

Trait-mediated nutrient resorption reveals element-specific conservation strategies in mangroves

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Research Article

Keywords: nutrient conservation, salt-regulation strategies, seasonality, leaf anatomy, macro- and micronutrients, halophytic woody plants

Posted Date: September 21st, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10823101/v1>

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Additional Declarations: No competing interests reported.

Abstract

Background

Nutrient resorption is an important nutrient conservation strategy in mangroves; however, its variation with respect to salt regulation strategy, season and leaf anatomical traits remains unclear. We investigated 10 cooccurring mangrove species in Dongzhaigang National Nature Reserve, Hainan, China, during the dry and wet seasons. Soil nutrients, green and senesced leaf concentrations of 12 elements, and six leaf anatomical traits were measured to quantify nutrient resorption efficiency (NuRE) and identify its main drivers. NuRE was strongly element specific.

Results

Nitrogen (N), phosphorus (P), potassium (K), copper (Cu) and zinc (Zn) showed positive resorption, ranging from 17.39% to 60.62%, whereas calcium (Ca), magnesium (Mg), iron (Fe), manganese (Mn), boron (B), sodium (Na) and aluminium (Al) showed negative resorption, ranging from – 164.91% to – 15.79%, indicating net accumulation during leaf senescence. Season and salt-regulation strategy significantly affected NuRE, although their interaction was not significant. N and Zn resorption was greater during the wet season; Cu resorption was greater during the dry season; and the negative resorption of Ca, Mg, Fe, Mn, B and Na was greater during the dry season. N and K resorption was greater in non-secretors than in secretors, whereas Mg accumulation was greater in secretors and B and Na in non-secretors. The green-leaf nutrient concentrations and anatomical traits explained most of the NuRE variation, accounting for 52.4–97.6%, whereas soil nutrients explained 2.4–47.6% of the variation. The green-leaf nutrient concentration was positively related to P, Mg, Fe, Mn, Zn, Na and Al resorption. Guard cell length, epidermal thickness, mesophyll structure, stomatal density, vein diameter and vein density showed element-specific associations with NuRE.

Conclusions

We conclude that mangrove nutrient resorption is highly element-specific and is governed mainly by internal leaf nutrient status and anatomy rather than soil nutrients. These findings show that element identity, leaf structure and salt-regulation strategies jointly shape nutrient conservation and nutrient cycling in coastal wetlands.

1. Background

Nutrient resorption during leaf senescence is a fundamental nutrient conservation strategy through which plants withdraw nutrients from senescing organs and reallocate them to actively growing tissues, thereby reducing their dependence on the current soil nutrient supply and improving nutrient use efficiency (Aerts, 1996; Nie et al., 2025; Yin et al., 2026). This process has important ecological

consequences because it regulates plant growth, alters litter nutrient quality and decomposition, and thereby influences nutrient return to soils, ecosystem productivity and biogeochemical cycling (Vergutz et al., 2012; Liu et al., 2026). Mangrove forests provide a particularly relevant system for examining nutrient resorption, as they occur in intertidal environments characterized by high salinity, tidal flooding, anoxic sediments and often low nutrient availability, where nitrogen (N) and phosphorus (P) frequently limit plant growth (Reef et al., 2010; Ishfaq et al., 2025). Compared with terrestrial plants, mangroves often exhibit highly efficient nutrient resorption as part of their conservative resource-use strategy. For example, while global perennial plants resorb approximately 50% of leaf N and 52% of leaf P before leaf abscission (Aerts, 1996), mangrove species can show N resorption efficiency as high as 95% and P resorption efficiency as high as 82% (Lovelock et al., 2004; Lin et al., 2010). Recent work further indicates that mangroves may differ from upland terrestrial plants in terms of trace element resorption, as the net accumulation of sodium (Na), manganese (Mn), boron (B), iron (Fe) and aluminum (Al) in senesced leaves, as well as increased copper (Cu) resorption and similar zinc (Zn) resorption (Nie et al., 2025). Despite this growing evidence, most studies on mangrove nutrient resorption have focused on the relationships between nutrient resorption and green-leaf nutrient concentrations (Chen et al., 2016; Shi et al., 2024; Jiang et al., 2025), whereas the role of leaf anatomical traits remains less well understood.

The salt regulation strategies of mangrove species differ markedly (Parida and Jha, 2010). Salt-secretors, including species of *Avicennia* and *Aegiceras*, can remove excess salts through leaf-associated secretion or elimination mechanisms, whereas non-secretors such as *Rhizophora*, *Bruguiera* and *Kandelia* rely more strongly on root salt exclusion, ion compartmentation and osmotic regulation (Inoue et al., 2025; Zhu et al., 2025). These contrasting strategies may be associated with differences in foliar nutrient composition and nutrient resorption during senescence. Previous studies comparing mangroves with contrasting salt regulatory mechanisms have reported species-specific patterns of element uptake, accumulation and resorption, reflecting differences in Na handling, nutrient requirements and adaptation to saline environments (Medina et al., 2015). Seasonal hydroclimatic variation may further modify these patterns. During the dry season, reduced rainfall and increased evaporative demand often increase soil salinity and salt accumulation, potentially constraining nutrient uptake and increasing reliance on internal nutrient conservation. In contrast, wet-season rainfall, freshwater input and tidal exchange can decrease salinity, alter nutrient fluxes and modify foliar nutrient status (Nasrin et al., 2019; Miao et al., 2022). Comparisons of nutrient resorption between salt-secretor and non-secretor mangroves across dry and wet seasons therefore provide a useful framework for evaluating how plant salt regulation strategies and seasonal environmental variation are associated with nutrient conservation.

The nutrient status of green leaves is widely recognized as an important predictor of nutrient resorption (Wei et al., 2020; Shi et al., 2024). In nutrient-limited mangrove ecosystems, species with higher green-leaf N and P concentrations may exhibit greater N and P resorption efficiencies, suggesting that nutrients accumulated in mature leaves can be remobilized during senescence to support subsequent growth (Jiang et al., 2025). However, nutrient resorption is not only a function of nutrient concentration. It also depends on the ability to mobilize nutrients from leaf tissues and export them before leaf

abscission, processes that may be influenced by leaf structure and vascular architecture (Clément et al., 2018; Estiarte et al., 2023). Anatomical traits associated with gas exchange, structural investment and internal transport—such as guard cell length (GCL), stomatal density (SD), epidermal thickness (ET), palisade-to-spongy mesophyll ratio (P:S ratio), leaf vein diameter (LV_{diameter}) and leaf vein density (LV_{density})—may therefore be linked to variation in nutrient resorption.

These anatomical traits may be particularly relevant in mangroves because salt stress imposes strong constraints on water balance, ion regulation and leaf structure (Feller et al., 1999; Bai et al., 2023). Smaller GCL and higher SD may be associated with more responsive stomatal regulation under fluctuating water availability and salinity (Qie et al., 2024). Thicker ET and greater P:S ratio investment may reflect stronger structural protection but may also be associated with greater nutrient retention in leaf tissues (Naskar et al., 2020; Zhang et al., 2024). Similarly, greater LV_{density} , expressed as total vein length per unit leaf area, may increase phloem transport capacity and facilitate the withdrawal of nutrients, particularly N, from senescing leaves (Zhang et al., 2015). In contrast, LV_{diameter} may reflect both transport capacity and structural investment and therefore may not be a simple indicator of enhanced nutrient withdrawal (Peng et al., 2022; Hong et al., 2025). Integrating green-leaf nutrient status with anatomical traits may thus provide a more complete understanding of interspecific variation in mangrove nutrient resorption than considering foliar nutrient concentrations alone.

Here, we examined multielement nutrient resorption in cooccurring mangrove species with different salt regulation strategies across dry and wet seasons. By measuring soil nutrient concentrations, green and senesced leaf nutrient concentrations and leaf anatomical traits, we evaluated how season, salt regulation strategy and leaf traits were associated with element-specific nutrient resorption efficiency (NuRE). Specifically, we asked the following questions: (i) How do salt regulation strategy and season affect element-specific NuRE in mangrove species? (ii) How are green-leaf nutrient concentrations and anatomical traits associated with multielement NuRE? (iii) Do leaf traits or soil nutrients explain more of the variation in element-specific NuRE?

We hypothesized the following:

1. The NuRE differed between salt-secreter and non-secreter mangroves and between dry and wet seasons, with responses depending on element mobility and physiological function.
2. Green-leaf nutrient concentrations and anatomical traits are associated with multielement NuRE. Specifically, higher green-leaf nutrient concentrations and anatomical traits related to stomatal regulation and transport architecture, such as lower GCL, higher SD and higher LV_{density} , are associated with higher NuRE for some elements, whereas traits reflecting greater structural investment, such as greater ET and a higher P:S ratio, are associated with lower NuRE for less mobile or structurally associated elements.
3. Leaf traits explain more of the variation in NuRE than soil nutrient status does because nutrient resorption occurs within leaves and is therefore expected to be closely linked to presenescent nutrient status and leaf anatomical structure.

2. Materials and methods

2.1 Study site

This study was carried out in the Dongzhaigang National Nature Reserve, a protected mangrove wetland situated on the northeastern coast of Hainan Province, China (110°32'–110°37' E, 19°51'–20°01' N). The reserve, which was established as the first national mangrove reserve in China, occupies approximately 3337.6 ha. It is located in a tropical maritime monsoon zone, where precipitation is strongly seasonal. Rainfall is concentrated mainly between May and October, whereas November to April is relatively dry. The mean annual precipitation is 1676.4 mm, with more than 80% occurring during the wet season (Zhang et al., 2022b), and the mean annual temperature is approximately 23.3–23.8°C (Jiang et al., 2024).

Hydrologically, Dongzhaigang forms a semienclosed estuarine system connected to four small rivers and characterized by muddy intertidal substrates. The area experiences regular semidiurnal tidal inundation, with an average tidal amplitude of approximately 1.6–1.8 m. The mangrove soils in the reserve are generally 1.0–1.5 m deep and mildly acidic, with pH values of approximately 5–6; these soils are classified mainly as saline marsh soils beneath the mangrove vegetation (Nie et al., 2025).

Large-scale deforestation in Dongzhaigang ended after the bay was formally designated as a national nature reserve in 1986 (Lu et al., 2022). The reserve now contains rich mangrove flora, including 35 species belonging to 25 genera and 18 families. Among these, 24 are true mangrove species from 14 genera and 10 families, while 11 are minor mangrove species from 11 genera and 8 families (Jiang et al., 2023). The major canopy-forming species include *Avicennia marina*, *Aegiceras corniculatum*, *Bruguiera sexangula*, *Ceriops tagal* and *Rhizophora stylosa*.

2.2 Experimental design

In September 2023, we conducted field sampling in the Dongzhaigang National Nature Reserve using 10 representative mangrove species that differ in their salt regulation strategies, including salt-secreting and non-salt-secreting species (Table S1). All the plant materials were collected from naturally occurring populations within the reserve. The species were chosen on the basis of our preliminary field observations and previous studies documenting mangrove salt regulatory mechanisms (Parida and Jha, 2010; Jiang et al., 2024). All the species were formally identified by Dalong Jiang and Erhui Feng, and voucher specimens were deposited at the Hainan Dongzhaigang National Nature Reserve Authority, Haikou, China. Permission for field investigation and plant material collection was granted by the Hainan Dongzhaigang National Nature Reserve Authority. All the sampling was conducted in accordance with the relevant institutional, national, and local regulations and guidelines for plant research and collection.

For each species, four 10 m × 10 m plots were distributed across the reserve. The distance between any two plots of the same species was kept greater than 1 km so that the samples were not spatially clustered and could better reflect the range of field conditions experienced by that species (Fletcher and

Fortin, 2018). This sampling design was intended to balance taxonomic coverage with field logistical feasibility while remaining suitable for mangrove ecosystems, where species richness and community composition are often strongly influenced by salinity stress (Hankin et al., 2019; Wang et al., 2024).

Given the pronounced zonation of mangrove species along intertidal gradients and the relatively narrow elevation and inundation ranges typically occupied by individual species (Twomey and Lovelock, 2024), this design was considered suitable for characterizing interspecific variation in nutrient resorption traits. In addition, analyses of nutrient use strategies across ten mangrove species have recently shown that substantial among-species variation can be recovered in these environmentally specialized ecosystems (Gille et al., 2024; Nie et al., 2025).

2.3 Leaf and soil sampling

In each plot, we first identified three conspecific trees whose DBH values were close to the plot-level average and marked them for seasonal leaf sampling. The same marked individuals were sampled during both the dry and rainy seasons. Mature green leaves and senesced leaves were taken from comparable shoots located in the middle canopy of each individual. For mature foliage, we collected 10 fully expanded, current-year leaves from each marked tree, yielding 30 green leaves per plot. The sampling was restricted to sun-exposed leaves located approximately 1–4 m above ground and was distributed among different compass directions to reduce positional bias. Leaves showing visible pathogen symptoms or more than 5% herbivore damage were not included (Pérez-Harguindeguy et al., 2013). Senesced leaves were collected from the same trees by gently flicking branches to detach leaves with a developed abscission layer at the petiole base (Zhang et al., 2015), with sampling time to match the peak senescence period of each species. Leaves from the three sampled trees within each plot were pooled by leaf type and season to generate one composite green-leaf sample and one composite senesced-leaf sample per plot. These plot-level composites were used as the experimental units in subsequent analyses.

For each plot and sampling season, soil was collected from the upper 20 cm of the profile using a corer with an internal diameter of 3.8 cm. Before sampling, loose litter and understory vegetation were removed from the soil surface. Six sampling points were then selected randomly within each plot, and the resulting cores were pooled to generate one composite soil sample. The 0–20 cm layer was targeted because it represents the main rooting zone of mangrove plants and is commonly used for evaluating soil properties in forest ecosystems (Lin et al., 2023; Shi et al., 2024). The leaf materials were placed in an ice-cooled container immediately after field collection. Both the leaf and soil samples were then returned to the laboratory, where they were processed for chemical and anatomical analyses.

2.4 Chemical and anatomical analyses

The green and senesced leaf samples were first heated at 105°C for 30 min to deactivate enzymes and then dried at 65°C until a constant weight was reached. The dried leaves were milled into powder and passed through a 0.45-mm sieve before elemental determination. Soil samples were initially passed

through a 2-mm sieve to remove roots, stones and visible plant residues. They were subsequently air-dried, thoroughly mixed and further sieved to 0.25 mm.

The total nitrogen concentrations in both the leaf and soil samples were quantified with an elemental analyzer (Flash 2000; Thermo Fisher Scientific Inc., Waltham, MA, USA). For leaves, concentrations of P, K, Ca, Mg, Fe, Mn, Cu, Zn, B, Na and Al were determined using inductively coupled plasma–optical emission spectrometry (ICP–OES; Optima 8000, PerkinElmer, Norwalk, CT, USA) after digestion in a nitric–perchloric acid mixture ($\text{HNO}_3\text{:HClO}_4 = 4\text{:}1$, v/v). The same elements in the soil were analyzed by ICP–OES following complete acid digestion with nitric, hydrofluoric and perchloric acids (Gaudino et al., 2007).

Leaf anatomical traits were assessed using mature, fully expanded green leaves collected from the individuals used for the chemical analyses. Stomatal characteristics were examined from impressions of the abaxial epidermis prepared with the nail-polish method (Li et al., 2015). Stomatal density (SD) was expressed as the number of stomata per unit of epidermal area. Guard cell length (GCL) was measured as the distance between the outer junctions of the paired guard cells at the proximal ends of the stomatal pore (Liu et al., 2023). All observations were made with a light microscope (DM2500, Leica Microsystems Vertrieb GmbH, Wetzlar, Germany). For each replicate of a given species, at least five leaves collected from three individuals were examined, and 15 microscope fields were randomly selected for measurement.

To determine the internal leaf structure, five leaves were chosen for each replicate. From each leaf, three hand-cut transverse sections of 1 cm × 1 cm were obtained from the upper, middle and lower portions of the lamina, while major veins were avoided. These sections were preserved in FAA solution consisting of 9 ml 70% ethanol, 9 ml deionized water, 1 ml formaldehyde and 1 ml acetic acid (Yang et al., 2025). Epidermal thickness (ET), palisade mesophyll thickness and spongy mesophyll thickness were measured under a Leica DM2500 microscope. For each transverse section, three fields of view were measured and averaged. ET represented the combined thickness of the adaxial and abaxial epidermis, and the palisade-to-spongy mesophyll ratio (P:S ratio) was obtained by dividing palisade mesophyll thickness by spongy mesophyll thickness.

Leaf vein traits were determined from paradermal sections. Rectangular leaf sections were soaked in 5% (w/v) NaOH solution for 2–10 days, depending on the species, and then rinsed and bleached in 6% (w/v) NaClO solution for approximately 15 min (He et al., 2024). After rinsing, the sections were stained with 1% (w/v) safranin in ethanol for 10 min, dehydrated in 100% ethanol for 20 min, and then returned to water prior to imaging. The sections were observed under a Leica DM2500 microscope. Leaf vein diameter ($\text{LV}_{\text{diameter}}$) and leaf vein density ($\text{LV}_{\text{density}}$) were quantified from digital images of the paradermal sections using ImageJ software (National Institutes of Health, Bethesda, MD, USA; <https://imagej.net>) (Inoue et al., 2025). For each replicate per species, 45 fields of view were measured from five leaves collected from three individuals. $\text{LV}_{\text{diameter}}$ was measured from two veins located in the

upper, middle, and lower portions of each leaf and averaged across all measurements. LV_{density} was calculated as the total vein length per unit of leaf area.

2.5 Leaf nutrient resorption efficiency

Nutrient resorption efficiency (NuRE) was defined as the proportion of a given nutrient withdrawn from leaves and reallocated to other tissues prior to leaf abscission (Aerts, 1996; Estiarte et al., 2023). To account for mass loss during leaf senescence, NuRE was calculated following van Heerwaarden et al. (2003), with further methodological considerations described by Vergutz et al. (2012) and Zhang et al. (2022a):

$$\text{NuRE} (\%) = \left(1 - \frac{\text{Nu}_{\text{sen}}}{\text{Nu}_{\text{gr}}} \times \text{MLCF} \right) \times 100$$

1

Here, Nu_{gr} is the dry-mass nutrient concentration of green leaves, whereas Nu_{sen} is that of senesced leaves. MLCF corrects for mass loss during leaf senescence and is calculated from the ratio of senesced-leaf dry mass to green-leaf dry mass.

2.6 Statistical analyses

To test our first hypothesis, we used linear mixed-effects models (LMMs) to evaluate the effects of salt regulation strategy, season, and their interaction on the NuRE of N, P, K, Ca, Mg, Fe, Mn, Cu, Zn, B, Na, and Al. The models were fitted using the *lme4* package (Bates et al., 2015). Plot identity was included as a random intercept to account for repeated measurements across sampling seasons, i.e., (1 | Plot). Model assumptions were assessed by inspecting residual normality and homoscedasticity using the *performance* package (Lüdtke et al., 2021). To improve conformity with the model assumptions, the NuRE values for all the elements were transformed using inverse hyperbolic sine (*asinh*) transformation prior to analysis (Burbidge et al., 1988; Bellemare and Wichman, 2020).

To test our second hypothesis, we adopted a sequential analytical approach to examine the effects of leaf nutrient and anatomical traits on the NuRE. First, for each continuous predictor (Nu_{gr} , P:S ratio, ET, GCL, SD, LV_{diameter} , and LV_{density}), we compared linear and logarithmic functional forms using Akaike's information criterion (AIC) to identify more appropriate relationships. These comparisons indicated that logarithmic transformations of predictors provided lower or comparable AIC values for P and Fe resorption efficiency, whereas linear forms were retained for the remaining NuRE variables (Table S2). Accordingly, logarithmic regressions were used to assess the relationships between PRE and FeRE and their corresponding green leaf nutrient concentrations and anatomical traits, whereas linear regressions were used for all other trait–NuRE relationships.

We then fitted LMMs using the *lme4* and *lmerTest* packages to identify the key leaf nutrient and anatomical predictors of each NuRE variable (Bates et al., 2015; Kuznetsova et al., 2017). All the

predictors were mean centered prior to analysis to facilitate interpretation of the model coefficients. Model selection was based on the corrected Akaike's information criterion (AICc) using the *dredge* function in the *MuMIn* package (Bartoń, 2022), and inference for fixed effects in the final selected model was based on the model summary. To further test whether these trait–NuRE relationships varied with season or salt regulation strategy, we fitted additional LMMs, including green leaf nutrient concentrations, leaf anatomical traits, season (or salt-regulation strategy), and their interaction terms as fixed effects, with the plot included as a random intercept. The significance of fixed effects was assessed using Type III ANOVAs with Satterthwaite's approximation.

To test our third hypothesis, we quantified the relative contributions of leaf traits and corresponding soil nutrients to the variation in NuRE using a two-group variance partitioning approach implemented with custom R functions. For each NuRE variable, we fitted three LMMs with Plot as a random intercept: a full model including both leaf traits and the corresponding soil nutrient, a leaf-only model, and a soil-only model. Models were fitted using the *lme4* package (Bates et al., 2015), and marginal R^2 values were calculated with the *performance* package (Lüdtke et al., 2021). These marginal R^2 values were then used to partition explained variance into leaf-unique, soil-unique, and shared fractions, with the shared fraction equally allocated to the two predictor groups to estimate their relative contributions. All the statistical analyses were performed via R version 4.3.0 (R Core Team, 2023), and statistical significance was defined as $P < 0.05$.

3. Results

3.1 Nutrient resorption efficiency across elements

NuRE differed significantly among the elements. Positive NuRE values were observed for N ($60.62 \pm 1.60\%$), P ($48.34 \pm 2.42\%$), K ($40.66 \pm 2.40\%$), Cu ($57.80 \pm 3.50\%$), and Zn ($17.39 \pm 4.00\%$), indicating net resorption during leaf senescence (Table S1). In contrast, Ca ($-25.30 \pm 5.61\%$), Mg ($-15.79 \pm 4.45\%$), Fe ($-123.63 \pm 18.00\%$), Mn ($-72.71 \pm 11.80\%$), B ($-77.36 \pm 14.50\%$), Na ($-29.06 \pm 6.87\%$), and Al ($-164.91 \pm 33.20\%$) presented negative NuRE values, indicating net accumulation in senescing leaves (Table S1).

3.2 Effects of season and salt regulation strategy on NuRE

Season and salt regulation strategy significantly affected NuRE, whereas their interaction was not significant (Table 1). The resorption of N and Zn was greater during the wet season than during the dry season, whereas the resorption of Cu was greater during the dry season ($P < 0.05$; Fig. 1). The negative NuRE values for Ca, Mg, Fe, Mn, B, and Na were more pronounced in the dry season than in the wet season ($P < 0.05$). Compared with secretors, non-secretors exhibited greater resorption of N and K ($P < 0.05$). In contrast, Mg resulted in more negative NuRE values for secretors, whereas B and Na resulted in more negative NuRE values for non-secretors ($P < 0.05$).

Table 1

Results of two-way ANOVA testing the effects of season and salt regulation strategy on the nutrient resorption efficiency of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), boron (B), sodium (Na), and aluminum (Al). For each term, the table presents the *F*-value and its statistical significance.

Nutrient resorption efficiency	Season	Salt regulation strategy	Season × Salt regulation strategy
	<i>F</i> , <i>P</i>	<i>F</i> , <i>P</i>	<i>F</i> , <i>P</i>
N	4.74*	6.03*	0.44
P	1.66	1.00	3.49
K	0.11	4.61*	0.25
Ca	5.15*	0.22	1.10
Mg	7.00*	6.74*	2.18
Fe	6.88*	0.13	0.27
Mn	4.28*	3.48	0.15
Cu	3.90*	0.17	0.78
Zn	4.65*	0.41	0.32
B	3.83*	3.91*	1.00
Na	6.73*	10.87**	0.03
Al	0.09	2.34	1.35
**: $P < 0.01$, *: $P < 0.05$.			

3.3 Relationships between the NuRE and leaf traits

Leaf nutrient and anatomical traits were significantly associated with NuRE. The NuRE of P, Mg, Fe, Mn, Zn, Na, and Al increased significantly with increasing nutrient concentration in green leaves ($P < 0.05$), whereas that of K showed a marginally positive relationship ($P = 0.088$; Table S3; Figs. 2 and 3). The NuRE of N, Mn, Cu, and B decreased significantly with increasing GCL ($P < 0.05$), whereas Mg showed a marginally negative relationship with GCL ($P = 0.061$). The NuRE of Mn increased significantly with increasing ET, whereas those of Ca, B, and Na decreased significantly with increasing ET ($P < 0.05$). The NuRE of P, Ca, B, and Na decreased significantly with increasing P:S ratio ($P < 0.05$), whereas Zn showed a marginally negative relationship with the P:S ratio ($P = 0.066$). The NuRE of P decreased significantly with increasing SD, whereas that of Fe increased significantly with increasing SD ($P < 0.05$). The NuRE of B and Na increased significantly with increasing LV_{diameter} ($P < 0.05$). P had a marginally positive relationship with LV_{diameter} ($P = 0.060$), whereas K had a marginally negative relationship ($P = 0.075$). The NuRE of Zn and Na also increased significantly with LV_{density} ($P < 0.05$).

These relationships were generally consistent across seasons and salt regulation strategies (Figures S1 and S2). However, several differed in strength between groups. Across seasons, the relationships of N resorption with GCL and of P resorption with ET, P_{gr} , SD, and $LV_{diameter}$ were stronger in the dry season than in the wet season ($P < 0.05$; Figure S1). In contrast, the relationships of Fe resorption with Fe_{gr} and of B resorption with $LV_{diameter}$ were stronger during the wet season ($P < 0.05$; Figure S1). Differences in relationship strength were also detected between salt regulation strategies. The relationships of N resorption with the GCL, K resorption with $LV_{diameter}$, B resorption with the GCL and $LV_{diameter}$, and Na resorption with $LV_{density}$ were stronger in secretors than in non-secretors ($P < 0.05$; Figure S2). In contrast, the relationship between Fe resorption and the SD was stronger in non-secretors ($P < 0.05$; Figure S2).

3.4 Relative importance of green leaf traits and soil nutrients

The variation in NuRE was explained primarily by green leaf traits, which accounted for 52.4%–97.6% of the total variation, whereas soil nutrients explained 2.4%–47.6% (Fig. 4).

4. Discussion

Our results revealed that the NuRE in mangroves varied with season, salt regulation strategy and leaf traits but that these effects were strongly element specific. Non-secretors generally showed greater resorption of N and K, whereas several less mobile or structurally associated elements presented negative NuRE values, indicating retention or accumulation in senescing leaves. Compared with soil nutrients, green-leaf nutrient concentrations and anatomical traits explained more of the variation in NuRE. Together, these findings suggest that mangrove nutrient resorption is closely linked to internal leaf status and structure, whereas seasonal conditions and salt regulation strategies affect the strength of these relationships.

4.1 Effects of salt-regulation strategy and season on NuRE

Season and salt-regulation strategy significantly affected NuRE, whereas their interaction was not significant. These findings indicate that seasonal variation and salt regulation type influenced nutrient resorption but did not result in strongly divergent seasonal responses between secretors and non-secretors. Non-secretors exhibited greater resorption of N and K than secretors did. This pattern suggests that non-secretors may rely more strongly on the internal conservation of these mobile nutrients during leaf senescence. Because non-secreting mangroves lack specialized salt-secreting structures, they generally depend more on root-level exclusion, tissue tolerance and conservative resource use to cope with saline conditions (Zhu et al., 2023). The increased resorption of N and K is consistent with this strategy, as both elements are relatively mobile and play important roles in photosynthesis, osmotic regulation, stomatal function and ionic balance (Luo et al., 2021; Mostofa et al.,

2022). However, these findings should be interpreted as an association between salt regulation strategies and nutrient conservation rather than direct evidence for different resorption mechanisms.

In contrast, Mg had more negative NuRE values for secretors, whereas B and Na had more negative values for non-secretors. A negative NuRE indicates that these elements were retained or accumulated in senescing leaves rather than being efficiently withdrawn. The stronger Mg accumulation in secretors may be related to differences in leaf ion balance or photosynthetic tissue function, given the role of Mg in chlorophyll structure and enzyme activation (Tian et al., 2021). However, species-level variation in Mg accumulation among mangroves is common (Table S1); thus, this pattern should be treated cautiously (Medina et al., 2015). The more negative NuRE of B and Na in non-secretors is consistent with the low phloem mobility of B in many species and the tendency for Na to accumulate in leaves under saline conditions (Brown and Shelp, 1997; Krishnamurthy et al., 2014). These patterns suggest that the salt regulation strategy is associated not only with the resorption of mobile nutrients but also with the retention of less mobile or salt-related ions.

Seasonal effects also differed among the elements. N and Zn resorption was greater during the wet season, suggesting more effective nutrient withdrawal under conditions that may favor growth and metabolic activity. In contrast, Cu resorption was greater during the dry season, which may reflect seasonal changes in the demand for or cycling of micronutrients involved in redox processes and stress responses (Mir et al., 2021). Several elements, including Ca, Mg, Fe, Mn, B and Na, presented more negative NuRE values during the dry season. This pattern is consistent with greater retention or accumulation of relatively immobile or structurally associated elements during dry-season senescence (Nie et al., 2025). Reduced water availability, stronger salinity stress and changes in xylem-driven ion delivery may contribute to such seasonal differences, although these mechanisms require further testing (White and Broadley, 2003; Sevanto, 2018).

4.2 Leaf nutrient and anatomical control of NuRE

Green-leaf nutrient concentrations were important predictors of NuRE. The NuRE of P, Mg, Fe, Mn, Zn, Na and Al increased significantly with the corresponding nutrient concentrations in green leaves, whereas K showed a marginally positive relationship. These findings suggest that presenescent nutrient status is closely related to the amount or proportion of nutrients that can be withdrawn before leaf abscission. Such a relationship is expected because nutrient resorption is calculated from the difference between green and senesced leaves, and green-leaf nutrient concentrations partly represent the nutrient pool available for resorption (Jiang et al., 2025; Nie et al., 2025).

Leaf anatomical traits were also associated with NuRE, but the direction of these relationships varied among elements. The NuRE of N, Mn, Cu and B decreased with increasing guard cell length (GCL), whereas Mg had a marginally negative relationship. These results suggest that species with smaller guard cells tend to exhibit greater resorption of several nutrients. Smaller and denser stomata are often associated with faster stomatal responses, and recent work on mangroves has shown that Rhizophoraceae species with smaller, denser stomata close more rapidly under high vapor pressure

deficit (Drake et al., 2013; Qie et al., 2024). Therefore, the negative GCL–NuRE relationships may reflect coordination between stomatal traits and nutrient conservation. This is particularly relevant for N, which is often limiting in mangrove ecosystems and is closely linked to photosynthetic capacity (Luo et al., 2021; Ishfaq et al., 2025). However, the relationships with Mn, Cu and B indicate that stomatal traits are associated not only with macronutrient resorption but also with micronutrient cycling.

Epidermal thickness (ET) and mesophyll structure showed contrasting relationships with different elements. Mn resorption increased with increasing ET, whereas Ca, B and Na resorption decreased. Similarly, a higher palisade to spongy mesophyll ratio (P:S ratio) was associated with lower resorption of P, Ca, B and Na, with a marginally negative relationship for Zn. These patterns suggest that more strongly developed structural tissues may be linked to greater retention of some elements during senescence. This interpretation is consistent with evidence that leaf anatomy can influence nutrient distribution among tissues and that nutrient resorption is constrained by cellular and subcellular processes during senescence (Hayes et al., 2019; Estiarte et al., 2023). The negative relationships for Ca and B are also consistent with their roles in cell-wall structure, whereas Na is closely related to osmotic and ionic regulation in saline environments (Shi et al., 2017; Thor, 2019; Xiao and Zhou, 2023). Nevertheless, these anatomical relationships should be interpreted as trait associations rather than direct evidence of causal constraints on nutrient withdrawal.

Stomatal density (SD) was related to P and Fe resorption in opposite directions. P resorption decreased with increasing SD, whereas Fe resorption increased. Because SD is related to stomatal conductance, transpiration and stomatal responsiveness, these results suggest that stomatal traits may be linked to nutrient resorption in an element-dependent manner (Qie et al., 2024). The negative relationship between SD and P resorption may reflect broader associations between leaf structure, nutrient status and senescence processes rather than a direct effect of stomatal density on P withdrawal (Estiarte et al., 2023). In contrast, the positive Fe–SD relationship indicates that Fe is associated with different traits than P is. Given that Fe is involved in chloroplast function and photosynthetic electron transport but is often involved in low or variable resorption globally, these results further highlight the element-specific nature of NuRE (Chen et al., 2021).

Leaf vein traits were also associated with NuRE. Zn and Na resorption increased with increasing leaf vein density (LV_{density}). Because LV_{density} represents total vein length per unit of leaf area and is related to leaf transport architecture, these results suggest that venation traits may be linked to nutrient resorption, although the relationship is not universal across elements (Sack et al., 2014). Previous work revealed a positive relationship between LV_{density} and N resorption in dipterocarp trees, whereas P resorption was not clearly related to vein traits (Zhang et al., 2015). In our study, the strongest LV_{density} relationships occurred for Zn and Na, suggesting that the association between venation and NuRE depends strongly on nutrient identity.

The leaf vein diameter (LV_{diameter}) was positively related to B and Na resorption, marginally positively related to P resorption, and marginally negatively related to K resorption. These contrasting findings

indicate that LV_{diameter} should not be interpreted as a general indicator of increased resorption capacity. Leaf veins contribute to transport, phloem export and mechanical support; thus, vein diameter may reflect several aspects of vascular and structural investment rather than a single function (Hong et al., 2025). Therefore, the positive relationships for B and Na should be interpreted as element-specific associations with vein size, not as direct evidence that larger veins enhanced nutrient withdrawal.

The trait–NuRE relationships were generally consistent across seasons and salt-regulation strategies, but several differed in strength. The relationships of N resorption with GCL and of P resorption with ET, P_{gr} , SD and LV_{diameter} were stronger in the dry season, suggesting that leaf traits may be more closely linked to N and P resorption under dry-season conditions. In contrast, Fe resorption was more strongly related to Fe_{gr} and B resorption to LV_{diameter} during the wet season. The salt-regulation strategy also modified the trait relationships: the secretors showed stronger associations of N resorption with the GCL, K and B resorption with LV_{diameter} , B resorption with the GCL, and Na resorption with LV_{density} , whereas the non-secretors showed stronger Fe resorption and SD relationships. These results indicate that mangroves share broadly similar trait–NuRE relationships, but the strength of these relationships depends on the seasonal and physiological context.

4.3 Green-leaf traits outweigh soil nutrients in explaining NuRE

Green-leaf traits explained most of the variation in NuRE, accounting for 52.4%–97.6% of the total variation, whereas soil nutrients explained 2.4%–47.6%. These findings indicate that nutrient resorption in mangroves is more closely related to leaf-level characteristics than to soil nutrient concentrations. The strong contribution of green-leaf traits suggests that nutrient status before senescence and leaf anatomical structure are important for NuRE. Green-leaf nutrient concentrations may reflect the nutrient pool available for resorption, whereas anatomical traits may be related to nutrient distribution and movement within leaves (Aerts, 1996; Zhang et al., 2015). By comparison, soil nutrients appeared to have a weaker direct contribution, although they may still influence NuRE indirectly through their effects on nutrient uptake and leaf trait development (Ishfaq et al., 2025). Therefore, our results should not be interpreted as showing that soil nutrients are unimportant. Rather, they suggest that the effects of soil nutrient availability on resorption may be partly mediated through leaf nutrient status and anatomical traits.

Overall, our findings show that NuRE in mangroves is closely associated with internal leaf traits but that these associations are element specific and context dependent. The resorption patterns of mobile nutrients such as N, P and K were generally relatively clear, whereas relatively immobile or structurally associated elements were often retained or accumulated in senescing leaves. Seasonal conditions and salt-regulation strategies modified the strength of the trait–NuRE relationships but did not fundamentally alter their overall direction. These findings suggest that nutrient resorption in mangroves reflects an integrated leaf-level nutrient conservation strategy shaped by nutrient identity, leaf structure and saline environmental conditions. These patterns may have implications for litter nutrient return and coastal

nutrient cycling, particularly where mangrove community composition or seasonal hydrology changes over time.

5. Conclusion

Nutrient resorption efficiency in mangroves was more strongly explained by green-leaf nutrient and anatomical traits than by soil nutrients. The green-leaf traits accounted for 52.4–97.6% of the variation in NuRE, indicating that leaf-level nutrient status and structure are important predictors of nutrient conservation during senescence. Season and salt-regulation strategy also influenced NuRE, but their interaction was not significant. N and K resorption was greater among non-secretors, whereas several less mobile or structurally associated elements were retained or accumulated, especially during the dry season. Trait–NuRE relationships were generally consistent across seasons and salt regulation groups, although their strength varied across contexts. Together, these findings indicate that mangrove nutrient resorption is element specific and closely linked to internal leaf traits. Integrating green-leaf nutrient concentrations, leaf anatomical traits and soil nutrient conditions can improve our understanding of nutrient conservation strategies and their potential consequences for litter quality and nutrient cycling in coastal wetlands.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing Interests

The authors declare that they have no conflicts of interest.

Funding

This study was financially supported by the National Natural Science Foundation of China (32201332), the Hainan Provincial Natural Science Foundation of China (322QN304, 423RC477), the Startup Foundation for Advanced Talents of Hainan Normal University (920193), the Hainan Provincial Higher Education Institutions Graduate Student Innovation Research Project (Qhys2024-408, Hys2025-407), and the College Students' Innovation Training Program (S202511658034, CXCXYXJ2025043).

Author Contribution

Z.X.: data curation, investigation, methodology, formal analysis, writing—original draft. T.N.: data curation, investigation, methodology. D.L.J.: project administration, conceptualization, supervision, funding acquisition, writing—review and editing. S.W.W.: data curation, investigation. W.Y.Z.: investigation. E.H.F.: investigation, resources. Q.Y.: writing—review and editing.

Acknowledgement

We sincerely thank the editor and anonymous reviewers for their valuable comments and constructive suggestions, which greatly improved the quality of this manuscript.

Data Availability

Data and R code supporting this study are included in a Mendeley dataset (doi: 10.17632/yrfy7d3zvv.1).

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Figures

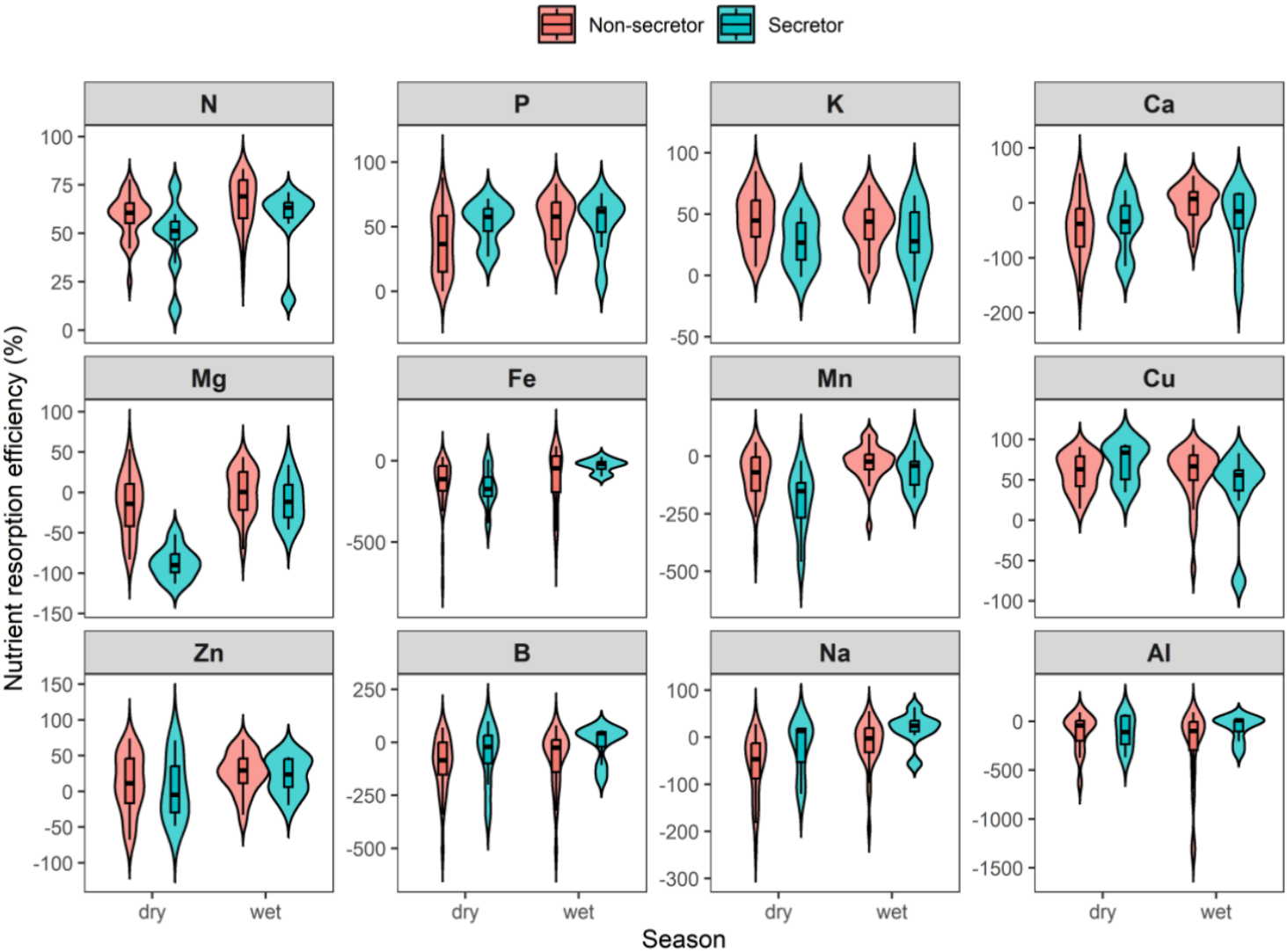


Figure 1

Nutrient resorption efficiencies of N, P, K, Ca, Mg, Fe, Mn, Cu, Zn, B, Na, and Al for non–secretor and secretor mangrove species during the dry and wet seasons. The element abbreviations follow those in Table 1.

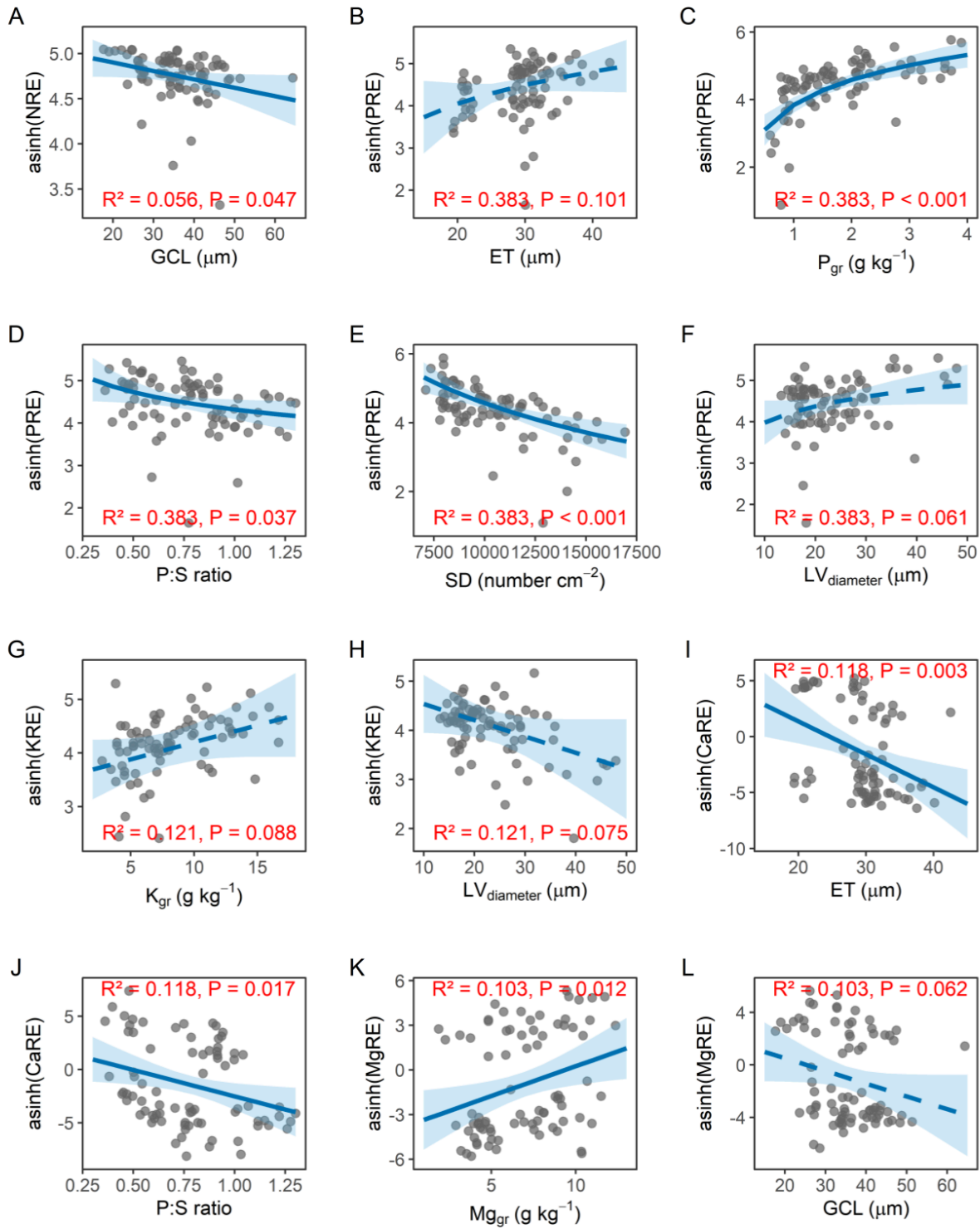


Figure 2

Partial regression plots showing the relationships of macronutrient resorption efficiency with nutrient concentrations in green leaves and leaf anatomical traits were constructed on the basis of multiple linear regression models (Table S3), while all other variables were statistically controlled. The shaded areas indicate 95% confidence intervals. The coefficients of determination (R^2) and significance values (P) are shown in each panel. P_{gr} : green leaf phosphorus concentration, K_{gr} : green leaf potassium

concentration, Mg_{gr} : green leaf magnesium concentration, P:S ratio: palisade to spongy mesophyll ratio, ET: epidermal thickness, GCL: guard cell length, SD: stomatal density, $LV_{diameter}$: leaf vein diameter, $LV_{density}$: leaf vein density.

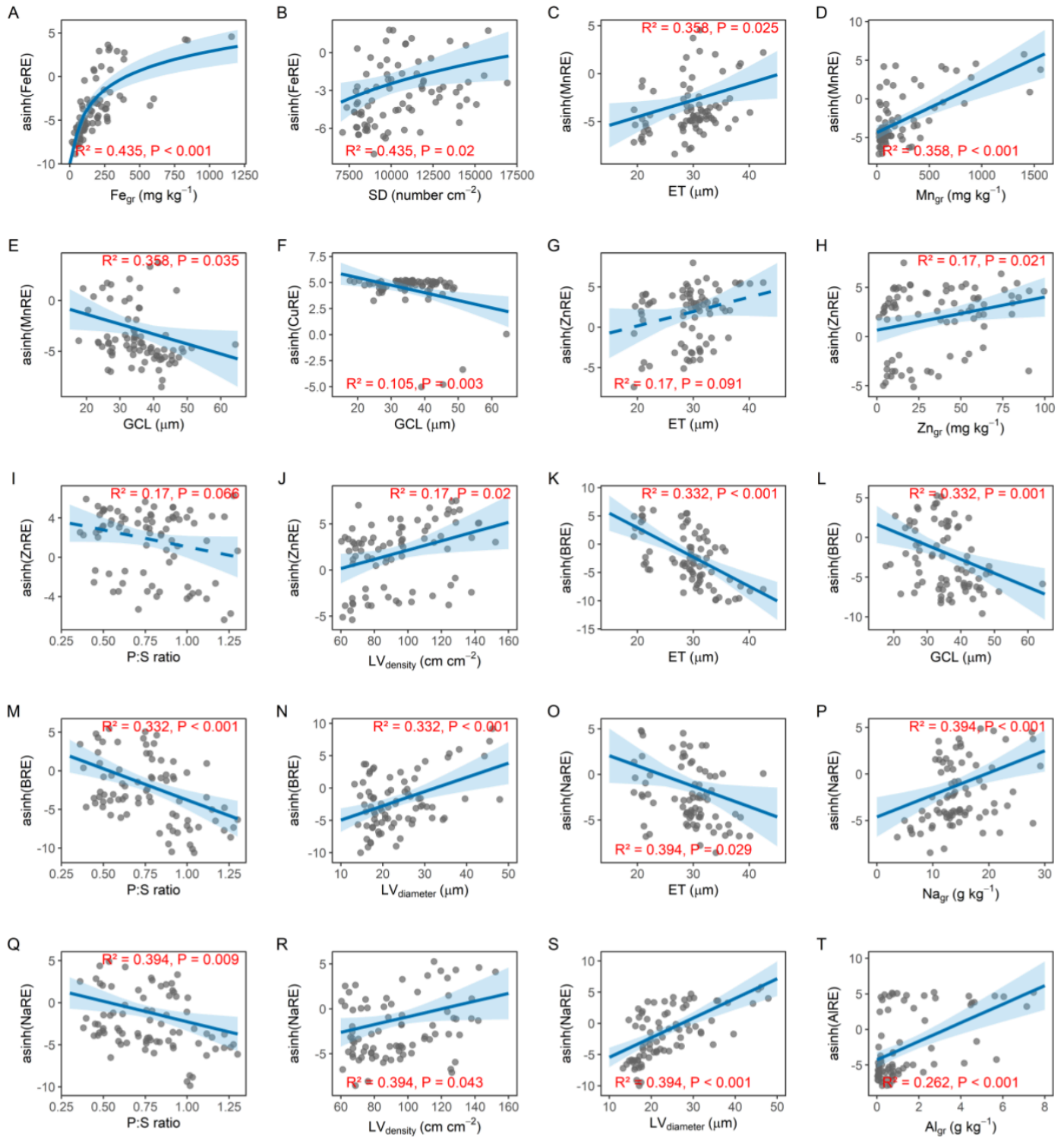


Figure 3

Partial regression plots showing the relationships of micronutrient resorption efficiency with nutrient concentrations in green leaves and leaf anatomical traits were constructed on the basis of multiple linear regression models (Table S3), while all other variables were statistically controlled. The shaded areas indicate 95% confidence intervals. The coefficients of determination (R^2) and significance values (P) are shown in each panel. Fe_{gr}, Mn_{gr}, Zn_{gr}, Na_{gr}, and Al_{gr} represent the iron, manganese, zinc, sodium, and aluminum concentrations, respectively, in green leaves. Other abbreviations of the explanatory variables are as defined in Figure 2.



Figure 4

Relative contributions of green leaf traits (nutrient and anatomical) and soil nutrient concentrations to thenutrient resorption efficiency of N, P, K, Ca, Mg, Fe, Mn, Cu, Zn, B, Na, and Al based on hierarchical variance partitioning and linear mixed–effects models. The element abbreviations follow those in Table 1.

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