

Diverse belowground resource strategies underlie plant species coexistence and spatial distribution in three grasslands along a precipitation gradient

Hongbo Li¹, Bitao Liu², M. Luke McCormack^{1,3}, Zeqing Ma¹ and Dali Guo^{1,4}

¹Center of Forest Ecosystem Studies and Qianyanzhou Station, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources

Research, Chinese Academy of Sciences, Beijing 100101, China; ²College of Forestry, Shanxi Agricultural University, Taigu, Shanxi 030801, China; ³Department of Plant Biology, University of Minnesota, St Paul, MN 55108, USA; ⁴University of Chinese Academy of Sciences, Beijing 100049, China

Summary

Author for correspondence:

Dali Guo

Tel: +86 10 64888153

Email: guodl@igsnr.ac.cn

Received: 3 April 2017

Accepted: 13 June 2017

New Phytologist (2017) **216**: 1140–1150

doi: 10.1111/nph.14710

Key words: adaptive strategy, foraging strategy, mycorrhizal colonization, root branching, species distribution, temperate steppe, trade-off, trait variation.

- Functional traits and their variation mediate plant species coexistence and spatial distribution. Yet, how patterns of variation in belowground traits influence resource acquisition across species and plant communities remains obscure.
- To characterize diverse belowground strategies in relation to species coexistence and abundance, we assessed four key belowground traits – root diameter, root branching intensity, first-order root length and mycorrhizal colonization – in 27 coexisting species from three grassland communities along a precipitation gradient.
- Species with thinner roots had higher root branching intensity, but shorter first-order root length and consistently low mycorrhizal colonization, whereas species with thicker roots enhanced their capacity for resource acquisition by producing longer first-order roots and maintaining high mycorrhizal colonization. Plant species observed across multiple sites consistently decreased root branching and/or mycorrhizal colonization, but increased lateral root length with decreasing precipitation. Additionally, the degree of intraspecific trait variation was positively correlated with species abundance across the gradient, indicating that high intraspecific trait variation belowground may facilitate greater fitness and chances of survival across multiple habitats.
- These results suggest that a small set of critical belowground traits can effectively define diverse resource acquisition strategies in different environments and may forecast species survival and range shifts under climate change.

Introduction

Variation in plant functional traits promotes diversity of resource foraging and ecological strategies (Lambers *et al.*, 2008; Zemunik *et al.*, 2015). These positive effects can directly drive species coexistence and distribution within and across plant communities (Zuppinger-Dingley *et al.*, 2014; Li *et al.*, 2015). For instance, interspecific trait variation is thought to be the cornerstone of niche partitioning and the fostering of species coexistence (Grime, 2006; Adler *et al.*, 2013; Williams *et al.*, 2017), whereas intraspecific trait variation may reflect plants' ability to adapt to climate change or environmental heterogeneity (Laughlin & Messier, 2015). Recent studies have indicated that the unique trait space arising from interspecific and intraspecific variation shapes the multifarious resource acquisition strategies across species (Díaz *et al.*, 2016; Kunstler *et al.*, 2016), and that a relatively small number of pivotal functional traits may be sufficient to describe species adaptive strategies in response to shifts in abiotic and biotic conditions (Kraft *et al.*, 2015). These advances

have been mainly achieved through studies of aboveground plant traits. However, traits of fine-root and mycorrhizal fungi, both of which are key for soil-based resource acquisition, should also play a decisive role in determining plant and ecosystem function (van der Heijden *et al.*, 1998; Bardgett *et al.*, 2014). Thus, clarifying the trade-offs among root and mycorrhizal traits as well as their variation is essential to understanding the diversity of belowground resource acquisition and whole-plant adaptive strategies (Comas & Eissenstat, 2004; Holdaway *et al.*, 2011; McCormack *et al.*, 2015), which underpin mechanisms of plant species coexistence and distribution.

Fine-root and mycorrhizal fungal traits may form multifarious combinations, resulting in diverse resource acquisition strategies in stable ecological communities (Kong *et al.*, 2014; Zemunik *et al.*, 2015). Several recent studies focused on woody plants observed that species with thinner absorptive roots (thin-root species) had lower mycorrhizal colonization but higher root branching than species with thicker absorptive roots (thick-root species) (Eissenstat *et al.*, 2015; Liu *et al.*, 2015a; Cheng *et al.*,

2016). These results indicate that fine roots and mycorrhizal fungi are complementary in nutrient acquisition among coexisting tree species. Furthermore, a trade-off between root branching intensity and lateral root length has also been proposed to optimize water acquisition (Lynch, 2013). These diverse trade-offs among belowground traits should lead to a multifaceted array of resource foraging strategies with each unique, viable strategy and particular trait space occupied by a given species (Chen *et al.*, 2016). Previous studies have also implied that several critical belowground traits – such as fine-root diameter, root branching, lateral root length and mycorrhizal colonization – may be essential in defining variation among global soil resource foraging strategies. Despite observations in woody plants at local scales (Eissenstat *et al.*, 2015; Liu *et al.*, 2015a; Cheng *et al.*, 2016), the universality of trade-offs among root and mycorrhizal fungal traits in different plant forms and communities has yet to be tested. Here, we chose 27 plant species from three grassland communities along a precipitation gradient, to test the hypothesis that there are various trade-offs among root traits and between root traits and mycorrhizal fungal trait. We expected that different combinations of traits will facilitate coexistence of diverse belowground strategies as each species occupies a unique trait space.

Given that available trait space often differs markedly in communities adapted to different environmental conditions (Dwyer & Laughlin, 2017), belowground strategies of species should change along environment gradients. Precipitation is the most important limiting factor in the temperate steppe (Yang *et al.*, 2011), and responses of belowground traits to increasing water stress can reflect diverse water acquisition and adaptive strategies. Generally, plants may increase lateral root length (Lynch, 2013), but often decrease lateral root branching (Zhan *et al.*, 2015) to improve drought tolerance. In addition to changes in root form, both increases and decreases in mycorrhizal colonization have been observed with increasing water stress (Liu *et al.*, 2015b; Ruiz-Lozano *et al.*, 2016). Plants may reduce mycorrhizal colonization, as mycorrhizal fungi can represent a large carbon cost to the plant (Douds *et al.*, 2000) yet have little direct effect on water uptake (Smith & Read, 2008). Conversely, increasing mycorrhizal colonization can improve plant drought tolerance by modifying root hydraulic properties (Augé, 2001). We hypothesize that regionally common species (observed across multiple communities) will decrease root branching but increase lateral root length in response to decreasing precipitation. We further predict that mycorrhizal colonization will probably decrease because of reduced overall resource availability in drier sites. However, it is important to note that trait sensitivity and/or intraspecific variation is not equal among all species (Violle *et al.*, 2012). Root traits of thin-root species often have higher sensitivity and greater plasticity in varied environments than those of thick-root species (Fitter, 1994). Similarly, the ability of plants to regulate mycorrhizal colonization with changes in soil resource environments also varies across species (Grman, 2012; Grman & Robinson, 2013). Therefore, we also predicted that the extent of trait variation will differ among species, with thin-root species generally

being more responsive across sites while thick-root species will express greater trait conservatism (i.e. be less responsive).

Interspecific and intraspecific trait variation is a crucial factor enabling plants to adapt to varied environments and may also determine the local dominance of individual species (Benito Garzón *et al.*, 2011). In tropical forests with little topographic complexity, Umaña *et al.* (2015) found that locally dominant species had lower variation around optimal trait values than rare species and occupied core positions within community trait space. In this case, a core position refers to a species that expresses a particular trait value that is similar to the average trait value for the entire community. This allows for high efficiency in exploiting resources in a given environment and may confer a significant growth advantage (Muscarella & Uriarte, 2016). Unfortunately, few studies combine observations from a locally homogeneous environment together with investigation into species abundances and their intraspecific trait variation at a regional scale with larger environmental heterogeneity. Despite this limitation, Umaña *et al.* (2015) predicted that regionally common species, as opposed to locally common species, might have higher intraspecific trait variation enabling them to maintain high fitness and ensure success across multiple habitats. Therefore, across communities along a resource gradient, we hypothesized that regionally common species have higher intraspecific trait variation compared with regionally rare species (species only present within a single community).

To test our hypotheses, we selected three temperate grassland communities along a precipitation gradient in Inner Mongolia, China. Based on the current expectations for trait variation within and among species (McCormack *et al.*, 2017), we chose to measure four critical traits for the first two lateral root branch orders, including root diameter, root branching intensity, lateral root length of first-order roots (first-order root length) and mycorrhizal colonization, across 27 coexisting species. These traits were selected, first, because of their potential and expected relationships to soil resource acquisition. Additionally, each trait is relatively easy to measure and can be readily incorporated into future trait studies if appropriate. They also represent a range of evolutionary and adaptive histories, with root diameter showing a strong phylogenetic signal and low intraspecific variation across environments while root length and root branching often show low phylogenetic signal but high intraspecific variation (Kong *et al.*, 2014; McCormack *et al.*, 2017; Valverde-Barrantes *et al.*, 2017). Finally, mycorrhizal fungi represent a crucial component of plant–soil resource acquisition strategies (Walder & van der Heijden, 2015) and may mediate advantages and disadvantages of root morphology and architecture. In a stable environment, plant and mycorrhizal fungi preferentially allocate resources to higher quality partners (Bever *et al.*, 2009; Werner & Kiers, 2015) and, under this scenario, mycorrhizal colonization can represent the relative mycorrhizal dependence of different plant species (Lekberg & Koide, 2005). Using these trait observations, we aimed to identify a trait space that can define shifts in belowground strategies among coexisting species, and to examine the link between species abundance distribution and intraspecific trait variation across multiple habitats.

Materials and Methods

Study sites

The three study sites are located within the semiarid steppe in Duolun County (DL; 42°02'N, 116°17'E; 1324 m above sea level (asl)), Zhengxiangbai Banner (ZB; 42°24'N, 115°17'E; 1269 m asl) and Sunitezuo Banner (SZ; 42°53'N, 114°04'E; 1182 m asl), within the Inner Mongolia Autonomous Region of China (Supporting Information Fig. S1a). Long-term mean annual precipitation (MAP) is *c.* 385, 326 and 223 mm in DL, ZB and SZ, respectively (Table 1), with *c.* 90% of the total annual precipitation distributed from May to October in all sites. Mean annual evapotranspiration (ET) is 267, 210 and 146 mm across the three sites, respectively (Table 1). Mean annual temperature is 2.1, 2.7 and 2.0°C in DL, ZB and SZ, respectively, and the sites are characterized by a short growing season extending from May to September. Precipitation in 2015 was measured using a rain gauge and recorded using a CR200X datalogger (Campbell Scientific, Logan, UT, USA) twice per hour beginning on 1 May 2015 and is presented in Table 1 and Fig. S1(b). The soil in the three sites is classified as 'chestnut' according to the Chinese classification or Haplic Calcisols according to the Food and Agricultural Organization classification. Initial soil test results showed that soil fertility was similar among the three sites. Soil total nitrogen content was 0.64, 0.75 and 0.72 g kg⁻¹, and soil total phosphorus content was 0.28, 0.35 and 0.33 g kg⁻¹ in the topsoil layer (0–40 cm) in DL, ZB and SZ, respectively (Table S1). The vegetation at each site is dominated by perennial herbaceous species.

At each site, a 40 × 40 m experimental area with roughly uniform vegetation was established. Within this experimental area, three 5 × 5 m square plots were randomly laid out with at least 10 m distance between the plots. Each 5 × 5 m plot was divided into 25 equally distributed 1 × 1 m subplots. We then selected five subplots in each plot: four subplots were arranged as a square in each corner of the main plot with the fifth subplot occurring in the center. Thus, 15 subplots were established to investigate the community structure of grassland within each of the three sites for a combined total of 45 subplots.

Vegetation survey

At each site, vegetation records were based on the 15 (1 × 1 m) vegetation subplots which were each divided into 100 (10 × 10 cm) equally distributed grids. The occurrence of species as well as the

number of individuals and per cent coverage of each species was recorded in each grid in early August 2015. A visual estimation method was used to obtain the per cent cover of each species in each grid, and summed across all 100 grids to obtain estimate of species cover in the subplot (Yang *et al.*, 2011). We then classified the recorded plants into four groups: nonmycorrhizal, grass, forb and allium species (Fig. S2). Detailed information of the species sampled across the three sites is presented in Table S2.

Root trait measurements

Ten individuals of each species cataloged during the vegetation survey were collected within the experimental area to measure root traits. For each individual plant, we gently excavated the 0–40 cm soil layer to obtain most of the roots. Previous samplings indicated that >85% of the biomass of the finest lateral roots (or first-order roots) was distributed in this layer (D. L. Guo, unpublished data). The intact root samples were carefully washed with tap water to remove the soil adhering to roots. Root samples were then frozen at –20°C until the measurement of root traits.

We measured four root traits related to the trade-off between carbon investment and resource acquisition to characterize the plant adaptive strategies along the precipitation gradient. These traits included root diameter and mycorrhizal colonization measured on the first two root orders together, root branching intensity, and first-order root length (Table S2). These parameters were assessed on a root order basis according to the morphometric (i.e. centripetal) root order classification (Pregitzer *et al.*, 2002). Root samples from each root order were arranged in water (such that there was no overlap between roots) and then scanned (Expression 10000XL; Epson, Suwa, Japan). From the scanned images, average diameter and total length for the first two root orders were measured using WINRHIZO software (Regent Instruments Inc., Quebec City, QC, Canada). For a given sample, manual counts were used to determine the numbers of first-order roots on each second-order root under a dissecting scope. Root branching intensity was then calculated as the number of first-order roots divided by the root length of second-order roots (Kong *et al.*, 2014).

To assess mycorrhizal colonization, root samples were first cleared in 10% (w/v) KOH solution at 90°C for 15 min to remove color from the root, acidified in 5% HCl at room temperature for 5 min and then stained with 0.05% (w/v) acid fuchsin (1.2 g acid fuchsin mixed with 2400 ml of solution, which included glycerin (70%), lactic acid (10%) and water in proportions of 1 : 1 : 1 by volume) at 90°C for 30 min. We then randomly selected 50 root segments of first and second orders with an

Table 1 Climatic characteristics of the three study sites

Site	Abbreviation	Latitude and longitude	Temperature (°C)			Precipitation (mm)		ET (mm)
			MAT	January	July	MAP	May–August	
Duolun County	DL	42°02'N, 116°17'E	2.1	–17.5	18.9	385	221	267
Zhengxiangbai Banner	ZB	42°24'N, 115°17'E	2.7	–19.1	17.6	326	143	210
Sunitezuo Banner	SZ	42°53'N, 114°04'E	2.0	–18.7	22.0	223	104	146

MAT, mean annual temperature; MAP, mean annual precipitation; May–August, growth stage in 2015; ET, evapotranspiration.

average length of 1 cm to measure mycorrhizal colonization according to the method described by McGonigle *et al.* (1990) with a Leica light microscope ($\times 200$; Leica DM 2500; Leica Mikrosysteme Vertrieb GmbH, Bensheim, Germany).

Data analysis

The mean values and coefficient of variation (CV) of all traits averaged across 27 species in three sites were calculated. To test our first hypothesis and determine multifarious trade-offs among the four key traits, pairwise trait relationships were assessed using linear regression in SPSS 19.0 (SPSS Inc., Chicago, IL, USA). These analyses were conducted with and without using phylogenetic independent contrasts (PICs) to analyze trait relationships after removing the influence of phylogeny using the R package PICANTE (Kembel *et al.*, 2010). Results reported as significant indicated that responses were consistent with and without using PICs. Cases where the significance of a test was changed with the PICs are specifically indicated in the text.

Next, we determined whether regionally common species (species that occurred across sites) tended to alter root branching intensity, root diameter, first-order root length and mycorrhizal colonization in response to the precipitation gradient to test our second hypothesis. Similarly, we tested whether plant species specifically altered a single trait or a combination of traits to respond to the precipitation gradient. Linear regression was used to examine the relationship between the degree of change among each of the four traits and MAP, total precipitation from May to August 2015 (growth stage) and precipitation in July 2015, respectively. The degree of change for each trait within each regionally common species represented the difference in mean trait value between the driest (or drier) site and the wettest site. We then used one-way ANOVA to test the influence of precipitation on four traits of each regionally common species, and, when appropriate, conducted post hoc means comparisons using least square difference (LSD) tests in SPSS 19.0 (SPSS Inc.).

Finally, we tested our third hypothesis that regionally common species have higher intraspecific trait variation than do regionally rare species, which relates to their differential success across multiple habitats. Linear regression was used to examine the relationship between the intraspecific variation of a single trait or combination of traits and the total abundances and the importance values of all species across three sites. Intraspecific variation of each trait was represented by variation of trait values among individuals of each species within the regional pool (Violle *et al.*, 2012). We used individual species relative occurrence frequency in three sites to represent species abundance (Klanderud & Totland, 2005). The importance value was calculated as the sum of the relative coverage, relative density and relative occurrence frequency of each species divided by 3. To facilitate comparison of multiple traits, the trait values were scaled before analysis by subtracting the mean and dividing by the standard deviation of each trait, across species (Muscarella & Uriarte, 2016). Furthermore, we wanted to address whether regionally common species occupy core positions within the regional pool while rare species occupy peripheral positions. To do this, we subtracted the community-

weighted mean (CWM) trait values for all sites from the median trait value of each species (Umaña *et al.*, 2015). We calculated the CWM values for each trait t and each habitat b (three sites along the precipitation gradient in the present study) as:

$$CWM_{th} = \sum_{j=1}^S I_{jb} \times t_j$$

where I_{jb} is the importance value of species j in habitat b and t_j is the mean trait value of species j . Thus, the distance of a species from CWM for each trait was calculated (ΔCWM_{tjb}). A small distance value indicates that a species is close to the mean trait value of the community, whereas a large distance value indicates that a species occupies an extreme position in the community-wide trait distribution (Umaña *et al.*, 2015). We also calculated Pearson's correlation coefficients between the mean trait value against the relative occurrence frequency and the importance value of each species across three sites, and between the absolute values of the distance and the importance value.

Results

Interspecific root trait variation across three sites

Across three sites, we observed wide variation in four root traits across 27 species (Fig. S2; Table S2). There was 4.7-fold variation in root diameter of the first two root orders across all the species, ranging from 0.128 mm in *Carex tristachya* (nonmycorrhizal species) to 0.605 mm in *Allium mongolicum* (CV = 58%). Species in the *Allium* genus generally had large root diameters, while grasses tended to have the smallest diameters (Fig. S2). Root branching intensity varied by nearly two orders of magnitude with a CV of 113% (from 0.26 cm^{-1} for *A. mongolicum* to 17.91 cm^{-1} for *C. tristachya*). First-order root length also varied widely, with a CV of 110%, and ranged from 0.048 cm for *C. tristachya* to 1.629 cm for *A. mongolicum*. The variation in mycorrhizal colonization was also large and ranged from 0 in several nonmycorrhizal species to 58% in *Allium bidentatum* (CV = 86%).

Multifarious trade-offs between critical belowground traits across species

Branching intensity across 27 species decreased with increasing root diameter across all species and sites ($R^2 = 0.72$; $P < 0.001$; Fig. 1a). Conversely, mycorrhizal colonization increased with increasing root diameter across all species and sites ($R^2 = 0.80$; $P < 0.001$; Fig. 1b), and first-order root length was also positively correlated to root diameter ($R^2 = 0.80$; $P < 0.001$; Fig. 1c). These correlations also remained robust within each site (Fig. 1; Table S3). However, these correlations between root diameter and branching intensity, between root diameter and first-order root length, and between root diameter and mycorrhizal colonization were greatly reduced after removing the influence of phylogeny via PICs across 27 species (Table S4).

Across the 27 species, mycorrhizal colonization ($R^2 = 0.61$; $P < 0.001$) and first-order root length ($R^2 = 0.62$; $P < 0.001$) showed a strong negative relationship with branching intensity

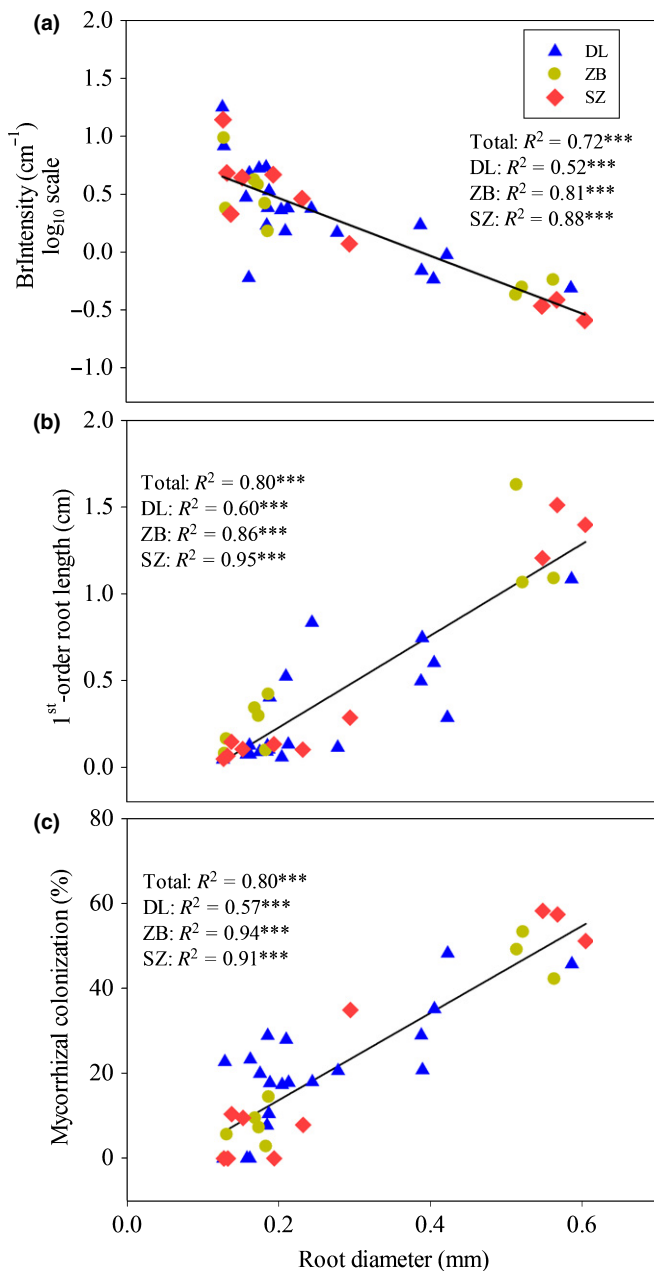


Fig. 1 The relationship of (a) root branching intensity (BrIntensity), (b) first-order lateral root length, and (c) mycorrhizal colonization with mean diameter of the first two order roots across the 27 species at three sites along a precipitation gradient (mean annual precipitation in Duolun County (DL), Zhengxiangbai Banner (ZB) and Sunitezuo Banner (SZ) is 385, 326 and 223 mm, respectively). Note that the y-axis of (a) has a log₁₀ scale. The solid line represents the linear correlation across all species at the three sites. The linear correlation coefficients across species within each site are also shown; there was no difference among the slopes of the regression lines of each site ($P > 0.05$). ***, $P < 0.001$.

(Fig. 2; Table S3). There was also a significant ($P < 0.001$) positive relationship between mycorrhizal colonization and first-order root length ($R^2 = 0.66$; $P < 0.001$). These correlations were nonsignificant after removing the influence of phylogeny via PICs (Table S4), indicating a strong influence of phylogeny on belowground strategies. Different plant groups often exhibited different root trait trade-offs and distribution patterns along a two-

dimensional space, suggesting a diversification of belowground strategies among groups. For example, allium species had relatively thick root diameters, long first-order roots, high mycorrhizal colonization and low branching intensity compared with forb and grass species. At the other end of the trait spaces (Fig. 2), nonmycorrhizal species had lower first-order root length and root diameter, but often had greater variation in branching intensity.

Belowground traits of regionally common species respond to precipitation gradient

The four traits measured across the regionally common species each showed a different degree of response (intraspecific trait variation) to the precipitation gradient. The fine-root diameter of regionally common species did not vary significantly along the precipitation gradient (Table S5). However, higher precipitation tended to be associated with higher mycorrhizal colonization and branching intensity but lower first-order root length (Fig. 3a,c; Table S5). For example, precipitation during the 2015 growing season was positively correlated with mycorrhizal colonization and branching intensity, but negatively correlated with first-order root length. The branching intensity of *C. tristachya* and *Cleistogenes squarrosa* in sites ZB and SZ was 22–46% and 72–75% lower than that in site DL, which had the highest precipitation (Fig. 3a). Similarly, the branching intensity of *A. bidentatum* and *Allium ramosum*, which had relatively thick roots, decreased by 31% and 32%, respectively, in sites with lower precipitation. While not always significant, this pattern was roughly consistent across all species occurring at more than one site. Mycorrhizal colonization also tended to be lower in sites with lower precipitation. This was clearest among thin-root species, which all reduced mycorrhizal colonization by 50–84%, while only a single thick-root species (*A. ramosum*) showed a significant, 27% increase (Fig. 3c). Conversely, the length of first-order roots tended to be higher in sites with lower precipitation. Five thin-root species (all except *Stipa krylovii*) reduced first-order root length by 38–75% in the wetter sites compared to the drier sites (Fig. 3b). One thick-root species (*Allium tenuissimum*) also showed a 33% decrease in first-order root length, while most other thick-root species remained unchanged. Overall, thin-root species exhibited greater plasticity in root traits than thick-root species.

Regionally common species employed diverse combinations of traits to respond to the decreasing precipitation (Table 2). For instance, *Agropyron cristatum* significantly altered three belowground traits (decreased root branching intensity and mycorrhizal colonization and increased first-order root length significantly), while *A. bidentatum* adjusted only one trait (decreased root branching intensity) to adapt to the decreasing precipitation. Furthermore, each trait of a given species had particular change degree (Fig. 3) and response direction (Table 2), suggesting diverse adaptive strategies.

Intraspecific root trait variation and species abundance at a regional scale

We found a positive correlation between intraspecific variation in traits or combinations of traits and a species' relative occurrence frequency and importance value across the three sites (Tables 3,

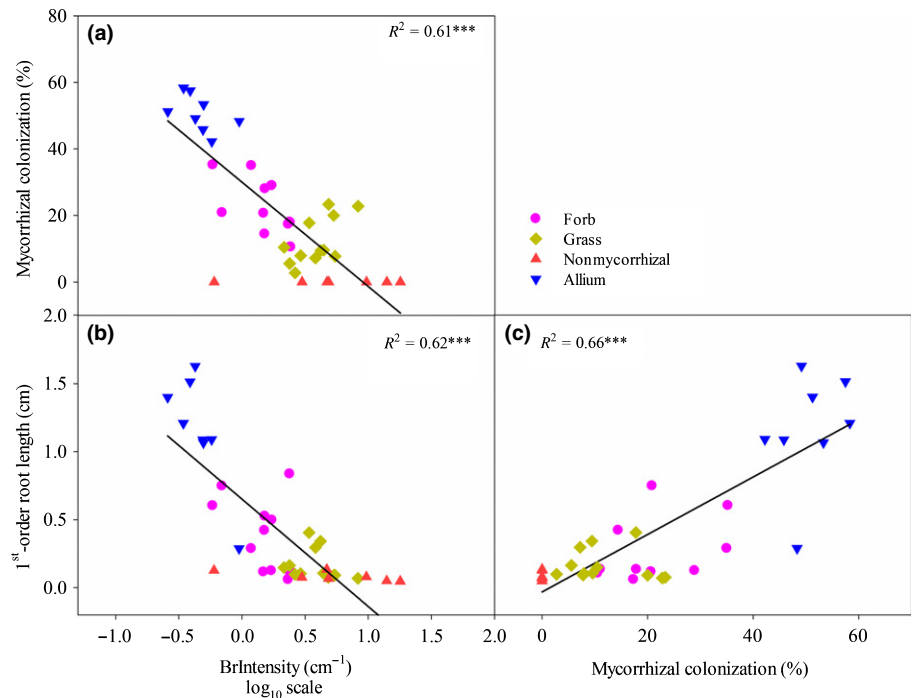


Fig. 2 The relationship of root branching intensity (BrIntensity, on a \log_{10} scale) with (a) mycorrhizal colonization and (b) first-order lateral root length, and (c) the relationship of mycorrhizal colonization with first-order lateral root length across the 27 species (belonging to four different plant groups) at three sites along the precipitation gradient. ***, $P < 0.001$.

S6; Fig. S3). This indicated that regionally common species tend to exhibit higher variance in traits than rare species across regionally heterogeneous precipitation environments. However, intraspecific variation of root diameter and first-order root length was not related to species abundance, suggesting that root branching intensity and mycorrhizal colonization may play more important roles in adapting belowground resource acquisition strategies along the precipitation gradient.

Next, the relative position of regionally common and rare species within the entire range of trait values was quantified across three habitats. For root branching intensity, most of the common species tended to occupy core positions and rare species tended to occupy extreme positions within the functional trait space observed across the total community across all sites (Fig. 4); that is, common species tended to not have very high or very low branching intensities compared with most other species. However, there was a notable exception, *C. tristachya*, which was a regionally common species occurring in all three habitats, yet also had an uncommonly high branching intensity compared with the typical community range. Moving across sites, root branching intensity was positively correlated with species relative occurrence frequency and importance value (Table S7), suggesting that species with higher lateral root branching intensity were better able to adapt to changing water availabilities. Unlike branching intensity, first-order root length, mycorrhizal colonization and fine-root diameter did not display a consistent pattern and both regionally common and rare species were found across the full range of observed trait values (Figs S4–S6).

Discussion

From the perspective of functional ecology, an important step towards understanding belowground foraging strategies is to

identify critical traits in which species differ markedly and which also confer adaptive advantages under different environmental conditions. The combination of these critical traits then forms a trait space that can define a particular belowground strategy. The four traits selected for our study, that is, root diameter, root branching intensity, first-order root length and mycorrhizal colonization, all showed marked variation among coexisting species in all sites (Fig. 1; Table S2), and within the same species across the precipitation gradient (Fig. 3).

Trade-offs between traits in resource acquisition strategies

Variation and covariation of critical traits can form a unique trait space for individual species and diverse belowground strategies within a stable community (Lambers *et al.*, 2008). Trade-offs between root traits and between roots and associated mycorrhizal fungi have been recognized across different plant populations (Seifert *et al.*, 2009) and across species (Postma *et al.*, 2014; Koziol & Bever, 2015), which together highlighted the diversity of resource foraging strategies. In this study, our results showed that, compared with thick-root species, thin-root species had a higher root branching intensity (Fig. 1a), but had shorter lateral root length (Fig. 1b) and lower mycorrhizal colonization (Fig. 1c). These results support our first hypothesis that a variety of trade-offs exist between belowground traits that form diverse resource foraging strategies among coexisting species. Specifically, thin-root species preferentially rely on highly branched lateral roots for resource acquisition, whereas thick-root species rely more on mycorrhizal fungi to explore for soil resources, suggesting that there exists a spectrum of effective resource acquisition strategies across thin- and thick-root species. Similar trade-offs in nutrient foraging strategies between fine roots and mycorrhizal fungi have also been observed across subtropical and temperate

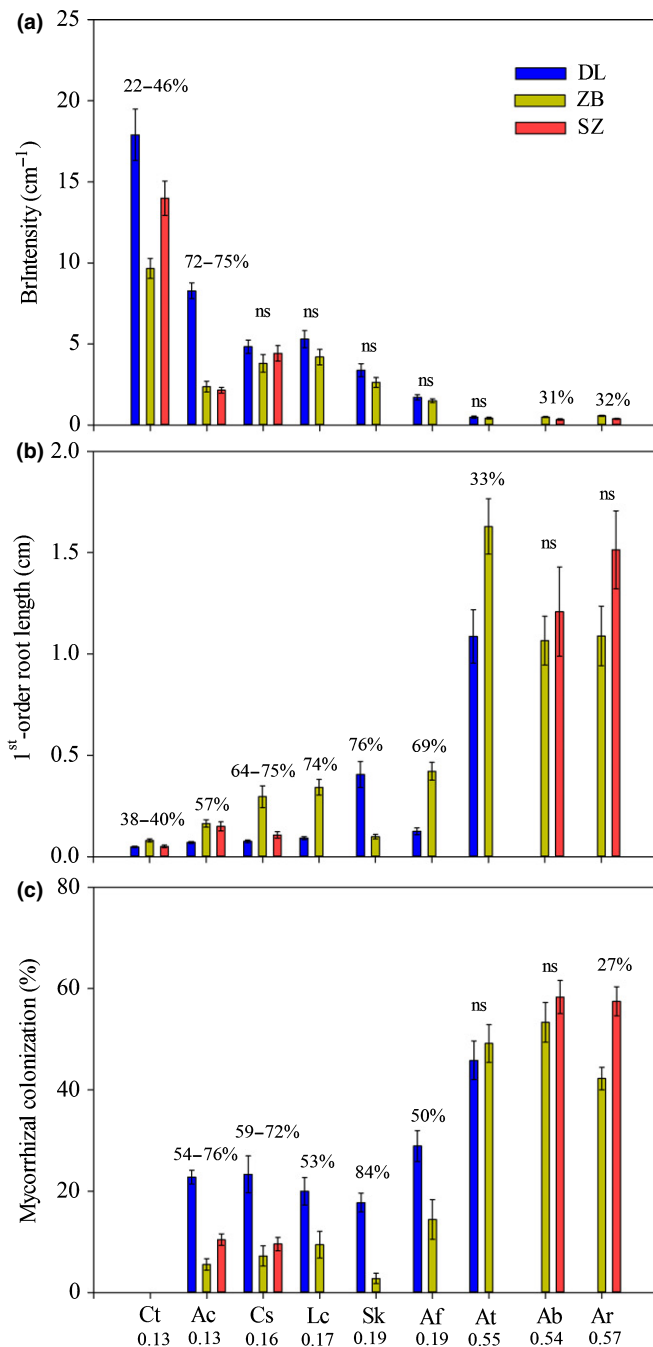


Fig. 3 The trait values (\pm SE) of nine regionally common species (appearing in two or three sites) at different sites. (a) root branching intensity, (b) first-order root length, (c) mycorrhizal colonization. The change of the trait values is shown above the column of each species, which was calculated as the percentage change in the trait between the site with lowest (or lower) trait value and the site with the highest trait value. The mean diameter (mm) of each species is listed below the species name. Ct, *Carex tristachya* (nonmycorrhizal species); Ac, *Agropyron cristatum*; Cs, *Cleistogenes squarrosa*; Lc, *Leymus chinensis*; Sk, *Stipa krylovii*; Af, *Artemisia frigida*; At, *Allium tenuissimum*; Ab, *Allium bidentatum*; Ar, *Allium ramosum*.

tree species (Eissenstat *et al.*, 2015; Liu *et al.*, 2015a; Chen *et al.*, 2016; Cheng *et al.*, 2016). Integrating our results and the results of these studies, we suggest that the diverse plant resource acquisition strategies resulting from trade-offs among belowground

Table 2 Four critical belowground traits of nine regionally common species (appearing in two or three sites) in response to the precipitation gradient

Species	Traits			
	Root diameter	Branching intensity	First-order root length	Mycorrhizal colonization
<i>Carex tristachya</i>	\leftrightarrow	\downarrow	\uparrow	●
<i>Agropyron cristatum</i>	\nearrow	\downarrow	\uparrow	\downarrow
<i>Cleistogenes squarrosa</i>	\nearrow	\searrow	\uparrow	\downarrow
<i>Leymus chinensis</i>	\leftrightarrow	\searrow	\uparrow	\downarrow
<i>Stipa krylovii</i>	\leftrightarrow	\searrow	\downarrow	\downarrow
<i>Artemisia frigida</i>	\leftrightarrow	\searrow	\uparrow	\downarrow
<i>Allium tenuissimum</i>	\downarrow	\leftrightarrow	\uparrow	\leftrightarrow
<i>Allium bidentatum</i>	\nearrow	\downarrow	\leftrightarrow	\leftrightarrow
<i>Allium ramosum</i>	\leftrightarrow	\downarrow	\nearrow	\uparrow

\uparrow , positive response; \nearrow , predominantly positive response; \downarrow , negative response; \searrow , predominantly negative response; \leftrightarrow , predominantly no response. Species are ordered from smallest first-order root diameter (*Carex tristachya*; nonmycorrhizal species ●) to largest first-order root diameter (*Allium ramosum*).

Table 3 Linear correlation between individual traits and relative occurrence frequency, and between combinations of traits and relative occurrence frequency among the 27 species across three sites

Variable	Coefficient	R^2	P -value	df
Root diameter	-4.2	0.03	0.35 ns	26
BrIntensity	20	0.37	<0.001***	26
First-order root length	0.40	0.00	0.97 ns	26
Mycorrhizal colonization	4.3	0.30	0.007**	22
BrIntensity + mycorrhizal colonization	23	0.53	<0.001***	26
Root diameter + first-order root length	-3.7	0.00	0.77 ns	26
Four traits combined	20	0.08	0.15 ns	26

Significance levels are shown: ns, nonsignificant at $P > 0.05$; **, $P < 0.01$; ***, $P < 0.001$. BrIntensity, root branching intensity.

traits may be common in both herbaceous and woody plant ecosystems.

The co-occurrence of diverse combinations of plant traits can facilitate community stability (Kraft *et al.*, 2015). Furthermore, the complementarity and trade-offs in resource foraging strategies between belowground traits may reduce interspecific competition across coexisting species, especially in resource-limited environments (Zemunik *et al.*, 2015). Supporting this idea, our results showed a distinct pattern of root trait dispersion across species groups that regularly coexisted within each site (Fig. 2). For example, alliums tended to have high mycorrhizal colonization and low branching intensity, while grasses had the opposite traits (Fig. 2a). Species that occupy dissimilar trait space are thought to

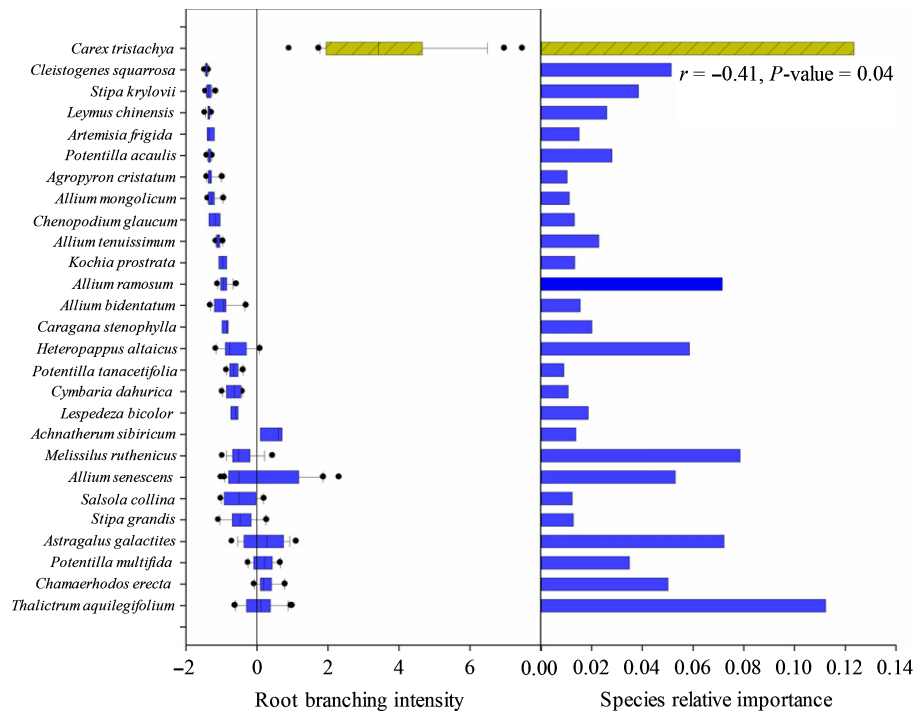


Fig. 4 The relative position of species in the root branching intensity (BrIntensity) distribution across the three sites. Left panel: the x-axis represents the difference between median BrIntensity for the species and community-weighted mean (CWM) BrIntensity for the entire community. The y-axis arrays species from bottom to top based on how close they are to the CWM value. Each boxplot represents the distribution of BrIntensity by species. Right panel: species importance value across all three sites. The result of Pearson correlation analysis of the absolute values of the differences between the median trait value of the species (except *Carex tristachya*; the dark yellow plot) and the CWM trait value of the community against the importance value of the species is provided at the upper right. Negative correlations indicated that common species tended to have mean trait values closer to CWM trait values, whereas rare species had mean trait values more distant from CWM trait values.

coexist more easily because each strategy can better adapt to unique local conditions (Kraft *et al.*, 2008; de Bello *et al.*, 2013). Thick-root species which depend more on mycorrhizal fungi (such as alliums and some forb species; Fig. 2a) may easily absorb nutrients at a distance via hyphae (up to 25 cm; Jansa *et al.*, 2003), whereas thin-root species (such as grasses and nonmycorrhizal species) may rely more on short and dense clustering of lateral roots (Fig. 2), which can maximally exploit nutrients in rhizosphere (Shen *et al.*, 2013). Thus, complementarity of lateral roots and mycorrhizal fungi across coexisting species can utilize the limited soil volume more fully and may also represent a form of niche partitioning that facilitates greater species coexistence (Silvertown, 2004). This also enables fine roots of thin-root species to invade the soil space of the thick-root species, as we observed in our field sites (H. Li, pers. obs.). For example, the nonmycorrhizal species *C. tristachya*, which has relatively thin roots, high root branching, and short length of first-order lateral roots (Table S2), commonly coexists in close proximity to many other species with relatively thick roots and high mycorrhizal colonization, potentially as a consequence of niche differentiation within the rhizosphere.

Root traits of regionally common species respond to precipitation gradients

In agreement with our second hypothesis, eight of nine regionally common species observed in this study significantly reduced root

branching and/or mycorrhizal colonization with decreasing precipitation (Fig. 3a,c). This suggests that plants tend to decrease the relative proportion of thin lateral roots and/or reduce plant carbon investments in mycorrhizal fungi and, in turn, are likely to promote thicker primary root elongation to obtain water from deeper soil layers (Schenk & Jackson, 2002; Zhan *et al.*, 2015). Despite the fact that the response patterns of these critical traits to water stress was directionally consistent for most of the common species, the degree of each response varied substantially among species. Thin-root species showed greater plasticity in response to water stress, both by decreasing root branching and/or mycorrhizal colonization and increasing first-order lateral root length (Fig. 3). Similar evidence for greater root plasticity in thin- than thick-root species has also been observed in woody plants (Eissenstat *et al.*, 2015; Liu *et al.*, 2015a), crops (Li *et al.*, 2014), and other grass species (Fitter, 1994), suggesting that thin-root species, generally speaking, are more responsive to variable environments.

We found that the plant adaptive strategies in this study were not always driven by directional changes in all four traits across the gradient. Instead, species adaptations to decreasing precipitation were often captured by just one, two or three traits, though the degree, and sometimes the direction of change varied among species (Table 2). These results are consistent with observations in previous studies demonstrating that different species may employ different strategies as they respond to their environment. For instance, when plants encounter a nutrient patch, some

species first express a distinct root physiological response (e.g. increased ion uptake) (Caldwell, 1994); some species proliferate new roots in the nutrient-rich zone to capture more nutrients and obtain competitive advantage; some species may use a combination of both strategies; and other species show no discernable adjustment (Fransen & de Kroon, 2001). Similarly, plant species and even individual genotypes often differ in their ability to alter allocation to arbuscular mycorrhizal fungi in different contexts (Grman, 2012; Chu *et al.*, 2013). These studies and our results reflect diverse adaptive strategies by which traits respond to various environmental factors and together form multifarious trait-based adaptive strategies. Meanwhile, intraspecific covariation of multiple traits also partly reveals the coexistence mechanism of species: even if some species have the same trait means and variances, but have opposite covariance, they may still occupy different trait spaces and niches (Laughlin & Messier, 2015).

Correlation between intraspecific variation in belowground traits and species' relative abundance

There was a positive correlation between intraspecific variation in root traits and a species' relative abundance at the regional scale (Table 3; Fig. S3). This indicated that high intraspecific trait variation and phenotypic plasticity may facilitate greater fitness and chances of survival in new or suboptimal environments across multiple habitats (Forsman, 2014; González-Suárez *et al.*, 2015). For example, previous studies have shown that invasive species often have higher phenotypic plasticity than noninvasive species, which may enable them to adapt to novel environments and rapidly respond to disturbance (van Kleunen *et al.*, 2010; Davidson *et al.*, 2011). In agreement with our third hypothesis, regionally rare species tended to exhibit lower trait variation than regionally common species (Table 3; Fig. S3). Thus, our results provide support for the prediction by Umaña *et al.* (2015), who proposed that regionally common species should have high intraspecific trait variation centered around optimal trait values on larger spatial scales with higher environmental heterogeneity. Conversely, the relative trait conservatism of regionally rare species may have given them an advantage for exploiting water within a site and locally homogeneous environment (Grime, 2006). Among the traits measured, we found that variation in plant abundance was best explained by the combination of root branching and mycorrhizal colonization (Table 3; Fig. S3). This strongly suggests the need to integrate observations of critical root traits together with direct consideration of their mycorrhizal associations to obtain clearer and more powerful assessments of trait variation and plant fitness across environmental gradients.

Our results showed that, for root branching intensity, the majority of regionally common species tended to exhibit median trait values closer to regional CWM trait values (Fig. 4), which could be explained by root branching intensity being able to determine the species distribution abundance (Table S7). Generally speaking, species are more likely to occur in areas where their median trait values are less distant from the CWM trait values (Muscarella & Uriarte, 2016), especially when the particular traits of interest are integral to a plant strategy for adapting to a

given environment (Umaña *et al.*, 2015). However, the species *C. tristachya* was a clear exception. It had a high importance value (e.g. high dominance) within the regional community, yet expressed traits that were distant from the CWM traits. One explanation for this may be that *C. tristachya* had a very distinct resource acquisition strategy, because this is a nonmycorrhizal species with higher lateral root branching intensity than all the other species in our study. In general, however, our results suggested that having high root branching intensity and short lateral root length seems to be an effective adaptive strategy in drought conditions.

Conclusions

Among a diverse array of herbaceous plants along a precipitation gradient, we found that there existed distinct trade-offs between root traits and a complementarity between lateral roots and mycorrhizal fungi in resource acquisition at both local and regional scales: thin-root species rely more on highly branched, fine lateral roots, whereas thick-root species rely more on mycorrhizal fungi. Furthermore, we found that, on the whole, regionally common species significantly decrease root branching intensity and/or mycorrhizal colonization, but increase lateral root length, in response to water stress, yet the specific degree and direction of response for individual traits or combinations of traits varied among species, resulting in diverse adaptive strategies across species. Meanwhile, regionally common species had higher intraspecific trait variation along the precipitation gradient compared with regionally rare species. Root branching intensity in particular appeared to be an especially important trait reflecting plant adaptive success across the gradient as branching intensity was positively correlated with plant abundance across the precipitation gradient and occupied a core position within the regional community trait distribution. Based on these results, we propose that a limited number of the principal belowground traits measured here can effectively define diverse resource foraging and environmental adaptation strategies in different environments, thus emphasizing the need to integrate observations of belowground strategies into assessments of whole-plant adaptations to changing environments.

Acknowledgements

We thank Biao Zhu (Peking University) for his helpful comments. This research was supported by the National Natural Science Foundation of China (grant no. 31600319) and the National Basic Research Program of China (no. 2013CB956303).

Author contributions

H.L. and D.G. designed the experiment with assistance from M.L.M. B.L. and Z.M. obtained the belowground trait data, and H.L. organized the data set. H.L. and M.L.M. coordinated the analysis and write-up of the work and all authors contributed to revisions.

References

- Adler PB, Fajardo A, Kleinhesselink AR, Kraft NJ. 2013. Trait-based tests of coexistence mechanisms. *Ecology Letters* 16: 1294–1306.
- Augé RM. 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza* 11: 3–42.
- Bardgett RD, Mommer L, De Vries FT. 2014. Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution* 29: 692–699.
- de Bello F, Vandewalle M, Reitalu T, Lepš J, Prentice HC, Lavorel S, Sykes MT. 2013. Evidence for scale- and disturbance-dependent trait assembly patterns in dry semi-natural grasslands. *Journal of Ecology* 101: 1237–1244.
- Benito Garzón M, Alía R, Robson TM, Zavala MA. 2011. Intra-specific variability and plasticity influence potential tree species distributions under climate change. *Global Ecology and Biogeography* 20: 766–778.
- Bever JD, Richardson SC, Lawrence BM, Holmes J, Watson M. 2009. Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. *Ecology Letters* 12: 13–21.
- Caldwell MM. 1994. Exploiting nutrients in fertile soil microsites. In: Caldwell MM, Pearcy RW, eds. *Exploitation of environmental heterogeneity of plants*. New York, NY, USA: Academic Press, 325–347.
- Chen WL, Koide RT, Adams TS, De Forest JL, Cheng L, Eissenstat DM. 2016. Root morphology and mycorrhizal symbioses together shape nutrient foraging strategies of temperate trees. *Proceedings of the National Academy of Sciences, USA* 113: 8741–8746.
- Cheng L, Chen W, Adams TS, Wei X, Li L, McCormack ML, DeForest JL, Koide RT, Eissenstat DM. 2016. Mycorrhizal fungi and roots are complementary in foraging within nutrient patches. *Ecology* 97: 2815–2823.
- Chu Q, Wang X, Yang Y, Chen F, Zhang F, Feng G. 2013. Mycorrhizal responsiveness of maize (*Zea mays* L.) genotypes as related to releasing date and available P content in soil. *Mycorrhiza* 23: 497–505.
- Comas LH, Eissenstat DM. 2004. Linking fine root traits to maximum potential growth rate among 11 mature temperate tree species. *Functional Ecology* 18: 388–397.
- Davidson AM, Jennions M, Nicotra AB. 2011. Do invasive species show higher phenotypic plasticity than native species and if so, is it adaptive? A meta-analysis. *Ecology Letters* 14: 419–431.
- Díaz S, Kattge J, Cornelissen JH, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Prentice IC *et al.* 2016. The global spectrum of plant form and function. *Nature* 529: 161–171.
- Douds DD Jr, Pfeffer PE, Shachar-Hill Y. 2000. Carbon partitioning, cost, and metabolism of arbuscular mycorrhizas. In: Kapulnik Y, Douds D Jr, eds. *Arbuscular mycorrhizas: physiology and function*. Dordrecht, the Netherlands: Springer, 107–129.
- Dwyer JM, Laughlin DC. 2017. Constraints on trait combinations explain climatic drivers of biodiversity: the importance of trait covariance in community assembly. *Ecology Letters* 20: 872–882.
- Eissenstat DM, Kucharski JM, Zadworny M, Adams TS, Koide RT. 2015. Linking root traits to nutrient foraging in arbuscular mycorrhizal trees in a temperate forest. *New Phytologist* 208: 114–124.
- Fitter AH. 1994. Architecture and biomass allocation as components of the plastic response of root systems to soil heterogeneity. In: Caldwell MM, Pearcy RW, eds. *Exploitation of environmental heterogeneity of plants*. New York, NY, USA: Academic Press, 305–323.
- Forsman A. 2014. Effects of genotypic and phenotypic variation on establishment are important for conservation, invasion, and infection biology. *Proceedings of the National Academy of Sciences, USA* 111: 302–307.
- Fransen B, de Kroon H. 2001. Long-term disadvantages of selective root placement: root proliferation and shoot biomass of two perennial grass species in a 2-year experiment. *Journal of Ecology* 89: 711–722.
- González-Suárez M, Bacher S, Jeschke JM. 2015. Intraspecific trait variation is correlated with establishment success of alien mammals. *American Naturalist* 185: 737–746.
- Grime JP. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science* 17: 255–260.
- Grman E. 2012. Plant species differ in their ability to reduce allocation to non-beneficial arbuscular mycorrhizal fungi. *Ecology* 93: 711–718.
- Grman E, Robinson TM. 2013. Resource availability and imbalance affect plant–mycorrhizal interactions: a field test of three hypotheses. *Ecology* 94: 62–71.
- van der Heijden MG, Klironomos JN, Ursic M, Moutoglou P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396: 69–72.
- Holdaway RJ, Richardson SJ, Dickie IA, Peltzer DA, Coomes DA. 2011. Species- and community-level patterns in fine root traits along a 120 000-year soil chronosequence in temperate rain forest. *Journal of Ecology* 99: 954–963.
- Jansa J, Mozafar A, Frossard E. 2003. Long-distance transport of P and Zn through the hyphae of an arbuscular mycorrhizal fungus in symbiosis with maize. *Agronomie* 23: 481–488.
- Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26: 1463–1464.
- Klanderud K, Totland Ø. 2005. Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. *Ecology* 86: 2047–2054.
- van Kleunen M, Weber E, Fischer M. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters* 13: 235–245.
- Kong D, Ma C, Zhang Q, Li L, Chen X, Zeng H, Guo D. 2014. Leading dimensions in absorptive root trait variation across 96 subtropical forest species. *New Phytologist* 203: 863–872.
- Kozioł L, Bever JD. 2015. Mycorrhizal response trades off with plant growth rate and increases with plant successional status. *Ecology* 96: 1768–1774.
- Kraft NJ, Godoy O, Levine JM. 2015. Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences, USA* 112: 797–802.
- Kraft NJB, Valencia R, Ackerly DD. 2008. Functional traits and niche based tree community assembly in an Amazonian forest. *Science* 322: 580–582.
- Kunstler G, Falster D, Coomes DA, Hui F, Kooyman RM, Laughlin DC, Poorter L, Vanderwel M, Vieilledent G, Wright SJ *et al.* 2016. Plant functional traits have globally consistent effects on competition. *Nature* 529: 204–207.
- Lambers H, Raven JA, Shaver GR, Smith SE. 2008. Plant nutrient-acquisition strategies change with soil age. *Trends in Ecology & Evolution* 23: 95–103.
- Laughlin DC, Messier J. 2015. Fitness of multidimensional phenotypes in dynamic adaptive landscapes. *Trends in Ecology & Evolution* 30: 487–496.
- Lekberg Y, Koide RT. 2005. Is plant performance limited by abundance of arbuscular mycorrhizal fungi? A meta-analysis of studies published between 1988 and 2003. *New Phytologist* 168: 189–204.
- Li HB, Ma QH, Li HG, Zhang FS, Rengel Z, Shen JB. 2014. Root morphological responses to localized nutrient supply differ among crop species with contrasting root traits. *Plant and Soil* 376: 151–163.
- Li R, Zhu S, Chen HY, John R, Zhou G, Zhang D, Zhang Q, Ye Q. 2015. Are functional traits a good predictor of global change impacts on tree species abundance dynamics in a subtropical forest? *Ecology Letters* 18: 1181–1189.
- Liu Z, Li Y, Ma L, Wei H, Zhang J, He X, Tian C. 2015b. Coordinated regulation of arbuscular mycorrhizal fungi and soybean MAPK pathway genes improved mycorrhizal soybean drought tolerance. *Molecular Plant–Microbe Interactions* 28: 408–419.
- Liu B, Li H, Zhu B, Koide RT, Eissenstat DM, Guo D. 2015a. Complementarity in nutrient foraging strategies of absorptive fine roots and arbuscular mycorrhizal fungi across 14 coexisting subtropical tree species. *New Phytologist* 208: 125–136.
- Lynch JP. 2013. Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. *Annals of Botany* 112: 347–357.
- McCormack ML, Dickie IA, Eissenstat DM, Fahey TJ, Fernandez CW, Guo DL, Helmsaari H-S, Hobbie EA, Iversen CM, Jackson RB *et al.* 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist* 207: 505–518.
- McCormack ML, Guo DL, Iversen CM, Chen WL, Eissenstat DM, Fernandez CW, Li L, Ma CE, Ma ZQ, Poorter H *et al.* 2017. Building a better foundation: improving root-trait measurements to understand and model plant and ecosystem processes. *New Phytologist* 215: 27–37.

- McGonigle TP, Miller MH, Evans DG, Fairchild GL, Swan JA. 1990. A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. *New Phytologist* 115: 495–501.
- Muscarella R, Uriarte M. 2016. Do community-weighted mean functional traits reflect optimal strategies? *Proceedings of the Royal Society B: Biological Sciences* 283: 1827.
- Postma JA, Dathe A, Lynch JP. 2014. The optimal lateral root branching density for maize depends on nitrogen and phosphorus availability. *Plant Physiology* 166: 590–602.
- Pregitzer KS, DeForest JL, Burton AJ, Allen MF, Ruess RW, Hendrick RL. 2002. Fine root architecture of nine North American trees. *Ecological Monographs* 72: 293–309.
- Ruiz-Lozano JM, Aroca R, Zamarreño ÁM, Molina S, Andreo-Jiménez B, Porcel R, García-Mina JM, Ruyter-Spira C, López-Ráez JA. 2016. Arbuscular mycorrhizal symbiosis induces strigolactone biosynthesis under drought and improves drought tolerance in lettuce and tomato. *Plant, Cell & Environment* 39: 441–452.
- Schenk HJ, Jackson RB. 2002. The global biogeography of roots. *Ecological Monographs* 72: 311–328.
- Seifert EK, Bever JD, Maron JL. 2009. Evidence for the evolution of reduced mycorrhizal dependence during plant invasion. *Ecology* 90: 1055–1062.
- Shen J, Li C, Mi G, Li L, Yuan L, Jiang R, Zhang F. 2013. Maximizing root/rhizosphere efficiency to improve crop productivity and nutrient use efficiency in intensive agriculture of China. *Journal of Experimental Botany* 63: 1181–1192.
- Silvertown J. 2004. Plant coexistence and the niche. *Trends in Ecology & Evolution* 19: 605–611.
- Smith SE, Read DJ. 2008. *Mycorrhizal symbiosis*. New York, NY, USA: Academic Press.
- Umaña MN, Zhang C, Cao M, Lin L, Swenson NG. 2015. Commonness, rarity, and intraspecific variation in traits and performance in tropical tree seedlings. *Ecology Letters* 18: 1329–1337.
- Valverde-Barrantes OJ, Freschet GT, Roumet C, Blackwood CB. 2017. A worldview of root traits: the influence of ancestry, growth form, climate and mycorrhizal association on the functional trait variation of fine-root tissues in seed plants. *New Phytologist* 215: 1562–1573.
- Violle C, Enquist BJ, McGill BJ, Jiang LIN, Albert CH, Hulshof C, Jung V, Messier J. 2012. The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution* 27: 244–252.
- Walder F, van der Heijden MG. 2015. Regulation of resource exchange in the arbuscular mycorrhizal symbiosis. *Nature Plants* 1: 15159.
- Werner GD, Kiers ET. 2015. Partner selection in the mycorrhizal mutualism. *New Phytologist* 205: 1437–1442.
- Williams LJ, Paquette A, Cavender-Bares J, Messier C, Reich PB. 2017. Spatial complementarity in tree crowns explainsoveryielding in species mixtures. *Nature Ecology & Evolution* 1: 0063.
- Yang H, Li Y, Wu M, Zhang ZHE, Li L, Wan S. 2011. Plant community responses to nitrogen addition and increased precipitation: the importance of water availability and species traits. *Global Change Biology* 17: 2936–2944.
- Zemunik G, Turner BL, Lambers H, Laliberté E. 2015. Diversity of plant nutrient-acquisition strategies increases during long-term ecosystem development. *Nature Plants* 1: 15050.
- Zhan A, Schneider H, Lynch J. 2015. Reduced lateral root branching density improves drought tolerance in maize. *Plant Physiology* 168: 1603–1615.
- Zuppinger-Dingley D, Schmid B, Petermann JS, Yadav V, De Deyn GB, Flynn DF. 2014. Selection for niche differentiation in plant communities increases biodiversity effects. *Nature* 515: 108–111.

Fig. S1 A map of the three sites (DL, ZB and SZ) and the precipitation from May to August in 2015.

Fig. S2 Root diameter of first- and second-order roots ranked in ascending order of 27 species in the Inner Mongolia grassland of China.

Fig. S3 The relationship between intraspecific trait variation (root branching intensity plus mycorrhizal colonization) and importance values of the species along the precipitation gradient.

Fig. S4 The relative position of species in the first-order root length distribution across the three sites.

Fig. S5 The relative position of species in the mycorrhizal colonization distribution across the three sites.

Fig. S6 The relative position of species in the root diameter distribution across the three sites.

Table S1 Soil nutrient (0–40 cm layer) characteristics of the three study sites

Table S2 Root traits of the 27 species in this study and their sampling sites (mean \pm SE; $n = 10$)

Table S3 Pearson's correlations for pairwise traits within and across three sites

Table S4 Pearson's correlations with phylogenetically independent contrasts (PICs) for four belowground traits across 27 species

Table S5 Linear correlation between precipitation and variance in trait for regionally common species across the three sites

Table S6 Linear correlation between individual traits and combinations of traits against relative importance value among the 27 species across the three sites

Table S7 Pearson's correlations between individual traits against relative occurrence frequency and relative importance value among the 27 species across the three sites

Please note: Wiley Blackwell are not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

See also the Commentary on this article by Comas, 216: 963–964.