



# Effect of slope position on leaf and fine root C, N and P stoichiometry and rhizosphere soil properties in *Tectona grandis* plantations

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**Abstract** Little is known about C–N–P stoichiometries and content in teak (*Tectona grandis*) plantations in South China, which are mostly sited on hilly areas with lateritic soil, and the effect of slope position on the accumulation of these elements in trees and rhizosphere soils. Here we analyzed the C, N, P content and stoichiometry in leaves, fine roots and rhizosphere soils of trees on the upper and lower slopes of a 12-year-old teak plantation. The Kraft classification system of tree status was used to sample dominant, subdominant and mean trees at each slope position. The results showed that the C, N and P contents in leaves were higher than in fine roots and rhizosphere soils. The lowest C/N, C/P and N/P ratios were found in rhizosphere soils, and the C/N and C/P ratios in fine roots were higher than in leaves. Nutrient accumulation in leaves, fine roots and rhizosphere soils were significantly influenced by slope position and tree class with their interaction mainly showing a greater effect on rhizosphere soils. Leaf C content and C/N ratio, fine root C and P contents, and C/N and C/P ratios all increased distinctly with declining slope position. The contents of organic matter (SOM), ammonium (NH<sub>4</sub><sup>+</sup>–N),

nitrate-nitrogen (NO<sub>3</sub><sup>–</sup>–N) and available potassium (AK) in rhizosphere soils were mainly enriched on upper slopes, but exchange calcium (ECa), available phosphorus (AP), and pH were relatively lower. Variations in the C, N and P stoichiometries in trees were mainly attributed to the differences in rhizosphere soil properties. N and P contents showed significant positive linear relationships between leaf and rhizosphere soil, and C content negative linear correlation among leaves, fine roots and rhizosphere soils. Chemical properties of rhizosphere soils, particularly C/N and NH<sub>4</sub><sup>+</sup>–N, had significant effects on the leaf nutrients in trees on the upper slope. Correspondingly, rhizosphere soil properties mainly influenced fine root nutrients on the lower slope, and soil AK was the major influencing factor. Overall, these results offer new insights for the sustainability and management of teak plantations in hilly areas.

**Keywords** *Tectona grandis* · Stoichiometric ratio · Rhizosphere soil · Dominant trees · Nutrient accumulation

## Introduction

Carbon (C), nitrogen (N) and phosphorus (P) play a pivotal role in regulating the nutrient balance between plants and soil (Zhang et al. 2019; Qiu et al. 2020) and for the cycling, transformation and feedback of mineral nutrients in biogeochemical processes (Yang et al. 2018). In plants, carbon participates in the structural basis of various tissues (Liu et al. 2011). Nitrogen is a necessary for the synthesis of amino acids and protein, foliar photosynthetic physiology and carbon fixation (Sinclair and Vadez 2002). Phosphorus is a vital component of ATP and cell membrane construction and nucleotides (Li 2008). The three elements are essential for feedback on nutritional status and adaptation to the external

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environment (Güsewell 2004). Many studies have suggested that the ratios of leaf N/P below 14 indicate N limitation and above 16 mean P limitation (Vitousek et al. 2010; Zhang et al. 2015). Furthermore, the relationships of stoichiometric ratios among C, N and P are critical in plant–soil interactions and can indicate the status of nutrient cycling, storage and limiting elements in plantation ecosystems (Mooshammer et al. 2014; Peñuelas et al. 2020).

Trees have different social statuses in stands as a result of their competition for nutrients, water and light and long-term adaptation to the habitats, resulting in different morphological structures and nutrient patterns (Contreras et al. 2011; Světlík et al. 2021). These differences also continue to affect tree functions and growth (Pretzsch 2021). A previous study showed that the status of trees shaped different levels of competition and biomass allocation patterns (Wertz et al. 2020); carbon priority allocates to the trunk over other organs (Nilsson et al. 1993). With a decrease in tree's social status, the stem fraction increases, while the branches fraction decreases (Ochał et al. 2013). Other studies have indicated that tree social status, which can alter crown characteristics and inter tree competition over time, is an important driver of variations in growth allocation (Trouvé et al. 2015; Gao et al. 2021). For example, dominant trees can access adequate light compared to suppressed or mean trees and thus produce more photosynthates, which also affects root development and vigor, eventually leading to large differences in tree growth and biomass (Scartazza et al. 2015; Wertz et al. 2020). The N and P content in the dominant trees are significantly higher than in mean trees because of the close correlations between nutrients and tree growth (Spohn 2016), and dominant trees generally occupy high ecological niches, reducing the competition for soil nutrients and water (Han et al. 2005; Shi et al. 2021). However, little is known about differences in the nutrient stoichiometry in leaves and fine roots among tree status classes. Additionally, tree growth is affected not only by C, N and P levels in different tissues, but also by soil factors such as soil acidity and available nutrients (Cleland 2011). Therefore, it is of great importance to understand the content and distribution of C, N and P among the leaves, roots and soils in plantations.

Slope position is a primary factor contributing to differences in soil properties and fertility (Tateno et al. 2010; Utin and Essien 2021). The contents of soil organic matter and available nitrogen significantly increased (Hirobe et al. 1998; Tsui et al. 2004), but total nitrogen and soil pH decreased with the rising of slopes (Miheretu and Yimer 2017). Affected by soil water storage, downhill soil microorganisms and enzymes were found to have higher activities, which resulted in a heterogeneous distribution of nutrient resources at different positions on a slope (Walkiewicz et al. 2021). Stable patterns of nutrient cycling and distribution among trees and environments are formed at smaller spatial

scales because N and P absorption by trees mainly depends on the supply in the soil (Ordóñez et al. 2009; Fang et al. 2021). Moreover, soil P is usually considered to be the major determinant for N and P assimilation by roots and leaves (Yang et al. 2016; Li et al. 2019). Soil N and pH also strongly affect nutrients in trees (Parfitt et al. 2005; Luo et al. 2021). The inconsistency of these results is attributed to differences in plant type and site conditions, highlighting the need for further studies to better understand plant–soil system interactions in specific stands.

Teak (*Tectona grandis* Linn f.; Verbenaceae) is a major exotic species commercially planted in China (Zhou et al. 2017), but it generally faces nutrient deficiency and soil acidification, which present tough technical problems for the efficient cultivation of plantations (Fernández-Moya et al. 2015; Zhang et al. 2022). In teak plantations in Nigeria, soil C and total nitrogen (TN) were higher and pH and available phosphorus were lower on higher slope positions (Lawal et al. 2014). The different slope positions shaped soil heterogeneity, which may indirectly affect nutrient supply and tree absorption. Therefore, we hypothesized that soil heterogeneity and tree size caused by the different slope positions and status classes would result in significant differences in C, N and P contents and their stoichiometric ratios in leaves and fine roots. We tested this hypothesis by measuring C, N and P contents in leaves and fine roots and chemical properties of rhizosphere soils in young teak plantation to analyze C, N and P stoichiometries in trees and rhizosphere soils among different slope positions and tree status classes and their relationships between trees and soils.

## Materials and methods

### Study area

The study area at the Experimental Center of Tropical Forestry in Pingxiang City, Qingshan Forest Farm, Guangxi Zhuang Autonomous Region, southern China (106°42' E, 22°12' N) has a southern subtropical monsoon climate with mean annual temperature of 21.6 °C and relative humidity of 82%. The extreme maximum and minimum temperatures are 38.7 °C and −1.2 °C. The mean annual precipitation is 1380 mm with more than 80% of the precipitation falling from May to September. The altitude of the experimental site ranges from 121 to 188 m with about 25° of a slope. The soil was lateritic red soil derived from granite (Zhou 2009). The initial soil organic matter of the test site for the 0–10 cm depth was 28.71 g·kg<sup>-1</sup> with a pH of 5.00. The total N was 1.21 g·kg<sup>-1</sup>, total P 0.38 g·kg<sup>-1</sup>, available N 139.37 mg kg<sup>-1</sup>, available P 1.68 mg·kg<sup>-1</sup>, and exchangeable calcium content was 10.82 mmol·kg<sup>-1</sup>.

The experimental plantation was established in April 2008 with teak seedlings started from cuttings of superior clones at the Research Institute of Tropical Forestry, Chinese Academy of Forestry in Guangzhou, China. The plantation area is about 1 ha with a planting spacing of 2 × 3 m.

### Plots and growth traits of trees

In August 2020, four replicate plots of 900 m<sup>2</sup> were established on the upper slope (mean altitude 175 m a.s.l.) and on the lower slope (mean altitude 134 m a.s.l.). All trees in the eight plots were measured for tree height (H), diameter at breast height (DBH), height to crown base (HCB) and crown width (CW, the mean of the crown in the east–west and north–south directions) (Table 1). Trees in the plots were then marked as dominant (DT), subdominant (SDT) or mean (MT) according to the Kraft class system described by Nicholas et al. (1991), and five trees were selected as sample tree, respectively.

### Sampling

Plant and soil samples in each slope position were taken from four plots (replications) in September 2020. Five pieces of healthy, mature leaves were taken from five sample trees in each status class (dominant, subdominant and mean) exposed to sunlight and having better growth in the central canopy. The leaves samples in each status class were then combined for nutrient analysis. The fine roots (diameter less than 2 mm) at the 0–10 cm soil layer was sampled 1 m from the bole base of each marked sample tree. Simultaneously, each fine root was followed to its origin and shaken gently to remove loosely adhering soil. Rhizosphere soil that tightly adhered to the root was carefully collected with a sterile brush. In total, we took 24 samples of leaves, fine roots and soil, respectively. All plant samples were oven-dried at 85 °C for 30 min and then at 65 °C for 48 h to determine the content of total C, N and P. All soil samples were passed through a 2–mm sieve, then divided into two parts. One part was air-dried at room temperature, then used to measure soil organic matter (SOM), total N (TN), total P (TP), available P

(AP) and K (AK), exchange calcium (ECa) and soil pH. The other part was stored at 4 °C until used to measure ammonia (NH<sub>4</sub><sup>+</sup>–N) and nitrate–N (NO<sub>3</sub><sup>–</sup>–N) contents.

### Sample analyses

Total C in leaves and fine roots and SOM were measured by wet combustion using potassium dichromate and sulfuric acid oxidation method (Schinner et al. 1996). Total N was measured using the Kjeldahl method (Mádlíková et al. 2020). Total P was determined by the molybdenum antimony colorimetric method (Yang et al. 2018). NH<sub>4</sub><sup>+</sup>–N and NO<sub>3</sub><sup>–</sup>–N content were measured by Nessler's reagent colorimetric and the phenoldisulfonic acid colorimetric method, respectively (Zha 2017). Soil available P (AP) was determined by colorimetry after extraction with NH<sub>4</sub>F–HCl. Soil AK was measured using flame atomic absorption spectrometry. The pH of a 1:2.5 soil–water mixture was measured using a pH meter (PHS-3C, Shanghai, China). Soil ECa was extracted with ammonium acetate and measured using atomic absorption spectrometry (Schroth et al. 2015; Yu et al. 2021).

### Statistical analyses

Statistical analyses of all variables were conducted using SPSS 21.0 software (IBM Armonk, NY, USA) at a significance level of 0.05. Homogeneity of each factor was tested, and a two-way analysis of variance was used to test for differences in all variables among the different slope positions and tree classes and followed by Tukey's honestly significant difference (HSD) test to separate means that differed. All values are presented as means and standard errors. A linear regression analysis was used to explore the relationships of C, N, P and their ratios among leaves, fine roots and rhizosphere soil. Pearson's correlation analysis (Origin Pro2021, Origin Lab Corp., Northampton, MA, USA) and redundancy analysis (RDA, CANOCO 5.0 software, Microcomputer Power, Ithaca, NY, USA) were used to discuss the relationships between soil chemical properties and the C, N and P stoichiometry of leaves and fine roots.

**Table 1** Mean values (±SE, n=20) for growth traits for sample trees on upper and lower slope positions and different tree status classes

Position	Status class	H (m)	DBH (cm)	HCB (m)	CW (m)
Upper	DT	17.40 ± 0.21	19.49 ± 0.25	6.18 ± 0.42	5.96 ± 0.11
	SDT	17.33 ± 0.62	18.28 ± 0.26	6.33 ± 1.03	5.61 ± 0.13
	MT	15.63 ± 0.31	17.53 ± 0.28	5.20 ± 0.41	4.89 ± 0.20
Lower	DT	17.80 ± 0.41	20.30 ± 0.63	5.38 ± 0.36	6.63 ± 0.11
	SDT	17.25 ± 0.54	18.40 ± 0.07	5.73 ± 0.18	5.97 ± 0.28
	MT	15.98 ± 0.25	17.65 ± 0.22	5.40 ± 0.38	5.23 ± 0.29

DT: dominant trees; SDT: subdominant trees; MT: mean trees. H: height; DBH: diameter at breast height; HCB: height to crown base; CW: crown width

**Results**

**Leaf C, N and P contents and stoichiometry ratios**

The leaf C, N contents and C/N, N/P ratios differed significantly between slope positions but leaf P content and C/P ratio did not (Table 2). Tree status also significantly affected leaf N and P contents and the ratios of C, N and P. Only leaf N/P ratio was significantly influenced by an interaction between slope position and status class.

Leaf C content and C/N ratio on the lower slope position (LS) were significantly higher than those on the upper slopes (US), whereas N content and N/P ratio were lower on the LS. The P content was slightly higher on the LS (Fig. 1). For both slope positions, leaf C, N and P contents by tree status class in decreasing order were dominant (DT) > subdominant (SDT) > mean (MT). On the US, leaf N and P contents of DT

were 15.62% and 20.42% significantly higher than those of MT and 16.66% and 15.13% higher on the LS, respectively. Leaf C/N ratio on the LS was significantly higher than on the US, while the N/P ratio was relatively small (< 14) on the LS (Fig. 1d, 1f,  $P < 0.05$ ). Leaf C/N and C/P ratios in increasing order by status class were DT < SDT < MT.

**Fine root C, N and P stoichiometry**

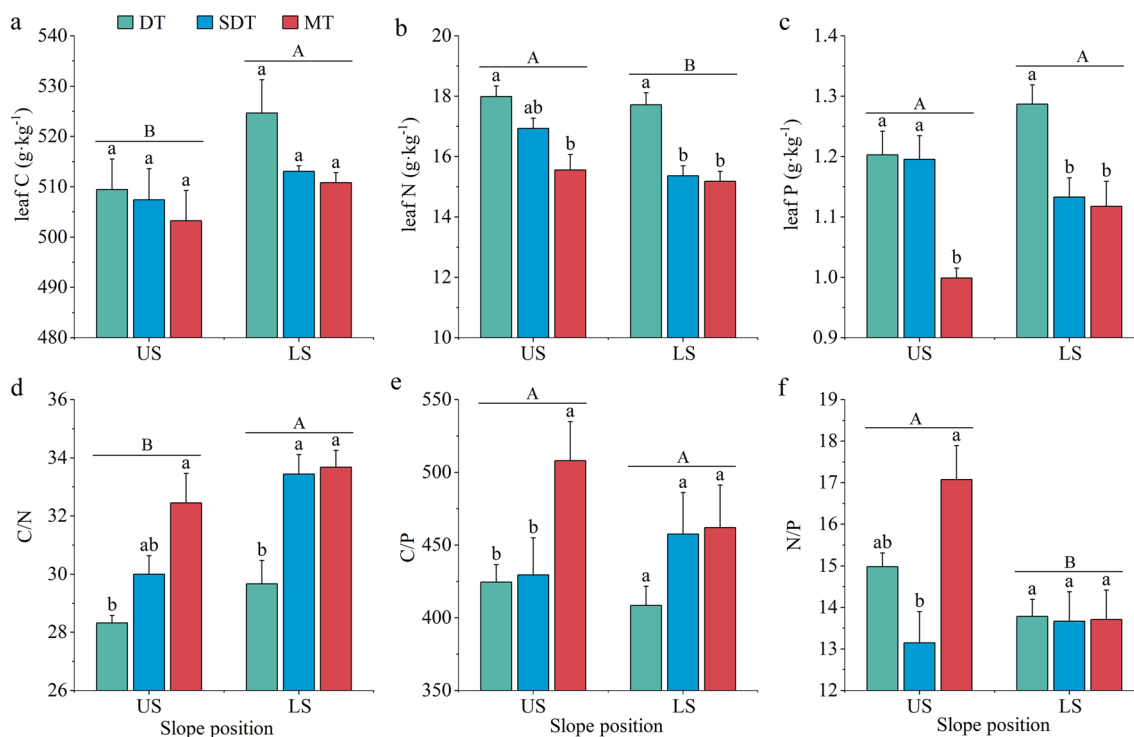
Fine root C and N contents and the ratios of C/N and C/P significantly differed between slope positions (Table 3). Only the C and P contents differed significantly among the tree status classes. The root N content and C/N ratio were also significantly affected by the interaction between slope position and status class.

The contents of C and P and the ratios of C/N and C/P in fine roots were significantly higher on the LS than on the

**Table 2** Two-way ANOVA of leaf C, N and P stoichiometries of different slope positions (SP), status classes (SC) and their interaction (SP×SC)

Variable	Leaf C (g·kg <sup>-1</sup> )	Leaf N (g·kg <sup>-1</sup> )	Leaf P (g·kg <sup>-1</sup> )	Leaf C/N	Leaf C/P	Leaf N/P
Slope (F1, 19)	5.02 *	5.68 *	0.98 ns	12.19 **	0.35 ns	6.50 *
Status (F2, 19)	1.95 ns	22.34 **	5.22 *	17.39 **	4.27 *	4.69 *
SP×SC (F2, 19)	0.48 ns	1.81 ns	1.38 ns	1.59 ns	1.24 ns	4.54 *

\* $P < 0.05$ ; \*\* $P < 0.01$ ; ns,  $P \geq 0.05$



**Fig. 1** C, N and P stoichiometry for leaves from trees in different status classes and slope positions. DT: dominant trees; SDT: subdominant trees; MT: mean trees; US: upper slope; LS: lower slope. Different capital letters indicate a significant difference in the variable

between slopes; different lowercase letters indicate a significant difference in the variable between the status classes on the same slope position

**Table 3** Two-way ANOVA of fine root C, N and P stoichiometries of different slope positions (SP), status classes (SC) and their interaction (SP×SC)

Variables	Root C (g·kg <sup>-1</sup> )	Root N (g·kg <sup>-1</sup> )	Root P (g·kg <sup>-1</sup> )	Root C/N	Root C/P	Root N/P
Slope (F1, 19)	28.93 **	3.03 ns	4.50 *	8.74 **	6.83 *	0.03 ns
Status (F2, 19)	3.64 *	0.76 ns	5.55 *	0.65 ns	3.50 ns	0.97 ns
SP×SC (F2, 19)	0.94 ns	11.95 **	0.48 ns	12.75 **	2.24 ns	2.34 ns

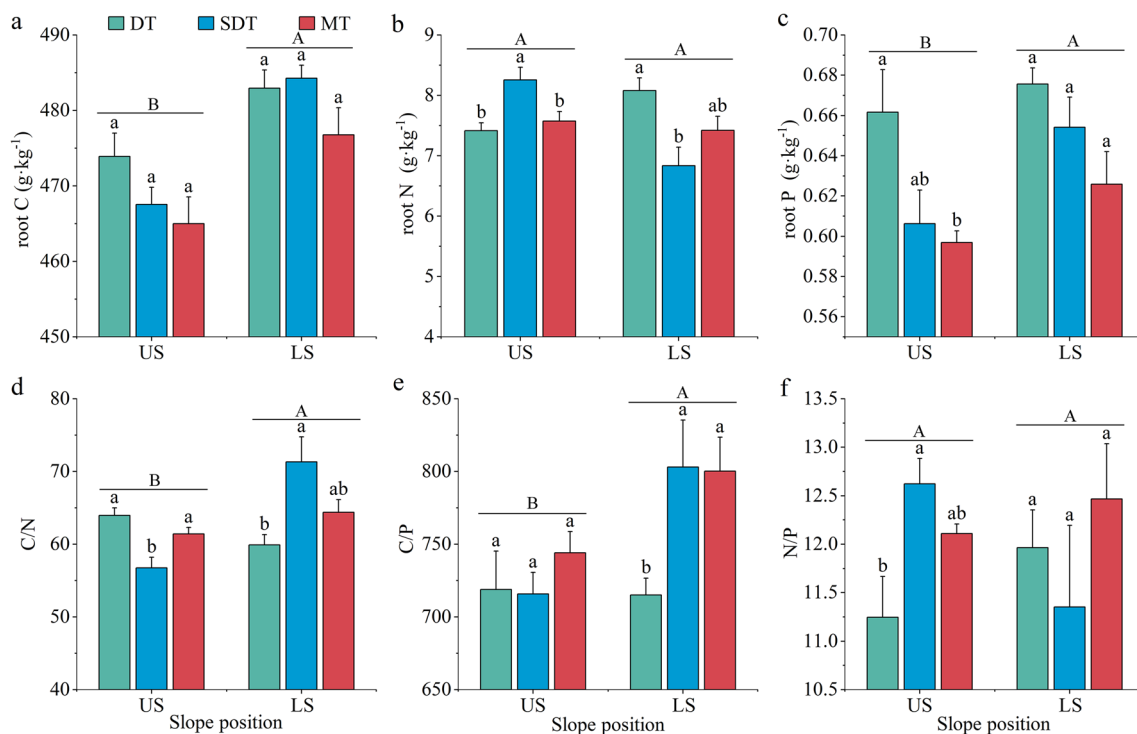
\**P*<0.05; \*\**P*<0.01; ns, *P*≥0.05

US (Fig. 2a, c, d, e). The C and P contents decreased with declining tree status class, however, C, N and P stoichiometry ratios among tree status classes showed the absence of obvious differences (Fig. 2 d–f).

### Soil chemical properties and C, N, P stoichiometric ratios

Slope position, tree status class and their interaction differently affected soil chemical properties and the stoichiometric ratios of C, N and P in rhizosphere soils (Table 4). There were significant differences in SOM, NH<sub>4</sub><sup>+</sup>-N, NO<sub>3</sub><sup>-</sup>-N, ECa and AK contents and in the soil pH values between the two slope positions, but not for TN, TP and AP (Table 4, Fig. 3). The SOM, NO<sub>3</sub><sup>-</sup>-N, NH<sub>4</sub><sup>+</sup>-N, AK content and soil C/P ratio were significantly higher on the US than on the LS, whereas ECa content and pH were significantly lower on the US than on the LS.

Although the TN content, C/N and N/P ratios in rhizosphere soil did not vary significantly between slope positions, they were distinctly influenced by the interaction between slope position and tree status class (Table 4). The TN content and N/P ratio of rhizosphere soil from DT had markedly higher. TN content was 19.34% and 38.46% higher and N/P ratio 15.26% and 29.55% higher, respectively, for the rhizosphere soils from SDT and MT than from DT. However, the C/N ratio from DT was 17.49% and 24.28% lower respectively, than from STD and MT, and NH<sub>4</sub><sup>+</sup>-N, NO<sub>3</sub><sup>-</sup>-N and AP of DT were higher on the LS than on the US (Fig. 3 g, i). Furthermore, the NH<sub>4</sub><sup>+</sup>-N and AP contents of DT were clearly higher than MT on the US, while the NO<sub>3</sub><sup>-</sup>-N content of DT was lower than MT. The changing trend of the ECa content was consistent with the pH value, both of them in DT maintained the highest levels on the LS (Fig. 3 j, k).



**Fig. 2** C, N and P stoichiometry for fine roots from trees in different status classes and slope positions. DT: dominant tree; SDT: subdominant tree; MT: mean tree; US: upper slope; LS: lower slope. Different

capital letters indicate significant difference in the variable between slope positions; different lowercase letters indicate a significant difference in the variable among tree status class

**Table 4** Two-way ANOVA of rhizosphere soil chemical properties by slope position (SP), tree status class (SC) and their interaction (SP×SC)

Variables	SOM (g·kg <sup>-1</sup> )	TN (g·kg <sup>-1</sup> )	TP (g·kg <sup>-1</sup> )	Soil C/N	Soil C/P	Soil N/P	NH <sub>4</sub> <sup>+</sup> -N (mg·kg <sup>-1</sup> )	NO <sub>3</sub> <sup>-</sup> -N (mg·kg <sup>-1</sup> )	AP (mg·kg <sup>-1</sup> )	ECa (mmol·kg <sup>-1</sup> )	pH	AK (mg·kg <sup>-1</sup> )
Slope (F1, 19)	20.84**	1.08 ns	1.52 ns	1.82 ns	17.59**	2.39 ns	43.84**	212.10**	0.01 ns	20.77**	11.02**	5.60*
Status (F2, 19)	1.25 ns	4.77*	3.00 ns	6.05*	3.19 ns	1.36 ns	4.37*	1.85 ns	4.36*	12.81**	7.75**	2.98 ns
SP×SC (F2, 19)	4.05*	9.65**	0.23 ns	6.32**	1.84 ns	8.24**	5.69*	5.21*	0.57 ns	1.90 ns	2.70 ns	0.86 ns

SOM: soil organic matter; TN: total nitrogen; TP: total phosphorus; NH<sub>4</sub><sup>+</sup>-N: ammonium nitrogen; NO<sub>3</sub><sup>-</sup>-N: nitrate-nitrogen; AP: available phosphorus; ECa: exchangeable calcium; pH: soil pH value; AK: available potassium. \**P*<0.05; \*\**P*<0.01; ns, *P*≥0.05

## Linear regression analysis of C, N and P stoichiometry among leaves, fine roots and rhizosphere soils

Leaf and fine root C contents were significantly negatively correlated with that in rhizosphere soils (Fig. 4a), while the N and P contents in leaves were significantly positively correlated with that in rhizosphere soils (Fig. 4b, c). The N/P ratio was negatively correlated between the fine roots and soils (Fig. 4f), while the C/P and N/P ratios had no obvious linear relationships among leaves, fine roots and rhizosphere soils (Fig. 4d, e).

## Correlations between nutrients in leaves and fine roots and rhizosphere soil factors

On upper slopes (Fig. 5a), Pearson's correlations indicated that leaf N and P contents were significantly positively correlated with the rhizosphere soil N/P ratio and TN content and negatively correlated with the soil C/N ratio. There was a significant positive correlation between leaf P and soil ECa contents, but a negative correlation between leaf C/P ratio and soil ECa content. Fine root C content was significantly negatively correlated with soil TN content and positively correlated with soil C/N ratio. Fine root N/P ratio had a significant negative correlation to soil NH<sub>4</sub><sup>+</sup>-N content. On the lower slope (Fig. 5b), leaf N and fine root P contents were positively correlated with rhizosphere soil pH value, AP and ECa contents, but leaf C/N ratio was negatively correlated with these rhizosphere soil properties.

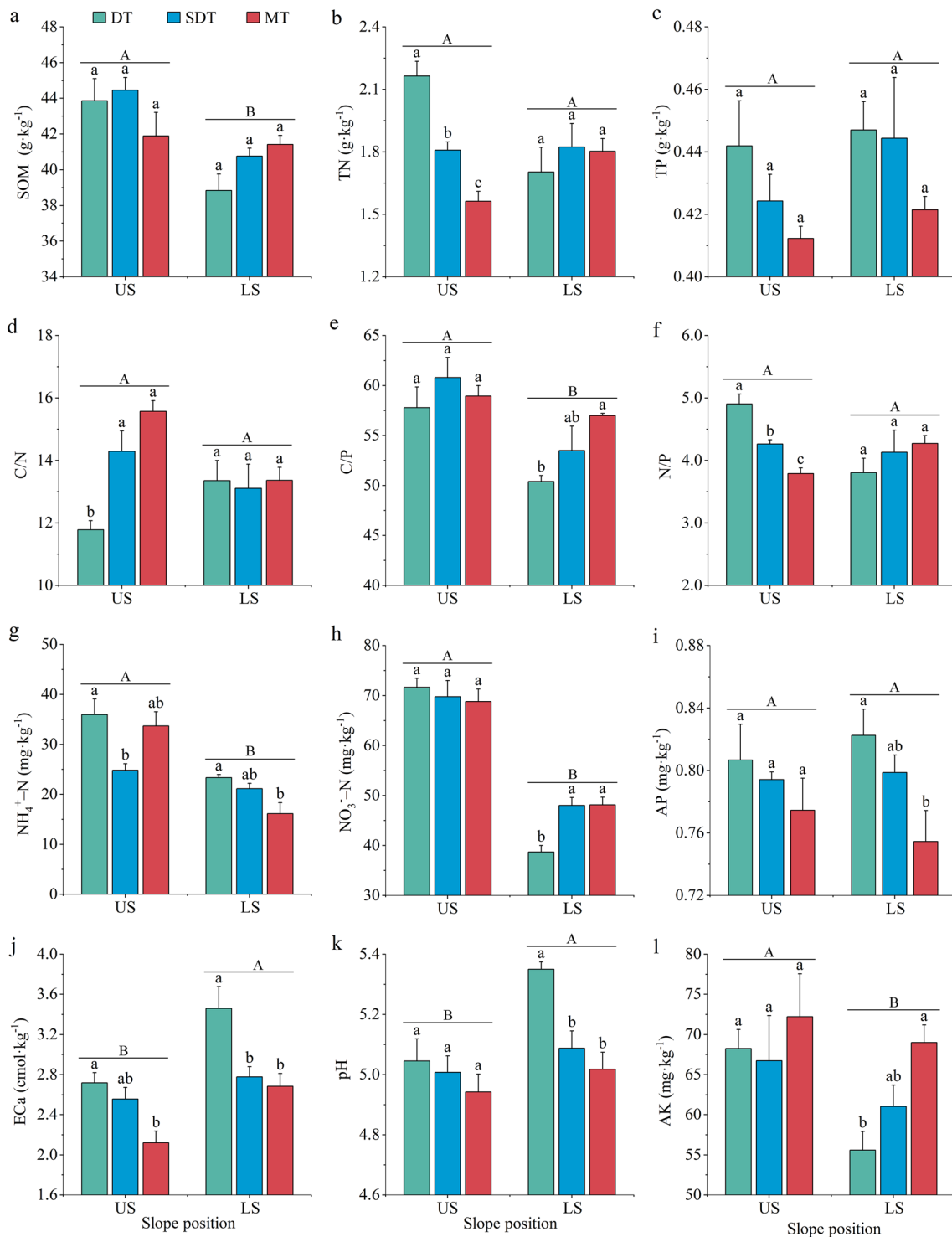
In the redundancy analysis of relationships between C, N and P stoichiometry of leaves and fine roots and rhizosphere soil variables (TN, TP, NH<sub>4</sub><sup>+</sup>-N, NO<sub>3</sub><sup>-</sup>-N, ECa, pH, AP, AK, soil C/N and soil C/P), rhizosphere soil chemical properties explained 89.44% of the total variation for the upper slope (Fig. 5c) and 97.64% for the lower slope (Fig. 5d). Soil factors had a major influence on leaf nutrient elements on the upper slope, whereas they had greater impact on fine root elements on the lower slope. Analysis of conditional effects indicated that the main factor affecting C, N and P stoichiometry in leaves and fine roots on the upper and lower slopes were soil C/N, NH<sub>4</sub><sup>+</sup>-N and AK, respectively (Table 5).

## Discussion

### Variations of C, N and P stoichiometry in leaf and fine root in two slope positions

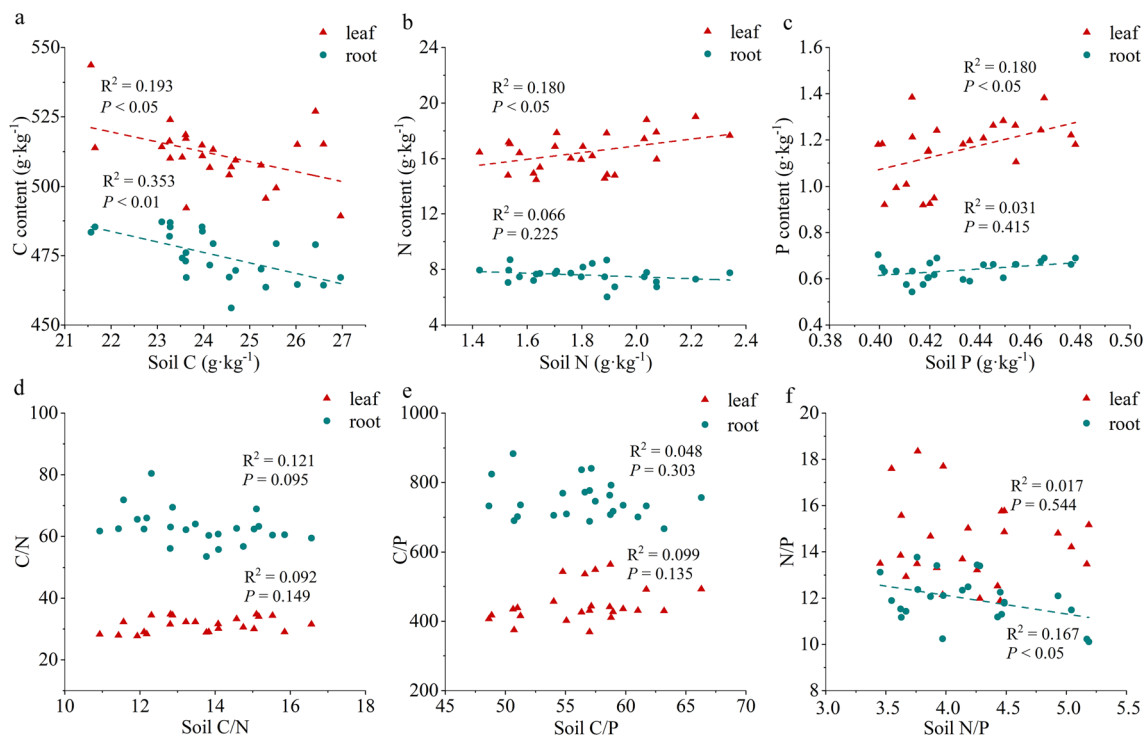
In the present study, the C, N and P contents in leaves were much higher than those in fine roots and rhizosphere soils. Leaf C content and C/N ratio was lower on the upper slope than the lower, but the N content and N/P ratio on the upper





**Fig. 3** Rhizosphere soil chemical properties (mean ± SE) at different slope positions by tree status class. DT: dominant tree; SDT: subdominant tree; MT: mean tree; US: upper slope; LS: lower slope. SOM: soil organic matter; TN: total N; TP: total P; NH<sub>4</sub><sup>+</sup>-N: ammonium N; NO<sub>3</sub><sup>-</sup>-N: nitrate N; AP: available P; ECa: exchangeable Ca;

pH: soil pH value; AK: available K. Different capital letters indicate a significant difference in the variables between slope positions; different lowercase letters indicate significant differences in the variable among status classes



**Fig. 4** Relationships of C, N and P contents **a–c** and their stoichiometric ratios **d–f** for leaves and fine roots with those of rhizosphere soils

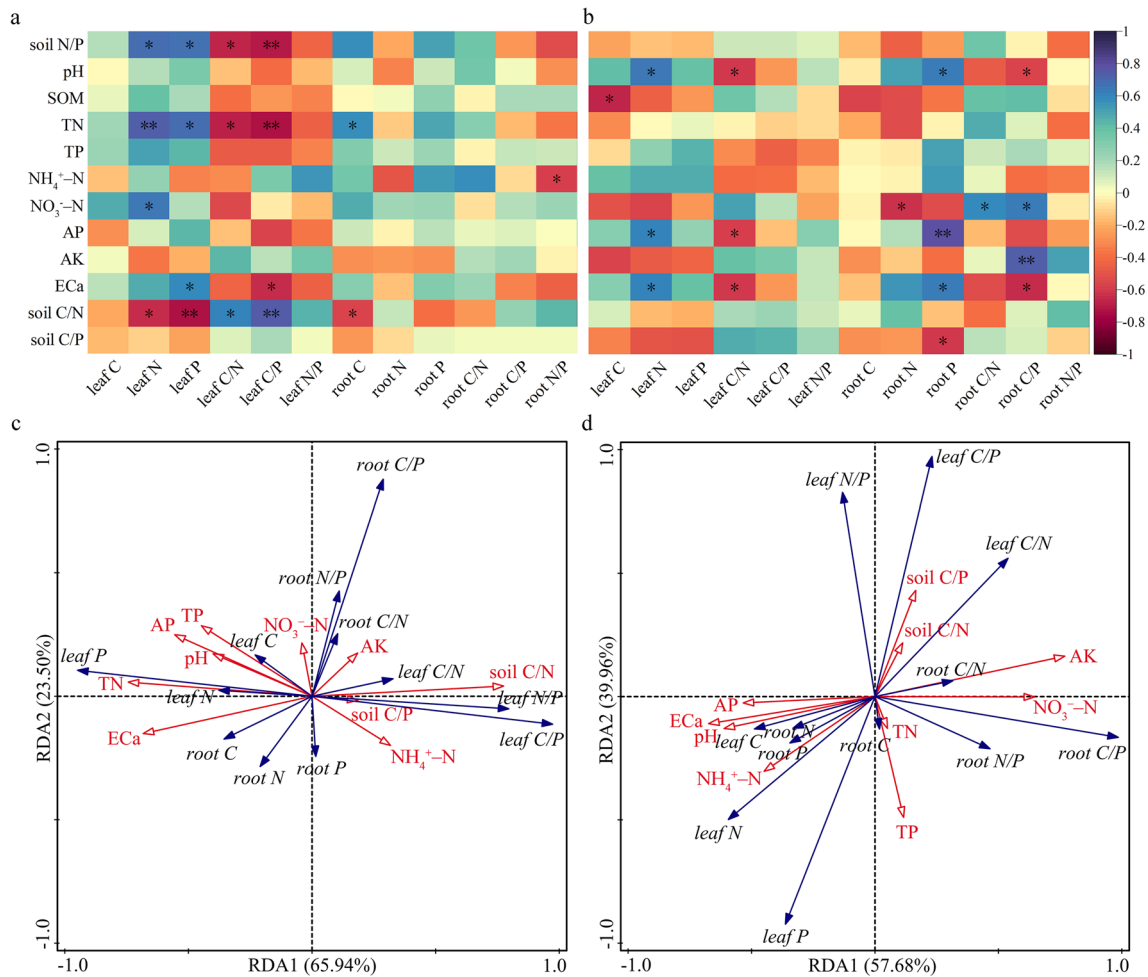
slope were significantly higher than on the lower slope. Differences in leaf P content and C/P ratio were not statistically significant between the two slope positions. With the exception of leaf C, these variables varied considerably among tree status classes, with dominant trees having higher levels of the leaf N and P contents than subdominant and mean trees (Table 2, Fig. 1). The leaf C level was higher on the lower slope than on the upper, but leaf N content was relatively low on the lower slope. The changes in leaf C/N ratio showed that the N utilization of trees was more efficient on the lower slope than on the upper slope.

The N/P ratios of leaves indicated that trees were deficient in N on the lower slope, and P was insufficient in trees on the upper slope. Although the P contents did not differ between slopes, it was clearly higher in dominant trees than in mean trees, which might reflect the absorption capacity of trees and nutrient availability in the soil (Fan et al. 2018; Hogan et al. 2021). Because dominant trees generally occupy a high ecological niche, in contrast to trees in other status classes reducing the competition for soil nutrients and water (Yu et al. 2003; Huang et al. 2020; Wang et al. 2021), the relatively stronger nutrient supply capacity in the soil can enhance the absorption of mineral elements for leaves (Yang et al. 2018). The linear relationships of N, P content between leaves and rhizosphere soils also supported these results (Fig. 4b, c). Moreover, an increase in leaf P content usually promotes N utilization efficiency and the synthesis

of photosynthetic pigments and ATP, improving the net photosynthetic rate and C content in leaves (Walker et al. 2014). Other studies have also suggested coupled relationships between N and P in plants (Crous and Ellsworth 2004; Yang et al. 2015; Netzer et al. 2019). Therefore, the changes in leaf N and P contents were consistent for different status classes of trees, and both of them were greater in dominant trees than the subdominant and mean trees. Leaf C content was not significantly different among the dominant, subdominant and mean trees in this study. A possible explanation is that C is not directly involved in biomass production activities in trees, but mainly contributing to a relatively stable skeleton of tissues (Zhang et al. 2019).

The C and P contents in fine roots were significantly higher on the lower slope than on the upper in our study (Fig. 2a, c). C compounds in aboveground tissues, especially leaves, are the major source of C in plant roots, so more C in the leaves is likely to promote the transport of nutrients from leaves to roots (Wu et al. 2004). Fine root P content was closely correlated to rhizosphere soil AP content, and they had significant and positive relationship in the lower (RDA analysis, Fig. 5b). Chen et al. (2016) also found that P in roots was mainly absorbed from the soil and increased with soil available P in *Larix olgensis* plantations. However, fine root P content on the upper slope clearly differed between dominant and mean trees, possibly because dominant trees possess a great ascendant in resource acquisition and the





**Fig. 5** Pearson's correlation analyses **a, b** and redundancy analysis **c, d** among leaf and fine root C, N, P stoichiometry and soil chemical properties for upper **a, c** and lower **b, d** slopes. pH: soil pH value; SOM: soil organic matter; TN: total N; TP: total P; NH<sub>4</sub><sup>+</sup>-N: ammo-

nium N; NO<sub>3</sub><sup>-</sup>-N: nitrate-N; AP: available P; AK: available K; ECa: exchangeable Ca. Blue indicates a positive correlation between the different variables, red a negative correlation. \**P* < 0.05, \*\**P* < 0.01

**Table 5** Conditional effects of soil properties on leaf C, N, P contents and their stoichiometric ratios in redundancy analysis

Response variables	Explanatory variables	Explains (%)	<i>F</i>	<i>P</i>
C, N, P stoichiometry for leaves and fine roots (upper slope)	soil C/N	39.8	6.6	0.004**
	NH <sub>4</sub> <sup>+</sup> -N	18.3	3.9	0.016*
	pH	6.9	1.3	0.352
	TP	5.9	1.3	0.278
C, N, P stoichiometry for leaves and fine roots (lower slope)	AK	35.3	5.5	0.008**
	ECa	14.7	3.0	0.074
	TP	10.7	1.8	0.200
	AP	8.7	2.2	0.162

\**P* < 0.05, \*\**P* < 0.01

soil is deficient of P on the upper slope. Fine root N content did not differ significantly between the two slope positions in this study (Fig. 2b), which may be related to other factors, such as N adaptation strategies, root morphology, and coupling relationships between elements. These findings are partially consistent with our hypothesis that the stoichiometric characteristics in C, N and P of leaves and fine roots are very sensitive to changes in slope positions; however, these elements in fine roots varied little among the different status classes, showing that nutrient uptake and accumulation by fine roots are not only dependent on tree's demands but also closely related to the level of soil nutrients.

### Changes in rhizosphere soil chemical properties and C, N, P stoichiometric ratios

The rhizosphere hosts abundant and diverse microbial groups, which drive edaphic carbon and nitrogen dynamics

(Ling et al. 2022). The distribution of the rhizosphere soil nutrients differs significantly due to the spatial heterogeneity of soils at different slope positions (Xu et al. 2021). In the present study, rhizosphere soils on the upper slope were significantly enriched in SOM,  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_3^-\text{-N}$  and AK, whereas soil pH values and the ECa content were higher on the lower slope (Fig. 3). These changes were basically consistent with the results of previous studies (Tsui et al. 2004; Utin and Essien 2021). The accumulation of soil organic matter is mainly related to soil pH (Wang et al. 2020; Muneer et al. 2022) and degradation by soil microbes (Liu et al. 2019; Vidal et al. 2021). Thus, the relative decrease in SOM on the upper slope is due to reduced decomposition at low pH, which inhibits the metabolic activities of the microbes (Müller et al. 2017), that need a moderately alkaline environment and grow poorly at lower soil pH (Rousk et al. 2009). In addition, SOM mainly originates from the decomposition of litter, so the litter quality will also affect SOM content to some extent (Lu et al. 2021; Angst et al. 2021). The higher C/N ratio of leaves and fine roots on the lower slope in this study could result in litter's less decomposition by microorganisms (Wang and Zheng 2021). Furthermore, soil microbes usually use labile carbon to decompose recalcitrant organic matter to accelerate N acquisition, when a higher level of soil available N is likely to lead to reduced decomposition of SOM (Wang et al. 2019).

In the present study, rhizosphere soil  $\text{NH}_4^+\text{-N}$  and  $\text{NO}_3^-\text{-N}$  on the upper slope were relatively high than those on the lower slope (Fig. 3g, h). On the one hand, soil N enrichment was related to the higher SOM level on this site because SOM is tight coupled relationship between C and N cycles (Sardans et al. 2017). On the other hand, the higher C/N ratios of the leaves and fine roots accelerated N consumption in the rhizosphere soil on the lower slope due to the greater N utilization efficiency. The lower C/N ratios in plants could result in rapid release of N from the litter during decomposition, elevating the available N in the soil (Zhao et al. 2021). We also found that the content of  $\text{NO}_3^-\text{-N}$  in rhizosphere soil was clearly higher than  $\text{NH}_4^+\text{-N}$ , indicating that nitrification is higher than ammonification in teak plantations, which may increase soil acidification (Krusche et al. 2003). As an indicator of soil fertility, soil pH can influence soil nutrient cycling directly and indirectly (Qiao et al. 2020). In our study, the rhizosphere soil pH and ECa content of dominant trees was significantly higher than those of subdominant and mean trees even more on the lower slope (Fig. 3j, k). The increase in the soil pH was mainly correlated with the decline in organic acids caused by the reduced SOM (Zhang et al. 2018a, b). Also, soil pH in tropical hilly plantations is strongly influenced by leaching resulting in further loss of Ca and P ions; thus, the pH and ECa content are relatively low on the upper slope in comparison to the lower slope (Tsui et al. 2004). Previous studies have also

shown a strong positive correlation between soil pH and ECa (Deforest and Otuya 2020; Pfahler et al. 2020).

Of the stoichiometric ratios for the rhizosphere soil C, N and P, only the C/P ratio differed significantly between slope positions (Fig. 3 d – f) as a result of the high C and low P in the rhizosphere soil on the upper slope, which is consistent with P deficiency on the upper slope based on the leaf N/P ratio, probably because of increased storage in the SOM and reduction of soil P (Turrión et al. 2000; Walkiewicz et al. 2021). P is commonly limited by soil pH and easily fixed in the form of insoluble phosphate with Al and Fe elements in acidic soils (Khanna et al. 2007).

### The relationship between plants and rhizosphere soil factors

Regression analysis suggested that the content of leaf and fine root C contents were had a significant negative linear relationship with rhizosphere soil C content (Fig. 4a). C in photosynthates is transported to roots, which can release C into the soil in the form of exudates such as carbohydrates, amino acids, organic acids and enzymes (Grayston et al. 1996). Subsequently, soil microorganisms can improve the mineralization of soil organic matter by using these exudates as energy sources, which is beneficial for tree absorption and growth (Maarastawi et al. 2021). Thus, the C enrichment in leaves and fine roots might indirectly reduce soil organic matter. Leaf N and P contents were positively correlated to the rhizosphere soil N and P contents, respectively (Fig. 4b, c), similar to the results of Bertilsson et al. (2003) and Zhou et al. (2018) because the contents of N and P aboveground mainly depend on the concentrations of nutrients at the surface soil. When more nutrients accumulate in the rhizosphere soil, fine roots can absorb more N and P for transport to the leaves for the synthesis of chloroplasts, proteins and other compounds for tree growth (Liao et al. 2014).

Soil nutrients primarily contribute to the growth and development of forest trees, and are present at differing C, N and P stoichiometries at various sites, as demonstrated in this study (Fig. 5). Simultaneously, rhizosphere soil C/N and  $\text{NH}_4^+\text{-N}$  were the main influencing factors for leaf and fine root nutrients on the upper slope, whereas AK had a stronger driving effect on the lower slope. On the upper slope, the rhizosphere soil TN content and N/P ratio were significantly positively related to leaf N and P contents, while the C/N ratio was negatively related to leaf N and P. The supply of soil N can promote N and P uptake by leaves, reducing leaf C/N and C/P (Parfitt et al. 2005). A significant negative correlation was shown between  $\text{NH}_4^+\text{-N}$  and root N/P, indicating that soil  $\text{NH}_4^+\text{-N}$  mainly plays an inhibitory role for N absorption by fine roots instead of a promoting effect in teak plantations. On the lower slope, root P and leaf N were positively correlated with soil pH, AP and ECa. An increase

in soil pH and ECa content can accelerate the mineralization rate of P by promoting microbial activity (Deforest and Otuya 2020; Pfahler et al. 2020). The transformation of organic P into an inorganic state enhances the absorption of P by roots and leaves (Hu et al. 2017). Moreover, there is a cooperative action between N and P (Augusto et al. 2013). However, a significance difference in C, N and P stoichiometric ratios was not observed between fine roots and rhizosphere soils (Fig. 5a, b), because plant absorption of mineral elements and their acquisition, transport and storage are impacted by many factors, such as soil moisture, temperature and microbial activity (Ren et al. 2016; Engelhardt et al. 2021; Kusbach et al. 2021). In summary, based on the condition of upper and lower slopes of teak plantations, different management strategies should be implemented in the future.

## Conclusion

Slope position in a hilly area had a strong effect on leaf and fine root C, N and P stoichiometry by shaping different soil properties, and strong correlations existed between leaf, fine root and rhizosphere soil factors. Leaf and fine root C content and C/N ratio were higher and SOM content and soil C/N ratio lower on the lower slope than on the upper. The C/N ratio,  $\text{NH}_4^+\text{-N}$  and AK in rhizosphere soil were the major drivers of these effects, leading to content changes in leaves and fine roots elements. The C, N and P stoichiometries varied strongly among the different status classes of trees only in the leaves. The interaction between slope position and tree status class seemed to have more profound effects on soil properties. These results provide a better understanding of nutrient accumulation patterns for devising management strategies for teak plantations. More attention is needed on the function of microorganisms in nutrient cycling in plant–soil systems.

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