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# Linkages among leaf nutrient concentration, resorption efficiency, litter decomposition and their stoichiometry to canopy nitrogen addition and understory removal in subtropical plantation

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## Abstract

**Background** The prevalence of understory removal and anthropogenic nitrogen (N) deposition has significantly altered the ecological processes of forest ecosystems at both regional and global scales. However, it remains a pressing challenge to understand how N deposition and understory removal affect leaf nutrient dynamics, nutrient resorption, litter decomposition, and their linkages for better managing forest ecosystems under nutrient imbalances induced by N enrichment. To address this research gap, a field manipulation experiment was carried out in a subtropical *Cunninghamia lanceolata* plantation with four treatments including: control (CK), canopy N addition (CN), understory removal (UR), and canopy N addition plus understory removal (CN × UR). Green and senesced leaf N and phosphorus (P) concentrations, N and P resorption efficiencies, litter decomposition, and their correlations were measured.

**Results** The results revealed that the average N concentrations of green early and late leaves in UR were increased by 6.61 and 18.89% compared to CK. UR had the highest whereas CN had the lowest P concentrations in green leaves across the two sampling seasons. Following this, UR, leaf type, season, and their interactions significantly affected leaf N, P, and N:P ( $P < 0.05$ ). The highest leaf N resorption (32.68%) and P resorption efficiencies (63.96%) were recorded in UR. Litter decomposition was significantly retarded in UR ( $P < 0.01$ ) relative to CN. The regression analysis demonstrated that leaf nutrient status was significantly interconnected with leaf nutrient resorption efficiencies. In addition, leaf nutrient dynamics were strongly correlated with litter nutrients, indicating that both were coupled.

**Conclusion** These findings can deepen our knowledge of biogeochemical cycling and reveal contrasting nutrient-acquisition strategies on N and P limitation in response to UR and CN. Considering the P limitation, it is important to note that P was resorbed more efficiently, illustrating a remarkable nutrient preservation approach for nutrient-limitations. Resorption may be a crucial mechanism for keeping nutrients in these forests, so better understory management practices are required to prevent reliance on external nutrient pools. Overall, this study sheds meaningful insights into the ability of forest adaptation in response to global climatic change.

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**Keywords** Nutrient resorption, Nitrogen deposition, Litter decomposition, Stoichiometry, Understory removal, Subtropical plantation

## Introduction

The Anthropocene has drastically altered global atmospheric nitrogen (N) deposition, leading to substantial nutrient alteration and elemental imbalances in forest ecosystems (Gundale 2022). The emission of total reactive N around the world has increased by 7.3 Tg N yr<sup>-1</sup> or 30% in recent years (Tian et al. 2020). China has emerged as a major hotspot for reactive N emissions (Cui et al. 2013), which are anticipated to reach 63 Tg N yr<sup>-1</sup> by 2050 (IPCC 2022). Despite the fact that N is a fundamental nutrient that restricts plant growth and alters leaf nutrient resorption efficiencies, as well as plant stoichiometry (Moreau et al. 2019), excessive N accumulation on the other hand, has a cascading impact on the stability and functioning of forest ecosystems (Liu et al. 2019). Thus, understanding the effects of increased N deposition on plant nutritional status and resorption efficiencies would provide more realistic and integrated insights into nutrient reactions to global environmental challenges.

Long-term management practices such as understory plant removal exhibited strong influence on the functioning of forest ecosystems by directly or indirectly modifying soil biogeochemical processes (Zhang et al. 2022a). However, understory removal and its consequences on subtropical ecosystem processes where atmospheric N deposition is rising are typically ignored mostly in ecological research (Kumar et al. 2018). On the one hand, understory plants were eliminated to prevent competition for resources utilization between trees and the understory plants (Giuggiola et al. 2018; Yang et al. 2018; Yu et al. 2022). On the other hand, understory vegetation is a pivotal stratum of forest ecosystems that has a considerable impact on key processes like forest regeneration, soil nutrient and carbon cycling (Landuyt et al. 2019). Numerous studies have demonstrated a strong connection between understory plants and belowground ecological processes such as altering organic carbon, microbial biomass, litter decomposition, nutrient inputs, and retention (Trentini et al. 2018; Zhang et al. 2022a). Understory vegetation usually has faster nutrient turnover rates compared with the canopy (Landuyt et al. 2019). Thus, understory management should be of greater concern in order to comprehensively understand their mechanistic linkages in subtropical ecosystem processes.

Acquisition of leaf nutrients and the recycling of nutrients are key ecological processes that are significantly regulated by anthropogenic N deposition in forest ecosystems. Increased N input generally leads

to higher foliar N concentrations and fulfills the plant N demands in N-limited forests (Minocha et al. 2015; You et al. 2018a). Meanwhile, this situation raises environmental concerns as it negatively affects ecosystem function and stability (Liu et al. 2019; Gundale 2022). The excessive influx of N can create a shift in nutrient limitation patterns from N to P, causing intense competition for scarce nutrients in N-saturated ecosystems. For instance, the addition of N can modify the leaf N:P ratio, further exacerbating phosphorus (P) limitation and potentially shifting it from N to P limitation (You et al. 2018b). Although extensive research on leaf nutrient dynamics and N deposition on ecosystem processes (Zhou et al. 2017a; Tong et al. 2021; You et al. 2021) had been conducted by adding N directly to the forest understory or soil (Wortman et al. 2012; Zhang et al. 2022b), most of these experiments failed to account for some key processes that occur in the forest canopy, such as canopy N interception and uptake (Liu et al. 2021). Recent literature has revealed that understory addition of N considerably overstated the detrimental effects of N deposition by 375–472% compared to canopy N-addition (Zheng et al. 2018). Therefore, emphasizing the importance of canopy N addition is a more realistic strategy for modeling the actual processes of atmospheric N deposition and will provide reliable information about the impact of ecological changes on nutrient cycling in forest ecosystems.

Nutrient resorption and litter decomposition play a significant role in controlling nutrient budgets and plant nutrient use efficiency in forest ecosystems (Wan et al. 2021). Nutrient resorption allows plants to withdraw nutrients such as N and P before abscission from senescent structures to developing tissues (Prieto and Querejeta 2020). Nutrient resorption reduces nutrient loss and minimizes plant reliance on soil nutrient availability (Li et al. 2020). Approximately 31% and 40% of the annual N and P requirements of plants, respectively, are fulfilled via the resorption process (Xu et al. 2017). In addition, a global meta-analysis estimated that nitrogen and phosphorus resorption efficiencies (NRE and PRE) were 62.1% and 64.9%, respectively (Vergutz et al. 2013). It has been found that anthropogenic N addition can have positive (Shen et al. 2018; Luo et al. 2022), negative (Lü et al. 2016), or neutral effects (Kou et al. 2017) on nutrient resorption efficiencies. Moreover, it is still debated whether plants in nutrient-poor environments resorb more nutrients

than those in nutrient-rich environments (See et al. 2015). These inconsistent patterns are most likely a response to nutrient limitations on plant growth (Yan et al. 2015). For instance, under low nutrient availability conditions, plants would increase variability in their own nutrient concentration and sustain high resorption efficiency (Additional file 1: Fig. S1a) (Chen et al. 2021). Similarly, in an environment of unbalanced nutrition supply, plants resorb nutrients based on their level of nutrient limitation status (Sun et al. 2023), a process known as “relative nutrient limitation” (Additional file 1: Fig. S1b). If a plant’s growth is limited by N, it will absorb more N than other nutrients. In contrast, if the plant is P-limited, more P will be resorbed. Furthermore, stoichiometric control of leaf multiple nutrient resorptions could also be regulated by “stoichiometry control” (Additional file 1: Fig. S1c) (Sun et al. 2023). To date, research on the impacts of canopy N addition and understory removal on nutrient resorption is relatively limited, which impedes our understanding of plant nutrient conservation strategies and nutrient recycling in forest ecosystems.

The N enrichment considerably affects leaf litter fall kinetics and decomposition by changing the soil or litter quality (Pichon et al. 2020). Litter decomposition is tightly linked with nutrient resorption, in general, high nutrient resorption capacities are usually associated with lower nutrient concentrations and slower decomposition rates in plants (Killingbeck 1996; Deng et al. 2018). Litter-derived nutrient is often considered to be an important factor influencing decomposition processes due to the nutrient demands of the decomposing microbiota (Tong et al. 2021). Specifically, the litter-derived C stimulates the decomposition of soil organic C by influencing the structure and activity of the soil microbial community (Zhang et al. 2023). Inversely, the rate of litter decomposition might be influenced by soil microbial biomass, which contributes to ensure optimal nutrient use efficiency (Müller et al. 2017). The effects of N addition on litter decomposition have been debated since inconsistent patterns have been observed (Keeler et al. 2009; Zhou et al. 2017b; Ren et al. 2018). Increased N-deposition can result in escalation of litter decomposition rates, because of the abundance of N that is available to decomposers in soil ecosystems (Gill et al. 2022). In addition, understory vegetation removal hinders the rate of litter decomposition by reducing substrate availability for soil microbiota (Additional file 1: Fig. S1) (Wu et al. 2011; Wan et al. 2021). On the contrary, Jonathan et al. (2016) pointed out that understory vegetation removal hastens the decomposition of the *Pinus sylvestris* litter. Therefore, it is imperative to develop conceptual frameworks for the better understanding of ecological processes by

predicting the interspecific variabilities of foliar litter decomposition and nutrient uptake among various forest ecosystems in response to N deposition. However, how and to what extent increased atmospheric N deposition and management practices affect the multiple nutrient-associated processes such as leaf nutrient dynamics, nutrient resorption, litter decomposition, and their linkages remains unclear in forest ecosystems.

In this study, we conducted canopy N deposition and understory removal in *Cunninghamia lanceolata* (Chinese fir) forests since they are high-yielding, evergreen conifers with leaves that typically grow and senesce simultaneously (Wu et al. 2019; Liu et al. 2022). The relationships between various nutrient-interlinked processes were detected to provide comprehensive empirical evidence such as leaf nutrient dynamics, nutrient resorption, and litter decomposition in response to canopy N addition and understory removal in subtropical Chinese fir plantations. We tested the following hypotheses: (i) Understory removal would significantly increase leaf nutrient concentrations and leaf nutrient stoichiometry by reducing field nutrient competition; (ii) Canopy N addition might increase litter decomposition while decreases NRE due to the increased N input, similarly leaf P concentration decreases and PRE increases because of N-induced acidification and lower P supply; (iii) The relationships between foliar nutrients, resorption, litter nutrients, and their stoichiometry should be coupled due to plant nutrient acquisition and conservation strategies in response to nutrient addition.

## Materials and methods

### Study area

The experimental site was situated in Sanming city, at the Guanzhuang National Forestry Farm (26° 30′ N and 117° 43′ E), Fujian Province, China. The ecosystem experiences typical subtropical monsoon climate, with mean annual rainfall between 1606 and 1650 mm and mean annual temperatures between 18.8 and 19.6 °C. Soil is classified as an Acrisol in the U.S. soil taxonomy. The basic soil properties were as follows: mean soil organic carbon 18.38 g kg<sup>-1</sup>, soil bulk density 1.06 g cm<sup>-3</sup> and soil pH 4.68. The average annual wet N deposition in this region from rainfall (including NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup>) was 4.2–5.7 g N m<sup>-2</sup> yr<sup>-1</sup> (Wu et al. 2019). The study was carried out in a *Cunninghamia lanceolata* (Chinese fir) plantation forest that was planted in 2008 at a density of 1660 trees ha<sup>-1</sup>. At the time of the study, the mean height and diameter at breast height were 5.11 m and 7.34 cm, respectively. The predominant species of understory were *Ardisia punctate*, *Ficus hirta*, *Arachniodes hasseltii*, and *Smilax china*.

### Experimental design

In this study, a randomized block experiment was deployed with 4 replicates when the plantation of *C. lanceolata* was 6 years old. In June 2014, eight blocks (40 m×40 in size) were established over a 6-ha section of the plantation, and each block was divided into two 15 m×15 m plots. Each plot was inset with a 5 m×5 m subplot for understory removal treatment. There were two factors, with four treatments randomly assigned to each of the four replicated blocks including: (i) CK, control; (ii) CN, canopy nitrogen addition (25 kg N ha<sup>-1</sup> yr<sup>-1</sup>); (iii) UR, understory removal; and (iv) CN×UR, canopy nitrogen addition plus understory removal. A 3–8 m buffer strip was used to avoid cross-contamination between adjacent plots. For each CN plot, the required amount of NH<sub>4</sub>NO<sub>3</sub> (269 g) was dissolved in 15 L of tap water, and the solution was sprayed over the forest canopy inside the plots. In order to apply the N on forest canopy, a high-pressure spraying equipment was placed in the center of each plot. Briefly, N solutions were pumped to a height of 5 m above the forest canopy using PVC pipes (10 cm in diameter) coupled to a tall supporting tower. The N solutions were sprayed evenly (rotating at 360°) over the canopy using crane sprinklers. The solution was sprayed once every 2 months for 15 months, starting in June 2014 and lasting until sampling in December 2016. The control plots received an equal amount of water without NH<sub>4</sub>NO<sub>3</sub>. For understory removal subplots, the existing and germinating understory vegetation were manually pulled out each month using a machete and hoe. The collected aboveground biomass of understory plants was completely removed from the experimental plots to avoid their onsite decomposition.

### Field sampling and analysis

Soil samples from 0 to 20 cm were randomly collected by taking three soil cores (3 cm diameter) from each plot. Before taking the cores, plant debris was scraped off from the top of the soil. One sample per subplot was created using the three combined cores. Stones and small, discernible plant residues were manually removed after the soil samples had been air-dried. Before measuring the soil properties, all samples were grounded to pass through a 2 mm sieve. The pH of soil was measured using 1:2.5 (w/v) ratio of soil to deionized water. Fresh soil was dried at 105 °C for 24 h in order to determine the gravimetric soil moisture content.

Both green and senesced leaves were sampled in late April and December 2016, a representative set of mature green and freshly senesced but still connected leaf were sampled. Plant samples were oven dried at 75 °C for

48 h and ground by using a ball mill (NM200, Retsch) prior to chemical analysis. For C, N, and P analysis, dried leaves were crushed into a fine powder and passed through a 0.15-mm sieve. The modified Walkley–Black acid–dichromate FeSO<sub>4</sub> titration technique was used to determine the organic C concentration of soil and plant samples (Bao 2000). A flow injection auto analyzer was utilized to determine the total N concentration following micro-Kjeldahl digestion. Following the digestion of pulverized leaf material in H<sub>2</sub>SO<sub>4</sub>–HClO<sub>4</sub>, the total P concentrations were determined colorimetrically using the molybdate/ascorbic acid procedure (Bao 2000).

The leaf litter decay experiment was performed by following the method of Wu et al. (2011). The fresh Chinese fir litter was collected from the tested plots and mixed to create a uniform mixture before filling the 1-mm mesh nylon litter bags (10 g of dried leaf litter per bag, 20 cm×20 cm). In each subplot of the four treatments, litter bags were randomly allocated across the surface soil in May 2016. Litter bags were collected (one per subplot) from each subplot every 2 months for a total of seven times between May 2016 and July 2017. To determine the percentage of litter mass loss, the retrieved litters were cleansed with forceps, dried for 72 h at 75 °C in an oven, and weighed. The C, N, and P concentrations were chemically analyzed using the same methods as described above (Bao 2000).

### Calculations and statistical analysis

Nutrient resorption efficiency (NRE/PRE) is defined as the percentage of the mature leaf nutrient pool that is resorbed from senescent leaves (Killingbeck 1996). It was calculated as follows

$$\text{NRE/PRE} = \left[ \frac{(N/P_{\text{green}} - N/P_{\text{senesced}} \times \text{MLCF})}{N/P_{\text{green}}} \right] \times 100\%$$

where  $N/P_{\text{green}}$  and  $N/P_{\text{senesced}}$  are the mass-based N or P concentrations of green and senescent leaves, respectively. The MLCF (mass loss correction factor) of 0.745 was used for the compensation of mass loss correction (Vergutz et al. 2013).

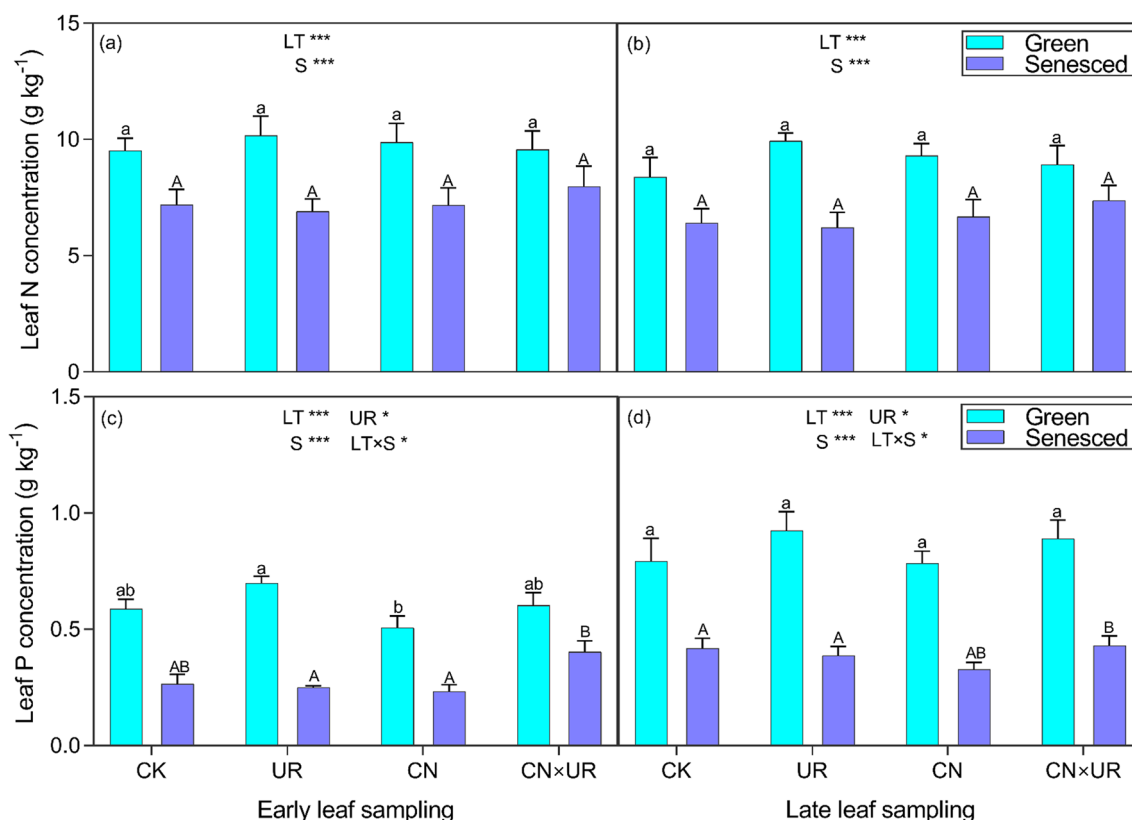
Prior to analysis, Shapiro–Wilk tests were run to examine the normality and homogeneity of the data. The effects of treatments on leaf nutrient concentrations and nutrient resorption efficiencies were examined discretely by one-way ANOVAs along with LSD tests. Two-way ANOVAs were applied to determine the main and interaction effects of CN and UR on foliar nutrient concentrations, resorption efficiency, and N:P ratio. Three-factor ANOVAs were carried out to analyze the main and interactional effects of

CN, UR, and season (S; April and December) on leaf nutrient resorption efficiencies. Similarly, a four-factor ANOVA was employed to investigate the main and interactional effects of CN, UR, leaf type (LT, Green vs Senesced), and season (S) on the concentrations of N, P, and N:P. Furthermore, the impacts of CN, UR, and their various interrelations on litter nutrient (N, P, and C) dynamics and litter decomposition were also investigated using repeated measures ANOVA. The various relationships between leaf nutrients, resorptions, and decomposition of litter were analyzed using the function of linear regression. The statistical analysis was carried out using SPSS 25 (SPSS Inc., Chicago, IL, USA), and a confidence level of  $P \leq 0.05$  was used to determine significance. All illustrations and analyses were accomplished by SigmaPlot 14.0 (Systat Software, Inc., San Jose, CA) and GraphPad Prism 10.0 software (GraphPad Software, Inc., San Diego, CA, USA).

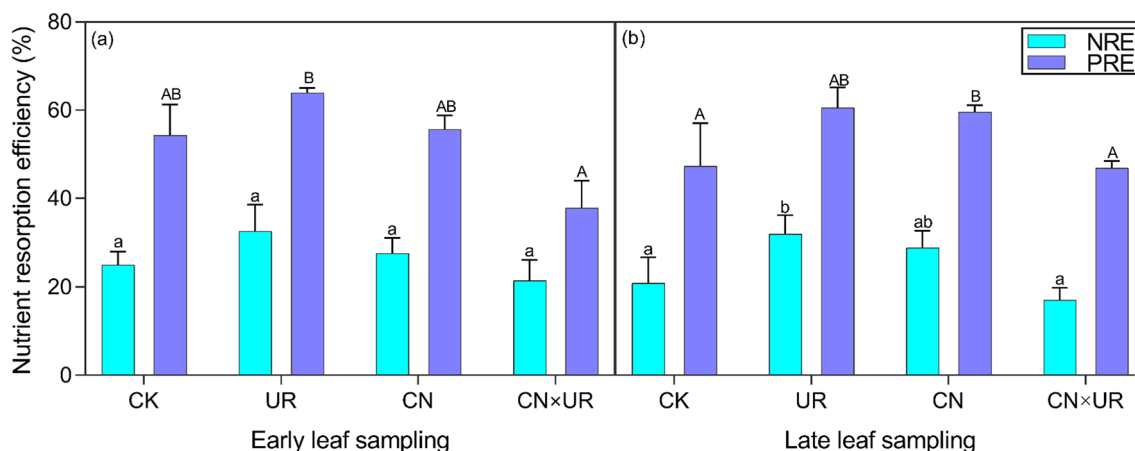
## Results

### Response of leaf nutrient concentration and resorption

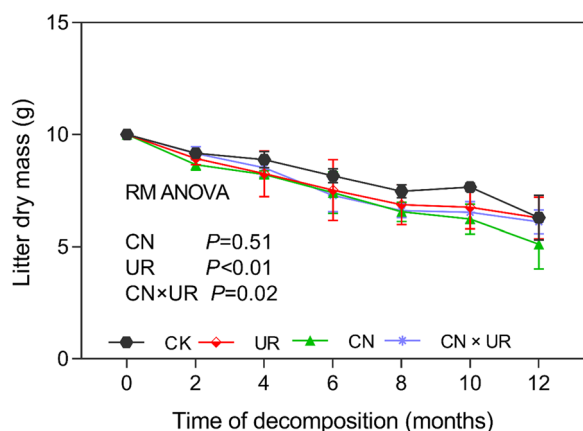
UR ( $P=0.02$ ), leaf type (LT,  $P<0.01$ ), season (S,  $P<0.01$ ), and their interactions significantly influenced leaf N, P, and N:P of early and late sampling (Fig. 1 and Additional file 1: Table S3). In contrast, CN and its interaction with UR had no significant effect on leaf nutrient concentrations but had a remarkable impact on N:P ratios and nutrient resorption efficiencies as determined by two-way ANOVAs (Additional file 1: Tables S1, S2). The concentrations of N in green early and late leaves were increased by 6.61% and 18.89% in UR and by 3.56% and 11.24% in CN compared to the control (Fig. 1a, b). In addition, UR had the highest, whereas CN had the lowest leaf P concentration in green early and late leaves (Fig. 1c, d and Additional file 1: Table S3). The highest level of senesced leaf P concentration was observed in the combined treatment of CN×UR (Fig. 1c, d).



**Fig. 1** Response of nitrogen and phosphorus concentrations in green and senesced leaves to canopy nitrogen addition (CN) and understory removal (UR) across two seasons. Data are presented as means ± SD, with four replicates. Within each of the four-bar groups (Green or Senesced treatment) values with a different letter are significantly different based on ANOVA with LSD ( $P < 0.05$ ). The lower and upper cases represent green and senesced subplots, respectively. CK, control; UR, understory removal; CN, canopy nitrogen addition; CN×UR, canopy nitrogen addition plus understory removal. Main effects of CN, UR, leaf types (green vs senesced), season (S) and their interactions were evaluated with four-way ANOVA analyses. \* $P < 0.05$ ; \*\*\* $P < 0.001$



**Fig. 2** Effects of canopy N addition and understory removal on nutrient resorption efficiencies across two seasons. Data are the means  $\pm$  SD of four replicates. Within each group, values with a different letter are significantly different based on ANOVA with LSD ( $P < 0.05$ ). The lower and upper cases represent NRE and PRE subplots, respectively. NRE: nitrogen resorption efficiency; PRE: phosphorus resorption efficiency; CK: control; UR: understory removal; CN: canopy nitrogen addition; CNxUR: canopy nitrogen addition with understory removal



**Fig. 3** The effects of canopy nitrogen addition (N), understory removal (UR), and their interactions on litter decomposition rate after 12 months in *Cunninghamia lanceolata* plantation. Data were presented as the mean  $\pm$  standard deviation (SD) of four replicates at a significance level of  $P < 0.05$  (The inserted  $p$ -values were from two-way repeated measures ANOVA). CK: control; UR: understory removal; CN: canopy N addition; CNxUR: canopy N addition plus understory removal

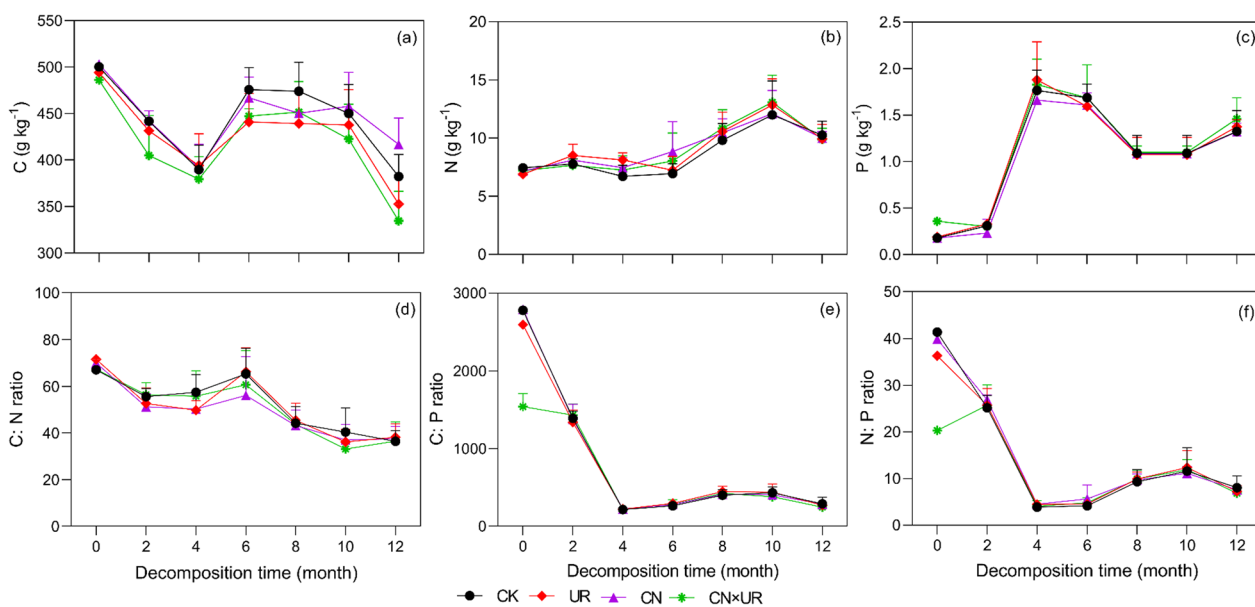
Leaf nutrient resorption efficiencies varied dramatically with interactions across early and late leaves (Fig. 2 and Additional file 1: Table S4). The average NREs and PREs were 32.68% and 63.96% for UR and 27.64% and 55.66%, respectively, for CN. UR recorded the highest while CN plus UR recorded the lowest leaf NRE and PRE across the sampling seasons (Fig. 2a). PRE was higher than NRE without statistical significance difference ( $P > 0.05$ , Additional file 1: Table S4).

### Response of leaf litter decomposition and nutrient dynamics

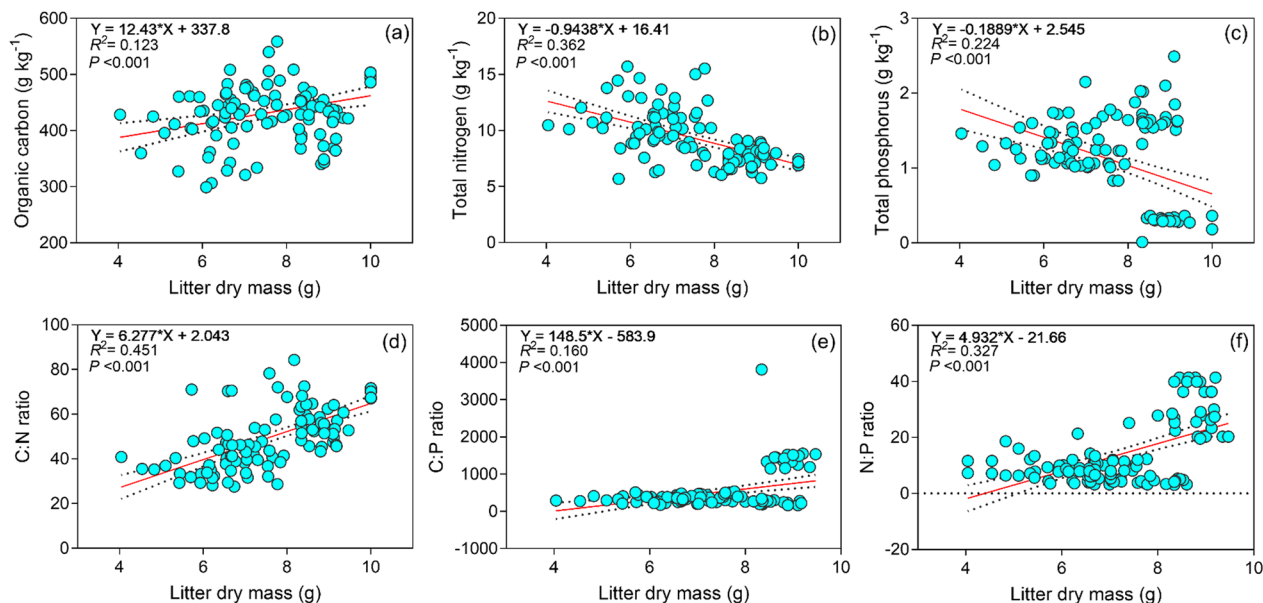
Two-way repeated measures ANOVA revealed that UR ( $P < 0.01$ ) significantly retarded leaf litter decomposition, whereas CN recorded remarkably faster decomposition rate (Fig. 3 and Additional file 1: Table S5). There was an interactive effect between CN and UR ( $P = 0.02$ ). The mean leaf litter C, N, and P concentrations were  $500.3 \text{ g kg}^{-1}$ ,  $7.1 \text{ g kg}^{-1}$ , and  $0.26 \text{ g kg}^{-1}$ , respectively. The effect of UR was more pronounced on C release relative to CN (Fig. 4a). Conversely, the high levels of residual N and P were usually noted in the UR plots (Fig. 4b, c). The average leaf litter stoichiometry ratios of C:N, C:P, and N:P were 65.8, 2600.9, and 38.4, respectively (Fig. 4d, f). UR, sampling date (T), and the interactions between CNxUR and URxT significantly impacted leaf litter P during the decomposition process ( $P < 0.05$ , Additional file 1: Table S5).

### Relationships among leaf nutrient concentration, resorption, litter decomposition, and their stoichiometry

Leaf litter organic carbon was positively correlated, while total N and P concentrations were negatively correlated with litter dry mass ( $P < 0.001$  for all, Fig. 5a–c). Litter dry mass and the stoichiometric ratios of C:N, C:P, and N:P were all positively correlated ( $P < 0.001$ , Fig. 5d–f). Furthermore, green leaf P concentrations increased linearly with litter TN ( $P = 0.018$ , Fig. 6a), whereas the relationships between the N:P of green and senesced leaves and the litter TN were negative



**Fig. 4** Dynamics of the remaining C, N, and P and the C:N, C:P and N:P ratios in leaf litter of *Cunninghamhamia lanceolata* plantation (a–e). CK: control; UR: understory removal; CN: canopy N addition; CN×UR: canopy N addition plus understory removal. Error bars represent the standard deviations of the means ( $n=4$ )

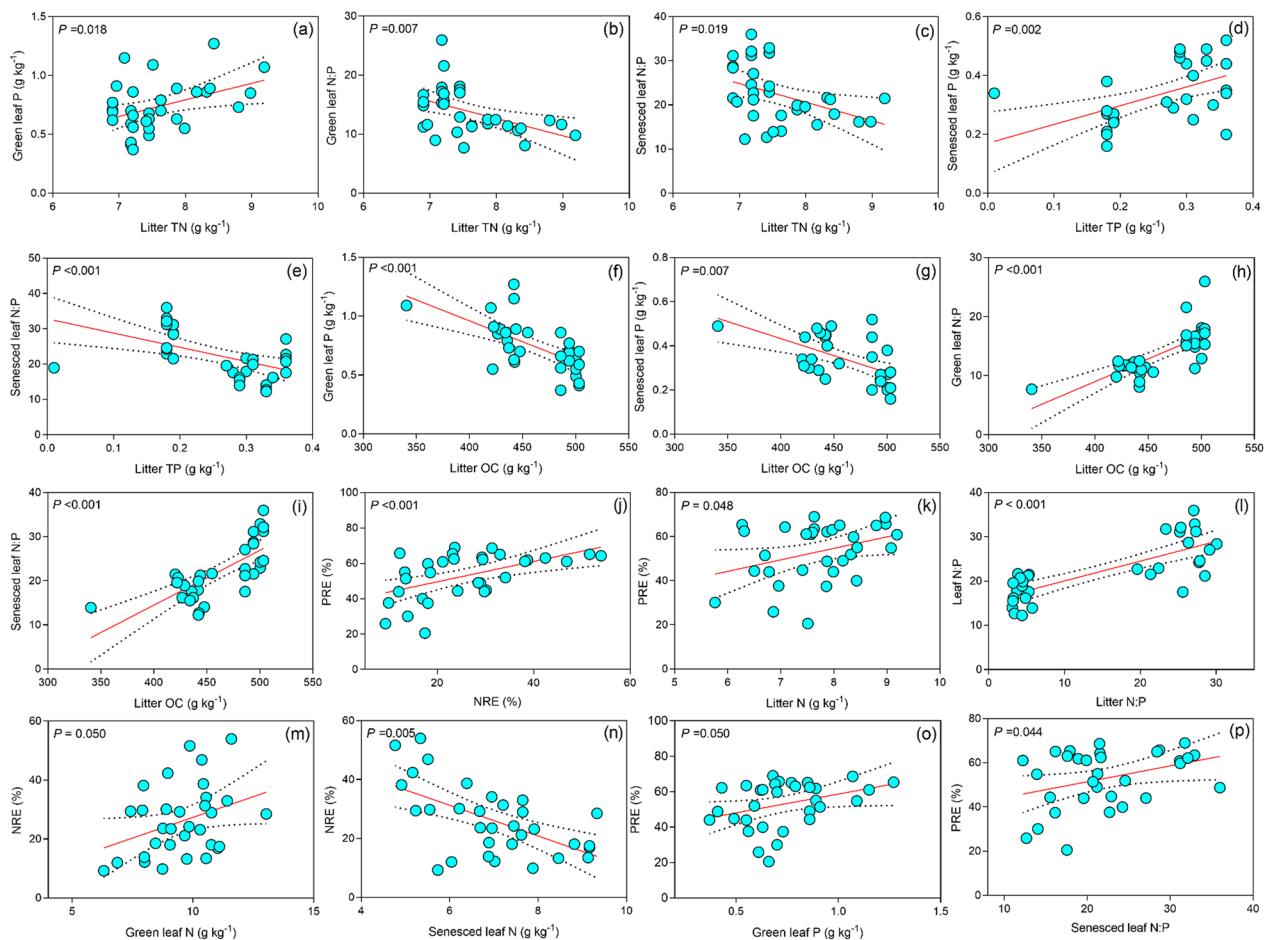


**Fig. 5** Relationships between stoichiometric characteristics of leaf litter C, N, P, C:N, C:P and N:P and litter dry mass of *Cunninghamhamia lanceolata* plantation

( $P=0.007$  and  $P=0.019$ , respectively, Fig. 6b, c). Contrastingly, the senesced leaf P was positively correlated, while N:P was negatively correlated with litter P ( $P < 0.01$ , Fig. 6d, e). The [N]g, [N]s, and NRE did not correlate with litter TN, TP, and OC ( $P > 0.05$  for all, Additional file 1: Figs. S2 and S3). Litter OC decreased

with increased [P]g and [P]s (Fig. 6f, g), whereas leaf N:P increased with litter OC ( $P < 0.001$ , Fig. 6h, i).

Strong correlations between NRE and PRE were observed ( $P < 0.001$ , Fig. 6j). Also, significant correlations among leaf and litter N:P ratios were found ( $P < 0.001$ , Fig. 6l). The relationship between PRE and litter N was



**Fig. 6** Relationships between green leaves ([N]<sub>g</sub> and [P]<sub>g</sub>), senescing leaves ([N]<sub>s</sub> and [P]<sub>s</sub>), and the nitrogen and phosphorus resorption efficiency (NRE and PRE) with litter derived nutrients. Solid lines denote significant relationships with  $P < 0.05$

positive ( $P=0.048$ , Fig. 6k), while NRE showed a negative relationship with senescent leaf N and a positive relationship with green leaf N (Fig. 6m, n). The correlations between PRE with green leaf P and senescent leaf N:P were positive (Fig. 6o, p).

## Discussion

### Dynamics of leaf nutrient concentration and resorption efficiencies

Our findings indicated that UR increased N and P concentrations in green early and late leaves (Fig. 1), which supported our first hypothesis and the nutrient limitation theory (Gruber et al. 2018; De Lombaerde et al. 2021). The proposed mechanism is attributed to modifying soil microclimate and enhancing the availability of soil nutrients with UR (Wu et al. 2011; Li et al. 2020). First, UR increases soil water availability and temperature by allowing more solar radiation to reach the forest floor, which has the potential to increase nutrient availability

by influencing soil microbial activities (Giuggiola et al. 2018). Second, soil nutrient availability was potentially increased as a result of the faster decomposition rate of the remaining detritus from understory plants (Fang et al. 2021). Understory vegetation removal allows faster growth rates of *Cunninghamia lanceolata* plantations due to the release of competition for other resources (Chen et al. 2022). For example, UR can facilitate tree growth via speeding up N mineralization (Fang et al. 2021).

CN substantially increased both green and senesced leaf N and N:P ratios but decreased leaf P concentration (Fig. 1 and Additional file 1: Table S3). High N deposition generally raises leaf N concentrations (Zhang et al. 2022b), while decreasing leaf P concentrations (Deng et al. 2017). The favorable responses of leaf N following N addition are well studied (Gurmesa et al. 2016; You et al. 2018a). However, CN aggravated ecosystem P limitations in our study. The first reason would be that



the significant decreases in N and P concentrations of senesced early and late leaves of Chinese fir plantations occurred as a result of homeostatic control and nutrient resorption (Chen et al. 2015). Green leaves in some plants retain their stability better than their senescent leaves because of internal homeostatic regulation (Zeng et al. 2021). Second, due to N-rich environments in the subtropical forests, N-induced soil acidification would decrease available P, especially in soils with P limitations (Deng et al. 2017; Luo et al. 2022). The evidence includes the values of N resorption (average 32.68%) in our study were notably lower than the mean NRE (62.1%), while P resorption (average 63.96%) was similar to the average PRE (64.9%) at a global scale estimation (Vergutz et al. 2013). Based upon this threshold, *Cunninghamia lanceolata* plantations exhibit effective P and ineffective N resorption in early and late leaves, respectively. Our data affirms the second hypothesis and showed that CN considerably reduced leaf NRE since more N from soils will be absorbed by plants and minimize reliance on internal N recycling from senescing leaves (You et al. 2018b; Hu et al. 2022). According to Killingbeck (1996), plants use P efficiently when the P concentration in senescent leaves is less than 0.5 g kg<sup>-1</sup>. Consistently, P concentration in senesced leaves were less than 0.5 g kg<sup>-1</sup>, indicating that *Cunninghamia lanceolata* had a greater P use efficiency in this study.

We also found the higher leaf PRE in both early and late leaf sampling with UR (Fig. 2 and Additional file 1: Table S4). This might be because: (i) P is abundantly present in leaves in an organic form (Estiarte and Peñuelas 2015), which likely makes the process of P resorption less expensive. (ii) P is frequently scarce because it is less soluble and mobile in subtropical soils (Vitousek et al. 2010). The twin stresses of soil P restriction and atmospheric N deposition affect forest ecosystems frequently in subtropical areas (Liu et al. 2013). Consequently, N deposition can change soil from N limitations to P limitations (Deng et al. 2017) and lead to a more conservative use of P (i.e., greater P resorption) in plantations (Luo et al. 2022). Concretely, higher PRE compared to NRE may indicate that Chinese fir is most likely to be limited by P rather than N and follows the mechanism of nutrient limitation control (Additional file 1: Fig. S1b).

#### Dynamics of leaf litter decomposition and nutrient stoichiometry

In this study, UR significantly ( $P=0.01$ ) retarded the rate of litter decomposition in Chinese fir plantations (Fig. 3). Previous studies have also found that removing the understory has a detrimental impact on litter decomposition in subtropical plantations (Wu et al. 2011; He et al. 2019; Wan et al. 2021). Since the rates of litter

decomposition are influenced by substrate quality and soil decomposers (Wu et al. 2019), the explanation should be that UR would hinder litter decomposition because the lower plant species resulted in varied soil microbial diversity and community composition. Although soil microbial community was not directly determined in this experiment, recent published literature (Xi et al. 2022) and other evidence (Yang et al. 2018; Qiu et al. 2021) revealed that removing the understory reduced substrate availability to soil microbes, which inhibited the microbial decomposition functions (Wu et al. 2011; Wan et al. 2021). Furthermore, *Cunninghamia lanceolata* litter frequently releases allelochemicals like cyclic dipeptide during decomposition (Xia et al. 2015), which can prevent the microbial degradation performance in understory removal. Consistent with our second hypothesis, CN slightly accelerated litter decomposition rates of *Cunninghamia lanceolata* (Fig. 3 and Additional file 1: Table S5) and supported the N limitation theory that N deposition would speed up the rate of decomposition (Gill et al. 2022). CN potentially increased the soil fungal diversity, which alternatively accelerated the litter decomposition process (Wu et al. 2019; Liu et al. 2021). In addition, the net N release only happens when the litter average C:N ratio is lower than 40 (Parton et al. 2007). In this study, the C:N ratio of *Cunninghamia lanceolata* litter was higher than 40 (Fig. 4d), resulting in a higher decomposition rate after N addition. Likewise, according to Dziadowiec (1987), P will release if the litter C:P values are in the range of 200 to 480, the obtained value was far lower than those in our study (Fig. 4e). Therefore, litter decomposition was enhanced and net P immobilization occurred.

#### Relationships among leaf resorption, nutrient stoichiometry, and litter decomposition

In this study, the relationships between green leaf N/P and NRE/PRE were significantly positive (Fig. 6). In general, the efficiency of nutrient absorption rises with lower soil nutrient levels and declines significantly when the corresponding nutrients are more readily available in soils (Xu et al. 2021). The higher resorption indicated a higher nutrient transformation from green leaves to senescent leaves (Brant and Chen 2015). These findings are compatible with some studies (Chen et al. 2021), but contradict other results (Liu et al. 2014; See et al. 2015). For instance, NRE substantially increased with leaf N concentration in the non-karst forest (Chen et al. 2021). However, Liu et al. (2014) noted that, as the concentrations of N and P in green leaves decreased, the efficiency of N and P resorption increased. The discrepancies about the nutrient resorption efficiencies would be attributed to the initial leaf and soil nutrient status (Xu et al.

2020; Chen et al. 2021). NRE and PRE had poor relationships with litter nutrient status in our study, which also supported these findings. Theoretically, if foliar concentrations indicate nutrient constraints and resorption represents a nutrient limitation, PRE will increase and NRE will decrease as leaf N:P increases (Sorrell et al. 2011). However, other than a positive relationship between leaf N:P ratios and PRE, we did not observe such a phenomenon (Fig. 6p). These unexpected results imply the possibility of additional plant strategies, such as the stoichiometry control strategy (Sun et al. 2023).

There was a strong positive relationship between NRE and PRE (Fig. 6j), which indicated that resorptions of N and P were coupled and increased concurrently. For example, a similar significant interrelation between NRE and PRE was noted in two 50-year-old forests (Chen et al. 2021). This was also supported by Liebig's law of the minimum (Marschner 2012), that multiple nutrient balances as well as nutrient availability are necessary for plant growth. Moreover, no significant relationships were noted between the stoichiometric ratios and the resorption efficiencies, which did not support our third hypothesis. The reason would be that the nutrients N and P in plants are coupled (Fig. 6l), while resorption is dominated by their concentrations but not their ratios, adding more concrete support for the nutrient limitation control (Killingbeck 1996; Sun et al. 2023). Litter OC was positively correlated with senesced leaf N:P and green leaf N:P, while litter TN and TP had a significant negative relationship with senesced leaf N:P and green leaf N:P (Fig. 6). Although these results appeared to be incongruous, they were also logical in light of the improved N affordance and P availability. Litter N:P ratios and leaf N:P ratios were significantly interrelated. It is confirmed by the retranslocation of nutrients between soil and plant, which is constrained by soil availability (Bui and Henderson 2013).

## Conclusion

The present study evaluated the unique empirical evidence of multiple nutrient-associated mechanisms of foliar nutrient status, resorption, litter decomposition, and their linkages in response to the increasing N deposition and understory removal in *Cunninghamia lanceolata* plantations. To our knowledge, this study is the first of its kind that sheds light on the intricate interrelationships amongst multiple nutrient cycling processes in subtropical ecosystems. Our results suggested that CN and UR can greatly affect ecosystem nutrient cycling and resorption efficiencies. We first found that UR consistently increased the concentration of foliar nutrients and resorption efficiencies. In contrast, CN enhanced foliar N concentration while decreasing P concentration and

NRE. NRE and PRE changed across treatments, being lower in CN and greater in UR, suggesting that UR is better capable of obtaining nutrients and may save more resources through absorption from senescing leaves. Second, UR appeared to be the dominant factor for retarded litter mass loss, and CN promoted leaf litter decomposition. UR provided a high concentration of C, N, and P from leaf litter decomposition processes. Except for the tight relationship between leaf N:P ratio and litter N:P ratio, few relationships were found between resorption efficiency and N, P, and C stoichiometric ratios. We conclude that nutrient resorption may be a key mechanism for nutrient conservation in these plantations, where P is the most limiting nutrient. Therefore, effective understory management is crucial for nutrient conservation cycling and enhancing nutrient uptake in subtropical plantation forests. However, exploring the long-lasting legacy impacts of understory removal by further edge cutting technologies merits further studies on global ecological challenges.

## Supplementary Information

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**Additional file 1: Figure S1.** A schematic diagram showing various leaf nutrient resorption control strategies under different nutrient limitation scenarios and litter decomposition processes in response to canopy nitrogen (CN) addition and understory removal (UR) in *Cunninghamia lanceolata* plantation. In the uppermost panel, (a) nutrient concentration control, the role of foliar nutrients in influencing resorption patterns is depicted. In the middle panel, (b) nutrient limitation control, certain nutrient restriction has the potential to influence resorption patterns. (c) stoichiometry control, this panel emphasizes the role of foliar N:P ratios in determining how much N versus P are resorbed during senescence. The CN addition follows the nutrient concentration control whereas UR follows the nutrient limitation control. The stoichiometric control is proposed for various relationships of leaf nutrient contents, nutrient resorption and litter decomposition. The CN addition accelerates litter decomposition process by boosting substrate availability for soil biota which in turn results in higher litter nutrient release in soil ecosystem. By contrast UR slows down the process of litter decomposition by decreasing the availability of substrate for soil biota and hence results in slow nutrient release into the soil ecosystem. **Figure S2.** Relationships between resorption efficiencies of N and P with leaf and litter nutrient contents in Chinese fir plantations. **Figure S3.** Relationships between N and P concentrations in green leaves ([N]<sub>g</sub> and [P]<sub>g</sub>), senesced leaves ([N]<sub>s</sub> and [P]<sub>s</sub>), with litter nutrient contents in Chinese fir plantations. **Table S1.** Results of two-way ANOVAs for leaf nutrient concentrations, leaf N:P ratio, and nutrient resorption parameters sampled in April, as dependent on canopy nitrogen addition (CN), understory removal (UR), and their interaction (CN × UR). **Table S2.** Results of two-way ANOVAs for leaf nutrient concentrations, leaf N:P ratio, and nutrient resorption parameters sampled in December, as dependent on canopy nitrogen addition (CN), understory removal (UR), and their interaction (CN × UR). **Table S3.** Results of four-way ANOVAs showing the effects of canopy nitrogen addition (CN), understory removal (UR), leaf types (LT) (Green vs Senesced), seasons (S) (April and December) and their interactions on N, P concentrations and N:P ratios in a Chinese fir plantation. **Table S4.** Effects of canopy nitrogen addition (CN), understory removal (UR), season (S) (April and December) and their interactions on leaf nutrient resorption parameters (NRE, and PRE) in a Chinese fir plantation. **Table S5.** Results of repeated measures ANOVA showing the effects

of canopy nitrogen addition (CN), understory removal (UR), sampling dates (T), and their interactions on leaf litter nutrient content of N, P and N:P during 2016–2017.

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### Author contributions

Jawad Ali Shah, Jianping Wu and Wenfei Liu conceived the idea, suggestions for data selection, preparation, analysis and interpretation. Jawad Ali Shah and Saif Ullah conducted data analysis. Jianping Wu, Fangfang Shen, Yingchun Liao, contributed ideas to analyses. Jawad Ali Shah and Jianping Wu wrote the manuscript. Jawad Ali Shah, Wenfei Liu, Saif Ullah, Syed Turab Raza, Fangfang Shen, Yingchun Liao, Honglang Duan, Jianping Wu contributed to the shaping of the manuscript, and made edits and suggestions leading to the final version.

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### Availability of data and materials

This paper is original and contains all crucial data produced or analyzed throughout this research. However more detailed information related to this current study will be provided on a reasonable request from the corresponding author.

### Declarations

#### Ethics approval and consent to participate

Not applicable.

#### Consent for publication

Not applicable.

#### Competing interests

The authors declare no conflict of competing interest for the submitted work.

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