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Importance of AM fungi and local adaptation in plant response to environmental change: Field evidence at contrasting elevations

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ABSTRACT

Predicting response of plants to environmental change is a great challenge for ecologists and requires a deeper understanding of the importance of biotic interactions such as the role of arbuscular mycorrhizal (AM) associations. Using reciprocal transplantation experiments we tested the performance of two plant species (*Primula atrodentata* and *Aster himalaicus*) and AM fungal associations and their interactions in response to environmental change at sites of contrasting elevation. The results show a clear home advantage of plant performance and fungal colonization in most cases, and the consistently positive responses of plants to AM fungi in all home-away combinations. Specifically, mycorrhizal responses showed home-site advantage in *P. atrodentata* and the AM fungi consistently increased the fitness of *A. himalaicus* at the high elevation site, suggesting that the stress gradient hypothesis and adaptation hypothesis are both important theoretically in the prediction of functional responses of AM associations to environmental change in alpine ecosystems.

1. Introduction

Predicting how terrestrial organisms will respond to environmental change is crucial because their responses can feedback to enhance or ameliorate plant adaptation (Ciais et al., 2005; Van der Putten, 2012). Alpine plant species are considered to be particularly vulnerable to climate change (Theurillat and Guisan, 2001). Previous studies indicate that alpine plants may respond to climate change directly via altered physiology, fitness, or phenology and also indirectly through altered biotic interactions (Tylianakis et al., 2008; Grassein et al., 2014; Nicotra et al., 2015). Arbuscular mycorrhizal (AM) associations occur contemporaneously with plant biomes (Remy et al., 1994; Heinemeyer et al., 2006) and it is therefore not surprising that they have experienced major biogeographic and environmental changes in the past. Some important work has been done on this topic during the last 10 y which suggests that the importance of plant and AM fungal interactions need to be taken into account to obtain a more accurate assessment of predictions of plant response to global environmental change (Yang et al., 2013; McCormack et al., 2014; Rudgers et al., 2014; Wilson et al., 2016).

The stress gradient hypothesis (SGH) provides a common conceptual model of species interactions, especially in alpine and arctic ecosystems (Callaway et al., 2002; Cavieres and Sierra-Almeida, 2012). The theory suggests that general interactions in plant communities can shift from competition towards facilitation with increasing environmental stress (Daleo and Iribarne, 2009; He et al., 2013). Evidence for the SGH has also been presented for plant-microbe interactions along an elevation gradient when fertile soil at low elevations had a microbial community with an overall negative effect on pine seeding growth while soil at higher elevations was less fertile and held a microbial community that

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promoted pine seedling growth (Wagg et al., 2011). However, the role of the AM fungi in plant performance along elevation gradients has rarely been considered (Yang et al., 2016), even though AM fungi are known to be able to ameliorate and mediate plant response to some adverse conditions such as drought, N deposition and warming (Kivlin et al., 2013). Increasing environmental stress such as temperature, precipitation, snow duration, atmospheric pressure and UV radiation with increasing elevation may determine the presence and performance of AM fungi and their mutualistic function in montane ecosystems (Lugo et al., 2012; Li et al., 2015). Wahl and Spiegelberger (2016) presented a working hypothesis along the parasitism - mutualism continuum based on the SGH and proposed that the relationship between plants and AM fungi becomes more mutualistic with increasing environmental stress and more parasitic under more benign conditions. However, this hypothesis still requires further experimental evidence, especially under field conditions, to assess the role and function of AM fungi in plant fitness and vegetation assemblages along elevation gradients.

Local adaptation, a consequence of the fitness trade-offs between habitats, is a mechanism that favors population differentiation and that may lead to eventual speciation (Kawecki and Ebert, 2004). This theory is commonly operationally defined as “home vs away”, where a focal genotype performs better in its habitat of origin than it does in another habitat (Blanquart et al., 2013). Sometimes a population may perform better at home than elsewhere, and sometimes not. For example, within species the growth of individuals from different elevation gradients differs significantly according to their optimum local environment (Grassein et al., 2014). Leger et al. (2009) supported this by presenting examples of local adaptation seen in a low elevation population but not in a population at a high elevation site using field reciprocal transplants on Peavine Mountain in western North America. However, another study found that a population of *Poa alpina* from the lowest elevation origin often performed best regardless of changes in elevation gradient ranging from 425 to 1921 m a.s.l. (Hautier et al., 2009). Moreover, recent results show no local adaptation in long-lived woody species (Sedlacek et al., 2015). These studies did not specifically consider the role of associated microorganisms, which may potentially be important because microorganisms are often considered to be less dispersal-limited than their host plants (Finlay, 2002). In particular, the relative importance of AM fungal symbionts to adaptation, compared with genetic changes in the plants themselves, remains unclear. Some studies have indicated that plants perform better when they grow in their local soil and when they are inoculated with their native AM fungi (Schultz et al., 2001; Johnson et al., 2010). In contrast, some other studies show that the responses of plants to both native arbuscular mycorrhizal fungi and local soil can vary greatly, from negative to positive effects (Klironomos, 2003; Pánková et al., 2014). The present study was, therefore, conducted to assess how elevational variation affects the functioning of AM associations in the local and in novel environments.

The Tibetan plateau has an average elevation >4000 m a.s.l. and is a global climate change ‘hotspot’ due to its highly sensitive and fragile ecosystems. Climate change has led to a temperature increase of 0.2 °C per decade on the plateau during the past 50 y. This rapid change has already exceeded that of the northern and southern hemispheres (Chen et al., 2013). In the present study we conducted reciprocal transplant experiments using two plant species and their AM fungal associations at two elevation sites, and investigated the potential for environmental stress and local adaptation to shape plant performance, fungal performance and plant growth responses to AM inoculation. The purpose of our study was to test the two different hypotheses: the SGH expecting higher and stronger symbiotic relationships at higher elevations (harsher conditions); and the adaptation hypothesis expecting that the local combination of factors (local AM fungal associations, conditions and plants) will outperform the non-local ones.

2. Materials and methods

2.1. Study sites and plant species

The experimental sites were located on the west slope of Mount Segrila (29°21′-29°50′ N, 94°28′-94°51′ E), Nyingchi region, on the Tibetan plateau. The maximum elevation of the mountain is 5200 m and the local climate is driven by the Indian monsoon in summer and the westerlies in winter. The annual average temperature is −0.73 °C and the average annual rainfall is 600–1000 mm on the experimental slope. Approximately 80–90% of the precipitation falls during the plant growing season (May to September).

Reciprocal transplant experiments were conducted at sites at 3270 and 4540 m a.s.l. during the plant growing season in 2015. The air temperature averages 13.2 and 4.1 °C, respectively, at the two sites and the amounts of precipitation are 795 mm and 740 mm during the growing season (Du et al., 2009). The cover of *Aster himalaicus* was 10% and 13% and that of *Primula atrodentata* was 20% and 10% at the two sites. The corresponding soil characteristics and vegetation details at the two elevation sites are shown in Table 1.

2.2. Experimental design

Two plant species that occur at the selected elevation sites,

Table 1
Chemical properties of soils and vegetation details at the two elevation sites (data are means ± SE, $n = 5$).

Elevation (m a.s.l.)	pH	Olson P ($mg \cdot kg^{-1}$)	Total C ($g \cdot kg^{-1}$)	Total N ($g \cdot kg^{-1}$)	SOM ($g \cdot kg^{-1}$)	Vegetation cover	Species richness	Dominant plant species (Cover)
3270	5.84 ± 0.06	8.67 ± 1.42	21.6 ± 1.79	2.29 ± 0.21	82.18 ± 1.44	*c.* 90%	11.8 ± 0.49	*Aster himalaicus* (*c.* 10%) *Primula atrodentata* (*c.* 20%) *Carex sp.* (*c.* 25%) *Poa annua* (*c.* 10%) *Ranunculus pedatifidus* (*c.* 8%) *Potentilla anserina* (*c.* 5%)
4540	5.01 ± 0.14	7.33 ± 0.41	48.93 ± 2.63	4.05 ± 0.26	95.28 ± 3.50	*c.* 85%	12.8 ± 0.37	*Aster himalaicus* (*c.* 13%) *Primula atrodentata* (*c.* 10%) *Carex sp.* (*c.* 10%) *Androsace umbellata* (*c.* 12%) *Aconitum naviculare* (*c.* 15%) *Euphorbia stracheyi* (*c.* 15%)

NB: At each elevation site the vegetation cover, dominant plant species cover and species richness were estimated on five plots of 1 × 1 m at each plant community using Sutherland's method (Sutherland and Krebs, 1997).