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# Patterns of Needle Nutrient Resorption and Ecological Stoichiometry Homeostasis along a Chronosequence of *Pinus massoniana* Plantations

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**Abstract:** Nutrient resorption and stoichiometry ratios are vital indicators to explore nutrient transfer and use efficiency for plants, particularly under the condition of nutrient limitation. However, the changing rules about nutrient resorption and ecological stoichiometry homeostasis are still unclear with the development of plantations. We determined carbon (C), nitrogen (N), and phosphorus (P) concentrations in soil and in fresh and senesced needles along a chronosequence of *Pinus massoniana* plantations (10, 20, 30, and 36 years old) in Guizhou Province, China. We also calculated the N and P resorption efficiency (NRE and PRE, respectively) and the homeostasis coefficient. The results showed that fresh and senesced needles' C and N concentrations maintained an increasing trend, whereas their P concentrations decreased initially and subsequently increased as the plantations' ages increased. Fresh needles' N:P ratios indicated that N limitation existed before 20 years old, while P limitation appeared in the 30-year-old plantations. The NRE and PRE showed patterns of increasing initially and decreasing subsequently along the chronosequence of *P. massoniana* plantations, which was coupled with weak stoichiometric homeostasis to reduce nutrient deficiency. Therefore, the appropriate nutrient management measurements should be induced to promote tree growth and the sustainable development of *P. massoniana* plantations.

**Keywords:** nutrient resorption; nutrient limitation; ecological stoichiometry homeostasis; *Pinus massoniana* plantations

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## 1. Introduction

Carbon (C), nitrogen (N), and phosphorus (P) are vital indicators of nutrient utilisation in trees. Their ecological stoichiometry ratios are closely related to the life histories and adaptation strategies of tree species [1,2]. Generally, nutrient accumulation and the transformation of tree and soil nutrient release often change because of the biotic and abiotic influence during the development of the plantation [3,4]. These variations in N and P concentrations in trees and soil often lead to the nutrient limitation of tree individuals within the background of the long growth cycle and the dynamic understory habitats [5,6]. According to previous reports, N and P limitations often happen because of insufficient nutrient supply in young and ageing forests, respectively [7–9]. Inevitably, these situations would have substantial effects on tree biomass accumulation and timber yield [10]. Hence, clarifying these effects will further strengthen the understanding of the adaptability of plantations under nutrient changes.

Ecological stoichiometry focuses on analysing the balance of chemical elements in ecological interactions [11]. To date, this related theory has been widely used to explain the relationship and feedback between plants and the environmental factors in the ecological system [12,13]. Leaf N:P ratios are acknowledged to be indicators of N or P limitation for plant growth. For example, N or P limitation occurred at the N:P < 14 or >16 for plant leaves, respectively [14]. Simultaneously, soil nutrient state and fertiliser supply capacity affect plant nutrient and growth characteristics. For one plant species, the values of its stoichiometry usually maintain a relatively constant composition regardless of the change in environmental factors, which is called stoichiometric homeostasis [15,16]. At present, these patterns have been discovered in many kinds of woody plants [17]. However, stoichiometric homeostasis may have different thresholds in various environments, including different growth stages in plants [18,19].

Nutrient resorption from ageing tissues is an important approach for plants to accumulate nutrient elements and optimise their use efficiency, which make them less dependent on soil nutrients to maintain stoichiometric homeostasis [15]. Hence, plants have greater N or P resorption efficiency (NRE/PRE, respectively) once N/P limitation occurs [20]. In addition to soil nutrient status, studies have reported that nutrient resorption efficiency (NuRE) could also be affected by fresh leaf and litter nutrients [21], leading to various patterns in response to different-age stands [17]. Many researchers found that NuRE presented a negative correlation with soil nutrients [22,23]. On the contrary, some studies reported that plants growing in infertile soil did not always show higher NuRE [24,25]. These results indicate that NuRE with plantation development and the correlations with stoichiometry and homeostasis are still uncertain. Therefore, clarifying the pattern of nutrient resorption and ecological stoichiometry homeostasis along a chronosequence of plantations is necessary.

*Pinus massoniana* is a pioneer afforestation species and the main timber tree species in South China, covering about one million hm$^2$ of afforestation area. *P. massoniana* plays an extremely important role in China's timber production and forest ecosystem service function [26]. Usually, the mature age of *P. massoniana* plantations is about 40 years in south of China. However, their rotation period could be from 20 to 25 years based on the different purpose of utilization and to maximize economic benefit. In recent years, the productivity and economic value of *P. massoniana* plantations have attracted much attention. For example, the earlier, pure *P. massoniana* plantations have begun to degenerate because of the simple community structure, the growth rate and timber productivity, and soil fertility reduction and acidification [27–29]. Previously, the majority of experiments on the ecological stoichiometry of *P. massoniana* plantations were carried out only at one growth stage [30], which made the nutrient dynamic and limitation status along a chronosequence of *P. massoniana* plantations unclear. Therefore, we measured the needle and soil total organic C, N, and P concentrations and calculated their stoichiometric ratios, including needle nutrient resorption in *P. massoniana* plantations across a chronosequence of 10- (young), 20- (middle-aged), 30- (near-mature), and 36-year-old (mature) stands in Guizhou Province, China. The aim was to illustrate the patterns of nutrient resorption and stoichiometric homeostasis along a chronosequence of *P. massoniana* plantations. Based on this, we want to verify two hypotheses: (i) NuRE would increase along the chronosequence of the *P. massoniana* plantation because nutrient demand may increase with tree growth, and (ii) NuRE would present a negative relationship between soil and needle nutrients to conserve nutrients for trees.

## 2. Materials and Methods

### 2.1. Study Site

A description of this study site (Figure 1) can be found in the study by Pan et al., 2021 [26]. The soil belongs to the alfisols type (the acidic siliceous yellow soil) and has moderate fertility, with a soil depth of 60–80 cm. The earliest local vegetation was a *P. massoniana*, *Pinus armandii,* and broadleaf tree (*Populus davidiana* and *Quercus fabri*) artificial forest, which was established as a pure forest of *P. massoniana* in the 1980s.

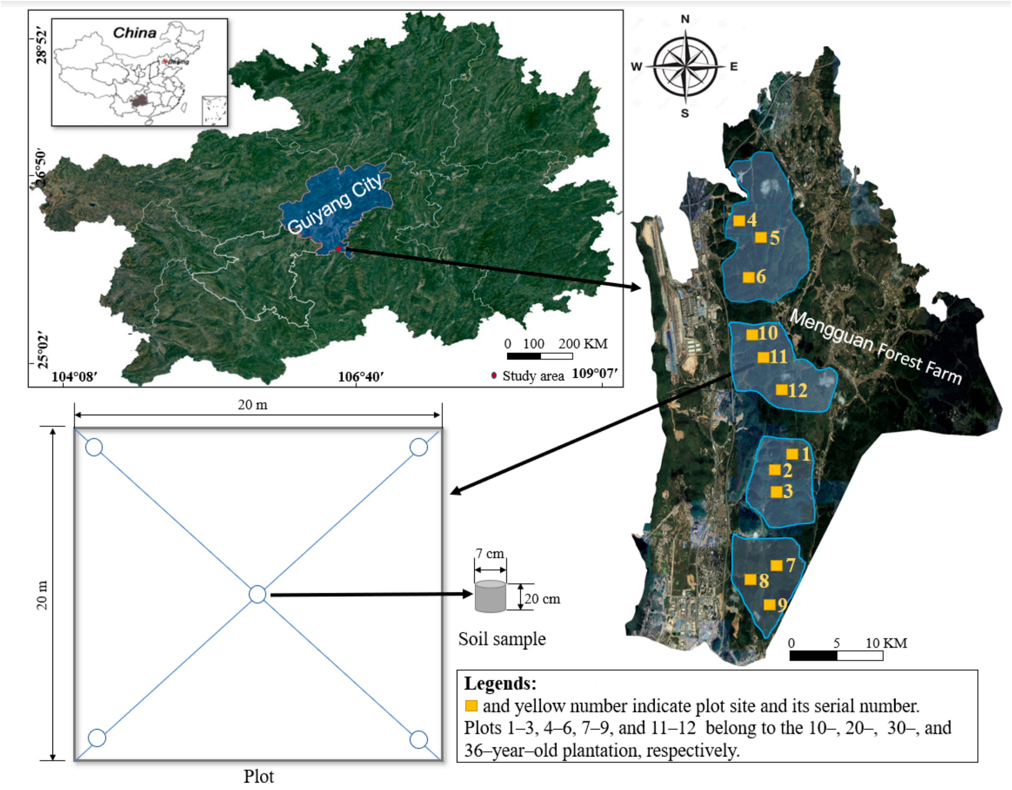

**Figure 1.** Location of Mengguan Forest Farm study area in Guizhou, China and soil sample distribution in each sample plot.

### 2.2. Experimental Design and Sample Collection

We selected four age classes (10, 20, 30, and 36 years old) of *P. massoniana* plantations as the research objects and carried out the preliminary investigation in August 2017. The four aged plantations were established in 2007, 1997, 1987, and 1981, respectively, with a plant/row distance of 1 m × 2 m. They were tended (irrigation and weeding) and managed (insect control and grazing prohibition) only in the first 3 years after afforestation. The first and the second thinning were conducted with 30% of trees being removed 10 and 20 years after establishment, respectively, and a density of approximately 1500 trees·ha$^{-1}$ was kept. Three typical 20 m × 20 m replicated sample plots were established within each of the same age plantations. All plots were on relatively flat topography as well as similar soil type, altitude, and climate conditions as much as possible (Table 1). Within each plot, the tree height, diameter at breast height (DBH), canopy, and others were measured and recorded. Meanwhile, three well-growing individuals were selected according to the average DBH, with a >10 m distance between any two sample trees, and were labelled.

**Table 1.** Characteristics of *Pinus massoniana* plantations along a chronosequence.

| Plantation Age | 10 Years Old | 20 Years Old | 30 Years Old | 36 Years Old |
|---|---|---|---|---|
| Altitude/m | 1194 ± 6.4 | 1175 ± 8.3 | 1206 ± 8.5 | 1214 ± 9.2 |
| Canopy density | 0.90 ± 0.07 | 0.85 ± 0.10 | 0.75 ± 0.09 | 0.80 ± 0.08 |
| Stand density/(trees·ha$^{-1}$) | 4675 ± 256 | 2812 ± 135 | 1356 ± 103 | 1083 ± 94 |
| Mean diameter at breast height (DBH)/cm | 8.53 ± 1.56 | 12.66 ± 2.55 | 18.46 ± 3.01 | 21.26 ± 5.26 |
| Mean tree height/m | 7.43 ± 1.83 | 15.64 ± 2.74 | 18.94 ± 2.43 | 19.87 ± 3.26 |

Note: each value denotes the mean (±SD).

Fresh (1- and 2-year-old matured leaves) and senesced needles from the same tree were sampled in August and September 2017, respectively, during vigorous growth and peak abscission. Twelve branches in the middle sun-exposed crown from the labelled individual were cut down and sampled in approximately equal quantities of 1- and 2-year-old-matured fresh needles, respectively, and mixed to form a single sample. The senesced needles were also collected from the same branches and mixed to form a litter needle sample. In the laboratory, all the samples were dried for 48 h at 65 °C and powderised using a mechanical grinder for chemical measurement.

Belonging to the shallow-rooted trees, the majority of *P. massoniana* fine roots were distributed in the topsoil layer [31]. Thus, soil samples were taken from the 0–20 cm soil layer in each sample plot (Figure 1). After clearing the surface plant litter, five soil samples were collected using the five-point method. A total of 60 soil samples were obtained from the 4 age stands.

### 2.3. Chemical and Physical Measurements

Fresh and senesced needles were ground with ball mill equipment (HM2L, Shandong, China) for chemical determination. Soil samples were also air-dried indoors and sieved (2 mm mesh) for chemical measurements. The total C of all the samples was determined using the $K_2Cr_2O_7$ oxidation method, and their total N concentrations were determined with the Kjeldahl method using a Kjeldahl autoanalyser (GK–600P, Shandong, China) [32]. The total P concentrations of the needles and soil samples were determined with the colourimetry method using a spectrophotometer (V–5600, Shanghai, China). Soil available N (AN) and available P (AP) concentrations were analysed using the alkali diffusion and colourimetric methods, respectively [33]. Each needle and soil sample was divided into three parts equally as three duplicate samples for chemical determination.

### 2.4. Calculations

NuRE was calculated using the formula of Vergutz et al. [34] as follows:

$$\text{NuRE} = \left( \frac{(Nu_{\text{g}} - Nu_{\text{s}}) \times \text{MLCV}}{Nu_{\text{g}}} \right) \times 10 \tag{1}$$

where the mass loss correction value (MLCV) was 0.745 for conifers [34], and $Nu_{\text{g}}$ and $Nu_{\text{s}}$ represented the nutrient concentrations in all age classes of fresh needles and senesced needles, respectively.

The homeostatic coefficient (H) was calculated using the method of Sterner and Elser [35], which was derived from the following model:

$$\text{y} = \frac{1}{\text{H}} \times \log\text{x} + \text{B} \tag{2}$$

where y is the concentration of N, P, or N:P ratio in the fresh needles of *P. massoniana* samples, respectively, whereas x is the corresponding value in soil. Mean N and P concentrations and the N:P ratio of the 0–20 cm soil layers were calculated, which were used as soil values. B and H values were calculated through a linear regression analysis. For the convenience of statistics, the slope (1/H with a value ranging from 0 to 1) was used to measure the homeostasis degree. According to Person et al. [15], homeostasis was divided into four patterns based on the values of 1/H, which were stability (the value ranges from 0 to 0.25), weak stability (the value ranges from 0.25 to 0.5), weak sensitivity (the value ranges from 0.5 to 0.75), and sensitivity (the value ranges from 0.75 to 1), respectively.

### 2.5. Statistical Analysis

C, N, and P stoichiometric ratios of all the samples were calculated using the mass ratios. One-way analysis of variance was used to compare the significant differences in soil total organic C, N, and P concentrations and NuRE along a chronosequence of *P. massoniana* plantations. A two-sample *t*-test was used to analyse the differences between NRE and PRE under the same-age plantation. Linear or quadratic regression was conducted to determine the relationships between plantation age and needle C, N, and P concentrations and their stoichiometric ratios, including NRE:PRE ratios. Covariance analysis was used to test the significant differences in the slopes of stoichiometry between fresh and senesced needles, including the slopes of stoichiometric homeostasis in all-aged plantations. Pearson's correlations were used to test the relationships between NuRE and nutrient concentrations of the needles and soil. All the statistical analyses were conducted with SPSS 24.0 (SPSS Inc., Chicago, IL, USA) for Windows, and all the figures were plotted with Origin 2022b (Microcal Inc., Northampton, MA, USA).

## 3. Results

### 3.1. Soil C, N, and P Concentrations and Their Stoichiometric Ratios

Soil C, N, and P concentrations and their stoichiometric ratios presented different change trends along a chronosequence of *P. massoniana* plantations (Table 2). C and AP concentrations and the AN:AP ratios all tended to increase with increasing plantation age. N and AN concentrations and the C:P ratio decreased initially and subsequently increased, with their lowest values appearing in the 20-year-old plantation. On the contrary, the P concentration and C:N ratio increased initially and then decreased, and both reached the highest values in the 20-year-old plantation.

**Table 2.** Soil main element concentrations and their stoichiometric ratios along a chronosequence of *P. massoniana* plantations.

| Nutrition Indexes | 10 Years Old | 20 Years Old | 30 Years Old | 36 Years Old |
|---|---|---|---|---|
| C (g·kg$^{-1}$) | 9.98 ± 1.89 b | 9.48 ± 1.24 b | 11.58 ± 1.50 a | 11.85 ± 1.14 a |
| N (g·kg$^{-1}$) | 1.95 ± 0.34 b | 1.51 ± 0.22 c | 2.32 ± 0.28 a | 2.37 ± 0.24 a |
| P (g·kg$^{-1}$) | 0.38 ± 0.05 b | 0.49 ± 0.04 a | 0.24 ± 0.04 c | 0.21 ± 0.05 c |
| C:N | 5.87 ± 0.34 b | 6.63 ± 0.25 a | 5.87 ± 0.26 b | 5.45 ± 0.31 c |
| C:P | 28.88 ± 7.36 b | 20.09 ± 5.20 c | 48.09 ± 5.09 a | 43.89 ± 5.87 a |
| N:P | 5.86 ± 1.41 c | 2.24 ± 1.11 d | 9.45 ± 1.43 a | 7.93 ± 1.26 b |
| AN (mg·kg$^{-1}$) | 12.96 ± 1.76 b | 11.04 ± 1.90 c | 13.62 ± 1.73 b | 15.35 ± 2.38 a |
| AP (mg·kg$^{-1}$) | 7.14 ± 0.93 a | 1.41 ± 0.22 b | 1.79 ± 0.13 b | 1.59 ± 0.14 b |
| AN:AP | 4.55 ± 0.78 c | 8.81 ± 1.20 b | 8.52 ± 0.76 b | 10.03 ± 0.79 a |

Note: Parameters include organic carbon (C); nitrogen (N); phosphorus (P); available nitrogen (AN); and available phosphorus (AP). Each value denotes the mean (±SD). Different lowercase letters represent differences among different stand ages under the same nutrition indexes ($p < 0.05$).

### 3.2. Needle C, N, and P Concentrations and Their Stoichiometric Ratios

The fresh- and senesced-needle C concentrations revealed a linear increasing trend along the chronosequence of *P. massoniana* plantations, ranging from 411.43 to 472.21 mg·g$^{-1}$ and from 368.02 to 451.13 mg·g$^{-1}$, respectively (Figure 2a). Meanwhile, both N concentrations increased quadratically from 11.42 to 18.45 mg·g$^{-1}$ and from 7.44 to 11.23 mg·g$^{-1}$, respectively (Figure 2b). In addition, both P concentrations tended to drop initially and subsequently rise along the chronosequence (Figure 2c). Fresh needle C:N ratios tended to decrease with increasing plantation age, whereas they increased initially and decreased subsequently in the senesced needles (Figure 2d). Generally, the fresh needle C:P ratios showed a trend of first decreasing and then increasing, which was opposite to the senesced needles (Figure 2e). Synchronously, the fresh- and senesced-needle N:P ratios increased along the chronosequence, whereas the fresh needle N:P ratios maintained the higher values before the approximately 23-year-old plantation, and then were exceeded by the senesced needles (Figure 2f).

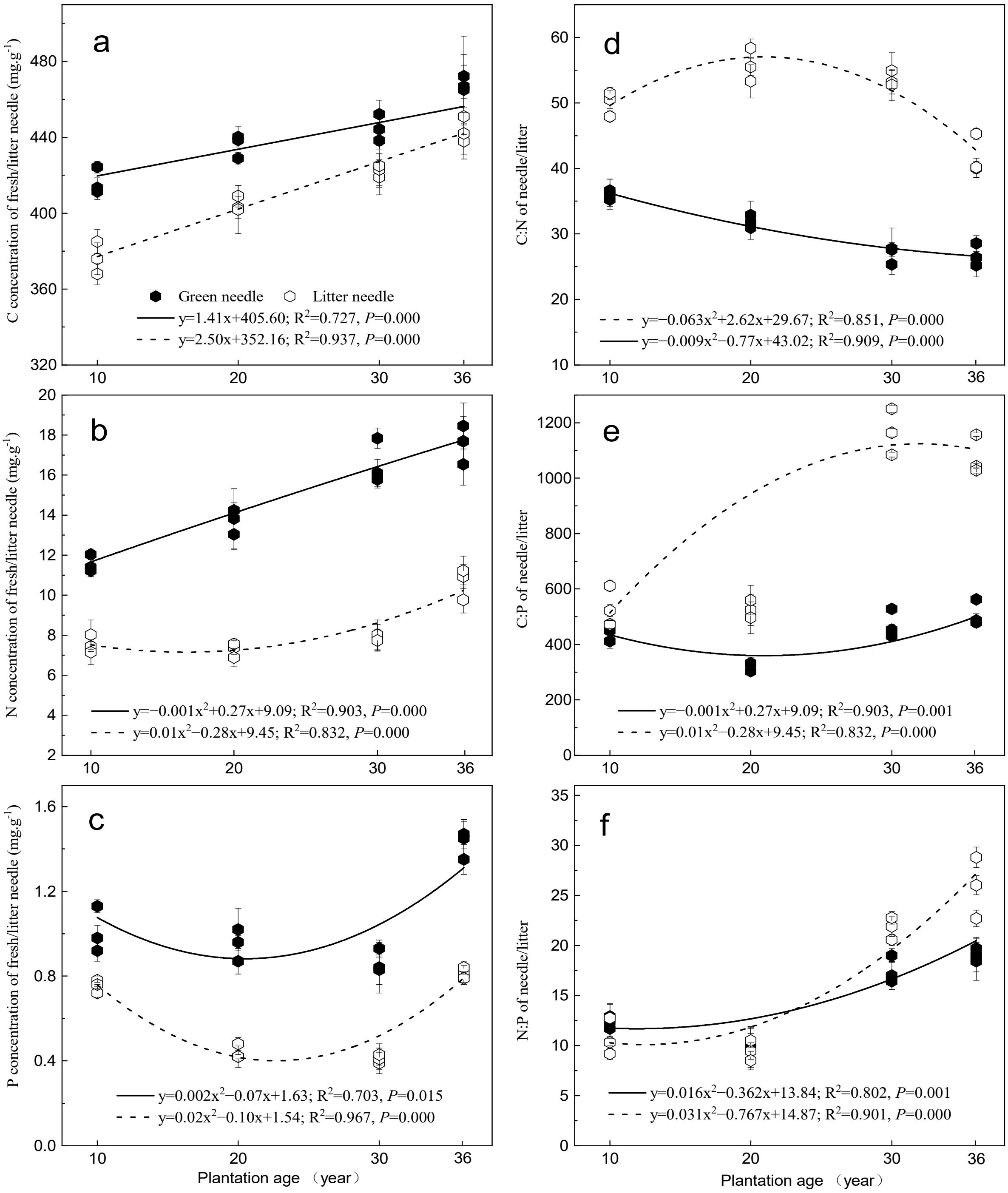

**Figure 2.** Fresh and senesced needles' C, N, and P concentrations (**a**–**c**) and their stoichiometry ratios (**d**–**f**) along the chronosequence of *P. massoniana* plantations.

### *3.3. Needle NuRE and Their Relationships with Soil Stoichiometry*

As shown in Figure 3a, the NRE and PRE exhibited the same change trend, which continually increased from the 10- to 30-year-old stage and then decreased in the 36-year-old stage. However, the NRE was higher than the PRE before the 20-year-old plantations, whereas it was the opposite after 30-year-old stages. NRE:PRE ratios showed a rapid decrease along the chronosequence of *P. massoniana* plantations (Figure 3b). The NRE was significantly negatively correlated with the senesced-needle N concentration (Table 3). However, the PRE was positively correlated with C concentrations and C:N ratios in the fresh needles, the ratios of C:P and N:P in the senesced needles, and the AN:AP ratio in the soil. Undoubtedly, the PRE was negatively correlated with the P concentration in the senesced needles, including the soil AP concentration (Table 3).

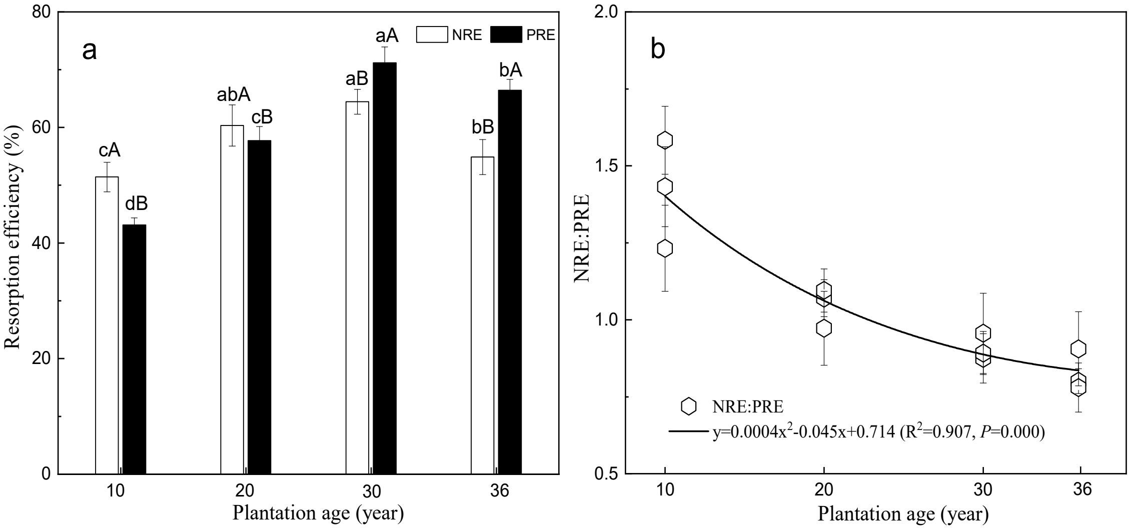

**Figure 3.** Resorption efficiency of N and P (**a**) and their ratios (**b**) in fresh and senesced needles along the chronosequence of *P. massoniana* plantations. Different capital letters represent differences between fresh and senesced needles in the same-age plantations, respectively ($p < 0.05$). Different lowercase letters represent differences amongst fresh or senesced needles along the chronosequence, respectively ($p < 0.05$).

**Table 3.** Pearson correlations between nitrogen/phosphorus resorption efficiency and element concentrations, and their stoichiometric ratios in needles and soil.

| Factors | Items | Pearson Correlations | |
|---|---|---|---|
| | | **NRE (*p* Value)** | **PRE (*p* Value)** |
| Fresh needle | C | | 0.866 ** (0.000) |
| | C:N | | 0.921 ** (0.000) |
| Senesced needle | P | | −0.790 ** (0.002) |
| | N | −0.615 * (0.033) | |
| | C:P | | 0.834 ** (0.001) |
| | N:P | | 0.756 ** (0.004) |
| Soil | AP | −0.665 * (0.018) | −0.777 * (0.003) |
| | AN:AP | | 0.769 ** (0.003) |

Note: Parameters include organic carbon (C); nitrogen (N); phosphorus (P); available nitrogen (AN); available phosphorus (AP); NRE (nitrogen resorption efficiency); and PRE (phosphorus resorption efficiency). Only the items with significant correlations are shown in this table. The value shows the correlation coefficient; positive values represent positive correlation and negative values represent negative correlation. * $p < 0.05$, ** $p < 0.01$.

### 3.4. Pattern of Needle Stoichiometric Homeostasis

The slopes (1/H) of linear regression relationships between the fresh needle and soil for N, P, and N:P ratios were 0.019, 0301, and 0.287, respectively (Figure 4). These results indicated that the homeostatic adjustment existed in N and P concentrations along the chronosequence of *P. massoniana* plantations. Comparatively, the N concentration had a stronger ability of homeostatic adjustment than the P concentration and N:P ratio during the development of *P. massoniana* plantations (Figure 3a).

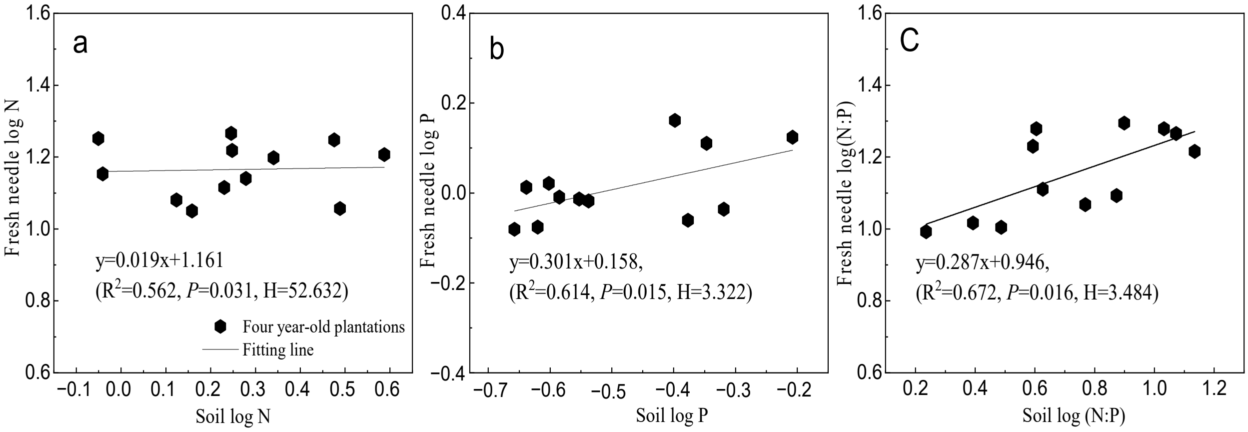

**Figure 4.** Line regression relationships between fresh needle and soil for N concentrations (**a**), P concentrations (**b**), and N:P ratios (**c**) along the chronosequence of *P. massoniana* plantations.

## 4. Discussion

### *4.1. Changes in Soil C, N, and P Concentrations along a Chronosequence*

In this research, soil C, N, and P concentrations showed significant fluctuation along the chronosequence of *P. massoniana* plantations. The previous researcher indicated that soil C concentration mainly depended on the quantity of organic matter and the size of the soil humus [36]. We observed the increasing C concentration in the soil, and this pattern was in agreement with some previous results [18,23,37]. The researchers also found that decaying plant litter would provide approximately 58% of the source of N in plantation ecosystems [38]. As we know, 30% of trees were removed during the 10 and 20 years of the plantations in this study area, which made the amount of litter decrease dramatically. This case greatly limited the input of topsoil nutrients, particularly the N element [39]. As is known, soil P transformation is mainly regulated by biochemical mineralisation under abiotic factors [40,41]. Here, we also found that the soil P concentrations quickly increased (Table 2) in plantations before year 20. Thus, the thinning was responsible for this change. After the thinning, more sunshine reaching the understory made the surface soil temperatures increase and accelerated the rate of P mineralisation. Eventually, this led to the P accumulation and concentration increasing in the soil.

### *4.2. Changes in Nutrient Limitation and Nutrient Resorption Efficiency along a Chronosequence*

The C, N, and P concentrations in fresh and senesced needles also showed significant correlations along the chronosequence of *P. massoniana* plantations. The C and N concentrations in the two kinds of needle also maintained the increasing trend along the chronosequence. Similar results have been reported in *C. lanceolata* [18] and *Larix kaempferi* [42]. Obviously, the senesced needle would transfer the N element to the fresh needle for the nutrient resorption strategy. The increasing NRE before the age of 30 years old also supported our opinion. The decreasing soil N concentration portended the N limitation appearing during the development process of the plantation, which was demonstrated further by the lower N:P ratio of 14 in the fresh needles (Figure 2f).

The P concentrations in the fresh needles showed that the changing trend decreased initially and then increased along the chronosequence of *P. massoniana* plantations. Lower P concentrations of the fresh and senesced needles were observed in the 20-year-old plantation. This case may be caused by the high demand for N in the early stage of plantations, which inhibited the uptake of the P element to some degree. After the 20-year-old stage, the demand for P increased rapidly with the further development of plantations. Generally, we found a higher N:P ratio of 16 after the age of 30 years old in plantations (Figure 2f), which indicated the appearance of a P limitation during this period. Based on the theory of the plant nutrient utilisation hypothesis [19], we also observed that *P. massoniana* continually maintained the increasing PRE to relieve the P deficiency until the age of 30 years old. However, the PRE began to decrease after the age 30 years old (Figure 3a).

Evidently, this study indicated that the NRE and PRE were contrary to our first hypothesis. This phenomenon could be caused by the growth variations in *P. massoniana* individuals at different ages. That is, NRE and PRE maintained the increasing trend until the plantation age reached 30 years old, which also illustrated that the increasing nutrient element resorption significantly improved the N and P concentrations of plants to promote tree growth. After 30 years, the *P. massoniana* plantations had rich understory soil and a developed root system, which could obtain more nutrients from the soil and reduce the nutrient utilization from senesced needles (Table 1). Meanwhile, as an effect of the natural closure of the canopy as the trees grew, the light intensity reaching the interior of the tree canopy was reduced. This shade condition sped up the senescence of needles, which shed from the tree earlier, shortening the time for nutrient transfer from the senesced leaves. Hence, the reducing NRE and PRE appeared after 30 years in the *P. massoniana* plantations.

This case was confirmed by the growth rhythm of *P. massoniana* plantations. According to Table 1, the mean DBH of *P. massoniana* individuals increased quickly before the 30-year-old plantations, and then slowly. Meanwhile, the DBH increment quickly increased until the 20-year-old plantation and tended to decrease gradually. Similar growth patterns have been reported about *P. sylvestris* var. *mongolica* [23], *Pinus tabulaeformis* [37], and *Robinia pseudoacacia* [43] along the chronosequence. Subsequently, the NRE and PRE decreased with plantation development after the 30-year-old stage, and a growing number of N and P elements in senesced needle were returned to the soil.

### *4.3. Interrelationship of Needle Nutrient Utilization, Stoichiometry, and Homeostasis*

The C and N concentrations in fresh and senesced needles all increased along a chronosequence (Figure 2a,b), which may have been caused by the accumulation of C structural compounds as the trees grew. Generally, a higher C concentration in the needles had a stronger self-protection ability [44], indicating that *P. massoniana* individuals obtained a strong resistance with increasing stand age in the plantation systems. Simultaneously, the increasing C concentration and C:N ratio in fresh needles could significantly improve the vegetative growth of *P. massoniana* and the PRE (Table 3). Generally, higher N concentrations and N:P in the senesced needles improve litter decomposition rates and nutrient release, which is helpful in enhancing soil nutrient availability and easing plant nutrient limitation [21]. As shown in Figure 2f and Table 3, the N limitation disappeared after the 20-year-old plantations, and soil N concentrations also kept an increasing trend. Evidently, the increasing NRE had a significant negative correlation with the senesced-needle N concentration to conserve nutrients for tree growth with the development of *P. massoniana* plantations, which was consistent with our second hypothesis.

The rapid growth of the young-aged trees requires more P for the composition of the genetic material [45]. Once the soil P concentration is deficient, the plant has to transfer the senesced needle P to a fresh needle [46]. Clearly, the above condition was consistent with our results, which eventually led to an increase in the PRE (Figure 3a). In most cases, the greater NuRE for plants is caused by soil nutrient deficiency [47]. In this study, the same result was found, supported by the negative correlations between the PRE and soil P and AP concentrations (Table 3). The change in the greater NRE and PRE before and after the 20-year-old stage in *P. massoniana* plantations led to the decrease in NRE:PRE ratio, respectively (Figure 3b), which also indicated that relatively more P from the senesced needles was reused along the chronosequence. The above findings were in line with the relative nutrient resorption hypothesis [48,49]. We also observed that *P. massoniana* individuals, in fact, resorbed more N or P elements during the N− or P−limited stage (Figure 2b,c). Generally, the increase in NRE and PRE in the fresh needle and the decreased P and AP concentrations in the soil confirmed our second hypothesis.

In this research, (1/H)N:P and (1/H)P ranged from 0.25 to 0.75 across all the ages of *P. massoniana* plantations (Figure 4c). Based on the homeostatic patterns, *P. massoniana* showed weak homeostasis in P concentration and N:P ratio across all the plantation ages, indicating it had the same stoichiometric characteristic as most subtropical tree species [50]. However, a lower value of (1/H)N ranging from 0 to 0.25 was observed (Figure 4a), which showed that the needle N concentration in *P. massoniana* plantations had stable nitrogenous homeostasis. According to scholars' previous reports, plants with stable stoichiometric homeostasis have an efficient nutrient regulation ability when the soil nutrients do not meet their growth needs, and they are obliged to regulate nutrient composition to store nutrients [51,52]. *P. massoniana* is a fast-growing species in South China, and the rapid biomass and volume increase must be supported by a stable nitrogen supply. The presence of the lower N concentration in soil and the N limitation in fresh needles made plants have to increase the NRE from the senesced needles, which was also consistent with the increasing trend in the NRE before 30-year-old *P. massoniana* plantations. As a whole, the relatively stable stoichiometric homeostasis is one of the adaptive strategies to cope with heterogeneous habitats for plants [53], which could be realised by regulating nutrient resorption from leaves [54].

### *4.4. Inspiration for P. massoniana Plantation Management*

The analysis of the N:P and NRE:PRE ratios in needles and soil along the chronosequence of *P. massoniana* plantations indicated that tree growth might improve the transfer from N to P limitation. Although the P concentration in soil decreased, the PRE maintained an increasing trend along the chronosequence. These results also implied that *P. massoniana* had a certain tolerance to low-P habitats in the earlier stage of the plantation, and a similar characteristic has been reported previously [55]. The soil nutrient concentration was low owing to the thin solum and serious leaching in most of Southern China, particularly N and P deficiency. Therefore, N and P limitations usually occur in artificial forest ecosystems. Similar results have been found in other forests or plantations, such as *C. lanceolata* plantations limited by N and P [2], *Metasequoia glyptostroboides* forests limited by P [56], and Eucalyptus plantations limited by P [57]. Evidently, N and P supplements should also be vital for not only younger but also older plantations. Therefore, introducing mixed tree species will be an effective way to alleviate nutrient demand conflict with the increasing age of artificial plantations. For example, introducing N-fixing tree species improved nitrogen absorption on Eucalyptus plantations [58], and the mixed-species tree plantations could significantly ease or eliminate P limitation in some forest ecosystems [59]. Certainly, the suitable tree species for mixing with *P. massoniana* still require further research in the future. Certainly, efficient fertilisation management strategies could also supply the appropriate means to alleviate nutrient limitations in timber forests.

## 5. Conclusions

In summary, our results found that a synergic relationship between leaf litter and soil in *P. massoniana* plantations. The significant differences in tree nutrient components at different ages suggested that their ecological stoichiometry and nutrient resorption may be flexible. The soil organic C concentration increased with the increasing age of *P. massoniana* plantations, whereas their N and P concentrations presented the opposite fluctuation trend. Generally, the nutrient element accumulation of fresh and senesced needles increased along the chronosequence. N and P limitation existed in *P. massoniana* plantations before the age of 20 years old and after 30 years old, respectively. The patterns of NRE and PRE initially increased and then decreased along the chronosequence of *P. massoniana* plantations, indicating the increasing nutrient element resorption could promote tree growth. The weak stoichiometric homeostasis would improve nutrient utilization during the development process of *P. massoniana* plantations. To ease nutrient limitation, introducing suitable tree species for mixing with *P. massoniana* should be advocated to realise the more effective cultivation of plantations.

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