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C:N:P stoichiometry of rhizosphere soils differed significantly among overstory trees and understory shrubs in plantations in subtropical China

Xiaoqin Dai, Xiaoli Fu, Liang Kou, Huimin Wang, and Clinton C. Shock

Abstract: Rhizosphere soil C:N:P stoichiometry is useful for identifying the linkage of plant species and soil nutrients, which can be particularly helpful for understory vegetation management of forest ecosystems. There has been limited research on rhizosphere soil stoichiometry, especially for co-existing overstory and understory plant species. We investigated the bulk and rhizosphere soil C:N:P stoichiometry of dominant overstory trees and understory shrubs (*Adinandra millettii, Eurya muricata,* and *Loropetalum chinense*) in *Pinus massoniana* Lamb., *Pinus elliottii* Engelm., and *Cunninghamia lanceolata* (Lamb.) Hook. plantations in subtropical China. Rhizosphere soil C, N, and P concentrations and ratios increased significantly compared with bulk soil, and those of overstory trees were higher than those of understory shrubs with the exception of *L. chinense*. Rhizosphere soil C:N, C:P, and N:P of *L. chinense* were not significantly different with those of overstory trees but were higher than those of *A. millettii* and *E. muricata*. Soil pH significantly influenced the profiles produced by soil C, N, and P concentrations and their stoichiometries. This study indicated that the difference in nutrient status between overstory trees and understory shrubs was related to shrub species, in which soil pH was the dominant driving factor. Understory shrub species should be considered in plantation management to reduce resource competition among species.

Key words: biogeochemical niche, nutrient limitation, pure coniferous forests, plant species, red soil.

Résumé : La stœchiométrie de C:N:P dans le sol de la rhizosphère est utile pour identifier le lien des espèces végétales avec les éléments nutritifs dans le sol, ce qui peut être particulièrement utile pour l'aménagement de la végétation du sous-bois des écosystèmes forestiers. La stœchiométrie dans le sol de la rhizosphère a été peu étudiée, particulièrement dans le cas des espèces végétales qui coexistent dans l'étage dominant et le sous-bois. Nous avons étudié la stœchiométrie de C:N:P dans l'ensemble du sol et dans le sol de la rhizosphère des arbres de l'étage dominant et du sous-bois (*Adinandra millettii*, *Eurya muricata* et *Loropetalum chinense*) dans des plantations de *Pinus massoniana* Lamb., *Pinus elliottii* Engelm. et *Cunninghamia lanceolata* (Lamb.) Hook. en Chine subtropicale. Les concentrations et les ratios de C, N et P ont significativement augmenté dans le sol de la rhizosphère comparativement à l'ensemble du sol et ceux des arbres de l'étage dominant étaient également plus élevés que ceux des arbres du sous-bois à l'exception de *L. chinense*. Les ratios C:N, C:P et N:P dans le sol de la rhizosphère de *L. chinense* étaient significativement différents de ceux des arbres de l'étage dominant mais plus élevés que ceux de *A. milletti* et *E. muricata*. Le pH du sol influençait significativement les profils générés par les concentrations de C, N et P dans le sol ainsi que leur stœchiométrie. Cette étude indique que les différences de statut nutritionnel entre les arbres de l'étage dominant et les arbustes du sous-bois sont reliées à l'espèce d'arbuste, chez lesquels le pH du sol est le principal facteur déterminant. On devrait tenir compte des arbustes du sous-bois dans l'aménagement des plantations pour réduire la compétition pour les ressources entre les espèces. [Traduit par la Rédaction]

Mots-clés : niche biogéochimique, limitation des éléments nutritifs, forêt pure de conifères, espèce végétale, sol rouge.

Introduction

Plantations often consist of overstory trees, understory shrubs, and herbs (Y. Liu et al. 2017), which grow together and compete for nutrient resources, including nitrogen (N) and phosphorus (P) (Wang et al. 2016). Understory vegetation is commonly removed in plantation management to reduce competition for belowground resources and improve the productivity of target tree species (Wagner et al. 2006). The positive role of understory vegetation has been increasingly recognized in forest ecosystem processes and functions in recent years, which includes increasing soil carbon (C) and nutrients (Qiao et al. 2014; Winsome et al. 2017), alleviating soil acidification (Fu et al. 2015), and promoting litter decomposition (Mao et al. 2016; Wang et al. 2016). Therefore, retaining some understory vegetation can be advantageous for forest production and ecological functions in plantation management (Fu et al. 2015). Understanding which understory species should be removed or retained is still a significant challenge in forest ecosystem management.

Niche differentiation, including biogeochemical niche differentiation, has been studied extensively as a theoretical mechanism

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of species coexistence (Peñuelas et al. 2008; Álvarez-Yépiz et al. 2017). Biogeochemical niche differentiation reflects that the coexisting different species tend to use the nutrients in differing proportions, thus producing the different stoichiometry for coexisting different species (Peñuelas et al. 2008; Urbina et al. 2017). Different ecological stoichiometry implies the potential for different nutrient limitations (Koerselman and Meuleman 1996; Zechmeister-Boltenstern et al. 2015).

Differences in ecological stoichiometry among plant species can be used as criteria for choosing understory vegetation to coexist with overstory trees. In particular, rhizosphere soil stoichiometry can help assess the linkage of plant species and belowground nutrient balances (Bell et al. 2014). It is feasible to choose some understory species with divergent biogeochemical niche to coexist with target trees in forest ecosystems by using the rhizosphere soil stoichiometry of different species to infer their nutrient limitation. However, most studies about soil stoichiometry have been conducted on bulk soil (Li et al. 2012; Heuck et al. 2015; Chen et al. 2016). For example, Li et al. (2012) examined the variations in soil stoichiometry of C, N, and P and the influencing factors based on 1069 soil samples at a depth of 0–20 cm from typical landscapes in southern subtropical China. A recent meta-analysis, based on 2736 observations along soil profiles of 0–150 cm depth, evaluated temporal changes in soil C:N:P stoichiometry over the past 60 years across subtropical China (Yu et al. 2018). In the grassland, rhizosphere soil C:N:P stoichiometry also was referred by Bell et al. (2014) and Carrillo et al. (2017). However, limited evidence has been collected from rhizosphere soil occupied by different species within the same forests (Bell et al. 2014). Moreover, the differences in the nutrient limitations of co-existing species have rarely been considered from the perspective of rhizosphere stoichiometry.

Because of the rhizosphere's tight linkage between soil and plants, its processes are important in terrestrial C and nutrient cycles. Photosynthetically assimilated CO_2 released via rhizodeposition is the primary C source in soil (Merbach et al. 1999). A meta-analysis conducted by Finzi et al. (2015) showed that root-induced mineralization accounted for up to one-third of the total C and N mineralized in temperate forest soils. It is known that nearly all plant species depend on the symbiotic associations with mycorrhizal fungi to facilitate their nutrient acquisition (van der Heijden et al. 2015). The type of mycorrhizal association is specific for each plant species (Toju et al. 2013), which determine rhizosphere priming and ecosystem C, N, and P cycling (Phillips and Fahey 2006; Lin et al. 2017; Sulman et al. 2017). There is emerging evidence that functional variations between arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) fungi induce differences in soil C and nutrient cycling (Cheeke et al. 2017). For example, owing to greater root exudates rates, ECM-associated plants have higher effects on the microbial properties of rhizosphere soil than AM-associated plants (Yin et al. 2014). Variations in the rhizosphere processes among plant species are likely to influence the outcomes of their competition for nutrient resources (Yin et al. 2012).

Previous studies have emphasized nutrient limitations, inferred from leaf or soil stoichiometry, among overstory species from different forests (Hume et al. 2016); however, few studies have focused on nutrient partitioning between the overstory and understory species from the same forest ecosystem. The lack of such knowledge inhibits forest ecosystem management.

Pinus massoniana Lamb., *Pinus elliottii* Engelm., and *Cunninghamia lanceolata* (Lamb.) Hook. have been widely planted since the 1980s and are the dominant plantation forests in mid-subtropical China. *Pinus massoniana* and *P. elliottii* associate with ECM fungi, whereas *C. lanceolata* associates with AM fungi (Lin et al. 2017). The shrubland under the three pure coniferous forests is mainly dominated by *Adinandra millettii* and *Eurya muricata* (associated with AM

fungi) and *Loropetalum chinense* (associated with ECM fungi) (Su et al. 1992).

We hypothesized that (*i*) rhizosphere soils have higher C:N and C:P ratios compared with bulk soils because of more C rhizodeposition and N and P uptake by plant roots; (*ii*) *P. massoniana* and *P. elliottii*, which have higher rhizosphere soil C concentrations, would induce greater C:N and C:P ratios compared with *C. lanceolata* due to their different fungal symbiosis; (*iii*) overstory trees have different rhizosphere soil C:N:P ratios with some understory shrubs, thus inducing different nutrient biogeochemical niches. Examining the differences in soil C, N, and P stoichiometry, advantageous understory species could be selectively retained to coexist with tree species of interest in the plantation ecosystem. Accordingly, the objectives of this study are (*i*) to examine the differences in concentrations and their stoichiometries of C, N, and P between bulk and rhizosphere soils; (*ii*) to determine how the plantations with different tree species affect rhizosphere soil C:N:P ratios; and (*iii*) to clarify whether rhizosphere soil C:N:P ratios differ among co-existing species within a specific plantation or among three plantations.

Materials and methods

Study site

The study was conducted at Qianyanzhou Ecological Research Station (26°44′N, 115°03′E) of the Chinese Academy of Sciences (CAS), located in Jiangxi Province in Southern China. The site is a typical red soil, hilly region with a subtropical monsoon climate. Average annual temperature and precipitation vary between 17.4 and 18.9 °C and between 945 and 2144 mm, respectively. The soils are weathered from red sandstone and mudstone and are classified as Typic Dystrudepts by the USDA system. The soil contains 17% sand, 68% silt, and 15% clay (Wen et al. 2010).

The zonal vegetation was evergreen broad-leaf forests that were largely destroyed due to human activities prior to the 1980 s. Grassland and scattered shrubland became the dominant vegetation, which induced severe soil degradation by 1983. Subsequent reforestation was initiated to prevent soil degradation in 1984–1986. The reforesting involved three main pure coniferous forests: *P. massoniana*, *P. elliottii*, and *C. lanceolata*. Both *P. massoniana* and *C. lanceolata* are native species, whereas *P. elliottii* was introduced from the southeastern United States. *Pinus massoniana* and *P. elliottii* were planted in the soils weathered from sandstone and *C. lanceolata* was planted in the soils weathered from mudstone. The properties of the soils for *P. massoniana*, *P. elliottii*, and *C. lanceolata* were similar before the plantation establishment (Fu et al. 2015). By 2016, the age of the three plantations was about 31 years old. The shrubland under the three pure coniferous forests was dominated primarily by *Adinandra millettii*, *Eurya muricata*, and *Loropetalum chinense*. The characteristics of overstory and understory vegetation in the three forest types are presented in Table 1.

Soil sampling

Soil samples were collected in mid-October of 2016. Five blocks were established on several spatially separate hilly slopes. Three forest types were randomly selected in each block, and a 20 m × 20 m plot was established in each forest type. The distance between blocks was more than 100 m and between plots was at least 50 m. No significant differences in soil properties of bulk soils were found among the five blocks ($P > 0.05$). In the study site, the roots of overstory trees and shrubs mainly spread on the 0–20 cm soil depth (Fu et al. 2016), so bulk soil and rhizosphere soil were sampled from 0–20 cm soil depth. The mulch layer was removed before taking the cores. In each plot, nine soil cores were randomly selected to acquire 0–10 and 10–20 cm bulk soil; then, these were combined and mixed thoroughly by soil layer. Meanwhile, the rhizosphere soils of overstory trees (*P. massoniana, P. elliottii,* or

Table 1. Stand characteristics.

Plantation	Diameter at breast height (cm)	Tree height (m)	Stand density (trees·ha⁻¹)	Canopy density (cm²·cm⁻²)	Important value of shrub species (%)		
					A. millettii	*E. muricata*	*L. chinense*
P. massoniana	19.6±1.4	20.2±0.6	1960±211	0.79±0.05	14.7	8.00	33.7
P. elliottii	24.6±1.2	22.0±0.8	2060±309	0.75±0.06	25.3	21.3	36.0
C. lanceolata	20.5±2.1	17.2±3.0	2440±357	0.77±0.04	37.9	29.7	22.2

C. lanceolata) and understory shrub species (*A. millettii*, *E. muricata*, and *L. chinense*) were sampled in each plot. Three to five plants of each species were randomly selected in each plot. Around the selected tree or shrub's trunk, the respective roots plus adhering soil at 0–20 cm soil depth were carefully dug out from the four sites of each plant. If some shrub species had a small root biomass, the plant was carefully dug to acquire its whole roots and adhering soils. The loosely adhering soil was gently shaken off the roots as rhizosphere soil, in which all visible portions of root were removed from the soil. Rhizosphere soil came from distances of less than 4 mm from the root surface (Riley and Barber 1970). The rhizosphere soil was combined and mixed for the same species within the same plot. Each soil sample was collected in a plastic bag, placed in a cooler in the field, and then carried to the laboratory. The soil was air-dried for subsequent total organic C, total N and P, and soil pH measurements.

Soil chemical analysis

Soil pH value was determined in a 1:2.5 soil to water ratio by a digital pH meter. Total organic C (SOC) and total soil nitrogen (TN) concentrations were measured using a Vario-Max N/CN elemental analyzer (Elementar Analysensysteme GmbH, Germany). Soil was digested with H_2SO_4–$HClO_4$, and the total P (TP) concentration was determined by ascorbic acid – molybdate blue colorimetry (Page et al. 1982). The ratios of SOC to TN (C:N), SOC to TP (C:P), and TN to TP (N:P) were calculated.

Data analysis

Soil C, N, and P concentrations and their ratios, as well as the soil pH value, were analyzed for rhizosphere soil for each species and 0–10 and 10–20 cm bulk soil from the same forest type, using linear mixed-effects models with soil sampling type fitted as a fixed effect and block fitted as a random effect. The differences in soil C, N, and P concentrations and their ratios between bulk and rhizosphere soils, and overstory tree and understory shrub, and among overstory species or shrub species were analyzed using linear mixed-effects models. All analyses of variance were conducted using IBM SPSS statistics 20. The standardized data matrix of C, N, and P and their stoichiometries (TC, TN, TP, C:N, C:P, and N:P) were subjected to principal component analysis (PCA) using the rda function of the vegan package of R software. The first two principal components (PCs) were chosen to account for as much of the variability in the data as possible. The resulting PCs are latent variables and are uncorrelated each other.

Results

Soil pH and C, N, and P concentrations

Bulk soils, rhizosphere soils of trees, and rhizosphere soils of shrubs had significantly different soil pH values. The rhizosphere soil pH value was lower compared with that of bulk soils (Fig. 1). Additionally, the decrease in overstory rhizosphere soil was higher than that in understory rhizosphere soils (Fig. 1). The average rhizosphere soil C, N, and P concentrations were significantly higher than those of bulk soils (*P* = 0.000), especially for overstory species and understory *L. chinense* (Fig. 2). The rhizosphere soil C, N, and P concentrations of overstory species were significantly higher than those of the average across the three understory species (*P* = 0.000 for C and N and *P* = 0.01 for P) and especially higher

than those of *A. millettii* and *E. muricata* except for soil P concentrations in *P. elliottii* forests (Fig. 2). Among understory shrub species, rhizosphere soil C, N, and P were also significantly different (*P* = 0.001 for C, *P* = 0.000 for N, and *P* = 0.003 for P). Rhizosphere soil C, N, and P concentrations of *L. chinense* respectively increased by 33%–310%, 31%–200%, and 1%–73% compared with those of *A. millettii* and *E. muricata*. The differences were greatest in the *P. massoniana* forest and least in the *P. elliottii* forest.

Soil C, N, and P stoichiometry

Bulk and rhizosphere soil C:N ratios were 9.6–19.6:1 and 13.3–28.9:1, C:P ratios were 51.1–132:1 and 114–499:1, and N:P ratios were 4.8–7.7:1 and 7.2–17.3:1, respectively. Generally, soil C:N, C:P, and N:P ratios of rhizosphere soil were significantly higher than those of bulk soil (*P* = 0.000; Fig. 3). The soil C:N ratio at the 0–10 cm soil depth was significantly higher than that at the 10–20 cm soil depth; however, C:P and N:P ratios were not significantly different between the 0–10 and 10–20 cm soil depths in the three plantations. Among overstory species, the rhizosphere soil C:N and C:P ratios of *P. massoniana* and *P. elliottii* were higher than those of *C. lanceolata* (*P* = 0.001), but no significant difference of rhizosphere soil N:P ratio was found among them (*P* > 0.05). Overstory rhizosphere soil C:N, C:P, and N:P ratios were significantly higher than those of the average across the three shrub rhizosphere soils (*P* = 0.000 for C:N and C:P and *P* = 0.001 for N:P) and especially higher than those of *A. millettii* and *E. muricata* (Fig. 3). In most cases, the rhizosphere soil C:N, C:P, and N:P ratios of *L. chinense* were not significantly different with those of overstory rhizosphere soil (Fig. 3).

Soil C, N, and P, and their stoichiometries differed significantly among bulk soils, rhizosphere soils of trees, and those of shrubs; PC1 and PC2 explained 86.1% and 13.3% of the total variance, respectively (Fig. 4*a*). Overstory species and understory species *L. chinense* grouped to the right had higher C, N, and P and stoichiometries, whereas bulk soil and understory species *A. millettii* and *E. muricata* grouped to the left had lower C, N, and P and stoichiometries along with PC1 (Fig. 4*b*). PC1 scores were significantly negatively correlated with soil pH (Fig. 5).

Discussion

Effects of bulk and rhizosphere soils on C:N:P stoichiometry

Plants allocate C via their roots to rhizosphere soil that drives microbes to mineralize N and P from organic matter in the soil (Meier et al. 2015). As a result, soil nutrients and microbial biomass in the rhizosphere are generally much more abundant than those in bulk soil (Finzi et al. 2015; Kuzyakov and Blagodatskaya 2015). This process is consistent with the result that rhizosphere soil C, N, and P concentrations were significantly greater than the bulk soil (Fig. 2). Rhizosphere soil C, N, and P concentrations were 3.5 times, 1.9 times, and 34% greater, respectively, compared with bulk soil. The imbalanced difference induced higher soil C:N, C:P, and N:P ratios in rhizosphere soil compared with bulk soil (Fig. 3). The high C:N and C:P ratios implied that rhizosphere soil microbes had relatively more nutrient (e.g., N and P) limitations than energy (C) limitations compared with bulk soil. This could be because approximately 11%–20% of the photosynthate is released

Fig. 1. Bulk and rhizosphere soil pH of overstory and understory species in (*a*) *P. massoniana*, (*b*) *P. elliottii*, and (*c*) *C. lanceolata* plantations in subtropical China. *P* < 0.05 indicates significant difference among six soil sampling types. [Colour online.]
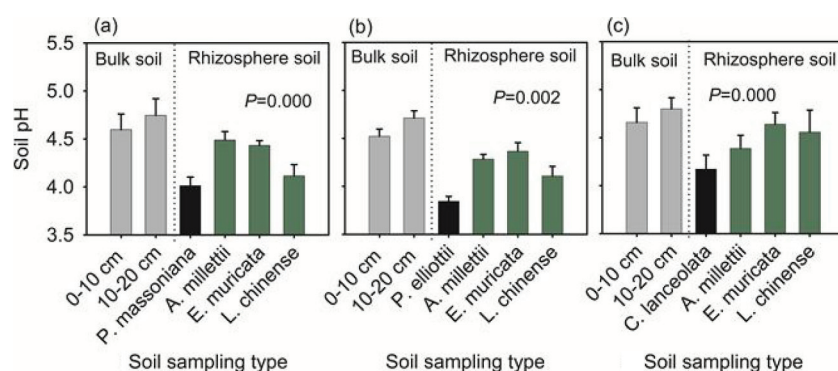
Fig. 2. Bulk and rhizosphere soil C, N, and P concentrations of overstory and understory species in (*a*, *d*, *g*) *P. massoniana*, (*b*, *e*, *h*) *P. elliottii*, and (*c*, *f*, *i*) *C. lanceolata* plantations in subtropical China. Different letters above the mean ± standard error indicate significant differences among bulk soils, rhizosphere soils of the tree species, and rhizosphere soils of the shrub species in each plantation at *P* < 0.05. [Colour online.]
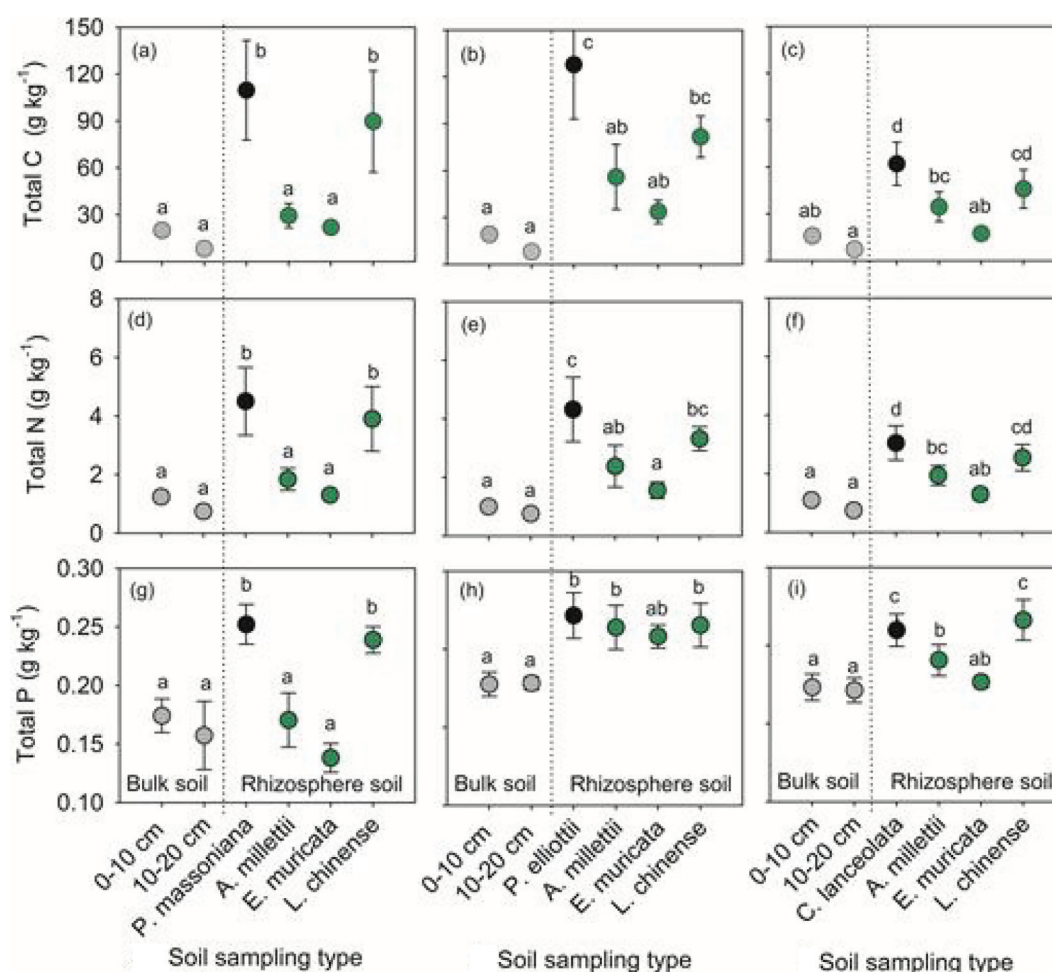

to the soil as root exudate, in which the most abundant components are carbohydrates and organic acids (Merbach et al. 1999). A large amount of rhizodeposited C makes rhizosphere soil microorganisms proliferate quickly and mineralize N and P for their needs from the organic matter in the soil (Mwafulirwa et al. 2017; Huo et al. 2017). Although soil N and P concentrations were greater in rhizosphere soil compared with bulk soils, the soil C concentration was 46 g·kg⁻¹ greater compared with the bulk soil. Theoretically, an extra 6 g N·kg⁻¹ and 1 g P·kg⁻¹ should be needed to meet the demand of soil microbial biomass (C:N:P 42:6:1) in

rhizosphere soil (Spohn 2016). However, only 1.63 g N·kg⁻¹ and 0.05 g P·kg⁻¹ more were present in rhizosphere soil compared with the bulk soil. It is obvious that rhizosphere soil microbes had greater N and P limitations compared with the bulk soil. Net nutrient mineralization also occurs at high C to nutrient ratios due to nutrient turnover in the microbial biomass (Spohn 2016), in that microbial N and P remineralization is taken up by plants and microbes, or loss from ecosystems.

Previous studies reported that *P. massoniana* forests with 4.4:1 soil N:P ratios were mainly limited by the availability of P in the

Fig. 3. Bulk and rhizosphere soil C:N:P stoichiometry of overstory and understory species in (*a, d, g*) *P. massoniana*, (*b, e, h*) *P. elliottii*, and (*c, f, i*) *C. lanceolata* plantations in subtropical China. Different letters above the mean ± standard error values indicate significant differences among bulk soils, rhizosphere soils of the tree species, and rhizosphere soils of the shrub species in each plantation at *P* < 0.05. [Colour online.]
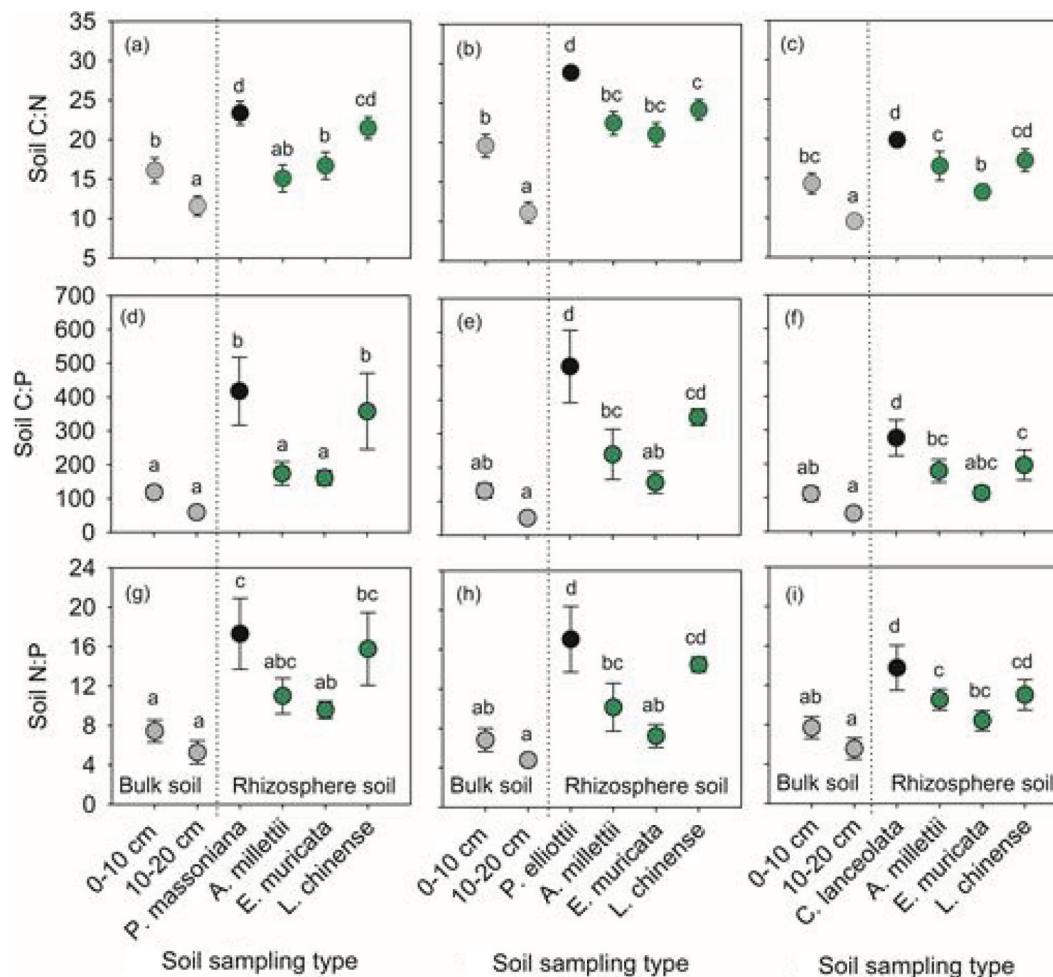
southern subtropics of China (Liu et al. 2016). Here, the bulk soil N:P ratio averaged to 6.3:1 whereas that of the rhizosphere soil was 12.2:1 (Fig. 3), indicating that P limitation also occurred at the study site. The P limitation was relatively more severe in rhizosphere soil, although higher soil P concentration was found in rhizosphere soil compared with the bulk soil, mainly due to the stoichiometric relationship between microbial biomass and its substrate controls the element cycling of ecosystems (Spohn 2016). Generally, the N:P ratio in microbes is 6–7:1 (Zechmeister-Boltenstern et al. 2015; Spohn 2016); thus, microbes will mine out more N to meet their P requirement in the rhizosphere soil (12.2 N coupled by 1 P) compared with bulk soil (6.3 N coupled by 1 P). A 34% increase in soil P concentration was not enough to meet rhizosphere soil P requirement where abundant soil microbial and crowded root masses exist.

Moreover, roots and rhizosphere microbes may reduce P availability in acid soils through acidification of the rhizosphere (Hinsinger 2001). J.X. Liu et al. (2017) reported that compared with N, soil P is deficient for plant demands in subtropical China. As a hotspot of root uptake, it is possible that rhizosphere soil P deficiency would be more severe compared with bulk soil due to the intense competition of plants and soil microbes, especially for acidic soil where most P is bound in insoluble complexes (Zhao and Wu 2014).

Effects of overstory and understory species on C:N:P stoichiometry

Due to different quantities and qualities of root exudate and rhizodeposits from different plant species (Ohta and Hiura 2016),

rhizosphere soil environments and microbial communities change with plant species (Zhang et al. 2011), further influencing soil nutrient cycling and its stoichiometry. Zhao et al. (2014) and Di Palo and Fornara (2015) showed that plant composition was more important in explaining plant C to nutrient stoichiometric variation than soil nutrient contents, e.g., SOC, TN, TP, and available N and P. In the present study, the rhizosphere soil C:N and C:P ratios of *P. massoniana* and *P. elliottii* were higher than those of *C. lanceolata* (Fig. 3). This result indicated that C deposition in roots was likely higher for *P. massoniana* and *P. elliottii* than for *C. lanceolata*. This finding is mainly because *C. lanceolata* roots are colonized by AM fungi, whereas *P. massoniana* and *P. elliottii* are colonized by ECM fungi (Lin et al. 2017). Previous investigations indicated that ECM trees would exude more C from roots than AM trees (Phillips and Fahey 2006). Yin et al. (2014) indicated that exudation rates of ECM tree species were nearly two times greater compared with those of AM tree species. Because the two mycorrhizal types exhibit striking differences in morphology, C sink strength, and hyphae spatial extent (Finlay and Söderström 1992), ECM tree species must invest more C to build their hyphae network. Thus, it is possible that microbes in the rhizosphere soil of *C. lanceolata* were more limited by energy than by nutrition compared with those of *P. massoniana* and *P. elliottii*. Under C limitation, microbes will mineralize C to meet their energy requirement, whereas extra N and P are released to the soil for plant uptake (Schimel and Weintraub 2003).

Fig. 4. Principal component analysis of soil C, N, P, and their stoichiometries of the bulk soil and rhizosphere soil of overstory and understory species. (*a*) Separation of soil samples by bulk soil (BS) and rhizosphere soil (RS) of plant species. The gray symbols are 0–10 cm depth of BS, the white symbols are 10–20 cm depth of BS, the red symbols are the RS of *A. millettii*, the purple symbols are the RS of *E. muricata*, the blue symbols are the RS of *L. chinense*, and the green symbols are the RS of overstory trees. (*b*) Distribution of soil C, N, P, and their ratios among different bulk soils, rhizosphere soils of trees, and rhizosphere soils of shrubs. [Colour online.]
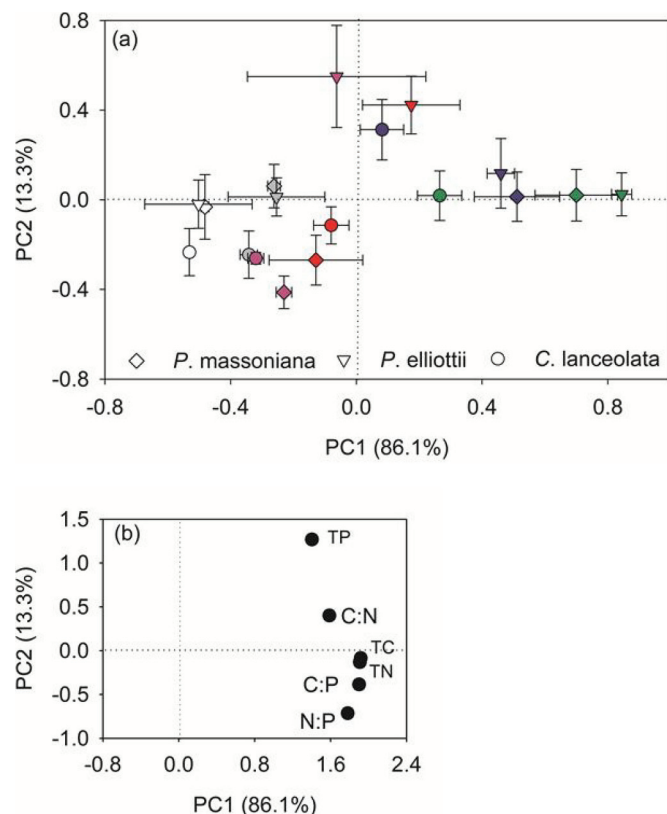
Fig. 5. Relationship of the first axis (PC1) scores of principal component analysis with soil pH.
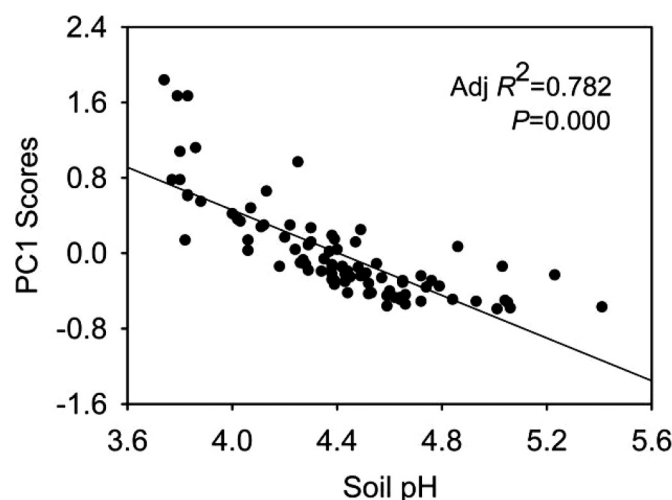
The released excess N and P could favor the formation of larger volumes of timber for *C. lanceolata*.

It is known that trees, shrubs, and herbs have significantly different leaf stoichiometries (Pan et al. 2015). Fan et al. (2015) showed higher leaf C:P and N:P ratios for overstory trees than for understory plants. They also found that soil and plant N:P ratio was strongly related. As we hypothesized, overstory rhizosphere soil C:N, C:P, and N:P ratios were significantly higher than those of shrub rhizosphere soil (Fig. 3). This is because rhizosphere soil C, N, and P concentrations of overstory trees increased by 54 g·kg⁻¹ (119%), 1.7 g·kg⁻¹ (77%), and 0.04 g·kg⁻¹ (20%) compared with those of understory shrubs, respectively (Fig. 2). Firstly, overstory trees may have greater C deposition to rhizosphere soil than do understory shrubs (Fig. 2), which induced higher rhizosphere soil C:N and C:P ratios of overstory trees. Carbon allocation to roots is closely linked with photosynthesis (Brzostek et al. 2015). Overstory trees generally have a higher photosynthetic capacity than understory shrubs (Sakai et al. 2005), implying the higher root exudation rate of overstory trees. It is well documented that the root exudation rate varies among herbaceous plants, crops, and tree seedlings (Badri and Vivanco 2009). Secondly, rhizosphere soil microbes of overstory trees would mineralize excess N accompanying with soil P mineralization according to the average soil microbial biomass C:N:P ratio (42:6:1) compared with those of understory shrubs. Thirdly, the foliar N:P ratio of overstory trees was 16:1 and that of understory shrubs was 20:1 in the study site, implying relatively less N and more P uptake of overstory trees compared with understory shrubs (unpublished results).

In most cases, the rhizosphere soil C:N, C:P, and N:P ratios of *L. chinense* were similar with those of overstory rhizosphere soil (Figs. 3 and 4*a*). The variations of the root exudation among co-existing species relate to their functional traits and demand for N and P (Sun et al. 2017). Root morphology has a strong effect on the C flux from roots to soil. For example, increased root branching can increase root exudation rates (Groleau-Renaud et al. 1998). Yin et al. (2012) indicated that differences in the altered morphological and functional characteristics of the roots could be largely responsible for rhizosphere N transformations. It has been verified that *L. chinense* fine root morphological plasticity is higher than that of *C. lanceolata*, which increases the fine root nutrient absorption rate, according to the study of Wang et al. (2015).

Among the shrub species, higher rhizosphere soil C, N, and P and their ratios were found for *L. chinense* compared with those of *A. millettii* and *E. muricata*, possibly because *L. chinense* roots are colonized by ECM fungi. Alternatively, *A. millettii* and *E. muricata* are colonized by AM fungi (Su et al. 1992), which suggests a higher exudation rate for *L. chinense* compared with *A. millettii* and *E. muricata*. Moreover, *L. chinense* fine root morphological plasticity was greater, which induced its roots to grow widely into the litter layer (Wang et al. 2016). In the current study, the roots of *L. chinense* occasionally also grew into the litter layers; however, the roots of *A. millettii* and *E. muricata* tend to extend into deeper soil. Although the rhizosphere soil came from the roots of 0–20 cm soil depth, it is possible that the parts of rhizosphere soil of *L. chinense* came from surface soil, whereas those of *A. millettii* and *E. muricata* were from deeper soil. Thus, the rhizosphere soil from the roots growing into the litter layer will have characteristics similar to surface soil, whwereas the rhizosphere soil from the roots growing to the deeper soil will have characteristics similar to subsurface soil. This is also a possible reason for the higher C:N, C:P, and N:P ratios for *L. chinense* and the lower C:N, C:P, and N:P ratios for *A. millettii* and *E. muricata*. The difference in soil C, N, and P concentrations and stoichiometries among understory species may not be the direct results of the presence of these species, but the root morphological plasticity led the roots to the different soil depths, which indirectly induced the different rhizosphere soil C, N, and P concentrations and stoichiometries. Further study concerning

the fine root morphological plasticity of *A. millettii* and *E. muricata* is required to confirm this result.

Effects of soil pH on soil C:N:P stoichiometry

Low molecular mass organic acids such as citric acid and oxalic acid are the main components of root exudate (Tyler and Ström 1995) and vary significantly among tree species (Aoki et al. 2012; Ohta and Hiura 2016). The profiles produced by soil C, N, and P and their stoichiometries of bulk soil and rhizosphere soil of different species were significantly correlated with soil pH (Fig. 5). The C:N, C:P, and N:P ratios were higher when the pH was lower (Fig. 4), indicating that lower pH values had higher N and P nutrition limitations, especially P nutrition limitations. Suo et al. (2016) also showed that soil pH was the most important predictor of soil C:N and N:P rather than tree composition or leaf litter input in temperate forests. Soil pH is an important determinant of microbial community composition and activity in forest ecosystems (Bååth and Anderson 2003; Zhou et al. 2017) that, in turn, affects ecological processes such as microbial C use efficiency, soil respiration, and N and P mineralization (Kuzyakov and Blagodatskaya 2015). In acid soils, amendment of soil pH can improve the soil available nutrient concentrations (Carrino-Kyker et al. 2016), thus promoting the growth of target trees. The understory could alleviate soil acidification in subtropical China (Fu et al. 2015); however, the understory also influences the growth of overstory trees. In plantation management, retaining a part of understory vegetation is desirable for forest production and the maintenance of ecological function (Fu et al. 2015). In the three plantations, the relative dominance of *L. chinense* was up to about 30% (Table 1). Meanwhile, biogeochemical niche of *L. chinense* was similar to the overstory trees, which possibly could induce competition for nutrients between *L. chinense* and the overstory trees. Thus our study suggested that of the three main understory shrubs, *L. chinense* could be considered for removal in plantation management to achieve higher productivity and ecological function.

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