased by 30%, but in lightly degraded and severely degraded grassland, it highly increased with 15.3% and 13.3%, respectively. The species diversity of genus *Glomus* in moderately degraded grassland and lightly degraded grassland were higher than for normal grassland. Significant differences were observed in a relative abundance of common dominant species among different degraded grasslands. The proportion of dominant species highly increased with the aggravation of grassland degradation. The results suggest that the grassland mild degradation increased the adaptability and stress resistance of species.

Keywords: alpine steppe, richness, species composition, *Stipa purpurea*

Introduction

Arbuscular mycorrhizal (AM) fungi are the most influential members of the soil microbiota (Smith and Read, 2008), which play a key role in improving the resistance of plants to drought (Wu *et al*., 2008), salt (Evelin *et al*., 2009) and nutrient deficiency (Smith and Read, 2008), restoration of degraded ecosystem (Bingham and Biondini, 2009; Zhang *et al*., 2012) and sustaining plant diversity and the ecosystem' stability (van der Heijden *et al*., 1998; O'Connor *et al*., 2002; Wagg *et al*., 2011). However, the composition and development of AM fungi are influenced by environmental changes and anthropogenic activity. A large number of studies have documented that overgrazing significantly reduced species diversity of AM fungi (Chaudhry *et al*., 2005; Su and Guo, 2007; Wearn and Gange, 2007). Moreover, several studies found that some other factors, such as drought, wind erosion and poor soil factors affect species diversity of AM fungi in grassland ecosystems (Landis *et al*., 2004; Uhlmann *et al*., 2004; Liu *et al*., 2009). Even so, the effects of grassland degradation on species composition of AM fungi in degraded ecosystem are not well understood, especially in extreme environment.

The Tibetan Plateau is called the third pole of the world, with an average altitude of 4,500 m above sea level (a.s.l.). The changes of plants and microorganisms can reflect the effects of climatic changes and human activities, on this distinctive ecosystem for the severe geographic and climatic conditions. Besides that, Tibetan Plateau is an important rangeland for the Tibetan herdsmen, occupying 82.07 million hectares of the Tibetan plateau (Gai *et al*., 2009). In the last decade, several studies focused on AM fungal species diversity in Tibetan Plateau, which includes warm steppe, alpine meadow and alpine steppe (Gao *et al*., 2006; Gai *et al*., 2009; Cai *et al*., 2010), and 111 species AM fungi belonging to 12 genera were observed. *Stipa* genus is one of the dominant species in arid and semiarid regions, which occupies the greatest area and plays a key role in the stability of the Tibetan Plateau ecosystem.

In recent years, the grassland degradation in Tibetan Plateau become more severe due to many exotic factors, which caused a significant decline of plant density and cover, and expanded desertification area. Although several previous projects have been studied the mycorrhizal structure of *Stipa breviflora* (Bao and Yan, 2004), the diversity of AM fungal species *Stipa capillata*, *S. purpurea*, *S. subsessiliflora* var. *basiplumosa*, *S. roborowskyi* and *S. glareosa*

(Shi *et al*., 2007), also AM fungal species composition and diversity of *Stipa* in degraded Tibet Plateau, are still not clear. In order to verify the influence of grassland degradation on AM fungal species composition on alpine steppe, *Stipa purpurea* community was selected as research subject, while *S. purpurea* is a dominant species of Tibet Plateau.

Materials and methods

Study area

The average altitudes of plateau surface in the study area range from 4300 to 5300 m. The climate types in the study area vary from plateau frigid semi-arid climate type, to arid climate. There are two seasons, cold (October to May) and warm (June to September) every year, and the mean annual temperature is -1.2-3.0 °C. There is no absolute frost free period, and annual accumulated temperature (≥0 °C) is 800-1100 °C; annual precipitation is 100-200 mm, annual evaporation is about 2000 mm, and the days with instantaneous wind speed ≥17.0 m s^{-1} are 100.3-158.2 d yr^{-1}. Within the study area, *S. purpurea* is a major component of alpine steppe. Currently, alpine steppe has already degraded to varying degrees, and desertification and vegetation thinning gradually become severely. Previous studies indicated that under the fragile and extreme environment of north Tibet Plateau, once desertification happens, it will be extremely difficult for native vegetation to spontaneously recover. Moreover, the desertification may be irreversible, and even more, other plants are difficult to colonize.

Sample collection

Samples were collected in the south of northern Tibetan Plateau (30°57.290'-31°51.147'N, 86°56.173'-90°59.424'E). The most representative and typical plant species in alpine steppe, *S. purpurea*, was selected as research subject. Twelve zones (10 × 10 m) (3 for normal, 3 lightly degraded, 3 moderately degraded and 3 severely degraded grasslands) were randomly selected as sampling zones, according to the classification standard of grassland degradation (Zhang, 2003), having 30-50 km interval between each two sampling zones; 3 sampling plots (1 m × 1 m) were randomly selected in each sampling zone, leaving 100-150 m interval between each two sampling plots. In each sampling plot, all surface soil (2 cm) was removed, and separately, the 2-30 cm soil samples with roots were collected. Afterwards, the samples from the 3 sampling plots in each sampling zone were mixed well, to make 1 mixture sample (about 2.5 kg). The collected samples with roots were put into bags, with marks and records. All soil samples were calcareous soil. Soil parent material and soil type were lacustrine deposits and alpine steppe soil, respectively. Soil texture was low-sand soil.

AM fungi identification

The AM fungal spore numbers in soil samples were isolated and counted. AM fungal spores from 20 g mixed air-dried samples were extracted using wet screening-sucrose gradient centrifugation. The spore colour, size and connective mycelia were observed under stereo light microscope; spores were placed on glass slide (with 30% glycerol as flotation reagent cover slip) to conduct microscopy observation, and spore colour, size and connective mycelia were recorded; spores were then disrupted to observe inclusion, sporoderm stratification, colour and thickness. For identification, Melzer's reagents were applied to test spore specific reaction. The species were identified according to the manual for identification of Vesicular-Arbuscular mycorrhizal fungi (Schenck and Péréz, 1988) and INVNAM (*http://invam.caf.wvu.edu/Myc-lnfo/*), as well as identification materials and new species identified in recent years.

Data analysis

The following data were collected and analyzed in order to evaluate the composition and the diversity of AM fungi.

1) Spore density (SD): number of all AM fungal spores per 20 g air-dried soil.

2) Species richness (SR): the number of AM fungal species per 20 g air-dried soil.

3) Species diversity (H): it is calculated by Shannon-Weiner index. If one random sample includes N individuals, and the individual number of species i is N_i, then $P_i = N_i / N$. H can be calculated with this formula:

$$H = -\sum_{i=1}^{k} (P_i \ln P_i)$$

where k is the number of a certain sampling site; P_i is the percentage of spore density of AM fungal species i in total spore density, of one sampling site.

4) Species evenness (J): it is calculated by Pielou index, that is $J = H/\ln S$, where H is Shannon-Weiner index, and S is the number of AM fungal species at a certain sampling site.

5) Isolation frequency (F): occurrence frequency of certain AM fungal genus or species in total samples, that is F = occurrence number of certain AM fungal genus or species/sample number ×100%. According to F value, AM fungi are classified to 4 grades: dominant genus or species (F > 50%), most common genus or species (30% < F < 50%), common genus or species (10% < F < 30%), rare genus or species (F < 10%).

6) Relative abundance (RA): number of certain AM fungal genus or species spores at a certain sampling site / number of all AM fungal spores at a certain sampling site.

7) Importance value (I): the mean value of isolation frequency (F) and relative abundance (RA), that is I = (F + RA) / 2.

Correlation analysis and significance test were performed using DPS software and *LSD* method.

Results

Grass degradation had negative effects on AM fungi population composition in soil of *S. purpurea* community. AM fungi were composed of *Acaulospora*, *Glomus* and *Scutellospora* in normal, lightly, moderately and severely degraded grassland, and the species richness followed the order: *Glomus* > *Acaulospora* > *Scutellospora* (Tab. 1).

Compared to normal grassland, the composition of AM fungi in degraded grasslands changed significantly (Tab. 2); the proportion of *Acaulospora* in lightly and severely degraded grasslands increased by 92.3% and 179.0%

respectively, compared with normal grassland, while it decreased by 36.5% in moderately degraded grasslands. The change of *Glomus* was totally different from *Acaulospora*. The proportion of *Scutellospora* species significantly increased with the grassland degradation (Tab. 2). Grassland degradation had important effects on AM fungi composition in soil of *S. purpurea* community.

Meanwhile, in all these four types of grasslands, the relative abundance of common species of AM fungi *Glomus* were higher than other dominant species.

As dominant species, *A. scrobiculata* and *A. spinosa* only occurred in normal and lightly degraded grasslands (Tab.1).

Glomus was dominant genus with a frequency of occurrence of 100% over all spore samples examined for all types of grasslands, and the relative abundance (77.0-96.1%) and importance value (88.5-98.0%) were higher than for other genus. In different degraded grasslands, the changes of AM fungi spore density, relative abundance and importance value were all the same (Tab. 2) and they showed a specific tendency: *Glomus*＞*Acaulospora*＞*Scutellospora*. Significant differences among the genus were observed (P<0.05).

Tab. 1. Genera and species of AM fungi in soil from different degraded grasslands of *S. purpurea*

Genus	Species	Normal grassland	Lightly degraded grassland	Moderately degraded grassland	Severely degraded grassland
Acaulospora	*A. delicat*	+	+	-	-
	A. laevis	+	+	+	+
	A. scrobiculata	+	-	-	-
	A. spinosa	-	+	-	-
Glomus	*G. aggregatum*	+	+	+	+
	G. claroideum	+	+	+	+
	G. convolutum	+	+	+	-
	G. dominikii	+	-	+	+
	G. etunicatum	+	+	+	-
	G. geosporum	+	+	+	+
	G. mosseae	+	+	+	+
	G. versiforme	+	+	+	+
Scutellospora	*S. calospora*	+	+	+	+

Note: "+" indicates that the AM fungi occurred in the site sample; "-" indicates that no AM fungi appeared in the site.

Tab. 2. Spore density, composition and importance value of AM fungi in soil samples from *S. purpurea* community, under different degraded grasslands

State of grasslands	AM fungal genera	Spore density (20 g^{-1} dry soil)	Species richness	Diversity (H)	Species evenness (J)	Relative Abundance (%)	Importance value
Normal grassland	*Acaulospora*	2.25 ± 1.90 ^{b}	0.41 ± 0.26 ^{b}	0.1940 ^{b}	0.0781 ^{b}	5.87 ^{b}	52.94 ^{b}
	Glomus	34.00± 20.35 ^{a}	1.42 ± 0.38 ^{a}	1.2367 ^{a}	0.4977 ^{a}	88.70 ^{a}	94.35 ^{a}
	Scutellospora	2.08 ± 1.44 ^{b}	0.17 ± 0.17 ^{c}	0.1576 ^{b}	0.0634 ^{b}	5.43 ^{b}	36.05 ^{c}
Lightly degraded grassland	*Acaulospora*	3.00 ± 2.35 ^{b}	0.42 ± 0.26 ^{b}	0.3153 ^{b}	0.1315 ^{b}	11.29 ^{b}	55.65 ^{b}
	Glomus	23.00 ± 11.98 ^{a}	1.25 ± 0.37 ^{a}	1.3200 ^{a}	0.5505 ^{a}	86.52 ^{a}	93.26 ^{a}
	Scutellospora	0.58 ± 0.58 ^{c}	0.08 ± 0.08 ^{c}	0.0840 ^{c}	0.0350 ^{c}	2.19 ^{c}	17.76 ^{c}
Moderate degraded grassland	*Acaulospora*	3.08 ± 3.08 ^{b}	0.17 ± 0.17 ^{b}	0.1220 ^{b}	0.0530 ^{b}	3.73 ^{b}	35.20 ^{b}
	Glomus	79.42 ± 44.29 ^{a}	1.33 ± 0.36 ^{a}	1.3374 ^{a}	0.5808 ^{a}	96.07 ^{a}	98.04 ^{a}
	Scutellospora	0.17 ± 0.17 ^{c}	0.08 ± 0.08 ^{c}	0.0124 ^{c}	0.0054 ^{c}	0.20 ^{c}	16.77 ^{c}
Severely degraded grassland	*Acaulospora*	3.92 ± 3.92 ^{b}	0.25 ± 0.25 ^{b}	0.2965 ^{b}	0.1426 ^{b}	16.38 ^{b}	58.19 ^{b}
	Glomus	18.42 ± 9.03 ^{a}	0.92 ± 0.31 ^{a}	1.2289 ^{a}	0.5910 ^{a}	77.00 ^{a}	88.50 ^{a}
	Scutellospora	1.58 ± 1.58 ^{b}	0.08 ± 0.08 ^{c}	0.1794 ^{c}	0.0863 ^{c}	6.62 ^{c}	19.98 ^{c}

Note: these data were means ± SD; different lowercase letters on the same column means the significant difference at 5% level.

Among all grasslands, there was no consistent variation in spore density, relative abundance and importance value of AM fungi. The spore density of *Glomus* in moderately degraded grassland were 133%, 245.2% and 341.2% higher than that in normal grassland, lightly degraded grassland and severely degraded grassland, respectively. The spore density of *Acaulospora* in degraded grasslands was higher than that in normal grassland. The relative abundance of *Acaulospora* in severely degraded grassland was averagely higher by 187% than other grassland, and the importance value were similar, except in moderately degraded grassland (Tab. 2).

Grassland degradation had negative effects on AM fungi population composition. AM fungi species diversity in soil samples of *S. purpurea* community was different under the four grasslands degraded states. The AM fungi species richness of degraded grasslands was much lower than that of normal grassland, and the decreased tendency increased with the degradation of grassland. The species diversity in lightly and severely degraded grasslands was higher than that in moderately degraded and normal grassland (Fig. 1b).

The species richness of *Acaulospora*, *Glomus* and *Scutellospora* in severely degraded grasslands decreased by 39.0%, 33.1% and 52.9% compared with normal grassland

(Tab. 2). There was no significant difference for species diversity and evenness between lightly and moderately degraded grasslands. Species diversity and evenness of *Glomus*, *Acaulospora* and *Scutellospora* in severely degraded grassland increased compared to normal grassland (Tab. 2). Different degraded grassland had negative effects on AM fungi genus and species richness, and the grassland degradation facilitated the increase of species diversity and evenness of *Glomus*.

The spore density and relative abundance of dominant species *Glomus* in moderately degraded grassland were much higher than other grasslands (Fig. 2).

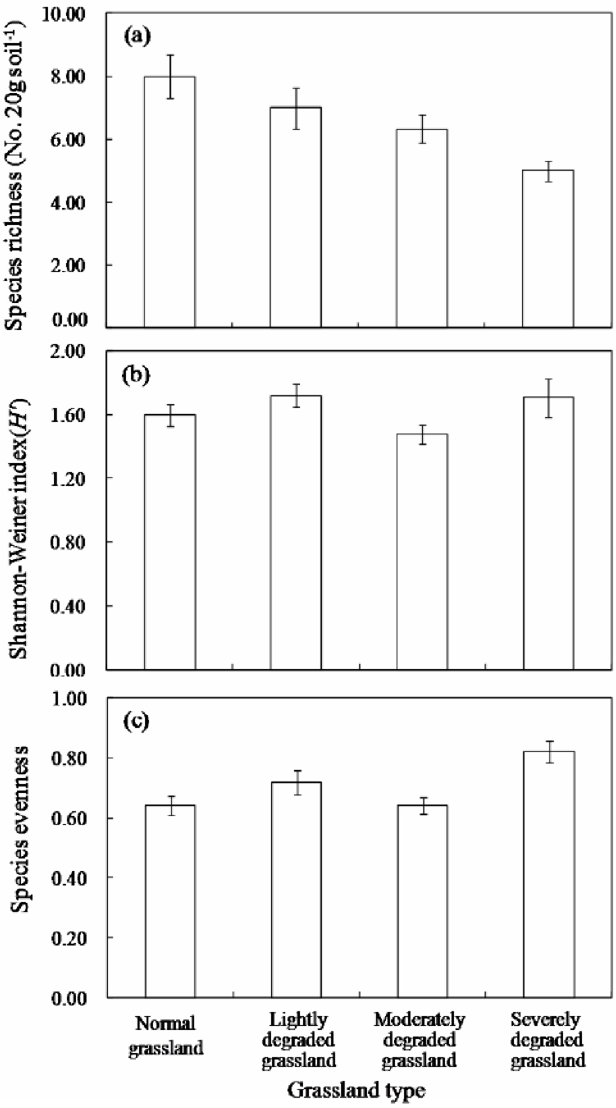

Fig. 1. Species richness (a), diversity (b) and evenness (c) of AM fungi in different grasslands

Compared with normal grassland, the dominant species of *Glomus* in moderately degraded grassland increased, while the genus *Acaulospora* decreased significantly (Tab. 2). Compared with normal grassland, the common dominant species of *Glomus* significantly increased in lightly and moderately degraded grassland, while it decreased in severely degraded grassland (Fig. 3).

In all these four grasslands, importance value of dominant species was greater than that of the most common species. Importance values of dominant species in degraded grasslands were much lower than the ones for normal grassland. The importance value of dominant species decreased lightly with the degradation aggravation, while the value of the most common species did not change significantly (Tab. 2). The importance values of *Acaulospora* in lightly and severely degraded grasslands were scant higher than that of *Glomus*, while the importance value of *Glomus* dominant species in moderately degraded grasslands was significantly higher than that of *Acaulospora*.

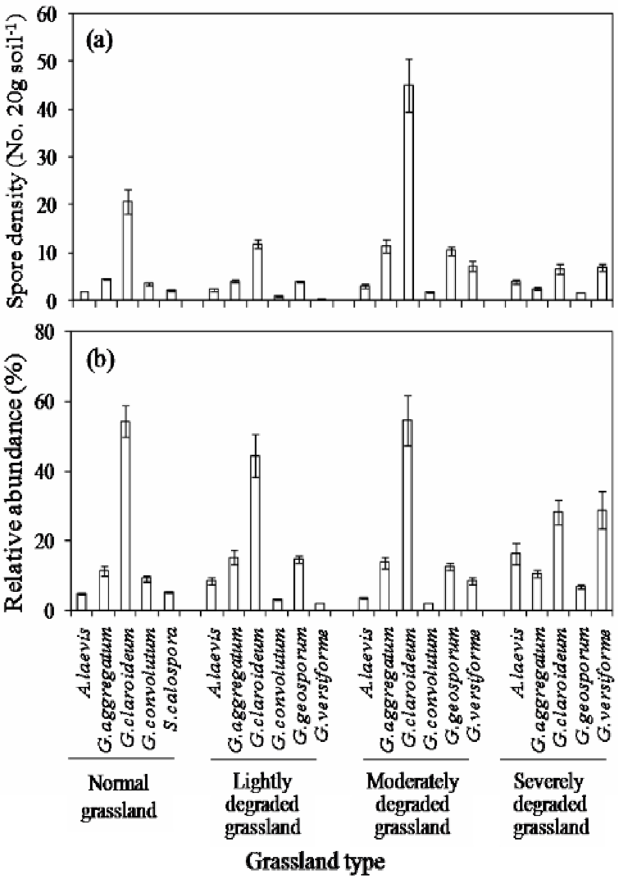

Fig. 2. Spore density (a) and relative abundance (b) of dominant AM fungi species in different grasslands

The relative abundance of dominant AM fungi in normal, lightly, moderately and severely degraded grasslands were 94.6%, 88.7%, 95.5% and 91.3%, respectively (Fig. 2b). The relative abundance of dominant species was significantly different among *Glomus,* as the proportion of *G. claroideum* species occupied about 30.9-57.5%.

Significantly positive correlations were observed between spore density and soil organic matter, spore density and altitude. There were significant negative correlations between diversity of AM fungi and soil available phosphorus, organic matter and altitude (Tab. 3).

Tab. 3. Correlation between environmental factors and AM fungal species density and the diversity of *S. purpurea*

	Soil water content	pH	Available phosphorus	Organic matters	Altitude
Spore density	0.1283	0.3051	0.7972**	0.9890**	0.9943**
Diversity	-0.2949	-0.3173	-0.9370**	-0.9223**	-0.9470**

Note: "**"denotes the significant difference at 1% level.

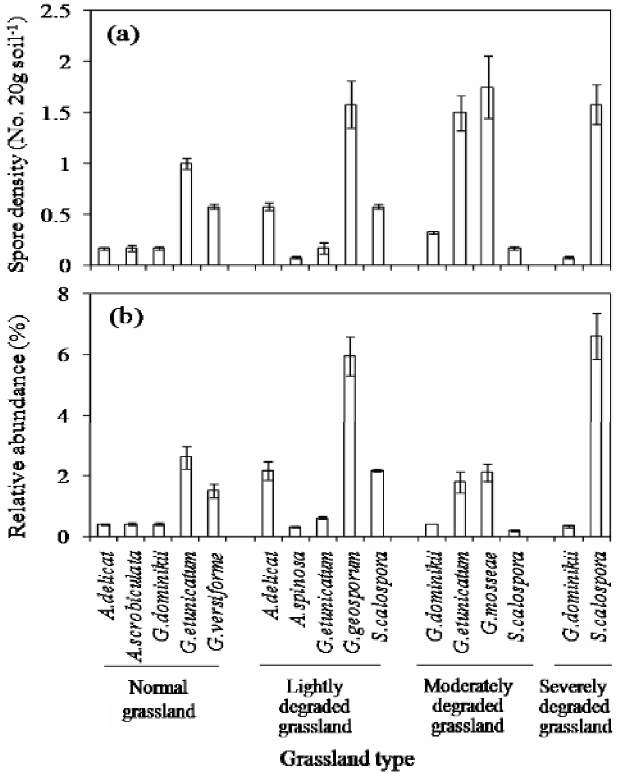

Fig. 3. Spore density (a) and relative abundance (b) of common dominant AM fungi species in different grasslands

Discussion

Several studies documented that degradation in Pakistan (Chaudhry *et al.*, 2005), Inner Mongolia steppe (Su and Guo, 2007) and southern England (Wearn and Gange, 2007) caused by overgrazing, declined species diversity of AM fungi. The current study found that grassland degradation had significant effects on AM fungal diversity of *S. purpurea* in Tibetan Plateau. Compared with normal grassland, AM fungal species richness in degraded grasslands significant declined with grassland degradation aggravation. However, AM fungi species diversity and evenness increased significantly in lightly and severely degraded grasslands, while it only decreased in moderately degraded grassland. The core of the grassland degradation is soil degradation, although the degradation of Tibet alpine grassland (which basically belongs to a natural process) is different from those caused by overgrazing (Gai *et al.*, 2006). Species diversity of AM fungi in Tibet alpine steppe showed the trend of lightly degraded grassland > severely degraded grassland > normal grassland > moderately degraded grassland, even though it was inconsistent with other previous results, that conclude that species diversity of AM fungi decline can be caused by overgrazing (Chaudhry *et al.*, 2005; Su and Guo, 2007; Wearn and Gange, 2007). This inconsistency might be related to the disruption of plant species caused by degradation in these areas, which grassland degradation may mainly decline with the proportion of non-mycorrhizal plant species, and little effects on mycorrhizal plant species. So that, in degraded grassland, the diversity of AM fungi till maintain at a higher level. Moreover, this also might be related to soil conditions and other environmental factors, caused by degradation, which can determine AM fungi community composition (Johnson *et al.*, 1992; Kernaghan, 2004). To obtain more information upon the impacts of degradation on alpine ecosystem, further studies on the influence of degradation on plant community composition, AM fungal colonization and soil conditions in Tibetan Plateau, are needed.

Previous results showed that AM fungi species *G. fasciculatum*, *G. geosporum*, *G. intraradices* and *G. mossea* were sensitive to overgrazing, while other *Glomus* fungi were not, obvious in Inner Mongolia (Su and Guo, 2007). The research on Namibia arid region showed that various grazing intensity affected the distribution of AM fungi, and *G. geosporum*, *G. mosseae* appeared in lightly grazing region, while they were not observed in moderately and severely grazing districts (Uhlmann *et al.*, 2006). These studies illustrate that AM fungi species have different reaction to environmental changes and grassland degradation in different ecosystems. In this study, *A. delicat* was found in normal grassland and lightly degraded grassland. *A. scrobiculata* was only observed in general grassland and it was not found in various degraded grasslands. However, 7 kinds of AM fungi, such as *A. laevis*, *G. aggregatum*, *G. claroideum*, *G. geosporum*, *G. mosseae*, *G. versiforme* and *S. calospora* had very strong adaptability, and were distributed also in normal grassland and all types of degraded grassland. Therefore, it might be concluded that different species of AM fungi have different response and sensitivity to grassland degradation.

Glomus species plays a dominant role, under different conditions of grasslands. In normal and degraded grasslands, the change trends of AM fungal species richness, spore density, relative abundance, importance value, diversity and evenness all followed the rule order of the three genera: *Glomus*>*Acaulospora*>*Scutellospora*. Unlike the relatively even distribution of AM fungal species in degraded steppe in Inner Mongolia (Wang and Liu, 2002), *Glomus* species had a dominant role (species richness, 63.6-80.0%; relative abundance, 77.0-96.1%) in AM fungal community structure of the normal and degraded grasslands in the ecological condition of alpine steppe of north Tibet Plateau. Moreover, *Glomus* species distributed widely (isolation frequency reached 100%). The result (Fig. 4) suggests that AM fungi in this region have a great tolerance to cold and arid environment, and also a high ability to adapt to degraded steppe, for long time co-evolution.

Although the composition of AM fungi dominant genera and species was simple, the percentage of dominant species increased with grassland degradation degree. The

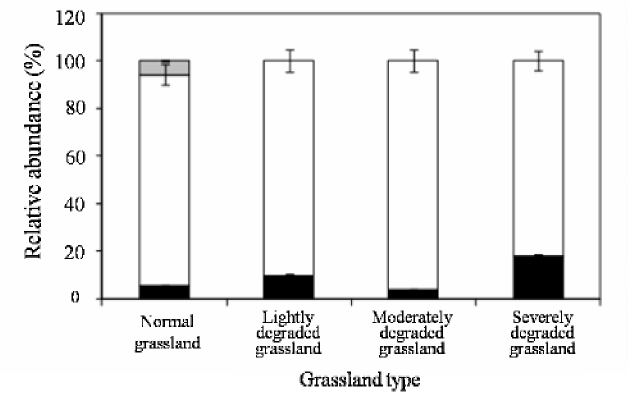

Fig. 4. Relative abundance of dominant AM fungi species in different grasslands. Black part in each column represents genus *Acaulospora*, white part in each column represents genus *Glomus* and grey part in each column represents genus *Scutellospora*

percentage of dominant species of *Glomus* genus (80.0-83.3%) in degraded grassland was significantly higher than for the normal one. This indicated that grassland degradation decreased AM fungal species richness. However, it promoted AM fungi adaptive ability to such an environment, and enhanced the survival of AM fungi of *Glomus* genera.

The role of AM fungal dominant species was very obvious in normal and degraded grasslands, with relative abundance of 88.7-95.5%. The relative abundances of the AM fungi and *Glomus* genera dominant species significantly decreased with degradation aggravation. It indicates that there is a significant relationship between plant species *S. purpurea* and AM fungal community composition. Generally, grassland degradation would thin and dwarf the vegetation, reduce the dominance of root system, which they all influence the survival and growth of AM fungi and inhibit the AM fungi variety and its infection on roots (Wang and Liu, 2002; Su and Guo, 2007; Wearn and Gange, 2007).

The study on alpine steppe of north Tibet Plateau found that the species abundance and richness of AM fungi in moderately degraded grassland reduced significantly, but species diversity and evenness were higher than the data for normal grassland. This might be related with the increase of soil organic matter. Under freezing low temperature in alpine steppe of north Tibet Plateau, the contact coverage of normal alpine grassland would lead to high soil water content and long term of soil freeze, as the soil organic matter is hard to decomposition and transform to sod layer, and therefore the formation and accumulation of organic matter would need a long time too. When the grass land were moderately degraded, the reduced soil water content might be suitable for microbe, and speed the decomposition of soil organic matter, and therefore increase the soil organic matter content, which would facilitate the propagation spore production of AM fungi, especially for *Glomus* genus.

It is worth to note that spore density, relative abundance, importance value, species diversity and evenness of *Acaulospora* and *Scutellospora* genera in moderately degraded grassland were lower compared to those in normal, lightly degraded and severely degraded grasslands, indicating that grassland degradation had adverse effects on AM fungal diversity.

Temperature (including soil temperature) is one of the most important ecological factors that determine AM fungal community composition, its development and infection in nature ecosystems (Heinemeyer and Fitter, 2004; Hawkes *et al.*, 2008). In the present study, with the increase of altitude, spore density increased significantly, while mycorrhizal infection decreased significantly (r = -0.6502*). This result is inconsistent with previous results obtained from warm steppe of south Tibet (Cai *et al.*, 2010). The ecological phenomenon may be associated with a series of factors, such as soil humidity, soil pH value, organic matter, available phosphorus content and bacteria number in soil, in cold and arid environment. The results indicate that altitude has an important impact on soil factors, soil temperature, soil pH value, organic matter, available phosphorus content and bacteria number. Species diversity and evenness decreased with the increase of altitude, which may ascribe to the decrease of temperature. This was consistent with the results that AM fungal diversity increased with the increase of temperature within a certain range (Shi *et al.*, 2007), suggesting that an environment at a higher altitude had adverse effects on AM fungal diversity.

Conclusions

The major conclusion from this study is that grassland degradation decreased AM fungal species richness and abundance, but the diversity of AM fungi in degraded grassland increased. The results suggest that grassland degradation increased the adaptability and stress resistance of AM fungi alpine grassland in Tibet Plateau. In spite this, reduced human caused disturbance (overgrazing, picking traditional Chinese medicinal materials, etc.) in this area is imperative, in order to sustain the species richness of AM fungi. Furthermore, the effects of AM fungi on revegetation in Tibetan Plateau need more consistent study in future.

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