Biochar Amendment Alters The Nutrient-Use Strategy of Moso Bamboo Under N Additions

Jinpei Gao
Zhejiang Agriculture and Forestry University: Zhejiang A and F University
Quan Li
Zhejiang Agriculture and Forestry University: Zhejiang A and F University
Junbo Zhang
Zhejiang Agriculture and Forestry University: Zhejiang A and F University
Kunkai Cui
Zhejiang Agriculture and Forestry University: Zhejiang A and F University
Zhizhuang Wu
China National Bamboo Research Center
Man Shi
Zhejiang Agriculture and Forestry University: Zhejiang A and F University
Xinzhang Song (songxinzhang@gmail.com)
Zhejiang Agriculture and Forestry University: Zhejiang A and F University https://orcid.org/0000-0003-2434-7466

Research

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Abstract

Background: While we know that N and biochar fertilizers affect soil nutrient concentrations and plant nutrient uptake, our understanding of how combined applications of N and biochar affect plant nutrient resorption in plantations is largely inadequate. A field experiment was conducted to investigate the effects of N (0, 30, 60, and 90 kg N ha^{-1} yr^{-1} or N0, N30, N60, and N90), in combination with biochar (0, 20, and 40 t biochar ha^{-1} or BC0, BC20, and BC40) on N and P resorption by young and mature bamboo plants as well as the relationship between nutrient resorption and leaf nutrient and soil concentrations. Fresh and senescent leaf samples were collected in July 2016 and March 2017, respectively.

Results: Young bamboo showed significantly greater foliar N resorption efficiency (NRE) and P resorption efficiency (PRE) than mature bamboo. N additions alone significantly increased the N resorption proficiency (NRP) and P resorption proficiency (PRP) but decreased the NRE and PRE of both young and mature bamboo. In both the N-free (control) and N addition treatments, biochar amendments significantly reduced the foliar NRE and PRE of young bamboo but had the opposite effect on mature bamboo. Foliar NRE and PRE were significantly correlated with fresh leaf N and P concentrations and soil total P concentration.

Conclusion: Our findings suggest that N addition inhibits plant nutrient resorption and alters the nutrient-use strategy of young and mature bamboo from “conservative consumption” to “resource spending.” Furthermore, biochar amendment enhanced the negative priming effect of N addition on nutrient resorption of young bamboo but reduced the negative effect on that of mature bamboo. This study provides new insights into the combined effects of N and biochar additions on the nutrient resorption of Moso bamboo and may assist in improving fertilization strategies in Moso bamboo plantations.

1. Introduction

Nutrient resorption, a physiological process by which plants reallocate nutrients from senescent structures to other living tissues for later use (Clark 1977; Turner 1977; Yuan and Chen 2015), can improve nutrient utilization (Chapin 1980; Vitousek 1984; Wu et al. 2020) and reduce plant nutrient uptake from the environment (Brant and Chen 2015; Lü et al. 2020; Yuan and Chen 2015). Nutrient resorption is most commonly quantified by nutrient resorption efficiency (RE) and resorption proficiency (RP) (Lü et al. 2020; Wu et al. 2020). Nutrient RE is the difference between the amount of a given nutrient in green versus fully senesced tissue relative to the amount in green tissue, and nutrient RP is the absolute level of nutrients found in senesced leaves (Chang et al. 2017; Killingbeck 1996). N and P resorption play an important role in affecting plant growth (Sterner and Elser 2002), contribute to leaf N and P, and determine plant photosynthesis, reproduction, and physiological processes (Kerkhoff et al. 2006; Koerselman and Meuleman 1996; Tian et al. 2018). Resorption is estimated to supply 31% and 40% of annual plant N and P demands on a global scale, respectively (Cleveland et al. 2013). Changes in nutrient (N and P) supply influence plant nutrient resorption (Chen et al. 2007). however, these findings remain highly controversial (Lü et al. 2020; Yuan and Chen 2015), especially for N addition.

The increase in atmospheric N deposition, mainly derived from burning fossil fuels and by using artificial fertilizers, is an important phenomenon in global climate change (Janssens et al. 2010). The latest research shows that the average annual N deposition in China reached 19.6 ± 2.5 kg N ha^{-1} yr^{-1}, which far exceeded that of Europe and the United States; thus, N deposition rates in China are among the most serious in the world (Yu et al. 2019). High N deposition can change plant N and P resorption by changing the N and P content in plants and soils, which in turn influences the N and P cycles in ecosystems (Du et al. 2016; Farrer et al. 2013; Lü et al. 2020; McNeil et al. 2007; Yuan and Chen 2015; Zhao et al. 2020). A meta-analysis by Yuan and Chen (2015) showed that N enrichment inhibited plant N resorption; however, other studies observed neutral and positive effects on plant N resorption (Li et al. 2010; Lü et al. 2010, 2013, 2020; van Heerwaarden et al. 2003). N addition also promoted (Lü et al. 2013), inhibited (Sardans et al. 2016), and/or had no effect (Lü et al. 2010; Zhang et al. 2017b) on foliar P resorption in forests. However, these studies have only partially observed N or P resorption; few studies have simultaneously considered resorption of both nutrients (N and P) in forests.

Biochar is produced by the pyrolysis of organic matter in a high-temperature and oxygen-limited environment (Antal and Grønli 2003) and is widely applied in forestry ecosystems (Li et al. 2018) for soil amendment (Jeffery et al. 2015). It has a high surface area and high pH and contains various forms of N and P nutrients (e.g., NH_4^+ and ortho-P) (Gul and Whalen 2016). Over the past few decades, most studies have focused on the effects of biochar amendments on soil physical and chemical properties, the soil organic carbon pool, and soil greenhouse gas emissions (Li et al. 2018; Song et al. 2016a). For example, biochar application enhanced soil fertility by increasing soil pH and cation exchange capacity (CEC), thereby increasing soil N and P concentrations (Biederman and Harpole 2013; Chan et al. 2007; Nelson et al. 2011), which affected foliar N and P concentrations (Major et al. 2010; Zhang et al. 2019). However, there are relatively few studies addressing the potential effects of biochar application on plant N and P resorption. By understanding these mechanisms, we can predict potential long-term changes in plant productivity in biochar-amended forests, especially in subtropical plantations where soils are usually acidic.

Moso bamboo (*Phyllostachys edulis*), one of the most economically important bamboo species, is widely distributed in the tropical and subtropical regions of East and Southeast Asia (Song et al. 2011, 2020). In China, it covers an area of 4.68 million hectares, accounting for 73% of the total bamboo forest area in China (Li and Feng 2019). Due to its rapid growth and strong regenerative ability (Song et al. 2016b), Moso bamboo is the main source of non-timber forest products in China (Song et al. 2015) and has a high potential for C sequestration (Song et al. 2017a). The subtropics of China, the main growing region of Moso bamboo, is subjected to high N deposition, with an average rate of 30 kg N ha^{-1} yr^{-1} (Jia et al. 2014), which is expected to continue to increase in the next few decades (Galloway et al. 2008; Liu et al. 2013). Our previous study found that N addition increased foliar N and P concentrations and soil available N (AN) and available P (AP) in Moso bamboo plantations (Li et al. 2016; Song et al. 2016c). In addition, biochar applications significantly increased soil bacterial diversity and decreased soil urease and acid phosphatase activities (Li et al. 2018; Peng et al. 2019). However, the effects of N deposition and biochar amendment on leaf nutrient resorption in Moso bamboo forests are still unclear.

In this study, we applied N and biochar to a Moso bamboo plantation to investigate leaf nutrient resorption by Moso bamboo plants and their responses to N deposition and biochar amendment. The primary hypotheses of this study were the following: (1) N addition reduces foliar nutrient (N and P) resorption due to an increase in soil nutrient availability; (2) biochar amendment reduces foliar nutrient (N and P) resorption due to an increase in soil nutrient availability; and (3) biochar amendment enhances the negative priming effect of N addition on foliar nutrient (N and P) resorption.

2. Materials And Methods

2.1 Study site

The experiment was conducted in the Lin'an District (30°14' N, 119°42' E), Hangzhou City, Zhejiang Province, China. The site has a subtropical monsoonal climate and distinct seasons. Mean annual air temperature and precipitation are 15.6 °C and 1420 mm, respectively. The topography consists of low hills, with an elevation of 100–300 m. The soil is classified as a Ferrosol, and derived from granite (Li et al. 2019).

Moso bamboo has a unique growth pattern. New bamboo shoots usually begin to emerge from the ground in March, and leaves appear in June of the same year. These leaves fall in the next spring, and new leaves quickly emerge. These new leaves have a life span of 2 years and are therefore, replaced biennially in spring (Zhang et al. 2017a). Moso bamboo forests are characterized by alternating high and low recruitment years. The recruitment of Moso bamboo shoots at the study site only occurred during even-numbered years (i.e., 2012, 2014, and 2016). Bamboo trunks are usually harvested after 4 years of growth to maximize economic benefits. Thus, Moso bamboo plantations are unevenly aged forests with leaves covering a 2-year interval (Song et al. 2016c). In our study site, Moso bamboo stands consisted of two growth stages: young bamboo shooting in the spring of 2016 (one-year-old) and mature bamboo shooting in the spring of 2014 (three-year-old). The initial stand and soil characteristics are listed in Table S1 (Li et al. 2018).

2.2 Experimental design

In November 2012, 12 plots of 20 × 20 m were established in the study site. Each plot was surrounded by a 20 m-wide buffer zone to avoid disturbing nearby plots. Based on the method of Fang et al. (2007) and the local N deposition rate of 30 kg ha^{-1} yr^{-1} of Jia et al. (2014), N additions were applied at a low (30 kg ha^{-1} yr^{-1}, N30), medium (60 kg ha^{-1} yr^{-1}, N60), and high (90 kg ha^{-1} yr^{-1}, N90) rate, with a control of 0 kg N ha^{-1} yr^{-1}. These treatments were randomly applied to three replicate plots per treatment. According to the chemical composition (NH_4^+:NO_3^- =1.28) of wet N deposition in China, NH_4NO_3, consisting of a similar composition ratio, was selected as the simulated N source (Song et al. 2017b).

Starting in January 2013, a quantitative NH_4NO_3 solution (10 L) was sprayed evenly on the forest floor of each plot at the beginning of each month for 21 months. The same amount of water (N-free) was sprayed on each control plot in the same manner. In September 2014, following the 21 month-period, two subplots of 10 × 10 m were established in each plot. Biochar (20 and 40 t ha^{-1}, defined as BC20 and BC40) was spread evenly over the ground, and then thoroughly mixed into the top 30 cm of the soil by plowing it. The remaining area inside the plot served as the control with no biochar application (BC0). Each sample plot was separated by an aluminum-plastic plate. All subplots received monthly N additions, as described above. Biochar was produced by pyrolysis of Moso bamboo chips at 600 °C (Yaoshi Coal Industry Co. Ltd., Hangzhou, China). The main characteristics of the biochar were the following: pH (H_2O) = 9.67; bulk density = 0.53 g cm^{-3}; CEC = 14.9 cmol kg^{-1}; carbon content = 81.73%; N content = 0.57%; and C/N ratio = 143.4.

2.3 Leaf N and P concentrations

We collected fresh leaf samples in July 2016 and senescent leaf samples in March 2017. Following the sampling methods of Song et al. (2020), three representative young Moso bamboo plants, with shoots emerging in April 2016, and three representative mature Moso bamboo, with shoots emerging in April 2014 were selected for sampling in each plot. Twenty healthy leaves on the south-facing side in the mid-upper canopy were collected from the 1-year-old and 3-year-old selected Moso bamboo plants. The leaf samples were transported to the laboratory in insulated cases at 4 °C. Samples were dried at 105 °C for 30 min, and then dried at 65 °C to a constant weight. Oven-dried leaves were milled for analysis of the N and P concentrations. Foliar N concentration was measured using an automatic CN analyzer (Sumigraph NC-80, Shimazu, Japan). Foliar P concentration was measured using the molybdenum antimony anti-colorimetric method (Lu 2000).

Leaf nutrient RE (%) was calculated for NRE and PRE using the following equation:

$$RE\ (\%) = (1 - MLCF * [Nutrient]_{senescent} / [Nutrient]_{green}) \times 100$$

where $[Nutrient]_{senescent}$ and $[Nutrient]_{green}$ are the concentrations of the nutrients in senesced leaves (March 2017) and green leaves (July 2016), respectively. MLCF is the mass loss correction factor that accounts for the mass loss occurring during leaf senescence (Vergutz et al. 2012), calculated according to the ratio of the dry mass of 50 senesced leaves and 50 green leaves with three replications in each treatment (Table S2). Nutrient RP was quantified as the nutrient concentrations of N (NRP) and P (PRP) (Killingbeck 1996).

2.4 Soil nutrients

Six surface soil cores (0–20 cm) were collected randomly from each plot and mixed together to form a soil sample in March 2017. The samples were kept in a thermotank, transported to the laboratory, and then sieved through a 2-mm mesh to remove the roots, plant residues, and stones. The samples were air-dried and then used for analysis of soil nutrient concentrations.

Soil pH was measured using a pH meter (FE20, Mettler Toledo, Switzerland) after shaking a soil water (1:2.5 w/v) suspension for 30 min (Lu 2000). Soil total N (TN) concentration was measured using an automatic CN analyzer (Sumigraph NC-80, Shimazu, Japan). Soil available N (AN) concentration was determined using the alkaline-$KMnO_4$ method (Patrick 1964). Soil total P (TP) concentration was determined by colorimetric analysis using a modified Kjeldahl method (Song et al. 2016c). Soil available P (AP) concentration was determined using the molybdenum blue method (Watanabe and Olsen 1965).

2.5 Statistical analysis

One-way ANOVA and least significant difference (LSD) multiple comparisons were used to determine significance differences in foliar N and P concentrations, N:P ratios, NRE, PRE, NRE:PRE ratios, and soil properties among the N and biochar addition treatments. Three-way ANOVA was used to analyze the interactions between N and biochar additions, and the effect of bamboo age on foliar N and P concentrations, N:P ratios, NRE, PRE, and NRE:PRE ratios. All data were checked for normality and homogeneity of variance before testing for treatment differences. Pearson correlation analysis was performed to test for correlations between leaf N and P concentrations, N:P ratio, NRE and PRE, and soil properties. All statistical analyses in this study were conducted using the SPSS 22.0 software package for Windows (SPSS Inc., Chicago, IL, USA).

3. Results

3.1 Soil physical and chemical properties

Compared to the control, N additions alone significantly decreased soil pH and AN:AP ratio but significantly increased TN, TP, and AP concentrations (Table 1). Soil pH, TN, TP, AN, and AP concentrations and AN:AP ratios were significantly higher in the biochar treatments than in the control (Table 1). Soil TN, AN, and AP concentrations and AN:AP ratios were significantly higher in the combined N (N30, N60, and N90) and biochar (BC20 and BC40) treatments than in the N addition alone.

Table 1
Soil physical and chemical properties in experimental plots in a Moso bamboo forest treated with different N (N0, N30, N60, and N90 is 0, 30, 60, and 90 kg N ha^{-1} yr^{-1}, respectively) and biochar (BC0, BC20, and BC40 is 0, 20, and 40 t biochar ha^{-1}) applications.

Treatment	pH	TN ($g \cdot kg^{-1}$)	TP ($g \cdot kg^{-1}$)	AN ($mg \cdot kg^{-1}$)	AP ($mg \cdot kg^{-1}$)	AN:AP ratio
N0 + BC0	4.667 ± 0.031bA	1.273 ± 0.052cD	0.412 ± 0.006bD	57.400 ± 2.090cB	13.545 ± 0.243cC	4.240 ± 0.230cA
N0 + BC20	4.750 ± 0.020a	1.998 ± 0.049b	0.490 ± 0.004a	202.113 ± 4.277b	19.304 ± 0.751a	10.478 ± 0.379b
N0 + BC40	4.773 ± 0.025a	2.281 ± 0.052a	0.487 ± 0.001a	219.847 ± 14.023a	16.004 ± 0.115b	13.736 ± 0.853a
N30 + BC0	4.443 ± 0.031cB	1.526 ± 0.031cC	0.653 ± 0.005aA	40.527 ± 1.901bD	18.368 ± 0.785cA	2.209 ± 0.129cC
N30 + BC20	4.577 ± 0.050b	1.919 ± 0.014b	0.439 ± 0.009c	203.980 ± 4.850a	20.354 ± 0.257b	10.021 ± 0.171a
N30 + BC40	4.660 ± 0.020a	2.128 ± 0.062a	0.541 ± 0.033b	207.247 ± 0.808a	31.838 ± 0.577a	6.511 ± 0.113b
N60 + BC0	4.297 ± 0.057bC	1.978 ± 0.034cA	0.473 ± 0.016cC	65.806 ± 0.562cA	18.941 ± 0.373cA	3.475 ± 0.049cB
N60 + BC20	4.393 ± 0.042ab	2.378 ± 0.043a	0.662 ± 0.033a	206.313 ± 3.233a	40.788 ± 0.656a	5.058 ± 0.052b
N60 + BC40	4.463 ± 0.051a	2.149 ± 0.018b	0.540 ± 0.003b	186.713 ± 2.139b	22.504 ± 1.097b	8.307 ± 0.326a
N90 + BC0	4.303 ± 0.065bC	1.736 ± 0.037bB	0.610 ± 0.023aB	50.376 ± 1.802cC	16.203 ± 1.283cB	3.126 ± 0.324cB
N90 + BC20	4.383 ± 0.025ab	1.968 ± 0.068a	0.492 ± 0.025c	174.113 ± 3.233b	19.671 ± 0.501b	8.858 ± 0.383a
N90 + BC40	4.473 ± 0.065a	2.041 ± 0.069a	0.550 ± 0.008b	181.113 ± 3.523a	38.438 ± 0.150a	4.712 ± 0.103b

TN, soil total nitrogen; TP, soil total phosphorus; AN, soil available nitrogen; AP, soil available phosphorus.

Capital letters indicate a significant difference between different N addition treatments in the BC0 treatment at the 0.05 level. Lowercase letters indicate a significant difference between different biochar treatments in the same N addition treatment at the 0.05 level.

3.2. Fresh leaf N and P concentrations

In the control treatment, fresh leaf N and P concentrations in young bamboo were significantly higher than those in mature bamboo (Fig. 1). Compared to the control, a high N addition (N90) significantly increased fresh leaf N and P concentrations in young bamboo but decreased these in mature bamboo (Fig. 1). Biochar amendment alone significantly increased fresh leaf N and P concentrations in young bamboo (Fig. 1a, c), and significantly decreased fresh leaf P concentration in mature bamboo (24.6–38.8%, Fig. 1d). In the N90 treatment, biochar amendment significantly increased fresh leaf N and P concentrations in young bamboo, while that in mature bamboo showed the opposite trend (Fig. 1). Three-way ANOVA indicated that the age of bamboo, N addition, and biochar amendment significantly affected fresh leaf N and P concentrations in young and mature bamboo, both independently and when combined (Table S3).

3.3 Nutrient resorption proficiency

The NRP of young bamboo was higher than that of mature bamboo under the N-free (control) treatment, while the PRP showed the opposite trend (Fig. 2). Compared to the control, N addition alone significantly increased the NRP and PRP of young bamboo (25.0–60.2% and 42.7–108.1%, respectively) and mature bamboo (25.4–49.0% and 8.7–13.0%, respectively) (Fig. 2a, c). Compared to the control, biochar amendment alone significantly increased the NRP and PRP of young bamboo (69.5–79.0% and 71.9–84.1%, respectively) (Fig. 2a, c) but significantly decreased the NRP and PRP of mature bamboo (7.11–11.82% and 30.5–51.5%, respectively) (Fig. 2b, d). Foliar NRP and PRP of young bamboo were significantly higher in the combined N addition (N30, N60, and N90) and biochar amendment (BC20 and BC40) treatments than in the treatments with N addition only (Fig. 2a, c), while that of mature bamboo showed the opposite trend (Fig. 2b, d). Three-way ANOVA indicated that the age of bamboo, N addition, and biochar amendment significantly affected the NRP and PRP of young and mature bamboo both independently and when combined (Table S3).

3.4 Nutrient resorption efficiency

Foliar NRE and PRE of young bamboo were significantly higher than those of mature bamboo under the N-free (control) treatment, while the NRE:PRE ratio showed the opposite trend (Fig. 3). Compared to the control, N addition alone significantly decreased foliar NRE and PRE of young bamboo (17.5–40.6% and 22.3–42.4%, respectively) and mature bamboo (32.3–51.0% and 20.2–25.3%, respectively) (Fig. 3). Biochar amendment alone significantly decreased the NRE and PRE of young bamboo (42.6–55.8% and 28.2–39.6%, respectively) but significantly increased that of mature bamboo (8.1–12.0% and 17.8–43.8%, respectively) relative to the control. Foliar NRE and PRE of young bamboo were significantly lower in the combined N addition (N30, N60, and N90) and biochar amendment (BC20 and BC40) treatments than in the N addition treatments alone (Fig. 3a, c), whereas mature bamboo showed the opposite trend (Fig. 3b, d). Compared to the control, N addition (N30 and N60) significantly increased the NRE:PRE ratio of young bamboo (6.3–15.1%; Fig. 3e) but significantly decreased that of mature bamboo (14.8–34.4%; Fig. 3f). Compared to the control, biochar amendment significantly decreased the NRE:PRE ratio of young and mature bamboo (Fig. 3e, f). In the N30 treatment, BC40 significantly decreased the NRE:PRE ratio of young bamboo by 15.2% (Fig. 3e). In the N60 treatment, BC40 significantly increased the NRE:PRE ratio of young bamboo by 10.8% (Fig. 3e). Foliar NRE:PRE ratio of mature bamboo was significantly lower in the combined N addition (N30 and N60) and biochar amendment (BC20 and BC40) treatments than that of the N addition treatments alone (Fig. 3f). Three-way ANOVA indicated that the age of bamboo, N addition, and biochar amendment significantly affected NRE, PRE, and NRE:PRE ratios of young and mature bamboo, both independently and when combined (Table S3).

NRE was significantly negatively correlated with fresh N and P concentrations, soil TN, TP, and AP concentrations ($P < 0.05$, Table 2). PRE was significantly negatively correlated with fresh N and P concentrations, soil TP and AP concentrations, and AN:AP ratio ($P < 0.05$, Table 2).

Table 2
Pearson's correlation coefficients indicating the relationships between N and P resorption efficiency (NRE and PRE) and fresh leaf N and P concentrations and soil characteristics in a Moso bamboo plantation.

Difference source	FLN	FLP	pH	TN	TP	AN	AP	AN:AP ratio
NRE	-0.275*	-0.384**	0.482**	-0.263*	-0.457**	0.035	-0.275*	0.224
PRE	-0.354**	-0.293*	0.462**	-0.006	-0.296*	0.284*	-0.021	0.316**

FLN, fresh leaf N concentration; FLP, fresh leaf P concentration; TN, soil total nitrogen; TP, soil total phosphorus; AN, soil available nitrogen; AP, soil available phosphorus. *$P < 0.05$; **$P < 0.01$.

4. Discussion

4.1 Effect of N addition on foliar nutrient resorption

In the present study, foliar NRE (45–52%) and PRE (34–54%) of Moso bamboo in the control plots were lower than the global average NRE and PRE of evergreen angiosperms (56% and 58%, respectively) (Vergutz et al. 2012), which may be attributed to the different tree species and soil nutrients. Furthermore, previous studies demonstrated that tree species with a high RE and low RP adopt a "conservative consumption" nutrient-use strategy, whereas those with a low RE and high RP adopt a "resource spending" strategy (Wright and Westoby 2003; Wu et al. 2020). In the present study, foliar NRE and PRE of young bamboo were higher than those of the mature bamboo, whereas foliar PRP exhibited the opposite trend. These results were similar to the findings of Wu et al. (2020), which found that leaf NRE and PRE decreased with stand age in Chinese fir (*Cunninghamia lanceolata*) plantations, indicating that young bamboo adopts a "conservative consumption" strategy while mature bamboo adopt a "resource spending" strategy. A possible reason for this is that rapid growth in young bamboo largely increases nutrient demands and further promotes plant nutrient uptake from the soil and nutrient resorption according to the growth rate hypothesis (Achat et al. 2018; Delgado-Baquerizo et al. 2016; Wu et al. 2020). Additionally, plant leaf NRE and PRE are used to estimate N and P limitations at the ecosystem scale according to the stoichiometric homeostasis theory and Liebig's law of the minimum (Du et al. 2020; Hooker 1917). A leaf NRE:PRE ratio > 1 indicates a stronger N limitation than P limitation. Alternatively, P is more limiting when the leaf NRE:PRE ratio is < 1 (Du et al. 2020). In this study, the foliar NRE:PRE ratio of young bamboo (< 1) was significantly different from the foliar NRE:PRE ratio of mature bamboo (> 1), indicating that young bamboo experienced P limitation while mature bamboo experienced N limitation.

In the present study, N addition significantly reduced foliar NRE and PRE but increased NRP and PRP of young and mature bamboo, which supports our first hypothesis and suggests that N addition alters the nutrient-use strategy of Moso bamboo from “conservative consumption” to “resource spending.” Previous studies have reported that N addition decreased plant N resorption (Lü et al. 2013; Yuan and Chen 2015; Zhao et al. 2020). For example, Zhang et al. (2017b) found that N input significantly decreased the leaf NRE of Chinese fir. A review by Yuan and Chen (2015) demonstrated that plant nutrient resorption decreased with increasing soil nutrient availability. In our study, N addition significantly increased soil TN concentration and decreased foliar NRE. Pearson correlation analysis showed that foliar NRE was significantly negatively correlated with soil TN concentration, which supports our argument that high nutrient availability reduces plant nutrient resorption. Moreover, enhanced N availability affected the resorption of other elements (Brant and Chen 2015; See et al. 2015). The effect of N addition on foliar PRE is highly variable, with negative, neutral, and positive effects (Kou et al. 2017; Lü et al. 2013, 2020; van Heerwaarden et al. 2003). Kou et al. (2017) observed that N enrichment led to increased P resorption, as plants increased P conservation during the transition from N-limitation to P-limitation. However, some studies found that N enrichment lowered P resorption (Lü et al. 2013, 2020; van Heerwaarden et al. 2003), because N enrichment enhanced soil P availability by stimulating extracellular phosphatase enzyme activity (Chen et al. 2020; Lü et al. 2020). In the present study and in our previous studies at the same site, N addition significantly increased soil TP and AP concentrations (Table 1) and acid phosphatase enzyme activity (Peng et al. 2019) but decreased PRE. In addition, foliar PRE was significantly negatively correlated with soil TP concentration (Table 2), which supports the argument that N addition decreases foliar PRE by increasing soil P availability.

Additionally, some studies have demonstrated a negative correlation between N and P resorption efficiency and fresh leaf N and P concentrations based on a global database analysis (Kobe et al. 2005; Vergutz et al. 2012). Our study found that fresh leaf N and P concentrations were significantly higher in the N addition treatments (Fig. 1) and negatively correlated with foliar NRE and PRE, which supports the above argument that N addition decreases nutritional resorption by increasing foliar nutrient concentrations.

Previous studies have suggested that nutrient RP is more sensitive than RE to nutrient additions (Ratnam et al. 2008; Yuan and Chen 2015) and less variable across time (Killingbeck 1996; Lü et al. 2020), which is attributed to RE being calculated from the percent changes in nutrients of green and senesced leaves. In this study, N addition significantly increased the NRP and PRP of young and mature bamboo, which was consistent with the findings of Lü et al. (2020) and Yuan and Chen (2015). A possible reason for this was that N addition increased soil nutrient availability (TN and TP; Table 1).

In summary, our study showed that young and mature Moso bamboo had a higher RE and lower RP in the N addition treatments, indicating that N addition altered the nutrient use strategy of Moso bamboo from “conservative consumption” to “resource spending.” In addition, the NRE:PRE ratios of mature bamboo were significantly lower in the N addition treatments than under the N-free treatment, which did not exceed 1, indicating that proportionally more P was resorbed than N, suggesting that N additions increased the P limitation of mature bamboo.

4.2 Effect of biochar amendment on foliar nutrient resorption

Biochar amendment significantly reduced the NRE and PRE but increased the NRP and PRP of young bamboo, supporting our second hypothesis. Biochar contains abundant nutrients (e.g., NH_4^+, Ortho-P) (Gul and Whalen 2016); its application in the experimental plots increased the soil AN and AP content (Table 1), thus reducing the plant’s dependence on the internal circulation of N and P, leading to decreased N and P resorption in young bamboo. Zhang et al. (2017c) also observed that biochar amendment increased soil nutrient availability in *Torreya grandis* plantations. Moreover, biochar application promoted the formation of soil aggregates (Brodowski et al. 2006) and greatly enhanced soil fertility, which is attributed to biochar having a highly porous structure, large specific surface area, and a high CEC of the soil (Bird et al. 2008; Cheng et al. 2008).

In the present study, NRE and PRE were significantly and negatively correlated with soil TN, TP, and AP concentrations (Table 2), supporting our hypothesis that biochar amendment reduces NRE and PRE by increasing soil nutrients. In addition, green leaf N and P concentrations in young bamboo were significantly higher in the BC20 and BC40 treatments than that in the control (Fig. 1) and were significantly and negatively correlated with the foliar NRE and PRE of young bamboo, which supports the argument that high green leaf N and P concentrations decreases nutrient RE. However, biochar amendment significantly decreased green leaf N and P concentrations in mature bamboo (Fig. 1) but increased foliar N and P resorption. Thus, the different responses of young and mature bamboo to biochar amendment may depend on the growth stage of the plant. These findings suggest that young bamboo adopts a “resource spending” strategy (with low RE and high RP), whereas mature bamboo adopts a “conservative consumption” strategy (with high RE and low RP) to biochar amendment, respectively. Biochar applications significantly decreased the foliar NRE:PRE ratios of young bamboo (< 1) and mature bamboo (> 1), indicating enhanced P limitation in young bamboo but no effect on P in mature bamboo.

4.3 Combined effects of N addition and biochar amendment

The combined application of biochar and N significantly decreased foliar NRE and PRE but increased NRP and PRP of young bamboo when compared with those of N addition treatments alone, which supports our third hypothesis and demonstrated that biochar amendment enhanced the negative priming effect of N addition on foliar nutrient resorption in young Moso bamboo. A possible reason could be that the combined application of biochar and N significantly increased soil N and P availability (Table 1), thereby increasing the fresh leaf N and P concentrations in young bamboo. The combined application of biochar and N increased soil AP and TP concentrations (Asai et al. 2019), which significantly enhanced fresh leaf N and P concentrations in *Torreya grandis* trees and seedlings (Zhang et al. 2019) and wheat (Huong 2016). However, mature bamboo showed the opposite response to combined biochar and N applications, suggesting that biochar amendment alleviates the negative priming effect of N addition on foliar nutrient resorption in mature bamboo. In the N60 treatment ($\leq$ 60 kg ha^{-1} yr^{-1}), biochar application significantly decreased the foliar NRE:PRE ratio of mature bamboo, indicating that biochar amendment enhanced P limitation of mature bamboo. However, the foliar NRE:PRE ratios of young bamboo in the combined N60 and N90 and BC20 and BC40 treatments were similar to those of the N addition treatments alone (both greater than or less than 1), suggesting that biochar amendments did not change the effect of N addition on the nutrition limitation of young bamboo.

5. Conclusions

Our findings showed that N addition alone significantly decreased leaf nutrition resorption (NRE and PRE) in both young and mature bamboo, indicating that N deposition reduced the internal nutrient cycling and altered the nutrient-use strategy of Moso bamboo from "conservative consumption" to "resource spending." Biochar amendment alone significantly decreased the leaf NRE and PRE of young bamboo but increased that of mature bamboo, suggesting that the effect of biochar amendment on nutrition resorption depends on the age of the bamboo. Furthermore, biochar amendment combined with N addition significantly decreased the leaf NRE and PRE of young bamboo but increased that of mature bamboo, indicating that biochar amendment altered the negative priming effect of N addition on leaf nutrition resorption, and the effect direction depended on bamboo age. There was a negative correlation between NRE and PRE and fresh leaf N and P concentrations and soil nutrient content. These findings will assist policymakers and managers with establishing efficient fertilization management strategies under changing N deposition rates in subtropical Moso bamboo plantations.

Declarations

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Author contributions

Xinzhang Song designed research, Jinpei Gao and Quan Li performed research, collected and analyzed data; All authors discussed the results and revised the manuscript.

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Data availability statement

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials.

Ethical Approval and Consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare no competing interests.

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Figures

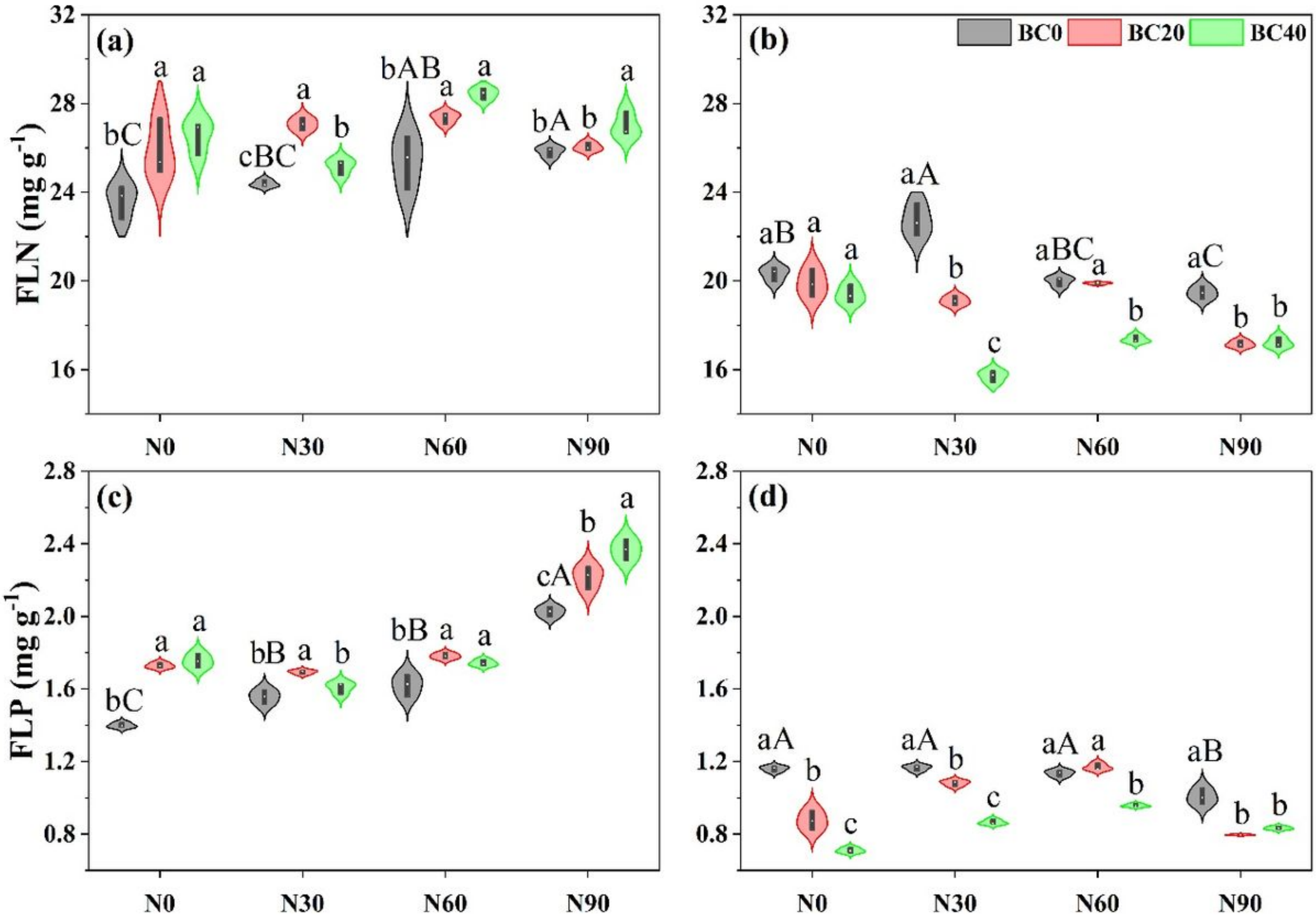

Figure 1

Fresh leaf nitrogen (FLN) and phosphorus (FLP) concentrations in young (a, c) and mature (b, d) bamboo under different N addition and biochar amendment treatments. N0, N30, N60, and N90 refers to 0, 30, 60, and 90 kg N ha-1 yr-1, respectively, and BC0, BC20, and BC40 refers to 0, 20, and 40 t biochar ha-1. Capital letters indicate a significant difference between different N addition treatments in the BC0 treatment at the 0.05 level. Lowercase letters indicate a significant difference between different biochar treatments in the same N addition treatment at the 0.05 level.

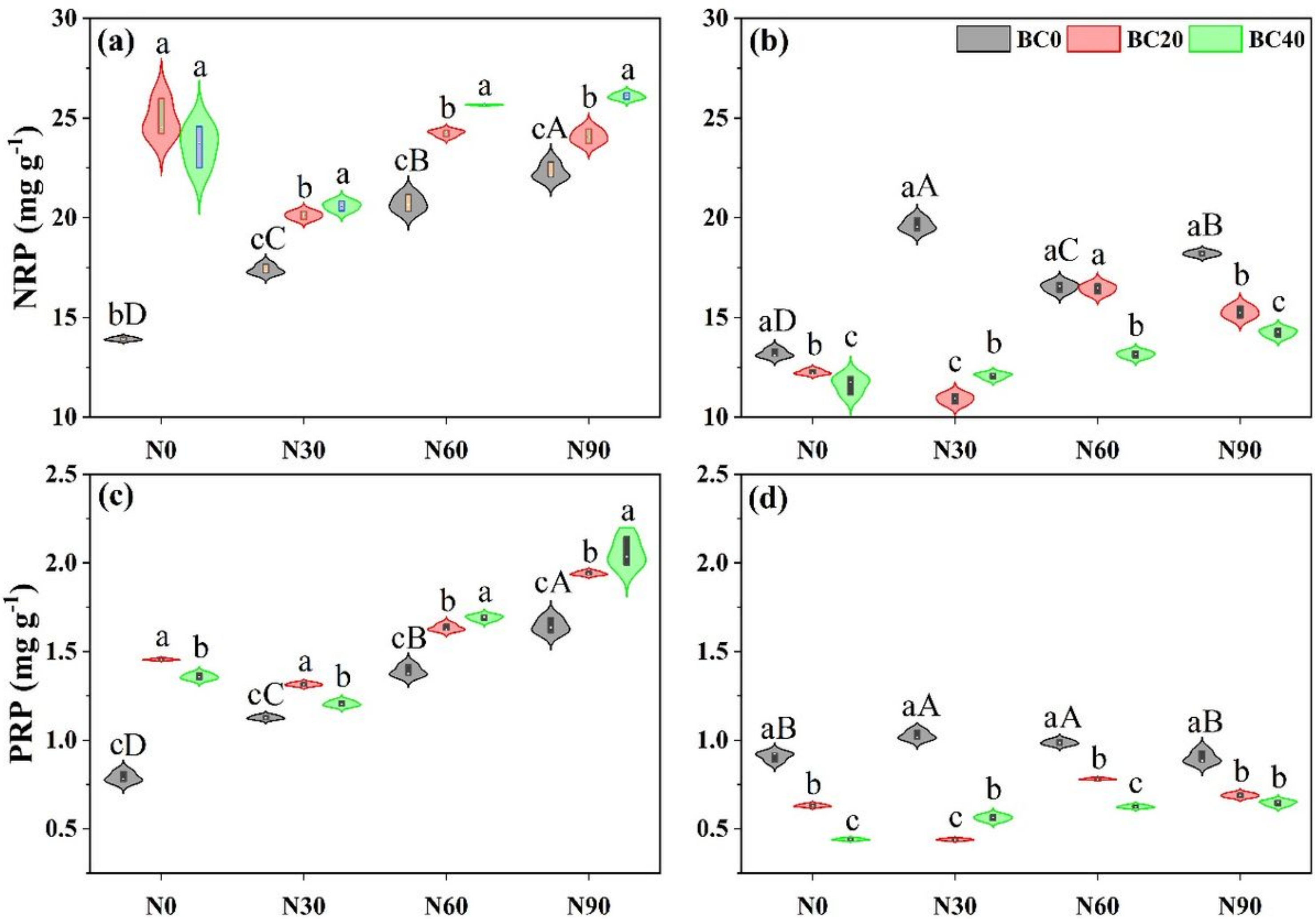

Figure 2

Nitrogen resorption proficiency (NRP) and phosphorus resorption proficiency (PRP) of young (a, c) and mature (b, d) bamboo under different N addition and biochar amendment treatments. N0, N30, N60, and N90 refers to 0, 30, 60, and 90 kg N ha-1 yr-1, respectively, and BC0, BC20, and BC40 refers to 0, 20, and 40 t biochar ha-1. Capital letters indicate a significant difference between different N addition treatments in the BC0 treatment at the 0.05 level. Lowercase letters indicate a significant difference between different biochar treatments in the same N addition treatment at the 0.05 level.

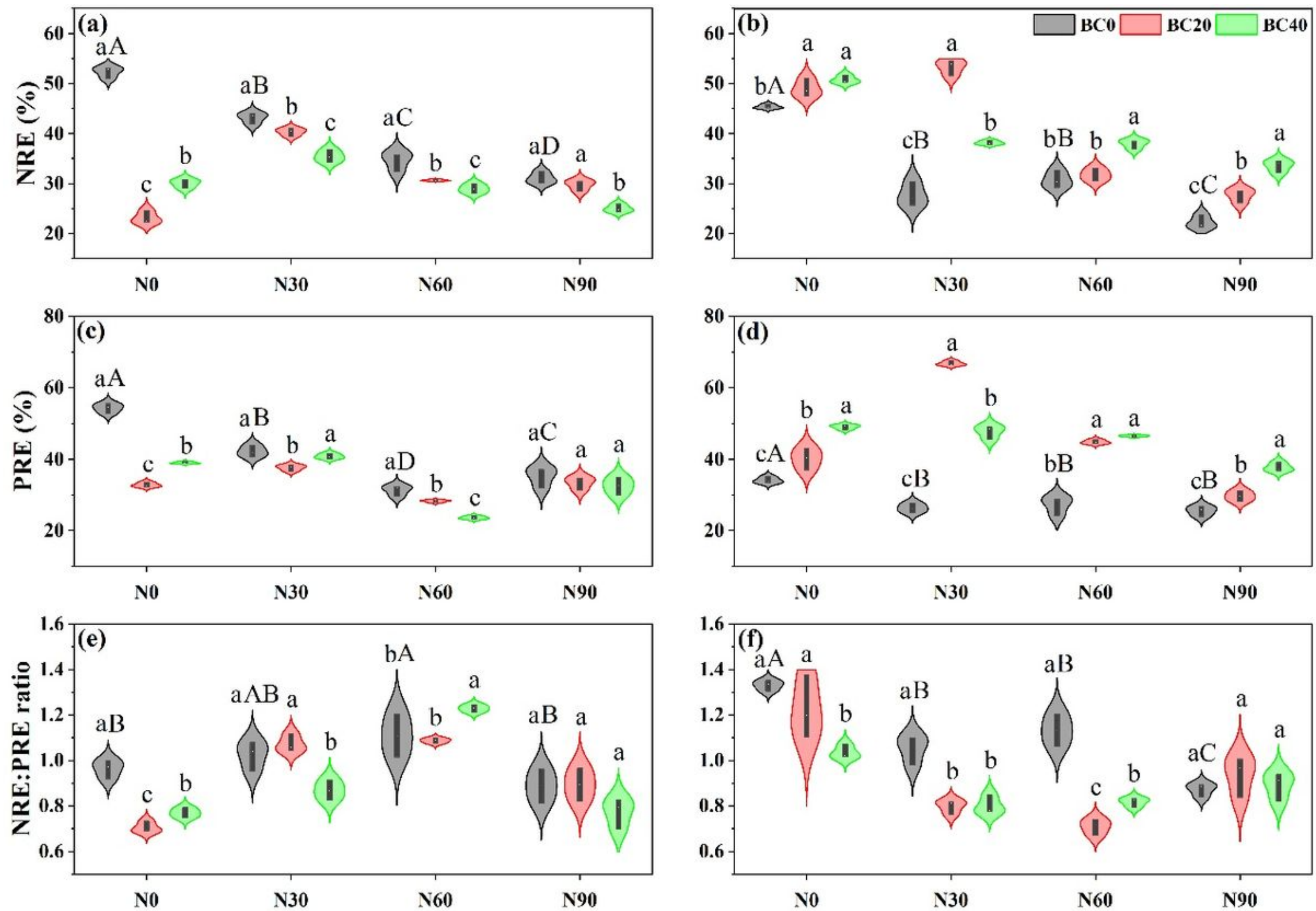

Figure 3

Nitrogen resorption efficiency (NRE), phosphorus resorption efficiency (PRE) and NRE:PRE ratio of young (a, c, and e) and mature (b, d, and f) bamboo under different N addition and biochar amendment treatments. N0, N30, N60, and N90 refers to 0, 30, 60, and 90 kg N ha-1 yr-1, respectively, and BC0, BC20, and BC40 refers to 0, 20, and 40 t biochar ha-1. Capital letters indicate a significant difference between different N addition treatments in the BC0 treatment at the 0.05 level. Lowercase letters indicate a significant difference between different biochar treatments in the same N addition treatment at the 0.05 level.

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