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REGULAR ARTICLE

Roots and arbuscular mycorrhizal fungi are independent in nutrient foraging across subtropical tree species

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Abstract

Aims Plant species with thin roots and high root-growth rate are thought to have greater root foraging precision than species with thick roots and low root-growth rate. However, whether root morphological traits (such as root diameter) are correlated with foraging precision of roots and mycorrhizal fungi in heterogeneous nutrient environments across tree species remains unclear.

Methods We examined 13 coexisting arbuscular mycorrhizal subtropical tree species, measured functional traits of roots, leaves and mycorrhizal fungi and assessed foraging precision of roots and mycorrhizal fungi in response to different nutrient patches using an in situ root-bag approach.

Results Thin-root species had greater specific root length and root growth rate than thick-root species, but they showed similar root and mycorrhizal hyphae foraging precisions. As root diameter increased, root foraging precision exhibited the U-shape patterns in the nitrogen and phosphorus patches, but hyphal foraging precision showed a slightly increasing trend only in the nitrogen patch. Foraging precisions of roots and hyphae were independent, and were not influenced by plant traits across species.

Conclusions Our findings challenge the notion that thin-root species with high root growth rate have greater foraging precision, suggesting that root morphological traits may not be correlated with the variation in foraging strategies of roots and mycorrhizal hyphae.

Keywords Mycorrhizal hyphae · Root morphology · Functional traits · Growth rate · Nutrient patches · Plant coexistence · Root foraging precision · Mycorrhizal hyphae foraging precision

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Introduction

Phenotypic plasticity is thought to be a cornerstone of plant adaptation to spatially and/or temporally heterogeneous environments (Valladares et al. 2007). Specifically, foraging precision of roots and mycorrhizal fungi can reflect plant strategies to acquire multiple soil resources from heterogeneous environments (Chen et al. 2018a). For instance, plants can proliferate roots or mycorrhizal hyphae to explore and acquire resources from nutrient-rich soil patches (Hodge 2006), and species with small root diameter were thought to have higher root foraging precision in nutrient-rich patches than thick-root species (Grime et al. 1986; Fitter 1994). However, in addition to root diameter, different types of nutrient patches in the natural environment and the distinct plant demands for different nutrients can also affect the degree of root response to a particular soil patch (Hodge 2004; Mariotte et al. 2017). Thus, although various studies have documented how roots and hyphae respond to nutrient patches (Robinson 1994; Hodge 2004; Kembel and Cahill 2005; Hodge and Fitter 2010; Li et al. 2018), it remains unclear (i) whether we can predict root and mycorrhizal hyphae foraging precisions using certain morphological root traits, and (ii) how root and hyphal proliferation in combination may shape the way plant forage for soil nutrients across a range of plant species.

Generally, the variation in root diameter is strongly constrained by plant phylogeny (Kong et al. 2014; Valverde-Barrantes et al. 2017). There is evidence that the species with a relatively small root diameter and high specific root length, on average, have faster-growing roots (Eissenstat 1991). Additionally, thin-root species are efficient in nutrient foraging, therefore they do not invest in arbuscular mycorrhizal (AM) fungi as much as thick-root species (Bates and Lynch 2001; Hodge 2004; Liu et al. 2015) that rely on the association with AM to enhance exploration of soil volumes (Comas et al. 2014; Eissenstat et al. 2015; Kong et al. 2016). These observations suggest that plant species may have a tradeoff between proliferating roots vs. supporting growth of mycorrhizal hyphae in response to nutrient patches (Chen et al. 2016). In addition, recent studies showed that root branching intensity and mycorrhizal colonization of thin-root species were more sensitive to environmental properties than those of thick-root species (Li et al. 2017; Wen et al. 2019). Together, these studies suggest that foraging precision of roots and/or mycorrhizal fungi across various species in heterogeneous nutrient environments may be influenced by root diameter. A better understanding of how foraging precision is regulated via proliferation of roots and mycorrhizal fungi in response to heterogeneous nutrient environments will deepen our knowledge of diverse foraging strategies across different species, especially in subtropical or tropical forests where root traits of tree species vary widely (Chen et al. 2013).

The attributes of nutrient patches may influence proliferation of root and mycorrhizal hyphae (Hodge and Fitter 2010; Liu et al. 2015; Chen et al. 2018b). However, few field studies have examined the responses of roots and mycorrhizal hyphae simultaneously to nutrient patches, especially with respect to different nutrients. For instance, Drew (1975) found that barley (*Hordeum vulgare*) plants proliferated roots in the nutrient-rich patches of phosphate (P), ammonium and nitrate (N), but not potassium (K), indicating that root proliferation in nutrient patches was nutrient-specific. Johnson et al. (2015) found that AM colonization and hyphal density responded strongly to soil P but not to soil N in the three grassland systems, indicating that the AM fungi responses to nutrient-rich patches are context-dependent. Therefore, understanding whether the responses of roots and mycorrhizal hyphae to nutrient patches are complementary or independent, in a range of coexisting species, can help us better characterize the plant foraging strategies.

A plant intrinsic demand for nutrients is another important driver regulating the response of plant roots and mycorrhizal hyphae to nutrient patches (de Kroon et al. 2009; McCleery et al. 2017). Though all plants need to acquire the same essential nutrients, there is large variation in root and leaf N and P concentration, and thus N:P ratio in terrestrial plants, which can reflect resource partitioning (Han et al. 2005; Zhao et al. 2016, 2018). Some tropical trees display clear preferences for certain forms of soil P (Nasto et al. 2017). Leguminous species generally do not proliferate roots in N-rich patches (Li et al. 2014), possibly because they get ammonium from their root association with N_2-fixing bacteria (Cornwell et al. 2014), decreasing their demand for soil N (Forde 2014). These differences in the nutrient demand may drive the differences in roots and mycorrhizal hyphae responding to a specific nutrient. Additionally, the generally consistent slopes of the relationship between respiration and nitrogen in leaves and roots indicate that broad generalization about resource

economics of leaves have parallels in roots (Reich et al. 2008). Therefore, the responses based on plant intrinsic demands for specific nutrients may influence the foraging precision of roots and mycorrhizal hyphae.

We experimentally examined root foraging of 13 dominant AM tree species in a subtropical forest, across a wide range of root diameters (the most distal first two order roots that are responsible for most of nutrient uptake). Root and mycorrhizal proliferation were evaluated in different nutrient treatments using a root-bag approach. The objectives of this study were to determine: 1) the degree of variation and the relationships of roots, leaves and mycorrhizal hyphae traits among different tree species; 2) whether the foraging precision of roots and mycorrhizal hyphae can be predicted by the root and leaf traits; and 3) how tree species and the types of nutrient patch (N, P or NPK) influence foraging precision of roots and mycorrhizal hyphae.

Materials and methods

Site and tree species description

The study was conducted in the Jiulianshan National Nature Reserve (24°34′ N, 114°27′ E) in the southern part of Jiangxi province, China. The mean annual temperature at our study site is 16.4 °C, and mean annual precipitation is 2156 mm. The soil is classified as clay loam, medium acidic ($pH_{water} = 4.8$), and on average contains 22 g kg^{-1} of total carbon and 1.7 g kg^{-1} of total nitrogen (N), 12 mg kg^{-1} of available N (KCl-extractable ammonium and nitrate), and 25 mg kg^{-1} of available phosphorus (P, ammonium carbonate extraction).

At this site, we selected 13 co-occurring and the most abundant AM tree species representing a wide range of fine root diameters, including 11 woody angiosperm species (*Acer fabri*, *Schima superba*, *Choerospondias axillaris*, *Liquidambar formosana*, *Elaeocarpus glabripetalus*, *Alniphyllum fortunei*, *Cinnamomum porrectum*, *Cinnamomum austrosinense*, *Machilus oculodracontis*, *Manglietia yuyuanensis* and *Neolitsea phanerophlebia*) and two woody gymnosperm species (*Cunninghamia lanceolata* and *Taxus chinensis*). All chosen trees were mature, canopy dominant or codominant, had healthy appearance and 17.5 ± 2.2 cm diameter at breast height (1.3 m from the ground).

Experimental design and nutrient addition study

This experiment was carried out during the 2013 growing season (March to September) using a root-bag technique (Comas and Eissenstat 2004). A ca. 5-mm diameter and 25-cm-long woody root of an identified tree was inserted into a root bag made from polyester fabric (30 cm long and 30 cm wide, with perforations of *c.* 0.5 mm). To ensure that future absorptive roots arising from this woody root represent new growth, all lateral fine roots were trimmed off before woody root was enclosed in the bag. In most cases, root pruning was minimal. The bag was then filled with 3 kg of sieved homogenized forest soil with different fertilizer treatments to simulate nutrient patchy environments, and then covered with the original litter layer and watered.

For each species, there were four treatments: 1) unfertilized control; 2) N-patch (+N, 0.06 g N kg^{-1} dried soil, in the form of slow-release urea); 3) P-patch (+P; 0.14 g P kg^{-1} dried soil, in the form of NaH_2PO_4); and 4) NPK-patch (+NPK; 0.06 g N, 0.03 g P and 0.05 g K kg^{-1} dried soil, in the form of Osmocote 19–6-12 slow-release compound fertilizer; Scotts-Sierra Horticultural Products Company, Marysville, WA, USA). The amount of fertilizer was four times the 'available' soil background N (for N- and NPK-fertilizer) or P (for P-fertilizer treatment) concentration on the site, which has been shown to effectively induce root proliferation (Adams et al. 2013). Four different nutrient addition treatments were assigned to an individual tree for all of the selected species, with four replicate trees per species. In total, there were 52 treatments (13 species × 4 nutrient additions) in 4 replicates.

Harvest and measurements

All root bags were harvested approximately 6 months after the initial placement. Intact bags were immediately placed in an icebox and transported to the laboratory. All regenerative root samples were then gently washed with running water and divided into different orders following the root-order classification approach suggested by Pregitzer et al. (2002). Following the dissection, samples from each root order were scanned on an Epson Expression 10,000 XL desktop scanner (resolution 400 dpi). Root images were analyzed using WinRHIZO software (Regent Instruments, Quebec, Canada) to obtain the average root diameter, and volume and total length of each root order. Here, the first two root orders were considered to be absorptive roots (McCormack et al.

2015) and were compared across species for root traits and AM colonization (Table 1). Root length growth rate for a given species under different nutrient addition treatments was expressed as the average absorptive root length proliferation of each root bag for the duration of the experiment.

Subsamples of all absorptive roots were cut into 1-cm segments, cleared with 10% (*w*/*v*) KOH at 90 °C for 15 min and stained with 0.05% (w/v) acid fuchsin for quantification of mycorrhizal colonization at ×200 magnification (Leica DM 2500; Leica Mikrosysteme Vertrieb GmbH, Bensheim, Germany) using the line-intersect method (McGonigle et al. 1990). Extraradical hyphae were extracted from fresh soil in each root bag using the membrane filter technique (Jakobsen et al. 1992): the blended suspensions composed of 4 g fresh soil, 100 mL deionized water and 12 mL sodium hexametaphosphate were shaken for 30 s and left to rest for 30 min; the supernatant was poured through a 38-μm sieve to retain hyphae, and the hyphae were washed into a flask with 200 mL deionized water; the flasks were shaken for 5 s, and 2 mL mixture was pipetted onto 25-mm-diameter, 1.2-μm Millipore filters. The filters were covered with 1% (w/v) acid fuchsin for 5 min and observed at ×200 magnification (Nikon 80i; Nikon, Tokyo, Japan) using the line-intersect method (McGonigle et al. 1990). Other root subsamples were oven-dried at 60 °C for 48 h and weighed for calculating specific root length (SRL, root length per unit root dry mass for each root order). The root tissue density was calculated as the ratio of root dry mass to its volume. Dried roots were then ground to fine powder, and root N concentration was determined using an elemental analyzer (Vario EL Cube, Elementar, Hanau, Germany).

For each species, mature and sun-exposed leaves were collected from the top-third of the tree canopy. Leaf thickness was measured immediately after sampling using digital calipers (SMCTW Company, Shanghai, China), avoiding the leaf major veins. Leaf samples were oven-dried at 65 °C for 48 h until constant weight for calculating specific leaf area (SLA, the leaf total area divided by its dry mass). Leaf tissue density was calculated from leaf thickness and SLA. The oven-dried leaf samples were ground to fine power. Leaf N concentration was determined using the same approach as for root N measurement. Leaf P concentration was determined by an ICP-MS analyzer (Elan DRC-e, PerkinElmer, USA)

Table 1 Abbreviations and descriptions of traits of roots, leaves and mycorrhizal fungi

Traits	Abbreviation	Units	Description
Roots			
Root diameter	RD	mm	Average diameter of first two order roots combined
Specific root length	SRL	m g^{-1}	Length per unit dry mass of first two order roots combined
Root tissue density	RTD	g cm^{-3}	Mass per unit root volume of first two order roots combined
Root nitrogen concentration	Root N	g kg^{-1}	Average root nitrogen concentration of first two root orders per root bag
Root length growth rate	RLGR	cm day^{-1}	Total length of absorptive roots (first two order roots) produced d^{-1} (standardized per root bag)
Leaves			
Leaf thickness	LT	mm	Leaf thickness
Specific leaf area	SLA	cm^2 g^{-1}	Leaf area/leaf dry mass
Leaf tissue density	LTD	g cm^{-3}	Mass per unit leaf volume
Leaf nitrogen concentration	Leaf N	g kg^{-1}	Leaf nitrogen concentration
Leaf phosphorus concentration	Leaf P	g kg^{-1}	Leaf phosphorus concentration
Leaf nitrogen-to-phosphorus concentration ratio	Leaf N/P		Leaf nitrogen-to-phosphorus concentration ratio
Mycorrhizal fungi			
Hyphal length density	HLD	m g^{-1}	Extramatrical hyphal length per unit soil dry weight in a root bag
Arbuscular mycorrhizal colonization	AMC	%	Percentage of absorptive root length colonized by arbuscules, hyphae, vesicles or coils

after digestion with sulfuric acid and 30% *v*/v H_2O_2 mixture with the volume ratio 5:8 (Johnson and Ulrich 1959; Li et al. 2014).

Data analysis

To meet the assumption of normality, all original data were log10-transformed before analyses. To accomplish our first goal, we calculated the mean values and standard error of root and leaf traits, AM colonization and extramatrical hyphal length density across 13 species in unfertilized control and different nutrient treatments. Moreover, one-way ANOVA was performed to test the difference of each trait across 13 species in each treatment separately, and when appropriate, post hoc means comparisons were made using Tukey HSD tests in SPSS 23.0 (SPSS Inc., Chicago, IL, USA). Additionally, for each plant and mycorrhizal fungal trait, we calculated its mean value, minimum, maximum and coefficient of variation averaged across all tree species in unfertilized control. We also tested the phylogenic conservativism in functional traits of roots, leaves and mycorrhizal fungi and calculated Blomberg's *K* statistic using the R 3.4.3 statistical platform (R Development Core Team 2014) and the packages plantlist (Zhang 2017), ade4 (Dray and Dufour 2004), adephylo (Jombart and Dray 2010), ape (Paradis et al. 2004), picante (Kembel et al. 2010), phytools (Revell 2012) and vegan (Oksanen et al. 2008). A larger *K* value indicates a greater phylogenetic conservativism for the given trait. In addition, pairwise trait relationships were calculated using Pearson's correlations with and without phylogenetically-independent contrasts (PICs). In order to test whether the absorptive root diameter across species had an effect on root length growth rate under all nutrient treatments, we used linear regression to examine the relationship between them. The slopes of the linear regressions under all nutrient treatments were compared with the R package smart (Higdon et al. 2004). Furthermore, we tested the influence of tree species and nutrient treatments on functional traits of roots and mycorrhizal fungi using two-way factorial ANOVA. Post hoc Tukey HSD tests were performed to determine significant differences.

To accomplish our second goal, we calculated foraging precision (*FP*) of roots as the percentage of increase in different nutrient addition patches (+N, +P or + NPK) compared with unfertilized control (Chen et al. 2016).

$$FP_{\text{roots}}\ (\%) = 100 \times \left(Root\ length_{\text{patch}} - Root\ length_{\text{control}}\right)/Root\ length_{\text{control}}$$

Similarly, we also calculated foraging precision of extramatrical hyphae and AM colonization using the same approach as for root foraging precision. To test whether each trait influenced foraging precision of roots, extramatrical hyphae and AM colonization under different nutrient patches, we analyzed the relationship between each trait and foraging precision using Pearson's correlations. In addition, we analyzed whether and how root diameter influenced the change in foraging precision of roots and mycorrhizal hyphae in different nutrient patches using regression analysis.

To accomplish our third goal, we analyzed the change in foraging precision of roots and mycorrhizal hyphae among different tree species in different nutrient patches. Also, we tested the influence of tree species and nutrient treatments on foraging precision of roots and mycorrhizal hyphae using two-way factorial ANOVA. Post hoc Tukey HSD tests were performed to determine significant differences.

Results

Variations and correlations between plant traits and mycorrhizal colonization across species

There were significant differences in plant traits and mycorrhizal colonization across 13 species in the unfertilized control (Table 2; Fig. 1). We also found large variation in root morphological traits (e.g. root diameter and specific root length) and root length growth rate across species in the unfertilized control (Table S2). For instance, the mean diameter of the first two root orders exhibited 4.5-fold difference between the smallest diameter of 0.19 mm in *Acer fabri* and the largest of 0.86 mm in *Taxus chinensis,* with an overall coefficient of variation (CV) of 48% ($P < 0.001$, Tables 2 and S2). Specific root length (SRL) exhibited almost 16-fold difference with the CV of 78% ($P < 0.001$, Tables 2 and S2). Root length growth rate exhibited a 12-fold difference with the CV of 61% ($P < 0.001$, Tables 2 and S2). Moreover, significant differences in root traits and mycorrhizal colonization across 13 AM tree species

persisted in the nutrient addition treatments (Table S1). Although there were significant differences in root and leaf N concentrations and leaf morphological traits across species in the unfertilized control ($P < 0.001$, Table 2), their CVs were smaller than those of root morphological traits (Table S2). Extramatrical hyphal length density and AM colonization exhibited a significant difference across species in the unfertilized control as well as the nutrient treatments ($P < 0.001$, Tables 2 and S1). In addition, root diameter and SRL were phylogenetically conserved as indicated by the high Blomberg's K values (Table S3). Nutrient addition treatments had no significant effect on SRL (Table S4). The root diameter responded to nutrient patches in some species more than others (species × treatment interaction, $P \leq 0.05$). *Taxus chinensis* was the only species with the root diameter significantly different between the unfertilized control and the nutrient addition treatments, especially in the P-patch (22% decrease; Tables 2 and S1; Fig. S1).

Across 13 species in the unfertilized control, root diameter was negatively correlated with SRL ($r = -0.99$, $P < 0.01$, Table 3) and root tissue density ($r = -0.60$, $P = 0.03$), but SRL was not significantly correlated with root tissue density ($r = 0.45$, $P = 0.12$). Root length growth rate was negatively correlated with root diameter ($r = -0.62$, $P = 0.02$) and positively correlated with SRL ($r = 0.62$, $P = 0.02$). However, after removing the influence of phylogeny via phylogenetically-independent contrasts, almost all of these correlations among root traits disappeared (Table 3). Furthermore, root length growth rate across all species decreased linearly with an increase in root diameter in different nutrient treatments (Fig. 2). Additionally, AM colonization was positively correlated with root diameter ($r = 0.77$, $P = 0.002$) and negatively correlated with SRL ($r = -0.76$, $P = 0.003$) (Table 3), and these correlations also disappeared after removing the influence of phylogeny via phylogenetically-independent contrasts (Table 3). However, extramatrical hyphal length density had no correlation with root traits regardless of whether phylogeny was considered or not.

Leaves displayed a correlation between morphological and chemical traits (Table 3). For instance, leaf thickness was negatively correlated with leaf tissue density ($r = -0.59$, $P = 0.04$), and specific leaf area (SLA) was positively correlated with leaf N concentration ($r = 0.72$, $P = 0.01$). Also, leaf N and P concentrations were highly positively correlated across species ($r = 0.66$, $P = 0.02$). Moreover, these correlations among leaf traits were maintained after removing the influence of phylogeny via phylogenetically-independent contrasts (Table 3).

The effects of plant traits on the foraging precision of roots and mycorrhizal hyphae

The results of Pearson's correlation showed that root traits such as root diameter, SRL, root tissue density and root N concentration, and leaf traits such as leaf thickness, SLA, leaf tissue density and leaf N or P concentration were not related to root and extramatrical hyphal foraging precisions and AM colonization in the three types of nutrient patches (Table S5). However, foraging precision of roots and extramatrical hyphae still could be influenced by root diameter (Figs. 3 and S2). As root diameter increased, root foraging precision exhibited the U-shape patterns (Fig. S2a, $R^2 = 0.19$, $P = 0.02$) especially in the N- and P-patches (Fig. 3a, $R^2 = 0.61$, $P = 0.009$ in N-patch, $R^2 = 0.69$, $P = 0.003$ in P-patch), whereas extramatrical hyphal foraging precision slightly increased (Fig. S2b, $R^2 = 0.09$, $P = 0.07$), mainly in the N-patch (Fig. 3b, $R^2 = 0.27$, $P = 0.07$).

Foraging precision of roots and mycorrhizal hyphae in response to nutrient patches

We observed that absorptive root foraging precision was significantly affected by tree species, nutrient types and their interaction (all $P < 0.001$, Fig. 4a). Three tree species (*Schima superba, Cunninghamia lanceolata* and *Taxus chinensis*) showed a positive response in all nutrient patches. By contrast, seven species (*Choerospondias axillaris*, *Liquidambar formosana*, *Elaeocarpus glabripetalus*, *Alniphyllum fortune*, *Machilus oculodracontis*, *Manglietia yuyuanensis* and *Neolitsea phanerophlebia*) showed relatively low sensitivity to nutrient patches. Unexpectedly, root foraging precision of five species (*Choerospondias axillaris*, *Cinnamomum porrectum*, *Machilus oculodracontis*, *Manglietia yuyuanensis* and *Neolitsea phanerophlebia*) was suppressed in the P-patch.

Extramatrical hyphal foraging precision and AM colonization plasticity were significantly influenced by species, nutrient types and their interaction ($P < 0.001$, Figs. 4b and S3). For extramatrical hyphal foraging precision, two tree species (*Acer fabri* and *Neolitsea*

Table 2 Functional trait mean values (SE) of absorptive fine roots, leaves and mycorrhizal fungi under unfertilized treatment for 13 arbuscular mycorrhizal tree species from a subtropical forest, southern Jiangxi Province, China.

Species	Abbr.	Family	Root traits					Leaf traits					Mycorrhizal fungi	
			RD (mm)	SRL (m g^{-1})	RTD (g cm^{-3})	Root N (g kg^{-1})	RLGR (cm day^{-1})	LT (mm)	SLA (cm^2 g^{-1})	LTD (g cm^{-3})	Leaf N (g kg^{-1})	Leaf P (g kg^{-1})	HLD (m g^{-1})	AMC (%)
Acer fabri	Acfa	Aceraceae	0.19^{h}	190^{a}	0.20^{abc}	0.20^{bcd}	2.3^{ab}	0.17^{d}	177^{a}	0.33^{bc}	0.19^{bc}	0.01^{c}	4.7^{abc}	21^{e}
			(0.00)	(17)	(0.02)	(0.01)	(0.5)	(0.10)	(103)	(0.19)	(0.01)	(0.0)	(1.1)	(3)
Schima superba	Scsu	Theaceae	0.21^{gh}	141^{ab}	0.22^{a}	0.12^{g}	4.5^{ab}	0.24^{bc}	88^{e}	0.49^{a}	0.12^{d}	0.00^{d}	5.4^{abc}	33^{d}
			(0.01)	(17)	(0.02)	(0.01)	(0.9)	(0.14)	(51)	(0.28)	(0.00)	(0.0)	(0.3)	(2)
Choerospondias axillaris	Chax	Anacardiaceae	0.25^{fg}	87^{bc}	0.24^{a}	0.17^{cdef}	3.0^{ab}	0.20^{cd}	149^{abc}	0.34^{bc}	0.24^{ab}	0.01^{c}	5.4^{bcd}	47^{c}
			(0.01)	(6)	(0.02)	(0.01)	(0.4)	(0.11)	(86)	(0.20)	(0.01)	(0.0)	(0.5)	(0)
Liquidambar formosana	Lifo	Hamamelidaceae	0.26^{efg}	89^{bc}	0.21^{ab}	0.13^{fg}	6.2^{a}	0.30^{ab}	172^{ab}	0.20^{e}	0.19^{bc}	0.01^{c}	5.3^{cd}	52^{c}
			(0.01)	(6)	(0.01)	(0.01)	(0.9)	(0.17)	(99)	(0.11)	(0.01)	(0.0)	(0.4)	(2)
Elaeocarpus glabripetalus	Elgl	Elaeocarpaceae	0.30^{ef}	69^{c}	0.21^{ab}	0.14^{efg}	4.9^{a}	0.20^{cd}	148^{abc}	0.35^{bc}	0.29^{a}	0.01^{c}	4.4^{a}	54^{bc}
			(0.01)	(9)	(0.02)	(0.01)	(0.5)	(0.11)	(85)	(0.20)	(0.01)	(0.0)	(0.9)	(1)
Alniphyllum fortunei	Alfo	Styracaceae	0.31^{ef}	74^{c}	0.19^{abc}	0.19^{bcde}	4.2^{ab}	0.38^{a}	123^{cd}	0.22^{e}	0.19^{bc}	0.01^{bc}	2.9^{d}	28^{de}
			(0.02)	(7)	(0.00)	(0.02)	(0.6)	(0.22)	(71)	(0.13)	(0.01)	(0.0)	(0.2)	(4)
Cinnamomum porrectum	Cipo	Lauraceae	0.33^{de}	67^{cd}	0.19^{abc}	0.23^{bc}	1.3^{bcd}	0.25^{bc}	112^{cde}	0.37^{ab}	0.17^{c}	0.01^{c}	4.0^{ab}	48^{c}
			(0.03)	(12)	(0.01)	(0.01)	(0.3)	(0.14)	(65)	(0.21)	(0.01)	(0.0)	(0.5)	(4)
Cinnamomum austrosinense	Ciau	Lauraceae	0.41^{cd}	39^{de}	0.21^{ab}	0.25^{b}	0.9^{cd}	0.37^{a}	110^{cde}	0.25^{cde}	0.24^{ab}	0.01^{c}	2.0^{abc}	28^{de}
			(0.03)	(6)	(0.01)	(0.01)	(0.5)	(0.21)	(63)	(0.14)	(0.01)	(0.0)	(0.6)	(0)
Machilus oculodracontis	Maoc	Lauraceae	0.51^{bc}	23^{ef}	0.23^{a}	0.17^{cdef}	2.5^{ab}	0.22^{cd}	131^{bc}	0.36^{ab}	0.19^{bc}	0.01^{c}	2.5^{abc}	59^{bc}
			(0.02)	(3)	(0.03)	(0.00)	(0.6)	(0.13)	(76)	(0.21)	(0.01)	(0.0)	(0.2)	(4)
Manglietia yuyuanensis	Mayu	Magnoliaceae	0.57^{b}	30^{ef}	0.13^{c}	0.23^{bc}	3.4^{ab}	0.34^{a}	137^{abc}	0.22^{e}	0.25^{ab}	0.02^{ab}	2.7^{a}	66^{abc}
			(0.02)	(2)	(0.01)	(0.01)	(0.5)	(0.20)	(79)	(0.13)	(0.02)	(0.0)	(0.3)	(2)
Neolitsea phanerophlebia	Neph	Lauraceae	0.55^{b}	32^{e}	0.14^{b}	0.35^{a}	1.8^{abc}	0.18^{d}	177^{a}	0.31^{bcd}	0.30^{a}	0.03^{a}	2.8^{abc}	91^{a}
			(0.03)	(3)	(0.01)	(0.02)	(0.3)	(0.10)	(102)	(0.18)	(0.03)	(0.0)	(0.3)	(2)
Cunninghamia lanceolata	Cula	Taxodiaceae	0.64^{b}	18^{fg}	0.18^{abc}	0.12^{g}	1.4^{bcd}	0.34^{a}	91^{de}	0.32^{bc}	0.14^{cd}	0.01^{c}	3.0^{ab}	76^{ab}
			(0.02)	(1)	(0.01)	(0.01)	(0.3)	(0.20)	(53)	(0.19)	(0.01)	(0.0)	(0.4)	(1)
Taxus chinensis	Tach	Taxaceae	0.86^{a}	12^{g}	0.17^{abc}	0.16^{defg}	0.5^{d}	0.25^{bc}	173^{ab}	0.23^{de}	0.32^{a}	0.03^{a}	2.5^{a}	84^{a}
			(0.07)	(1)	(0.03)	(0.01)	(0.2)	(0.15)	(100)	(0.13)	(0.03)	(0.0)	(0.7)	(2)

For each trait, different letters in each column indicate significant differences among tree species ($P \leq 0.05$). See Table 1 for abbreviations of traits

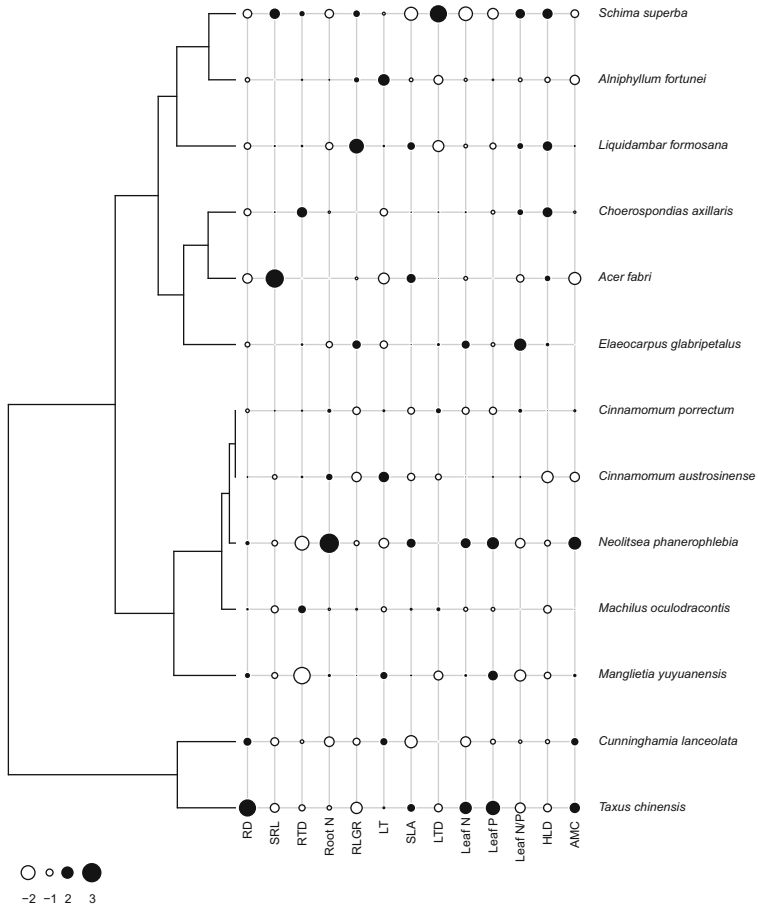

Fig. 1 Phylogeny and trait value distribution for 13 arbuscular mycorrhizal tree species in this study. The symbol size indicates relative trait values for each species, with smaller symbols closer to the mean value; white and black symbols represent values below and above the mean, respectively. See Table 1 for abbreviations of traits

phanerophlebia) showed a positive response in all nutrient patches (Fig. 4b), whereas *Cinnamomum porrectum* was suppressed in all three types of nutrient patches. *Schima superba* was suppressed in the N- and NPK-patches. *Elaeocarpus glabripetalus* and *Taxus chinensis* were suppressed in the P- and NPK-patches. Two tree species (*Cinnamomum austrosinense* and *Cunninghamia lanceolata*) were suppressed in the NPK-patch.

For AM colonization plasticity, five species showed a negative response in all nutrient patches (Fig. S3). In contrast, four species (*Elaeocarpus glabripetalus*, *Cinnamomum porrectum, Cinnamomum austrosinense* and *Machilus oculodracontis*) exhibited a positive response in the P-patch, and two species (*Alniphyllum fortune* and *Cinnamomum austrosinense*) showed a positive response in the N-patch.

The foraging precision of roots and extramatrical hyphae across species in different nutrient addition treatments were not related significantly (Fig. 5). Moreover, this independent tendency was also found between AM colonization plasticity and foraging precision of roots (Fig. S4a) or extramatrical hyphae (Fig. S4b).

Discussion

Root traits and plant growth strategy

Our results showed that recently-evolved species with thinner roots had higher specific root length and root length growth rate than ancient species with thicker roots (Table 3; Figs. 1 and 2). These findings, together with previous studies in other systems (Comas and Eissenstat 2004; McCormack et al. 2012), partially support the idea of the 'fast-or-slow' plant growth strategies (Reich 2014). Thin-root species adopt the 'fast strategy' with fast proliferation (Eissenstat et al. 2015) and quick root turnover (McCormack et al. 2012) as their resource acquisition strategy, whereas thick-root species adopt the 'slow strategy' with slow proliferation and long root lifespan as a resource conservation strategy. The fast root length

Table 3 Coefficients of Pearson's correlation with original data (lower-left part) and phylogenetically-independent contrasts (upper-right part) among functional traits of absorptive fine roots, leaves and mycorrhizal fungi across 13 tree species under unfertilized treatment.

	RD	SRL	RTD	Root N	RLGR	LT	SLA	LTD	Leaf N	Leaf P	Leaf N/P	HLD	AMC
RD		**−0.70***	−0.12	0.54	0.09	0.15	0.51	−0.48	**0.79****	**0.78****	−0.56	−0.56	0.32
SRL	**−0.99****		−0.27	−0.12	−0.12	−0.49	0.01	**0.59***	**−0.61***	−0.33	0.12	0.53	0.01
RTD	**−0.60***	0.45		**−0.69***	−0.21	0.57	**−0.65***	−0.24	−0.11	−0.43	0.38	−0.41	**−0.75***
Root N	0.18	−0.09	−0.51		−0.20	−0.11	0.70*	−0.30	**0.69***	**0.88****	**−0.79****	−0.21	0.41
RLGR	**−0.62***	**0.62***	0.27	−0.31		−0.39	0.26	0.27	−0.11	−0.11	0.27	0.33	0.53
LT	0.30	−0.31	−0.15	−0.15	−0.09		−0.49	**−0.83****	0.33	0.11	−0.23	**−0.69***	**−0.82****
SLA	0.02	0.02	−0.25	0.32	0.04	−0.49		−0.08	0.50	**0.71***	−0.57	0.00	**0.67***
LTD	−0.33	0.30	0.40	−0.16	0.06	**−0.59***	−0.42		**−0.68***	−0.55	**0.59***	**0.77****	0.49
Leaf N	0.41	−0.37	−0.40	0.47	−0.27	−0.22	**0.72****	−0.45		**0.89****	**−0.60***	−0.51	0.07
Leaf P	**0.65***	−0.53	**−0.83****	0.43	−0.33	−0.04	0.43	−0.36	**0.66***		**−0.84****	−0.47	0.26
Leaf N/P	**−0.60***	0.50	**0.82****	−0.50	0.46	−0.12	−0.35	0.47	−0.39	**−0.77****		**0.64***	−0.04
HLD	0.44	−0.41	−0.36	0.02	−0.38	−0.26	0.02	0.25	0.29	0.25	−0.15		0.45
AMC	**0.77****	**−0.76****	−0.49	0.01	−0.24	−0.06	0.19	−0.11	0.40	0.56	−0.27	0.48	

Significant correlations are in bold

*, $P \leq 0.05$; **, $P < 0.01$. See Table 1 for abbreviations of traits

growth rate of thin-root species may allow plants to rapidly recolonize soil after disturbance (Eissenstat et al. 2015). In contrast, thick-root species appear to have relatively low capacity to forage soil resource in the heterogeneous nutrient-rich patches, but these species can still acquire nutrients in the stable nutrient patches because of a long root lifespan (McCormack et al. 2012).

Despite root diameter and root length growth rate significantly negatively correlating across 13 coexisting species, neither of these root traits was correlated with root N concentration (Table 3). This suggests that morphological and chemical traits are decoupled at the root system level, which is different to the results of the leaf economics spectrum (Wright et al. 2004; Bergmann et al. 2017). This is likely due to leaf traits being more phylogenetically constrained than root traits, as shown by Laughlin (2014) and Kramer-Walter et al. (2016). Moreover, roots may display a broader array of possible trait combinations than foliar tissues in order to maximize functional gains and minimize the construction

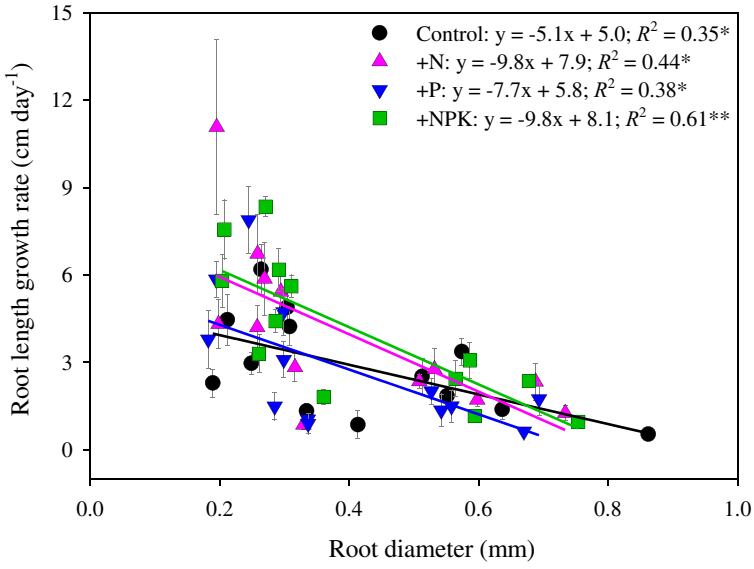

Fig. 2 The relationship of root diameter and root length growth rate across 13 arbuscular mycorrhizal tree species in four treatments (unfertilized control; +N, N-patch; +P, P-patch; +NPK, NPK-patch). Error bars represent ± SE of the mean. Differences among the slopes of the regression lines were not significant. *, $P \leq 0.05$; **, $P < 0.01$

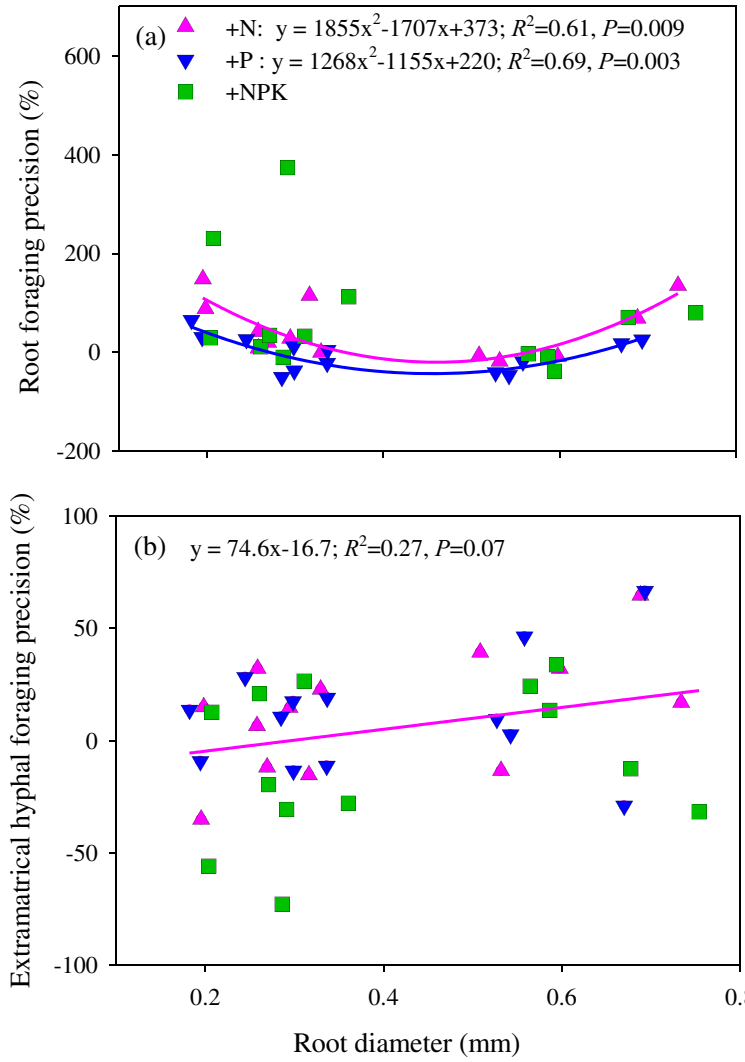

Fig. 3 The relationship of (**a**) root foraging precision and (**b**) extramatrical hyphal foraging precision with the mean diameter of the first two root orders across 13 arbuscular mycorrhizal tree species in different nutrient patches (+N, N-patch; +P, P-patch; +NPK, NPK-patch). Foraging precision of roots or extramatrical hyphae was calculated as a percentage increase in the nutrient patches compared with the unfertilized control. The data for individual nutrient patch treatments across all species were used in the regression analysis

and maintenance costs (Donovan et al. 2011). On one side, roots are typically associated with mycorrhizal communities (Brundrett 2002) in which the fungal partnerships allow plants to acquire nutrients without necessarily adjusting root morphology (Kong et al. 2017). On the other side, roots are always exposed to more complex abiotic and biotic environments than leaves (Weemstra et al. 2016).

Species with thick root diameter tended to have high leaf P concentration (Table 3). This result may be due to species with thicker roots relying more on arbuscular mycorrhizal fungi (Fitter and Merryweather 1992) that are effective in acquiring soil P (Baylis 1975), when sharing the same environment with species that have thinner roots. However, whether the negative correlation between root diameter and leaf P concentration is a general pattern across other biological systems remains to be investigated further.

Root proliferation in response to nutrient patches

We found diverse root foraging precision across species, regardless of nutrient types (Fig. 4a): as root diameter increased, root foraging precision initially decreased and then slightly increased (Fig. S2a). These findings do not support the general notion that thin-root species with higher growth rate have higher root foraging precision than thick-root species (Chen et al. 2016). Although root foraging precision and root diameter as well as the growth rate were considered phylogenically conserved (Kembel and Cahill 2005; Valverde-Barrantes et al. 2017), our results suggested that the relationship

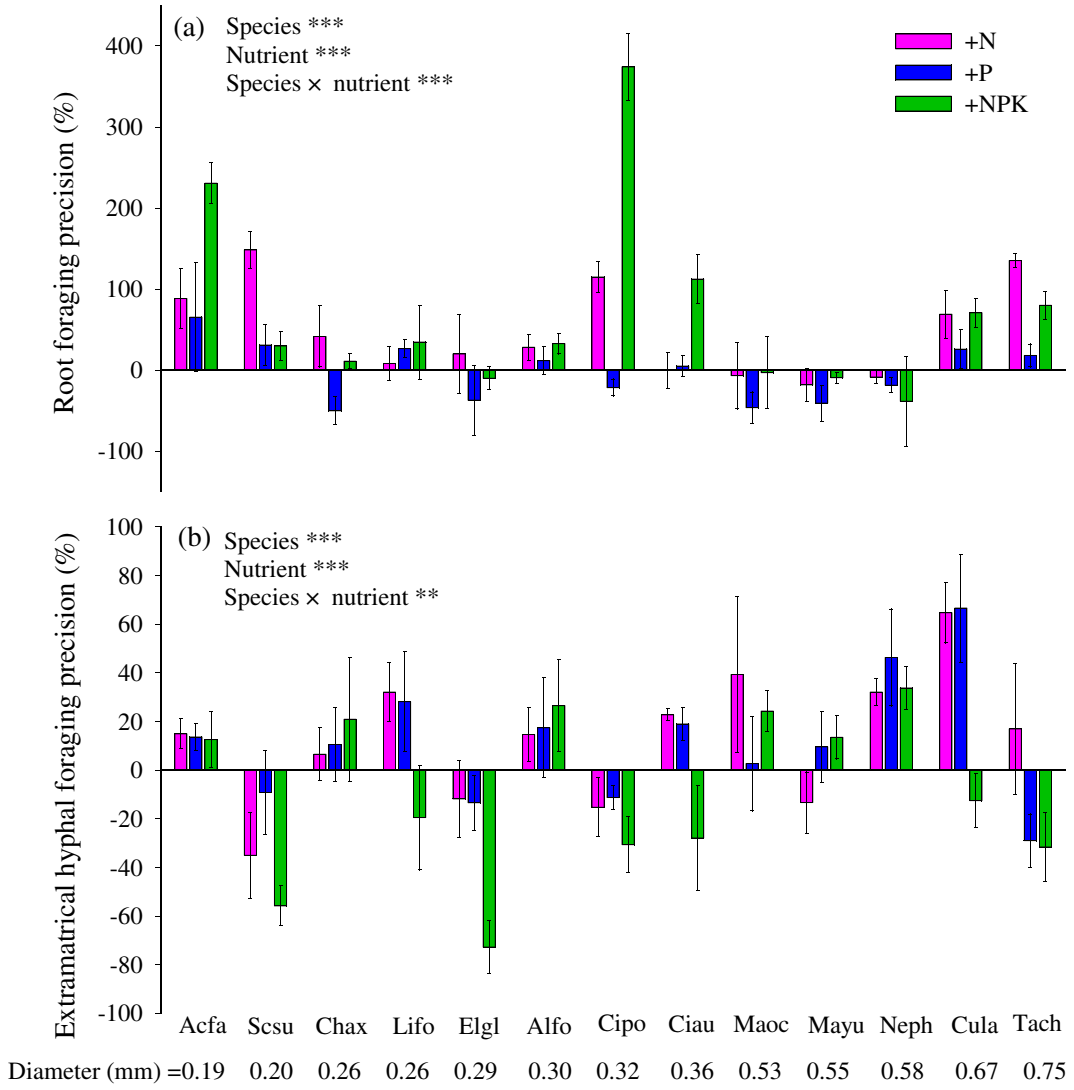

Fig. 4 Foraging precision of (**a**) roots and (**b**) extramatrical hyphae in different nutrient patches (+N, N-patch; +P, P-patch; +NPK, NPK-patch) for 13 arbuscular mycorrhizal tree species (see Table 2 for abbreviations of tree species). Values are means ± standard error ($n = 4$). The mean diameter in different treatments of each species is listed below the species name. The influence of both factors (species and nutrient addition treatments) on foraging precision was tested using two-way ANOVA. **, $P < 0.01$; ***, $P < 0.001$

between root diameter and foraging precision was complex.

For a given species, contrasting foraging precision responses were found in different nutrient patches (Fig. 4a). For instance, root foraging precision of *Cinnamomum porrectum* was positive in the N- and NPK-patches but negative in the P-patch. This finding may has been caused by the varied nutrient requirements of plant species, as the plant demand for specific nutrients can regulate the local root responses (Forde 2014). Additionally, the resource-driven niche partitioning may occur among the coexisting species. For example, Ceulemans et al. (2017) found that some European grass species prefer to acquire soil inorganic P, but other species prefer to acquire organic P. Similarly, there was also a significant difference in the absorption of different N forms among species in the tropical forest (Andersen et al. 2017). The preference of plant species for different nutrient forms may determine the responses of root systems to specific nutrient patches across species. In addition, species with high respiration tend to have high leaf N and root N concentrations (Reich et al. 2008),

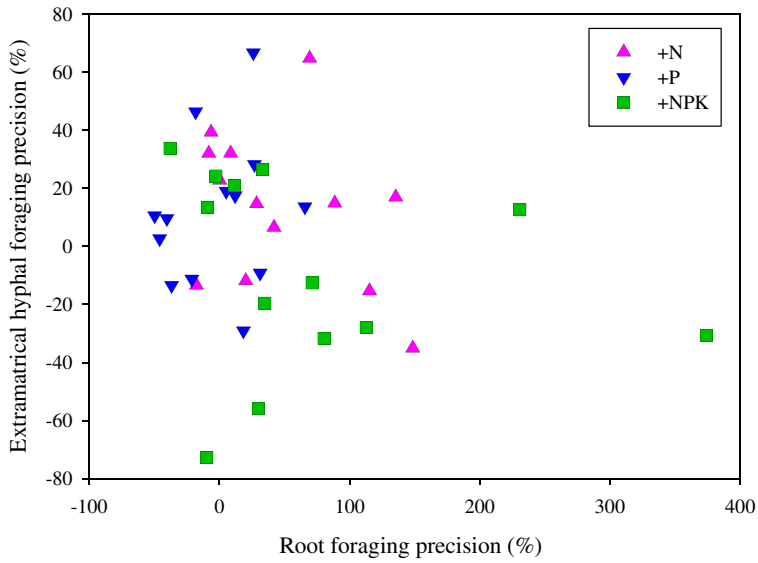

Fig. 5 A lack of relationship between foraging precision of roots and extramatrical hyphae across 13 arbuscular mycorrhizal tree species in different nutrient patches (+N, N-patch; +P, P-patch; +NPK, NPK-patch)

indicating that these species may adopt a fast-growth strategy and have high demand for nutrients. However, across all tree species in the present study, leaf nutrient concentrations (N and P) were not related to root foraging precision in different nutrient patches (Table S5), indicating a potential decoupling between nutrient acquisition strategies by roots and nutrient transport to above-ground organs. Also, Kramer-Walter et al. (2016) showed that the root traits are multidimensional in contrast to the leaf traits, suggesting that plants may have different adaptation to nutrient limitations above- and below-ground. Together, the integration of nutrient-specific and species-specific responses can generate a diversity of root foraging precision responses (Li et al. 2014), which may underpin species co-existence (Adler et al. 2013).

The foraging precision of mycorrhizal hyphae responding to nutrient patches

Root diameter had a marginally significant correlation with extramatrical hyphal foraging precision ($P = 0.07$, Fig. S2b) and none with AM colonization plasticity (Fig. S2c) in nutrient patches across all tree species studied. This finding suggests that predicting foraging precision of mycorrhizal hyphae to local environmental heterogeneity using a single root morphological trait is unreliable. Other factors, including supplies of soil available nutrients and the plant nutrient demands, also can influence foraging precision of extramatrical hyphae and AM colonization (Smith and Read 2008). Additionally, the interaction of nutrient treatments and plant species would influence extramatrical hyphal foraging precision and AM colonization plasticity (Figs. 4b and S3).

Root foraging precision was not associated with extramatrical hyphal foraging precision and AM colonization plasticity among species in all types of nutrient patches (Figs. 5 and S4a). Chen et al. (2016) also found no correlation between foraging precision of roots and AM hyphae, and suggested that AM trees rely more on their root proliferation than hyphae to respond to nutrient-rich patches. However, this explanation is rather speculative because roots of tree species studied here exhibited more complex foraging precision than hyphae (Fig. 3). A deeper reason for the independence of foraging precision of roots and mycorrhizal hyphae may be that plants cannot fully control their symbiotic relationship (van der Heijden et al. 2015). For example, some mycorrhizal fungi can colonize plant roots in the high-nutrient environments, and even cause a reduction in plant growth (Johnson 2010). Abiotic stress may have effects on AM fungi that are independent of the effects on the host plant (Millar and Bennett 2016). A recent study also demonstrated that AM fungal morphological traits cannot predict host plant growth, suggesting evolutionary asymmetry in plant-mycorrhizal symbiosis and a high degree of independence between mycorrhizal traits and plant performance (Koch et al. 2017).

The turnover of roots and hyphae in nutrient patches, albeit not measured in this study, may also be a reason for independence of foraging precision of roots and mycorrhizal hyphae. For instance, some plant species

increased the rates of initiating new roots as well as the rates of root death in the fertilized patches, together resulting in no root proliferation (Gross et al. 1993), whereas other species increased root proliferation in the nutrient-rich patches (Pregitzer et al. 1993). These findings suggest profound differences in plasticity of root lifespan across plant species, which may explain species-specific differences in root foraging precision in the nutrient-rich patches. On the other hand, Staddon et al. (2003) found that a large proportion of extraradical mycorrhizal hyphae turned over in 5 to 6 days, but the AM hyphal turnover could depend on the changes in the soil environment, which may explain species-specific and nutrient-specific alterations in mycorrhizal hyphae foraging precision.

Apart from the turnover of roots and mycorrhizal hyphae, non-mycorrhizal fungi (as an alternative strategy for absorbing soil nutrients) may also obscure the relationships between foraging precisions of roots and mycorrhizal hyphae. Recent studies have reported that non-mycorrhizal fungi can promote plant P acquisition by mineralizing P or transferring P in the form of soluble orthophosphate (Richardson and Simpson 2011; Almario et al. 2017). Indeed, diverse non-mycorrhizal fungi associated with roots were found to potentially interact with mycorrhizal fungi (e.g. AM fungi) positively or negatively (Toju et al. 2016; Toju and Sato 2018).

Our results showed that foraging precisions of hyphae and AM colonization in the nutrient patches across plant species were not related (Fig. S4b). The asynchronism of responses between these two mycorrhizal traits is also found across maize genotypes along a P gradient (Chu et al. 2013) and under various temperatures (Gavito and Olsson 2003). Mycorrhizal fungal species and genotypes can differ substantially in the morphological traits (Hazard and Johnson 2018) and capacity to capture nutrients (Smith and Read 2008), whereas plant species have some influence over selecting suitable mycorrhizal species according to relative resource abundance in soil and the plant intrinsic demand (Werner and Kiers 2015). These findings suggest that multiple mycorrhizal traits may need to be considered in characterizing plant foraging strategies.

In our study, a lack of correlation between foraging precision of roots and mycorrhizal fungi appeared to suggest that these two types of nutrient acquisition were relatively independent. A combination of multiple independent traits from multiple organs may result in a specific adaptation or growth strategy for each species (Laughlin 2014). Moreover, plant differences in the root and mycorrhizal fungi responses to heterogeneous environments may reduce species competition and thus promote species coexistence and community stability.

Conclusions

We found a diversity of root and mycorrhizal fungi foraging strategies across species exploring nutrient-rich patches, and there was also large variation in foraging precision of roots and mycorrhizal hyphae in response to different nutrient patches for a given species (from negative to positive). Moreover, foraging precision of roots and mycorrhizal hyphae in different nutrient patches was independent, generating diversity of plant foraging strategies in the heterogeneous nutritional environments. In addition, thick-root species with slow root growth showed similar root foraging precision as thin-root species with fast root growth regardless of the nutrient patches. This finding challenges the idea that thin-root species are more sensitive to environmental heterogeneity than thick-root species. We thus suggest that root morphological traits alone (such as root diameter) are unlikely to fully characterize the diversity of plant foraging strategies across species. Future studies should define the foraging strategy of plant species by integrating morphological and physiological traits of roots and mycorrhizal fungi.

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