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SOIL AND NEEDLE C:N:P STOICHIOMETRY AND NUTRIENT RESORPTION AT DIFFERENT GROWTH STAGES OF *PINUS MASSONIANA* PLANTATIONS IN SUBTROPICAL CHINA

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Stoichiometry and nutrient resorption are key indicators for assessing nutrient use efficiency in plants, particularly in nutrient-limited environments. However, the dynamic changes of these metrics in plantation ecosystems remain poorly understood. This study investigates nutrient use efficiency in *Pinus massoniana* plantations in Guangxi, China, focusing on the dynamics of carbon (C), nitrogen (N), and phosphorus (P) in soil and needles across different growth stages. Results show that soil C:N and C:P ratios increased with plantation growth, while the soil N:P ratio remained stable. Needle analysis revealed high C content, and low N and P contents, reflecting efficient nutrient utilisation and carbon storage. The N:P ratio in green needles suggested an initial co-limitation of N and P, with a shift towards increasing N limitation as the plantation matured. While needle N resorption efficiency (NRE) showed no significant variation across growth stages, the P resorption efficiency (PRE) and PRE:NRE ratio declined, indicating a reduction in P limitation over time. These findings provide new insights into nutrient dynamics in plantation ecosystems in subtropical China, offering valuable guidance for sustainable forest management practices.

Keywords: *Pinus massoniana*, stoichiometry, nutrient resorption, nutrient limitation, growth stage

INTRODUCTION

Ecological stoichiometry examines the balance and interactions of chemical elements in ecosystems (Ding et al. 2021, Wang et al. 2021, Guo et al. 2023b). It has been widely used to explore plant-environment relationships and feedback mechanisms, especially in subtropical forest ecosystems (Ding et al. 2021, Jiang et al. 2022, Qiao et al. 2020, Ali et al. 2022, Chang et al. 2022). Carbon (C), nitrogen (N), and phosphorus (P) are key elements for plant growth and central to ecosystem biochemical cycles (Niu et al. 2020, Ding et al. 2021, Chang et al. 2022). Understanding C:N:P stoichiometry in subtropical forests is essential for revealing tree life history strategies, adaptation mechanisms, and soil condition influences (Wang et al. 2021, Ding et al. 2021, Chang et al. 2022).

The leaf N:P mass ratio is a key indicator of N and P limitations in plant growth (Wang et al. 2021, Zhang et al. 2022a, Guo et al. 2023a). According to the N:P Threshold Hypothesis, specific N:P ratios indicate nutrient limitation status (Koerselman & Meuleman 1996, Gūsewell 2004). For subtropical forests, the thresholds proposed by Koerselman and Meuleman (1996) were widely used, defining a leaf N:P ratio below 14 as N limitation, above 16 as P limitation, and between 14 and 16 as co-limitation of N and P (Zhang et al. 2022a, Guo et al. 2023a). Soil C:N:P stoichiometry is another critical indicator of ecosystem quality in subtropical forests. The C:N ratio evaluates the carbon-nitrogen nutritional balance, while soil C:P and N:P ratios influence organic matter decomposition, nutrient cycling, and microbial community activity (Xu et al. 2019, Ding et al. 2021, Guo et al. 2023b). Nutrient dynamics in trees and soil often shift during forest plantation development, potentially leading to nutrient limitations in individual trees (He et al. 2022). Nitrogen and P limitations are particularly common in young and overmature forests, significantly affecting tree biomass accumulation and wood production (Hou et al. 2020, Guo et al. 2023a). Understanding stoichiometric relationships and their underlying mechanisms is essential for the sustainable management of subtropical forest ecosystems.

Nutrient resorption is the process by which plants reallocate nutrients from senescing leaves to other tissues for reuse (Jiang et al. 2021, Zhang et al. 2022b). This process shortens nutrient cycling, enhances nutrient use efficiency, and reduces plant dependence on soil nutrients (Wang et al. 2021, Guo et al. 2023a). Studies often report a negative correlation between nutrient resorption efficiency (NuRE) and soil nutrient availability (Wang et al. 2021, Guo et al. 2023a). However, some findings challenged this pattern, showing that plants under N or P limitations do not always exhibit higher N resorption efficiency (NRE) or P resorption efficiency (PRE) (Gerdol et al. 2019). This suggests that the relationship between NuRE and soil nutrients remains complex and uncertain, requiring further investigation, particularly in plantation ecosystems.

Forest plantations in southern China provide critical economic and environmental benefits, including soil erosion control, enhanced geochemical cycling, and increased productivity (He et al. 2022, Jiang et al. 2022, Guo et al. 2023b). In the past two decades, driven by forest degradation and growing recognition of ecosystem services, plantations in subtropical regions of China have rapidly expanded, with *Pinus massoniana* emerging as a key afforestation species (Jiang et al. 2021, Jiang et al. 2022, Guo et al. 2023a). However, the expansion of these plantations has brought challenges, such as slower growth rates and reduced timber productivity (He et al. 2022). To ensure the sustainable management of *P. massoniana* forests, a deeper understanding of nutrient dynamics and plant-soil interactions is essential (Guo et al. 2023a).

In subtropical China, we studied *P. massoniana* plantations at different growth stages: young, middle-aged, near-mature, and mature forests. We measured the C, N, and P contents of soil and needles (both green and senesced), their stoichiometric ratios, and the NuRE of the needles. This study aimed to investigate variations in N and P limitations and uptake strategies across growth stages. Our research was guided by three hypotheses: 1) Soil and needle C:N:P stoichiometry varies across growth stages; 2) NuRE increases with rising nutrient limitations; 3) N and P use strategies are shaped by the interaction between soil nutrients and growth stages.

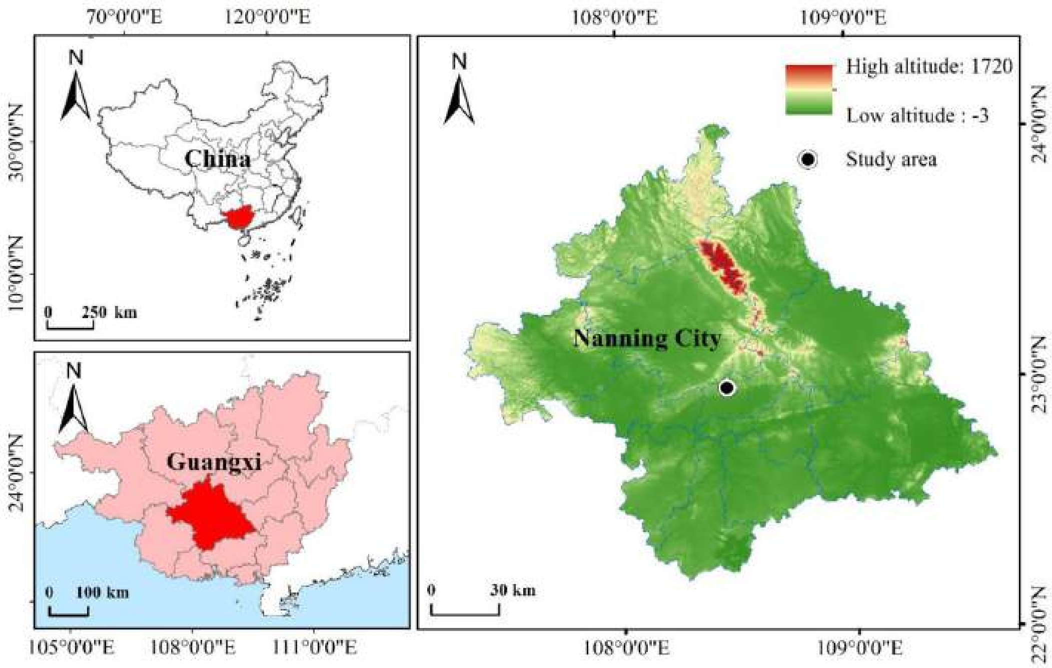

Figure 1 Study area location in Nanning, Guangxi, China

MATERIALS AND METHODS

Site description

The study area is located in *P. massoniana* plantations in central Nanning, Guangxi, southern China (22°51'N, 108°42'E) (Figure 1). It has a subtropical monsoon climate, characterised by abundant sunshine, warm temperatures, and ample rainfall. The average annual precipitation is 1477.85 mm, with an average temperature of 21.4 °C, 1758.6 sunshine hours, and a frost-free period of 312 days. The soil is mainly red soil and lateritic red soil, developed from sandy shale, and classified as Ferralsols.

The plantations were irrigated, weeded, and subjected to insect control and grazing prohibition during the first 2 years after afforestation. Initial thinning occurred when the trees were 10–15 years old, typically removing overcrowded, underperforming, or diseased trees. The first thinning intensity ranged from 25–35% of the total tree count, with canopy closure maintained at no less than 0.7. Thinning continued approximately every 10 years, reducing tree density by 20–30% until maturity. The understory vegetation mainly includes *Litsea cubeba*, *Schefflera octophylla*, *Ficus hirta*, *Sapium discolor*, *Euodia lepta*, *Ficus esquiroliana*, *Adiantum capillus-veneris*, *Dicranopteris linearis*, *Blechnum orientale*, and *Miscanthus floridulus*. During our study, no N-fixing plants were observed in densities sufficient to significantly impact the N dynamics of the ecosystem.

Sample collection and analysis

In August 2022, 23 pure *P. massoniana* plantations of varying stand ages were randomly selected in the study area. To ensure consistent site conditions, the plots were located at elevations of 300–500 m, on slopes with gradients between 18°–27°, in the middle section of the slope. The slopes faced southeast to southwest, ensuring uniform sunlight exposure, and the soil types were generally consistent across plots. The plantations included 6 plots of young forests (0–20 years), 5 plots of middle-aged forests (21–30 years), 7 plots of near-mature forests (31–40 years), and 5 plots of mature forests (>40 years). The youngest forest was 5 years old, and the oldest was 62 years old. Each tree was labeled with a unique number, and growth parameters, including diameter at breast height and height, were recorded. An overview of the plot characteristics is provided in Table 1.

In August 2022, three healthy trees exhibiting robust growth and showing no signs of disease, pest infestation, or physical damage were selected from each plot. These trees were chosen from the plot interior to avoid edge effects or recent thinning activities (Qiu et al. 2020). For each tree, branches of similar diameter were collected from the middle canopy in the east, west, south, and north directions using an averruncator. Green and senesced yellow needles were harvested from these branches. Needles of the same type (green or senesced) collected from each tree were combined into a single composite sample. In total, 69 composite samples of green and senesced needles were collected. Soil samples were collected within a 0.5–1.5 m radius around each sample tree. After removing plant residues, gravel, and debris, soil samples were taken from three depths: 0–20 cm, 20–40 cm, and 40–60 cm. Three samples from each soil layer within each plot were combined into a single composite sample, resulting in a total of 69 soil samples.

Table 1 Overview of *Pinus massoniana* plantations

Growth stage	Average stand age (years)	Average altitude (m)	Average slope (°)	Average density (tree hm^{-2})	Average diameter at breast height (cm)	Average tree height (m)
Young forest	12.6 ± 2.1	338 ± 32	21.5 ± 1.5	1634 ± 133	12.53 ± 3.14	10.87 ± 2.24
Middle-aged forest	25.6 ± 1.4	326 ± 17	20.0 ± 0.9	1123 ± 112	26.71 ± 2.95	23.38 ± 2.66
Near-mature forest	36.4 ± 0.7	343 ± 26	22.0 ± 1.8	874 ± 79	35.56 ± 4.43	30.24 ± 2.75
Mature forest	54.6 ± 3.7	332 ± 37	25.0 ± 1.11	752 ± 43	41.64 ± 5.41	33.27 ± 3.34

After returning the plant and soil samples to the laboratory, initial pre-processing steps were carried out. Plant samples were heated at 105 °C for 30 minutes, then dried at 85 °C until they reached a constant weight. They were then ground using a grinder. Soil samples were air-dried, cleaned of impurities, ground, and sieved. The soil organic C (SOC) and plant C content were measured using the $K_2Cr_2O_7$ heating oxidation method. The sample was heated in an oil bath with a 0.8 mol L^{-1} $K_2Cr_2O_7$ solution until boiling for 5 minutes, and the remaining potassium dichromate was titrated with a standard ferrous ammonium sulfate solution to determine organic C content. Total N content in soil and needles was measured by the Kjeldahl method (TecatorAB, Sweden), where the samples were digested with concentrated sulfuric acid, distilled to convert N into ammonia, and then titrated with 0.02 mol L^{-1} hydrochloric acid. Total P content in both soil and needles was measured using the molybdenum blue colorimetric method. P in the samples reacted with a 5% ammonium molybdate solution to form molybdenum blue, and its intensity was measured to determine the total P content. In this study, soil C, N, and P content refer to SOC, total N, and total P.

Data calculations and analysis

NuRE of needles can be calculated using Formula (1):

$$NuRE(\%) = \left(1 - \frac{Nu_s}{Nu_g} \times MLCF\right) \times 100\% \qquad (1)$$

where Nu_g and Nu_s represent the N or P content of green and senesced needles, respectively. MLCF represents the correction factor for mass loss, which in needle trees is 0.745 (Vergutz et al. 2012).

Before conducting statistical analyses, normality and homogeneity of variance tests were performed on all data. One-way analysis of variance (ANOVA) and LSD tests were used to examine differences in nutrient content of green needles, senesced needles, and soil, as well as NuRE and stoichiometric ratios among the different growth stages of *P. massoniana* plantations. Pearson correlation analysis was conducted to explore the correlations between needle (green and senesced) and soil C, N, and P contents, stoichiometric ratios (C:N, C:P, and N:P), and needle NuRE (NRE, PRE, and NRE:PRE). All statistical analyses were performed using SPSS 22.0 (SPSS Inc., Chicago, IL, USA) with a significance level of 0.05. Figures were created using Origin 2022 (OriginLab Corporation, Northampton, MA, USA). Redundancy analysis was used to clarify the relationships between NuRE and the C:N:P stoichiometry of soil and needles, performed with Canoco 5 (Microcomputer Power, Ithaca, NY, USA).

RESULTS

Soil C, N, and P contents and stoichiometry

Soil C, N, and P contents, along with their stoichiometric ratios, varied at different depths and growth stages in *P. massoniana* plantations (Figure 2). The average soil C, N, and P contents at the 0–60 cm depth were 15.05, 1.19, and 0.29 g kg^{-1}, respectively (Figures 2a, 2b, and 2c). The surface soil layer (0–20 cm depth) showed higher C and N contents ($p < 0.05$) than deeper layers across all growth stages (Figures 2a and 2b). However, this trend was only observed for soil P content in the mature forest stage (Figure 2c). Soil C content in the surface layer increased with growth stage (Figure 2a, $p < 0.05$). Soil N content did not vary significantly among growth stages (Figure 2b, $p > 0.05$). Soil P content in the deeper layers decreased with growth stage (Figure 2c).

The C:N ratio in the surface soil layer was significantly higher ($p < 0.05$) than in the deeper soil layer in young plantations, but this difference was not significant in other growth stages (Figure 2d, $p > 0.05$). The C:P and N:P ratios in the surface soil layer were higher ($p < 0.05$) than in deeper layers across all growth stages (Figures 2e and 2f). The C:N and C:P ratios in each soil layer generally increased with growth stage, while the N:P ratio remained relatively stable across growth stages (Figures 2d, 2e, and 2f).

Green and senesced needle stoichiometry and NuRE

In *P. massoniana* plantations, the C content of both green and senesced needles increased over

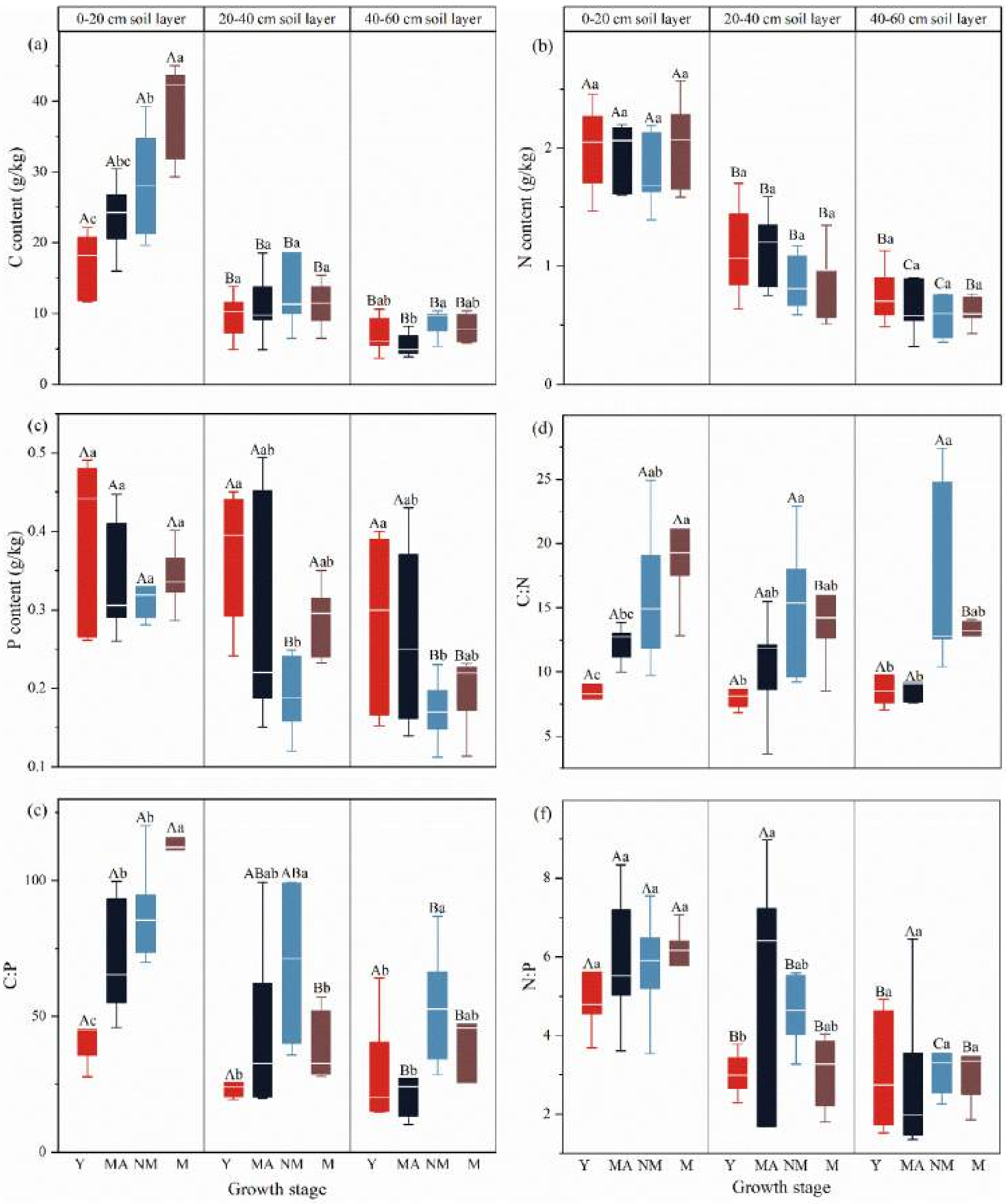

Figure 2 The soil C (a), N (b), and P (c) contents, as well as the C:N (d), C:P (e), and N:P (f) ratios at various soil layers and growth stages in *P. massoniana* plantations. Y, young forests; MA, middle-aged forests; NM, near-mature forests; M, mature forests. Significant differences among the growth stages and soil layers ($p < 0.05$) are denoted by distinct lowercase and uppercase letters

time (Figure 3a). The N and P contents in green needles showed an initial increase, followed by a decrease, with their maximum values occurring during the middle-aged forest stage (Figures 3b and 3c). The trends in N content of senesced needles were similar to those of green needles (Figures 3a, 3b, and 3c). Senesced needle P content in the young forest stage was significantly lower than in other growth stages (Figures 3a, 3b, 3c). The average C, N, and P contents in pooled green needle samples were 501.70, 12.54, and 0.89 g kg^{-1}, respectively, while those in senesced needles were 500.69, 10.18, and 0.52 g kg^{-1}.

As the growth stages progressed, the C:N ratio of both green and senesced needles first decreased and then increased, reaching its minimum in the middle-aged forest stage (Figure 3d). The variation in the C:P ratio was less pronounced, with the highest C:P ratio recorded in green needles during the mature forest stage and in senesced needles during the young forest stage (Figure 3e). The N:P ratio of green needles initially declined and then increased, while that of senesced needles showed a consistent downward trend (Figure 3f).

No significant differences in NRE values were observed across growth stages ($p > 0.05$), while PRE values and the PRE:NRE ratios decreased significantly with increasing growth stages (Figure 4).

Relationship between NuRE and C:N:P stoichiometry of soil and needle

The C contents of both green and senesced needles were positively correlated with stand age (0.857, $p < 0.05$), as well as with stoichiometric ratios related to C in the surface soil layer (Figure

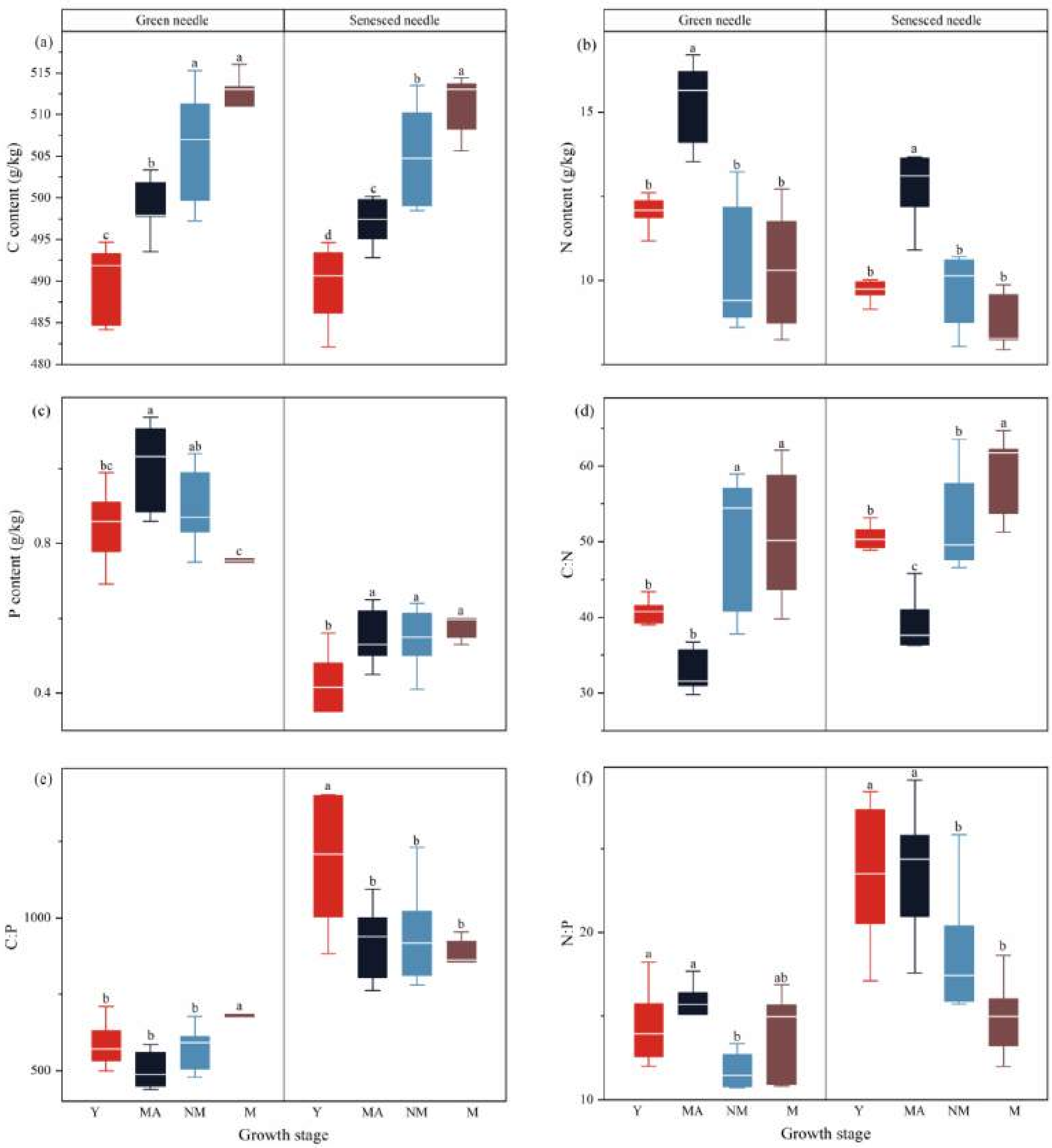

Figure 3 The green and senesced needle C (a), N (b), and P (c) contents, as well as the C:N (d), C:P (e), and N:P (f) ratios at various growth stages in *P. massoniana* plantations. Y, young forests; MA, middle-aged forests; NM, near-mature forests; M, mature forests. Significant differences among the growth stages ($p < 0.05$) are denoted by distinct lowercase letters

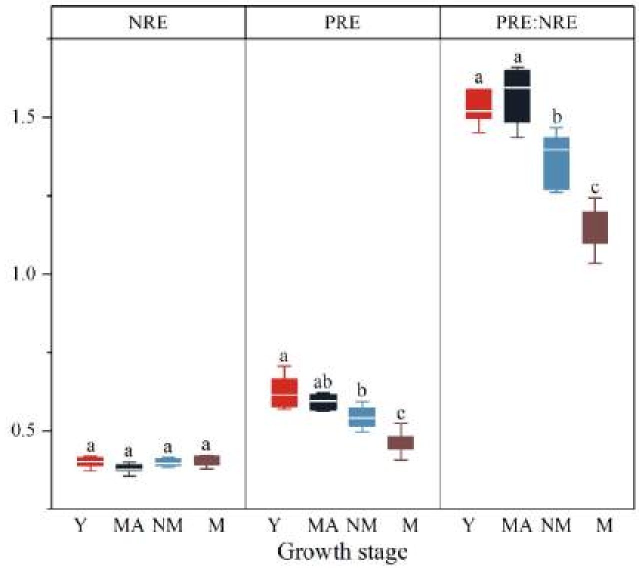

Figure 4 Needle N and P resorption efficiency at various growth stages in *P. massoniana* plantations. NRE, N resorption efficiency; PRE, P resorption efficiency; Y, young forests; MA, middle-aged forests; NM, near-mature forests; M, mature forests. Significant differences among the growth stages ($p < 0.05$) are denoted by distinct lowercase letters

5). The N contents of green and senesced needles showed no significant correlation with soil stoichiometric ratios ($p > 0.05$, Figure 5). Green needle P content was positively correlated with soil N content (0.509, $p < 0.05$) and the N:P ratio (0.456, $p < 0.05$) in certain soil layers (Figure 5). Senesced needle P content exhibited a positive correlation with stand age (0.667, $p < 0.05$), soil C:P ratio (0.509, $p < 0.05$), and N:P ratio (0.488, $p < 0.05$), while it was negatively correlated with P content in the surface soil layer (-0.487, $p < 0.05$).

The C:N ratios of both green and senesced needles were positively correlated with stand age (0.473, $p < 0.05$). Both the C:P and N:P ratios of green and senesced needles were negatively correlated with the N:P ratio in the surface soil layer ($p < 0.05$, Figure 5). Additionally, the C:P and N:P ratios of senesced needles were negatively correlated with stand age (-0.621, $p < 0.05$; -0.733, $p < 0.05$). NRE was negatively correlated with senesced needle N content (-0.43, $p < 0.05$) and positively correlated with soil C content (0.53, $p < 0.05$), showing no correlation with stand age ($p > 0.05$).

PRE was positively correlated with senesced needle C:P (0.69, $p < 0.05$) and N:P ratios (0.79), and negatively correlated with stand age (-0.88, $p < 0.05$). The NRE:PRE ratio showed a positive correlation with green and senesced needle N contents (0.45, $p < 0.05$; 0.49, $p < 0.05$), as well as senesced needle C:P and N:P ratios (0.57, $p < 0.05$; 0.77, $p < 0.05$). It was negatively correlated with stand age (-0.87, $p < 0.05$) and the C:N ratio of both green and senesced needles and surface soil layer (-0.61, $p < 0.05$; -0.53, $p < 0.05$; -0.61, $p < 0.05$).

The RDA analysis revealed that Axis 1 and Axis 2 explained 66.83% and 32.49% of the total variance in NuRE attributes, respectively (Figure 6). NRE was influenced by soil C content and senesced needle N content (Figure 6). PRE was primarily affected by stand age, as well as senesced and green needle C contents (Figure 6). Additionally, PRE showed a gradual decline with increasing stand age, with this shift occurring during the near-mature forest stage (Figure 6). The NRE:PRE ratios were primarily influenced by stand age, along with the C and N contents in green needles, C and P contents in senesced needles, and soil C content (Figure 6).

DISCUSSION

Soil C:N:P stoichiometry in different soil layers and growth stages

The surface soil layer had higher C and N contents than the deeper layers, consistent with previous studies (Zheng et al. 2021, Guo et al.

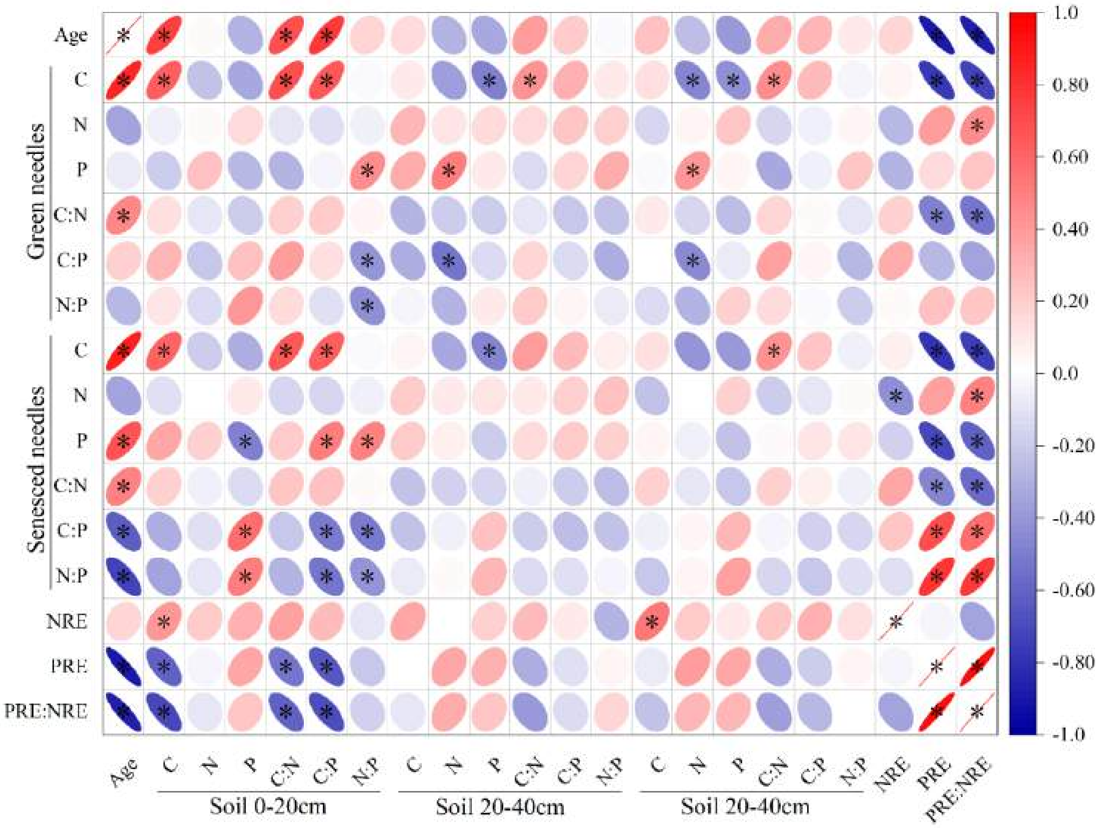

Figure 5 Correlation between stand age, C:N:P stoichiometry of green needles, senesced needles and soil, and nutrient resorption efficiency. NRE, N resorption efficiency; PRE, P resorption efficiency. The asterisks represent significant correlations at the 0.05 level

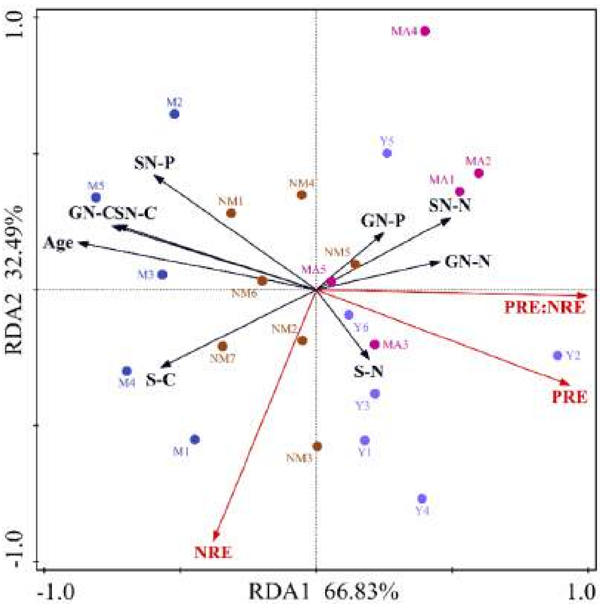

Figure 6 Redundancy analysis of NuRE attributes (in red) and nutrient status (in blue) in green and senesced needles, as well as soil at depths of 0–60 cm. NRE, N resorption efficiency; PRE, P resorption efficiency; GN-C, green needle C content; GN-N, green needle N content; GN-P, green needle P content; SN-C, senesced needle C content; SN-N, senesced needle N content; SN-P, senesced needle P content; S-C, soil organic C content; S-N, soil total N content

2023a). Litterfall decomposition contributes to C and N accumulation in the surface soil layer (Zheng et al. 2021, Obidike-Ugwu et al. 2023). However, in our study, there was no significant difference in soil N content among different growth stages, which contrasts with studies suggesting that soil N content increases in mature plantations (Guo et al. 2023a, Guo et al. 2023b). This discrepancy may be due to the high initial soil N accumulation at the study site during early plantation growth stages (Ali et al. 2022, Guo et al. 2023). In older plantations, surface soil P content was significantly higher than in deeper layers, likely due to root uptake and subsequent return via litter decomposition as the forest matures (Ali et al. 2022). However, soil N and P content in our study area were lower than the Chinese average (second national land resource survey), likely due to heavy rainfall causing N leaching (Guo et al. 2023a) and acidic red soil promoting P mineralization, reducing its availability to plants (Jiang et al. 2022).

The mature stands had the highest soil C:N ratio, followed by near-mature, middle-aged, and young forests. This variation likely results from slower nitrogen (N) decomposition compared to carbon (C) during forest maturation, which increases the C:N ratio (Piaszczyk et al. 2019, Xu et al. 2019). The soil C:P ratio averaged 52.06 in the 0–60 cm layer, well below the threshold of 200 proposed by Huang and Xu (2000), indicating net P mineralization in *P. massoniana* plantation soils. We observed higher N:P ratios in surface soils compared to deeper layers, consistent with prior studies showing a trend of increasing N:P ratios with decreasing soil depth (Qiao et al. 2020, Ding et al. 2021). This is due to P accumulating more slowly than N, particularly in surface soils, leading to elevated N:P ratios (Ding et al. 2021). Across growth stages, soil N:P ratios ranged from 1.35 to 8.98, averaging 4.31, which is significantly lower than the national average of 9.3 (Yang et al. 2021). This suggests that N limitation is stronger relative to P at our study site.

Green needle C:N:P stoichiometry in various growth stage

In this study, needle P content showed a positive correlation with soil N content. According to Gūsewell (2004) and Han et al. (2013), plants tend to prioritize the absorption of limited nutrients while reducing uptake of more abundant ones. Consequently, the strong N limitation at our study site likely influences the P absorption of *P. massoniana*. Needle N and P contents initially increased and then decreased with stand age. Previous studies have shown varying patterns in needle C, N, and P content with forest maturity. For example, in the Qianzhong region, needle C and N increased with age, while P initially decreased before rising (Guo et al. 2023b). In contrast, no significant changes in N and P were observed across stand ages in the Wuling Mountains (Wang et al. 2022). These differences can be attributed to regional variations in precipitation, soil types, and climate. Higher rainfall in our study area (1500 mm) compared to Qianzhong (1072.8 mm) and the Wuling Mountains (1300 mm) likely increases nutrient leaching and affects soil nutrient availability. Similarly, soil types—red and lateritic red soils in our study area versus yellow and yellow-brown soils in other regions—affect nutrient absorption. Additionally, climatic differences, such as the humid subtropical climate of Qianzhong and the warm temperate climate of the Wuling Mountains, further influence nutrient dynamics. These factors, along with stand age, shape the observed trends in needle nutrient content.

The average C:N and C:P ratios in green needles were 40.89 and 574.38, respectively, both higher than the global averages of 22.50 and 469.16 (Elser et al. 2000). This indicates that *P. massoniana* has strong C sequestration capabilities and efficient N and P utilisation, supporting its rapid growth and resin metabolism in nutrient-limited environments (Jiang et al. 2022). A global meta-analysis shows that plantation forests shift from N to P limitation as they mature (Zhang et al. 2022a). In our study, green needle N:P ratios ranged from 14.41 to 13.43 across different growth stages, indicating dual N and P limitations (14 < N:P < 16) in early stages, with N becoming the primary limitation (N:P < 14) in later stages (Koerselman & Meuleman 1996). The early-stage N and P limitations are likely due to high N leaching and P mineralisation in the subtropical monsoon climate (Chen et al. 2019). However, as N is depleted faster than P, the N:P ratio continuously declined in the later growth stages.

Nutrient use strategies and resorption patterns across various growth stages

Compared to green needles, *P. massoniana* senesced needles had lower N and P content but higher C:N and C:P ratios, reflecting its nutrient resorption capacity (Guo et al. 2023b). Notably, NRE remained stable across growth stages, while PRE declined significantly, likely due to changing nutrient demand and availability during growth (Guo et al. 2023a). Nitrogen is essential for synthesising proteins, nucleic acids, and chlorophyll, and plants typically require higher N concentrations than P for growth (Guo et al. 2023a). Throughout its life cycle, *P. massoniana* relies heavily on N to sustain rapid biomass accumulation, making nutrient resorption crucial for N acquisition. This explains the stable NRE across stand ages (Guo et al. 2023a). In contrast, P demand decreases as the tree matures, and its relative availability increases, leading to a gradual decline in PRE (Gūsewell, 2004, Han et al. 2013). The PRE:NRE ratio is commonly used to assess relative N and P limitations (Guo et al. 2023a). In this study, a negative correlation between the PRE:NRE ratio and stand age indicated reduced P limitation compared to N limitation as plantations matured. This finding aligns with previous studies, supporting the observation that N becomes the primary growth-limiting factor in later stages (Guo et al. 2023a, Han et al. 2013). Furthermore, the NRE:PRE ratio positively correlated with needle and soil N content, as well as related stoichiometric ratios, suggesting that PRE:NRE is primarily driven by the most limiting nutrient (Guo et al. 2023a).

Inspiration for plantation management

Nitrogen and P limitations are common in plantations across southern China (Jiang et al. 2022), including in Chinese fir (Wu et al. 2020), Chinese sweetgum (Zhang et al. 2018), and eucalyptus plantations (Cui et al. 2023). Our study indicates that N and P limitations vary with growth stages. Young *P. massoniana* plantations are co-limited by both N and P, while older plantations are primarily N-limited, with this shift occurring in the near-mature stage. Therefore, fertilisation strategies should be adjusted based on stand age (Guo et al. 2023b). Mixed forests have been shown to alleviate nutrient limitations (Yao et al. 2021, Kabzems et al. 2023). Since Chinese fir is another key species for afforestation in southern China, Wu et al. (2020) observed a shift from N to P limitation in Chinese fir plantations with age, which aligns with our findings in *P. massoniana*. Future research should explore the potential benefits of mixed *P. massoniana* and Chinese fir plantations for improving the development of subtropical forests.

CONCLUSIONS

Our study reveals significant variations in soil and needle stoichiometry across different growth stages of *P. massoniana* plantations, highlighting its adaptability to changing environmental conditions. Green needles of *P. massoniana* had high C content and low N and P content, demonstrating a strong capacity for C sequestration and efficient nutrient utilisation. This makes it a suitable afforestation species for subtropical China. In the early growth stages, *P. massoniana* plantations are co-limited by both N and P, with N becoming the primary limiting factor in later stages. We recommend adjusting fertilisation practices based on the growth stage of *P. massoniana* plantations in subtropical regions. Stable NRE and declining PRE further confirm reduced P limitation over time. This suggests that *P. massoniana* may help alleviate common P limitations in subtropical plantations. These findings provide valuable insights for the sustainable management of subtropical artificial forest plantations.

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REFERENCES

Ali A, Hussain M, Ali S et al. 2022. Ecological stoichiometry in *Pinus massoniana L.* plantation: increasing nutrient limitation in a 48-year chronosequence. *Forests* 13: 469. https://doi.org/10.3390/f13030469

Chang Y, Zhong Q, Yang H, Xu C, Hua W & Li B. 2022. Patterns and driving factors of leaf C, N, and P stoichiometry in two forest types with different stand ages in a mid-subtropical zone. *Forest Ecosystems* 9: 100005. https://doi.org/10.1016/j.fecs.2022.100005

Chen J, Kuzyakov Y, Jenerette GD et al. 2019. Intensified precipitation seasonality reduces soil inorganic N content in a subtropical forest: greater contribution of leaching loss than N2O emission. *Journal of Geophysical Research: Biogeosciences* 124: 494–508. https://doi.org/10.1029/2018JG004821

Cui Y, Yan Y, Wang S et al. 2023. Mixed Eucalyptus plantations in subtropical China enhance phosphorus accumulation and transformation in soil aggregates. *Frontiers in Forests and Global Change* 6: 1269487. https://doi.org/10.3389/ffgc.2023.1269487

Ding X, Li X, Qi Y, Zhao Z, Sun D & Wei H. 2021. Depth-dependent C-N-P stocks and stoichiometry in Ultisols resulting from conversion of secondary forests to plantations and driving forces. *Forests* 12: 1300. https://doi.org/10.3390/f12101300

Elser JJ, Sterner RW, Gorokhova E et al. 2000. Biological stoichiometry from genes to ecosystems. *Ecology Letters* 3: 540–550. https://doi.org/10.1111/j.1461-0248.2000.00185.x

Gerdol R, Iacumin P & Brancaleoni L. 2019. Differential effects of soil chemistry on the foliar resorption of nitrogen and phosphorus across altitudinal gradients. *Functional Ecology* 33: 1351–1361. https://doi.org/10.1111/1365-2435.13327

Guo W, Jiao P, Lopez Cml et al. 2023a. Nitrogen and phosphorous dynamics with stand development of *Pinus massoniana* plantations in Southeast China. *Frontiers in Plant Science* 14: 1139945. https://doi.org/10.3389/fpls.2023.1139945

Guo Q, Li H, Sun X, An Z & Ding G. 2023b. Patterns of needle nutrient resorption and ecological stoichiometry homeostasis along a chronosequence of *Pinus massoniana* plantations. *Forests* 14: 607. https://doi.org/10.3390/f14030607

Güsewell S. 2004. N:P ratios in terrestrial plants: variation and functional significance. *New Phytologist* 164: 243–266. https://doi.org/10.1111/j.1469-8137.2004.01192.x

Han W, Tang L, Chen Y & Fang J. 2013. Relationship between the relative limitation and resorption efficiency of nitrogen vs phosphorus in woody plants. *PloS One* 8: 83366. https://doi.org/10.1371/journal.pone.0083366

He J, Dai Q, Xu E, Yan Y & Peng X. 2022. Variability in soil macronutrient stocks across a chronosequence of Masson pine plantations. *Forests* 13: 17. https://doi.org/10.3390/f13010017

Hou E, Luo Y, Kuang Y, Chen C, Lu X et al. 2020. Global meta-analysis shows pervasive phosphorus limitation of aboveground plant production in natural terrestrial ecosystems. *Nature Communication* 11: 637. https://doi.org/10.1038/s41467-020-14492-w

Huang Cy & Xu JM. 2000. *Soil science*. China Agriculture Press, Beijing.

Jiang D, Yang B, Cheng XY, Chen HY, Ruan H & Xu X. 2021. The stoichiometry of leaf nitrogen and phosphorus resorption in plantation forests. *Forest Ecology and Management* 483: 118743. https://doi.org/10.1016/j.foreco.2020.118743

Jiang J, Lu Y, Chen B, Ming A & Pang L. 2022. Nutrient resorption and C:N:P stoichiometry responses of a *Pinus massoniana* plantation to various thinning intensities in Southern China. *Forests* 13: 1699. https://doi.org/10.3390/f13101699

Kabzems R, Harper G & Elkin C. 2023. Growing space management in boreal mixedwood forests: 22 year results. *Journal of Sustainable Forestry* 42: 655–674. https://doi.org/10.1080/10549811.2022.2090381

Koerselman W & Meuleman AFM. 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *The Journal of Applied Ecology* 33: 1441–1450. https://doi.org/10.2307/2404783

Niu J, Lu T, Lin Y & Zhang WX. 2020. Effects of nitrogen addition on the characteristics of foliar and soil ecological stoichiometry in Xishuangbanna tropical rainforest, Southwest China. *Journal of Tropical Forest Science* 32: 1–7. https://doi.org/10.26525/jtfs32.1.1

Obidike-Ugwu E, Ariwaodo J & Nwafor O. 2023. Evaluation of soil physio-chemical properties under a young *Albizia lebbeck* (rattle tree) plantation in a savanna ecosystem. *Journal of Tropical Forest Science* 35: 66. https://doi.org/10.26525/jtfs2023.35.1.66

Piaszczyk W, Błońska E, Lasota J & Lukac M. 2019. A comparison of C:N:P stoichiometry in soil and deadwood at an advanced decomposition stage. *Catena* 179: 1–5. https://doi.org/10.1016/j.catena.2019.03.025

Qiao Y, Wang J, Liu HM et al. 2020. Depth-dependent soil C-N-P stoichiometry in a mature subtropical broadleaf forest. *Geoderma* 370: 114357. https://doi.org/10.1016/j.geoderma.2020.114357

Qiu X, Wang H, Peng D et al. 2020. Thinning drives C:N:P stoichiometry and nutrient resorption in *Larix principis-rupprechtii* plantations in North China. *Forest Ecology and Management* 462: 117984. https://doi.org/10.1016/j.foreco.2020.117984

Raihan A. 2024. Enhancing carbon sequestration through tropical forest management: A review. *Journal of Forestry and Natural Resources* 3: 33–48.

Vergutz L, Manzoni S, Porporato A, Novais Rf & Jackson RB. 2012. Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. *Ecological Monographs* 82: 205–220. https://doi.org/10.1890/11-0416.1

Wang YH, Zhou JG & Fu YH. 2022. Effects of stand ages on C, N and P stoichiometry of *Pinus massoniana* secondary forests in Wuling Mountain Area of Chongqing. *Acta Ecologica Sinica* 42: 9537–9547. https://doi.org/10.5846/stxb202201100093

Wang Z, HE G, Hou Z, Luo Z & Zhao J. 2021. Soil C:N:P stoichiometry of typical coniferous (*Cunninghamia lanceolata*) and/or evergreen broadleaved (*Phoebe bournei*) plantations in South China. *Forest Ecology and Management* 486: 118974. https://doi.org/10.1016/j.foreco.2021.118974

Wu HL, Xiang WH, Ouyang S et al. 2020. Tree growth rate and soil nutrient status determine the shift in nutrient-use strategy of Chinese fir plantations along a chronosequence. *Forest Ecology and Management* 460: 117896. https://doi.org/10.1016/j.foreco.2020.117896

Xu HW, Qu Q, Li P, Guo ZQ, Wulan E & Xue S. 2019. Stocks and stoichiometry of soil organic carbon, total nitrogen, and total phosphorus after vegetation restoration in the Loess Hilly Region, China. *Forests* 10: 27. https://doi.org/10.3390/f10010027

Yang SB, Feng C, Ma YH et al. 2021. Transition from N to P limited soil nutrients over time since restoration in degraded subtropical broadleaved mixed forests. *Forest Ecology and Management* 494: 119298. https://doi.org/10.1016/j.foreco.2021.119298

Yao X, Zhang Q, Zhou H, Nong Z, Ye S & Deng Q. 2021. Introduction of *Dalbergia odorifera* enhances nitrogen absorption on Eucalyptus through stimulating microbially mediated soil nitrogen–cycling. *Forest Ecosystems* 8: 1–12. https://doi.org/10.1186/s40663-021-00339-3

Zhang H, Sun M, Wen Y et al. 2022a. The effects of stand age on leaf N:P cannot be neglected: A global synthesis. *Forest Ecology and Management* 518: 120294. https://doi.org/10.1016/j.foreco.2022.120294

Zhang H, Wang J, Wang J et al. 2018. Tree stoichiometry and nutrient resorption along a chronosequence of *Metasequoia glyptostroboides* forests in coastal China. *Forest Ecology and Management* 430: 445–450. https://doi.org/10.1016/j.foreco.2018.08.037

Zhang P, Lü XT, Li MH, Wu T & Jin G. 2022b. N limitation increases along a temperate forest succession: Evidences from leaf stoichiometry and nutrient resorption. *Journal of Plant Ecology* 15: 1021–1035. https://doi.org/10.1093/jpe/rtac017

Zheng Y, Hu Z, Pan X et al. 2021. Carbon and nitrogen transfer from litter to soil is higher in slow than rapid decomposing plant litter: A synthesis of stable isotope studies. *Soil Biology and Biochemistry* 156: 108196. https://doi.org/10.1016/j.soilbio.2021.108196.