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Differential Response of Soil Respiration and Total Belowground Carbon Allocation to Simulated Nitrogen and Phosphorus Deposition in Moso Bamboo Forests

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Abstract: Elevated nitrogen (N) and phosphorus (P) depositions have greatly affected belowground carbon processes in forest ecosystems. However, open questions still remained on the effects of N and P depositions on belowground carbon processes, including soil respiration (RS), its source components—autotrophic respiration (RA) and heterotrophic respiration (RH), and total belowground carbon allocation (TBCA) in Moso bamboo forests—one of the most important forest types with wide distributions in subtropical China. To fill this knowledge gap, a two-year N, P, and NP experiment was conducted in Moso bamboo forests. Results showed that RS, RA, and RH had a strong seasonal variability and were exponentially correlated with soil temperature. N and P depositions did not change RS and RA. However, P deposition increased RH due to the stimulation of microbial activities, indicating a significant soil carbon loss under P deposition. N and P depositions did not affect TBCA. However, NP deposition significantly increased root carbon-use efficiency. Net ecosystem production (NEP) varied from 198 ± 104 to 529 ± 225 g C m⁻² year⁻¹, indicating that Moso bamboo is an important carbon sink. P deposition marginally decreased NEP, while N and NP depositions did not affect NEP, which indicates that N deposition alleviated the suppression of P deposition on NEP. These findings highlight the inconsistent responses of RA, RH, and NEP to N, P, and NP depositions, which should be differently considered to increase the accuracy of predicting belowground carbon dynamics.

Keywords: N and P deposition; autotrophic respiration; heterotrophic respiration; net ecosystem production; root carbon-use efficiency



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1. Introduction

Soil respiration (RS) is one of the most important processes in global carbon cycling, and has received great attention in recent decades for several reasons. First, RS is one of the largest outfluxes from soil to the atmosphere. For example, approximately 76% ecosystem respiration is from RS in temperate forests [1]. Second, RS is roughly divided into autotrophic (RA, respiration by roots, their associated mycorrhizal fungi, and other microorganisms in the rhizosphere which are directly dependent on labile carbon compounds leaked from roots) [2] and heterotrophic respiration (RH, carbon fluxes from the decomposition of litter detritus and soil organic matter by microorganisms) [3]. Different controlling mechanisms of RA and RH have remarkable implications for soil and ecosystem

carbon balance. Thirdly, RH can impact climate change through the mineralization of long-stored soil carbon, offsetting net primary production (NPP) and even transforming terrestrial ecosystems from a carbon sink into a carbon source [4].

Total belowground carbon allocation (TBCA), a direct indicator to quantify carbon allocation to belowground [5], is another important but less studied carbon component in global carbon cycling. Among different ecosystems, TBCA can amount to as high as 21%–61% of the total gross primary production or to two-thirds of RS [6], which may be even higher than aboveground NPP or litterfall production [1,7]. Although the role of TBCA in carbon cycling has been highlighted [8], the driving mechanisms of the temporal and spatial variability of TBCA are still not fully understood. Because of the difficulties in the direct measurement of belowground carbon cycling processes in the field, indirect approaches, e.g., the mass-balance approach [9], have been widely used. Moreover, root carbon-use efficiency (RCUE), defined as the ratio of root NPP and TBCA, is far less intensively studied due to challenges in direct measurement of belowground carbon components.

Since 1850, atmospheric N deposition has increased up to threefold due to human activities, e.g., fossil fuel combustion and nitrogen fertilization application [10–13]. As one of the highest deposition areas across the globe, N deposition increased by 60% in the past thirty years in China [10]. It has been proved that increased N deposition may influence carbon cycling in terrestrial ecosystems by altering vegetation growth and soil organic carbon (SOC) accumulation or decomposition [14–17]. For example, primary production in N-limited ecosystems is commonly stimulated by N deposition [18]. However, because of high spatial variability in N deposition rates and ecosystem N availabilities [10,19], an accurate quantification of the contribution of N deposition to carbon cycling is still uncertain [18].

In recent decades, P deposition has increased rapidly. Such an increase in P deposition has no historical precedent [20]. The confounded effects of N and P depositions may cause substantial changes in ecosystem structure and function and, thus, in carbon cycling. However, conflicting results are often observed [21,22]. For instance, N deposition increases RS in *Pleiblastus amarus* bamboo forests [21] but decreases RS in a subtropical forest [22]. Similarly, P deposition increases RS in *Acacia mangium* and *Eucalyptus urophylla* forests [23] but decreases RS in a subtropical secondary forest [24]. These conflicting findings suggest that the responses of RS to N and P depositions are highly context dependent.

Moso bamboo (*Phyllostachys heterocycla* (Carr.) Mitford cv. *Pubescens*) forest, an important and unique forest type in subtropical China, is well known for its amazingly rapid growth, which can achieve a maximum height of up to 20 m and a diameter at breast height (DBH) of up to 16 cm within about 60 days of the bamboo shoot emergence [25,26]. For ecological protection, natural forests are not allowed to be felled in China; thus, Moso bamboo is a valuable substitute wood resource and it can be harvested every year. Consequently, the areas of Moso bamboo forests have increased from 3.87 million hectares during 2004–2008 to 4.68 million hectares during 2014–2018 [27,28], accounting for 15–36% of the net ecosystem production (NEP) of all forests across China [29]. Therefore, Moso bamboo forests play a critical role in regional, national, and even global carbon cycling [26,30].

Recent studies have analyzed the effects of N deposition on RS in Moso bamboo forests [31,32]. For instance, N deposition increases RS but decreases the temperature sensitivity of RS in a Moso bamboo forest in Zhejiang province, China [31]. The effects of P deposition or the interactions of N and P depositions on RS in Moso bamboo forests have been less studied. Furthermore, the majority of studies applied NaNO_3 [33,34], $(\text{NH}_4)_2\text{SO}_4$ [34,35], NH_4Cl [36], and NH_4NO_3 [37] as the only N forms to simulate N deposition. However, the ratio of NH_x and NO_y in atmospheric N deposition varies spatially [10]. A previous study already demonstrated that N forms have different impacts on RS [38]. Thus, N deposition with different N forms could potentially improve our understanding of realistic atmospheric N deposition on carbon cycling in forest ecosystems [26]. To our knowledge, no such study has been conducted to evaluate the effects of N and P depositions on TBCA in Moso bamboo forests.

To fill this knowledge gap, we conducted an experiment where N and P (and their combination) were added in the understory of a Moso bamboo forest. N was amended with a ratio of NH_x : NO_y of 2.08:1, aiming to (1) investigate the effects of N and P depositions and their interactions on RS, TBCA, and NEP; (2) explore the controlling mechanisms underlying the responses of RS, TBCA, and NEP to N and P depositions; (3) compare whether RS, TBCA, and NEP have similar responses to N and P depositions. The outcome would be a great assistance to improve our understanding of carbon balance to increasing N and P depositions in one of the least-intensively studied forest types—bamboo forests.

2. Materials and Methodology

2.1. Study Site

This study was conducted at the National Observation and Research Station of Bamboo Forests of Changning, Sichuan, which is located in the South Sichuan Bamboo Sea in Changning County ($26^{\circ}33'17''$ – $28^{\circ}26'46''$ N, $104^{\circ}5'11''$ – $105^{\circ}4'54''$ E), China. It is a mountainous area with an elevation from 260 to 1000 m and is characterized by a subtropical humid monsoon climate, with a mean annual precipitation from 1200 to 2000 mm with 334–356 fog days per year [39]. Temperature ranges from 8.1 °C in January to 30 °C in July or August, with averages between 14.5 and 18 °C [39]. More than ninety percent of the study area is covered by Moso bamboo forests mixed with *Bambusa intermedia* Hsueh et Yi, *Neosinocalamus affinis* (Rendle) Keng, *Dendrocalamus membranaceus* Munro, etc. [39].

2.2. Experimental Design

To evaluate the effects of N and P depositions and their combinations on RS and TBCA, a randomized block design with three replicates was employed in March 2019. In each replicate, a circle plot with a 5 m radius was established. A buffer zone of at least five to ten meters was set between two nearby plots. Within each block, four treatments were randomly assigned—pure water irrigation without N and P deposition (NP0), N deposition with 100 kg N ha^{−1} year^{−1} (N100), P deposition with 50 kg P ha^{−1} year^{−1} (P50), and N and P deposition with 100 kg N ha^{−1} year^{−1} and 50 kg P ha^{−1} year^{−1} (N100P50), which was conducted through an understory spray in all plots following Wei et al. [22]. An irrigation system, with a spraying device set in the plot center, was used for N and P deposition. N and P solutions were evenly sprayed down with a sprinkler that could freely turn 360°. Sprays were conducted in the morning to reduce the effects of sunshine and wind speed.

Two-year N and P deposition was conducted in the growing season of the Moso bamboo forests from April 2019 to September 2021, with six spraying events per year. To avoid the bias of N forms on RS and TBCA, according to Tian et al. [40], the local ratio of NH_x and NO_y was 2.08:1. To represent the local NH_x and NO_y in a realistic way, we used NH_4Cl and NH_4NO_3 as the N source with a ratio of NH_x and NO_y of 2.08:1, while KH_2PO_4 was the P source. In each plot except NP0 plot, a mixed solution of NH_x and NO_y was added in a volume equivalent to 1 mm of precipitation, which accounted for 6 mm per year [26]. This water deposition amounted to less than 0.5% of the mean annual precipitation. Therefore, the confounding effects from water addition was negligible.

2.3. Partitioning of RA and RH

The trenching approach was applied to partition RA and RH [30,41,42]. Specifically, a subplot of 1 m × 1 m was trenched down to a soil depth of 0.8 m in each plot center in March 2019. Four 0.5 cm thick polyethylene boards were inserted into the trenches vertically to prevent root ingrowth after trenching. Because the majority of roots were distributed within a soil depth of 0.4 m [43], a trench depth of 0.8 m was sufficient to prevent the root growth in trenched plots [30]. We carefully removed all living vegetation during the whole study period to reduce as much as possible the soil disturbances from litterfall and living vegetation [44].

In each plot, two sampling polyvinyl chloride (PVC, 20 cm in diameter and 12 cm in height) collars for untrenched soil and one PVC collar for trenched soil were inserted into

the soil at a depth of 6 cm. The PVC collars remained during the whole study period. Soil carbon fluxes in intact soil and the trenched plots represented RS and RH, respectively. The difference between RS and RH was treated as RA [30,45].

2.4. RS Measurement

Soil CO₂ flux measurement started in July 2019, four months after trenching [26], and continued monthly for two years until June 2021 using a Li-Cor-8100 (Li-Cor Inc., Lincoln, NE, USA). The measurement was conducted between 9:00 and 12:00 am because the soil CO₂ fluxes during this period could represent the diurnal average [44–46]. Soil temperature (ST) and moisture (SM) at a 5 cm soil depth were measured by the temperature and moisture sensors of Li-Cor 8100 as well as during CO₂ flux measurements. Due to instrument problems, ST and SM in July 2019 were not measured.

2.5. Vegetation Production

In each plot, DBH of each bamboo was measured using a diameter tap to the nearest 0.1 cm in July 2019, 2020, and 2021. Bamboo age was recorded according to visual examination of the culm color, eyelash on cycle of culm sheath, powder under cycle of culm sheath, and sheath in culm base [30,47]. Total biomass, including aboveground and belowground biomass, of each individual bamboo was estimated as per Zhou et al. [48]:

$$\text{Biomass} = 747.784 \times \text{DBH}^{2.771} \times ((0.148 \times A) / (0.028 + A))^{5.555} + 3.772 \quad (1)$$

where A is age ('du', a special expression of age for bamboo forest) [48].

Root NPP was estimated by the maximum–minimum approach, the difference of the highest biomass and the lowest biomass [5,49,50]. Root samples were collected using five sequential soil cores with a diameter of 5 cm every two months during the study period. Three layers were established: 0–10 cm, 10–30 cm, and 30–50 cm. After sample collection, roots were carefully washed to remove the soil and then were dried to a constant weight at 65 °C.

Three litterfall collectors (1 m × 1 m) were set at 0°, 120°, and 240°, three meters away from the plot center within each plot for each month. Roots and litterfall samples were dried to a constant weight at 65 °C. Carbon content of 0.5 g g^{−1} of vegetation samples was used to convert biomass to carbon stock [51].

2.6. Data Analysis

One-way analysis of variance (ANOVA) was applied to compare annual carbon fluxes, including RS, RA, RH, litterfall, NPP, NEP, TBCA, ST, and SM, among different N and P deposition treatments, at $p = 0.05$. Repeated measures of ANOVA [24] were used to study the interactions of N and P depositions and month (as a categorical variable) on ST, SM, RS, RA, and RH. All data analysis and figure processes were conducted in R 3.6.2 [52].

A linear regression analysis and an exponential regression analysis were employed to study the correlations between RS/RA/RH and SM/ST, respectively [30,53,54]:

$$\text{RS (RA or RH)} = a + b \times \text{SM} \quad (2)$$

$$\text{RS (RA or RH)} = c \times e^{d \times \text{ST}} \quad (3)$$

where a, b, c and d are the coefficients.

Temperature sensitivity (Q_{10}), the increase in respiration rate as temperature increasing by 10 °C, was calculated using monthly RS, RA, and RH fluxes and ST for each treatment, expressed as [55]:

$$Q_{10} = \frac{c \times e^{d \times (\text{ST} + 10)}}{c \times e^{d \times \text{ST}}} = e^{10d} \quad (4)$$

where d is taken from formula (3).

The annual cumulative CO₂ emission was calculated by:

$$\text{annual RS (RA or RH)} = \sum_{i=1}^{12} \text{monthly RS (RA or RH)} \times 12 \times 10^{-6} \times 3600 \times 24 \times \text{day}_i \quad (5)$$

where day_i is the number of days in each month; 12 is the molecular weight of carbon; the 10^{−6} is the unit conversion of 1 μmol to 1 mol. Due to COVID-19, soil CO₂ fluxes in February, March, and December 2020 were not measured. Therefore, we used soil CO₂ fluxes in February and March 2021 and December 2019 instead when calculating annual CO₂ fluxes [26].

2.7. Carbon Balance Calculations

NEP can be calculated as the balance between NPP (the sum of the biomass increment and litterfall production) and RH [30,56]:

$$\text{NEP} = \text{NPP} - \text{RH} = \text{biomass increment} + \text{litterfall} - \text{RH} \quad (6)$$

where biomass increment (including aboveground and belowground) is the sum of the biomass increments of new bamboos and growing bamboos of 2, 3, and 4 'du'. RH is the annual carbon flux from heterotrophic respiration (g C m^{−2} year^{−1}), respectively.

2.8. TBCA

Two approaches were applied to calculate TBCA: the component-cumulative approach [57] and the mass-balance approach [9]. The component-cumulative approach was expressed as [5,57]:

$$\text{TBCA} = \text{NPP}_{\text{root}} + \text{RA} \quad (7)$$

where NPP_{root} is the root NPP (g C m^{−2} year^{−1}), which was calculated as maximum-minimum approach [50]. RA is annual autotrophic respiration (g C m^{−2} year^{−1}).

Based on the assumption of near-steady state that the carbon input equals carbon output, the mass-balance approach was first proposed by Raich and Nadelhoffer [9], and TBCA was expressed as:

$$\text{TBCA} = \text{RS} - \text{litterfall} \quad (8)$$

where litterfall is the annual litter production (g C m^{−2} year^{−1}).

RCUE was calculated as the ratio of root NPP and TBCA [44,58]:

$$\text{RCUE} = \text{NPP}_{\text{root}} / \text{TBCA} \quad (9)$$

3. Results

3.1. Monthly Variabilities of ST and SM

ST at a depth of 5 cm showed seasonal variability in both untrenched and trenched plots under N and P and their combinations (Figure 1). Month led to a significant impact on ST ($p < 0.001$, Table 1). Mean annual ST was 18.5 °C for both trenched and untrenched soils. Simulated N and P depositions and the interactions of N and P depositions and month had no impact on ST ($p \geq 0.606$).

Monthly changes of SM at 5 cm depth were also observed in both untrenched and trenched soils (Figure 1c,d, $p < 0.001$, Table 1). However, the interactions of N and P depositions and month did not affect SM (Table 1, $p > 0.052$). Mean annual SM was 23.2% for untrenched soils, which was lower than that of trenched soils for N and P deposition treatments (26.8%, $p < 0.01$).

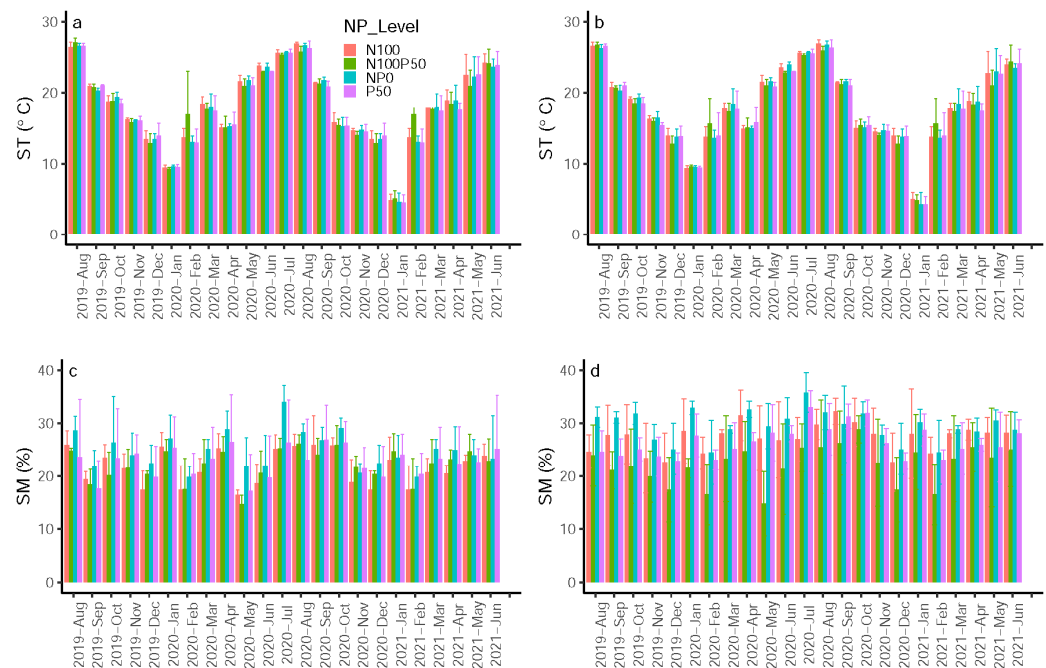


Figure 1. Monthly changes of soil temperature (ST, °C) and moisture (SM, %) in trenched (a,b) and untrenched (c,d) soils from August 2019 to June 2021. NP0: pure water irrigation without N and P deposition; N100: simulated N deposition with 100 kg N ha^{−1} year^{−1}; P50: simulated P deposition with 50 kg P ha^{−1} year^{−1}; N100P50: simulated NP deposition with 100 kg N ha^{−1} year^{−1} and 50 kg P ha^{−1} year^{−1}. The same below.

Table 1. *p* values of repeated measures of ANOVA of N and P depositions and month and their interactions with soil temperature (ST, °C) and moisture (SM, %) at 5 cm depth, total soil respiration (RS), autotrophic respiration (RA), and heterotrophic respiration (RH).

Factor	ST		SM		RS	RA	RH
	Untrenched	Trenched	Untrenched	Trenched			
N	0.835	0.606	0.241	0.007	0.460	0.316	0.558
P	0.927	0.891	0.997	0.621	0.841	0.492	0.112
N × P	0.646	0.686	0.347	0.261	0.130	0.567	0.078
Month	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Month × N	0.673	0.897	0.646	0.312	0.400	0.258	0.997
Month × P	0.729	0.828	0.052	0.968	0.319	0.277	0.064
Month × N × P	0.770	0.988	0.169	0.915	0.242	0.630	0.337

3.2. Monthly Variabilities of Soil Carbon Fluxes

Monthly RS rates varied greatly and the mean annual RS rates were $2.13 \pm 0.46 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, 2.18 ± 0.20 , 2.49 ± 0.25 , and $2.02 \pm 0.23 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for NP0, N100, P50, and N100P50, respectively. Month significantly influenced RS ($p < 0.001$, Table 1). However, N and P depositions and the interactions of the N and P depositions and month had no significant impact on RS ($p \geq 0.13$, Table 1).

Seasonal variabilities were also found for RA and RH (Figure 2b,c). Month had a significant impact on RA and RH (Table 1). However, N and P depositions and the interactions of the N and P depositions and month did not significantly influence RA and RH.

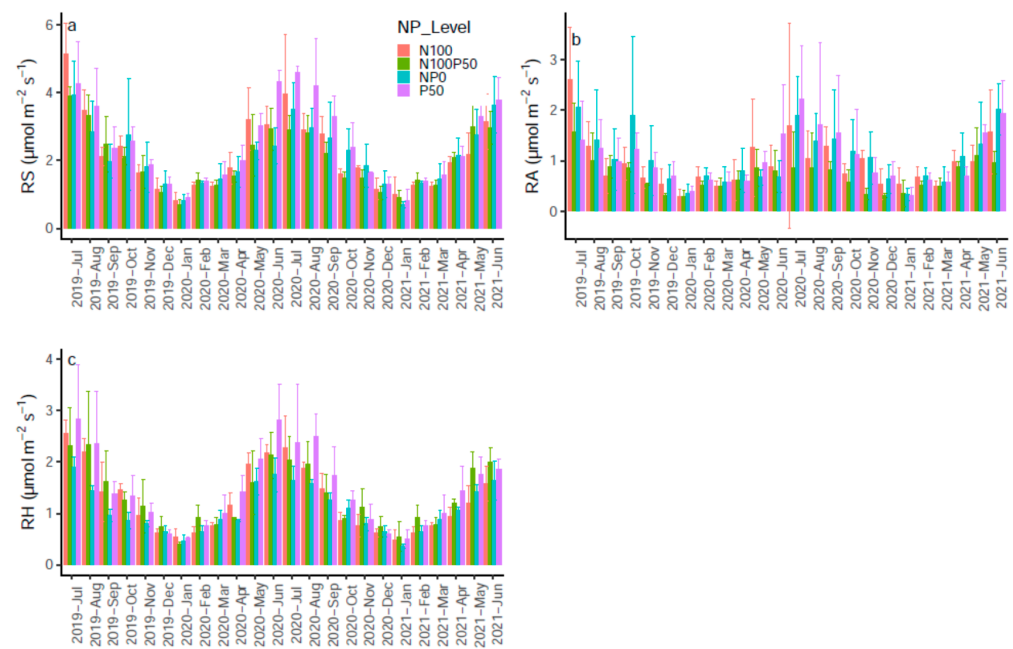


Figure 2. (a) Monthly changes of total soil respiration (RS), (b) autotrophic respiration (RA), and (c) heterotrophic respiration (RH) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) from July 2019 to June 2021.

3.3. Correlation between Soil Carbon Fluxes and ST/SM

Regardless of N and P deposition, RS, RA, and RH rates were significantly and exponentially correlated with ST at a 5 cm depth (Figure 3). ST explained 55%–75% variations of RS, while ST explained 30%–46% variations of RA and 63%–77% variations for RH, respectively (Figure 3).

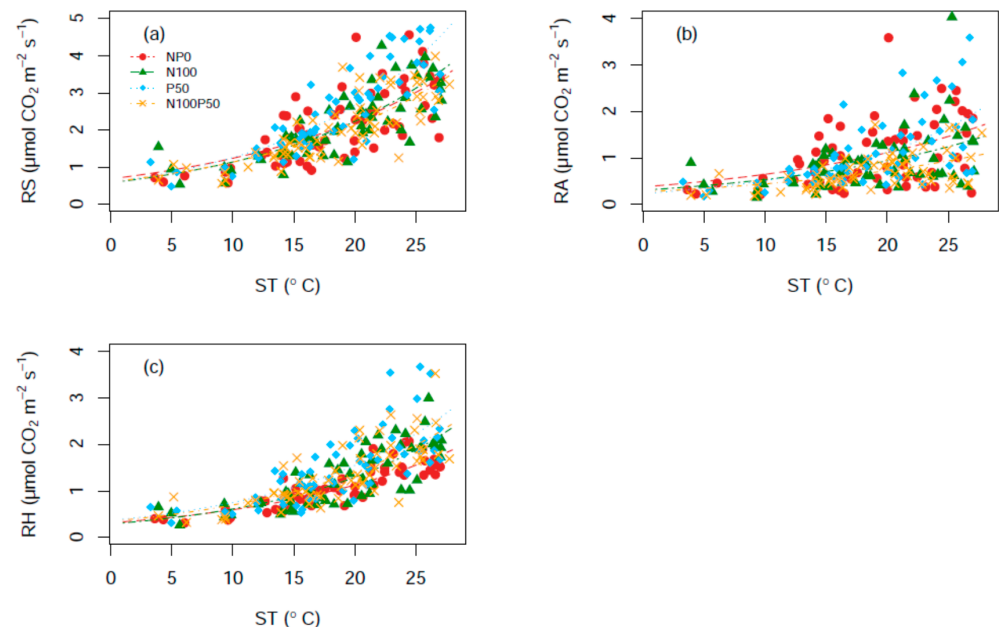


Figure 3. The correlations between (a) total soil respiration (RS), (b) autotrophic respiration (RA), and (c) heterotrophic respiration (RH) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and soil temperature (ST, $^{\circ}\text{C}$) at 5 cm depth.

Calculated Q_{10} values of RS were 1.96, 1.96, 2.12, and 1.88 under NP0, N100, P50, and N100P50 (Table 2), respectively. Similarly, the calculated Q_{10} values were 1.72, 1.76, 2.20, and 1.65 for RA and 1.65, 1.90, 2.12, 2.07, and 2.01 for RH under NP0, N100, P50, and

N100P50, respectively. However, there were no significant correlations between SM and RS, RA, and RH (Figure S1 and Table S1).

Table 2. Temperature sensitivity and coefficients of the models between RS, RA, and RH rates and soil temperature (ST, °C, $RS/RA/RH = c \times e^{d \times ST}$) at 5 cm depth.

Respiration Components	Treatment	c	d	R ²	Q ₁₀
RS	NP0	0.554 (0.422, 0.947)	0.067 (0.042, 0.077)	0.547	1.96
	N100	0.580 (0.364, 0.796)	0.067 (0.051, 0.084)	0.718	1.96
	P50	0.593 (0.405, 0.782)	0.075 (0.061, 0.089)	0.752	2.12
	N100P50	0.605 (0.415, 0.795)	0.063 (0.049, 0.077)	0.698	1.88
RA	NP0	0.375 (0.109, 0.641)	0.054 (0.022, 0.087)	0.302	1.72
	N100	0.303 (0.084, 0.525)	0.056 (0.023, 0.090)	0.446	1.76
	P50	0.232 (0.070, 0.395)	0.078 (0.048, 0.110)	0.400	2.20
	N100P50	0.266 (0.127, 0.404)	0.050 (0.026, 0.074)	0.463	1.65
RH	NP0	0.312 (0.231, 0.393)	0.064 (0.053, 0.076)	0.771	1.90
	N100	0.287 (0.179, 0.394)	0.075 (0.059, 0.092)	0.713	2.12
	P50	0.362 (0.204, 0.519)	0.073 (0.053, 0.092)	0.637	2.07
	N100P50	0.346 (0.209, 0.483)	0.070 (0.052, 0.088)	0.634	2.01

Note: the values in brackets of coefficients a and b are the confidence interval at 2.5% and 97.5%. RS: total soil respiration; RA: autotrophic respiration; RH: heterotrophic respiration; ST and SM: soil temperature and moisture at 5 cm depth, respectively.

3.4. Annual Cumulative Carbon Fluxes

N, P, and NP depositions did not affect annual RS ($p = 0.105$). Annual RS was $810 \pm 163 \text{ g C m}^{-2} \text{ year}^{-1}$ for NP0 and it was $881 \pm 97 \text{ g C m}^{-2} \text{ year}^{-1}$ for N100, $945 \pm 91 \text{ g C m}^{-2} \text{ year}^{-1}$ for P50, and $766 \pm 89 \text{ g C m}^{-2} \text{ year}^{-1}$ for N100P50 (Table 3). Similarly, N, P, and NP depositions did not affect RA ($p = 0.275$). However, P deposition significantly increased RH ($p = 0.024$). The contribution of RH to RS was higher than that of RA, which was 0.52 ± 0.11 for NP0, 0.59 ± 0.10 for N100, 0.65 ± 0.04 for P50, and 0.58 ± 0.10 for N100P50, respectively.

Vegetation NPP was $475 \pm 109 \text{ g C m}^{-2} \text{ year}^{-1}$ for NP0. N, P, and NP deposition did not affect vegetation NPP ($p = 0.739$). Similarly, litterfall production was $463 \pm 139 \text{ g C m}^{-2} \text{ year}^{-1}$ for NP0, which was not significantly different from that of N100, P50, and N100P50 ($p = 0.338$). Root NPP was affected by N and P deposition, and root NPP of P50 was significantly lower than that of N100P50 ($p = 0.002$).

NEP was $529 \pm 225 \text{ g C m}^{-2} \text{ year}^{-1}$ for NP0, which was marginally significantly higher than that of P50 ($p = 0.088$). However, NEP of N100 and N100P50 were not significantly different from that of NP0 ($p > 0.443$).

TBCA calculated from the component-cumulative approach was $594 \pm 174 \text{ g C m}^{-2} \text{ year}^{-1}$ for NP0 (Table 3), which was not significantly different from that of N100, P50, and N100P50 ($p > 0.73$). TBCA calculated from the mass-balance approach (TBCA_mba) was generally lower than that from the component-cumulative approach. However, TBCA_mba differed significantly between P50 and N100P50 ($p = 0.031$).

RCUE varied greatly (0.27 ± 0.10 to 0.48 ± 0.03 (Table 3)). RCUE was in order of $P50 < NP0 < N100 < N100P50$. N100P50 increased RCUE ($p = 0.036$), and RCUE of P50 and N100P50 was also different ($p = 0.002$).

Table 3. Annual cumulative carbon fluxes (mean $\pm$ standard deviation, $n = 3$) from July 2019 to June 2021 among N and P depositions.

Treatment	RS (g C m ⁻² year ⁻¹)	RA(g C m ⁻² year ⁻¹)	RH (g C m ⁻² year ⁻¹)	RH/RS (Unitless)	Litterfall (g C m ⁻² year ⁻¹)	Root NPP (g C m ⁻² year ⁻¹)	Vegetation NPP (g C m ⁻² year ⁻¹)	NEP (g C m ⁻² year ⁻¹)	TBCA (g C m ⁻² year ⁻¹)	TBCA_mba (g C m ⁻² year ⁻¹)	RCUE (Unitless)
NP0	810 $\pm$ 163 a	401 $\pm$ 158 a	409 $\pm$ 15 b	0.52 $\pm$ 0.11 a	463 $\pm$ 139 a	192 $\pm$ 41 ab	475 $\pm$ 109 a	529 $\pm$ 225 a	594 $\pm$ 174 a	348 $\pm$ 227 ab	0.34 $\pm$ 0.10 b
N100	881 $\pm$ 97 a	368 $\pm$ 130 a	513 $\pm$ 51 ab	0.59 $\pm$ 0.10 a	479 $\pm$ 162 a	195 $\pm$ 56 ab	364 $\pm$ 298 a	331 $\pm$ 341 a	563 $\pm$ 142 a	401 $\pm$ 179 ab	0.41 $\pm$ 0.15 ab
P50	945 $\pm$ 91 a	393 $\pm$ 112 a	551 $\pm$ 107 a	0.65 $\pm$ 0.04 a	407 $\pm$ 102 a	149 $\pm$ 53 b	342 $\pm$ 143 a	198 $\pm$ 104 a	542 $\pm$ 106 a	538 $\pm$ 141 a	0.27 $\pm$ 0.10 b
N100P50	766 $\pm$ 89 a	265 $\pm$ 50 a	500 $\pm$ 60 ab	0.58 $\pm$ 0.10 a	486 $\pm$ 148 a	245 $\pm$ 44 a	407 $\pm$ 217 a	393 $\pm$ 274 a	510 $\pm$ 88 a	280 $\pm$ 121 b	0.48 $\pm$ 0.03 a

Note: RS: total soil respiration; RA: autotrophic respiration; RH: heterotrophic respiration; NPP: net primary production; NEP: net ecosystem production; TBCA: total belowground carbon allocation; RCUE: root carbon-use efficiency. Different letters after the number mean significant difference at $p = 0.05$. Vegetation NPP, including aboveground and belowground NPP, was calculated as the biomass increment of new bamboos and growing bamboos.

4. Discussion

4.1. Monthly Dynamics of Carbon Fluxes and Their Correlations with ST and SM

Regardless of N and P deposition, there were strong monthly variabilities in RS, RA, and RH, which were similar to previous studies [24,53]. Some studies found that temporal variabilities of soil carbon fluxes were driven by precipitation or SM through regulating root and microbial activities [59,60]. However, SM was not the regulating factor controlling RS, RA, and RH, because there were no significant correlations between RS, RA, and RH and SM in the current study (Figure S1). ST may be the driving variable controlling the monthly changes in RS, RA, and RH, and ST could explain 30%–77% of the variations in RS, RA, and RH. Moreover, some previous studies also found that vegetation production could also be another controlling variable on RS, RA, and RH [61]; however, the strong correlation between RS, RA, and RH and ST may mask the correlation between vegetation production and soil carbon fluxes [62]. Because of special characteristics of Moso bamboo forests, the DBH of Moso bamboo did not change after bamboo shoot emergence [25,26]. Therefore, it was difficult to measure the monthly production of Moso bamboo forests.

ST and SM are well-recognized and important environmental variables driving the dynamic changes of soil carbon fluxes [22,26,30]. RS, RA, and RH were exponentially correlated with ST (Figure 1), which was consistent with many previous studies, e.g., Cai et al. [26] and Song et al. [63]. The degree of correlation (R^2) between RS, RA, and RH and ST varied, which may have resulted from the different driving mechanisms of RA and RH. However, there was no significant correlation between RS, RA, and RH and SM (Figure S1), indicating that SM was not a limiting factor of soil carbon fluxes in our study area. The finding supported previous studies in a Moso bamboo forest [64] and a temperate forest in subtropical China [65]. However, this study was not consistent with Tang et al. [30] and Liu et al. [66], who found significant and positive correlations between RS and SM. These conflicting findings demonstrate that the correlations between SM and RS are complicated and warrant further investigation into biome-specific or climate-zone-specific correlations between SM and RS in developing biogeochemical models to predict soil carbon fluxes.

Q_{10} of RS of N100, P50, and N100P50 were 1.96, 2.12, and 1.88, respectively, which were not significantly different from that of NP0 (1.96), indicating that N and P deposition did not affect the temperature sensitivity of Q_{10} . This result was similar to Zhang et al. [24], who found that N and P deposition did not significantly alter Q_{10} in a secondary forest. The unchanged Q_{10} to N and P deposition may be largely associated with nonsignificant changes in ST to N and P deposition (Figure 1); however, a previous study found that N, P, and NP depositions reduced Q_{10} [67].

Regardless of N and P deposition, Q_{10} varied slightly from 1.88 to 2.12, which was similar to Tang et al. [30] and Wang et al. [68] in Moso bamboo forests (1.9 and 2.08) and was within the reported Q_{10} range of 1.09–5.47 in Chinese forest ecosystems [69]. However, the Q_{10} of the Moso bamboo forest was lower than the average Q_{10} of 2.46 across forest ecosystems in China [69], indicating that RS in Moso bamboo was less sensitive to increasing temperature compared to the average of Chinese forests.

4.2. Effects of N and P deposition on RS and NEP

P deposition increased annual RH ($p = 0.024$, Table 3). The result was consistent with Liu et al. [70], who also found an increase in RH after P deposition in subtropical forests in China. Previous studies attributed the increased RH under P deposition to increased vegetation production [71]. However, we did not find significant differences between root NPP, total vegetation NPP, and litterfall (Table 3) among N and P depositions; therefore, the increased RH may be not have resulted from the changes in vegetation production. On the other hand, soil labile organic carbon (LOC), microbial biomass carbon (MBC), and dissolved organic carbon (DOC) were important indicators of microbial activities. According to the definition, RH represented the carbon loss from the decomposition of litter detritus and SOC due to microbial activities [3], and any environmental changes altering microbial activities may impact RH. In our study, we found significant correlations

between RH and MBC, DOC, and LOC (Figure S3) and an increase in LOC, MBC, and DOC ($p = 0.035$ for P50, Figure S2). These results indicated that the increased RH under P deposition was caused by the increase in soil microbial activities in this study, because increased soil P availability from increased P deposition could eliminate the nutrient limitation of microbial growth, causing increased microbial biomass and respiration [72]. However, our result was different from Zhang et al. [24], who found that RH was suppressed by P deposition due to the suppression of soil enzyme activities, microbial compositions (indicated by phospholipid fatty acids), and soil MBC. These different results may be associated with different soil nutrient levels.

N and P depositions increased the contributions of RH to RS from 0.52 to 0.65 (Table 3). According to a global analysis of the RH/RS ratio, Bond-Lamberty et al. [73] attributed the increasing RH/RS ratio from 1990 to 2014 to the elevated temperature under global climate change. This study proposed that another new potential mechanism that increased the RH/RS ratio may have resulted from increasing N and P depositions in the last several decades.

We also found that N and P depositions did not individually affect root NPP (Table 3), which supported previous studies in that root NPP was not responsive to N addition or P addition [15,74]. Previous studies attributed such a result to the shift in carbon allocation between aboveground and belowground [75]. However, such an explanation may not be applicable to our study because we did not find significant differences in NPP among the N and P depositions. We attributed such a phenomenon to the colimitation of N and P of Moso bamboo growth, supporting the previous conclusion from a meta-analysis in bamboo forests across China [76]. As indicated by Luo et al. [77] and Capek et al. [78], increasing N availability may enhance the limitation of P. However, vegetation and soil microbes could change their functional traits to increase P acquisition, e.g., releasing carboxylate exudates and phosphatases, modifying root morphological traits, and formatting symbiotic associations with mycorrhizal fungi [77]. Nonetheless, the N and P limitations cannot be isolated because nutrient limitations interact depending on nutrient conditions. As a result, N100P50 increased root NPP and the difference between N100P50 and P50 was significant (Table 3). Moreover, the majority of previous studies mainly focused on the response of fine-root production to simulated N and P additions; however, it was a pity that we did not separate fine and coarse roots, and we cannot draw the conclusion whether simulated N and P depositions increased fine-root production. Simulated N and P depositions tended to decrease RA because RA reflects the need of energy for many ecological processes, e.g., the uptake of ions from soil and the assimilation of nitrogen and sulfur into organic compounds [79]. Therefore, increasing nutrient availability may alleviate energy demand and decrease RA.

Although P was the limiting element in Moso bamboo forests [76], in this study, P deposition marginally decreased NEP, indicating that P deposition decreased carbon sequestration capability at an ecosystem scale. This phenomenon may be due to the stimulation of carbon outflux from RH under P deposition and no significant change in vegetation NPP (Table 3). Our results further indicated that the deposition of limited nutrient elements in forests may not necessarily increase ecosystem production because ecosystem production was determined by complex carbon cycling processes, including carbon fixation through photosynthesis and carbon release from respiration. Additionally, attentions should be paid to carbon outfluxes dominated by microbial activities because microbes are very sensitive to nutrient deposition. However, such an increasing trend in RH and a decreasing trend in NEP with a long-term P deposition is still an open question because a long-term P deposition could alleviate P shortage in Moso bamboo forests.

NEP ranged from 198 ± 104 to 529 ± 225 g C m⁻² year⁻¹ (Table 3), indicating that Moso bamboo was a carbon sink regardless of N and P deposition, falling within the range of NEP in subtropical forests in China, varying from 63 to 603 g C m⁻² year⁻¹ [29,80]. However, NEP in this study was higher than that of the world average of global forests (236 g C m⁻² year⁻¹) [81], indicating that Moso bamboo was one of the greatest vegetation

types with high efficiency of carbon sequestration compared to other forest types [29,80], acting as an important role in alleviating global climate change [26].

4.3. Effects of N and P Deposition on TBCA

Compared to root NPP and RA, TBCA is a more direct indicator to characterize the amount of the carbon allocation to belowground. Although many studies have been conducted to calculate TBCA [5,57], to the best of our knowledge, this study was the first attempt to explore the interactive effects of N and P depositions on TBCA in Moso bamboo forests. TBCA was $594 \pm 174 \text{ g C m}^{-2} \text{ year}^{-1}$ for NP0 (Table 3), which was not significantly different from that under N and P depositions. Such a result can be explained by no significant change in RA and a slight change in root NPP because TBCA was calculated as the sum of the RA and root NPP. Since there was no study to detect the interactions of N and P depositions on TBCA, we could not directly compare our result with other studies. However, we found a similar study on the effects of understory removal on TBCA [5], which found that understory removal did not affect the TBCA, with a slightly lower TBCA (417.7 to $486.9 \text{ g C m}^{-2} \text{ year}^{-1}$) compared to our study. Given the fact that few studies explored the effects of N and P deposition on the TBCA, further studies are encouraged to explore the underlying mechanisms of the interactions of N and P deposition on the TBCA.

However, the TBCA calculated from the mass balance was lower than the TBCA from the component-cumulative approach (Table 3) and differed significantly among N and P depositions. Such a difference may be associated to the assumption of the mass-balance approach, in which the soil carbon input is approximately equal to the carbon output at near-steady state [9]. Practically, such an assumption is difficult to meet in the field, and this is particularly true for Moso bamboo forests. Due to the biological characteristics of rapid growth, Moso bamboo is allowed to fell every year and a large amount of biomass is taken out from the stand. In view of the critical role of the TBCA in global carbon cycling, these findings suggest that method selection is extremely important to precisely estimate the TBCA because the belowground process is complex [5].

Consistent with other studies [9,82], the TBCA was higher than the litterfall and biomass increment. The result highlighted the critical role of the TBCA in Moso bamboo forests. RCUE ratio is a key ecological parameter in ecosystem carbon cycling modeling; however, the constant ratio of 0.5 has been widely used due to the difficulties and uncertainties in measuring root NPP and TBCA [8,83]. In our study, RCUE varied significantly among N and P deposition, indicating that N and P deposition could potentially affect RCUE. Moreover, RCUE was 0.34 for NP0 and 0.27 for P50, which were much lower than the assumed constant value of 0.5 that has been widely used in modeling terrestrial carbon cycling. Therefore, using a constant RCUE ratio of root-NPP-to-TBCA may lead to great uncertainties when estimating the belowground carbon cycling.

4.4. Limitation and Uncertainty

In our study, few limitations and uncertainties still exist. First, the short duration of N and P deposition would be an important limitation. In the current study, the duration of the N and P deposition lasted two years, which was relatively short for detecting belowground carbon dynamics. Previous studies have already found that the duration of N deposition had a significant impact on RA and RH and the dominant driving factors of RA and RH differed with N deposition duration [74,84]. Therefore, a long-term N and P deposition would greatly improve our understanding of the effects of N and P depositions on belowground carbon cycling.

Second, partitioning RA and RH would be an important source of uncertainty. Although the trenching approach has been widely used to separate RA and RH [24,26,30], it is well known that uncertainty may arise due to the decomposition of the remaining roots and associated root exudates in the trenched plot [41]. To minimize this uncertainty, the trenched plots were set four months before the soil carbon flux measurement in this study. Due to the termination of water uptake by roots after trenching, a previous study found

that soil water content in trenched plots was significantly higher than that of untrenched plots [30]. Although our study found that soil water content in trenched plots was significantly higher than that of untrenched plots (Figure 1), no significant relationship was found between soil water content and RH (Figure S1). Therefore, increased soil water content in trenched plots would not be the influence factor affecting RH in the current study.

Third, we applied an understory N deposition in this study, which ignored some critical ecological processes comparing realistic atmospheric N deposition, e.g., N retention, interception, absorption, and transformation of atmospherically deposited N [85]. Thus, simulating the canopy N deposition would be more realistic to represent the true effects of N deposition on belowground carbon cycling.

5. Conclusions

Through two-year field measurements in Moso bamboo forests in subtropical China, we found that ST was the most important environmental driver of RS, RA, and RH, and that N and P depositions did not affect ST and SM. N and P depositions did not alter RA, but P deposition significantly increased RH due to the stimulation of microbial activities. N and P depositions did not affect TBCA, but significantly impacted RCUE, indicating that N and P may change the total carbon allocation through the partition of belowground production and respiration. Regardless of N and P deposition, NEP varied from 198 to 529 g C m⁻² year⁻¹, suggesting that bamboo forests are an important carbon sink. However, P deposition marginally affected NEP, while N and NP depositions did not affect NEP. Furthermore, it should be highlighted that this study was conducted over a relatively short duration, whereas the delayed response of RS, NEP, and TBCA to N and P depositions may lead to different patterns with time. Long-term field experiments are still needed to disentangle the temporal effects of N and P depositions on TBCA.

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