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Response of Arbuscular Mycorrhizal Fungi to Simulated Climate Changes by Reciprocal Translocation in Tibetan Plateau

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Abstract

Arbuscular mycorrhiza (AM) fungi are considered as an important factor in predicting plants and ecosystem responses to climate changes on a global scale. The Tibetan Plateau is the highest region on Earth with abundant natural resources and one of the most sensitive region to climate changes. To evaluate the complex response of arbuscular mycorrhizal fungi colonization and spore density to climate changes, a reciprocal translocation experiment was employed in Tibetan Plateau. The reciprocal translocation of quadrats to AM colonization and spore density were dynamic. Mycorrhizal colonization frequency presented contrary changed trend with elevations of quadrat translocation. Colonization frequency reduced or increased in majority quadrats translocated from low to high or from high to low elevation. Responses of colonization intensity to translocation of quadrats were more sensitive than colonization frequency. Arbuscular colonization showed inconsistent trend in increased or decreased quadrat. Vesicle colonization decreased with changed of quadrat from low to high elevations. However, no significant trend was observed. Although spore density was dynamic with signs of decreasing or increasing in translocated quadrats, the majority enhanced and declined respectively in descent and ascent quadrat treatments. It is crucial to understand the interactions between AM fungi and prairie grasses to accurately predict effects of climate change on these diverse and sensitive ecosystems. This study provided an opportunity for understanding the effect of climate changes on AM fungi.

Keywords: arbuscular mycorrhizas; climate changes; colonization frequency; colonization intensity; spore density

Introduction

Arbuscular mycorrhiza (AM) fungi form symbiosis with ~80% of vascular plants being widely claimed to be an important mechanism for biochemical cycling in natural ecosystems, and more recently is being increasingly studied under current and projected global climate changes (van der Heijden *et al.*, 1998; Hughes *et al.*, 2008; Averill *et al.* 2014; Mohan *et al.*, 2014). AM fungi are considered as an important factor in predicting plants and ecosystem responses to climate changes on a global scale (Compant *et al.*, 2010; Mohan *et al.*, 2014).

The Tibetan Plateau is known as the 3rd Pole with abundant ice fields and is also the highest region on Earth with abundant natural resources. However, observed current and projected climate changes have produced numerous impacts including increases in temperature (0.25 °C decade^{-1}) (Hu *et al.*, 2013), and annual precipitation with the wettest year in 2010 being during 3,500 year by tree-ring record (Yang *et al.*, 2014), which makes this region a susceptive zone. More recently, greater attention has focused on climate changes in the Tibetan plateau vegetation ecology, and how the below-ground microbial communities respond to both variations in the soils environment and above ground vegetation type (Farrington, 2009; Zhang *et al.*, 2013). Moreover, many studies have shown that prairie plant communities are closely connected with their AM fungi community, and this relationship between plant and fungi displays positive reciprocal effects (Hartnett and Wilson, 1999; Eom *et al.*, 2000). There is also evidence that AM fungi community composition are not randomly distributed throughout tall grass prairies landscapes, but show some degree of host specificity (Eom *et al.*, 2000). Consequently, it is crucial to develop a firm understanding of the interactions between AM fungi and prairie grasses to accurately predict effects of climate change on these diverse and sensitive ecosystems (Araújo and Luoto, 2007). However, Jumpponen

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Table 1. Ecological characteristics of each plot in different elevations

Elevation (m)	Vegetation types	Dominated or common plant species	Mean annual temperature (°C)	Soil types	Soil organic matter ($g kg^{-1}$)	Soil total nitrogen ($g kg^{-1}$)
3200	*Kobresia* meadow	*Kobresia humilis, Anaphalis lactea, Elymus nutans, Stipa aliena, Taraxacum dissectum, Potentilla anserina*	-0.4	Mat Cry- gelic Cambisols	109.13	5.87
3400	Deciduous shrub meadow	*Potentilla fruticosa, Elymus nutans, Stipa aliena, Aster flaccidus, Saussurea nigrescens*	-0.7	Mollic- Gryic Cambisols	104.07	5.77
3600	Forbs meadow	*Polygonum viviparum, Kobresia humulis, Carex pachyrrhiza, Galium verum, Thalictrum alpinum*	-0.8	Mollic- Gryic Cambisols	126.47	7.57
3800	Sparse vegetation	*Leontopodium nanum, Galium verum, Corydalis melanochlora*	-1.6	Mollic- Gryic Cambisols	84.20	6.77

Note: Organic matter and total nitrogen of soil are the average in 0 to 30 cm soil.

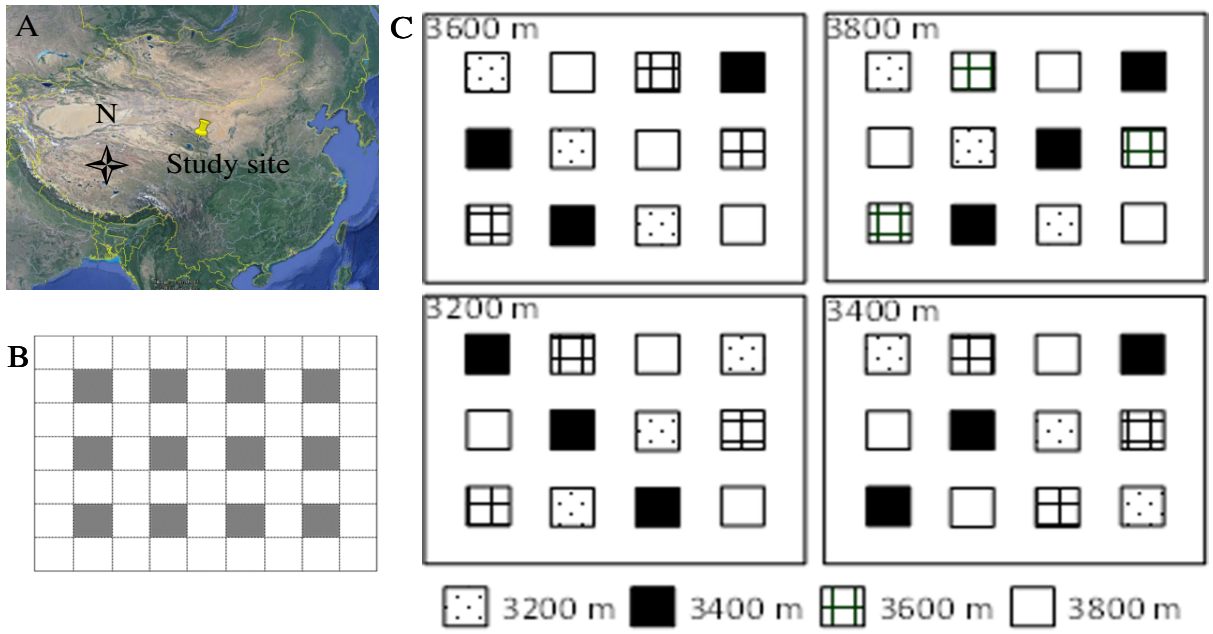

Fig. 1. The sketch of study site (A) and experimental design (B)

and Jones (2014) did not show fungal species richness or diversity changes to abiotic climate changes e.g. elevated CO_2, O_3, UV and Drought. Shi *et al.* (2014) indicated AM fungal richness and diversity are positively correlative with temperature in Mount Taibai. Currently, most of the AM fungi studies are laboratory, not field studies and this may be a limitation.

Here, we conduct a *in situ* study to determine the response of AM fungi colonization and spore density to elevational changes by using a reciprocal translocation experiment at the Haibei Alpine Meadow Research Station (101°19'E, 37°35'N), located in the northeast of the Tibetan Plateau to study the effects of climate changes on AM fungi colonization and spore density.

Materials and Methods

Study site and experimental design

This study site located at the Haibei Alpine Meadow Research Station, Chinese Academy of Sciences (101°19′E, 37°35′N) (Fig. 1 A) in the northeast of the Qinghai-Tibetan Plateau of China. Four plots of 7×9 m plots were selected in flat (aspect < 3°) and homogenous plots of four altitudinal gradients of 3200 m, 3400 m, 3600 m and 3800 m. The experiment was completed in early May 2007 when most alpine plants were dormant. The characteristics of each plot including vegetation, soil and climate were showed in Table 1. Then, each plot was divided into sixty-three (7×9) quadrats of 100×100 cm (Fig. 1 B). Among of them, twelve spaced quadrats were selected as the objects of this study (Fig. 1 B). Three quadrats were kept at original elevation, while nine with the depth of 0.3-0.4 m were translocated to the three other elevations. Twelve quadrats were semi-randomly distributed at each elevation (Fig. 1 C).

Samples collection

Five soil cores of 0-30 cm depth with 2 cm in diameter were collected in each quadrat according five-spot sampling model in August, 2011. The five soil cores in the same quadrat were mixed as a sample. Therefore, there are three replicas in each treatment (Fig. 1 C). The roots were picked out carefully from soil cores for the measurement of arbuscular mycorrhizal colonization. The soil was reserved for isolating arbuscular mycorrhizal fungal spores.

Assessment of arbuscular mycorrhizal colonization

Fresh roots were washed free of soil and cleared in 10% (w/v) KOH at 90°C in a water bath for 20–30 min, the exact

Table 2. Arbuscular mycorrhizal colonization and spores density in translocated quadrats in different elevation in Tibet

Elevation before translocation (m)	Elevation after translocation (m)	F%	M%	m%	a%	A%	v%	V%	Spore density
3200	3200	71.2 b	6.7 b	9.3 b	1.16 c	0.10 c	10.57 a	0.80 a	83.3 bc
3400	3200	74.0 ab	11.1 ab	14.5 ab	3.72 bc	0.46 bc	6.09 a	0.67 a	110.0 abc
3600	3200	81.4 ab	16.3 ab	19.3 ab	1.03 c	0.16 c	14.53 a	2.00 a	96.7 abc
3800	3200	81.4 ab	12.3 ab	14.7 ab	2.58 c	0.31 bc	6.93 a	1.14 a	60.0 c
3200	3400	81.0 ab	11.6 ab	13.7 ab	9.16 ab	1.84 a	9.38 a	1.36 a	105.0 abc
3400	3400	82.4 ab	21.5 a	26.0 a	11.84 a	2.68 a	13.09 a	3.33 a	156.7 a
3600	3400	88.9 a	14.3 ab	16.1 ab	3.93 bc	0.48 bc	7.99 a	1.25 a	105.0 abc
3800	3400	89.2 a	18.1 ab	20.0 ab	4.67 bc	0.90 bc	11.78 a	2.17 a	76.7 c
3200	3600	66.7 b	6.8 b	10.2 b	6.07 abc	0.45 bc	4.96 a	0.41 a	113.3 abc
3400	3600	71.9 b	12.9 ab	15.4 ab	0.62 c	0.02 c	8.15 a	1.68 a	116.7 abc
3600	3600	82.5 ab	10.3 ab	12.1 ab	1.44 c	0.16 c	3.06 a	0.36 a	86.7 bc
3800	3600	76.5 ab	9.0 ab	11.2 b	1.27 c	0.14 c	2.11 a	0.25 a	146.7 ab
3200	3800	72.5 b	8.0 b	10.8 b	0.31 c	0.03 c	7.21 a	0.68 a	76.7 c
3400	3800	75.9 ab	11.9 ab	15.8 ab	0.70 c	0.10 c	11.83 a	1.31 a	63.3 c
3600	3800	77.0 ab	16.9 ab	21.4 ab	2.45 c	0.40 bc	5.69 a	0.87 a	63.3 c
3800	3800	73.5 ab	10.3 ab	13.7 ab	1.95 c	0.13 c	8.50 a	0.68 a	70.0 c

Note: F% and M% mean colonization frequency and intensity in the root system, respectively. m% means intensity of the mycorrhizal colonization in the root fragments. A% and a% mean arbuscule abundance in the root system or in mycorrhizal parts of root fragments, respectively. V% and v% mean vesicle abundance in the root system or in mycorrhizal parts of root fragments, respectively. Spore density was calculated using the spore number in 100 g dried soil. Different letters between elevation denote significant differences (Duncan test, $P<0.05$).

time depending on the degree of lignification of the roots and their pigmentation. The root subsamples were cooled, washed, and cut into 0.5 to 1.0-cm-long segments and stained with 0.5% (w/v) acid fuchsin (Biermann and Linderman, 1981). At least thirty root fragments (ca. 1 cm long) were mounted on slides in polyvinyl alcohol-lactic acid-glycerol (Koske and Tessier, 1983) and examined at ×100-400 magnification using microscope. The colonization parameters were:

F% = Colonization frequency in the root system

M% = Colonization intensity in the root system

m%=Intensity of the mycorrhizal colonization in the root fragments

A%=Arbuscule abundance in the root system

a%= Arbuscule abundance in mycorrhizal parts of root fragments

These specific terms were calculated according to Trouvelot *et al.* (1986). Moreover, we calculated vesicle abundance in mycorrhizal parts of root fragments v% and V% referring to the formulas of (a%) and (A%) at Trouvelot *et al.* (1986).

V%=Arbuscule abundance in the root system

v%= Arbuscule abundance in mycorrhizal parts of root fragments

Extraction and counting of AM fungal spores

Spores or 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). Spore density was calculated using the spore number in 100 g dried soil.

Statistical analysis

The data were subjected to one-way of analysis of variance and means were compared by least significant difference (LSD) at the 5% level. The changes of colonization parameters and spore density were calculated by the following formula: [(translocated quadrats-primary elevation quadrats)/ primary elevation quadrats)]*100%. The statistical tests were applied using SPSS software package version 13.0 developed by SPSS Inc., Chicago, IL 60606, USA.

Results and Discussion

Decreasing altitude produced the highest observed colonization frequency in the root system in translocated quadrats from 3800 m to 3400 m (Table 2), which may be explained by the combination of changes in all kinds of factors including climate and soil etc. due to the translocated quadrats among different elevations. The changes of temperature have shown in Table 1 in different elevations. The changes of soil nutrition have also confirmed (Li *et al.*, 2010). Usually, the CO_2 concentration also increased with the decrease of elevations. The effect of soil nutrition on mycorrhizal colonization was well known (Smith and Read, 2008). It has also been widely claimed that increased CO_2 can improve the AM colonization (Monz *et al.*, 1994; Godbold *et al.*, 1997; Staddon *et al.*, 1999a; Rillig *et al.*, 1999), but increased temperature have variable impacts on colonization (Heinemeyer and Fitter, 2004; Wilson, 2012). Additionally, we tested the effect of stressing temperature on AM fungi colonization, which showed that temperature stress did not significantly affect AM fungi colonization with colonized rate of 56.9% and 60.8 in temperature stress and control treatment, respectively. Further, when the high or low temperature stress was considered, the same findings were obtained with the colonization values of 60.8% in low temperature stress comparing to 66.9% in control. The colonization in high temperature stress and control was 48.9 % and 47.9%, respectively. Interestingly there are some contrary findings, where elevated CO_2 decreased or do not significantly change the AM fungi colonization (Monz *et al.*, 1994; Staddon *et al.*, 1999b). The highest of vesicle frequency presented at translocated quadrats from 3600 to 3200 m. Further, the highest colonization intensity in the root system and root fragment, arbuscule abundance in mycorrhizal parts of root fragments, arbuscule and vesicle abundance in the root system and spore density presented the non-translocated quadrat of 3400 m. The response of AM fungi colonization parameters to climate changes were varied, which is in accordance with by previous reports (Staddon *et al.*, 1998; Mohan *et al.*, 2014). Such changes of host plant community possibly account for the colonization, because host plants regulate tightly internal mycorrhizal colonization, and do not allow the fungal partner to utilize all the soluble carbon in the root potentially

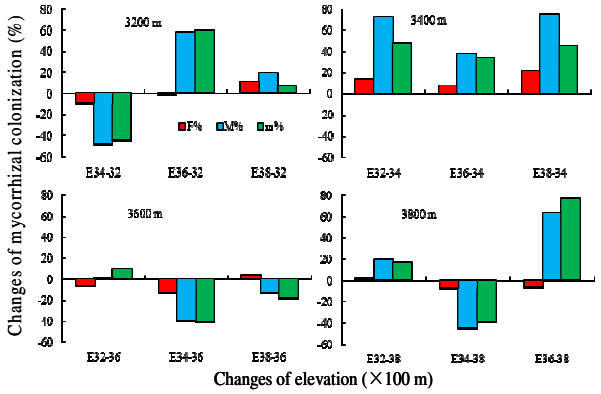

Fig. 2. The changes of total percentage of arbuscular mycorrhizal colonization in translocated quadrats comparing to these *in situ* quadrats at different elevation in Tibet

Note: E34-32 means the quadrat that was translocated from elevation 3400 m to 3200 m. The rest can be done in the same manner. The same are as below. F% and M% mean colonization frequency and intensity in the root system, respectively. m% means intensity of the mycorrhizal colonization in the root fragments.

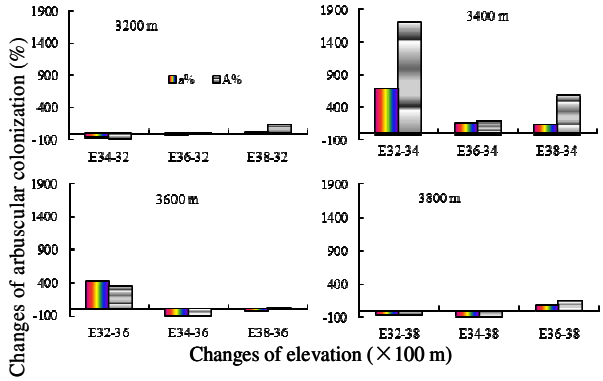

Fig. 3. The changes of percentage of arbuscule colonization in translocated quadrats comparing to these *in situ* quadrats at different elevation in Tibet

Note: A% and a% mean arbuscule abundance in the root system or in mycorrhizal parts of root fragments, respectively.

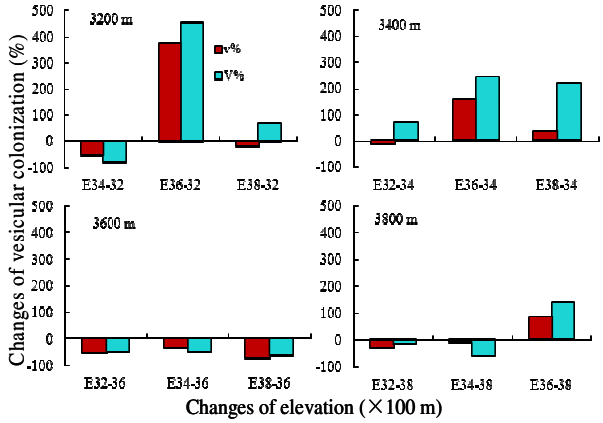

Fig. 4. The changes of total percentage of vesicle colonization in translocated quadrats comparing to these *in situ* quadrats at different elevation in Tibet

Note: V% and v% mean vesicle abundance in the root system or in mycorrhizal parts of root fragments, respectively.

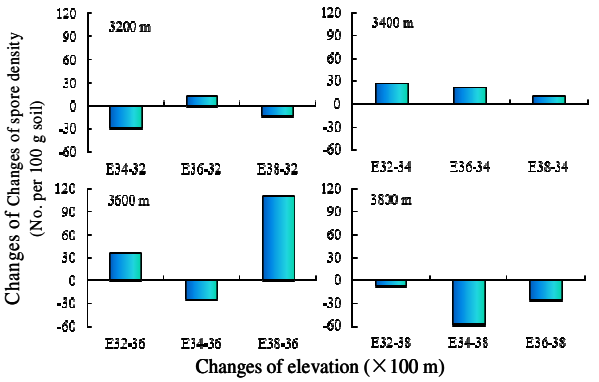

Fig. 5. The changes of spore density of arbuscular mycorrhizal fungi in translocated quadrats comparing to these *in situ* quadrats at different elevation in Tibet

available (Lewis *et al.*, 1994). Indeed, the plant communities have changed with the translocation of quadrats at different elevation (Zhang *et al.*, 2011). Additionally, the sampling season may have affected the responses of AM fungi colonization to climate changes. Zavalloni *et al.* (2012) showed the responses of AM fungi root colonization to elevated temperature and CO_2 varied with the growing season in grassland communities, which was previously confirmed under elevated CO_2 by Staddon *et al.* (1998).

The colonization frequency in the root system has lower changes than colonization intensity in the root system and intensity of the mycorrhizal colonization in the root fragments (Fig. 2), this result supports previous observations in newly established grasslands where AM fungi root colonization intensity, but not colonization frequency increased with elevated CO_2 and temperature (Zavalloni *et al.*, 2012). These data show that AM fungi colonization intensity is more sensitive than colonization frequency, which may be attributed to the root characteristics of host plants as AM fungi mainly colonize in absorption roots (Smith and Read, 2008). There were dynamic changes across all AM fungi colonization parameters, with the ascent or descent of translocated quadrats (Figs. 2-4), which is in accordance with majority studies in elevated CO_2 (Staddon and Fitter, 1998). Moreover, Staddon and Fitter (1998) reported CO_2 effects on AM fungi are indirect and are a result of plant growth changes at higher CO_2 concentrations. The observation of changes in arbuscule and vesicle are similar with previous findings that these presented different change trends with the elevated CO_2 (Sanders, 1996).

The spore density reduced in 4 out of 6 treatments of ascent quadrats (Fig. 5). Contrarily, they increased in 4 out of 6 treatments of descent quadrats. These results showed that climate changes impacted the spore density of AM fungi, which is similar to the findings made by Sun *et al.* (2013). Gong *et al.* (2013) confirmed spore density was closely related with climatic and edaphic factors. With the translocation of quadrats among different elevations, the climatic and edaphic factors and plant community and growth inevitably changed. Therefore, the exact response of AM fungi colonization, spore density and even community structure to translocation of quadrats needs to be further studied by the time-course samples owing to the importance of plant developmental stage in analyses of effects of CO_2 on mycorrhizal colonization (Staddon *et al.*, 1998).

Conclusions

The responses of colonization intensity to translocation of quadrats were more sensitive than colonization frequency. The majority spore density decreased or increased in ascent and descent quadrat treatments, respectively.

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