Absorptive roots trait plasticity explains the variation of root foraging strategies in *Cunninghamia lanceolata*

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A B S T R A C T

The architecture and morphology of absorptive roots show substantial plasticity in response to forest management practices. These traits are known to play important roles in the acquisition of soil resources by trees. However, the effects of nutrient addition, thinning and pruning on absorptive root traits and their feedback to root foraging strategies remain unclear.

We investigated the values and plasticity of traits related to nutrient foraging (root architecture, growth and morphology) for first- and second-order roots (absorptive roots) following nitrogen (N) addition, phosphorous (P) addition, thinning and pruning treatments in a young Chinese fir (*Cunninghamia lanceolata*) plantation.

We measured twelve traits of absorptive roots under the five treatments (control, N addition, P addition, thinning and pruning) and determined relationships between the values and plasticity of root traits and stem growth rate. We demonstrated clear patterns of root traits and their plasticity in response to the treatments. N and P addition increased root biomass (B) and root tissue density (RTD). Thinning and pruning led to larger specific root length (SRL) and root nitrogen concentrations (N), but resulted in lower root length (L) and root length density (RLD). Principal component analysis of the measured traits and plasticity provided evidence for two suites of traits related to resource acquisition and conservation strategies among treatments. The trait syndromes exhibiting resource acquisition strategy (SRL and N) is arrayed well along the positive part of the first axis, whereas the opposite trait syndromes with resource conservation strategy (root diameter and RTD) is along the negative part of the first axis. The first axis also separates nutrient-induced treatments (N and P addition) from light-mediated treatments (pruning and thinning). Furthermore, first-order root exhibited higher foraging sensitivity and precision (expressed as relative fine root length difference) in response to P addition than to the other treatments. The foraging sensitivity and precision, plus B, L and RLD showed that first-order roots are more responsive to environment than second-order roots across the treatments. Stem growth rate was correlated positively with absorptive root traits (biomass, root surface area index, root length density, and root tip number) after thinning, but negatively with these traits after N and P addition.

These findings demonstrate that *C. lanceolata* finely tuned root foraging strategies between first- and second-order root traits and their plasticity at the intraspecific level in response to forest management practices. Further studies may explore nutrient-induced and light-mediated foraging strategies between absorptive roots across root branch orders in mature Chinese fir plantation.

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1. Introduction

Absorptive fine roots (ephemeral first- and second-order roots) play key roles in regulating plant and ecosystem function through foraging and acquiring nutrients and water from the surrounding soil. These root structures are the most dynamic part of the root system (Robinson et al., 2003). Recent studies have shown that absorptive root traits vary widely across nutrient patches, plant species and ecosystems (Chen et al., 2013a,b; Eissenstat et al., 2015; Kong et al., 2015; Kou et al., 2015; Lambers et al., 2011; Liu et al., 2015; Pregitzer et al., 2002). Mechanisms underlying this variability rely on genotypic variability (genetically determined intrinsic pathway) and phenotypic plasticity (environmentally triggered responsive pathway) (Malamy, 2005). For example, Kong et al. (2014) found that there are two dimensions of cross-species root trait variation, a diameter-related dimension of phylogenetic

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conservation and a branching architecture dimension expressing root plastic responses to the environment. Together, this implies that absorptive root trait plasticity appears to be an important factor influencing nutrient foraging strategy in response to environmental conditions.

Given that absorptive roots show a high degree of plasticity by acclimating to local environmental conditions, it is valuable to understand how plants modify biomass allocation to root tip morphology to develop an efficient root system for nutrient foraging. As reported by Fort et al. (2014), grasses' root foraging strategies are linked to root traits. Grasses may compete with other species by adapting root trait values to tolerances for water and P stress, resulting in stronger competitive ability through modifying investment in root production, the type of root produced and root trait plasticity. Furthermore, Fort et al. (2015a,b) performed a greenhouse experiment and showed that root trait values and plasticity can not only explain the mechanism of species coexistence and ecological niche differentiation in the Fabaceae, but also reflect root foraging behavior and the diversity of belowground resource acquisition strategies (Bardgett et al., 2014; McCormack et al., 2015).

Absorptive root foraging strategies in response to nutrient availability have been linked to root morphology and physiology. For instance, Ostonen et al. (2011) reported that ectomycorrhizal root biomass, length and root tip number per stand basal area is higher in northern spruce forests than in comparable southern forests. This finding is consistent with the hypothesis that plants may optimize resource foraging strategy by modifying fine root growth, morphological and physiological traits (Mou et al., 2013; Wang et al., 2013a,b). Additionally, forest trees respond differently to management practices such as nutrient addition and thinning, highlighting multiple suites of root traits that impact nutrient foraging strategies (Noguchi et al., 2011; Kou et al., 2015). More recently, Liu et al. (2015) and Eissenstat et al. (2015) established that after fertilization, for 14 subtropical and 6 temperate arbuscular mycorrhizal (AM) tree species, thin-root species forage relatively more through absorptive fine root proliferation whereas thick-root species forage relatively more with the assistance of arbuscular mycorrhizal fungi. Overall, previous studies have evaluated how absorptive roots respond to climate gradients or nutrient patches, but few studies have examined the plastic responses of absorptive roots in the field, especially to forest management practices.

Plant functional traits and their plasticity are useful for explaining species' abilities to cope with environmental change (Callaway et al., 2003). The functional trait approach can be used to characterize the trade-off between resource acquisition and resource conservation across plant organs from leaf, stem to root, thus depicting the plant's economic spectrum (Kong et al., 2015; Prieto et al., 2015; Wright et al., 2004). Furthermore, root trait plasticity is also an important factor influencing plants' abilities to change trait values in response to environmental conditions (Fort et al., 2015a) due to the central role of root traits in resource foraging (Kou et al., 2015; Liu et al., 2015). Two important plastic responses of root resource foraging are variation in sensitivity and precision (Einsmann et al., 1999). Root foraging sensitivity (growth value gained as the spatial heterogeneity of nutrients increases, measured as total biomass) and precision (the preferential proliferation of roots in nutrient-rich patches compared with less fertile patches, as conceptualized by marginal value theory) has, to our knowledge, not yet been explicitly studied in field experiments on forest management practices.

Chinese fir (*Cunninghamia lanceolata*) is an important evergreen conifer species in China. Chinese fir plantations cover 8.54 million ha, representing 14% of the total plantation area in China. Moreover, the stock volume of Chinese fir is as much as 620 million m^3, representing approximately 32% of the total plantation stock volume in China (Yang et al., 2015). Here, we measured a variety of traits of the first two root branch orders under the treatments of N addition, P addition, thinning and pruning in a young Chinese fir plantation. The absorptive root traits covered several key aspects of foraging behavior, including architectural and morphological traits, chemical and growth traits (Table 1). Root foraging sensitivity and precision are also used to characterize root foraging behavior (Einsmann et al., 1999; Bliss et al., 2002). The aim of our study was to examine the influence of management practices on traits, plasticity, and foraging strategy of absorptive fine roots in a Chinese fir plantation. We hypothesized that (i) patterns of trait value and plasticity in absorptive fine roots vary along the trade-off between acquisitive and conservative root traits with management practices, while the effects of nutrient addition diverge from those of pruning and thinning; (ii) variations

Table 1
List of root traits measured and their presumed or demonstrated functional significance, adapted from Roumet et al. (2006). Symbols (+) and (−) indicate positive and negative relationships involving traits and functions, respectively.

Root trait	Abbreviation	Units	Functional significance	References
Architectural traits				
Root length density	RLD	$m\,m^{-2}$	Nutrient and water uptake (+)	Bayala et al. (2004)
			Nutrient uptake (+)	Bardgett et al. (2014)
Morphological traits				
Diameter	D	mm	Root turnover (+)	McCormack et al. (2015)
Root area index	RAI	$m^2\,m^{-2}$	nutrient potential and stand productivity (+)	Craine (2006)
Root tissue density	RTD	$g\,kg^{-1}$	Longevity (+)	Eissenstat and Yanai (1997)
Root tip frequency	RTFW	$N\,mg^{-1}$ DW	Nutrient forging strategy	Ostonen et al. (2011)
Surface area	S	cm^2	Nutrient forging strategy	Ostonen et al. (2011)
Specific root area	SRA	$m^2\,kg^{-1}$	Nutrient forging strategy	Ostonen et al. (2011)
Specific root length	SRL	$m\,g^{-1}$	Growth rate (+)	Comas and Eissenstat (2004)
			Competitive ability (+)	Fort et al. (2014)
			Root turnover (+)	McCormack et al. (2015)
			Rate of P uptake (+)	Hodge (2004)
Growth traits				
Biomass	B	$g\,m^{-2}$	Root foraging sensitivity and precision (+)	Mou et al. (2013)
Length	L	m	Nutrient uptake (+)	Kou et al. (2015); Ostonen et al. (2011)
Tips no.	Tips	No. m^{-2}	Nutrient forging strategy, standing biomass (+)	Ostonen et al. (2011)
Chemical traits				
N content	N	$mg\,g^{-1}$	Nutrient foraging behavior	Liu et al. (2015)

of root foraging sensitivity and precision reflect a tradeoff between nutrient and light resource economy, qualifying as a nutrient-induced foraging strategy (absorptive root functional parameters associated with N and P addition) and a light-mediated foraging strategy (those functional parameters associated with pruning and thinning).

2. Methods and materials

2.1. Study site and experimental design

The study site was located adjacent to the Huitong Experimental Station of Forest Ecology, Hunan Province, China (26°40′–27°09′N and 109°26′–110°08′E). This area belongs to a typical subtropical monsoon climate with mean January, July and annual temperatures of 1.9, 29.0 and 16.5 °C, respectively. The average annual precipitation is approximately 1200 mm. The soil is reddish oxisol (developed from slate and shale) and is relatively uniform with a depth of >1 m.

In April 2012, 15 study plots were established in an eight-year-old Chinese fir (*C. lanceolata*) plantation, with stand density, diameter at breast height (DBH) and mean height of 2380 stems ha^{-1}, 12.8 cm and 8.2 m, respectively. The experiment was conducted according to a randomized block design with three replicates. Within each block, one plot (240 m^2), selected at random, served as the control. The remaining four plots received the treatments of pruning (removing the lower 50% of the green crown length), thinning (50% thinning density), N (urea, 200 kg N ha^{-1} yr^{-1}) and P (KH$_2$PO$_4$, 50 kg P ha^{-1} yr^{-1}) addition. Additionally, the stem growth rate was calculated as the difference in DBH between the current year and the previous year, ΔDBH.

2.2. Root sampling and trait measurements

In May 2014, fine roots were sampled by 20 cm × 20 cm × 20 cm (8000 cm^3) soil monoliths excavated from each plot by the complete method of Taylor et al. (2014). Generally, one monolith was sampled from each tree, and five trees were randomly selected in each plot. The data for the five monoliths in the same plot were averaged. Monoliths were washed over three superimposed screens (3, 1 and 0.5 mm). All visible roots were removed from the screens by hand, rinsed with deionized water and stored at 4 °C until cleaned. *C. lanceolata* roots were separated from neighboring roots using fine forceps. The clean, living roots were hierarchically dissected into branch orders following the protocol described by Pregitzer et al. (2002). Morphological traits of the absorptive roots (the first-order and second-order roots), such as root diameter, length and projection area at 400 dpi were measured with WINRHIZO image analysis software (Regent Instruments Inc., Quebec, Canada). After scanning, roots were oven-dried (65 °C for 48 h) to constant weight and weighed to 0.001-mg accuracy. Root tissue density (RTD, kg m^{-3}), specific root area (SRA, m^2 g^{-1}) and specific root length (SRL, m g^{-1}) were calculated as M/V, S/M and L/M, respectively, where S, M and L are the mean root tip surface area, dry mass and length, respectively. Root tip frequency was expressed as the number of root tips per mg DW (RTFW). The root area index of the absorptive roots (RAI, cm^2 m^{-2}) was calculated as SRA multiplied by root biomass (Ostonen et al., 2011). In order to distinguish between the traits of first-order and second-order root, B1 and B2 was used to signify first-order root biomass and second-order root biomass, respectively. Total C and N concentrations in the absorptive roots were determined using a CHN analyzer (Elementar Analysensysteme GmbH, Hanau, Germany).

2.3. Data analysis

For each treatment pair (e.g., Control_1 & N addition_1, Control_1 & P addition_1, Control_1 & Pruning_1, Control_1 & Thinning_1), the variation in the trait value was calculated as Tt − Tc, where Tt is the trait value for the treatment (Pruning, Thinning, N and P addition) and Tc is the trait value for the control. Similarly, we also calculated trait plasticity for the four treatment conditions as ((Tt − Tc)/Tc) × 100 (Fort et al., 2015a), where Tt is the trait value of Chinese fir grown under a given treatment condition and Tc is the corresponding trait value of Chinese fir for the control. In addition, the root foraging sensitivity for a given treatment was examined by calculating the ratio of root biomass or length for the treatment to that of the control. This foraging sensitivity value was calculated as Bt/Bc and Lt/Lc, where Bt and Lt are the absorptive root biomass or length, respectively, of Chinese fir grown under a treatment condition, and Bc and Lc are the corresponding values for Chinese fir for the control. Root foraging precision was evaluated as the ratio of the root biomass (or total root length) for the treatment to that of the control. Root foraging precision was measured by (Bt − Bc)/Bc and (Lt − Lc)/Lc, with greater ratios considered to represent higher precision (Hodge, 2004).

The normality of the root variables and the homogeneity of the group variances were evaluated with Lilliefors and Shapiro–Wilk tests (for normality), and the F and Levene tests (for homogeneity), respectively. An analysis of variance (ANOVA) was performed for traits and trait plasticity with the treatments (pruning, thinning, N and P addition) and root order as factors. Pearson's correlation coefficients were calculated to test for the strength of the relationships between two sets of traits: (i) absorptive root traits and stem growth rate (ΔDBH) and (ii) absorptive root trait plasticity and stem growth rate (ΔDBH). A principal component analysis (PCA) and discriminant analysis (DA, Statistica 10 package, StatSoft Inc., Tulsa, OK, USA) were conducted on the traits for the various treatments to characterize root foraging strategies.

3. Results

3.1. Responses of root traits and plasticity to treatments

The effect of N addition was significant for all variables (Table 2) except for morphological traits (D, RAI, RLD and S) and growth traits (Tips). B, L, RTD, RTFW, SRA and SRL were significantly affected by P addition. The thinning treatment had a significant effect for four traits (D, RTD, SRA and SRL), while the effect of pruning treatment was not significant for any root traits. Moreover,

Table 2
F-ratios and statistical significance of ANOVAs for 12 traits and stem growth rate (ΔDBH).

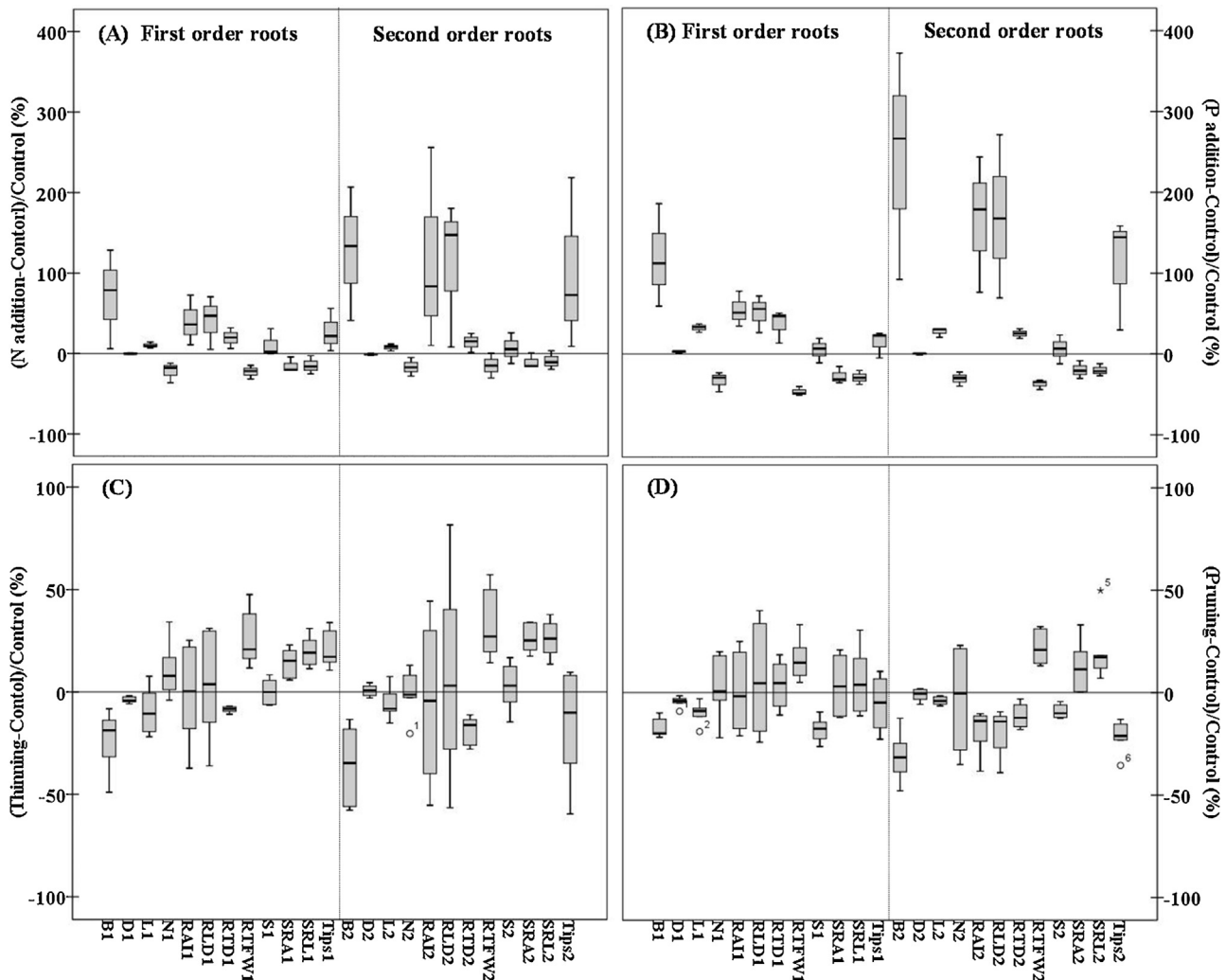| Trait	N addition		P addition		Pruning		Thinning	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
B	5.144	**0.050**	6.469	**0.032**	0.377	0.701	1.596	0.278
D	1.178	0.370	1.167	0.373	2.050	0.210	5.677	**0.041**
L	20.439	**0.002**	15.566	**0.004**	0.157	0.858	0.155	0.860
N	6.242	**0.034**	4.939	0.054	1.683	0.263	1.598	0.278
RAI	2.377	0.174	2.425	0.169	0.162	0.854	1.033	0.412
RLD	1.954	0.222	1.977	0.219	0.254	0.783	1.136	0.382
RTD	8.958	**0.016**	5.601	**0.042**	0.446	0.660	6.615	**0.030**
RTFW	12.839	**0.007**	9.549	**0.014**	1.425	0.312	1.130	0.383
S	0.256	0.782	0.550	0.604	0.562	0.597	0.396	0.690
SRA	8.239	**0.019**	6.061	**0.036**	0.462	0.651	10.405	**0.011**
SRL	8.059	**0.020**	6.591	**0.031**	0.664	0.549	9.574	**0.014**
Tips	0.417	0.677	0.498	0.631	0.427	0.671	2.014	0.214
ΔDBH	5.614	**0.042**	4.768	**0.048**	18.162	**0.003**	7.173	**0.026**

Fig. 1. Boxplots of the responses of absorptive root (first- and second-order roots) traits to (A) N addition (N), (B) P addition, (C) thinning, and (D) pruning factors. The center lines within each box show the location of the sample medians. The lower whisker is drawn from the lower quartile to the smallest point within 1.5 interquartile ranges from the lower quartile. The other whisker is drawn from the upper quartile. See Table 1 for trait code.

the trait of stem growth rate (ΔDBH) was significantly affected by all four treatments (Table 2).

The variation of trait plasticity in response to N and P addition, pruning and thinning was displayed using boxplots (Fig. 1). On average, trait plasticity ranged from −36.4% (N1) to 128.4% (B1) for first-order roots and from −30.4% (RTFW2) to 256.1% (RAI2) for second-order roots in response to N addition (Fig. 1A). Additionally, the average trait plasticity ranged from −50.1% (N1) to 186.0% (B1) for first-order roots and from −44.1% (RTFW2) to 372.0% (B2) for second-order roots in response to P addition (Fig. 1B). Under the thinning treatment, the minimum and maximum values of root trait plasticity were −49.0% (B1) and 47.5% (RTFW1) for the first-order roots and −59.5% (Tips2) and 81.5% (RLD2) for the second-order roots, respectively (Fig. 1C). The effect of pruning on trait plasticity varied from −26.3% (S1) to 33.7% (RLD1) for first-order roots and from −47.9% (B2) to 49.9% (SRL2) for second-order roots (Fig. 1D).

Positive values indicated increases in trait values with different treatments (Fig. 1). Hence, both N and P addition resulted in an increase in all root trait plasticity values except for RTFW, SRA, SRL and N. Moreover, the positive effect of P addition was greater than that of N addition (Fig. 1A and B). Conversely, the effect of thinning on RTFW, SRA, SRL and N was positive, while pruning slightly

increased the trait plasticity of RTFW and SRL for second-order roots. These results indicated that absorptive root traits differed in response to N and P addition and in response to thinning and pruning (Fig. 1C and D). In addition, the variation in absorptive root trait value responded to N and P addition as well as to pruning and thinning. This finding showed the general effect of the treatments on the trait values of B, L, SRL, RLD, RTD and ΔDBH (Fig. S1).

3.2. Root trait syndromes and plasticity and their correlation with stems growth rate

The first two axes of a PCA analysis based on absorptive root traits and their plasticity explained a total of 75.3% and 82.0%, respectively, of the variance for first-order roots (Fig. 2A and B). The first axis of the PCA (explained 44.8% and 69.2% of the variance for trait value and trait plasticity, respectively) differentiated the root traits of N, RTFW, SRA, SRL from those of B, D, L, RAI, RLD, RTD, S and Tips (Fig. 2). The second axis (30.3% and 12.8% of the variance for trait value and trait plasticity, respectively) was positively correlated with RTD and negatively correlated with Tips (Fig. 2A and Table 3), but the RTD and D (indicating a potential increase of the conservative capacity of species) of trait plasticity showed effects contrary to those of trait value (Fig. 2B and Table 3).
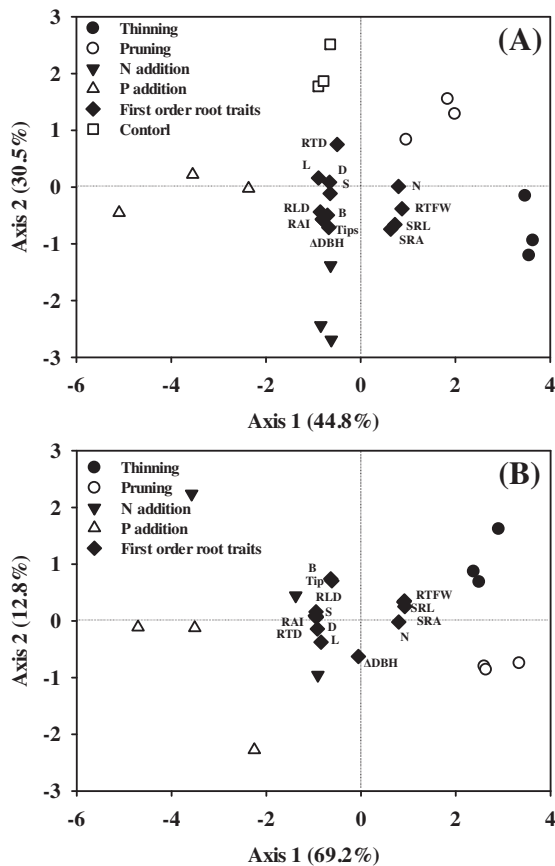
Fig. 2. Principal component analysis (PCA) for 12 traits measured in first-order roots of *C. lanceolata* under N addition, P addition, pruning, and thinning. (A) Trait value coordinates on PCA components 1 and 2. (B) Trait plasticity coordinates on PCA components 1 and 2. See details of abbreviations in Table 1.

Interestingly, both the suites of root traits and the treatments formed two distinct clusters along PCA axis 1. One cluster of N and P addition (change of soil nutrient availability) was found to the left along axis 1, while the other cluster of pruning and thinning treatment (shift on light environment) was found to the right along axis 1 (Fig. 2A and B). The suites of root traits and trait plasticity responsible for the differences among the treatments are plotted in Fig. 2. The traits of D and RTD of first-order roots were to the left along axis 1 according to N and P addition. Whereas those of SRL and N concentration (associated with a resource acquisition strategy) as well as SRA and RTFW was to the right along axis 1 according to pruning and thinning treatment (Fig. 2; Table 3). Stem growth rate was negatively and strongly correlated with axis 2 (Fig. 2B; Table 3). The same trend also occurred in second-order root trait values and trait plasticity (Fig. S2). Additionally, a discriminant analysis of the absorptive root trait value and trait plasticity pattern showed that the effects of N and P addition were clearly separated from those of thinning and pruning. The strongest effect occurred in response to P addition (Fig. S3).

For the absorptive root traits, a positive correlation was found between N1 and ΔDBH in response to N addition ($P < 0.05$), whereas a negative correlation was found between D1 and ΔDBH in response to thinning ($P < 0.05$, Table 4). Variation in growth rate (ΔDBH) was positively correlated with B, RAI, RLD and Tips plasticity in response to thinning and was negatively correlated with that of plasticity in response to N and P addition (Table 4). These results suggest that this coordinated pattern was strongly influenced by nutrient addition and thinning management. In

contrast with these significant correlations, variation in growth rate was uncorrelated with or not significantly related to all the root trait plasticity values in response to pruning (Table 4).

3.3. The sensitivity and precision of absorptive root foraging

Absorptive root foraging behavior (e.g., sensitivity and precision) was influenced by the treatments of N and P addition, pruning and thinning (Fig. 3). A comparison of the treatment and control biomass showed the effect of N and P addition on foraging precision of the first- and second-order roots was significant, while that on foraging sensitivity was not significant (Fig. 3A and B). The variation in foraging precision for thinning for the first- and second-order roots was 0.16 and 0.57, respectively, whereas the variation in foraging precision for pruning clearly decreased from the first-order roots (0.17) to the second-order roots (−0.33). Furthermore, we used the total root length (L, another growth trait) to illustrate the effect of the treatments on foraging sensitivity and precision of the absorptive roots. Both first- and second-order roots were more sensitive and showed a clearer response to P addition than to the other treatments (Fig. 3). Together with foraging sensitivity and precision, P addition significantly enhanced root foraging capacity by increasing the biomass and the total length of first-order roots (Fig. 3B).

4. Discussion

The results of this study showed that absorptive roots displayed a clearly differentiated pattern of functional traits in response to nutrient supply (N and P addition) and plantation management (pruning and thinning) in a ten-year-old Chinese fir plantation. The absorptive roots syndrome and foraging behaviors (e.g., sensitivity and precision) also differed between the first-order roots and the second-order roots among the selected treatments. The different responses to nutrient-induced and light-mediated forestry practices might result from trade-offs between different root foraging strategies and resource-management strategies in the managed Chinese fir plantation.

4.1. Trait plasticity in response to nutrient-induced and light-mediated forestry practices

The nutrient-induced treatments, e.g., N and P addition, can result in increased nutrient availability in soil and can then affect

Table 3
Functional parameter loadings on the first two axes of the principal component analyses (PCA) for trait values and trait plasticity in first-order roots.

Traits parameter	Trait value PCA axis		Trait plasticity PCA axis	
	1	2	1	2
Root area index (RAI)	**−0.839**	−0.483	**0.958**	0.077
Root biomass (B)	**−0.858**	−0.406	**0.940**	0.058
Root diameter (D)	−0.498	0.167	**0.929**	−0.077
Root length (L)	**−0.767**	0.172	**0.864**	−0.232
Root length density (RLD)	**−0.828**	−0.500	**0.936**	0.129
Root nitrogen concentration (N)	0.533	−0.476	**−0.837**	0.306
Root tip number (Tips)	**−0.690**	−0.617	0.599	**0.765**
Root tip frequency (RTFW)	**0.746**	−0.636	**−0.936**	0.273
Root tissue density (RTD)	−0.349	**0.799**	**0.936**	0.048
Specific root area (SRA)	0.434	**−0.822**	**−0.938**	0.159
Specific root length (SRL)	0.494	**−0.792**	**−0.923**	0.235
Surface area (S)	**−0.662**	−0.122	0.587	**0.787**
Stem growth rate (ΔDBH)	**−0.654**	−0.622	0.076	**−0.836**

Loadings in bold have squared loadings >0.65 and indicate the significance of the associated root trait parameter in the PCA, according to Prieto et al. (2015).

Table 4
Correlation statistics (Pearson *r* value) for the relationships ($n = 24$): (A) between the root traits' average values and variations in stem growth rate (ΔDBH), and (B) between trait plasticity and stem growth rate (ΔDBH) in response to N addition, P addition, pruning, and thinning.

Trait	Trait value				Trait plasticity			
	N	P	Pruning	Thinning	N	P	Pruning	Thinning
First order root								
B1	−0.685	−0.550	0.197	0.029	**−0.933**[**]	**−0.979**[**]	0.692	**0.930**[**]
D1	−0.351	−0.281	0.142	**−0.745**[*]	−0.661	−0.404	0.583	−0.510
L1	−0.506	−0.160	−0.110	−0.112	−0.707	**−0.947**[**]	−0.520	−0.360
N1	**0.917**[*]	0.603	−0.447	0.064	0.157	**−0.905**[*]	0.388	−0.573
RAI1	−0.438	−0.476	0.025	0.111	**−0.932**[**]	**−0.932**[**]	0.269	**0.971**[**]
RLD1	−0.409	−0.453	−0.020	0.206	**−0.851**[*]	**−0.840**[*]	0.139	**0.945**[**]
RTD1	−0.619	−0.239	0.384	−0.144	−0.757	**−0.929**[**]	−0.109	0.115
RTFW1	0.624	0.256	−0.199	0.351	0.414	**0.968**[**]	−0.405	0.710
S1	0.752	0.251	−0.072	−0.235	−0.476	**−0.900**[*]	−0.517	**−0.963**[**]
SRA1	0.667	0.256	−0.302	0.398	0.047	**0.851**[*]	0.066	−0.758
SRL1	0.669	0.271	−0.266	0.518	−0.571	0.762	0.149	−0.703
Tips1	−0.166	−0.434	0.017	0.312	**−0.940**[**]	**−0.960**[**]	−0.010	**0.877**[*]
Second order root								
B2	−0.642	0.030	−0.076	−0.352	**−0.959**[**]	**−0.981**[**]	0.324	**0.988**[**]
D2	−0.105	−0.412	0.305	0.157	**−0.948**[**]	−0.283	−0.366	−0.657
L2	−0.676	−0.601	0.026	0.065	−0.662	**0.932**[**]	−0.399	−0.716
N2	0.764	0.684	−0.446	0.118	0.650	**0.961**[**]	0.020	**−0.881**[*]
RAI2	−0.685	0.048	−0.346	−0.247	**−0.970**[**]	**−0.976**[**]	−0.057	**0.924**[**]
RLD2	−0.694	0.135	−0.336	−0.286	**−0.968**[**]	**−0.986**[**]	−0.055	**0.860**[*]
RTD2	−0.513	0.156	0.429	−0.531	**−0.959**[**]	**−0.978**[**]	0.154	−0.060
RTFW2	0.627	0.462	−0.473	0.264	0.341	**0.950**[**]	−0.557	0.640
S2	0.807	0.506	0.157	0.074	−0.523	−0.389	−0.322	**−0.870**[*]
SRA2	0.505	0.013	−0.403	0.468	**0.815**[*]	**0.944**[**]	−0.037	−0.251
SRL2	0.452	0.134	−0.399	0.399	0.754	**0.940**[**]	−0.115	−0.439
Tips2	−0.492	0.455	−0.330	−0.323	**−0.970**[**]	**−0.962**[**]	−0.087	**0.960**[**]

[*] $P < 0.05$.
[**] $P < 0.01$.

root dynamics through changes in root morphological and physiological traits (Mou et al., 2013). Our results confirmed an higher increase of absorptive root trait plasticity (B, L, RTD, RTFW, SRA and SRL) and foraging precision in response to P addition, and revealed the quantitative effect of nutrient supply on root foraging behavior (Figs. 1 and 3; Table 2). The nutrient-induced root trait plasticity also indicated their intimate relationships with foraging strategies in absorptive roots (Lohmus et al., 2006), e.g., the extensive foraging strategy (increased root growth and biomass) (Ostonen et al., 2011). This finding is, however, inconsistent with some previous studies. For example, a recent meta-analysis of simulated N deposition on root traits showed that N addition resulted in a significant decline in fine root biomass (<2 mm diameter; −12.8%) and a clear decrease in total root length (Li et al., 2015). In addition, Ostonen et al. (2007) argued that SRL was indicative of interspecific differences in environmental change response but was poorly plastic to N addition within species (George et al., 1997; Mei et al., 2010; Liu et al., 2015). In contrast, we observed that SRL and SRA showed significant responses to N and P addition in the young Chinese fir plantation (Table 2). These results underscore that various species show changes in root morphology as differential responses to changes in nutrient availability and that this phenomenon outlines an essential strategy for nutrient acquisition (Chen et al., 2013b; Lambers et al., 2011). Apart from interspecies differences, our results focus on absorptive roots (first-order and second-order roots) and were based on root order classes, whereas the approach used by previous studies differed significantly because those studies used root diameter classes. Interestingly, the effect of P addition on root traits was greater for first-order roots than for second-order roots (Fig. 3 and S1).

The light-mediated forest management practices such as thinning and pruning can also affect the morphological and physiological characteristics of fine roots. Our results confirmed that thinning significantly changed root trait parameters, with increases in SRA and SRL but decreases in D and RTD (Table 3). These results are consistent with the findings of previous studies of *Platycladus orientalis* (Chen et al., 2013a,b) and *C. lanceolata* (Wang et al., 2013a,b), but not consistent with previous results for *Chamaecyparis obtusa* (Noguchi et al., 2011). In part, these differences can result from species and site factors and also from the difference between root diameter classes and root order classes. Note that no root trait parameters showed a significant response to pruning. This finding is not in agreement with previous workers who reported different responses of tree species to pruning (Jones et al., 1998; Bayala et al., 2004; Chesney, 2008), suggesting that absorptive root trait values are not sensitive to pruning.

This study opens the opportunity to assess absorptive root trait syndromes and plasticity in response to thinning, pruning and nutrient addition in the same plantation, confirming response mechanisms vary between treatments. The nutrient supply (e.g., N or P addition) inducing a foraging strategy (higher root biomass, length and foraging ability), often increases growth by enhancing photosynthesis and resource-use efficiencies, and shifts the partitioning of carbon more above-ground (Forrester, 2013). For light-mediated treatment, thinning also can increase resource-use efficiencies and change in carbon partitioning between above- and below-ground by providing trees with more space to expand their root and crown zones. Consequently, thinning and pruning positively feedback on morphological plasticity of absorptive roots (SRL, SRA, RTFW and N concentration), resulting in a light-mediated foraging strategy. Additionally, it should be noted that the relative insensitivity of absorptive root morphology to pruning occurs at least partly because the reduction in resource acquisition is countered by an increase in the light-use and water-use efficiency of the remaining crown (Forrester and Baker, 2012).
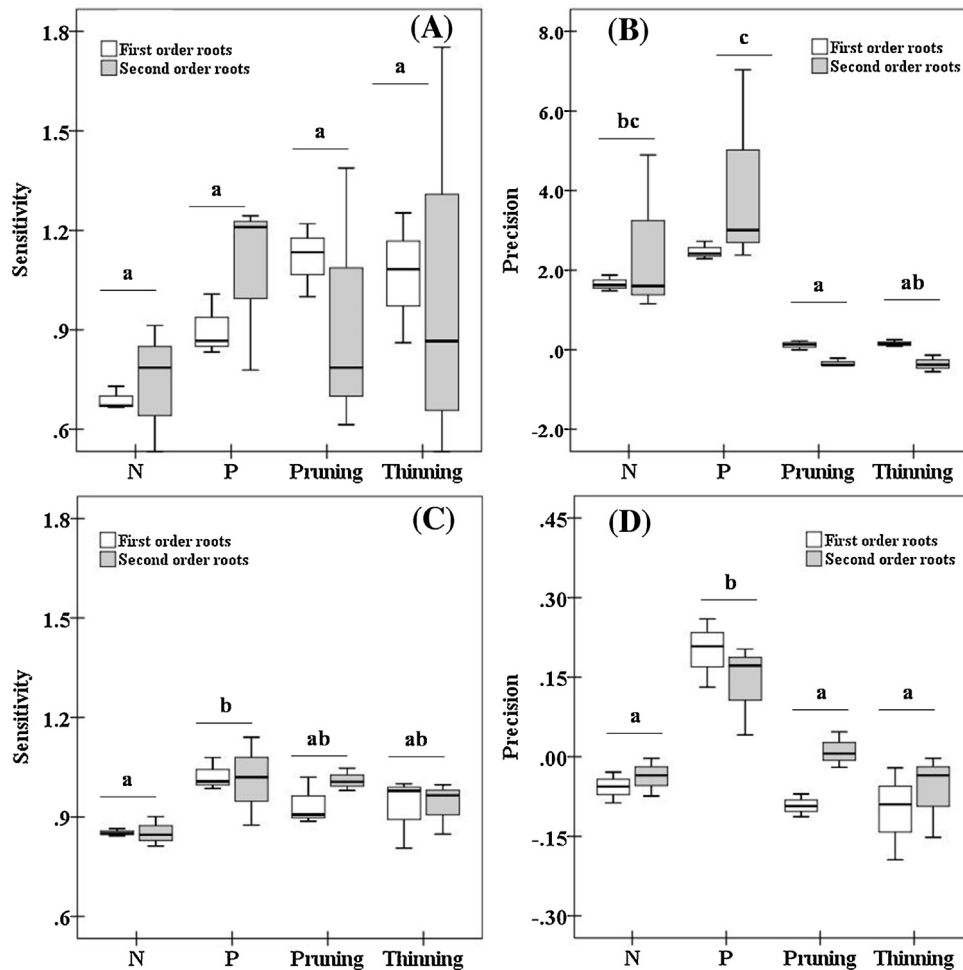
Fig. 3. Effect of N addition, P addition, pruning and thinning on absorptive root foraging sensitivity and precision, calculating as root biomass (A for sensitivity; B for precision) and total root length (C for sensitivity; D for precision).

4.2. Resource use trade-off and root foraging strategy

Both nutrient supply and forestry practices result in changes in resource use and alterations of root traits and their plasticity. As a consequence, different root foraging strategies occur with resource-management trades-off (Fort et al., 2015a). We determined that N and P addition induced shifts in morphological traits (increase of B, RAI, RLD and Tips but decrease of N, RTFW, SRA and SRL) and resulted in root foraging strategies that were driven by nutrient availability (Fig. 1). In contrast, thinning and pruning also affected the pattern of absorptive root traits and shaped different root foraging strategies driven by resource use efficiency. For example, thinning improved the light environment in the crowns and subsequently changed leaf physiological traits (increase of the photosynthetic rate and leaf nitrogen concentration per unit area) in a *C. obtusa* plantation (Han et al., 2006; Han and Chiba, 2009). This rapid response of leaf functional traits to environmental changes after thinning could decrease the biomass and production of fine roots but showed few effects on the characteristics of fine roots (e.g., D, RTD and SRL) in a young *C. obtuse* plantation (Noguchi et al., 2011). In contrast, a significant effect of thinning on morphological traits (D, RTD, SRA and SRL) was observed in our young *C. lanceolata* plantation (Table 2, Fig. 1), highlighting species-specific effects on leaf traits and feedback on root traits and their plasticity and a subsequent alteration of root foraging strategies. In a word, absorptive root foraging strategy is determined by species identity, environmental conditions and their interaction.

To adapt to the heterogeneity of soil nutrients, plant roots have evolved foraging behaviors. One of the important foraging behaviors is that root proliferation often occurs in nutrient-rich patches such as those produced by N and P addition treatments (Drew, 1975; Hodge 2004), whereas root morphological traits (e.g., D, RTD and SRL) showed a lack of response to fertilization treatments in results averaged across 14 AM tree species (Liu et al., 2015) and, similarly, a lack of results in a slash pine plantation (Kou et al., 2015). In our study, both root growth and morphological traits showed significant responses to nutrient supply and forest management practices (Table 2; Fig. 1). This finding suggests that the integrated responses of absorptive roots depend on nutrient and light availability, resource use and trade-offs among them, supporting the hypothesis that plants integrate the signals associated with nutrients and environmental conditions (Cahill et al., 2010; Fang et al., 2011). Furthermore, our results showed that root foraging sensitivity and precision in Chinese fir were enhanced under N addition, P addition and thinning, but decreased in response to pruning treatment based on the parameters of root biomass and total root length (Fig. 3). The promoted root foraging precision could be a reason for the advantageous response of suites of root traits (B, RAI, RLD and tips) in response to P addition. There

appear to be clear trade-offs between maximizing resource acquisition and minimizing costs associated with root tissue construction and maintenance (Eissenstat and Yanai, 1997). Our results supported a link between root economic spectrum and absorptive root foraging strategy in which first- and second-order roots given P addition tended to show higher RAI and RLD, higher root foraging sensitivity and precision than first- and second-order roots associated with the other treatments (Figs. 1 and 3). Indeed, a suite of morphological and chemical characteristics shaped by N or P addition reflects a root behavioral strategy as a result of adaptation to variation in nutrient availability, which qualified as a nutrient-induced foraging strategy. In contrast, canopy pruning and thinning can change photosynthesis and carbohydrate allocation pattern, consequently contributes another root behavioral strategy, a suite of absorptive root traits and trait plasticity mediated by plant light economy, which qualified as a light-mediated foraging strategy.

We conclude that there is a clear pattern of root traits and their plasticity in response to nutrient supply and forest management practices and that a strong trade-off exists among the resource use and root foraging strategies in the young *C. lanceolata* plantation. Although stem growth rate was affected significantly by the four treatments, it was correlated positively with absorptive root traits (B, RAI, RLD and Tips) after thinning but negatively with these root trait parameters after N and P addition. Furthermore, multiple suites of trait plasticity are more useful than those of trait values to explain differential responses to environment change. Interestingly, an evident difference between first-order roots and second-order roots was observed in response to the treatments, suggesting that multiple suites of traits between root orders operate simultaneously to impact absorptive root foraging strategies. Further studies may explore nutrient-induced and light-mediated foraging strategies between absorptive roots across root branching orders in mature Chinese fir plantation.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.envexpbot.2016.01.001.

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