



Nitrogen addition promotes foliar litterfall and element return in a subtropical forest, southwestern China

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Abstract Nitrogen deposition has a considerable impact on biogeochemical cycling in terrestrial ecosystems. However, how litter production and element return respond to N addition remains poorly understood in nitrogen-rich subtropical regions. In this study, a 4-year nitrogen addition experiment explored its effects on foliar litter production and carbon, nitrogen and phosphorus in a subtropical *Michelia wilsonii* forest. A clear seasonal pattern in foliar litterfall was observed, regardless of nitrogen treatments, with a peak in spring and a smaller one in autumn. Foliar litter increased with increasing nitrogen but did not affect litter carbon concentrations and often decreased nitrogen and phosphorus concentrations. The effect of nitrogen addition was dependent on time (month/year). Carbon, nitrogen and phosphorus return showed similar bimodal seasonal patterns. Nitrogen

addition increased carbon and nitrogen return but did not affect phosphorus. Our results suggest that the addition of nitrogen stimulates carbon and nutrient return via litterfall.

Keywords Nitrogen addition · Litterfall · Seasonal patterns · Element return · Subtropical forest

Introduction

Forest litterfall is a key pathway connecting above- and below-ground ecological processes and has a crucial role in maintaining long-term carbon (C) and nutrient balance (Vitousek and Sanford 1986). In forests, over 80% of the carbon fixed via photosynthesis falls as litter and most of the nitrogen (N) and phosphorus (P) absorbed by plants is derived from decomposed litter (Bowden et al. 2019; Jia et al. 2019). The quality and quantity of C, N, and P from foliar litter are important in regulating the biogeochemical cycle in forest ecosystems (Jasinska et al. 2020).

Atmospheric N deposition has been increasing because of the rapid development of agriculture and industry in China (Liu et al. 2013; Stevens 2019). As one of the most important research fields of global change, increasing atmospheric N deposition can alter ecosystem carbon and nutrient cycling (Cabal et al. 2017; Liu et al. 2021a). Changes in litterfall and concentrations of C and nutrients, which is a vital component of biogeochemical cycling, can reflect ecosystem nutrient status and acquisition mechanisms (Liu et al. 2016; Wen et al. 2020). Recent meta-analyses indicated that N addition stimulates plant growth and alters leaf nutrient contents (Tian et al. 2018; You et al. 2018b). The effects of the addition of N on litterfall, however, have been inconsistent, depending on ecosystem types, site conditions, and levels of N addition (Cabal et al. 2017; Lu et al.

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2018; Mao et al. 2020). For example, the addition of 30 and 60 kg N ha⁻¹ a⁻¹ accelerated litterfall production in a Moso bamboo plantation, while 90 kg N ha⁻¹ a⁻¹ had no effect (Zhang et al. 2017a).

Litter nutrient return varies with biotic (species and composition) and abiotic factors (climate and soil fertility) (You et al. 2017; Shen et al. 2019; Park et al. 2020). Earlier studies have shown that N addition-induced changes in soil properties affected litter production, which in turn influenced nutrient return in forest ecosystems (Fu et al. 2019; Li et al. 2021). In addition to altering the amount of litterfall, the addition of N also affects litter quality, and further regulates litter nutrient return (Chen et al. 2015; Mao et al. 2020). For example, litter nutrient concentrations are regulated by the absorption and dilution by plants under N addition (Zhang et al. 2017b; Feng et al. 2019). However, current N deposition studies have scarcely focused on litterfall and nutrient return, particularly in medium- and long-term (3–10 years) studies. A clearer understanding of the effects of N deposition on biotic and abiotic factors and the dynamics of litterfall and nutrient return is essential for accurately modeling and predicting C and nutrient cycling in N-enhanced subtropical regions.

Soils of the western edge of the Szechwan Basin in southwest China are undergoing pronounced N accumulation because of heavy rainfalls and active N input (Xu et al. 2013). Previous studies have indicated that N addition significantly inhibited litter decomposition in this area (Liu et al. 2018). However, the effects of the addition of N on the dynamic of litter production and element return remain unknown in the unique subtropical ecosystems in this area. A 4-year experiment was conducted to determine the effect of N addition (0 controls, 20 and 40 kg N ha⁻¹ a⁻¹) on foliar litter production and on C, N and P return in a subtropical *Michelia wilsonii* Finet & Gagnepain forest. The questions addressed were: (1) Does the addition of N affect foliar litterfall and C, N and P fluxes accompanying litterfall? (2) What are the roles of seasonal changes in regulating N effects? It was hypothesized that (1) N addition would increase foliar litter production, C and nutrient concentrations and returns; (2) the effect of N addition would be dependent on seasonal changes of biotic and abiotic factors.

Materials and methods

Study site

This study was conducted in a subtropical forest stand at the Forest Research Station of Lingyan Mountain of the Sichuan Agricultural University on the western edge of the Szechwan Basin (31°01′–31°04′ N, 103°37′–103°43′ E, 896–1320 m a.s.l.). The research area is characterized by a temperate

continental monsoon climate. The mean annual temperature is 14.4 °C, with a minimum of 4.9 °C in January and a maximum of 23.5 °C in August. The mean annual precipitation is approximately 1475 mm, with 80.9% occurring in the growing season (May to September) (Fig. 1). This stand is mainly dominated by *Michelia wilsonii* (> 80% of the basal area), a rare native species of the Szechwan Basin. The canopy cover is approximately 0.9 and the average diameter at breast height (DBH) is 18.9 cm. The soil is a ferralsol with old alluvial yellow loam according to the Chinese Soil Taxonomy (RGCST 2001). The organic C, N, P and pH in the upper 20-cm layer were 15.8 g kg⁻¹, 1.9 g kg⁻¹, 0.3 g kg⁻¹ and 5.7, respectively (Liu et al. 2018).

Experimental design

In November 2015, nine 10×10 m plots at 10-m intervals were established. According to the ambient atmospheric wet N deposition (36.2 kg N ha⁻¹ a⁻¹) in the study site (Yang et al. 2018), three treatments, three replicate plots per treatment, were set up: controls (0 kg N ha⁻¹ a⁻¹), low-N addition (20 kg N ha⁻¹ a⁻¹), high-N addition (40 N ha⁻¹ a⁻¹). Both low-N and high-N addition simulate the scenarios that wet N deposition would be approximately increased by 50% and 100%, respectively. Our previous study has shown that both NH₄⁺ and NO₃⁻ account for about 80% of the wet N deposition in the study area (Yang et al. 2018). In addition, a recent study has reported that atmospheric wet N deposition is dominated by almost equal parts NH₄⁺ and NO₃⁻ in China (Yu et al. 2019). Therefore, a solution of NH₄NO₃ was sprayed on the forest surface once a month from December 2015 to December 2019. NH₄NO₃ was weighed, and dissolved in 10 L of water; each control plot received 10 L of nitrogen-free water. The total solution applied per year to

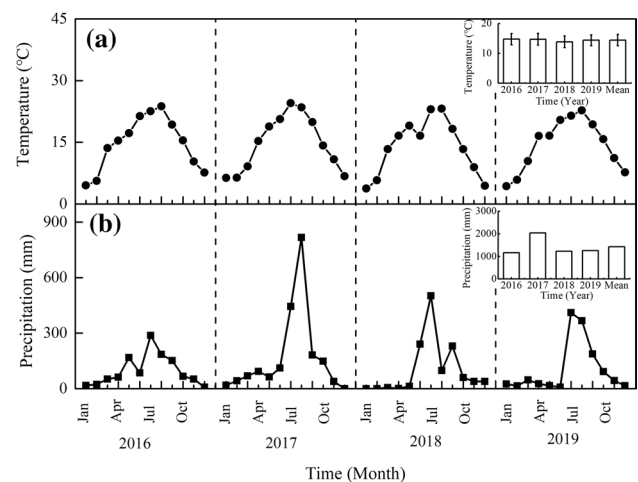


Fig. 1 Monthly dynamics of **a** temperature and **b** precipitation from 2016 to 2019 in the study area

each plot was equivalent to 1 mm of precipitation, less than 1% of the total annual precipitation (1475 mm). The small amount of additional water was considered to have no effect on the rainfall distribution pattern (see Zhuang et al. (2020) for further details).

Litterfall collection and chemical analysis

Eighteen litter traps (two traps/plot) were set in the plots 2-m from the quadrat boundary. The litter traps were funnel shaped with a 1-m diameter opening and a collection area of 0.78 m². The litter of each trap was collected monthly from January 2016 to December 2019. Several studies have demonstrated that forest litter production is dominated by foliage, and the other components have great spatial heterogeneity (You et al. 2017; Zhu et al. 2019). Our prior study also showed that litter production is mainly from foliar input in this forest stand (Pu et al. 2019). As a result, this study only focused on the foliar litter of the dominant tree species. Litter production was estimated after oven drying (65 °C, 72 h) to constant weight. Organic C, total N and total P concentrations were measured using dichromate oxidation, Kjeldahl determination (KDN, Top Ltd., Zhejiang, China) and phosphomolybdenum yellow spectrophotometry (TU-1901, Puxi Ltd., Beijing, China), respectively (Zhuang et al. 2018). The amount of C, N and P returned from forest litter was calculated by multiplying the monthly litter production by the corresponding C, N and P concentrations:

$$\text{Element return} = \text{Litter production} \times \text{Element concentration} \quad (1)$$

Data and statistical analyses

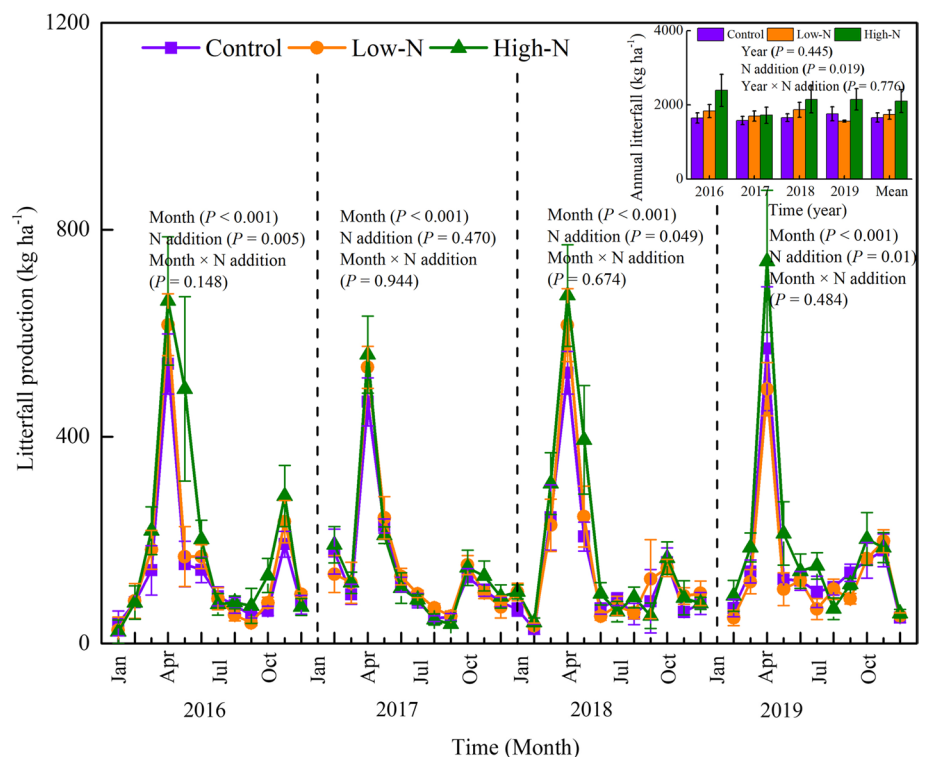
Repeated measure analysis of the variance was used to test the effect of N addition, time (month or year), and their interaction on foliar litter production and element (C, N and P) concentration and return. A correlation analysis assessed the relationships between the measured variables and environmental factors. Partial least squares (PLS) with coefficients and variable importance were performed to assess the relative importance of climate factor, element concentration and litter production to the element return under N addition. Statistical tests were considered significant at the $P < 0.05$ level. All statistical analyses were performed with SPSS software (SPSS 25.0 for windows; SPSS Inc., Chicago, IL, USA) and SIMCA 14.1 (Umetrics, Umeå, Sweden). Graphs were drawn with Origin (version 9.0 and 2019b).

Results

Dynamics of foliar litter production

There was a significant seasonal variation in foliar litterfall (Fig. 2). Regardless of N treatments, the monthly foliar litter

Fig. 2 Monthly dynamics of *M. wilsonii* foliar litter production; control (0 kg N ha⁻¹ a⁻¹), low-N addition (20 kg N ha⁻¹ a⁻¹), high-N addition (40 kg N ha⁻¹ a⁻¹), values are means \pm standard errors



production showed a bimodal pattern, with a major peak in spring (April) and a minor one in autumn (October–November) (Fig. 2). Annual production was 1957.2 kg ha⁻¹, 1665.1 kg ha⁻¹, 1890.8 kg ha⁻¹ and 1823.2 kg ha⁻¹, respectively, in 2016, 2017, 2018 and 2019 (Fig. 2). The addition of N significantly increased litter production (Fig. 2). Particularly, high-N addition increased annual litterfall by 45.3%, 9.3%, 29.8%, and 22.0%, respectively. However, time (year) did not affect foliar litter production (Fig. 2).

Dynamics of C, N and P concentrations

C, N and P concentrations of the foliar litter showed monthly and yearly variations regardless of N treatments (Fig. 3). C concentration did not change monthly but there were inter-annual variations (Figs. 3 and 4). N and P concentrations were higher in the warm months (June to October) compared to the other seasons (Fig. 3). The annual average concentrations of

C, N and P were 363.6–468.5 g kg⁻¹, 11.7–13.4 g kg⁻¹ and 0.6–0.8 g kg⁻¹, respectively (Fig. 3). The addition of N did not affect the concentration of C in the litter but it decreased N and P (Fig. 4). The effect of N addition on litter N and P concentrations was regulated by time (month or year) (Figs. 3 and 4).

3.3 Dynamics of C, N and P return.

Like litter production, the monthly fluctuations in C, N and P showed a bimodal pattern under both treatments, with a major peak in spring and a minor one in autumn (Fig. 5). Regardless of the addition of N, annual C, N, and P return were 672.2–854.1 kg ha⁻¹ a⁻¹, 19.9–22.3 kg ha⁻¹ a⁻¹, and 1.0–1.4 kg ha⁻¹ a⁻¹, respectively (Fig. 5). The addition of N increased foliar litter C and N return but did not affect P (Figs. 4 and 5). High-N addition increased annual C return by 32.2%, 16.0%, 24.2%, and 20.2% in 2016, 2017, 2018, and 2019, respectively (Fig. 4). In general, the interaction between the addition of N and time (year and month) had no effect on element return (Figs. 4 and 5).

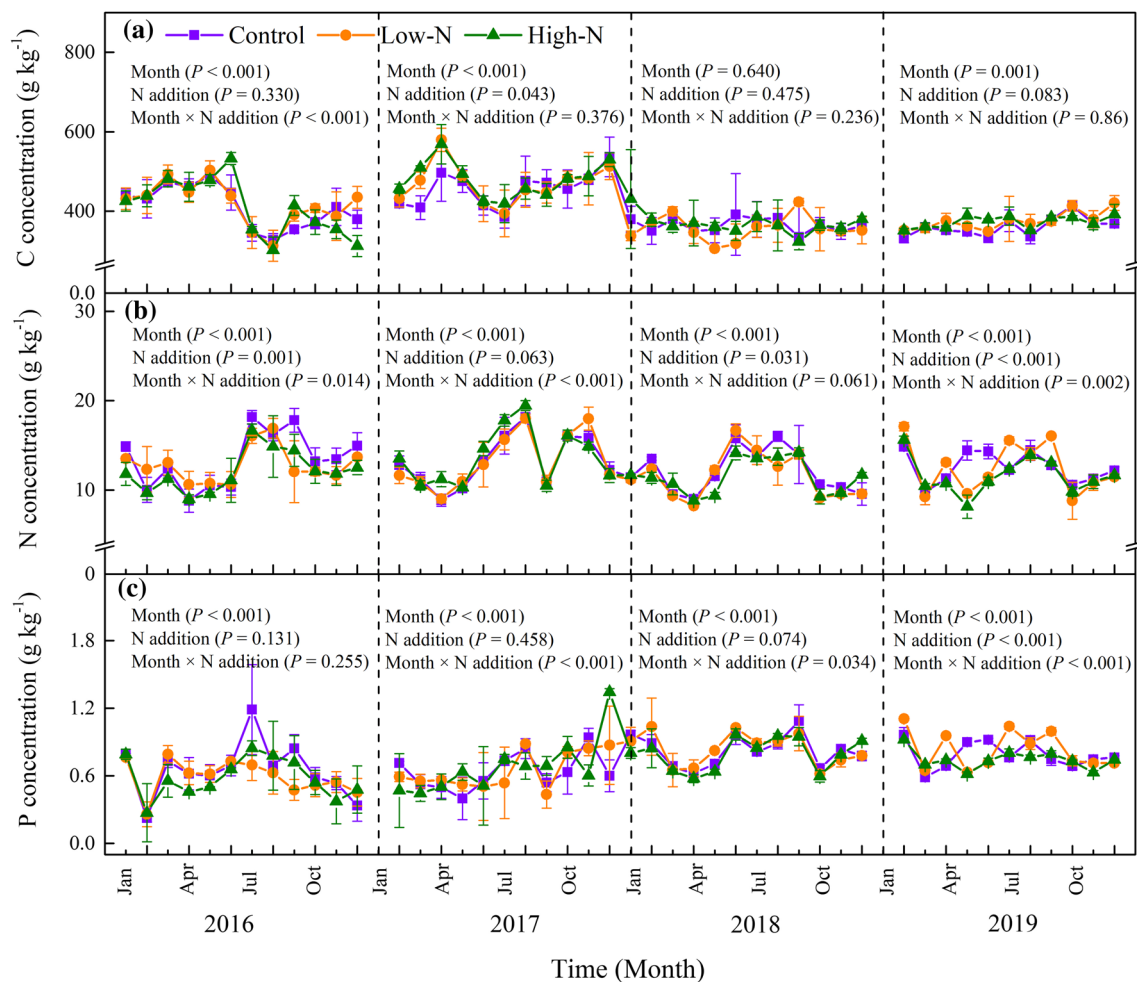
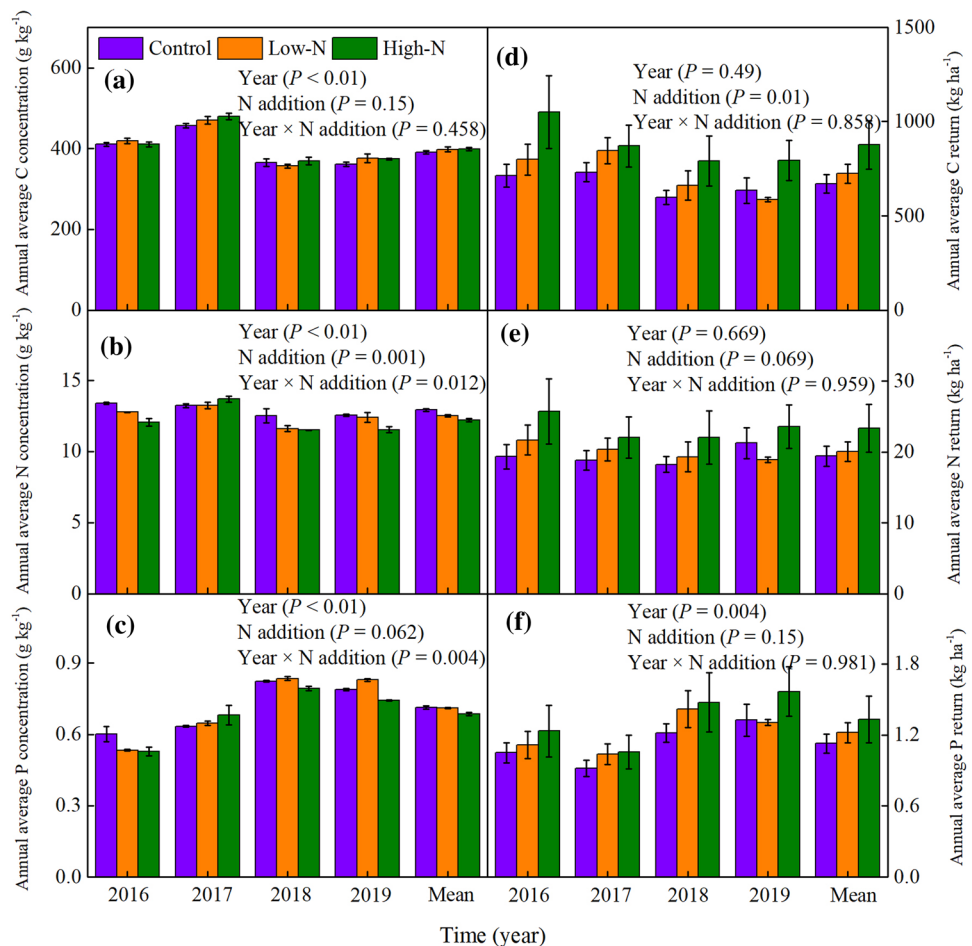


Fig. 3 Monthly fluctuations of carbon (C), nitrogen (N) and phosphorus (P) concentrations in *M. wilsonii* forest under different N additions; control (0 kg N ha⁻¹ a⁻¹), low-N addition (20 kg N ha⁻¹ a⁻¹), high-N addition (40 kg N ha⁻¹ a⁻¹); values are means \pm standard errors

Fig. 4 Annual fluctuations of carbon (C), nitrogen (N) and phosphorus (P) in *M. wilsonii* forest under different N additions; control (0 kg N ha⁻¹ a⁻¹), low-N addition (20 kg N ha⁻¹ a⁻¹), high-N addition (40 kg N ha⁻¹ a⁻¹), values are means \pm standard errors



Relation between element return and climate factors

Correlation analysis showed that temperature was positively correlated with litter N concentration and precipitation was negatively correlated with litterfall, C, N and P return (Fig. 6). Litter production was negatively correlated with N and P concentrations (Fig. 6). In addition, PLS analysis showed that N addition induced increases in element return were attributed to litter production rather than climate or element concentration (Fig. 7).

Discussion

Effects of N addition on litterfall

A recent synthesis indicated that litterfall of evergreen broadleaved forests accounted for 37% of total global forest litterfall (Shen et al. 2019). Therefore, quantifying the leaf litterfall of subtropical evergreen broadleaved forests is crucial to understanding the global biogeochemical cycle. The litter production noted in this study is similar to observations of other evergreen broad-leaved forests, such as

Dendrocalamus brandisii (Munro) Kurz (2072 kg ha⁻¹ a⁻¹) (Bahru and Ding 2020) and *Cunninghamia lanceolata* (Lamb.) Hook. (2655 kg ha⁻¹ a⁻¹) (Guo et al. 2015) in subtropical China but much lower than observed in other subtropical forests (Yang et al. 2005; Zhou et al. 2016; Park et al. 2020). The relatively low litter production in this study may be because only foliar litter was collected but other tissues (flowers, branches, fruits) were excluded (You et al. 2017). In addition, litter production varies with forest types (You et al. 2017; Shen et al. 2019) and depends on community composition, species abundance and basal area (Huang et al. 2018; Park et al. 2020).

The addition of N resulted in greater soil nutrient availability, leading to an increase in litter production (Tu et al. 2011; Li et al. 2021). Consistent with previous studies (Maaroufi et al. 2016; Zhang et al. 2017a; Zhao and Zeng 2019), and our initial hypothesis, the addition of N increased litter production. In contrast, N addition decreased litter production in a *Larix gmelinii* (Rupr.) Kuzen. forest and a *Cinnamomum camphora* (L.) Presl forest (Lv et al. 2013; Fu et al. 2019). Meta-analysis suggests that the response to N addition by litter is closely dependent upon plant functional types (Xia and Wan 2008). For example, the positive effect

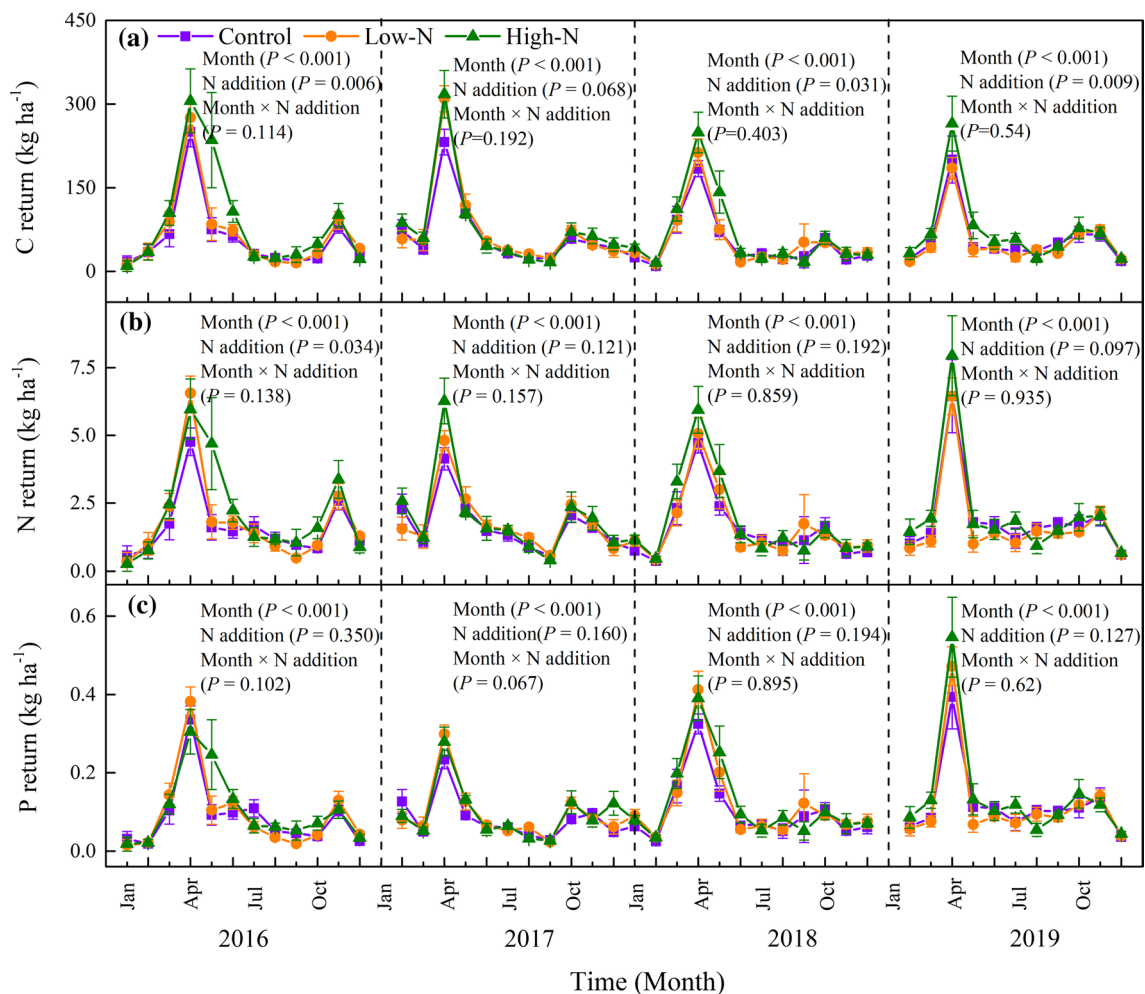


Fig. 5 Monthly fluctuations of carbon (C), nitrogen (N) and phosphorus (P) return in *M. wilsonii* forest under different N additions; control (0 kg N ha⁻¹ a⁻¹), low-N addition (20 kg N ha⁻¹ a⁻¹), high-N addition (40 kg N ha⁻¹ a⁻¹), values are means \pm standard errors

of N addition on broadleaved tree biomass is greater than that of coniferous trees (Xia and Wan 2008). Nutrient-limited conditions determine the response of plants to N addition (You et al. 2018b). In a N-rich forest, excessive N may acidify soils which in turn could reduce litter production (Fu et al. 2019). Further, the effects of adding N on stoichiometric and reabsorption efficiency of N and P in leaves varied with nutrient-limited conditions (You et al. 2018a, 2018b). The effects of N addition could also be modulated by the level of N addition. A previous study noted that low dose and medium dose N (30 and 60 kg N ha⁻¹ a⁻¹) increased litterfall production, whereas high dose N (90 kg N ha⁻¹ a⁻¹) addition had no effect in a *Moso* bamboo plantation (Zhang et al. 2017a).

Most subtropical forests are characterized by strong seasonality in leaf litterfall (Zhang et al. 2014; Park et al. 2020; Peng et al. 2020). Our results show a similar clear bimodal seasonal litterfall with a major peak in spring and a minor one in autumn. In addition, significant inter-annual

differences in climate variables (e.g., temperature and rainfall) have potential to alter the phenology of tree species, which in turn may result in irregular production of leaves, flowers, and fruit, and ultimately affects inter-annual variations in litterfall (Ehbrecht et al. 2021). However, there were no inter-annual differences in litterfall detected in this study, which could be due to the lack of reproductive litter, i.e., flowers and fruit (You et al. 2017).

Effect of the addition of N on C and nutrient concentration

The average concentrations of C, N, and P were 413.7 g kg⁻¹, 12.6 g kg⁻¹, and 0.6 g kg⁻¹, respectively. Litter C concentration is lower than in other subtropical evergreen forests (Ge et al. 2017; Zeng et al. 2017; Huang et al. 2021). However, N and P concentrations were comparable to the average values in Chinese forest ecosystems (Tang et al. 2015). In addition, higher concentrations of N and P in the warm season (June

Fig. 6 Correlation analysis of N addition, month, temperature, precipitation, litterfall, concentration and return of C, N, P; asterisks indicate significant differences (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

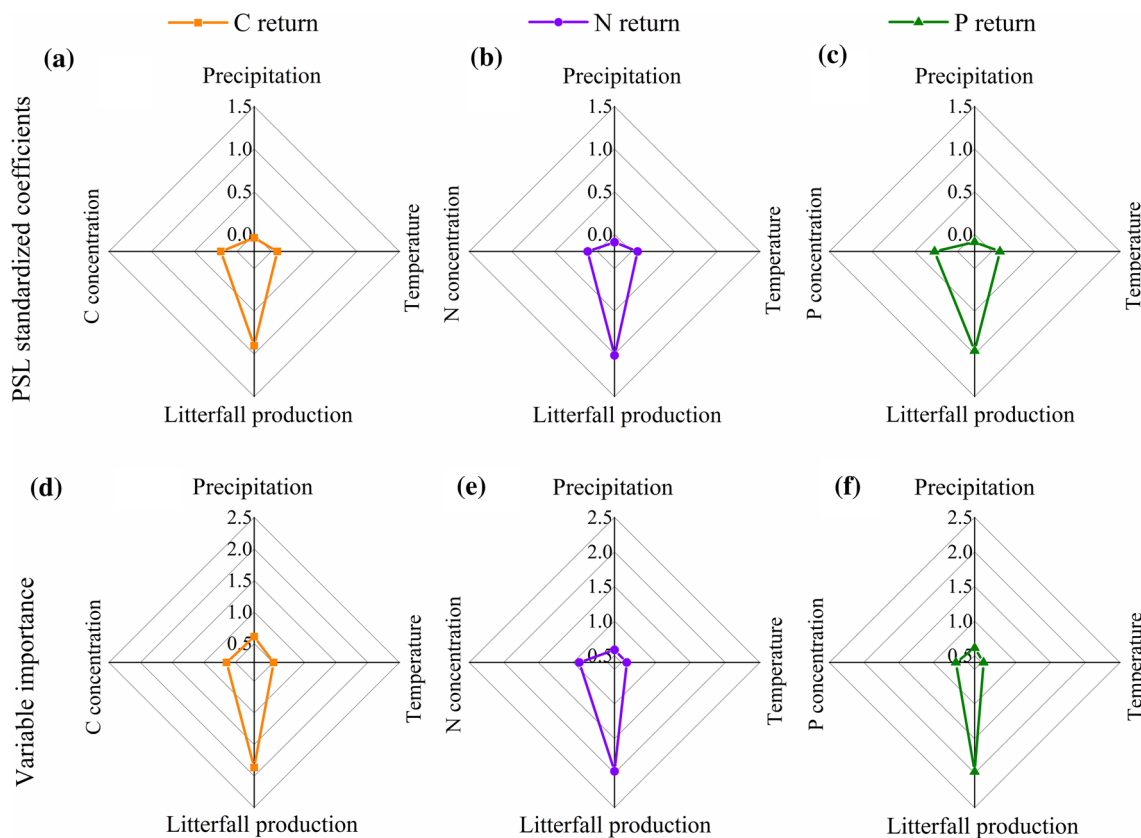
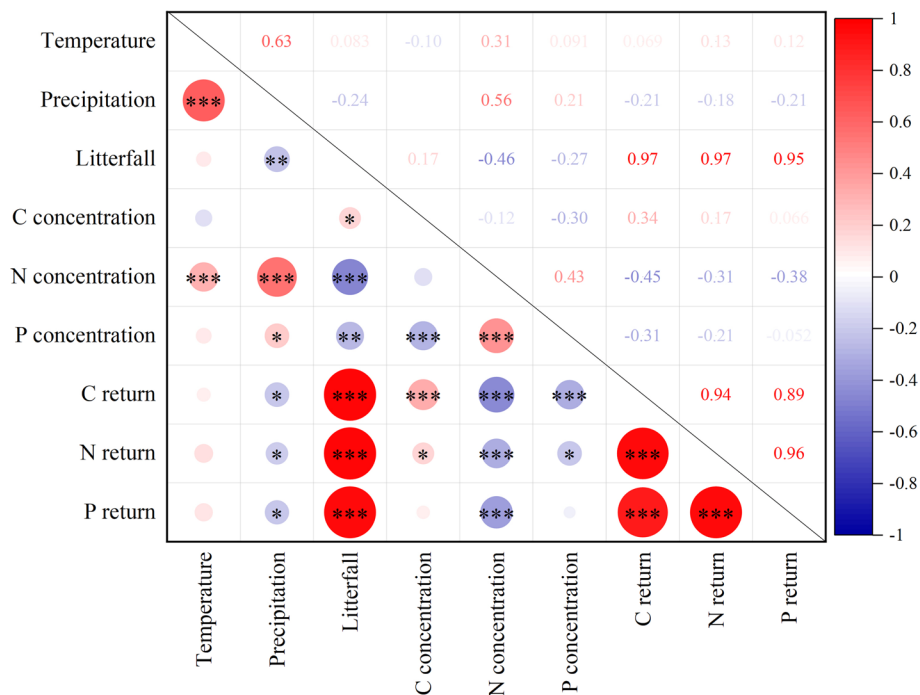


Fig. 7 Results of partial least squares (PLS) analysis for the effects of litterfall, element concentration and environmental factors on element return. PLS standardized coefficients show the direction and magnitude of each variable on the element return, the variable impor-

tant values (VIP) greater than 1 are significant ($P < 0.05$). **a**, **b** and **c** are PLS standardized coefficients of each variable to C, N, P return, respectively; **d**, **e** and **f** are the importance value of each variable to C, N and P return, respectively

to September) reflect a high nutrient demand for new leaves. In contrast, lower N and P concentrations in the dormant season might be a nutrient-conserving strategy to reduce nutrient losses through retranslocation to new tissue production and/or storage in twigs (You et al. 2018b). Further, the relatively high availability of nutrients in the growing season is favorable for nutrient uptake (You et al. 2018b; Zhang et al. 2018). Lastly, heavy rainfalls or strong winds in the growing season can lead to irregular litterfall and corresponding nutrient return (Park et al. 2020).

The addition of N has potential to mediate nutrients in both green leaves and the subsequent litter across global biomes (Liu et al. 2016; Yang et al. 2019). In this study, litter C was not affected by N addition. Similar results have been reported for other forest ecosystems (Smaill et al. 2008; Maaroufi et al. 2016; Fu et al. 2019). As a poorly mobile element, C is steadily accumulated in plant tissues (Jasinska et al. 2020). However, the addition of N decreased the concentration of N in the litter. Similar results were also found in a savanna in central Brazil (Kozovits et al. 2007) and in a Norway spruce forest (Maaroufi et al. 2016). On one hand, N addition can promote photosynthesis and consumption of the element (Fu et al. 2019). On the other hand, N addition can stimulate the accumulation of biomass, which may in turn dilute N concentration in leaf tissues (Zhang et al. 2017b). In addition, high-N addition decreased litter P in this study, which agrees with the findings in a *Larix gmelinii* forest (Fu et al. 2019) and a savanna in central Brazil (Kozovits et al. 2007). Nitrogen and P have been widely reported to interactively affect plant growth (Liu et al. 2021b). Thus high-N addition may increase P demand and reabsorption efficiency in leaves, which could in turn decrease litter P (Li et al. 2016).

It is important to note that the effects of the addition of N on litter N and P were time dependent (year and month). This may be attributed to the lag and superposition effect of N addition on the ecosystem, which is often regulated by season-related temperatures (Kozovits et al. 2007; Zhang et al. 2017c). For example, the positive effect of N addition on litter production increased with the extent of the duration of N addition (Kozovits et al. 2007).

Effect of the N addition on C and nutrient return

In contrast to decreases of N and P concentrations after N addition, this study found that litter C and nutrient return increased. Similar results were found in a *Cinnamomum camphora* (L.) Presl forest (Zhao et al. 2016) and a *Schima superba* Gardn. et Champ. forest (Lv et al. 2013). As noted earlier, element return is determined by both litter production and element concentration, and the former is more important in this study (Figs. 6, 7). As a result, nutrient return also showed a bimodal pattern.

It can be predicted that increased litter C and nutrient return will increase C and nutrient input to the soil through litterfall in this subtropical forest ecosystem (Tu et al. 2011; Bowden et al. 2019). Our previous study found that simulated N deposition delayed nutrient release by *M. wilsonii* leaf litter over a 1-year deposition in the same experimental stand (Zhuang et al. 2020). The residual C, N and P levels in *M. wilsonii* litter, were approximately 1.2–1.3, 1.6–1.9 and 1.6–3.2 times greater, respectively, in the N addition treatments than the controls. A previous study in a bamboo ecosystem in southwestern also reported that simulated N deposition can promote soil C sequestration by increased litter input (Tu et al. 2011). These results indicate that increasing nitrogen increased soil C and nutrient pools in this specific subtropical forest ecosystem.

Conclusions

This study examined the effects of the addition of N on monthly and yearly dynamics of foliar litter production, C, N, and P concentration and return in a N-rich subtropical *M. wilsonii* forest on the western edge of the Szechwan Basin. Foliar litterfall and C, N, and P return exhibited a bimodal pattern (a major peak in spring and a minor one in autumn). Nitrogen and P concentrations in foliar litter in the growing season were higher than in the dormant period. The addition of N stimulated foliar litter production during the 4-year experiment, and promoted C, N and P return, although their concentrations were not affected by the addition of N, indicating that increased C and N return was mainly attributed to stimulated litter production. Based on the results of litter decomposition in *M. wilsonii* forests, nitrogen deposition may increase carbon and nutrient pools in N-rich subtropical forest ecosystems.

Author contribution YZ: Methodology, formal analysis, investigation, writing—original draft. Shichen Xiong: Investigation. CY: Conceptualization, writing—original draft. SL, LW, LZ, HL: Investigation, software. BT: Project administration, validation. YL: Validation. ZX: Conceptualization, supervision, writing—original draft and editing.

Availability of data and materials The datasets used during the current study are available from the corresponding author on reasonable request.

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