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Differential responses of phosphorus accumulation and mobilization in Moso bamboo (*Phyllostachys edulis* (Carrière) J. Houz) seedlings to short-term experimental nitrogen deposition

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Abstract

Key message Short-term nitrogen (N) deposition stimulates phosphorus (P) demand owing to the growth improvment of *Phyllostachys edulis* seedlings. Increased N loads led to the acquisition and utilization of sufficient P, while the limitation of P starvation could be alleviated by the higher activity of soil acid phosphatase and P use efficiency rather than P resorption from senescent organs.

Context Plants in most terrestrial ecosystems are usually subjected to natural phosphorus (P) deficiency or surplus by overfertilization associated with increasing global nitrogen (N) deposition. As the widely distributed gramineous plant in Southern China, moso bamboo (*Phyllostachys edulis* (Carrière) J. Houz) grows fast and it also shows a relatively good growth performance under the variable N and P conditions. However, few studies focus on the special mechanism of P mobilization and utilization of moso bamboo, especially with the N loads.

Aims The objective of this study was to figure out the mechanisms of P mobilization and utilization in *P. edulis* seedlings under varying levels of soil P and N deposition conditions in the subtropical region of China.

Methods We grew *P. edulis* seedlings under 3 experimental N deposition rates (0 (N −), 30 (N +), and 60 (N + +) kg N $ha^{-1}·a^{-1}$) and 3 levels of soil P (2.99 $mg·kg^{-1}$, soil available P content under natural conditions, denoted as P_1; 20 $mg·kg^{-1}$, P_2; and 40 $mg·kg^{-1}$, P_3). We measured growth traits and analyzed the related P use indices.

Results Dry weight and P accumulation of new leaves and stems increased with increasing N loads under the 3 P treatments, with the positive effects of N deposition being stronger in the P_2 and P_3 treatments. Compared with N −, N +, and N + + significantly increased P use efficiency (PUE) (+ 15.54% and + 12.47%, respectively) regardless of soil P

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conditions. The P resorption efficiency showed a decreasing tendency under variable P conditions with increasing N, whereas PUE was further increased. Acid phosphatase (APase) activity and soil available P content were significantly improved by N loads in P_1.

Conclusion *Phyllostachys edulis* seedlings showed high growth plasticity and P mobilization mechanisms under different soil P availability with N loads. In general, N addition stimulated P demand of *P. edulis* seedlings owing to the growth promotion in the short period of experiment. A special P use mechanism in P deficiency conditions was that the limitation of P starvation was alleviated by the higher soil APase activity and PUE instead of P resorption from senescent organs. The long-term effect of N deposition on P mobilization and utilization in *P. edulis* forests requires further monitoring.

Keywords Nitrogen deposition, Phosphorus resorption, Growth trait, Phosphorus use efficiency, Soil phosphorus activation

1 Introduction

Nitrogen (N) and phosphorus (P) play pivotal roles in plant growth and have attracted increasing attention in studies of forest restoration and ecosystem development (Ågren et al. 2012; Braun et al. 2010). The threat of P deficiency, owing to its low availability caused by its slow diffusion and metal fixation in soils, has been a common barrier to plant development and productivity. In particular, P deficiency seriously constrains both the plant acquisition and mobilization efficiency of P, which represent the ability of plants to acquire P from the soil and the internal efficiency of P mobilization to produce higher biomass with lower P input, respectively (Wang et al. 2010). Several strategies help plants cope with P deficiency, such as changes in root distribution (López-Bucio et al. 2003), shifts in plant mass allocation (Zhang et al. 2016), and the stimulation of internal and exocrine acid phosphatase (APase) activities (Wasaki et al. 1997). Short-term economic benefits from higher yields of crops and wood have been suggested to be closely related to the abundant artificial application of P fertilizers (Higgs et al. 2000). However, the excessive addition of P is not a sustainable method to fundamentally solve the problem of P starvation in terrestrial ecosystems (Yan et al. 2016). Therefore, emphasis has been given on the development of environmental strategies for increased P utilization efficiency and regulation of the capacities of plants to cope with a low P environment (Aslam et al. 2020).

Meanwhile, the rapidly increasing N deposition in terrestrial ecosystems has also attracted increased attention (Liu et al. 2011). There has been a marked increase in the N deposition rate, particularly in subtropical China, with an increment of 30 kg ha^{-1} a^{-1} in the last few years (Jia et al. 2014). High N availability might stimulate plant requirements for other mineral elements like phosphorus. However, the supply of soil available P might be far less than the increasing P requirement of the plant (Marschner 2012), making it harder to maintain the long-term balance of N and P utility of ecosystems, which could potentially aggravate P limitation and alter the P cycle in forest ecosystems (Li et al. 2016; Marklein and Houlton 2012). N deposition sometimes has limited effects on P acquisition and utilization by plant. Plant growth could be stimulated by N deposition under variable soil P conditions (Fujita et al. 2010; Liu et al. 2013).

Moso bamboo (*Phyllostachys edulis* (Carrière) J. Houz) is a major bamboo species that widely distributed in southern China, covering an area of 4.43 Mha (Song et al. 2011; Wang et al. 2013; Zhou et al. 2010). Previous studies have mostly focused on the sequestration of carbon in *P. edulis* forests and its effect on the mitigation of climate change (Song et al. 2011), as well as carbon cycling and the related nutrient return mechanism under global nitrogen deposition conditions (Song et al. 2015; Zhang et al. 2017a, b; Zhang et al. 2021). Few studies focused on P utilization under different carbon sequestration or nitrogen deposition conditions (Xing et al. 2021), and they screened some microorganisms that could improve the activity of phosphorus availability in bamboo rhizosphere. It is necessary to determine the characteristics of acquisition and utilization of P by *P. edulis* seedlings under different N deposition rates and delineate the related mechanisms.

We conducted a pot experiment to explore the characteristics of mobilization and utilization of P by *P. edulis* seedlings under variable levels of soil P availability and N deposition conditions in the subtropical region of China. In particular, we investigated the accumulation and mobilization of P by *P. edulis* seedlings under low, medium, and high levels of soil P to 3 short-term N deposition rates. We proposed 3 hypotheses: (*i*) increasing N deposition might promote plant growth and therefore increase the demand for P nutrition; (*ii*) to satisfy increasing P demand, plants might reabsorb more P sources from senescent organs, particularly under low P availability, and P remobilization might delay the occurrence of P limitation; and (*iii*) extensive N loading probably stimulates P utilization, especially under sufficient soil P availability, while worsening plant growth under P deficiency conditions.

2 Material and methods

2.1 Plant material

Healthy seeds of *P. edulis* were collected in September 2017 from Lingchuan County, Guangxi Province (110° 27′ E, 25° 60′ N). After natural air drying, all collected seeds were placed in clean and sealed sampling bags (polyethylene, 18 × 27 cm) and then stored in a stable environment (temperature: 4 °C; humidity: 60%). The experiment began by soaking the seeds on April 27, 2018. After 12 h of soaking, the seeds were sown in rectangular plastic containers (55 × 33 × 5 cm; length × width × depth) filled with soil at a depth of 0.3–0.5 cm. We used the soil collected from a typical site of Moso bamboo forests without intensive management in Changxing County, Zhejiang Province (119° 7′ E, 30° 9′ N) to conduct the pot experiment (Table 5 in Appendix). This soil is a typical subtropical red soil with poor nutrient conditions. Soil pH was 4.75, and the content of organic matter, total N, hydrolyzable N, total P, and available P were 12.2 g·kg^{-1}, 430 mg·kg^{-1}, 48.0 mg·kg^{-1}, 350 mg·kg^{-1}, and 2.99 mg·kg^{-1}, respectively. All sown containers were placed in a climate chamber (FPQ-300C-20D, Life Technology Co., Ltd., Ningbo, China) at a temperature of 25 ± 2 °C, humidity of 70–90%, and the irradiance was 300–400 μmol m^{-2} s^{-1}. The soil samples were sprayed with distilled water daily before and during seedling emergence. On May 30, 2018, uniformly sized seedlings (approximately 5.7 ± 1.5 cm in height) were selected and transplanted to growth pots (32 × 20 × 15 cm, top diameter × bottom diameter × height). Six seedlings were evenly distributed per pot and 8 kg of the same soil, which was the same as the emergence medium, was added to each pot. In addition, a tray was placed in each pot. All pots were moved into a greenhouse located at Zhejiang A&F University, China (119° 72′ E, 30° 23′ N) on the same day, where the day/night temperature was controlled at approximately 28 °C/16 °C, and the average relative humidity was 65.3%.

2.2 Experimental design

A two-factor completely randomized design was applied in our experiment, using different levels of soil P availability and different N deposition rates. Soil P availability was set to low, middle, and high levels (2.99, 20, and 40 mg·kg^{-1} soil available P content, denoted as P_1, P_2, and P_3, respectively) based on our previous study (Pan et al. 2020) and the seedling P acquisition traits of other Poaceae species (i.e., *Oryza sativa*) (Julia et al. 2018). Potassium dihydrogen phosphate (KH_2PO_4) is a physiologically neutral compound fertilizer with stable properties. Subsequently, 1 L KH_2PO_4 solution at concentrations of 0, 4.39, and 9.56 mol L^{-1} per pot was applied in P_1, P_2, and P_3, respectively, on May 31, 2018. P_1 was the natural soil conditions (2.99 mg kg^{-1}). The same amount of water was applied to each pot to maintain a stable water content among different treatments. Three levels of N supplementation treatments were included: 0 kg N·ha^{-1}·a^{-1} (N−, as a control), 30 kg N·ha^{-1}·a^{-1} (N+, low N supplementation), and 60 kg N·ha^{-1}·a^{-1} (N++, high N supplementation). N was provided by spraying ammonium nitrate (NH_4NO_3) solution from the top of the canopy of *P. edulis* seedlings using a small electric sprayer. Spraying was evenly applied in the middle of each month for a total of 12 times from June 2018 to May 2019. N+ and N++ were applied using 2.4 L NH_4NO_3 solution per pot at concentrations of 0.008 and 0.016 mol L^{-1}, respectively. Control seedlings were sprayed with 0.2 L of deionized water each time (i.e., a total of 2.4 L) to maintain a stable water content among different treatments. The emergence of weeds was controlled throughout the experiment. We performed 9 treatments, with 4 replicates per treatment. Each replicate had 1 pot, with a total of 36 pots containing 216 seedlings during the entire experiment.

2.3 Measurements

Four seedlings without injury were randomly selected and uprooted with minimal damage to the root system from 4 pots for each treatment on May 28, 2019 (He et al. 2023). The rhizosphere soil, which was adhering to the root, was separated by gentle tapping, collected with a brush in plastic bags, and then stored in a refrigerator at −20 °C for further analysis. We first measured the diameter and height of seedlings (Table 6 in Appendix) and then divided them into 5 parts: old stem, old leaf, new stem, new leaf, and root. The stems and leaves tillered before 2019 were regarded as old. All fallen leaves were collected during the experiment. Each component of the sampled seedlings and fallen leaves were oven-dried at 105 °C for 30 min and then at 80 °C until constant weight to obtain the biomass data. Shoot mass was calculated as the sum of the aboveground biomass, including old and new stems and leaves. The root-to-shoot mass ratio (R/S), fallen leaf ratio (LFR), and total mass of the whole seedling were also calculated. Rhizosphere soil samples were used to measure the soil available P content and soil acid phosphatase (APase) activity. Soil available phosphorus was determined by colorimetry after soil extraction with 0.5 M $NaHCO_3$ adjusted to pH 8.5, according to the method by Bao (2000). Soil APase activity was measured using the *p*-nitrophenyl phosphate (PNP) method by Tabatabai and Bremner

(1969) with some modifications by Redel et al. (2019). This approach involves the colorimetric estimation of the *p*-nitrophenyl released by phosphatase activity following the incubation of soil samples (1 g) with 1 mL 50 mM PNP and 4 mL 0.1 M Tris buffer pH 5.5 for 1 h at 20 °C.

The P concentration of each component was determined using a molybdenum antimony anticolorimetric method (Bao 2000) and analyzed using a UV spectrophotometer (UV2500, Japan). Certain P use indices (i.e., P accumulation of different components, P partitioning ratio, P use efficiency (PUE), and P loss rate) are defined in Eqs. (1)–(4). In addition, the P resorption efficiency (PRE) of new leaves and stems was calculated using the formula by Chen et al. (2015) (defined in Eq. (5)). The related formulas are as follows:

$$\text{P accumulation of component} = \text{P concentration of component} \times \text{dry weight} \quad (1)$$

$$\text{P partitioning ratio} = \text{P accumulation of component/P accumulation of the whole plant} \quad (2)$$

$$\text{PUE} = \text{Plant biomass/P accumulation of the whole plant} \quad (3)$$

$$\text{P loss rate} = \text{P accumulation in fallen leaves/P accumulation of the whole plant} \quad (4)$$

$$\text{PRE} = [(\text{P content in living leaf or twig tissue} - \text{P content in the litter component corresponding to the same organs})/(\text{nutrient in living leaf or twig tissue})] \times 100\% \quad (5)$$

2.4 Statistical analysis

Two-way analysis of variance (ANOVA) was adopted to test the effects of N deposition rate, soil P availability, and their interactions on seedling growth traits and the related P use indexes (i.e., P concentration of different component, Eqs. (1)–(5), soil available P content, and soil Apase activity). Multiple comparisons among different treatments were conducted by Tukey's HSD test at $\alpha = 0.05$. Before ANOVAs, all the data were checked for normality and homogeneity of variance, and no data transformation was necessary. All statistical analysis was conducted using SPSS 22.0 (IBM, Chicago, Illinois, USA). All figures were derived using SigmaPlot 12.5 (Systat Software, Inc., USA).

3 Results

3.1 Seedling growth

Soil P availability and experimental N deposition rate had significant interactive effects on the component mass, root-to-shoot mass ratio (R/S), and fallen leaf ratio (LFR) of *P. edulis* seedlings (Table 1). The shoot mass was significantly lower under low P availability (P_1) despite N deposition, but it was significantly higher under high N deposition (N++) despite soil P availability. However, the root mass peaked in the medium soil P availability (P_2), except for that in N++, but we did not detect any significant differences in root mass among the $N-P_2$, $N+P_2$, $N++P_1$, $N++P_2$, and $N++P_3$ treatments (ranging from 1.02 to 1.41 g). We also found that the stem (old and new stem) and foliage (old and new foliage) biomass were significantly lower in P_1 than that in other soil P availability under different N deposition, except for the new foliage mass under low N deposition conditions (N+), with the highest stem and foliage biomass being found in the $N++P_2$ treatment ($P<0.05$). We noticed that R/S in P_1 was more than twice that of P_2 and P_3 without N deposition rate (N−), but no difference detected among soil P conditions in N+ and N++, with R/S being 72.4% lower in $N++P_2$ than the averaged R/S of $N-P_2$ and $N+P_2$ (0.16 vs 0.58) ($P<0.05$). In addition, LFR in P_1 was significantly higher than that of P_2 and P_3 under different N deposition rates (ranging from 33.84 to 34.48%) and was 28.16% higher in $N+P_2$ than the average LFR of $N-P_2$ and $N++P_2$ (25.25% vs 18.14%) ($P<0.05$), while the LFR of $N+P_3$ was significantly lower (26.37%) than the average LFR of $N-P_3$ and $N++P_3$ (16.45% vs 22.34%).

Table 1 Analysis of variance for the effects of soil P availability (P_s), N deposition rate (N_{dep}), and their interactions ($P_s \times N_{dep}$) on seedling component mass and the related morphology traits (i.e., fallen leaf ratio (LFR), root to shoot ratio (R/S)) of *P. edulis* seedlings at the time of final harvest (May 7, 2019). N-, N+, and N++ represent 0, 30, and 60 kg N·ha^{-1}·a^{-1} of experimental N deposition rate, respectively; P_1, P_2, and P_3 represent 2.99, 20, and 40 mg·kg^{-1} of soil available P content, respectively. Statistically significant effects ($P < 0.05$) are highlighted in bold text

Sources	Seedling component mass (g)						R/S	Fallen leaf mass (g)	LFR (%)
	Root	Old stem	New stem	Old leaf	New leaf	Shoot			
N − s									
P_1	0.679 ± 0.07 cd	0.0850 ± 0.01 g	0.177 ± 0.02 g	0.129 ± 0.02ef	0.106 ± 0.02e	0.496 ± 0.04a	1.43 ± 0.28a	0.122 ± 0.01f	34.5 ± 1.44a
P_2	1.13 ± 0.16ab	0.374 ± 0.03 cd	0.662 ± 0.08ef	0.391 ± 0.04 cd	0.440 ± 0.03d	1.87 ± 0.12bcd	0.597 ± 0.06b	0.191 ± 0.01e	18.7 ± 0.76 cd
P_3	0.732 ± 0.02 cd	0.211 ± 0.03ef	0.665 ± 0.11ef	0.335 ± 0.04d	0.367 ± 0.08d	1.60 ± 0.18bc	0.477 ± 0.05bc	0.197 ± 0.02e	22.1 ± 2.94bc
N +									
P_1	0.503 ± 0.08d	0.177 ± 0.01 fg	0.637 ± 0.03 fg	0.00 ± 0.00f	0.480 ± 0.05d	1.29 ± 0.04b	0.385 ± 0.05bc	0.243 ± 0.02de	33.8 ± 1.80a
P_2	1.29 ± 0.15ab	0.476 ± 0.04bc	1.02 ± 0.10d	0.395 ± 0.03 cd	0.521 ± 0.05d	2.41 ± 0.18d	0.546 ± 0.08b	0.308 ± 0.02d	25.3 ± 0.82b
P_3	0.902 ± 0.11bc	0.407 ± 0.05 cd	1.53 ± 0.06 cd	0.482 ± 0.02bc	0.904 ± 0.05c	3.32 ± 0.12e	0.270 ± 0.03bc	0.273 ± 0.02d	16.5 ± 1.11d
N + +									
P_1	1.02 ± 0.15abc	0.310 ± 0.04de	0.959 ± 0.09de	0.00 ± 0.00f	0.791 ± 0.09c	2.06 ± 0.15 cd	0.500 ± 0.07bc	0.402 ± 0.03c	34.1 ± 3.06a
P_2	1.20 ± 0.13ab	0.904 ± 0.06a	3.72 ± 0.15a	0.688 ± 0.04a	2.30 ± 0.09a	7.61 ± 0.26 g	0.157 ± 0.02c	0.638 ± 0.04a	17.6 ± 0.83 cd
P_3	1.41 ± 0.15a	0.566 ± 0.05b	2.32 ± 0.16b	0.527 ± 0.06b	1.26 ± 0.13b	4.67 ± 0.19f	0.302 ± 0.03bc	0.514 ± 0.02b	22.5 ± 1.05bc
F(P) values									
Soil P availability (P_s)	11.1 (< **0.001**)	72.6 (< **0.001**)	122 (< **0.001**)	169 (< **0.001**)	58.9 (< **0.001**)	375 (< **0.001**)	13.5 (< **0.001**)	24.1 (< **0.001**)	276 (< **0.001**)
N deposition rate (N_{dep})	7.77 (**0.002**)	65.7 (< **0.001**)	271 (< **0.001**)	11.7 (< **0.001**)	204 (< **0.001**)	226 (< **0.001**)	20.8 (< **0.001**)	200 (< **0.001**)	90.2 (< **0.001**)
$P_s \times N_{dep}$	2.83 (**0.044**)	5.53 (**0.002**)	50.9 (< **0.001**)	13.7 (< **0.001**)	37.4 (< **0.001**)	70.5 (< **0.001**)	7.61 (< **0.001**)	5.50 (**0.002**)	32.1 (< **0.001**)

3.2 Seedling P accumulation, allocation, and resorption

We observed a significant interactive effect of soil P content and simulated N deposition rate on P concentration in old and new tissues as well as in fallen leaves (Table 2). In particular, we found that low soil P availability (P_1) reduced P concentration in old, new, or fallen tissues under different N deposition conditions, except in old stems (Fig. 1A–F). P concentrations ranged from 0.680 to 1.290 mg g^{-1} in the P_1 treatment. In the case of medium (P_2) and high (P_3) soil P availability, we did not detect any significant differences in component P concentration under non-simulated N deposition (N−) conditions, except for the old stem P concentration in P_3, which was significantly higher (21.71%) than that in the P_2 treatment. However, under low N deposition (N+) conditions, we noticed that the P concentration of stems was significantly higher in the P_2 treatment, reaching 0.910 and 1.276 mg g^{-1} in old and new stems, respectively. We did not identify any differences in new leaf P concentration between P_2 and P_3 treatments; the P concentration of old leaves and roots peaked in the P_3 treatment, reaching 1.190 and 1.096 mg g^{-1}, in contrast with

Table 2 Effects of soil P availability (P_s), N deposition rate (N_{dep}), and their interactions ($P_s \times N_{dep}$) on the component P concentration of *P. edulis* seedlings and fallen leaves ($n = 4$) indicated by *F* and (*P*) values derived from ANOVA analyses. Statistically significant effects ($P < 0.05$) are highlighted in bold text

Sources	P concentration (mg g^{-1})					Fallen leaf P concentration (mg g^{-1})
	Root	Old stem	New stem	Old leaf	New leaf	
Soil P availability (P_s)	109 (< **0.001**)	68.8 (< **0.001**)	349 (< **0.001**)	2.33×10^3 (< **0.001**)	268 (< **0.001**)	155 (< **0.001**)
N deposition rate (N_{dep})	12.6 (< **0.001**)	60.3 (< **0.001**)	582 (< **0.001**)	803 (< **0.001**)	148 (< **0.001**)	47.9 (< **0.001**)
$P_s \times N_{dep}$	9.77 (< **0.001**)	23.6 (< **0.001**)	54.3 (< **0.001**)	339 (< **0.001**)	5.95 (**0.001**)	34.6 (< **0.001**)

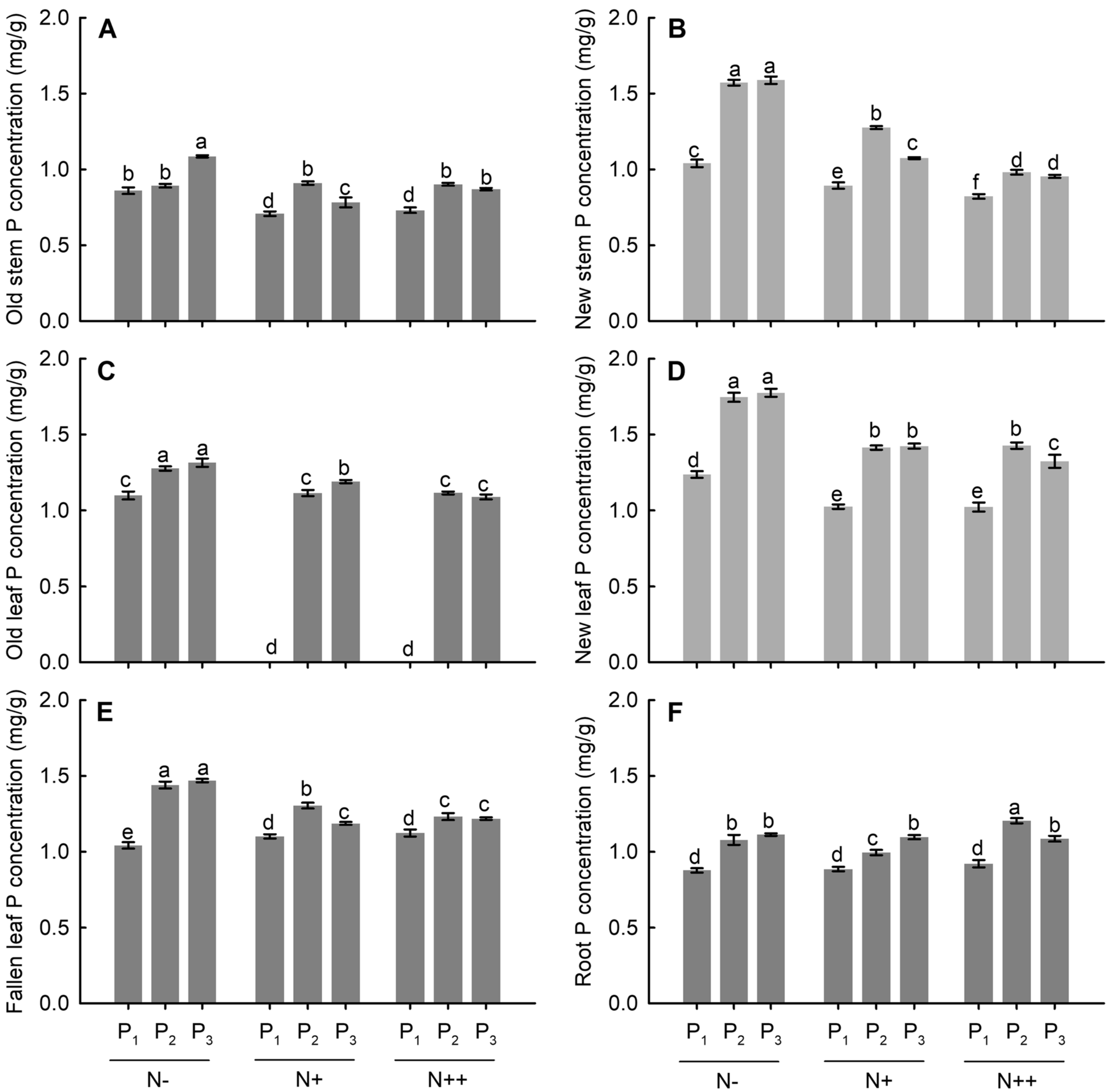

Fig. 1 P concentration of different component of *P. edulis* seedlings in response to experimental N deposition rate under different soil P availability. Different lowercase letters indicate significant differences among different treatments (Tukey's HSD, $\alpha = 0.05$). Vertical bars represent standard error from the mean at each sampling ($n = 4$)

that of fallen leaves. In addition, we observed that the effect of P addition on P concentrations of different components was reduced under high N deposition conditions (N++), except for new leaves and roots, wherein P concentrations were significantly higher (7.83% and 10.93%, respectively) in P_2 than those in P_3.

We further found that plant P content and related P partitioning were significantly affected by the interaction between soil P availability and experimental N deposition rates (Table 3). We observed an upward trend in plant P content with increasing N deposition rate under the same soil P availability (Fig. 2A), while the plant P content of P_1 was significantly lower than that of other treatments under the same N deposition rates. However, we did not detect any significant differences between the P_2 and P_3 soil P availability under N− or N+ conditions, with average plant P contents of 3.538 and 4.496 mg, respectively. We observed the highest plant P content in the N++P_2

Table 3 Effects of soil P availability (P_s), N deposition rate (N_{dep}), and their interactions ($P_s \times N_{dep}$) on component P content of *P. edulis* seedlings and the fallen leaves ($n = 4$) indicated by *F* and (*P*) values derived from ANOVA analyses. Statistically significant effects ($P < 0.05$) are highlighted in bold text

Sources	Seedling component P content (mg)					Fallen leaf P content (mg)
	Root	Old stem	New stem	Old leaf	New leaf	
Soil P availability (P_s)	21.8 (**<0.001**)	88.0 (**<0.001**)	128 (**<0.001**)	20.7 (**<0.001**)	102 (**<0.001**)	55.1 (**<0.001**)
N deposition rate (N_{dep})	11.2 (**<0.001**)	56.9 (**<0.001**)	120 (**<0.001**)	11.3 (**<0.001**)	171 (**<0.001**)	208 (**<0.001**)
$P_s \times N_{dep}$	1.46 (**0.035**)	6.60 (**<0.01**)	28.6 (**<0.001**)	7.10 (**<0.01**)	47.1 (**<0.001**)	6.90 (**<0.01**)

treatment, which was 54.07% higher than that of the $N++P_3$ treatment.

Plant P partitioning of different components varied among different treatments (Fig. 2B). Interestingly, we noticed that $N++P_2$ had the highest plant P content, with the lowest root P partitioning (14.45%) in contrast to that in the $N-P_1$ treatment (52.7%). Moreover, the new leaf P partitioning was significantly lower in P_1 than in P_2 and P_3 under N− conditions, with the highest new leaf P partitioning being shown in the $N+P_1$

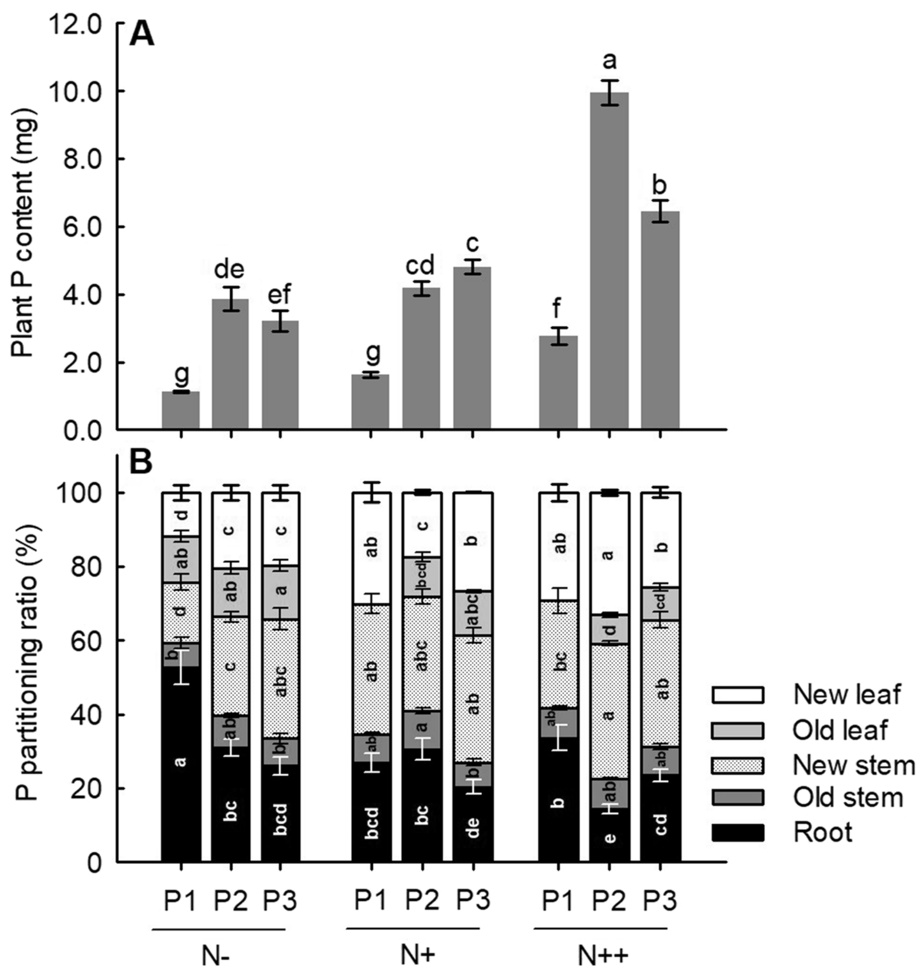

Fig. 2 Plant P content (**A**) and P partitioning ratio (**B**) of *P. edulis* seedlings in response to experimental N deposition rate under different soil P availability. Different lowercase letters in panel **A** represent significant differences among different treatments (Tukey's HSD, $\alpha = 0.05$). Different lowercase letters in the same component in panel **B** represent significant differences among different treatments (Tukey's HSD, $\alpha = 0.05$). Vertical bars represent standard error from the mean at each sampling ($n = 4$)

and N + + P_1 treatments, whereas the old leaf P partitioning was decreased with increasing N deposition rates. We did not observe any significant interactions between soil P availability and experimental N deposition rates in old stem P partitioning (Table 4); however, we found that P_3 had a significantly lower old stem P partitioning than that in the P_2 treatment. We detected few differences in new stem P partitioning among different treatments, except for the significantly lowest ratio in the N − P_1 treatment (16.45%).

We observed a significant interaction between soil P content and experimental N deposition rates on the fallen leaf P content and fallen leaf P proportion (Table 3, Fig. 3). In particular, we detected a clear upward trend in fallen leaf P content with increasing N deposition rates under the same soil P availability, ranging from 0.127 to 0.785 mg. Interestingly, the fallen leaf P content was significantly higher in P_2 and P_3 treatments under N + + conditions, in contrast to the significantly lower fallen leaf P content in the N − P_1 treatment. Likewise, the fallen leaf P proportion was significantly higher in P_1 under N + (16.57%) and N + + (16.80%) conditions.

We also identified that the P resorption efficiency of new stems (PRE_{ns}) and new leaves (PRE_{nl}) was also significantly influenced by the interaction between soil P content and experimental N deposition rates (Fig. 4). Notably, we found that the average PRE_{ns} and PRE_{nl} among different soil P availability ranged from 30.65 to 9.25% and 39.32 to 33.10%, respectively, showing a decreasing tendency with increasing N deposition rates. We detected the lowest PRE_{nl} in the P_1 treatment irrespective of N deposition rates, while the

Table 4 Effects of soil P availability (P_s), N deposition rate (N_{dep}), and their interactions ($P_s \times N_{dep}$) on plant P content of *P. edulis* seedlings and P partitioning ratio (*n* = 4) indicated by *F* and (*P*) values derived from ANOVA analyses. Statistically significant effects (*P* < 0.05) are highlighted in bold text

Sources	Plant P content (mg)	P partitioning ratio (%)				
		Root	Old stem	New stem	Old leaf	New leaf
Soil P availability (P_s)	204 (**< 0.001**)	24.9 (**< 0.001**)	4.36 (**0.023**)	6.82 (**0.004**)	42.8 (**< 0.001**)	0.0320 (0.968)
N deposition rate (N_{dep})	165 (**< 0.001**)	19.0 (**< 0.001**)	0.445 (0.645)	13.0 (**< 0.001**)	43.0 (**< 0.001**)	36.6 (**< 0.001**)
$P_s \times N_{dep}$	29.6 (**< 0.001**)	9.30 (**< 0.001**)	1.27 (0.305)	4.77 (**0.005**)	7.39 (**< 0.001**)	13.1 (**< 0.001**)

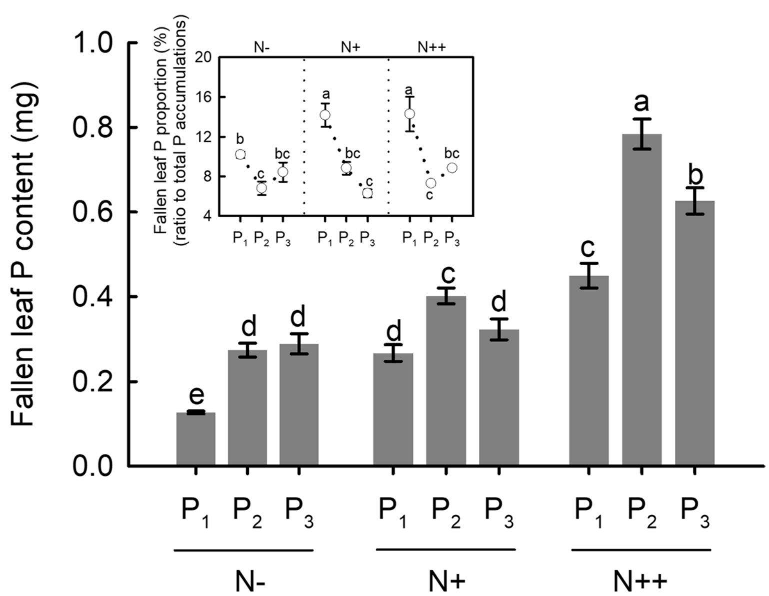

Fig. 3 Fallen leaf P content and the fallen leaf P proportion of *P. edulis* seedlings in response to experimental N deposition rate under different soil P availability. Different lowercase letters indicate significant differences among different treatments (Tukey's HSD, *α* = 0.05). Vertical bars represent standard error from the mean at each sampling (*n* = 4)

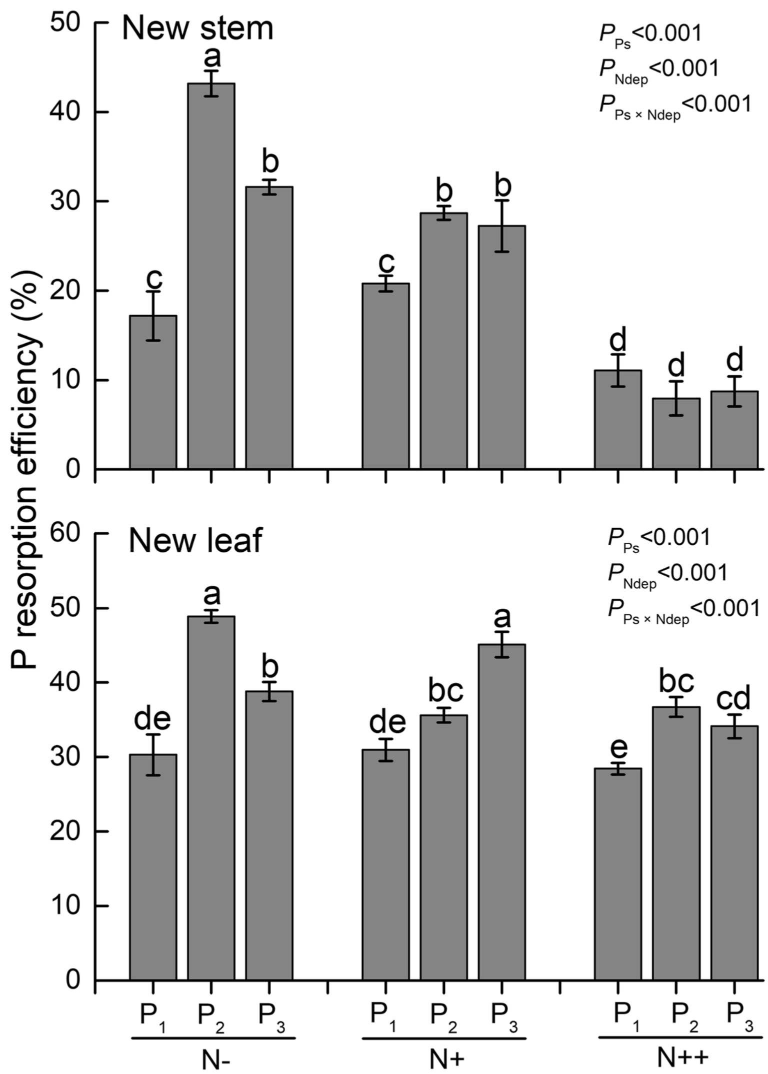

Fig. 4 P resorption efficiency in new stem and new leaf of *P. edulis* seedlings in response to experimental N deposition rate under different soil P availability. Different lowercase letters indicate significant differences among different treatments (Tukey's HSD, $a = 0.05$). Vertical bars represent standard error from the mean at each sampling ($n = 4$)

lowest PRE_{ns} was observed in the P_1 treatment under N+and N++conditions. We did not detect any significant differences in PRE_{ns} among $N++P_1$, $N++P_2$, and $N++P_3$ or between $N-P_1$ and $N+P_1$, or in the PRE_{nl} among $N-P_1$, $N+P_1$, and $N++P_1$. Interestingly, $N-P_2$ had the highest PRE_{ns} and PRE_{nl}, reaching 43.19% and 48.86%, respectively. However, we did not find any difference in the PRE_{nl} between $N-P_2$ and $N+P_3$.

3.3 P use efficiency and soil P activation

We found that the interaction between soil P availability and experimental N deposition rates was significantly influenced by plant P use efficiency (PUE), soil available P content, and acid phosphorus (APase) activity in the rhizosphere soil (Fig. 5). In particular, we observed that PUE peaked in P_1 treatments under different N deposition conditions. Both $N+P_1$ and $N++P_1$ had significantly higher PUE than $N-P_1$. $N-P_3$ had the highest available P content. Likewise, we observed the highest APase activity in the P_1 treatment under N+and N++conditions, which was consistent with PUE. We also detected a significant decrease in APase activity in the P_2 and P_3 treatments under N+and N++conditions, with the lowest APase activity being 0.146 μmol PNP·g^{-1}·h^{-1}.

4 Discussion

4.1 Seedling growth, P acquisition, and allocation of different organs

There were significantly interactive effects of N deposition and soil P availability on plant growth and P

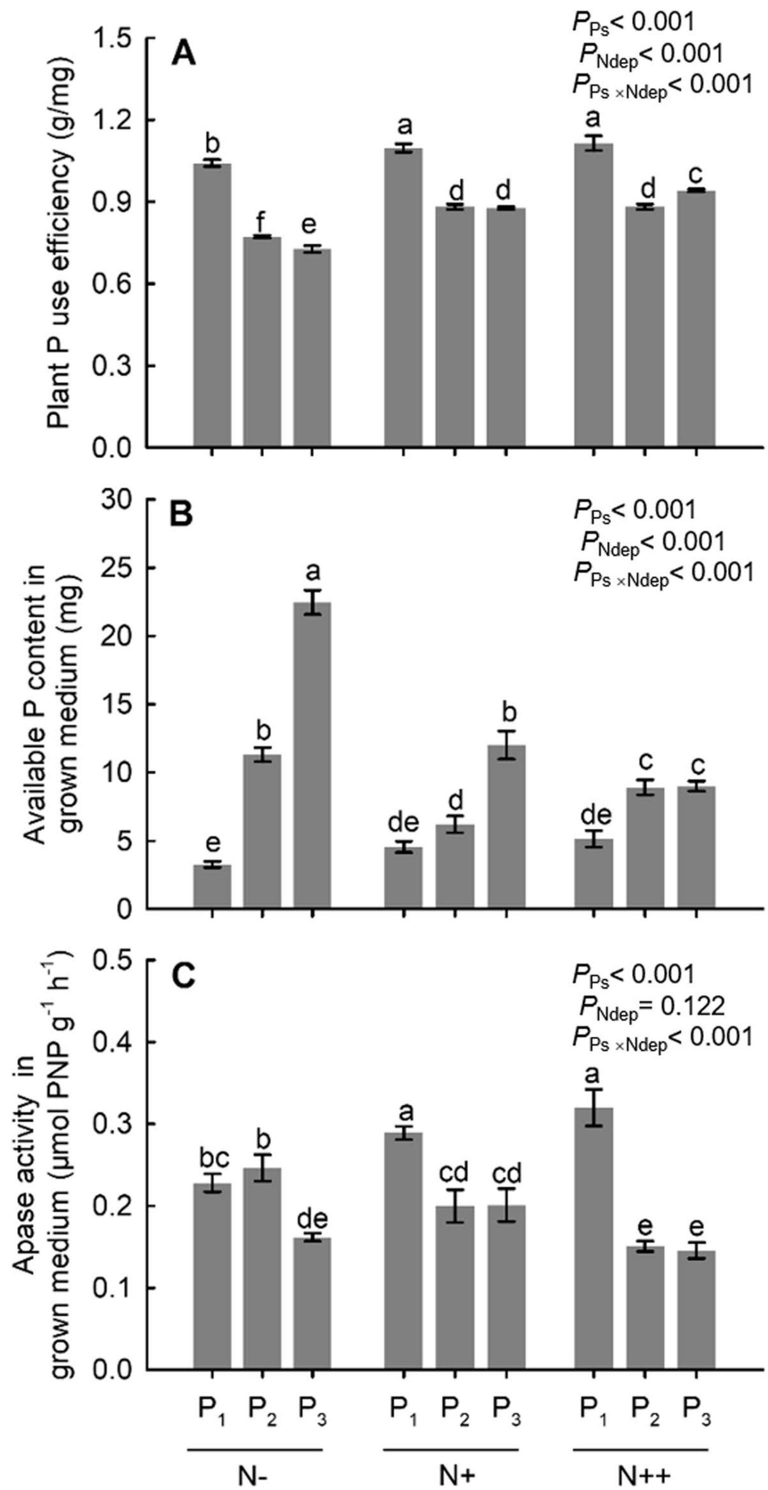

Fig. 5 Plant P use efficiency (PUE) (**A**), available P content (**B**), and acid phosphatase (Apase) activity (**C**) of rhizosphere soil in response to experimental N deposition rate under different soil P availability. Different lowercase letters indicate significant differences among different treatments (Tukey's HSD, $a = 0.05$). Vertical bars represent standard error from the mean at each sampling ($n = 4$)

acquisition of Moso bamboo seedlings. Numerous studies have reported the synergistic effects of N and P on plant growth and nutrient utilization indices (Heuck et al. 2018; Lin et al. 2020; Li et al. 2021). This could be explained by a compensative or limiting effect of N deposition on plant P utilization under variable P conditions and vice versa (Bragazza et al. 2004; Lambers 2022). Our study also revealed a similar phenomenon in which the short-term N deposition enhanced the growth of Moso bamboo seedlings, particularly the aboveground growth of new tillering organs irrespective of soil P availability, which supported the first hypothesis. In addition, the relatively lower seedling P absorption under low soil P conditions revealed a probable restriction in the acquisition and utilization of P, indicating that the unbalanced status of ambient nutrients restricts nutrient absorption and utilization, which supported the third hypothesis to some extent. The stoichiometry of C, N, and P varies among different species under different conditions (Bell et al. 2014; Chen and Chen 2021; Zhao et al. 2018). Some researchers have focused on the foliar or soil stoichiometry of bamboo forests (Guo et al. 2020; Song et al. 2016; Zhao 2021); however, this depends on various factors, such as stand age, management practices, soil properties, and site conditions. Besides, the relatively greater promotion of N deposition in medium and high soil P availability also revealed that the compensative effect of N deposition was still limited by P deficiency under natural soil P conditions, following Liebig's law of minimum nutrients (Warsi and Dykhuizen 2017).

Under the short-term experimental conditions, Moso bamboo seedlings under natural conditions ($N-P_1$) showed worse growth performance, including significantly smaller aboveground biomass, a lower P concentration in different organs, and a lower plant P content, but it had exhibited the highest root-to-shoot mass ratio and a relatively higher P use efficiency. This indicated an extensive resource foraging strategy under nutrient-limited conditions, which was consistent with the higher APase activity of the tested soils. Fine roots can adopt an extensive foraging strategy under water- or nutrient-limited conditions (He et al. 2022). This plasticity has been demonstrated in poplars, Scots pines, Norway spruce forests, and *Gramineae* species (Helmisaari et al. 2009; Ostonen et al. 2011; Wang et al. 2020). Considering the P partitioning of different organs (Fig. 2), the $N-P_1$ treatment led to a significantly higher root P proportion than other treatments, with the root P proportion declining with increasing N loads, which was in contrast to the new leaf P partitioning tendency. All these traits explained the functional equilibrium theory (Brouwer 1983; Poorter and Nagel 2000) and resource economics spectrum (Mommer and Weemstra 2012; Wright et al. 2004), as these traits were beneficial for nutrient absorption under resource-deficient conditions, especially for the easily fixed element P. More attention should be paid to fine root structure and its morphological traits, mycorrhizal fungi, and the root released- or microbial phosphatases (Lambers 2022). The better growth performance of Moso bamboo seedlings grown in medium with high P concentrations under N deposition conditions indicated the necessity for the application of P fertilizers in fast-growing *P. edulis* forests under relatively higher N deposition conditions.

4.2 P utilization, resorption, and the related soil APase activity

Seedling P acquisition was stimulated by short-term N deposition irrespective of the soil P availability, with the highest P partitioning in new organs in consistency with the highest P partitioning ratio of new stems and new leaves. This indicated that the new tillering organs in the second year had a larger amount of acquired nutrients, which was in line with the fast-growing species having a more rapid nutrient uptake caused by their higher growth rate (Lambers and Poorter 1992). The available P content in the rhizosphere showed a decreasing tendency in P_2 and P_3 under N deposition conditions (i.e., N+and N++) compared with that under N− conditions. It appeared that N deposition was an important driving factor for stimulating plant P uptake under P-sufficient conditions, which was similar to the compensation effect of N loads on seedling growth. N deposition might provide an advantage for plant growth by enhancing P uptake, particularly for faster-growing species, such as Moso bamboo (Yu et al. 2015). Phosphorus use efficiency (PUE) peaked under low levels of soil P and N deposition conditions, which could reduce the limitation of seedling growth under lower exogenous P supply. Acid phosphatase (APase) is believed to be important for P utilization and remobilization in plants, and its activity might be related to PUE (Yan et al. 2001). Low P availability has been suggested to increase the secretion of APase in the rhizosphere of many Poaceae species, including rice (*Oryza sativa*), wheat (*Triticum aestivum*), maize (*Zea mays*), and clover (*Trifolium spp.*) (Clark 1975; Tarafdar and Jungk 1987; Tadano et al. 1993). Moreover, the secretion of APase under P stress has been closely related to the transformation of organic and inorganic P toward increasing the soil available P content (George et al. 2018; Tarafdar and Claassen 1988). It was not surprising that the highest APase activity was observed in the $N+P_1$ and $N++P_1$ treatments in our study. We thus confirmed that the growth of Moso bamboo seedlings could be stimulated in a low P environment by improving soil APase activity, in consistency with the extensive foraging strategy of Moso bamboo seedlings under nutrient-limited conditions. Consequently, APase activity might decrease with the addition of P fertilizer, reducing the supply of P from the soil P pool and increasing the reliance on P fertilizer (Redel et al. 2019). Therefore, our study underlined the role of Moso bamboo seedlings in controlling soil APase activity and hence improving P availability to moderate P deficiency with higher N loads, which supported our third hypothesis. Similar P-utilization traits have been widely observed in semi-arid temperate grasslands and herbage (Colvan et al. 2001; Long et al. 2016; Sardans et al. 2006).

Resorption is an important mechanism for nutrient conservation (Aerts 1996). Nutrient resorption is the process by which nutrients are withdrawn from leaves before abscission and redeployed in developing tissues (e.g., leaves or reproductive structures such as seeds) or stored for later use (Wright and Westoby 2003). In our study, there was little difference in phosphorus resorption efficiency among different N loads under variable ambient P conditions, which rejected the second hypothesis. This suggested that the primary method for Moso bamboo seedlings to acquire nutrients might not be from old organs, but rather, from the soil through their roots. Plants adopt various strategies to increase P acquisition, especially under P deficiency conditions, such as acidification of the rhizosphere and mobilization of P by APase and other low molecular weight organic anions, the higher biomass proportion or some morphological plasticity of the root system, and the symbiotic relationships between plants and mycorrhizal fungi. All these strategies increase the ability of plants to explore the soil volume and mobilize P from inorganic and organic P sources (White and Hammond 2008).

Another interesting phenomenon was the abnormally higher fallen leaf ratio of senescent leaves in the $N+P_1$ and $N++P_1$ treatments with less P transfer. It also rejected our second hypothesis. We speculated that this might be related to energy consumption (Su 2021). P is an essential precursor of ATP synthesis and participates in energy metabolism (Ruprecht et al. 2019). We assumed that more P was transferred to energy metabolism first rather than seedling P acquisition and absorption. Furthermore, fallen senescent leaves reduce P consumption and energy, allowing seedlings to acquire more P from the soil (Wright and Westoby 2003), which suggests that Moso bamboo seedlings could have another P utilization mechanism. Nitrogen deposition might aggravate P starvation by transferring P from old organs to new tillering organs.

5 Conclusion

Phyllostachys edulis seedlings showed high growth plasticity and P mobilization mechanisms under different soil P availability with N loads. In general, N addition stimulated P demand of *P. edulis* seedlings owing to the growth promotion. A special P use mechanism in P deficiency conditions was that the limitation of P starvation was alleviated by the higher soil APase activity and PUE instead of P resorption from senescent organs. The long-term effects of N deposition on the growth and P utilization traits of *P. edulis* forests remain to be explored, and quantitative analysis of the expression of relevant genes, especially those regulating the reutilization of P from senescent organs and acid phosphatase regulated genes, is warranted in future studies.

Appendix

Table 5 Soil physical and chemical properties in seed provenance in Lingchuan County and the natural Moso bamboo forest in Changxing County

Site	OM (g kg^{-1})	TN (mg kg^{-1})	TP (mg kg^{-1})	AH-N (mg kg^{-1})	available P (mg kg^{-1})	pH
Lingchuan County, Guangxi Province	11.6 ± 0.27	420 ± 2.89	338 ± 4.44	43.7 ± 1.21	2.73 ± 0.05	4.63 ± 0.05
Changxing County, Zhejiang Province	12.2 ± 0.31	430 ± 3.57	350 ± 2.48	48.0 ± 1.63	2.99 ± 0.10	4.75 ± 0.02

OM (organic matter) was measured by potassium dichromate-volumetric method (dilution heating method); TN (total nitrogen) and TP (total phosphorus) were determined by digestion with concentrated sulphuri-perchloric acid and measured using an AutoAnalyzer 3 (Seal, Germany); AH-N (alkaline hydrolyzable nitrogen) was quantified by conductometric titration; available P (phosphorus) was measured by molybdenum antimony anti colorimetry; soil pH was measured using a standard pH meter with a soil/water ratio of 1/2.5. Five soil samples were collected in 0–20 cm soil layer at each site

Table 6 Diameter and height of *P. edulis* seedlings at the final harvest (May 7, 2019) in different treatments

Indices	N−			N+			N++		
	P_1	P_2	P_3	P_1	P_2	P_3	P_1	P_2	P_3
Diameter (cm)	1.73 ± 0.05 e	2.43 ± 0.04 d	2.58 ± 0.06 cd	2.37 ± 0.03 d	2.79 ± 0.07 c	3.50 ± 0.04 b	2.42 ± 0.06 d	3.62 ± 0.04 b	4.10 ± 0.04 a
Height (cm)	16.6 ± 1.85 d	26.4 ± 2.47 cd	28.6 ± 2.52 cd	28.7 ± 3.63 cd	37.3 ± 0.44 bc	47.2 ± 2.18 b	48.8 ± 3.14 b	70.8 ± 3.22 a	66.9 ± 2.47 a

N−, N+, and N++ represent 0, 30, and 60 kg N·ha^{-1}·a^{-1} of experimental N deposition rate, respectively; P_1, P_2, and P_3 represent 2.99, 20, and 40 mg·kg^{-1} of soil available P content, respectively. The same letter among different treatment indicates no significant difference (Tukey's HSD, $\alpha = 0.05$)Acknowledgements

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Authors' contributions
Conceptualization: Wenhui Shi, Yilei Tang, and Yuelin He; Methodology: Wenhui Shi and Yilei Tang; Formal analysis and investigation: Yilei Tang, Lin Lin, and Yuelin He; Writing—original draft preparation: Yilei Tang and Wenhui Shi; Writing—review and editing: Yuelin He and Wenhui Shi; Funding acquisition: Yeqing Ying and Wenhui Shi; Resources: Yeqing Ying; Supervision: Yeqing Ying and Wenhui Shi. The authors read and approved the final manuscript.

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Available of data and materials
Data deposited in the Mendeley data: https://data.mendeley.com/datasets/rwcjrvksmx (He et al. 2023).

Declarations

Ethics approval and consent to participate
The experimental protocol was established, according to the ethical guidelines. Written informed consent was obtained from individual or guardian participants.

Consent for publication
We give our consent for the publication of this manuscript.

Competing interests
The authors declare that they have no competing interests.

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