

Time-lagged precipitation drives the alternation of nitrogen and phosphorus limitations via nutrient resorption, constraining productivity in temperate forests

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ABSTRACT

Drought limits forest productivity, yet rewetting after drought does not fully restore productivity to its maximum potential. Whether this incomplete recovery is linked to plant nutrient limitations remains unclear. Here we continuously investigated nitrogen and phosphorus resorption efficiency (NRE and PRE) of three deciduous oak species for ten years (from 2013 to 2022) in a dry warm-temperate forest in Central China, and assessed their relationships with interannual climate variability and forest net primary productivity (NPP). Our results demonstrated that nutrient resorption did not differ among tree species but across years. With increasing precipitation, NRE initially decreased (9 %) and then increased (7 %), while PRE showed a consistent linear increase. In most years, PRE was higher than NRE, indicating that plant growth in this region is generally P-limited. However, in the second year following extreme precipitation events (2017 and 2021), the NRE:PRE ratio increased and exceeded 1, suggesting that the time-lag effects of extreme precipitation can shift the ecosystem from P to N limitation in the next year. PRE was positively correlated with NPP, while NRE was negatively correlated with NPP. A sudden decline in NPP was observed when the NRE:PRE ratio exceeded 1. Our results suggest that the lagged effects of extreme precipitation may switch N and P limitations via nutrient resorption in warm-temperate forest ecosystems, further constraining forest productivity. This study provides scientific guidance for forest management under global climate change.

1. Introduction

Climate change is driving not only a steady increase in global temperatures but also more frequent and intense extreme weather events, such as droughts and storms (Zhou et al., 2019). These changes pose

significant threats to tree growth and forest ecosystem functioning (Pugnaire et al., 2019; Weiskopf et al., 2020; Ma et al., 2025). Drought, in particular, limits forest productivity (Xu et al., 2024), and rewetting after drought often fails to restore productivity to pre-drought levels (Knapp et al., 2008). This incomplete recovery may be linked to nutrient

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limitation, though the underlying mechanisms remain unclear (Bünemann et al., 2013; Guo et al., 2022; Peng et al., 2024). Previous research has highlighted the combined influence of precipitation and nutrient availability on forest productivity (Xu et al., 2020; Guo et al., 2022; Manu et al., 2024). However, much of this evidence derives from spatial-scale analyses and manipulative experiments (Prieto and Querejeta, 2020; Hou et al., 2021; Cunha et al., 2022), leaving a gap in understanding how interannual climate variations interact with nutrient dynamics to shape forest productivity over time. Therefore, long-term field-based studies over decades are urgently needed to elucidate the underlying mechanisms (Drenovsky et al., 2019), especially in the face of increasingly frequent and intense extreme weather events.

Nitrogen (N) and phosphorus (P) are the two primary nutrients driving forest productivity (Du et al., 2020). Globally, high-latitude temperate and boreal forests are typically N-limited, while low-latitude tropical forests are P-limited (Reich and Oleksyn, 2004; Du et al., 2020). Although long-term field fertilization experiments are considered the best approach for assessing nutrient limitation in plant growth, directly testing these limiting elements in the field remains challenging (Reed et al., 2012; Peng et al., 2023). Nutrient resorption, the process by which plants transfer nutrients from senescing tissues to growing or storage tissues, is a key strategy for coping with nutrient limitations (Killingbeck, 2004). Nutrient resorption efficiency (NuRE) is widely used to assess plant nutrient status and limitation (Reed et al., 2012; Du et al., 2020; Peng et al., 2023). Globally, NuRE for N and P typically exceeds 50 %, with higher NuRE indicating stronger nutrient limitation (Yuan and Chen, 2009; Vergutz et al., 2012).

Nutrient resorption varies substantially due to various factors, including climate factors, soil nutrient conditions, and plant species or functional types (Reed et al., 2012; Vergutz et al., 2012; Prieto and Querejeta, 2020; Xing et al., 2024; Wang et al., 2025). On a broad geographical scale, drought tends to increase nitrogen resorption efficiency (NRE) but may either increase or decrease phosphorus resorption efficiency (PRE) (Yuan and Chen, 2009; Sun et al., 2015). In nutrient-poor environments, plants generally exhibit higher NuRE compared to nutrient-rich environments (Yuan and Chen 2015; Drenovsky et al., 2019). However, how plant nutrient resorption varies with interannual climate fluctuations remains unclear (Du et al., 2021). Undoubtedly, interannual drought–rewetting cycles significantly influence nutrient resorption through their effects on nutrient cycling in both plant and soil systems (Chen et al., 2021). Drought reduces soil nutrient availability by limiting nutrient diffusion and mass flow, while also directly impairing plant nutrient uptake due to decreased mineralization rates (He and Dijkstra, 2014; Müller and Bahn, 2022). These constraints can lead to higher NuRE in plants, serving as a strategy to conserve and recycle limited resources (Brant and Chen, 2015). Rewetting events after drought often trigger enhanced mineralization and nutrient release, temporarily alleviating nutrient limitations and supporting plant growth (He and Dijkstra, 2014). However, the extent to which these nutrient resorption dynamics are influenced depends on factors such as drought severity and duration, rewetting intensity, and the specific nutrient in question (e.g., N or P) (Sardans and Peñuelas, 2007; He and Dijkstra, 2014). For instance, P cycling may be more sensitive to soil moisture changes than N cycling, potentially leading to decoupled nutrient dynamics under extreme climatic conditions (Delgado-Baquerizo et al., 2013; Liang et al., 2022). As expected, the interplay between drought and rewetting shapes nutrient resorption patterns, affecting plant nutrient conservation strategies and forest productivity. Understanding these processes is crucial for predicting how forest ecosystems will respond to increasing climate variability and extreme weather events.

In warm temperate regions, precipitation is predominantly concentrated in the summer, and these areas are characterized by widespread oak trees distributions (Chen et al., 2024), which are generally P-limited (Du et al., 2020; Chai et al., 2015). Recently, due to global climate change, extreme precipitation events in this region have become increasingly frequent (Zhang et al., 2021). Increased precipitation can

enhance soil P release, alleviating P limitation in forest ecosystems (Vitousek et al., 2010). Moreover, previous studies have demonstrated that P resorption efficiency (PRE) exhibits greater variability compared to N resorption efficiency (NRE) (Drenovsky et al., 2019). As expected, plants can grow rapidly once P limitation is alleviated. However, due to the greater N stability, resorbed N may not sufficiently meet plant demands for maximum productivity, potentially shifting the ecosystem from P limitation to N limitation, a phenomenon that requires further study. Furthermore, nutrient resorption is closely linked to plant growth (Tully et al., 2013). Previous studies have reported that plant growth rates are positively correlated with NRE (Zhang et al., 2015; Xing et al., 2024), and resorbed N is primarily used for the growth of new leaves and reproductive parts in early spring (Bausenwein et al., 2001). Xing et al. (2024) found that in N-limited boreal forests, N addition leads to higher PRE (see also (Zhao et al., 2020)), effectively shifting the system toward P limitation and resulting in a decline in plant photosynthesis. Therefore, whether extreme climate events can reshape N and P limitations in ecosystems, and whether such shifts further impact forest productivity still require further confirmation.

In this study, we investigated the interannual variations in NRE and PRE for three deciduous oak species in temperate forests over ten consecutive years, and evaluated their relationships with annual climatic factors, green leaf nutrient content, and soil nutrient availability. First, we hypothesized that drought reduces PRE but increases NRE. This is because drought usually decreases soil nutrient availability, especially for N while having less pronounced effect on P (Delgado-Baquerizo et al., 2013). As a result, plants are expected to resorb more N and less P. Second, increased PRE induces a shift from P limitation to N limitation in plant growth. This is because higher PRE, combined with precipitation-induced soil P release, can alleviate P limitation, thereby increasing the demand for N to support growth. Third, relieving P limitation does not enhance forest productivity. This is because excess P availability can lead to N limitation, restricting further increases in productivity. Our findings will provide scientific guidance for forest management in the context of global climate change.

2. Materials and methods

2.1. Study area

This study was conducted from 2013 to 2022 at the Forest Ecological Research Station of the Baotianman Natural Reserve (111°47′–112°04′E, 33°20′–33°36′N, 500–1845 m a.s.l.) in Henan Province, Central China (Fig. 1). This area belongs to a temperate-subtropical ecotone zone with mean annual precipitation of 936 mm, and a mean air temperature of 12.4°C over the past thirty years (from 1981 to 2010) (<http://climateap.net/>). The dominant soil type is haplic luvisol. The forest vegetation primarily consists of deciduous oak species, including *Quercus aliena* var. *acuteserrata*, *Q. glandulifera*, and *Q. variabilis*, along with several other deciduous woodland species and shrubs as minor components, such as *Forsythia suspense*, *Cornus controversa*, and *Spiraea salicifolia*.

2.2. Soil and leaf sampling

Baotianman Natural Reserve is dominated by three oak species—*Q. aliena* var. *acuteserrata*, *Q. glandulifera* and *Q. variabilis*—all of which were selected when the project began in 2013. *Q. variabilis* litter usually contains the highest concentration of phenolic compounds and is therefore expected to be the most recalcitrant, yet this trait did not generate interspecific differences in NuRE (Du et al., 2021). As a direct continuation of previous work, we again included stands of three oaks, but we formulated no a-priori hypotheses regarding oak species identity. Therefore, the same three study sites were selected, where each site represented a stand of a subject tree species (Table 1). For each site, three 20 m × 20 m plots were demarcated and the latitude, longitude,

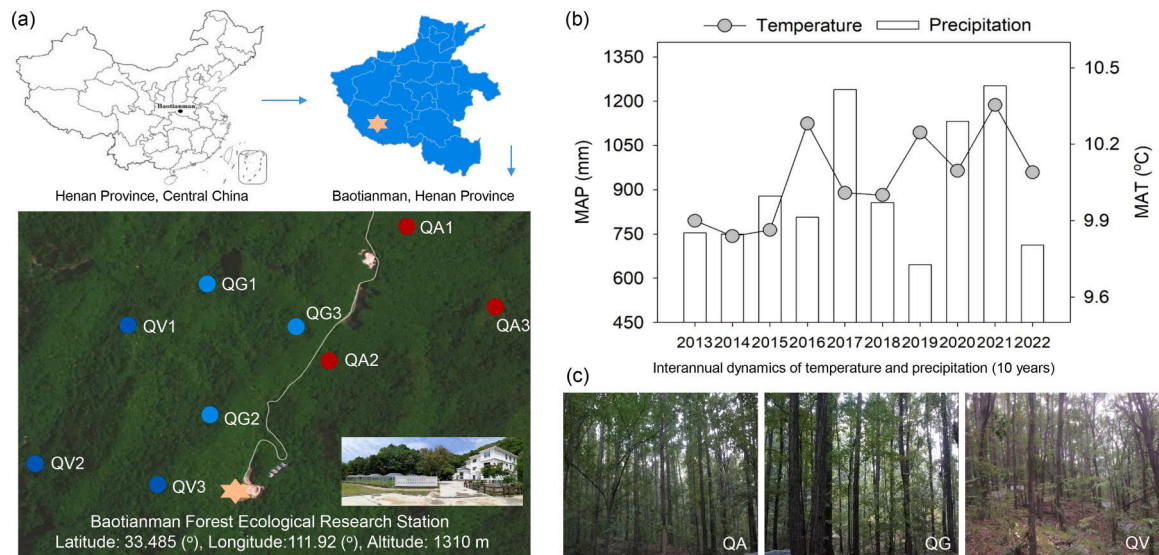


Fig. 1. The research site and climatic dynamics over the past decade. The study site is located in the Baotianman Mountains, within the temperate zone of Central China. QA represents *Quercus aliena* var. *acuteserrata*, QG is *Quercus glandulifera*, and Qv is *Quercus variabilis*.

Table 1
Site and vegetation characteristics of the three studied oak species.

Stands	Tree age (a)	Tree density (trees ha ⁻¹)	Tree height (m)	DBH (cm)
<i>Q. aliena</i> var. <i>acuteserrata</i>	98	950 ± 109	20.3 ± 2.0	33.5 ± 3.7
<i>Q. glandulifera</i>	98	1100 ± 156	19.9 ± 1.2	30.2 ± 1.3
<i>Q. variabilis</i>	105	641 ± 137	22.6 ± 0.8	35.4 ± 4.2

and altitude were recorded with a global positioning system (Thales Navigation, Santa Barbara, CA, USA). Within each plot, five healthy and medium-sized dominant trees were randomly selected for the collection of leaf samples from the upper central south-facing part of the crown. For each plot, we collected 100 green leaves in August and 100 senesced leaves in December. The green and senesced leaves were obtained by cutting the upper middle branches with a retrofitted fishing rod from the ground. A total of five soil cores (0–10 cm) were randomly extracted using a 2 cm diameter stainless-steel earth borer from each plot, which were combined to produce a composite sample. The soil samples were air-dried, while the green leaf and senesced leaf samples were oven dried (65 °C) for 72 h. The soil and leaf samples were ground and sieved through a 60-mesh sieve (0.25 mm diameter) for chemical analysis.

Study plot characteristics showing that each 400 m² plot was surveyed for all trees with diameter at breast height (DBH) ≥ 5 cm, including measurements of tree density (stems/plot), DBH (recorded at 1.3 m above ground level), and height (estimated with an ultrasonic altimeter).

Nutrient resorption was expressed as the difference in the elemental concentrations between the green (X_{gr}) and senescent (X_{sen}) leaves by dry mass.

$$\text{Nutrient resorption efficiency} = (1 - \frac{X_{sen}}{X_{gr}} \text{MLCF}) \times 100$$

Where MLCF is the mass loss correction factor and ~ 0.784 for deciduous broadleaved species (Vergutz et al., 2012), and X represents leaf N or P concentration.

The ratio of NRE:PRE was widely used to estimate local, regional and global N limitation or P limitation in terrestrial ecosystem (Du et al., 2020). If NRE:PRE was > 1, plants withdrew more N than P, which

suggested stronger N limitation than P limitation. Alternatively, when the NRE:PRE was < 1, plants absorbed more P compared to N, and thus P was more limiting in local forest ecosystems.

2.3. Chemical analyses

The total N concentrations of the fresh leaves, senesced leaves, and soil were assessed using an elemental analysis (Vario EL cube, Elementar, Germany). The total P concentrations were determined using an inductively coupled plasma optical emission spectrometer (ICP-OES) (Iris Advantage 1000, Thermo Jarrell Ash, Franklin, MA, USA). For the soil samples, digestion was performed with hydrofluoric and nitro-hydrochloric acid, while nitric and perchloric acid were used for the leaf samples. The detailed methodology for these analyses was reported by Sun et al. (2012) and Du et al. (2021).

2.4. NPP and meteorological data

NPP (g C·m⁻²·yr⁻¹) data were collected from MOD17A3HGF V6.1 provided by NASA Moderate Resolution Imagine Spectroradiometer (MODIS) MOD17 products (<https://doi.org/10.5067/MODIS/MOD17A3HGF.061>, accessed on 2 April 2024). Annual NPP was determined by computing an 8-day interval of Net Photosynthesis (PSN) products (MOD17A2H) from the given year. The product has been widely used in calculating forest water cycle, carbon dynamics, and biogeochemistry of vegetation (Wang et al., 2022). This study used 2013–2022 annual NPP data at a 500 m (m) pixel resolution. Due to the mismatch between the NPP resolution (500 m×500 m) and the sample area (20 m×20 m), to reduce the evaluation error of NPP between sample plots for each oak species, the average NPP data of seven points in this study were used to determine the NPP data of each oak tree species for a given year. During these seven points, three points were the center of the three repeated sample plots, the other three points were the middle points between every two sample plots connected by the three sample plots, and the seventh point was the center point of the triangle composed of three sample plots.

The climatic data and tree age were provided by the Baotianman Forest Ecological Research Station from the local meteorological system. During the study decade, the mean values of mean annual temperature (MAT) and mean annual precipitation (MAP) were 10.07 °C and 858.83 mm, respectively. The interannual precipitation from 645.60 to 1256.60 mm exhibited higher variability compared to the interannual

temperature, which ranged from 9.84 to 10.35 °C (Fig. 1b), with coefficients of variation of 1.80 % and 23.16 %, respectively. Extreme precipitation events were defined as total annual precipitation changes with a frequency distribution of more than 90 % within 50 years (IPCC, 2001). According to this definition, 2017 and 2021 were extreme precipitation years.

2.5. Data analyses

One-way ANOVA was employed to determine the differences in nutrient resorption between the different species. One-way repeated measures ANOVA was used to evaluate whether NRE, PRE and their interacting effects differed between years and species. Subsequently, linear and/or quadratic regressions were conducted to determine the nutrient resorption correlations with MAT, MAP, and leaf and soil nutrients, as well as the relationships between NPP and MAP and nutrient resorption. Hierarchical partitioning (HP) analysis was performed to test the combined effects of MAT, MAP, as well as leaf and soil element concentrations on nutrient resorption efficiencies. The above analyses were carried out with R version 3.6.1 (R Development Core Team, available from www.r-project.org/, accessed 2019) and SigmaPlot 10.0 (Systat Software, Inc., Richmond, CA, USA).

3. Results

3.1. Interannual dynamics of nutrient resorption efficiency in the temperate oak forests

Nutrient resorption varied significantly among years but did not differ between tree species (Fig. 2). PRE was generally greater than NRE in the three oak species. The three oak species showed analogous nutrient resorption patterns in response to interannual climatic variability. For instance, NRE in 2016 was lower than that in other years (Fig. 2a), and PRE in 2018, 2019, and 2022 was lower than that in other

years (Fig. 2b). In most years, the NRE:PRE ratio was < 1, which indicated that the local oak forests were mainly P-limited. However, after extreme precipitation events (2017 and 2021), the NRE:PRE ratio in 2018, 2019 and 2022 was > 1 (Fig. 2c), which revealed that the local oak forests shifted from P limitation to N limitation.

3.2. Effects of climatic and nutrient variations on nutrient resorption efficiency

NRE decreased with MAT in *Q. glandulifera* and *Q. variabilis* (Fig. 3a), and initially decreased (9 % in *Q. aliena*) and then increased (7 % in *Q. aliena*) with MAP in both *Q. aliena* and *Q. variabilis* (Fig. 3d). PRE first decreased (average: 34 %) and then increased (average: 43 %) with MAT (Fig. 3b), and significantly increased with MAP in the three oak species (Fig. 3e). NRE:PRE generally declined with MAP. There were positive relationships between NRE and leaf N concentration, and no relationships between PRE and leaf P concentration (Fig. 3). Soil nutrients did not influence NuRE.

Hierarchical partitioning analysis showed that 33–44 % variation for NRE, 53–74 % variation for PRE, 34–44 % variation for NRE:PRE were explained by climatic factors, and leaf and soil nutrient concentrations (Table 2). NRE was significantly correlated with leaf N concentration in the three oak species, PRE with MAT and MAP, and NRE:PRE also with MAT and MAP.

3.3. Relationship between nutrient resorption efficiency and NPP

Forest productivity, like nutrient resorption, was variable in response to annual climatic variability (Fig. S1). Forest productivity was closely associated with nutrient resorption, showing that NPP decreased with NRE, while increased with PRE. There was a cubic function relationship between NRE:PRE and NPP, showing that once NRE:PRE was greater than 1, NPP steeply decreased (Fig. 4). Moreover, we found that NPP initially increased with increasing precipitation and then decreased

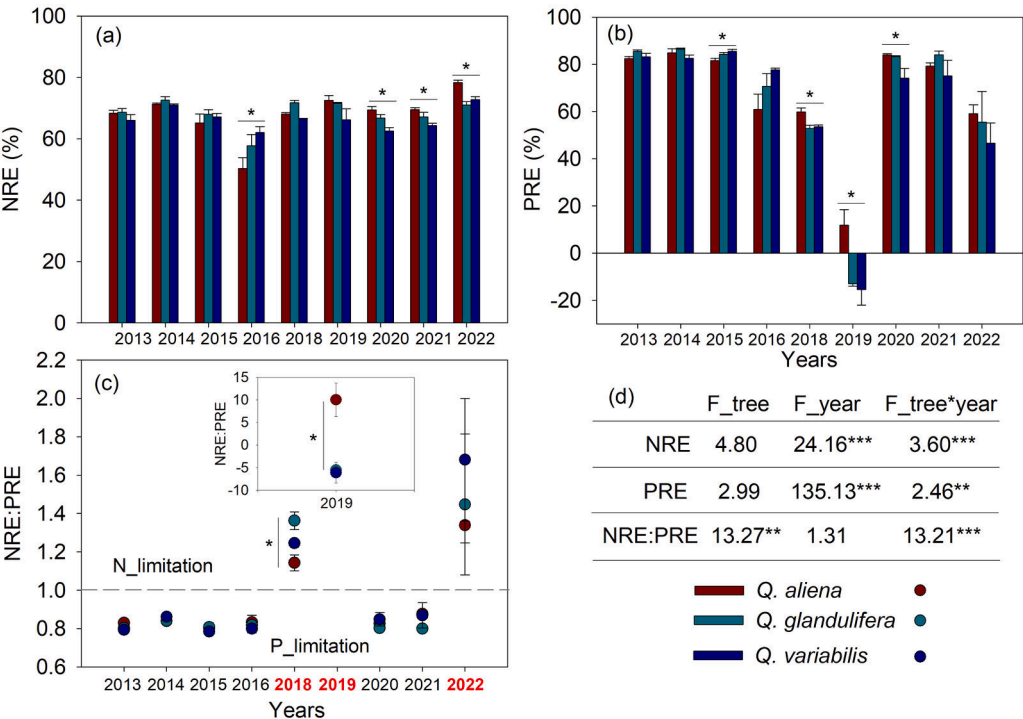


Fig. 2. Interannual dynamics of nitrogen resorption efficiency (NRE, a), phosphorus resorption efficiency (PRE, b), and NRE:PRE (c) of three oak species in temperate forests. When NRE:PRE < 1, it indicates that P resorption is greater than N, indicating P limitation; when NRE:PRE > 1, it indicates that N resorption is greater than P, indicating N limitation (c). The differences in nutrient resorption between species and years were evaluated by one-way repeated measures ANOVA (d). Red text represents the years of N limitation (c). The missing study in 2017 was triggered by accidental damage to the professional sampling equipment.

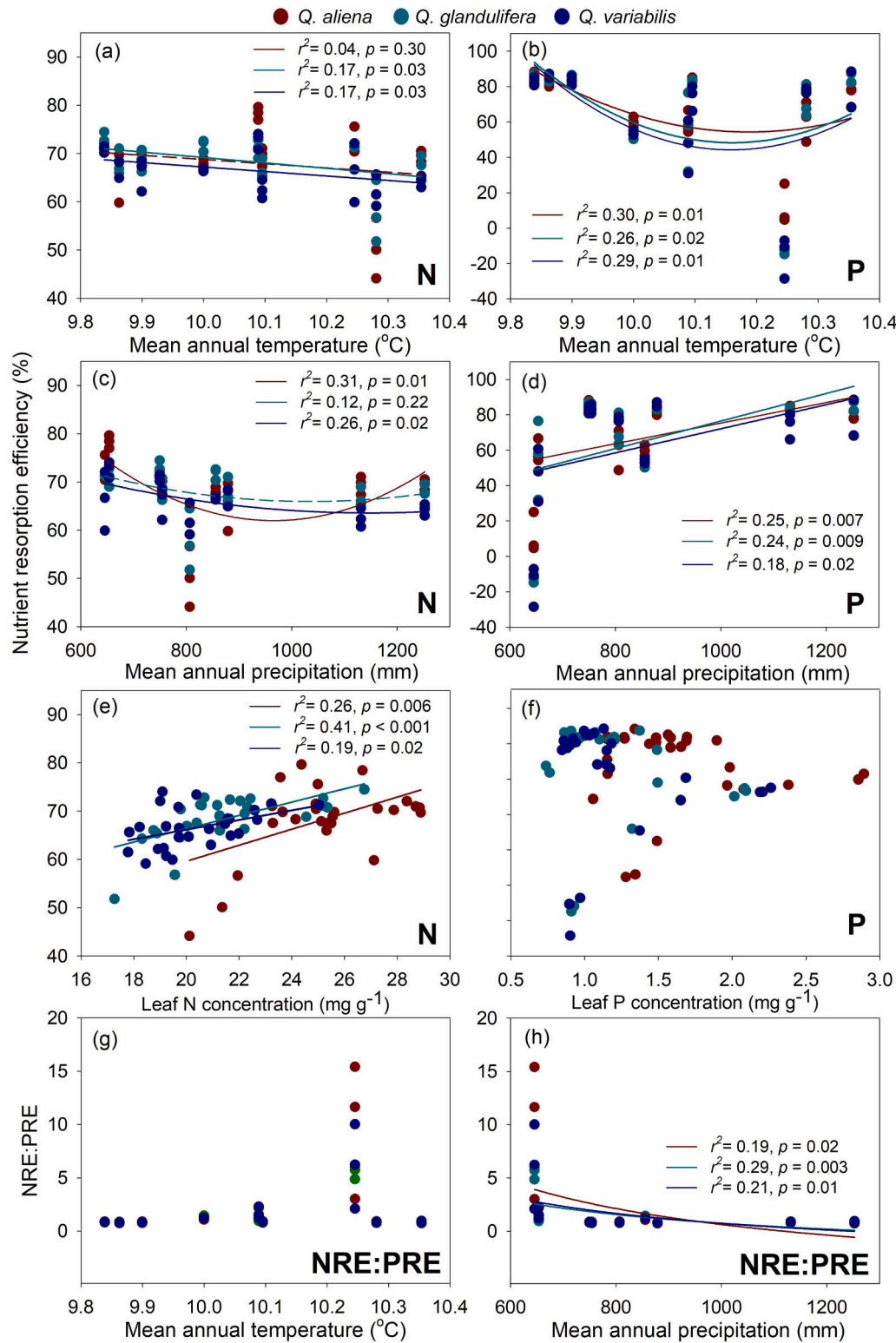


Fig. 3. Effects of climate and plant nutrient concentrations on nutrient resorption efficiency in three oak species.

for the three oak species (Fig. 4a). PRE in previous years was negatively correlated with soil P concentration in current years, and soil P concentration was positively correlated with NPP (Fig. 5 and Fig. S2).

4. Discussion

Nutrient resorption is a critical plant nutrient conservation strategy

(Brant and Chen, 2015), which plays important roles in determining biogeochemical cycling and plant growth (Xing et al., 2024). However, previous studies primarily focused on spatial scales, communities, and ecosystem levels (Du et al., 2020, Peng et al., 2023, Wang et al., 2025). Using a decade-long dataset from three temperate oak forests, we show that extreme precipitation events alleviated P limitation by increasing soil total P which is a widely accepted proxy for P availability (Luo et al.,

Table 2

Fraction of variance (%) accounted by climatic factors, leaf and soil nutrients in resorption efficiencies for the three oak species. *Q. aliena* var *acuteserrata* (QA), *Q. glandulifera* (QG), and *Q. variabilis* (QV).

Element	Species	Full model (r ²)	MAT	MAP	Leaf nutrient	Soil nutrient
NRE	QA	0.33	8.08	3.02	69.29*	18.81
	QG	0.44	17.82	5.94	72.74*	3.50
	QV	0.44	16.49	42.60*	36.94*	3.96
PRE	QA	0.74	45.24*	48.96*	1.92	3.88
	QG	0.60	39.73*	53.24*	2.65	4.37
	QV	0.53	46.388	47.31*	3.24	3.07
NRE:PRE	QA	0.34	43.65*	43.12*	5.55	7.67
	QG	0.41	46.76*	33.07*	17.62	2.55
	QV	0.44	35.18*	43.67*	7.42	13.72

2025). This precipitation-driven P enrichment, in turn, shifted the stoichiometric balance of nutrient limitation experienced by the vegetation. This transition occurred as the P pulse stimulated rapid plant growth, consequently increasing N demand beyond soil supply capacities. Importantly, this transition from P- to N-limitation exhibited a distinct time lag, ultimately constraining forest primary productivity through asynchronous nutrient availability.

4.1. Effects of interannual climate variability on nutrient resorption

In this study, PRE was greater than NRE in 6 out of the 10 years of study, indicating that P was more limiting than N for plant growth in this temperate forest, as demonstrated by other studies (Du et al., 2021). Furthermore, our results revealed that nutrient resorption varied significantly between years but did not differ between species, consistent with previous findings (Du et al., 2021). The analogous responses in nutrient resorption between species have been well-documented by

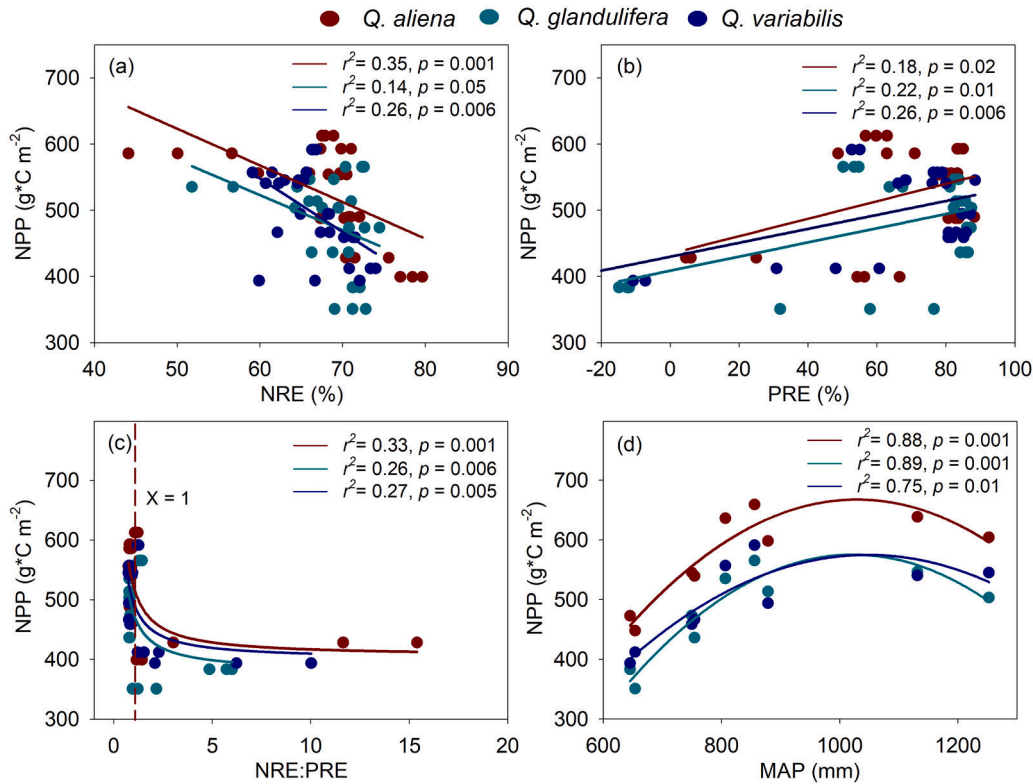


Fig. 4. Relationships between nutrient resorption and forest net primary productivity.

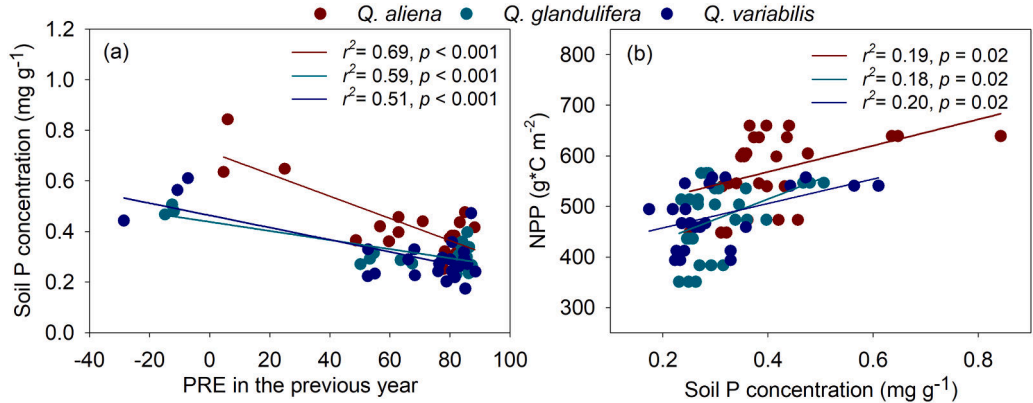


Fig. 5. Relationships between soil P concentration, and PRE of the previous year, and NPP.

other field works (Prieto and Querejeta, 2020), and manipulative experiments (Lü et al., 2013). These results suggest that the plants occupying the same niche and growing in the same region might have parallel or convergent nutrient absorption and conservation strategies (Bahamonde et al., 2019).

Interannual variability in nutrient resorption (Fig. 2d) underscores its sensitivity to climate fluctuations. There was a negative relationship between NRE and temperature (Fig. 3a), as demonstrated in previous studies (Yuan and Chen, 2009, Prieto and Querejeta, 2020). This is because low temperature not only inhibits the metabolic activity of plants, but also restricts soil nutrient release and root nutrient uptake (Reich and Oleksyn, 2004). Thus, plants need to withdraw additional N to maintain normal metabolic activity and growth, which can reduce their dependence on soil nutrient availability (Brant and Chen, 2015). On the other hand, high temperature enhances soil N mineralization (Dai et al., 2020), which can increase soil N availability and thereby lowering N resorption. However, the temperature-PRE relationship exhibited more complex dynamics, showing a unimodal pattern that contrasts with previous reports of either positive (Yuan and Chen, 2009) or negative (Sun et al., 2015) linear responses. This is largely due to the fact that low temperature restricts P mineralization and uptake, thus requires greater P resorption. At elevated temperature, warm-induced enhancement of N availability stimulates plant growth (Dai et al., 2020), thereby increasing P demand (Chen et al., 2020) and driving higher PRE to maintain stoichiometric balance (Van de Waal et al., 2018).

In line with previous studies (e.g. Yuan and Chen, 2009), PRE increased with increasing precipitation (Fig. 3e). Under drought conditions, soil P availability decreased (Sardans and Peñuelas, 2004), but organic P mineralization, driven by extracellular phosphatase enzyme, increased (Zhang et al., 2020, Peng et al., 2023). This process can improve soil P concentration, thereby alleviating P limitation for plant growth. Previous studies also demonstrated that N inputs would accelerate P cycling rates through the enhancement of soil and root phosphatase activity (Marklein and Houlton, 2012). However, since enzyme production and activity require a large amount of N supply (Allison and Vitousek, 2005, Peng et al., 2023), we observed higher NRE in low precipitation years (Fig. 3). Our findings indicate that a higher N requirement may be an adaptive strategy for local plants to cope with P limitation under drought conditions.

In contrast to drought, increasing precipitation enhances the solubility and mobility of soil P (Lucas et al., 2023), thereby improving soil phosphorus availability (He and Dijkstra, 2014). As a result, plants may rapidly absorb more P to alleviate P limitation, as demonstrated by Bünnemann et al. (2013). In response to changes in nutrient conditions caused by extreme precipitation, plants maximize the external acquisition and internal conservation of the most limiting element (Peng et al., 2023). Thus, plants also need to store more P through nutrient resorption to cope with long-term P shortages and maintain rapid growth after precipitation (Fig. 3). The high leaf P concentration in the second year of extreme precipitation further supports this hypothesis (Fig. S3). Our results suggest that high P utilization and resorption after high precipitation may be an adaptive strategy for plants to alleviate P limitation and adapt to long-term low P environments.

4.2. Extreme precipitation reshapes N and P limitations through nutrient resorption

The ratio of NRE:PRE was greater than 1 after extreme precipitation events. This indicates that N resorption was greater than P resorption, suggesting a shift in plant growth limitation from P to N after extreme precipitation. One potential explanation is that P limitation was alleviated following extreme precipitation (He and Dijkstra, 2014) and higher P was stored in plant organs through nutrient resorption. This allowed plants to grow rapidly in the second year, leading to higher N demand to match the increased P supply and maintain stoichiometric balance

(Sterner and Elser, 2002). However, plant N reserves were relatively stable (low C.V.) compared to P. When plants experienced P supply pulses during extreme precipitation, the supply of N became insufficient or limited caused by N leaching (Gao et al., 2014). Consequently, plants need to mineralize and withdrawn more N (Fig. 2) after extreme precipitation to maintain a balanced source-sink relationship and stoichiometric equilibrium (Wang et al., 2017), resulting in the N limitation for plant growth. The conversion of N and P limitations has previously been attributed to P limitation caused by long-term anthropogenic N deposition (Chen et al., 2020, Xing et al., 2024). However, our findings suggest that extreme precipitation can also reshape N and P limitations in temperate forest ecosystems.

Interestingly, the phenomenon of $NRE:PRE > 1$ was observed twice, in 2018 and 2022.

However, the two extreme precipitation events occurred in 2017 and 2021, respectively. This indicates that N limitation was delayed by one year and occurred in the second year following extreme precipitation. Other studies have also reported time delay effects (Hahn et al., 2021), primarily focusing on the spatiotemporal changes in primary productivity but lacking mechanistic explanations. Our results suggest that the time lag effect is primarily driven by seasonal and interannual fluctuations in plant nutrients. Plants can regulate their regrowth by controlling the resorption process to store key nutrients such as N and P for growth in the following year (May and Killingbeck, 1992, Silla and Escudero, 2003), depending on climatic conditions. To our knowledge, this is the first study to demonstrate the time lag effect of extreme precipitation reshaping nutrient limitation in forest ecosystems. However, while our study shows that extreme precipitation can reshape N and P limitations, the threshold of precipitation required to trigger this shift remains unclear (Linger et al., 2020), and requires further investigation.

4.3. Nutrient resorption significantly affects forest primary productivity

Precipitation and nutrient are the two predominant factors controlling forest productivity. Our results indicate that NPP did not always increase with precipitation in the temperate forests but declined when precipitation exceeded a certain range (Fig. 4a). This finding differs from previous studies that reported a linear increase in NPP with increasing precipitation, but aligns with the study by Zhou et al. (2008) which found a non-linear relationship between precipitation and NPP. One potential explanation is that although extreme precipitation released P, alleviated plant P limitation (Vitousek et al., 2010), the lack of sufficient N supply to match the high P supply pulse constrained plant growth under high precipitation conditions (Fig. 3e). This explanation is supported by the high stability of NRE between years. Additionally, previous studies have shown that extreme precipitation can cause soil N leaching and denitrification, reducing soil N availability for plant growth.

Moreover, we found that nutrient resorption is closely associated with forest productivity. There was a positive correlation between PRE and NPP. According to the growth rate hypothesis, rapidly growing plants require more P to synthesize proteins and support growth, particularly in areas with long-term P deficiency. Therefore, plants at the end of the growing season may withdraw more P to rebalance their source-sink relationships for the following year's growth. High precipitation supported rapid plant growth (Fig. 4a), and also promoted PRE (Fig. 3e), which aligns with our explanation. However, there was a negative correlation between NRE and NPP, contrasting with previous studies (Zhang et al., 2015, Xing et al., 2024). For instance, Zhang et al. (2015) found NRE was positively correlated with plant growth rates across the dipterocarp species. One possible explanation for this negative correlation is that in the P-limited areas with high NPP, the priority of P resorption exceeds that of N resorption. Thus, the more P withdrawn, the less N can be accommodated. In addition, based on the complex relationships between precipitation and NRE (Fig. 3d), it is evident that plants exhibit strong N regulation abilities to adapt to

P-deficiency environments. Furthermore, these opposing relationships between NPP and PRE/NRE suggest that the antagonistic effects of N and P control the interannual dynamics of NPP in local ecosystems, preventing unlimited plant growth even under favorable conditions.

The NRE:PRE ratio has been proven to be an effective measure of plant nutrient limitation across different terrestrial ecosystems (Reed et al., 2012, Du et al., 2020, Xing et al., 2024). We found that when the NRE:PRE ratio was < 1 (indicating P limitation), NPP was elevated. However, when NRE:PRE exceeded 1, indicating a shift from P to N limitation, NPP decreased rapidly. Xing et al. (2024) found that in N-limited boreal forests, plant growth was increasingly constrained by relative P deficiency induced by N addition. These findings suggest that shifts in nutrient limitations can reduce forest productivity. In 2022, following extreme precipitation, although P limitation was alleviated by high P resorption in the previous year (Fig. 2), drought conditions restricted the increase in forest productivity (Fig. S1). In contrast, in 2017, also following extreme precipitation, forest productivity significantly improved. This was due to the combination of high precipitation in 2018 and alleviated P limitation, both of which facilitated plant growth. These results imply that nutrient resorption may affect forest productivity through time lag effects, as further demonstrated by our analysis (Fig. 5).

We found that soil P concentration was closely related to forest productivity but was negatively associated with the previous year's PRE, which is in line with previous study (Cunha et al., 2022). Our study sites lie in a P-deficient region where litter decomposition and plant nutrient resorption are key regulators of soil nutrient status. We found that plant-mediated conservation of nutrients imposes a pronounced time-lag on soil fertility, because recurrent drought slows both litter breakdown and overall soil nutrient cycling (Liu et al., 2024). Consequently, the buffering effect of vegetation on soil P may dampen—or even offset—short-term gains in soil P triggered by extreme precipitation. This lagged feedback complicates predictions of how future precipitation regimes will influence nutrient limitation in temperate oak forests. Additionally, we emphasize that while a significant correlation between precipitation and nutrient resorption has been established, plant growth is collectively determined by environmental factors (primarily precipitation in temperate forests) and nutrient conservation strategies (Linger et al., 2020, Gao et al., 2023).

5. Conclusions

Our study demonstrated how nutrient resorption varies over time and evaluates its relationships with annual climate factors and forest productivity. We found that interannual climate variability significantly affects plant nutrient resorption stoichiometry, particularly P, which exhibits high annual variability and increases with precipitation. In long-term P-limited ecosystems, extreme precipitation events can alleviate P limitation. However, due to the mismatch between N supply and P pulses, plant growth shifts from P limitation to N limitation, and this shift exhibits a time lag effect. Moreover, the lagged effects of extreme precipitation on N and P limitation, combined with the climatic conditions of the current year, jointly determine forest productivity. Our findings suggest that increasing water supply in temperate forests is not the only solution to improve forest productivity, as the conversion of nutrient limitation can constrain plant growth and forest productivity. Therefore, nutrient stoichiometry adjustments should also be considered in future forest management strategies. This study highlights the importance of long-term field ecosystem monitoring and provides new insights into plant nutrient adaptation strategies and forest carbon dynamics under climate change, particularly in the context of extreme weather events.

CRedit authorship contribution statement

Yanhua Zhu: Resources, Conceptualization. Xinxin Liu: Formal

analysis. Chang Zhao: Data curation. Zhicheng Chen: Resources. Xiaobo Yuan: Writing – review & editing, Conceptualization. Saeed ur Rahman: Writing – review & editing. Zhengbing Yan: Writing – review & editing. Nan Hui: Writing – review & editing, Writing – original draft, Funding acquisition. Zhenyu Hu: Writing – original draft, Methodology. Chunjiang Liu: Methodology, Conceptualization. Baoming Du: Writing – review & editing, Writing – original draft, Investigation, Formal analysis. Shan Yin: Resources, Methodology. Hongzhang Kang: Resources, Funding acquisition.

Declaration of Competing Interest

The authors declare no conflict of interest.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123191.

Data availability

Data will be made available on request.

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