Effects of Long-Term Fertilization and Stand Age on Root Nutrient Acquisition and Leaf Nutrient Resorption of *Metasequoia glyptostroboides*

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The plant nutrient acquisition strategies are diverse, such as root nutrient acquisition and leaf nutrient resorption, playing important roles in driving soil processes, vegetation performance as well as ecosystem nutrient cycling. However, it is still in a debate whether there is a synergy or tradeoff between above- and below-ground nutrient acquisition strategy under nitrogen (N) and phosphorus (P) addition, or with stand age. Herein, this study investigated the responses of root-soil accumulation factor (RSAF) and leaf nutrient resorption efficiency (NuRE) to long-term N and P fertilization, and further explored the trade-off between them in *Metasequoia glyptostroboides* plantations with different stand age. Results showed that under N fertilization in young plantations, leaf N resorption efficiency (NRE) increased, and root-soil accumulation factor for P (RSAF-P) decreased. For young forests under P fertilization, the NRE increased whereas RSAF-P decreased. For middle-aged forests under P fertilization, the NRE and leaf P resorption efficiency (PRE) increased and the RSAF-P decreased. Under P fertilization in young and middle-aged plantations, PRE had a significant positive correlation with RSAF-P. Under N fertilization in young plantations, NRE was significantly positive correlated with root-soil accumulation factor for N (RSAF-N). The covariance-based structural equation modeling (CB-SEM) analysis indicated that stand age had positive effects on PRE whether under N or P fertilization, as well as on RSAF-P under N fertilization, whereas had no effects on the NRE or RSAF-N. Overall, our results can shed light on the nutrient acquisition strategies of *M. glyptostroboides* plantations under future environmental changes and the results could be applied to the nutrient management practices.

**Keywords:** nutrient acquisition strategies, N and P fertilization, stand age, leaf, root
INTRODUCTION

The plant nutrient acquisition strategies cannot be underestimated in forest ecosystems, given that the plants usually do not have sufficient amounts of biologically available nutrients to support growth, survival, and reproduction, especially in nutrient-impoverished habitats (Abrahão et al., 2018; Wang et al., 2020). It has been always considered that roots are the major tissue for the plant to acquire nutrients, and root nutrient acquisition strategies play a decisive role in the maintenance of forest ecosystem health and vitality (Andersen et al., 2017; Ma et al., 2018; Li et al., 2019). In recent decades, some other plant nutrient acquisition strategies have also been proposed, such as leaf nutrient resorption proficiency and efficiency (Reed et al., 2012; He et al., 2020; Xu et al., 2020). Naturally, whether these plant nutrient acquisition strategies co-vary or exhibit coordinated responses to a changing environment has drawn great attention from ecologists.

Allocation of effort toward nutrient capture and resorption depends on both the environment nutrient availability and the cost involved in these processes (Wright and Westoby, 2003; Wang et al., 2014a). In barren soils, plants should bear traits that prioritize conservation over active absorption of resources, whereas the opposite was expected in nutrient-rich soils. Specifically, since nutrients derived from capture become less expensive than those from resorption as soil nutrient availability increases, the root capture strategy would be more favored than leaf resorption (Wright and Westoby, 2003; Kou et al., 2017). Inversely, species from nutrient-impoverished habitats also reduce nutrient losses by remobilizing a large fraction of the nutrients before senesced organ shedding (high remobilization efficiency), and shedding leaves with very low final nutrient concentrations (Killingbeck, 1996; Kobe et al., 2005; Hayes et al., 2014). Nevertheless, in cases of consistent environmental nutrient availability, the costs of the different plant nutrient acquisition strategies have not been effectively evaluated.

Increasing anthropogenic nitrogen (N) and phosphorus (P) deposition has enhanced N and P availability in many forest ecosystems, respectively, providing ideal venues for the studies of the trade-off relationships of plant nutrient acquisition strategies. It is well known that plants can maintain high nutrients level under nutrient enrichment through increasing above-ground nutrient conservation or improving below-ground nutrient uptake (Deng et al., 2016; Hofmann et al., 2016). Several studies showed the trade-off relationships between root nutrient acquisition and leaf nutrient resorption while only considering these two mechanisms (Deng et al., 2016; Kou et al., 2017). In contrast, other studies found the synergy relationship between these two mechanisms, and emphasized that only adopting above-ground nutrient conservation of below-ground nutrient uptake may not be applicable (Ushio et al., 2015; Hofmann et al., 2016).

The corresponding alterations in tree nutrient capture capacity during forest stand development had been widely demonstrated (Brant and Chen, 2015; Chen and Chen, 2022). For instance, the NRE rose and then dropped, and the PRE increased with stand age in Medicago sativa, which was closely related to the

MATERIALS AND METHODS

Study Site

The study was conducted in Dongtai Forest Farm (121° 45′ E, 33° 42′ N), a site located in the central coast of the Jiangsu Province, China. The climate of the study site is that of the monsoon subtropical moist marine climate zone. The altitude is 0–4 m, the annual average temperature, frost-free period, precipitation, and sunshine duration is 14.5°C, 220 days, 1055.7 mm, and 2130.5 h. The soil is alkaline sandy soil, which was more infertile than yellow-earth soil in the natural range of M. glyptostroboides. The study site was the pioneer area to plant the M. glyptostroboides in coastal China (Figure 1).

Experiment Design and Sample Collection

N and P experiment was initiated in 2014 of different ages (young forest: 6-year old; middle-age forests: 24-year old) with three 300 m × 100 m plots of M. glyptostroboides plantations in Dongtai forest farm, and ten 20 m × 30 m plots of each plot were selected for completely random block N and P addition experiments, of which 5 plots were used for N addition treatments and 5 plots for P addition treatments in each age class. Each plot was separated by a buffer zone. The basic information is shown in Table 1. N and P addition gradients setting: set the N addition treatments as CK, 0.8, 2.4, 4.0, and 6.0 mol·m⁻², respectively, and the fertilization was added in the form of urea [CO(NH₂)₂]; P fertilization treatment was set as CK, 0.05, 0.2, 0.6, and 1.0 mol·m⁻², respectively, and fertilization was added in the form of superphosphate [Ca(H₂PO₄)₂]. The fertilization gradients were based on a pretest and a previous seeding pot
study (Wang et al., 2018). Fertilization dosage and time: the first addition time is from the end of March to the beginning of April, 60% of the total amount of fertilization added; the second addition time is in the middle of June, 40% of the total amount of fertilization added. In addition, N and P were applied to the field directly every year.

Three average trees in each plot were selected for collecting leaves, branches, and roots. Fully expanded leaves and branches from the upper and outer part of tree crowns were sampled. The fine roots (<2 mm) of each selected individual were sampled through the careful removal of the soil surrounding the roots. Five soil cores (2.5 cm in diameter) per plot were randomly collected from 0 to 10 cm depth following the removal of understory plants and surface litter, and thoroughly mixed to homogenize a sample. Leaves, branches, roots, and soils were sampled in August 2018 (the end of the growing season). Five litter traps (1.0 m², made of nylon mesh) per plot were fixed 1.0 m above the ground. Leaf litter was collected in late November 2018.
TABLE 1 | General characteristics of the young and middle-aged *M. glyptostroboides* stands.

| Basic properties | Parameter | Young plantations | Middle-aged plantations |
|------------------|-----------|-------------------|-------------------------|
| Stand structure  | Average height (m) | 10.33 ± 2.21 | 15.91 ± 2.20 |
|                  | DBH (cm)     | 17.8 ± 0.86 | 27.75 ± 0.84 |
|                  | DBH (growth) | 4.8 ± 1.52 | 2.39 ± 0.69 |
|                  | Density (tree/ ha²) | 417 | 417 |
|                  | Crown width (m) | 4.61 ± 0.65 | 5.01 ± 0.52 |
| Soil physical properties | Water content (%) | 0.22 ± 0.02 | 0.32 ± 0.03 |
|                  | Total porosity (%) | 44.09 ± 2.81 | 46.49 ± 2.39 |
|                  | Capillary porosity (%) | 42.46 ± 3.68 | 45.75 ± 2.37 |
| Soil chemical properties | Organic C content (g kg⁻¹) | 8.19 ± 0.38 | 13.18 ± 4.09 |
|                  | Available N content (mg kg⁻¹) | 90.90 ± 4.27 | 132.67 ± 12.66 |
|                  | Total P content (g kg⁻¹) | 0.85 ± 0.03 | 0.68 ± 0.10 |
|                  | Available P content (mg kg⁻¹) | 14.27 ± 3.91 | 2.85 ± 0.15 |

The DBH (growth) is the DBH increasement during 2015–2019 year.

Chemical Measurements

All plant organs samples were dried in the oven at 105°C for 2 h, then dried at 75°C to constant weight, crushed with a mechanical grinder, and the samples were sieved to determine nutrient content. The C and N concentrations were determined for each sample using an autoanalyzer (Kjeltec 2300 Analyzer Unit, Foss, Sweden). P concentration was determined using the standard ammonium molybdate method (reference code GBW08513; General Administration of Quality Supervision, PRC).

Soil samples were air-dried after being sieved (2-mm mesh). Soil pH was determined by the potentiometric method, soil organic carbon (SOC) was determined with wet oxidation by sulfuric acid and potassium dichromate and back titration with ferrous sulfate. The total N concentration was determined by Kjeldahl method, Hydrolysable N concentration was determined by titration with a dilute solution of H₂SO₄ after extraction with a mixture of ferrous sulfate and sodium hydroxide. The total P and available P concentrations were determined with a molybdate blue colorimeter after extraction with 0.5 M sodium bicarbonate (Zhang et al., 2018).

Data Analysis

Nutrient resorption efficiency (NuRE) was defined as the proportional withdrawal of a nutrient during senescence and was calculated as follows:

\[
\text{NuRE} = \left(1 - \frac{\text{Nu}_{\text{senesced}}}{\text{Nu}_{\text{green}}} \times \text{MLCF}\right) \times 100\%
\]

Where NuRE is N or P resorption efficiency, Nu_{\text{senesced}} and Nu_{\text{green}} represent N or P concentration (mass-based) in leaf and litter, respectively, and MLCF is mass loss correction factor with a value of 0.745 for deciduous coniferous species (Vergutz et al., 2012).

Root-soil accumulation factor (RSAF) for N and P were defined to describe the root N or P acquisition (Kou et al., 2017), as follows:

\[
\text{RSAF} = \frac{\text{Nu}_{\text{root}}}{\text{Nu}_{\text{soil}}}
\]

Where RSAF is root N or P accumulation factor, Nu_{\text{root}} and Nu_{\text{soil}} represent N or P concentration (mass-based) in absorptive fine root and soil, respectively.

Data analysis using the single factor variance (One-way ANOVA) analysis of the different fertilization gradients of plant organs stoichiometric characteristics, nutrient acquisition, nutrient recycling, and nutrient absorption efficiency under different stand ages, respectively, the influence of significance level set as \( p = 0.05 \), with minimal process significantly difference (LSD) determined the level of significance in SPSS 23.0 (SPSS Inc., Chicago, IL, United States). The covariance-based structural equation modeling (CB-SEM) analysis was conducted in SPSS Amos 26 (SPSS Inc., Chicago, IL, United States) to explore the effects of stand age on NuRE and RSAF under N and P fertilization. All data were tested to fulfill the assumptions of normality and homogeneity of variance, and transformations were carried out when necessary. Figures were plotted using Origin 2018 (Origin Lab Corporation, Northampton, MA, United States).

RESULTS

Effect of Nitrogen and Phosphorus Fertilization on Leaf Nutrient Resorption Efficiency and Root-Soil Accumulation Factor

Under N fertilization in young plantations, the NRE and PRE of CK treatment were 31.02 and 64.25%, respectively. The NRE remarkably increased while PRE kept relatively stable along N fertilization gradients (Figure 2A). The RSAF-N and RSAF-P of CK treatment were 131.75 and 198.49, respectively. The RSAF-P remarkably decreased while RSAF-N kept relatively stable along N fertilization gradients (Figure 2B).

Under P fertilization in young plantations, the NRE and PRE of CK treatment were 32.17 and 68.31%, respectively. The NRE remarkably increased, while PRE kept relatively stable along P fertilization gradients (Figure 2C). The RSAF-N and RSAF-P of CK treatment were 108.38 and 189.6, respectively. The RSAF-N and RSAF-P remarkably increased and decreased along P fertilization gradients (Figure 2D).

Under N fertilization in middle-aged plantations, the NRE and PRE of CK treatment were 45.02 and 54.24%, respectively. The NRE and PRE both kept relatively stable along N fertilization gradients (Figure 3A). The RSAF-N and RSAF-P of CK treatment were 82.59 and 126.71, respectively. The RSAF-N and RSAF-P both kept relatively stable along N fertilization gradients (Figure 3B).

Under P fertilization in middle-aged plantations, the NRE and PRE of CK treatment were 39.07 and 54.24%, respectively. The NRE and PRE both remarkably increased remarkably along P fertilization gradients (Figure 3C). The RSAF-N and RSAF-P of CK treatment were 83.64 and 121.24, respectively. The RSAF-N and RSAF-P both kept relatively stable along P fertilization gradients (Figure 3D).
Effect of Nitrogen and Phosphorus Fertilization on Leaf N Resorption Efficiency/leaf P Resorption Efficiency and Root-Soil Accumulation Factor for N/Root-Soil Accumulation Factor for P

The NRE/PRE of CK treatment was 0.49 and 0.83 in young and middle-aged plantations under N fertilization, respectively. The NRE/PRE for young plantation increased significantly under N fertilization, while the NRE/PRE for middle-aged plantations kept relatively stable along N fertilization gradients (Figure 4A). The RSAF-N/RSAF-P of CK treatment were 0.69 and 0.68 in young and middle-aged plantations under N fertilization, respectively. The RSAF-N/RSAF-P for young plantation increased significantly under N fertilization, while the RSAF-N/RSAF-P in middle-aged plantations kept relatively stable along N fertilization gradients (Figure 4B).

The NRE/PRE of CK treatment was 0.50 and 0.88 in young and middle-aged plantations under P fertilization, respectively. The NRE/PRE in young and middle-aged plantations both kept relatively stable along P fertilization gradients (Figure 4C). The RSAF-N/RSAF-P of CK treatment were 0.59 and 0.70 in young and middle-aged plantations under P fertilization, respectively. The RSAF-N/RSAF-P remarkably increased under P fertilization, while the RSAF-N/RSAF-P in middle-aged plantations kept relatively stable along P fertilization gradients (Figure 4D).

The Relationships Between Leaf Nutrient Resorption Efficiency and Root-Soil Accumulation Factor Under Nitrogen and Phosphorus Fertilization

Under N fertilization, NRE showed no association with RSAF-N, while PRE was significantly positive correlated with RSAF-P in young and middle-aged plantations (Figures 5A,C). Under P fertilization, NRE was significantly positively correlated with RSAF for N in young plantation, whereas no significant relationships were found between NRE and RSAF-N in middle-aged plantation, as well as PRE and RSAF-P in both young and middle-aged plantations (Figures 5B,D).
The Direct and Indirect Effect of Nutrient Fertilization and Stand Age on Leaf Nutrient Resorption Efficiency and Root-Soil Accumulation Factor

The covariance-based structural equation modeling (CB-SEM) analysis indicated that N fertilization and stand age together explained 84.3% of variations in NRE and 73.5% of variations in PRE (Figure 6A). N fertilization had a positive indirect effect on NRE via leaf N, and a negative indirect effect on PRE through leaf P and soil pH. Stand age had a positive direct effect on PRE via leaf P, and a negative indirect effect via soil total N and leaf P. N fertilization and stand age together explained 62.8% of variations in RSAF-N and 56.0% of variations in RSAF-P (Figure 6B). N fertilization and stand age had a negative and positive direct effect on RSAF-P, respectively. N fertilization had a positive indirect effect on RSAF-N via fine root N. Stand age had a negative indirect effect on RSAF-N via soil N:P.

P fertilization and stand age together explained 60.9% of variations in PRE (Figure 6C). Stand age had a positive direct effect on PRE, and P fertilization had a positive indirect effect on PRE via leaf P. P fertilization and stand age together explained 78.1% of variations in RSAF-N, and 44.4% of variations in RSAF-P (Figure 6D). P fertilization had a negative direct effect on RSAF-P, and stand age had a negative direct effect on RSAF-N. Stand age had a negative indirect effect on RSAF-N via fine root N and P.

DISCUSSION

Effects of Nitrogen Fertilization on Plant Nutrient Acquisition

Bioavailable N is increasing due to human activity, which greatly alters nutrient availability for plant growth and affects fundamental ecological processes (Wang et al., 2019a). Nutrient resorption from senescing leaves is one of the plants’ essential nutrient conservation strategies, accounting for a large property of the nutrient demand for plants (Aerts, 1996). In this study, N fertilization increased leaf N concentration in young plantation, which was in line with the observations from the global-scale meta-analysis (Ostertag and DiManno, 2016;
However, in contrast to most previous studies, we found a significant increase in NRE for young plantation and no significant changes for middle-aged plantation under N fertilization (Yuan and Chen, 2015; Lu et al., 2019; Zhao et al., 2020). Our study also found that leaf litter N concentration kept relatively stable under N fertilization whether in young and middle-aged plantations (Wen et al., 2021). Thus, considering the violent strong natural and human-activities disturbances, we deemed that nutrient return of leaf litter to the soil, i.e., litter decomposition, might not be so essential, especially in the coastal man-made forests. Moreover, the RSAF-P decreased remarkably under N fertilization, which was not consistent with Kou et al. (2017), who reported that the RSAF-P kept relatively stable in Pinus elliottii plantations.

The NRE/PRE in leaf was recently developed to indicate the theoretical framework of N or P limitation for plant growth, which could be applied to quantitatively evaluate the spatial characteristics and key influencing factors of N and P limitation in the terrestrial ecosystems (Du et al., 2020). In this study, the NRE/PRE was always less than 1 under N fertilization, indicating that the plant growth was mostly limited by N. This result was consistent with one of our previous studies, which found N was the main limiting factor for M. glyptostroboides growth combining with the concept of stoichiometric homeostasis (Wang et al., 2019b). Moreover, the NRE/PRE of young plantation increased along the gradient of N fertilization, demonstrating that the N limitation got relieved to some extent (Li et al., 2016; Du et al., 2020).

It was always expected that plant tissues exhibited trade-offs relationships in water and nutrient acquisition, which is of great significance for plant stoichiometric homeostasis and the balance of matters and energy in the terrestrial ecosystems. While these trade-off relationships became unpredictable under the background of global change. In this study, we observed significant and positive associations between PRE and RSAF-P in both young and middle-aged plantations under N fertilization, which was not in line with Kou et al. (2017) for Pinus elliottii plantations. However, most of the trade-off relationships between leaf nutrient resorption and fine root nutrient acquisition had been lost under N fertilization. Therefore, we referred that the changes in environmental nutrient conditions might lead to the absence of trade-off relationships between under- and above-ground plant tissues.
Effects of Phosphorus Fertilization on Plant Nutrient Acquisition

Atmospheric P deposition brought by agricultural activities, dust transport, and combustion source emissions had greatly altered the soil P availability that greatly influenced plant growth (Widdig et al., 2019; Pan et al., 2021). Generally, the availability of one nutrient would inevitably affect relative availability of other nutrients, particularly in the status of nutrient deficiency or imbalance (Kou et al., 2017). In the current study, the NRE of young and middle-aged plantation increased along the gradient of P fertilization, which was also reported in Yan et al. (2015). Furthermore, the RSAF-N/RSAF-P increased remarkably whether under P fertilization in young plantation, and kept relatively stable in middle-aged plantation. This finding was also in line with the above observations for above-ground plant tissues. Therefore, fine root nutrient acquisition might play an important role in indicating the nutrient limitation of plant growth. Meanwhile, we observed that the RSAF-P decreased significantly under P fertilization whether in young or middle-aged plantation, which might be attributed to the fact that the fine root nutrient acquisition existed some delayed effects.

Notably, the NRE and RSAF-N in young plantation under P fertilization, were significantly correlated with each other, even exhibiting synergy relationships to some extent. These findings were also observed in previous research, which emphasized that only adopting aboveground N and P conservation or belowground N and P uptake might not be accurate (Ushio et al., 2015; Hofmann et al., 2016). Therefore, we concluded that the synergistic relationship for P acquisition might be explained by the two following reasons. Firstly, the relationships between fine root nutrient acquisition and leaf nutrient resorption were indeed positively related, whereas there might exist some other mechanisms which could balance these two nutrient conversation mechanisms. Secondly, there was no trade-off evolutionary mechanism between leaves and roots, which might leading to the consistent responses of leaf nutrient resorption and fine root nutrient acquisition to environment changes by chance.

Stand Age Mediates Fertilization Effects on Plant Nutrient Acquisition

Trees at different growth stages have great differences in physiological processes and nutrition requirements, resulting in

fine roots (Pregitzer et al., 2002; Kou et al., 2018), which might lead to an underestimate of the RSAF.

FIGURE 5 | (A) Relationships between NRE and RSAF-N under N fertilization in young and middle-aged plantations (no significance). (B) Relationships between NRE and RSAF-N under P fertilization in young ($R^2 = 0.468$, $P < 0.01$) and middle-aged (no significance) plantations. (C) Relationships between PRE and RSAF-P under N fertilization in young ($R^2 = 0.266$, $P < 0.05$) and middle-aged plantations ($R^2 = 0.291$, $P < 0.05$). (D) Relationships between PRE and RSAF-P under P fertilization in young and middle-aged plantations (no significance).
in changes of nutrient acquisition strategies along an age sequence (Sun et al., 2016; Zhang et al., 2018). However, most previous studies considered the stand age effects on nutrient acquisition strategies in natural conditions, while little was known about its combination with environmental changes. In the current study, we used SEM analysis to explore the direct and indirect effects of stand age on NuRE and RSAF under N and P fertilization. Generally, stand age had positive effects on PRE whether under N or P fertilization, as well as on RSAF-P under N fertilization, which indicated that plant intended to resorb more P from senescing leaves and soil by fine root to deal with strengthening P-limitation during stand development (Zhang et al., 2018; Wang et al., 2019b). Thus, these findings confirmed that stand age mediated the fertilization effects on nutrient acquisition strategies.

CONCLUSION

This study evaluates how N and P fertilization affects nutrient acquisition strategies in M. glyptostroboides plantations with different stand ages of the coastal in China. We found that N fertilization increased NRE, while decreased RSAF-P in young plantations. P fertilization increased NRE and PRE, while decreased RSAF-P in middle-aged plantations. Little synergistic relationships were observed between NuRE and RSAF whether under N and P fertilization, as well as in young and middle-aged plantations. Stand age had positive effects on PRE and RSAF-P, whereas had no effects on the NRE or RSAF-N. These findings provided new insights into the predictions for the facts that how variations in nutrient availability induced by the global change will influence plant nutrient uptake and nutrient conservation strategies.

Please confirm that the Data Availability statement is accurate. Note that we have used the statement provided at Submission. If this is not the latest version, please let us know.
further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

TW and XY designed the project and participated in the manuscript. RS, RT, and GW wrote and revised the manuscript. RS and HZ analyzed the data and constructed the database.

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