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Variations in root chemistry of three common forest species, southwestern China

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Abstract Root chemistry varies with tree species and root diameter but little information is available about Tibetan forest species. The root chemistry of three root diameter classes (fine: 0-2 mm, medium: 2-5 mm, coarse: 5-10 mm) of three subalpine species (Abies faxoniana Rehd. and Wild, Picea asperata Mast., and Betula albosinensis Burkill) were investigated. Carbon concentrations, and carbon/nitrogen and carbon/phosphorus ratios increased but nitrogen, phosphorus and nitrogen/phosphorus ratios decreased with increasing root diameter. The roots of the conifers had higher carbon levels, and higher carbon/nitrogen and carbon/phosphorus ratios than birch roots. The opposite was found with nitrogen and phosphorus levels and nitrogen/phosphorus ratios. Lignin concentrations decreased but cellulose concentrations increased with greater root diameters. The results indicate that diameter-associated variations in root chemistry may regulate their contribution to detrital pools which has important implications for below-ground carbon and nutrient cycles in these subalpine forests.

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Zhenfeng Xu sicauxzf@163.com **Keywords** Root diameter · Lignin · Cellulose · Stoichiometry · Subalpine forest

Introduction

Plant root systems are important components of terrestrial ecosystems. In forests, fine root turnover accounts for approximately 30-50% of net primary production (Vogt 1991). Turnover rates and decomposition patterns generally vary with root diameters (Silver and Miya 2001; Joslin et al. 2006). Moreover, large diameter roots play an important role in the transport and storage of C (carbon) and nutrients (Ludovici et al. 2002; Melin et al. 2009), and also provide a slow delivery of C to the soil which affects long-term ecosystem productivity and CO₂ emissions through slow decomposition (Johnsen et al. 2005).

Root chemistry is thought of as substrate quality, which not only can reflect the distribution of chemicals, but can also predict functional processes (Birouste et al. 2012). Carbon is the main element of plant tissues; nitrogen (N) and phosphorus (P) are the most important nutrients for a variety of proteins and genetic materials (Hessen et al. 2004; Ladanai et al. 2010). Cellulose and lignin are the main components of cell walls and of natural lignocellulosic materials. Their concentrations or stoichiometry are widely used as predictors of root decomposition or respiration (Silver and Miya 2001; Jia et al. 2013). Root chemistry differs widely between species (Roumet et al. 2006; Birouste et al. 2012). Compared to broadleaved species, conifer roots usually have lower N, P and lignin (Silver and Miya 2001; Newman and Hart 2006). Root diameters integrate both chemical and physical properties (Andrén et al. 1992). With the increase in diameters, N and P concentrations decrease but the C/N ratios, and lignin

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and cellulose increase (King et al. 2002; Pregitzer et al. 2002). Research has mainly focused on diameter-associated variations within a fine-root system (e.g., < 0.5 mm vs. 0.5–1 or 0.5–2 mm), (Yang et al. 2004; Sun et al. 2013; Wang et al. 2014). However, chemical differences between fine roots and larger roots are still poorly understood in forests such as Tibetan forest ecosystems.

Subalpine forests on the eastern Tibetan Plateau play important roles controlling headwaters, conserving soils, maintaining biodiversity and regulating regional climates (Yang et al. 2005). Minjiang fir (*Abies faxoniana* Rehd. and Wild, dragon spruce (*Picea asperata* Mast.), and red birch (*Betula albosinensis* Burkill) are three dominant species in these forests. Previous studies have shown that there are significant differences in above-ground litter quality among the three species (Xu et al. 2016). In order investigate the chemical traits of below-ground roots of these species, C, N, P, lignin and cellulose concentrations in three diameter classes (0–2.0, 2.1–5.0 and 5.1–10.0 mm) were determined. The main objective in this study was to determine if root chemistry and stoichiometry vary with species and root diameter.

Materials and methods

The research was carried out at the Long-term Research Station of Alpine Forest Ecosystems of Sichuan Agricultural University located on the eastern Tibetan Plateau. Annual mean precipitation is approximately 850 mm and annual mean temperature 3 °C. The ground is snow covered from mid-November to early April. Soils are typical dark brown forest soils classified as Cambic Umbrisols according to the IUSS Working Group (IUSS 2007). Minjiang fir, dragon spruce and red birch are dominant forest species.

Sampling and dissection

In July 2013, root samples of the three species were collected from a mixed forest stand with slope $< 5^{\circ}$, aspect NE 46°, and a canopy cover of approximately 80%. Topsoil properties (0–15 cm) were organic C 89 g kg⁻¹, N 5.5 g kg⁻¹, and pH 6.3. Three plots (100 m × 100 m) were established as replicates for root collection. For each species, three trees were chosen and soil trenches 50 cm × 50 cm × 20 cm 1–2 m from each sample tree were dug to give access to the root system. Soil particles and other materials were removed from roots by washing and brushing with deionized water (Yang et al. 2004). Following the methods of Camiré et al. (1991), the intact root system was classified into three diameter classes using a vernier caliper: fine roots (0.0–2.0 mm), medium roots

(2.1-5.0 mm) and coarse roots (5.1-10.0 mm). Each sample was mixed to get one composite sample which was then passed through a 0.15 mm sieve and used for chemical analyses.

Chemical analyses

Levels of C, N and P were determined as described by Lu (1999). Carbon contents were determined using the dichromate oxidation-sulphate-ferrous titration method. N and P levels were evaluated by the Kjeldahl method and the phosphomolybdenum yellow colorimetry method, respectively. Lignin and cellulose were measured using the acid detergent lignin procedure (Vanderbilt et al. 2008; He et al. 2016). Briefly, 1.0 g root samples were oven-dried and ground, transferred to digestion tubes, and suspended in an 80 mL solution of 1.0 mol L^{-1} H₂SO₄ and cetyl trimethyl ammonium bromide (CTAB; 20 g L^{-1}). The tubes were heated at 169 °C for 1 h. After cooling, they were transferred to a sand core funnel and washed with acetone until the solution through the suction filtration was clean. After oven drying at 170 °C for 1 h, the sample and tube were weighed and designated as W1. Subsequently, the sample was soaked for 3 h in a 72% H₂SO₄ solution, subjected to suction filtration, washed with acetone as described above, and oven-dried at 170 °C for 1 h. Sample and tube were weighed, designated as W2, and placed in a muffle furnace (Box Furnace; Lindberg/Blue M, Asheville, NC, USA) at 550 °C for 3 h, weighed after cooling and designated as W3. The cellulose concentration was determined from the difference between W1 and W2 divided by the sample weight (1.0 g), and multiplied by 100. The lignin concentration is the difference between W2 and W3.

Statistical analyses

Two-way ANOVA examined the effects of species, root diameter, and their relationship on C, N, P, lignin, and cellulose concentrations and theirs ratios. One-way ANOVA with Tukey post hoc test were used to compare the differences in all variables among root diameters for a given species, and for species for a given root diameter. Pearson correlation analysis examined relationships between all variables. The statistical tests were considered significant at the P < 0.05 level and were performed using the Software Statistical Package for the Social Sciences (SPSS) version 19.0.

Results

C, N and P concentrations

Tree species and root diameter often had significant effects on C, N and P concentrations (Table 1). Carbon levels increased with root diameter while there were no significant differences between fine and medium roots of spruce and birch (Fig. 1; Table 1). The average C concentrations of fir, spruce and birch were 526.8, 501.7 and 476.5 mg g⁻¹, respectively (Fig. 1). However, N and P levels often decreased with increasing diameter within all

 Table 1
 Results of two-way ANOVA for response of chemistry and stoichiometry to tree species (TS) and root diameter (RD)

Parameters	Variables source	d.f.	F	Р
С	TS	2	69	< 0.001
	RD	2	45.91	< 0.001
	$TS \times TS$	4	13.26	< 0.001
Ν	TS	2	1071.83	< 0.001
	RD	2	657.14	< 0.001
	$TS \times TS$	4	59.35	< 0.001
Р	TS	2	78.43	< 0.001
	RD	2	97	< 0.001
	$TS \times TS$	4	17.01	< 0.001
C/N	TS	2	191.76	< 0.001
	RD	2	222.65	< 0.001
	$TS \times TS$	4	6.62	0.002
C/P	TS	2	31.25	< 0.001
	RD	2	71.33	< 0.001
	$TS \times TS$	4	3.98	0.017
N/P	TS	2	123.12	< 0.001
	RD	2	38.37	< 0.001
	$TS \times TS$	4	5.69	0.004
	TS	2	138.19	< 0.001
	RD	2	86.98	< 0.001
	$TS \times TS$	4	21.6	< 0.001
Cellulose	TS	2	59.78	< 0.001
	RD	2	1851.79	< 0.001
	$TS \times TS$	4	58.56	< 0.001
Lignin/N	TS	2	263.43	< 0.001
	RD	2	94.5	< 0.001
	$TS \times TS$	4	12.33	< 0.001
Lignin/P	TS	2	67.01	< 0.001
	RD	2	13.56	< 0.001
	$TS \times TS$	4	0.4	0.804
Lignin/cellulose	TS	2	285.65	< 0.001
	RD	2	1111.29	< 0.001
	$TS \times TS$	4	101.57	< 0.001

three species. Regardless of diameter, birch roots generally had higher N and P concentrations than those of the two conifers (Fig. 1).

C/N, C/P and N/P

Root C/N, C/P and N/P were also influenced by tree species, root diameter (Table 1). In general, both C/N and C/P tended to increase with increasing root diameter but the opposite pattern was found in N/P (Fig. 2). However, root C/P was similar between fine and medium roots for all three tree species and root diameter did not affect N/P of birch root. Irrespectively of root diameter, both fir and spruce had higher C/N and C/P compared to birch. Conversely, the N/P of birch was higher than those of two coniferous trees in each diameter (Fig. 2).

Lignin and cellulose concentrations

ANOVA results indicated that lignin and cellulose concentrations were significantly affected by tree species and root diameter (Table 1). Individual lignin concentration ranged from 188.1–394.3 mg g⁻¹ and individual cellulose concentration varied between 131.1 and 360.4 mg g⁻¹ (Fig. 3). Both lignin and cellulose concentrations peaked in the fine root of fir and coarse root of birch, respectively. Regardless of tree species, fine roots exhibited higher lignin concentration but lower cellulose concentration compared to larger diameter roots. The effect of tree species on lignin and cellulose concentration was dependent on root diameter (Table 1).

Lignin/N, Lignin/P and Lignin/cellulose

There were significant differences in lignin/N, lignin/P and lignin/cellulose among tree species or root diameters (Table 1). However, no significant interaction of species \times diameter on lignin/P was observed (Table 1). The highest lignin/N and lignin/P was found in the coarse root of fir. In all species, the lignin/N and lignin/P increased with increasing root diameter but the opposite was true for lignin/cellulose (Fig. 4). Irrespectively of root diameter, both fir and spruce roots exhibited higher lignin/N and lignin/P than birch roots.

Correlations between root variables

When pooled over all data of root diameter and tree species, significant correlations between variables were observed (Table 2). C concentration showed a negative relationship with N and P concentration but N concentration had a positive correlation with P concentration. Root C was positively associated with C/N and C/P. However,

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Fig. 1 Variations of root C, N and P concentrations among diameters and species (mean \pm SD). Different lowercases represent significant differences among root diameters for a given tree species and

different uppercases represent significant differences among species for a given root diameter



Fig. 2 Variations of C/N, C/P and N/P among root diameters and species (mean ± SD). Different lowercases represent significant differences among root diameters for a given tree species and different uppercases represent significant differences among species for a given root diameter

Fig. 3 Variations of lignin and cellulose concentrations among root diameters and species (mean \pm SD). Different lowercases represent significant differences among root diameters for a given tree species and different uppercases represent significant differences among species for a given root diameter





Fig. 4 Variations of lignin/N, lignin/P and lignin/cellulose among root diameters and species (mean \pm SD). Different lowercases represent significant differences among root diameters for a given

tree species and different uppercases represent significant differences among species for a given root diameter

there were no significant correlations between root lignin and C, N, P, C/N, C/P and N/P. Root lignin concentration was correlated negatively with cellulose concentration but no correlation was found between lignin and lignin/N and lignin/P. A positive correlation was found between lignin/cellulose and lignin. Additionally, root C, C/N and C/P showed positive relationships with cellulose, lignin/N and lignin/P (Table 2).

Discussion

According to the theory of ecological stoichiometry, there exist complex coupling relationships among C, N and P, which were largely affected by biotic and abiotic factors (Ladanai et al. 2010). Previous studies have revealed that C concentration and C/N was greater in conifer roots than in broad-leaved roots (Silver and Miya 2001). Regardless of root diameter, root C/N and C/P generally exhibited a tendency of fir and spruce > birch in the present case. This is mainly due to the fact that root growth and C investment strategy are different between needle-leaved evergreen and broad-leaf deciduous tree species (Chang and Guo 2008). N and P are considered as major limiting factors for plant growth in terrestrial ecosystems (Vitousek and Howarth 1991; Vitousek et al. 1994). Regardless of root diameter, birch root had higher N and P concentration than fir and spruce, which was similar to the performances of leaf litter and fine roots of three tree species (Wei et al. 2013; Xu et al. 2016). In general, broad-leaved tree species have higher photosynthesis and respiration rates compared to coniferous trees. Thus, more N and P are needed via root system to meet rapid metabolism activity (Tang et al. 2015a, b). Moreover, the C/N and C/P ratios are often used to reflect organismic utilization efficiency for substrate. Root litter with low C/N has a faster decomposition rate (Chapin et al. 2002; Zhang and Wang 2015). In this study, higher nutrient concentrations and lower C/N and C/P in birch roots reflect its better decomposability compared to conifer roots. This deduction is partly line with the reported results that the fine root of birch decay more rapidly as compared to those of two conifers (Wei et al. 2013; Wu et al. 2010).

Root diameter integrates both chemical and physical properties and is widely used as an agent of litter quality (Andrén et al. 1992). Irrespective of tree species, lower C/N and C/P and higher N, P and N/P were observed in fine roots compared to larger roots. This finding was in consistent with most reported results (Silver and Miya 2001; John et al. 2002; Yuan et al. 2011; Wang et al. 2014). Compared to larger diameter roots, fine roots with higher P concentration supported that the growth rate hypothesis that faster growing tissues such as fine roots need more P-rich RNA to support protein synthesis (Yuan et al. 2011). However, higher N/P of fine roots relative to coarser roots implied that P concentration decreased proportionally less than N concentration with increasing root diameter. In addition, this also indicates that C, N and P are disproportionally allocated to new biomass as plant roots grow from fine to coarse roots.

Lignin and cellulose are well known as a recalcitrant component and they are two key components in root substrate (Melillo et al. 1982). Lignin concentration of broadleaved tree roots seems to be higher compared to conifer roots (Silver and Miya 2001). In the current case, birch roots often had higher lignin concentrations than spruce roots, but lower relative to fir roots. Moreover, a recent study has found that there was no significant difference in

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	С	N	Р	C/N	C/P	N/P	Lignin	Cellulose	Lignin/N	Lignin/P	Lignin/cellulose
C	1										
Ν	-0.883^{**}	1									
Ρ	-0.865^{**}	0.946^{**}	1								
C/N	0.807^{**}	-0.893^{**}	-0.823^{**}	1							
C/P	0.850^{**}	-0.883^{**}	-0.957^{**}	0.878^{**}	1						
N/P	-0.689^{**}	0.839^{**}	0.635^{**}	878**	-0.608^{**}	1					
Lignin	-0.093	0.189	0.306	-0.081	-0.274	-0.084	1				
Cellulose	0.590^{**}	-0.655^{**}	-0.754^{**}	0.678^{**}	0.801^{**}	-0.378	-0.668^{**}	1			
Lignin/N	0.749^{**}	-0.805^{**}	-0.701^{**}	0.937^{**}	0.762^{**}	-0.875^{**}	0.264	0.426*	1		
Lignin/P	0.718^{**}	-0.735^{**}	-0.725^{**}	0.796^{**}	0.779^{**}	-0.657^{**}	0.378	0.333	0.912^{**}	1	
Lignin/Cellulose	-0.464^{*}	0.602^{**}	0.674^{**}	-0.545^{**}	-0.661^{**}	0.340	0.824^{**}	-0.923^{**}	-0.256	-0.122	1
*P < 0.05; **P <	0.01										

lignin concentration between Douglas fir and European beech (Thomas et al. 2014). A meta-analysis has also shown that there are substantial variations in root lignin among tree species (Newman and Hart 2006). Therefore, root lignin content is likely to be attributed to species itself traits and the environments of tree growth. In addition, there existed certain difference in root cellulose and lignin/cellulose between coniferous and broad-leaved tree species, but this tendency was dependent on root diameter root cellulose was found to be lower in Douglas fir as compared to that of European beech (Thomas et al. 2014). This may be explained by thicker secondary cell walls of beech roots, especially sclerenchymatous and xylem cells (Kutschera and Lichtenegger 2002). Combined with lower N and P concentration, conifer roots tend to exhibit higher lignin/N and lignin/P than birch roots. In general, lignin/N and lignin/P are commonly considered as one of key factors controlling long-term decomposition (Dickison 2000; Yang et al. 2004). Thus, we further speculate that birch roots could decay faster than those of conifer roots (fir and spruce) during the long-term decomposition process.

Besides, lignin concentrations tended to decrease with increasing root diameter irrespective of tree species. Similar performances were observed in many other forest tree species, including Douglas fir, European beech and Black alder (Thomas et al. 2014; Camiré et al. 1991). The higher lignin concentration in fine roots compared to larger roots is likely to be due to the fact that fine roots often had greater component of lignified tissue (e.g., the xylem) compared to coarser roots (Dickison 2000). Conversely, cellulose concentration showed an increasing tendency with increasing root diameter. This is probably because fine roots commonly had lower secondary cell walls relative to larger diameter roots (Guo et al. 2008). Secondary walls generally are thicker than primary walls, and typically contain a higher proportion of cellulose than primary walls (Guo et al. 2008). A negative correlation between lignin and cellulose concentrations was found in this study, which was line with the results observed in Douglas fir and European beech (Thomas et al. 2014). Compared to fine roots, higher lignin/N in the coarse roots can result in lower decomposition rates (Stump and Binkley 1993; Rahmana et al. 2013). A one-year incubation experiment has supported the deduction that mass loss of fine roots was greater than those of coarse root in the subalpine forest tree species (Tang et al. 2015a, b).

Conclusions

This study explored diameter-associated variations in root chemistry and stoichiometry in three common subalpine forest tree species of southwestern China. Irrespectively of root diameter, conifer roots (fir and spruce) tend to have lower N and P concentrations but higher C/N, C/P, lignin/N and lignin/P than birch roots. In addition, regardless of tree species, fine roots exhibited higher N and P concentrations and lower cellulose, lignin/N and lignin/P as compared to larger diameter roots. In general, there are significant relationships among root chemical variables. Taken together, there are remarkable differences in chemical traits among diameter classes and tree species, which have important implication for below-ground carbon and nutrient cycles in this specific area.

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