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Nutrient resorption responses of female and male *Populus cathayana* to drought and shade stress

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Abstract

Nutrient resorption can increase nutrient use and play important roles in terrestrial plant nutrient cycles. Although several studies have reported individual responses of plant nutrient resorption to drought or shade stress, the interaction of drought and shade remains unclear, especially for dioecious plants. This study explored whether nutrient resorption is correlated to growth characteristics (such as biomass and root/shoot ratio [R/S ratio]) and leaf economics (such as leaf thickness, leaf mass per area [LMA] and leaf vein density [LVD]) in female and male *Populus cathayana* across different conditions. We found that drought stress significantly increased nitrogen (N) resorption efficiency (NRE) in both sexes, but shade and interactive stress decreased NRE in *P. cathayana* females. Under drought stress, nutrient resorption was sexually dimorphic such that *P. cathayana* males have higher NRE than females. Furthermore, NRE and phosphorous (P) resorption efficiency (PRE) were positively related to R/S ratio, leaf thickness, LMA, and LVD in both sexes across different treatments. Our study is the first to present how nutrient resorption is related to biomass accumulation and allocation, and leaf economics, suggesting that nutrient uptake may be modulated by R/S ratio and leaf economics, which is important for understanding the conservation mechanism of plant nutrients.

1 | INTRODUCTION

Increasing attention is given to how to improve the nutrient use efficiency in plants, which usually suffer nutrient limits, such as nitrogen (N) and phosphorus (P). Nutrient resorption can transfer nutrients (i.e., N and P) from senesced leaves to other tissues and increase nutrients residence times in plants (Chen et al., 2021; Drenovsky et al., 2019; Xu et al., 2020; Zhang, Tang, et al., 2015). Thus, nutrient resorption as one important nutrient conservation mechanism can increase plant nutrient reuse and plays an important role in ecosystem nutrient cycling (Killingbeck, 1996; Vergutz et al., 2012; Zhu et al., 2022). The percentage of nutrients in green leaves resorbed from senescing leaves represents the nutrient resorption efficiency (Aerts, 1996; Brant & Chen, 2015; Yuan & Chen, 2009), which is largely influenced by soil resources. Plants usually increase N and P resorption efficiency (NRE and PRE) to promote nutrient uptake and reuse in barren areas, whereas they are decreased in fertile regions (Brant & Chen, 2015; Xu et al., 2020; Zhao et al., 2017). A previous study has reported that precipitation affects soil moisture and fertility at regional and district scales, thereby regulating soil nutrient and nutrient resorption (Brant & Chen, 2015). Recent research on nutrient resorption has focused on nitrogen and phosphorus addition (Zhang et al., 2021), nitrogen enrichment and drought (Zhao et al., 2020), and different latitudes (Li et al., 2016; Zhang et al., 2022), however, the knowledge is still limited on plant nutrient resorption, especially in dioecious plants.

Drought limited plant growth and biomass accumulation, and climate change will lead to more frequent and severe drought (Anderegg et al., 2015; Angon et al., 2022; Choat et al., 2018; Xu et al., 2022). Tree species have different adaptive strategies to cope with drought stress, for example, changing biomass allocation with a higher

root/shoot ratio (Nolan et al., 2017; Wang et al., 2020; Yu et al., 2020) leads to a greater water uptake capacity (Poorter et al., 2012; Yu et al., 2023). Recent studies have shown that plant nutrient resorption is closely linked with plant body size and R/S ratio (Peng et al., 2019). For instance, NRE and PRE increased with increasing plant body size but decreased with increasing R/S ratio. According to Wright et al. (2004), leaf economics can be assessed by calculating revenues and expenditures per unit investment, typically measured as biomass, or C, N, P. For example, leaf mass per area (LMA) determines the leaf dry matter investment per unit of light-intercepting leaf area deployed. In addition, plant leaves that respond to drought stress usually have higher leaf thickness and LMA. Compared with females, *Populus euphratica* males had higher leaf thickness, LMA and leaf vein density (LVD), which were positively correlated with NRE under drought and nutrient-deficient environment (Yu et al., 2022). Therefore, it is important to know the driving and modulating factors of nutrient resorption, which improves our knowledge of nutrient uptake and use strategies of plants.

Light plays a key role in the whole growth process of plants (Cheynier et al., 2013). Shade tolerance is an expression of a plant's ability to capture and utilize light resources (Myers & Kitajima, 2007). On the one hand, as plants continue to grow, mutual shading between leaves can increase, with some negative effects on plant growth (Niinemets, 2010), for example, a decrease in plant growth rate, biomass, and photosynthetic capacity (Liu et al., 2018; Sevillano et al., 2016; Valladares & Niinemets, 2008). On the other hand, it has also been shown that shade attenuates stomatal limitation and photoinhibition of leaves, increases the relative water content of leaves and thus alleviates the adverse effects of drought on photosynthesis (Wang & Wang, 2023). Current studies on plant shading have focused on different shade levels (Huang et al., 2022) and shade periods (Song et al., 2022). Little is known about how shading affects the growth and nutrient uptake of dioecious plants.

In nature, dioecious plants are an integral part of forest ecosystems, although they only constitute 5%–6% of the total plant species (Renner, 2014). Due to the higher reproduction costs in females, there is a sexual dimorphism in dioecious trees such that *Populus* males are more resistant to unfavorable conditions and perform better compared with females (Juvany & Munné-Bosch, 2015; Liu et al., 2020; Xia et al., 2022; Xu et al., 2008). For example, Liu et al. (2022) showed that under drought conditions, *Populus cathayana* males adopted a more conservative water use strategy by reducing the xylem lumen area and increasing the number of ducts and cell wall thickness to withstand drought. *P. cathayana* is a typical representative of dioecious plants, and there have been many studies on the differences between female and male *P. cathayana* under different environmental stress (Liu et al., 2020, 2022; Xia et al., 2022; Xu et al., 2008).

Our study is the first to investigate the differences in nutrient uptake associated with growth and leaf economic traits in a dioecious plant across different conditions. Specifically, we investigated the resorption of nitrogen and phosphorus and their relationships between biomass accumulation and allocation, and leaf economic traits of female and male *P. cathayana* under drought, shade and their interaction. We hypothesized that (1) nutrient resorption of *P. cathayana* females and males is related to growth and leaf economic traits across different environmental conditions. (2) Nutrient resorption of *P. cathayana* has sex-specific responses to drought and shade stress.

2 | MATERIALS AND METHODS

2.1 | Plant materials and experimental design

Populus cathayana Rehd. cuttings of two sexes were collected from 20 trees, sampled from five populations in Datong (35°56′ N, 101°35′ E) in Qinghai, China (Xia et al., 2022). After sprouting and growing for 4 weeks in a glasshouse, 80 healthy cuttings (40 females and 40 males) of approximately the same crown sizes and equal heights were selected for the experiment. This study was conducted at the experimental site of Hangzhou Normal University, Cangqian Campus, Hangzhou City, Zhejiang Province (29°38′ N, 119°54′ E). All plants were grown in a greenhouse with a temperature of 21–25°C at day and 15–18°C at night, with a 12–14 h photoperiod during the experimental period (Guo et al., 2022). This experimental layout was completely randomized with three factors (sex, drought and shade), including two sexes (female and male), two watering regimes (well-watered, CK, and drought), and two shade levels (natural irradiance and low irradiance, shade). We determined the soil water content (SWC) with a time-domain reflectometer (Yu et al., 2018, 2020), and the well-watered (control) treatments were watered to a minimum of 80% of field capacity with a SWC range between 29% and 33%, and the drought treatments with a SWC range between 9% and 13%. Black nylon nets were used for the shade treatments, with irradiance levels at 50% of the natural irradiance (Dong et al., 2015), the irradiance was determined with a Li-Cor 190-SA quantum sensor (Li-Cor Inc.) on a sunny day.

2.2 | Determination of growth

At the end of the experiment, we randomly selected 5 cuttings from each treatment to measure dry matter accumulation and divided the plants into three parts: roots, stems and leaves, and washed the soil from the roots, put them in an envelope and put them to dry in an oven set at 70°C for 72 h until the dry mass reached a constant value. We used a scanner with a resolution of 600 dpi (Cannon Scanner 5600F) to take photos of the leaves and measured the leaf area by Image J imaging software. The leaf mass per area (LMA) was calculated as dry mass/leaf area.

2.3 | Determination of nutrient resorption

Green and mature yellow leaves were taken before the plants dropped their leaves, and all leaf collections were done in 1 day. After drying the leaves, stems and roots, appropriate amounts were taken

to determine nutrient (N and P) contents in the leaves. We used the semi-micro-Kelda hydrogen method (Mitchell, 1998) to determine the N content of leaves and induced plasma emission spectrometry (Lotscher & Hay, 1997) to determine the P content of leaves. The nutrient resorption efficiency (RE) is usually defined as the percentage of nutrients absorbed from senesced leaves compared to green leaves (Aerts, 1996; Killingbeck, 1996), calculated as follows:

$$RE = \frac{Xgr - Xsen}{Xgr} \times 100$$

where Xgr represents mature (green) leaves' nutrient content, and Xsen represents the nutrient content of senesced leaves. Senesced leaves are usually characterized by overall color (often yellow), and can be detach with a gentle flick. In addition, senesced leaves exhibit an abscission layer at the base of the petiole to prevent further nutrient withdrawal (Zhang, Zhang, et al., 2015).

2.4 | Determination of anatomical and morphological traits of leaves

Prior to harvest, three clean and intact green fresh leaves were taken from each female and male plant in each treatment and then placed in a plastic bag and stored in a household

TABLE 1 Biomass accumulation and allocation in *P. cathayana* females and males under drought, shade and their interactive stress.

Treatment	Sex	Leaf biomass	Stem biomass	Root biomass	Total biomass	R/S ratio
CK	Female	6.75 ± 0.31a	8.52 ± 0.18a	6.27 ± 0.13a	21.54 ± 0.57a	39.31 ± 1.38b
	Male	7.08 ± 0.35a	8.08 ± 0.20a	5.67 ± 0.08b	20.83 ± 0.54a	38.53 ± 1.46b
Drought	Female	4.73 ± 0.21bc	5.52 ± 0.09b	4.62 ± 0.14c	14.87 ± 0.30c	44.26 ± 0.53a
	Male	5.37 ± 0.03b	5.71 ± 0.11b	5.25 ± 0.13b	16.32 ± 0.19b	46.51 ± 0.75a
Shade	Female	5.02 ± 0.18b	5.52 ± 0.12b	3.82 ± 0.12d	14.36 ± 0.29c	35.02 ± 0.74b
	Male	5.17 ± 0.13b	5.39 ± 0.06b	3.77 ± 0.14d	14.33 ± 0.25c	36.36 ± 0.84b
DS	Female	3.15 ± 0.08d	3.35 ± 0.18c	2.65 ± 0.13e	9.15 ± 0.27d	35.75 ± 0.74b
	Male	3.88 ± 0.20cd	3.29 ± 0.05c	2.4 ± 0.12e	9.57 ± 0.28d	36.23 ± 1.29b

Note: Each value is the mean ± SE ($n = 5$). Different letters denote significant differences according to Tukey's test at a significance level of $p < 0.05$. Abbreviations: CK, control treatment; DS, the combined stress of drought and shade.

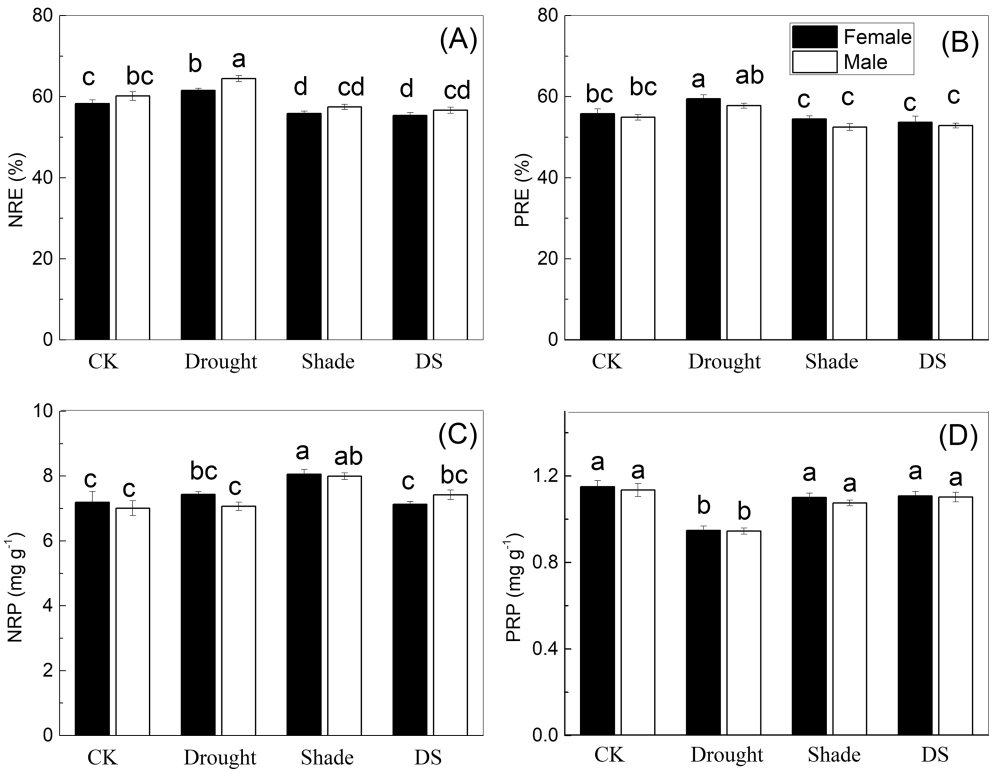

FIGURE 1 (A) N resorption efficiency, (B) P resorption efficiency (PRE), (C) N content in senesced leaves (NRP) and (D) P content in senesced leaves in female and male *P. cathayana* under drought, shade and their interactive stress. Each value is the mean ± SE ($n = 5$). Different letters above bars denote significant differences according to Tukey's test at a significance level of $p < 0.05$.

refrigerator at 4°C for subsequent measurement of leaf vein density, leaf thickness, and other indices. Three intermediate leaf slices from each leaf were taken as hand-cut cross-sections (Yu et al., 2022) to measure leaf thickness, and then a Nikon Eclipse Ni–U microscope (Nikon Corporation) was used to photograph. Finally, leaf thickness was measured by using Image J imaging software (National Institutes of Health). The middle part of the leaf was taken and boiled in 5% NaOH solution for about 4–5 min, placed in sodium hypochlorite solution for bleaching for about 15–20 min, and stained with 1% methylene blue for about 20–30 s (the leaves were fully unfolded), and leaf vein density measurement and calculation were described in detail in Zhang, Zhang, et al. (2015).

2.5 | Statistical analyses

All analyses were performed using the Statistical Package for the Social Sciences (SPSS) version 18.0. Prior to analyses, data were checked for normality and homogeneity of variances and log-transformed where necessary to correct for deviations from these assumptions when needed. Individual traits among treatments were compared by Tukey's tests of one-way ANOVA at a significance level of $p < 0.05$. Linear regressions were conducted to determine the relationships between nutrient resorption and total biomass, R/S ratio, leaf thickness, leaf mass per area and leaf vein density. All the figures were done using the Origin 9.0 (OriginLab) software.

3 | RESULTS

3.1 | The effect of drought and shade stress on biomass accumulation and allocation

Drought, shade and their interactive stress significantly decreased the leaf, stem, root and total biomass of female and male *P. cathayana*, while drought stress increased the R/S ratio (Table 1). In addition, the root and total biomass of *P. cathayana* males were higher than those of females under drought stress.

3.2 | The effect of drought and shade stress on nutrient resorption

Compared with the control treatment (CK), drought stress significantly increased NRE by 5.5% in females and 7.1% in males, but shade and interactive stress decreased NRE in *P. cathayana* females by 4.3% and 5.0%, respectively (Figure 1A). There were no significant differences in PRE of female and male *P. cathayana* across different treatments, but PRE of females was significantly higher under drought stress. In addition, shade stress significantly increased NRP (N content in senesced leaves) by 12.1% in females and 14.3% in males, while drought stress significantly reduced PRP (P content in senesced leaves) by 17.4% in females and 16.7% in males (Figure 1).

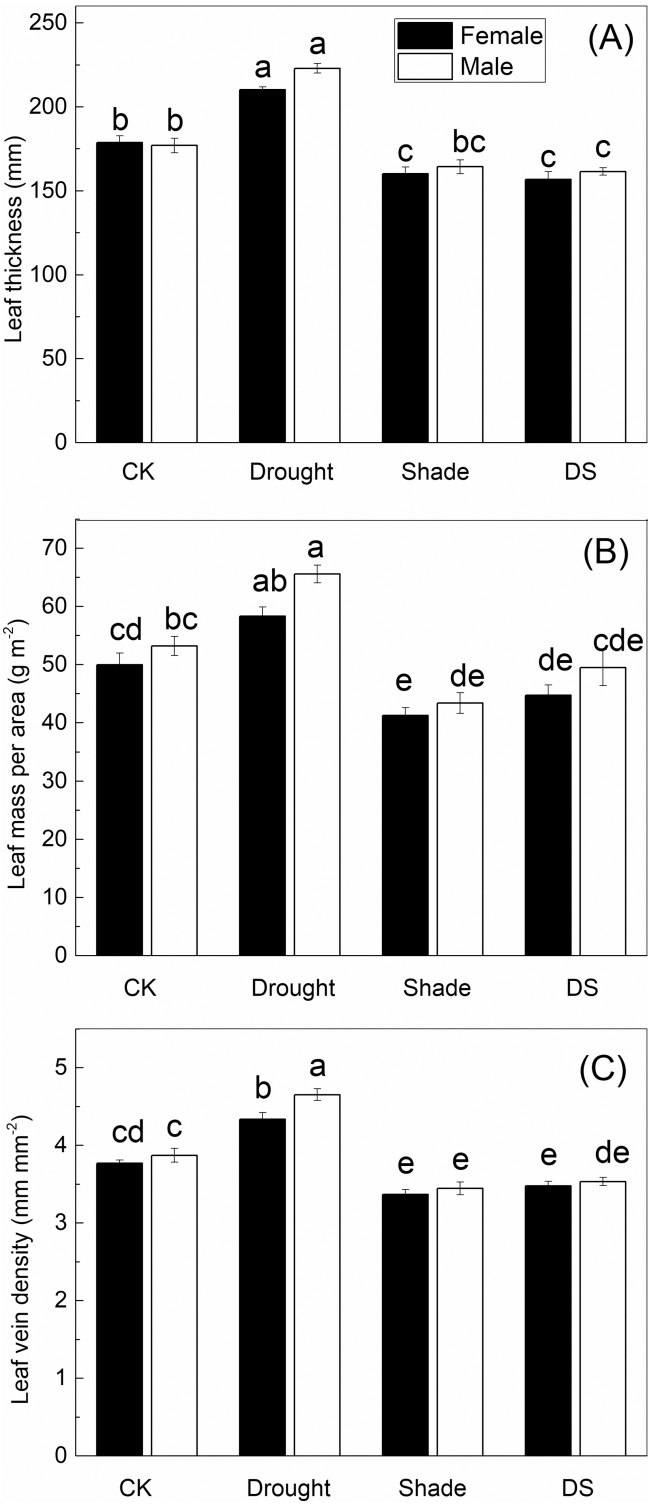

FIGURE 2 (A) Leaf thickness, (B) leaf mass per area, and (C) leaf vein density in female and male *P. cathayana* under drought, shade and their interactive stress. Each value is the mean ± SE ($n = 5$). Different letters above bars denote significant differences according to Tukey's test at a significance level of $p < 0.05$.

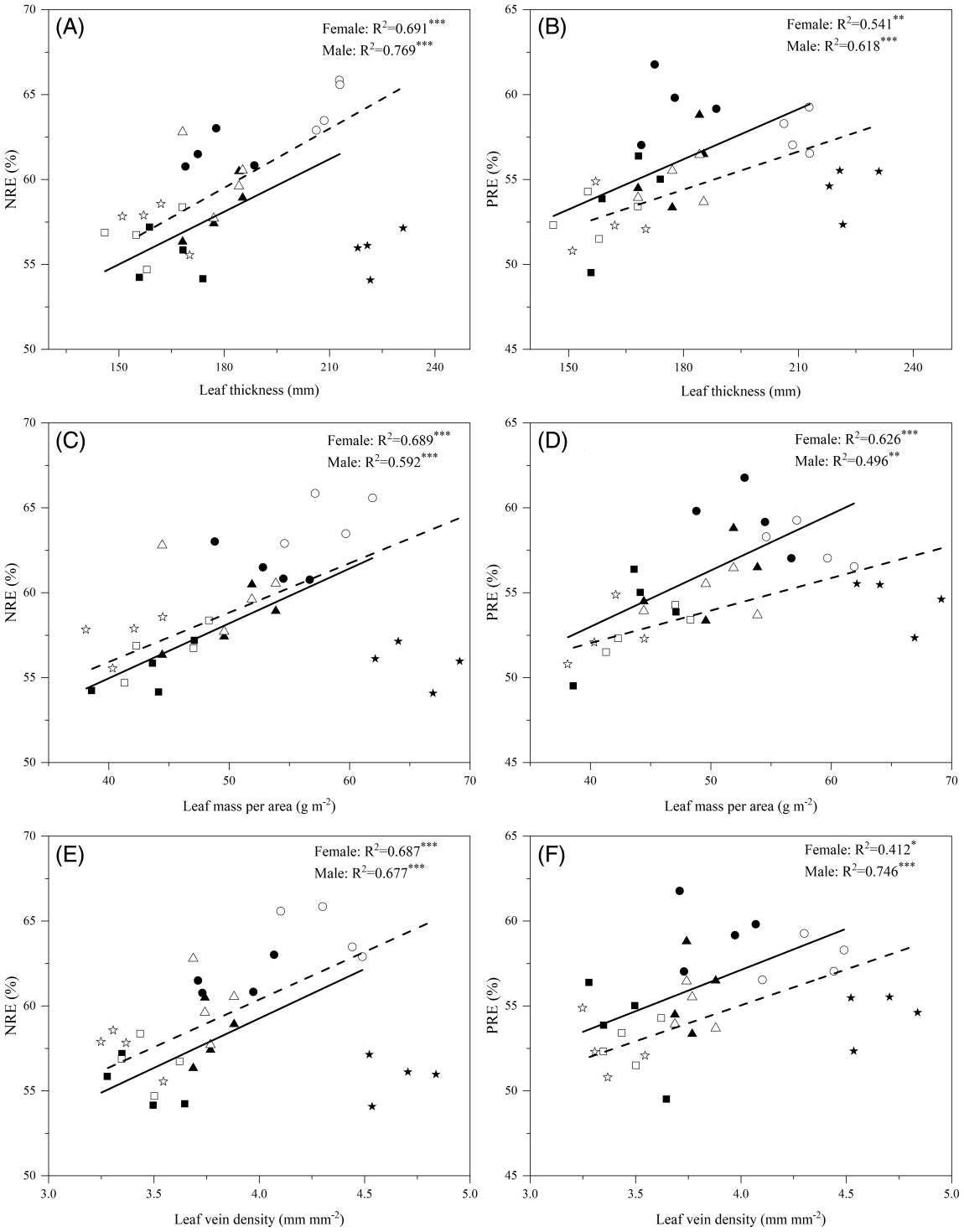

FIGURE 3 Relationships of leaf N and P resorption efficiencies with leaf thickness (A,B), leaf mass per area (C,D) and leaf vein density (E,F) in female and male *P. cathayana* across different drought and shade levels. The white triangle, circle, star and square indicate *P. cathayana* males under CK, drought, shade and their interactive stress, respectively. The black triangle, circle, star and square indicate *P. cathayana* females under CK, drought, shade and their interactive stress, respectively. *F* value and *p*-value are shown. **p* < 0.05; ***p* < 0.01; ****p* ≤ 0.001.

3.3 | The effect of drought and shade stress on leaf economic traits

Under drought stress, leaf thickness, leaf mass per area (LMA), and leaf vein density (LVD) were significantly higher in both sexes, and *P. cathayana* males had higher LVD than females (Figure 2). In addition, these three leaf traits showed a declining trend under shade and the interactive stress. Shade stress significantly decreased LMA and LVD and the interactive stress decreased leaf thickness and LVD in both sexes (Figure 2).

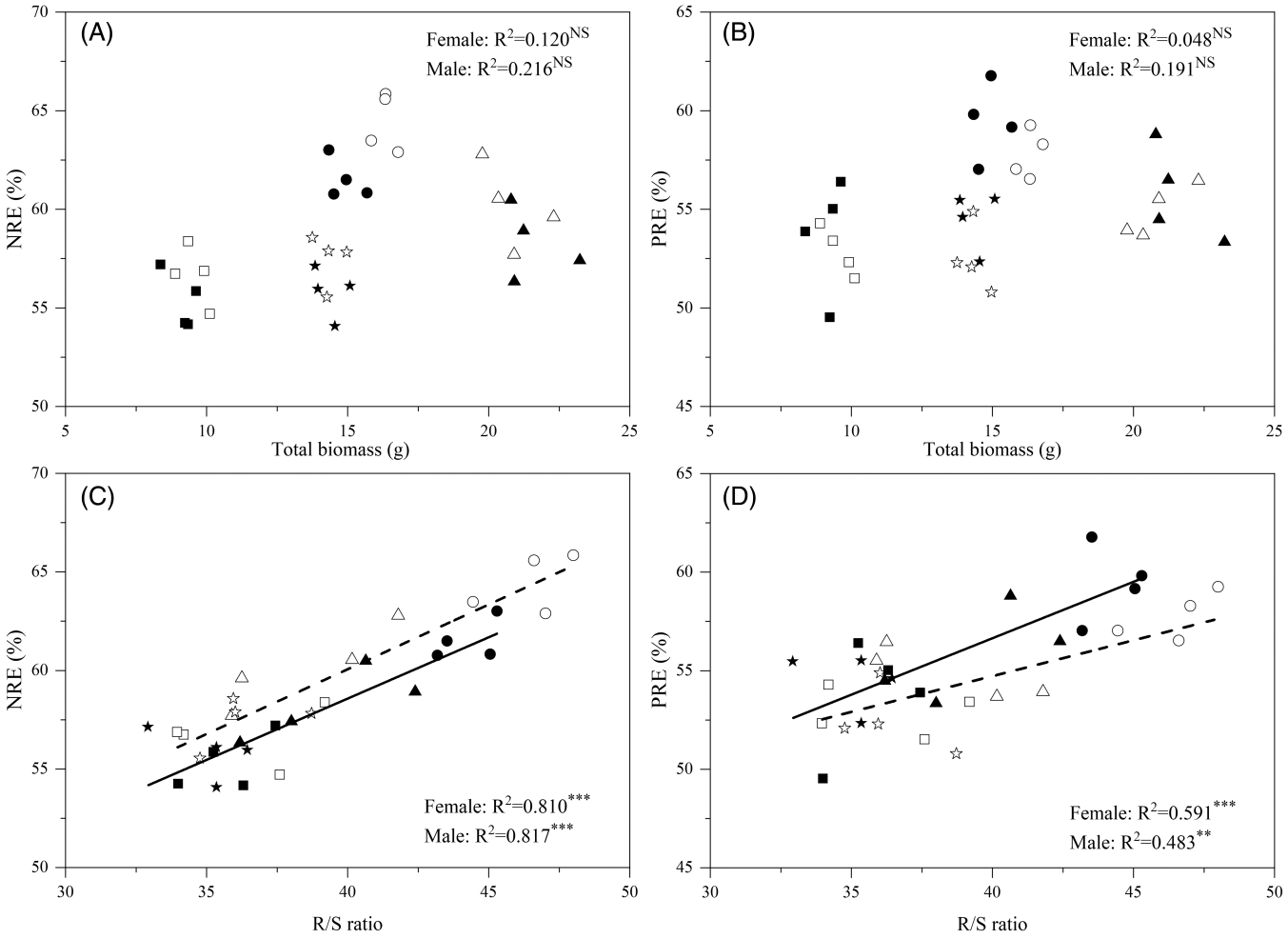

FIGURE 4 Relationships of leaf N and P resorption efficiencies with total biomass (A,B), and R/S ratio (C,D) in female and male *P. cathayana* across different drought and shade levels. The white triangle, circle, star and square indicate *P. cathayana* males under CK, drought, shade and their interactive stress, respectively. The black triangle, circle, star and square indicate *P. cathayana* females under CK, drought, shade and their interactive stress, respectively. *F* value and *p*-value are shown. NS, $p > 0.05$; $^{**}p < 0.01$; $^{***}p \leq 0.001$.

3.4 | Correlations between nutrient resorption and leaf economic and growth traits

NRE and PRE increased linearly with leaf thickness, LMA, and LVD in both sexes of *P. cathayana* across different treatments ($p < 0.05$; Figure 3). Nitrogen content in senesced leaves of *P. cathayana* males decreased linearly with LMA and LVD, while phosphorus content in senesced leaves of both sexes decreased linearly with leaf thickness, LMA and LVD under different treatments ($p < 0.05$; Figure 5). Additionally, NRE and PRE of *P. cathayana* showed no correlations with total biomass, but they increased linearly with the R/S ratio in both sexes of *P. cathayana* across different treatments ($p < 0.05$; Figure 4). Nitrogen content in senesced leaves (NRP) of males and phosphorus content in senesced leaves (PRP) of both sexes decreased linearly with the R/S ratio ($p < 0.05$; Figure 6).

4 | DISCUSSION

4.1 | Drought and shade stress affect growth and leaf economic traits

Many studies have shown that drought and shade stress inhibited plant growth and decreased biomass accumulation (Guo et al., 2020; Sevillano et al., 2016; Yu et al., 2020, 2023). Our results are consistent with these earlier studies indicating that the biomass in female and male *P. cathayana* are significantly reduced under drought, shade and interactive stress (Table 1). In addition, plants usually respond to environmental stress by altering biomass allocation and R/S ratio, for example, drought (Ledo et al., 2018; Wang et al., 2020; Ye et al., 2021). Previous studies have reported that larger root systems generally have a better nutrient and water uptake capacity (Boonman et al., 2020; Portsmuth & Niinemets, 2007). These results are consistent with those

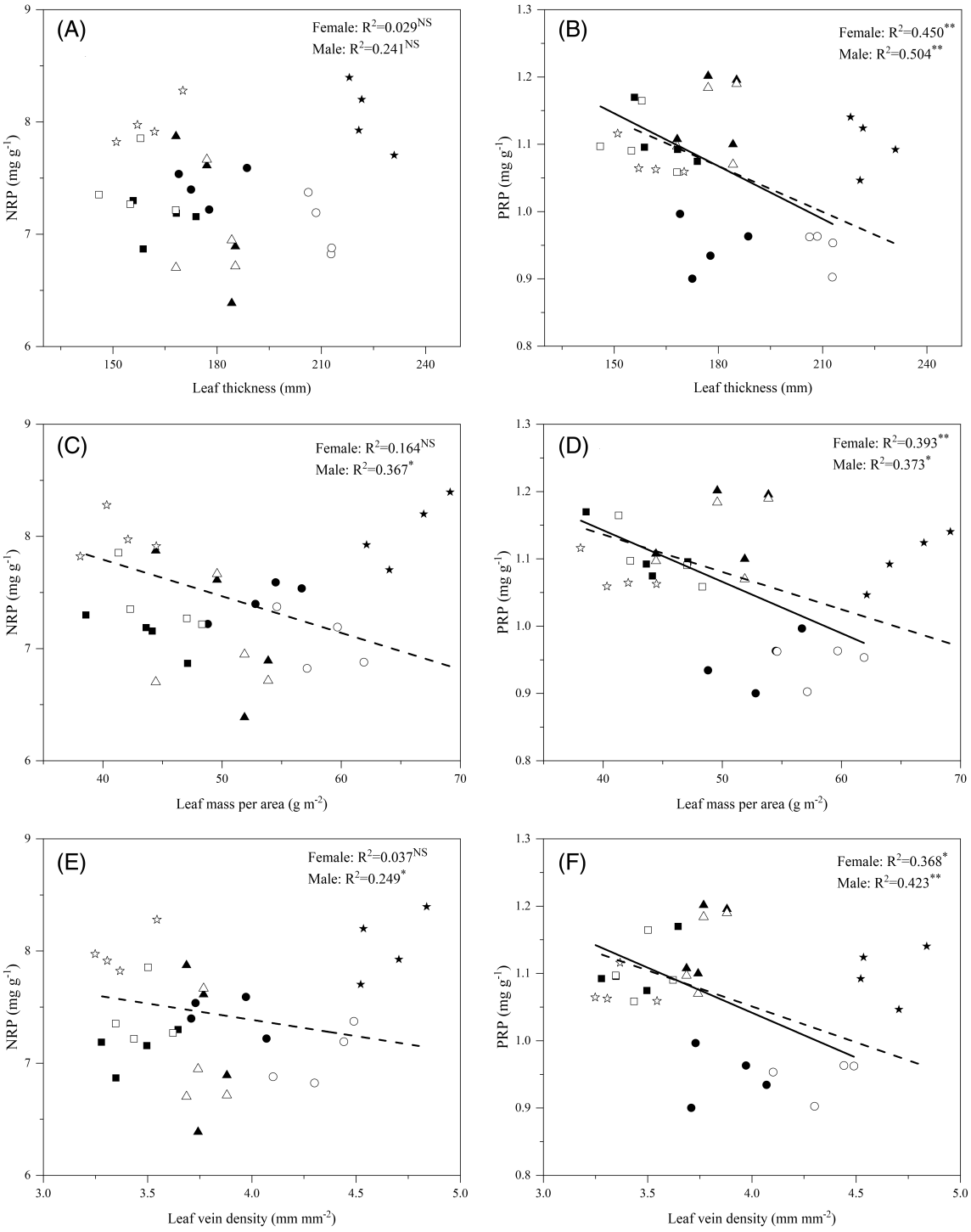

FIGURE 5 Relationships of N and P contents in senesced leaves with leaf thickness (A,B), leaf mass per area (C,D) and leaf vein density (E,F) in female and male *P. cathayana* across different drought and shade levels. The white triangle, circle, star and square indicate *P. cathayana* males under CK, drought, shade and their interactive stress, respectively. The black triangle, circle, star and square indicate *P. cathayana* females under CK, drought, shade and their interactive stress, respectively. *F* value and *p*-value are shown. NS, $p > 0.05$; $^{*}p < 0.05$; $^{**}p < 0.01$.

studies suggesting that drought stress significantly increased root/shoot ratio in both sexes (Table 1), indicating *P. cathayana* has a better nutrient and water uptake under drought stress.

Plants can change leaf structure to cope with varied environmental conditions, such as increased leaf thickness and leaf mass per area (LMA) under drought stress (Han et al., 2013; Júnior et al., 2019; Khan et al., 2023; Peña-Rojas et al., 2005; Yu et al., 2022). Leaf thickness and LMA are important leaf functional and economy traits, which are closely related to nutrient and water use efficiency in plants. For example, plants typically increase leaf thickness and LMA to extend

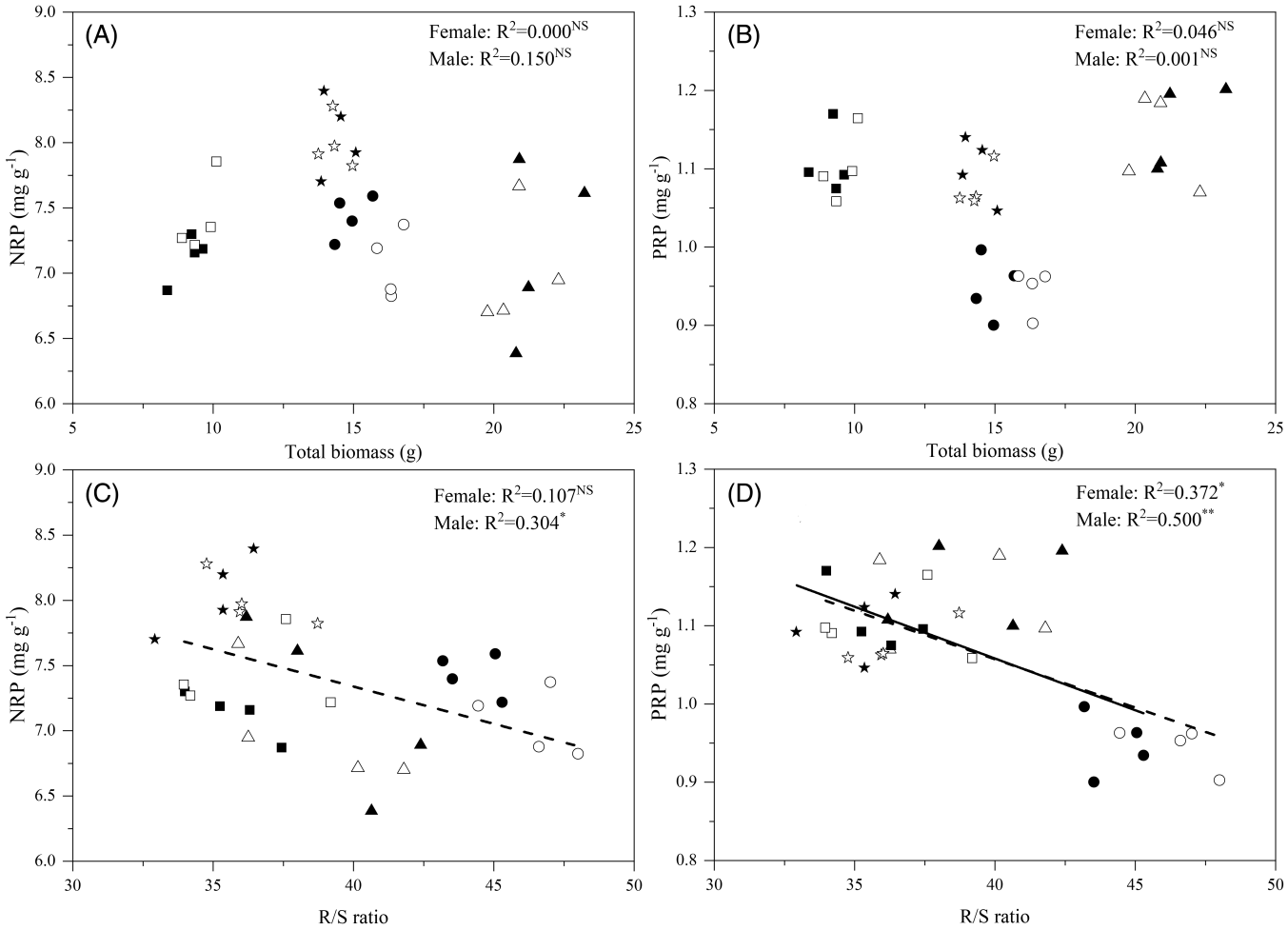

FIGURE 6 Relationships of N and P contents in senesced leaves with total biomass (A,B), and R/S ratio (C,D) in female and male *P. cathayana* across different drought and shade levels. The white triangle, circle, star and square indicate *P. cathayana* males under CK, drought, shade and their interactive stress, respectively. The black triangle, circle, star and square indicate *P. cathayana* females under CK, drought, shade and their interactive stress, respectively. *F* value and *p*-value are shown. NS, $p > 0.05$; $^{**}p < 0.01$.

water diffusion distance, prevent excessive water transpiration and improve the water use efficiency (Fahmy, 1997) to cope with drought stress. Additionally, leaf vein density (LVD) is closely associated with the nutrient and water transport in phloem (Brodribb et al., 2007; Sack & Scoffoni, 2013). In our study, we observed that drought stress significantly increased leaf thickness, LMA and LVD in female and male *P. cathayana*, indicating a conservation strategy that enhances nutrient and water use. On the other hand, plants had lower LMA and LVD under shade stress (Lusk et al., 2010; Sack & Scoffoni, 2013). Our data agreed with those results showing a significant reduction in LMA and LVD in female and male *P. cathayana* under shade stress.

4.2 | Drought and shade stress affect nutrient resorption

In arid environments, the high temperature and low rainfall result in slow plant decomposition and slow nitrogen and phosphorus biogeochemical cycling, ultimately decreasing soil nutrient use efficiency (Delgado-Baquerizo et al., 2013). Previous studies have reported that increased NRE and PRE with increasing levels of water stress (Brant & Chen, 2015; Lü & Han, 2010; Vergutz et al., 2012; Yuan & Chen, 2009), indicating plants have a conservative nutrient strategy with enhance the nutrients retention and use efficiency. Our results agreed with these statements that drought stress significantly increased NRE of both sexes and PRE of females. In addition, we observed no significant difference in nitrogen content in senesced leaves, but phosphorus content in senesced leaves was significantly lower under drought stress. These results were consistent with early studies that nitrogen content in senesced leaves was almost unchanged under water stress (Zhao et al., 2017), while phosphorus content in senesced leaves was significantly reduced (Tang et al., 2013). A recent study showed that nitrogen and phosphorus content in senesced leaves did not differ significantly between sun and shade leaves (Doğan et al., 2015). Our results partially agreed with this report that the nitrogen content in senesced leaves of both sexes was significantly higher, while phosphorus content in senesced leaves showed no significant difference under shade stress. Furthermore, compared to the control treatment, there was no

significant difference in nitrogen and phosphorus content in senesced leaves of female and male *P. cathayana* under the combined drought and shade stress, implying the unique responses to the interactive stress.

4.3 | Correlations between nutrient resorption and R/S ratio and leaf economics

Plants obtain nutrients mainly through the soil and senesced organs (Peng et al., 2019). The R/S ratio is closely linked with the nutrient conditions, for example, a high R/S ratio usually occurs in a resource-limited environment (Wang et al., 2020; Yu et al., 2020, 2023). The higher R/S ratio means a greater root system, which normally has a better nutrient and water uptake capacity (Boonman et al., 2020; Portsmuth & Niinemets, 2007). Our study found that NRE and PRE of both sexes showed no significant correlation with biomass but was positively correlated with R/S ratio across different conditions. These results indicated that nutrient resorption might be modulated by R/S ratio, and *P. cathayana* both taking up soil nutrients and resorption from senesced leaves nutrients.

In this study, we found that NRE and PRE were positively correlated with leaf thickness, LMA and LVD in female and male *P. cathayana* across different conditions. Our results suggest that leaf economic traits are closely linked with nutrient uptake from senesced leaves in a dioecious plant. Plants can enhance nitrogen and phosphorus retention and increase nutrient uptake from senesced leaves to decrease their dependence on the external environment (Yu et al., 2022). Furthermore, the higher leaf thickness and LMA generally imply a longer leaf life span (Wright et al., 2004, 2005), resulting in a longer nutrient residence time and photosynthetic assimilation time (Poorter et al., 2006). In addition, nitrogen and phosphorus content in senesced leaves were negatively correlated with LMA and LVD in *P. cathayana* males, indicating that higher LMA and LVD are usually associated with lower nitrogen and phosphorus content in senesced leaves (Yu et al., 2022). Thus, *P. cathayana* males had a more conservative strategy and may have a better water and nutrient (i.e., N) uptake capacity.

5 | CONCLUSIONS

To the best of our knowledge, this work is the first to reveal how nutrient resorption is related to biomass accumulation and allocation and leaf economics in a dioecious plant across different conditions. We found that drought stress significantly increased NRE in both sexes, but shade and the interactive stress decreased NRE in *P. cathayana* females. There was sexual dimorphism in nutrient resorption, *P. cathayana* males had higher NRE than females under drought stress. In addition, NRE and PRE were positively related to R/S ratio, leaf thickness, LMA, and LVD in both sexes of *P. cathayana* across different conditions. These results indicated that nutrient resorption may be modulated by R/S ratio and leaf economics, and *P. cathayana* both take up soil nutrients and resorption from senesced leaves nutrients. Our findings are helpful in understanding the conservation nutrient mechanism in dioecious plants under future climate change with more frequent and extreme droughts.

AUTHOR CONTRIBUTIONS

Shuanglei Tang had the main responsibility for data collection, analysis and writing, Xiazhen Lin contributed to English-language improvement, Wen Li and Chengjin Guo contributed to data analysis, Jungang Han and Lei Yu (the corresponding author) had the overall responsibility for experimental design and project management.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as all new created data is already contained within this article and the supplementary material of this article.

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