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ORIGINAL ARTICLE

Inconsistent interannual variations between net primary production and soil CO_2 effluxes in a Moso bamboo forest

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ABSTRACT
Understanding the link between interannual variations in net primary production (NPP) and soil CO_2 efflux (R_s) is essential for evaluating carbon dynamics in forest ecosystems, particularly in ecosystems such as Moso bamboo (*Phyllostachys pubescens*) forests with distinctive 2-year cycles of new shoot production. In this study, we measured NPP and R_s components in a Moso bamboo forest over a 5-year period to clarify the consistency of their interannual variation patterns. Our results revealed significant year-to-year variations in NPP (CV = 41%), primarily attributable to above-ground productivity, while R_s components (i.e. autotrophic (R_a) and heterotrophic (R_h) respiration) exhibited less year-to-year variations (CV = 10%–22%). Although NPP and R_s did not exhibit synchronized interannual variations, we observed marginal positive correlations between litterfall, fine root production, and R_a (Spearman's correlation coefficient = 0.9, $p < 0.1$). These findings suggest that while current-year NPP components may influence R_a, R_h variations appear to be relatively independent from NPP variations in Moso bamboo forests. We discuss the simplification of net ecosystem production (NEP = NPP – R_h) estimates in Moso bamboo forests for regional C assessment, highlighting the importance of long-term monitoring of above- and below-ground processes in these ecosystems.

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KEYWORDS
Year-to-year fluctuations; soil C cycling; Moso bamboo; carbon allocation

Introduction

Moso bamboo (*Phyllostachys pubescens*) is one of the dominant and economically important vegetation types in East Asia (Benton 2015). Owing to its rapid growth, Moso bamboo forest has been recognized as an important carbon (C) sink that has ecological benefits, such as climate change mitigation (Shinohara et al. 2014; Song et al. 2016; Lin et al. 2017; Xu et al. 2018; Zhou et al. 2019). The sizes of C sinks in Moso bamboo forests, similar to those of woody forest ecosystems, are evaluated using a net ecosystem production (NEP) index derived from net primary production (NPP) minus heterotrophic respiration (R_h). NPP is generally quantified from the increments in above- and below-ground biomass and litterfall production (Lf) (e.g. Waring et al. 1998), although measuring below-ground biomass increments remains challenging compared with above-ground measurements (Finér et al. 2011; Osawa and Aizawa 2012; Katayama et al. 2019). NPP has been quantified in various types of forest ecosystems, including Moso bamboo forests (Song et al. 2017; Lin et al. 2017; Chen et al. 2018; Shimono et al. 2022). However, few studies have quantified Moso bamboo NEP owing to the lack of soil CO_2 efflux (R_s) measurements, including R_h (Tang et al. 2016, Lin et al. 2017; Li et al. 2022; Yuan et al. 2023). Because NEP can substantially affect long-term C storage compared with NPP (Riuta et al. 2021), NEP estimates, including R_s and its components, in Moso bamboo forests should be encouraged to assess their effectiveness for climate change mitigation.

The R_s is commonly separated into autotrophic and heterotrophic components. Autotrophic respiration (R_a) includes the respiration from live plant parts and can represent ~50% of the total R_s (Högberg et al. 2002). Heterotrophic respiration (R_h) includes respiratory processes from soil microbes, which depend on the availability of organic substrates in the soil (Hanson et al. 2000). The R_s and its components vary with fluctuations in environmental factors such as precipitation and temperature (Raich et al. 2002; Chen et al. 2010; Zhang et al. 2023). The interannual variations in the R_s and its components have been quantified globally in various types of woody forest ecosystems (Irvine et al. 2008; Kume et al. 2013; Makita et al. 2018; Sun et al. 2020, Li et al. 2022). Although recent studies have quantified the R_s and its components in Moso bamboo forests with measurements on an annual basis (Hsieh et al. 2016; Huang et al. 2021; Jin et al. 2023), significant uncertainty remains regarding the interannual variations in the R_s and its components in these forests due to the lack of long-term R_s measurements.

Long-term Moso bamboo NPP measurements show significant interannual variations (Song et al. 2017; Lin et al. 2017), which might affect the interannual variations in R_s and its components. These variations are mainly caused by the 2-year cycles of new shoot production in Moso bamboo, whereby

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a high number of new shoots are produced in an “on-year”, followed by a low number of new shoots in an “off-year” (Li et al. 1998; Kleinhenz and Midmore 2001; Song et al. 2016; Lin et al. 2022). This can cause more than two-fold interannual differences in NPP (Song et al. 2017, Lin et al. 2017). It is possible that the 2-year cycles in Moso bamboo new shoot production might cause large interannual variations in below-ground processes, such as in R_s and its components (R_a and R_h). However, it is not known whether the 2-year cycles in NPP in Moso bamboo forests are accompanied by 2-year cycles in annual R_s and its components.

Previous studies show a linkage between NPP and R_s in vegetative ecosystems (Xu et al. 2015; Endsley et al. 2022; Yan et al. 2022). Although the mechanisms for the linkage between NPP and R_s are still under discussion, R_s might increase with NPP because high NPP might accompany high Lf, and there is a positive relationship between Lf and R_s (Raich and Nadelhoffer 1989; Davidson et al. 2002; Hibbard et al. 2005). Such potential strong linkages between NPP and R_s are important from a practical viewpoint because long-term NPP measurements might enable us to understand interannual variations in R_s and its components without the direct measurements of R_s. Indeed, a previous study found strong correlations between annual NPP and R_s over a 5-year study period in grassland ecosystems (Yan et al. 2022).

This study was conducted to clarify whether interannual variations in R_s were linked with those of NPP in a Moso bamboo forest that shows large interannual variations in new shoot production. To do this, we measured NPP and R_s components in a Moso bamboo forest, central Taiwan over a 5-year period. Then, we (1) compared the size of the interannual variations between NPP and R_s components and (2) examined the correlation between year-to-year variations in NPP and R_s.

Materials and methods

Site

A 20 × 25 m study plot was established in a pure Moso bamboo forest with the area of about 18 ha in the Experiment Forest of National Taiwan University (23′40″ N, 120′48″ E), located in Nantou County, central Taiwan, in 2012. The study plot was located at 1120 m.a.s.l., and it experiences a subtropical monsoon montane climate with a mean annual air temperature of 18.6°C and mean annual precipitation of 2407 mm (Chiu et al. 2016; Tseng et al. 2017). The soil at the study site had a sandy-loam texture with a pH of 4.1, and understory vegetation was rare.

Conventional management practices, including annual selection cutting, fertilization and weeding in September–October, have been implemented since 1949 at this site. All treatments, such as felling and weeding, were halted within the experimental area during the study period. Stand culm density in the study plot was 3954 culms ha^{-1} in April 2012 with a mean diameter of breast height (DBH) of 9.0 cm. New culms sprouted annually in late April to early May. The annual stand culm densities after the appearance of new culms were 5632, 5793, 6000, and 7925 culms ha^{-1} in 2013, 2014, 2015, and 2016, respectively. Accordingly, total above-ground biomass was 27.3, 36.4, 39.7, 42.0, and 49.4 Mg C ha^{-1} in 2012, 2013, 2014, 2015, and 2016, respectively. Total below-ground biomass measurements were performed only in 2013, which was 33.7 Mg C ha^{-1}consisting of 6.5 and 27.2 Mg C ha^{-1} in roots and rhizomes, respectively. At the study site, dead and fallen culms were removed from the plot every year. More detailed site information is available in Hsieh et al. (2016) and Lin et al. (2017).

NPP and NEP definitions

According to previous studies (Clark et al. 2001; Luyssaert et al. 2007), NPP (Mg C ha^{-1} yr^{-1}) was derived from the annual increment in biomass (ΔB) (Mg C ha^{-1} yr^{-1}), consisting of the biomass of culms (ΔB_c), branches (ΔB_b), leaves (ΔB_l), roots (ΔB_r), and litterfall (Lf) (Mg C ha^{-1} $year^{-1}$) as follows:

$$\mathrm{NPP} = \Delta \mathrm{B} + \mathrm{Lf} \tag{1}$$

$$\Delta \mathrm{B} = \Delta \mathrm{B}_c + \Delta \mathrm{B}_b + \Delta \mathrm{B}_l + \Delta \mathrm{B}_r \tag{2}$$

Total NPP can be divided into above-ground productivity (ANPP) and below-ground productivity (BNPP). Here, ANPP (Mg C ha^{-1} yr^{-1}) consisted of culms (ΔB_c), branches (ΔB_b), leaves (ΔB_l), and litterfall (Lf) as follows:

$$\mathrm{ANPP} = \Delta \mathrm{B}_c + \Delta \mathrm{B}_b + \Delta \mathrm{B}_l + \mathrm{Lf} \tag{3}$$

Below-ground productivity (Mg C ha^{-1} yr^{-1}) was defined as follows:

$$\mathrm{BNPP} = \Delta \mathrm{B}_{r\_f} + \Delta \mathrm{B}_{r\_c} \tag{4}$$

where ΔB_{r_f} and ΔB_{r_c} are the increment in fine and coarse roots, respectively. In this study, we did not consider rhizome increments (Kobayashi et al. 2023) or the root litter effect (Osawa and Aizawa 2012) in the estimation of BNPP because of the difficulty in quantifying them.

NEP (Mg C ha^{-1} yr^{-1}) was defined simply using the following equation:

$$\mathrm{NEP} = \mathrm{GPP} - \mathrm{R}_{eco} - \mathrm{R}_h \tag{5}$$

in which

$$\mathrm{NPP} = \mathrm{GPP} - \mathrm{R}_{eco} \tag{6}$$

where GPP, R_{eco}, and R_h are the gross primary productivity (Mg C ha^{-1} yr^{-1}), total above- and below-ground autotrophic respiration (Mg C ha^{-1} yr^{-1}), and heterotrophic respiration (Mg C ha^{-1} yr^{-1}), respectively. Hence, NEP was calculated by

$$\mathrm{NEP} = \mathrm{NPP} - \mathrm{R}_h \tag{7}$$

Measurements

Above-ground biomass

Above-ground biomass was estimated from the DBH data measured from each culm in the experimental plot using allometric equations for leaves, branches, and culms developed near the study plot (Liu and Kao 1988). The DBH data were measured during an annual culm census after completion of new shoot sprouting (ca. late May) during the 5-year study period. The ΔB_c, ΔB_b, and ΔB_l (Mg C ha^{-1} yr^{-1}) were estimated from the annual biomass increments owing to new culm development in each year and the C contents in each organ at this site (Lin et al. 2017).

Litterfall measurement

Five litter traps (1 m^2) were set 1 m above the ground level in the plot to capture above-ground Lf consisting of leaves, twigs, and sheaths. The Lf was collected monthly from 2012 to 2016, and it was weighed after oven-drying at 70°C for 72 h. The monthly values converted using the C content at this site (Lin et al. 2017) were summed to determine the annual Lf (Mg C ha^{-1} yr^{-1}).

Root productivity

Root productivity, including both fine and coarse roots, was assessed using the root mesh method (Hirano et al. 2009). Five nylon meshes (measuring 10 cm in length, 20 cm in depth, with a mesh size of 1 mm) were randomly placed within the experimental plot each year. After 1 year, soil samples surrounding the meshes were extracted from the ground, forming soil blocks measuring 10 cm in length, 4 cm in width, and 20 cm in depth. Fine roots, with a diameter of <2 mm, were distinguished from coarse roots with a diameter of >2 mm. Subsequently, all root samples were oven-dried at 60°C for 72 h and weighed. Five new meshes were then randomly inserted into the soil following the collection of the previous year's meshes. On the basis of the methodology outlined by Hirano et al. (2009), root productivity (ΔB_r: Mg C ha^{-1} yr^{-1}), including both fine (ΔB_{r_f}) and coarse (ΔB_{r_c}) root production, was calculated using the dry weight of roots (g), the projected area of soil blocks (10 cm × 4 cm), and the root carbon contents determined at the site (Lin et al. 2017).

Soil CO_2 efflux

The R_s was measured using a portable, closed, dynamic infrared gas analyzer (EGM–4 CO_2 gas analyzer, PP Systems, MA, U.S.A.) equipped with a chamber that was 15 cm high and 10 cm in diameter (SRC–1, PP Systems, MA, U.S.A.). Twenty measurement locations were selected randomly from the plot at the study site. In each measurement location, a polyvinyl chloride (PVC) collar (10 cm internal diameter, 5 cm height) was inserted in the soil. Measurements were recorded every 1–2 months during the 5-year period, with three replicates at each point, and averaged. The measurements were carried out during the daytime on a single day (07:00–14:00).

The R_h was determined by the trenching method (Kuzyakov 2006; Bond-Lamberty et al. 2011). Three 1 × 1 m trenching plots outside the study plot were prepared in December 2012, which were surrounded by ditches of 50–70 cm depth and 40 cm width. The trenches prevented other live roots and rhizomes from extending into the trenching plots. Three PVC collars were placed in the center of each trenched plot to minimize boundary effects. We recorded R_s every 1–2 months from February 2013 to March 2016. We assumed that R_s in the trenching plots after August 2013 was available to represent R_h, because the ratio of the trenching-plot R_s to the 20-location R_s showed stable values (≈0.4) after August 2013. Thus, we estimated the R_h data before August 2013 by multiplying the R_s measured in the 20 locations by the mean R_h/R_s ratio (0.4). This study calculated the annual R_h and R_s for each year (Mg C ha^{-1} yr^{-1}) from the arithmetic mean of the monthly measurements of R_s and R_h, respectively, to estimate annual R_a (= R_s − R_h) and NEP (= NPP − R_h). Note that the arithmetic means basis annual R_s corresponded well to annual R_s estimated from the interpolated R_s using modeled R_s and continuous measurements of environmental variables such as soil temperatures at this site (Hsieh et al. 2016). More detailed information on the R_s-related methodology at this site is provided by Hsieh et al. (2016) and Lin et al. (2017).

Statistical analysis

This study used an annual value basis. The coefficient of variation (CV) was calculated to estimate the interannual variability in NPP and R_s components. We calculated the CV of each component as CV = S.D./mean, where mean and S.D. represent the mean and standard deviation of each component (Mg C ha^{-1} yr^{-1}) across 5 years (2012–-2016). To assess whether the interannual variation differed between NPP and R_s components, we compared the CVs of R_s, R_a, and R_h with BNPP, ANPP, and NPP using the asymptotic test in the "cvequality" package (Marwick and Krishnamoorthy 2019) in R (ver. 4.3.2; R Core Team 2023). This test assesses whether the CVs across multiple groups are significantly different by estimating a population CV (i.e. a combined measure of variability from all sampled data) and comparing it to each group's CV. The test statistic, *D′AD*, quantifies the deviation of each group's CV from the estimated population CV, allowing us to calculate a p-value to assess the statistical significance. Spearman rank correlation was conducted to assess the association among NPP (ANPP and BNPP) and R_s components using the "cor()" function in R, with the method specified as "spearman".

Results

We found large year-to-year variations in NPP, while R_s, R_a, and R_h showed small year-to-year variations (Figure 1). NPP ranged between 5.0 and 15.5 Mg C ha^{-1} yr^{-1}. The year-to-year variations in NPP were mainly caused by ANPP rather than BNPP. ΔB_c was the dominant component in ANPP and accounted for 26.3%–67.4% of ANPP with an average of 53.3%. In contrast, R_s showed a smaller range (11.2–16.1 Mg C ha^{-1} yr^{-1}) than that of NPP. In particular, R_h exhibited minor year-to-year variations with a range of 4.4–5.6 Mg C ha^{-1} yr^{-1}.

The CV in NPP (41.3%) was larger than that of R_s (17.2%) (Figure 2). The CV values in ANPP (47.5%) and its components (27.0%–62.6%) were mostly larger than that of BNPP (28.7%), R_s (17.2%), R_a (22.4%), and R_h (10.1%). R_s and its components (R_a and R_h) had significantly lower CVs compared with ANPP and NPP ($D'AD = 7.51$, $p = 0.05$ and $D'AD = 9.64$, $p = 0.02$, respectively). There was no significant difference in CV between R_s, R_a, R_h, and BNPP ($D'AD = 3.61$, $p > 0.05$).

Strong linkages between NPP and R_s components were not found in the interannual variations at this site (Table 1). However, marginal correlations were found between R_a, R_s, and some NPP components (Table 1). R_s had a small positive correlation with ΔB_c ($\Delta = 0.9$, $p < 0.1$), ANPP ($\Delta = 0.9$, $p < 0.1$), and NPP ($\Delta = 0.9$, $p < 0.1$). Additionally, R_a had a small positively correlation with Lf ($\Delta = 0.9$, $p < 0.1$) and ΔB_{r_f} ($\Delta = 0.9$, $p < 0.1$). R_h was not correlated with NPP components. In additional analysis, Pearson correlation tests supported

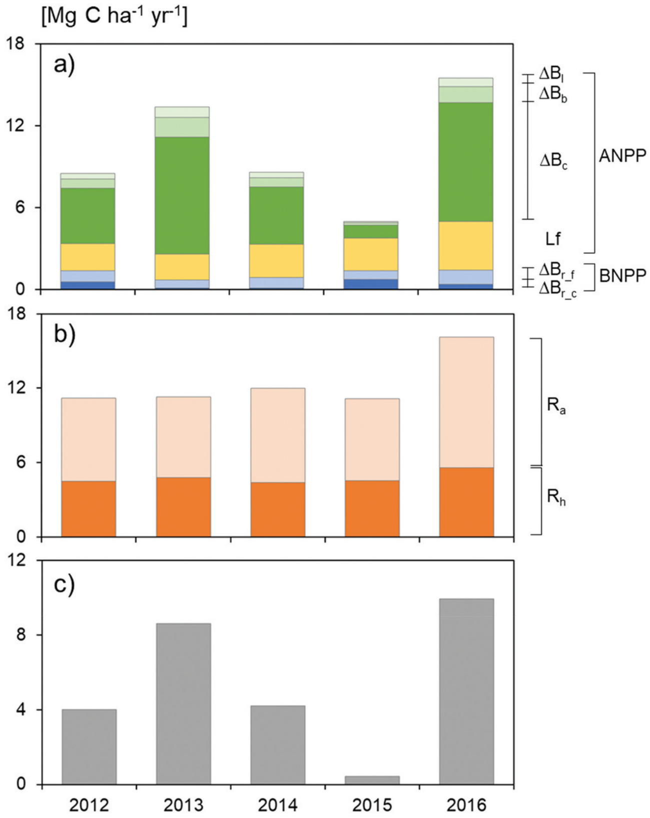

Figure 1. Year-to-year fluctuations in a) net primary production (NPP) and b) soil CO_2 efflux (R_s) components with c) net ecosystem production (NEP) for 5-years. See abbreviations in Materials and Methods section.

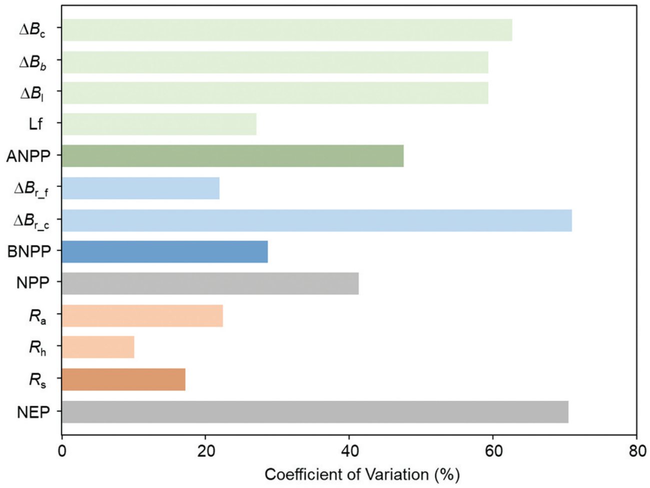

Figure 2. Coefficient of variations (CVs) in net primary production (NPP) and soil CO_2 efflux (R_s) components with net ecosystem production (NEP). See abbreviations in Materials and Methods section.

the positive correlation between R_a, Lf, and ΔB_{r_f}, but they did not support the correlation between ΔR_s, ΔB_c, ANPP, and NPP (Supplementary Table S1).

Discussion

Size of interannual fluctuations in NPP and R_s

We assumed that the large interannual variations in NPP (mainly attributable to ANPP) might be accompanied by similar R_s interannual variations; however, we did not find synchronized interannual variations between NPP and R_s (Figures 1 and 2). Although we cannot identify the mechanisms for the large and small interannual variations in NPP and R_s, respectively, such tendencies also can be inferred from previous studies (Supplementary Table 2C and 2F). These studies showed that the interannual CV of NPP was approximately 2%–38% with a mean of 20.3% in various types of woody forest ecosystems (Supplementary Table 2C), which was larger than that of most R_s observations in woody forests (CV = 11.1%) (Supplementary Table 2F). Our interannual CV in NPP (41.3%) was close to the upper range of the previous studies. The interannual CV for Lf at this site (27.0%) was also in the top 15% of

Table 1. Spearman's correlation coefficients and significance (ms: $p < 0.10$, *: $p < 0.05$) among NPP and R_s components ($n = 5$). Here, above-ground net primary production (ANPP) is the sum of annual biomass increment of culm (DB_c), branch (DB_b), leaves (DB_l), and litter fall (lf). Below-ground net primary production (BNPP) is the sum of fine root (DB_{r_f}) and coarse root (DB_{r_c}) productions. Annual soil CO_2 effluxes (R_s) consists of heterotrophic (rh) and autotrophic (ra) respiration. Net ecosystem production (NEP) is calculated from ANPP + BNPP − Rh.

	DB_c	DB_b	DB_l	Lf	ANPP	DB_{r_f}	DB_{r_c}	BNPP	NPP	R_a	R_h	R_s	NEP
DB_c	1.00												
DB_b	**0.90** $^{\text{ms}}$	1.00											
DB_l	**0.90** $^{\text{ms}}$	**1.00 ***	1.00										
Lf	0.30	−0.10	−0.10	1.00									
ANPP	**1.00 ***	**0.90** $^{\text{ms}}$	**0.90** $^{\text{ms}}$	0.30	1.00								
DB_{r_f}	0.30	−0.10	−0.10	0.70	0.30	1.00							
DB_{r_c}	−0.70	**−0.90** $^{\text{ms}}$	**−0.90** $^{\text{ms}}$	0.20	−0.70	0.30	1.00						
BNPP	0.00	−0.40	−0.40	0.70	0.00	0.70	0.70	1.00					
NPP	**1.00 ***	**0.90** $^{\text{ms}}$	**0.90** $^{\text{ms}}$	0.30	**1.00 ***	0.30	−0.70	0.00	1.00				
R_a	0.40	0.00	0.00	**0.90** $^{\text{ms}}$	0.40	**0.90** $^{\text{ms}}$	0.10	0.60	0.40	1.00			
R_h	0.60	0.50	0.50	0.10	0.60	0.10	−0.10	0.40	0.60	0.00	1.00		
R_s	**0.90** $^{\text{ms}}$	0.70	0.70	0.60	**0.90** $^{\text{ms}}$	0.50	−0.60	0.10	**0.90** $^{\text{ms}}$	0.70	0.30	1.00	
NEP	**1.00 ***	**0.90** $^{\text{ms}}$	**0.90** $^{\text{ms}}$	0.30	**1.00 ***	0.30	−0.70	0.00	**1.00 ***	0.40	0.60	**0.90** $^{\text{ms}}$	1.00

The significance of bold values is $p < 0.10$ (ms) and $p < 0.05$ (*).

observations in previous studies (range of 5%–47%, mean of 15.6%) (Supplementary Table 2A). In contrast, interannual CV in R_s (17.2%) at this site was closer to the mean of previous R_s studies (11.1%) (Supplementary Table 2).

The trend from the Moso bamboo forest was identical to those of woody forest ecosystems (i.e. interannual CV in NPP was larger than that of R_s). However, the Moso bamboo was unique in the size of the year-to-year fluctuations of the NPP. Because ANPP accounted for more than half of NPP at this site, the large interannual variations in NPP were caused, first, by the 2-year cycles of new shoot production (Lin et al. 2022) and, second, by episodic events such as drought in the early spring. According to the biennial cycles of Moso bamboo new shoot production, 2015 should have been "on-year", but we observed the smallest NPP during the study period, probably owing to below-average rainfall during the period April–June 2015 (around 50% of rainfall in normal years). Such reduced rainfall might lead to soil drought conditions, potentially suppressing photosynthesis and thereby declining new shoot production. A previous study reported that severe summer drought significantly reduced Moso bamboo productivity (Song et al. 2017). A 20-year long-term monitoring project in a Moso bamboo forest also suggested the biennial cycles could be disturbed by environmental conditions (Li et al. 1998), although the mechanisms are still uncertain. Further studies including long-term monitoring with environmental variables are needed to clarify the factors disturbing the biennial cycles of the new shoot productions.

Possible mechanisms for the marginal linkage between NPP and R_s

Although we did not find a strong relationship between the NPP and R_s components, we observed marginal correlations between ΔB_{r_f}, Lf, and R_a (Table 1, Supplementary Table S1). Although the mechanism of their marginal correlations was unclear, some previous studies might imply the mechanism behind the correlations. First, fine roots substantially contributed to total R_a in woody forests due to their high productivity (Desrochers et al. 2002; Chen et al. 2009; Makita et al. 2012; Hirano et al. 2023), suggesting ΔB_{r_f} could affect R_a. However, contribution of fine roots to total R_a is still unknown in Moso bamboo forests; further sophisticated studies covering separations of R_a components with root phenology monitoring (Kume et al. 2018; Cui et al. 2021; Hirano et al. 2023) are needed there. Second, the large amount of Lf occurring biennially (or every few years) in the period between April and May might affect R_a through the changes in culm-leaf age structure at the stand level. Note that Moso bamboo leaves have a 2-year lifespan and that new first-year leaves can have higher photosynthesis rates than those of 2-year-old leaves (Huang et al. 1989; Lin et al. 2022). The possible biennial (or every few years) increases in first-year leaves at the stand level could increase R_a, probably because of increased total below-ground C allocation from the new first-year leaves at the stand level (Raich and Nadelhoffer 1989; Davidson et al. 2002; Hibbard et al. 2005). The culm-leaf age structure at the stand level might be a key for understanding the relationship Lf and R_a.

Although Wang et al. (2023) showed week positive relationships between R_h and NPP components, such as Lf probably due to enhanced microbial activities, the interannual fluctuations in R_h were largely independent of the NPP components in this study, which suggested that current-year NPP components had little effect on R_h at this site. We should note that we have only a 5-year dataset, which is not statistically adequate to understand the linkage between NPP and R_s components. Further long-term monitoring would enable us to clarify the mechanisms linking NPP and R_s components, including the effect of time lags between Lf productions and microbial activities. Note that more than 1 year is needed to complete the decomposition of Moso bamboo organs (Orrego et al. 2023). Additionally, stable isotope labeling could be a useful way to understand the linkage between above- and below-ground C dynamics (Dannoura et al. 2011; Rog et al. 2021).

Implications for NEP estimates in Moso bamboo forests

The inconsistent interannual variations in NPP and R_s components observed in this study (Figures 1 and 2) suggest that a simpler method could be applied to estimate NEP in Moso bamboo forests. Although the regular and irregular occurrences of large interannual variations in NPP indicate that it is important to monitor NPP (i.e. ANPP), the constant R_h observed in this study suggests that it is possible to use the constant values of R_h for NEP estimates in Moso bamboo forests. Actually, we could reproduce 5-year NEP variations using the constant values of R_h (i.e. 5-year mean R_h) plus measured NPP with high accuracy, i.e. the mean difference between measured and estimated NEP of 0.3 Mg C ha^{-1} yr^{-1}

with a tight relationship between measured and estimated NEP ($y = 1.1x - 0.5$, y: estimated NEP; x: measured NEP, $R^2 = 0.99$).

Recently, NPP has been estimated from remote sensing techniques such as airborne LiDAR, as these technologies can provide forest stand structural data (e.g. stand density and vegetation height), which allows for estimating annual biomass increment (e.g. Næsset and Gobakken 2005; Dial et al. 2021). Although we need a careful discussion if these techniques can be applied to Moso bamboo forests, these techniques might enable us to estimate regional and global scale monitoring for the interannual fluctuations more easily compared with the plot-based intensive measurements for NPP and ANPP adopted in this study. Because Moso bamboo forests are distributed over large areas in East Asia (Song et al. 2017), fluctuations in Moso bamboo C cycling may affect the regional-scale C balances. Furthermore, Moso bamboo habitat could be enlarged to the north under future global warming scenarios (Takano et al. 2017). Currently, although regional-scale assessments for land-surface C cycling have considered various types of vegetation (Kondo et al. 2017; Sha et al. 2022; Xi et al. 2023), they have not considered bamboo forests explicitly.

This study had several limitations. First, there is a level of uncertainty in our BNPP measurements in Moso bamboo forests. Our study did not consider the year-to-year fluctuations in rhizome production. Kobayashi et al. (2023) reported the importance of rhizome production, which accounted for 9.5% of DB. Furthermore, it is possible that the rhizome production could contribute to 20–30% of total NPP at this site, which was roughly estimated from a rhizome turnover rate ($= 0.11$ g g^{-1}) reported by Kobayashi et al. (2023) and rhizome biomass at this site. Second, the management intensity level also can substantially affect NEP. This study was conducted under the transitional management condition, i.e. conventional managements such as fertilization and harvesting were performed before our measurements and the management practices were stopped during our study period. Such treatments could affect C balances in this study, as a recent study suggested that unmanaged Moso bamboo stands could have low C sequestration ability compared with fertilized well-managed stands (Yuan et al. 2023). Changes in culm density resulting from harvesting could also affect NEP as a consequence of the density-dependency effects of new shoot production (Lin et al. 2022). Further studies, including long-term monitoring of the rhizome system under the different levels of management practices, are needed to clarify the linkage between ANPP, BNPP, and R_s in Moso bamboo forests. While monitoring the rhizome system of Moso bamboo remains challenging, the use of larger-sized root windows (Silva and Beeson 2011) than those of the A4-sized optical scanner method (e.g. Dannoura et al. 2008; Kume et al. 2018; Endo et al. 2019; Tamura et al. 2022) and/or radar systems (Hirano et al. 2012) might enable us to observe long-term BNPP including the rhizome system.

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Disclosure statement

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