Nutrient Resorption Strategies of Three Oak Tree Species in Response to Interannual Climate Variability

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Research Article

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Abstract

Background Nutrient resorption is critical for plants toward balancing their nutritional requirements and adapting to environmental variabilities, which further impacts litter quality and nutrient cycling. However, the interannual variability of nutrient resorption under climate change remains unclear.

Methods: We investigated the five-year nutrient resorption efficiencies (NuRE, %) of 14 elements in three deciduous oak tree species, *Quercus aliena* var. *acuteserrata*, *Q. glandulifera*, and *Q. variabilis* species in a warm-temperate forest of Central China, and assessed their relationships with interannual climate and soil factors.

Results Nutrient resorption did not differ between species but varied significantly between different years. For each year, nucleic acid-protein elements (N, P, S, and K) were preferentially resorbed in all of the oak species in contrast to photosynthesis-enzymic (C, Mg, and Zn) and structural (Ca, Na, Mn, and Ba) elements, which were to some extent discriminated, and toxic (Al and Fe) elements that were completely excluded. Among the 14 elements, the NuRE of N, P, S, Ca, and Mg was closely associated with interannual climate in the three oak species, showing N and S resorption efficiency were reduced with temperature, while N, P, and S resorption efficiency initially decreased and then increased with precipitation. Moreover, the elemental coefficient variations between different years generally decreased with higher NuREs in all three oak species.

Conclusions: Different oak species have analogous nutrient conservation strategies in response to annual climate variability, and interannual climate variations strongly impacted plant nutrient resorption. Deciduous plants may establish a trade-off mechanism to rebalance somatic nutrients for regrowth at the end of growing season.

Background

Plants obtain their nutrient requirements externally through soil nutrient cycling, which includes inputs from litter decomposition, biological fixation, atmospheric deposition, weathering, removal by root uptake, and leaching losses (Pallardy 2010; Cronan 2017), and internally through the reallocation of nutrients to different structures (Killingbeck 2004; Marschner and Marschner 2012). Nutrient resorption is a process through which plants reallocate nutrients from senescing structures to developing tissue, which contributes to reducing their dependence on nutrient uptake (Aerts and Chapin 1999; Killingbeck 2004; Brant and Chen 2015). This assists plants with adapting to environmental variabilities (May and Killingbeck 1992; Killingbeck 1993; Prieto and Querejeta 2020), as well as influencing plant reproduction, litter decomposition, and ecosystem nutrient cycling (Attiwill and Adams 1993; Aerts, 1996; Xu et al. 2020a). Therefore, the significance of nutrient resorption is being increasingly recognized, in terms of the functions of plant adaptation and nutrient cycling in response to climate change (Fujita et al. 2014; Yan et al. 2016; Drenovsky et al. 2019).

Nutrient resorption varies substantially with temperature and precipitation along geographical/ to pographical gradients (Kobe et al. 2005; Yuan and Chen 2009; Reed et al. 2012; Vergutz et al. 2012; Du et al. 2017; Tong et al. 2021). Climate change issues, including global warming, extreme drought, and N deposition, also influence nutrient resorption (Suseela et al. 2015; Zheng et al. 2018; Huang et al. 2018; Prieto and Querejeta 2020; Lü et al., 2021). For instance, climatic warming may delay leaf senescence and potentially reduce nutrient resorption, while drought can advance leaf senescence and increase resorption (Rivero et al. 2007). Aside from climatic factors, nutrient resorption also fluctuates with the availability of soil nutrients, plant nutrient status, and functional groups (Chapin and Moilanen 1991; Wright and Westoby 2003; Liu et al. 2014; Bahamonde et al. 2019; Gerdol et al. 2019; Xu et al. 2020b), as well as source-sink relations (Killingbeck 2004), and the mobility of nutrients in the phloem (Bukovac and Wittwer 1957; Hill 1980). Since most species are unlikely to migrate quickly enough to keep pace with environmental changes (IPCC 2015), their ability to adapt to variations in local environments might help them to survive under altered climatic environments that are anticipated in the near future (Jump and Peñuelas 2005; Prieto and Querejeta 2020). However, it is largely unknown how local plants might respond to disparities in environmental factors that are induced by interannual climate variations, which is critical toward elucidating the physiological and evolutionary adaptation of plants under climate change.

The level of nutrient resorption is, to a certain extent, associated with the elements within plants (Han et al. 2011). Nitrogen (N), phosphorus (P), potassium (K), and sulphur (S) are preferentially withdrawn from senescing leaves, showing high resorption, while calcium (Ca), magnesium (Mg), aluminum (Al), and iron (Fe) are accreted in senesced leaves, and therefore show low, or negative resorption (Killingbeck 1993; Liu et al. 2014; Estiarte and Peñuelas 2015; Du et al. 2017; Prieto and Querejeta 2020). Previous studies have revealed that different elements are often distributed in a coordinated pattern during the nutrient resorption process (Killingbeck 1993) in a trade-off manner, as reported by Du et al. (2017). Further, in adapting to environmental changes, plants have also evolved a homeostasis mechanism that is based on the stability of the limiting elements hypothesis, i.e. with higher element concentrations and lower variability (low coefficient of variation) (Han et al. 2011). However, less is known about how different nutrients interact to rebalance somatic nutrients during the resorption process. Moreover, plants growing at the same sites may exhibit parallel or convergent localized adaptations in terms of functional traits, physiology, and genetics (Aspinwall et al. 2016; Yeaman et al. 2016; Bauters et al. 2017; Bahamonde et al. 2019). Whether different local plants also exhibit analogous responses in nutrient resorption remains unclear. These findings will assist ecologists with optimizing their biogeochemical models, while improving their understanding of nutrient cycling.

The genus *Quercus* are widely distributed in the Northern Hemisphere especially in temperate forests, which plays important roles in ecological and economic perspectives (Aldrich and Cavender-Bares 2011). In our study area, three *Quercus* species come to dominate a stand. Previous studies mainly focused on soil carbon dynamic and plant stoichiometry in different oak forests (Du et al. 2017; Liu et al. 2017). For this study, we investigated the interannual variations in multiple element stoichiometry and resorption for three deciduous oak species over five years. Our objectives were to examine the nutritional responses of different plants to climatic differences driven by interannual variability, while exploring the regulation

patterns and driving factors of nutrient resorption based on climate change and multiple additional elements. To achieve our objectives, we measured the NuRE variations of seven macroelements (C, N, P, S, K, Ca, and Mg), four microelements (Fe, Mn, Zn, and Cu), and three trace elements (Na, Al, and Ba), and evaluated the effects of interannual temperature, precipitation, as well as green leaf and soil nutrient status, on the nutrient resorption of multiple elements.

Materials And Methods

Study area

This study was conducted from 2013 to 2016, and 2018 (Fig. S1) at the Forest Ecological Research Station of the Baotianman Natural Reserve (111°47'- 112°04'E, 33°20'- 33°36'N, 500 to 1845 m a.s.l) of Henan Province, in Central China. This area belongs to a temperate and subtropical ecotone zone. The mean annual precipitation and ambient air temperature are 900 mm and 15.1°C, respectively. With the primary soil type being haplic luvisol (Liu et al. 2017), the forest consists mainly of deciduous oak, including *Q. aliena* var. *acuteserrata*, *Q. glandulifera*, and *Q. variabilis*, in addition to some minor components of other deciduous woodland species and shrubs, such as *Forsythia suspense*, *Spiraea salicifolia*, and *Carex lanceolata*.

Soil and leaf sampling

Three study sites were selected, with each site representing a stand of the subject tree with recorded GPS locations, including latitude, longitude, and altitude (Table S1). At each site, three 20 m × 20 m plots were established. Within each plot, soil samples were randomly collected at a 0-10 cm depth at five locations to create a composite sample. Leaf samples were collected from the upper middle of south-facing crown of five sampling trees. A total of two hundred leaves were collected for each of the two leaf types (green leaves – August, and senesced leaves - December), where the senesced leaves were obtained by shaking the upper middle branches. Both green and senesced leaf samples were dried at 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. The collection of the soil and leaf samples followed the national standards of “Observation Methodology for Long-term Forest Ecosystem Research from (GB/T 33027-2016)”.

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 that was fixed at ~ 0.784 for deciduous broadleaved species (Vergutz et al. 2012).

Chemical analyses

The total C and N concentrations of the leaves and soil were determined using elemental analysis (Vario EL cube, Elementar, Germany), whereas the total P, S, K, Na, Ca, Mg, Al, Fe, Mn, Zn, and Cu were assessed using an inductively coupled plasma optical emission spectrometer (ICP-OES) (Iris Advantage 1000, Thermo Jarrell Ash, Franklin, MA, USA) following digestion with hydrofluoric and nitrohydrochloric acid for the soil samples, and nitric and perchloric acid for the leaf and seed samples.

Data analyses

One-way ANOVA was conducted to test the variations in nutrient resorption between the different years. Linear regressions were employed to examine the correlations of nutrient resorption between different elements, as well as with mean annual temperature (MAT), mean annual precipitation (MAP), and green leaf element concentrations. Cluster analysis was run to group elements by NuRE. Hierarchical partitioning (HP) analysis was performed to test the effects of MAT, MAP, and leaf and soil element concentrations on nutrient resorption efficiencies. Canonical discriminant analysis (CDA) was employed to distinguish multiple-nutrient resorption efficiencies between species and years. To further compare nutrient resorption between species, we performed one-way MANOVA with repeated measures (MANOVAR) over different years for each element using SPSS 16.0 (IBM, Chicago, IL, USA). The remaining analyses were carried out using Rversion 3.6.1 (R Development Core Team, accessed 2019) and SigmaPlot 10.0 (Systat Software, Inc., Richmond, CA, USA).

Results

Interannual and interspecies variations in nutrient resorption efficiencies

For all elements examined, NuRE generally followed an order of P, K, N, S, Mg, C, Zn, Mn, Na, Ca, Ba, Fe, Cu, and Al from high to low in the three oak species. Generally, the NuRE of P, K, N, S, Mg, C, and Zn was greater than zero, while that of Mn, Na, Ca, Ba, Fe, Cu, and Al was less than zero (Fig. 1). In the three oak species, with the exception of Zn, no significant differences were found in the NuREs of other elements, and over the five years of the study, the NuREs of all elements (except for K, Mn, and Ba) had significant differences (Table1). Canonical discriminant analysis further indicated that the NuREs did not differ between species, but varied significantly between years ($p < 0.001$) (Fig. 2, Tables S2, S3).

Effects of climatic and nutritional conditions on plant nutrient resorption

It was observed that NRE and SRE were generally reduced with higher MAT, while CaRE and MgRE initially increased and then decreased with MAT (Fig. 3). The CRE and CuRE were typically decreased with higher MAP. Additionally, NRE, PRE, and SRE initially decreased and then increased with MAP, whereas CaRE and MgRE initially increased and then decreased with MAP (Fig. 4). The NuREs of most elements were positively correlated with the elemental concentrations of green leaves; however, PRE was negatively related to the P concentrations of green leaves (Fig. S3).

Hierarchical partitioning analysis indicated variations in NuRE over the different years, from 18.13% KRE to 96.04% PRE in the three oak species (Table S4). The NRE was strongly associated with MAT and leaf N, CuRE with MAP in the three species, PRE with MAT and leaf P, MgRE with MAT in *Q. aliena* var. *acuteserrata* and *Q. glandulifera*, and CaRE, MnRE, and BaRE, with MAT and leaf elements in *Q. glandulifera* and *Q. variabilis*. The NuRE of the remaining elements was mostly related to leaf element concentrations except for K, Na, and Cu. Soil elements did not influence NuRE, except for CRE in *Q. glandulifera* and ZnRE in *Q. variabilis*.

Homeostatic regulation of nutrient resorption and correlations

Cluster analysis indicated five similar clusters in three species (Fig. 5). Nucleic acid-protein elements (N, K, P, and S) exhibited low variability (strong homeostasis), whereas photosynthesis-enzymes (C, Mg, and Zn) and toxic (Al and Fe) elements showed medium variability, and structural elements (Mn, Ba, Ca, and Na), as well as Cu, had high plasticity (Fig. 6, Table S5). For all three species, the coefficient of variation (CV, %) of elements between the different years generally decreased with higher NuREs (Fig. 6). There were positive relationships between NRE and SRE, NaRE and BaRE, and AIRE and FeRE in all three species, and CaRE was positively correlated with MnRE, BaRE, and NaRE (Fig. S3).

Discussion

Analogous response of interspecies NuREs to interannual climate variability

In contrast to deciduous plants on a global scale (Vergutz et al. 2012), the three oak species under study demonstrated higher N, P, and K resorption efficiencies, but lower C and Mg resorption efficiencies. The NuRE of N and P in this study was higher than that of deciduous plants in a subtropical karst region (Liu et al. 2014), and higher than that of *Q. variabilis* across China (Sun et al. 2015). This signified that plant growth in this region was more restricted by N and P. This may be because the plants grew at high altitudes, where due to the low temperature, they required higher levels of nutrient resorption to store nutrients for the following growing season. This was demonstrated by Du et al. (2017), who found that the resorption of N, P, and S, at least in *Q. variabilis*, was the greatest at high altitudes. Moreover, PRE in the three oaks was greater than NRE (except for 2018). This was in alignment with the research of Chai et al. (2015) and Du et al. (2017), who revealed that in the same or neighboring regions, the growth of oaks was commonly restrained by P compared with N.

As a conservation mechanism, nutrient resorption plays a key role in balancing plant nutrient demands and acquisition (Brant and Chen 2015; Killingbeck 2004). Our results revealed that NuRE varied significantly among the different years but did not differ between species. Interestingly, the three oak species displayed analogous NuRE responses to interannual climate variability, particularly for C, N, P, S, Mg, Fe, Mn, and Cu (Fig. 1). The similarity in NuRE between different plants indicated that the same plant types (only deciduous plants were investigated in the study) growing at the same sites might have parallel or convergent mechanisms in terms of nutrient conservation (Yeaman et al. 2016). This aligned well with a study by Bahamonde et al. (2019), who found that the NuRE did not vary between *Nothofagus*

pumilio and *N. Antarctica* at the sites they investigated. Similar results were reported from a five year manipulative field study by Prieto and Querejeta (2020), and demonstrated by Lü et al. (2013), who found that with N inputs, plants exhibited a convergent response in the resorption of N and P. These results indicated that plants growing under the same conditions, or occupying the same niche, may experience analogous limitations for nutrient absorption and conservation processes (Bahamonde et al. 2019). Thus, our findings may have important implications for the study of localized plant adaptations and evolution.

Effects of interannual climate, and leaf and soil nutrient status on NuRE

Significant fluctuations in nutrient resorption due to interannual variabilities in temperature and precipitation were reported in two prior studies (May and Killingbeck 1992; Killingbeck 1993). Which elements are more sensitive to interannual climate variability? Of the 14 elements examined, the NuRE of N, P, S, Ca, and Mg was closely associated with MAT and MAP (Figs. 3, 4). The results suggested that these elements were more sensitive to interannual climate variability compared to others, which due to their importance, translated to limitations in photosynthesis and growth in plants (Elser et al. 2000; Marschner and Marschner 2012). This finding signified that responses of resorption to climatic variability were contingent on element type (Vergutz et al. 2012; Sun et al. 2015; Du et al. 2017), where some elements directly related to growth (such as nucleic acid-proteins and photosynthetic elements) may be more sensitive to climate change.

The NRE decreased with higher temperatures across all species, which has been demonstrated in numerous previous studies (Yuan and Chen 2009; Sun et al. 2015; Prieto and Querejeta 2020). This is mainly because colder temperatures not only inhibited the metabolic activity of plants, but also restricted nutrient release and root N uptake. Therefore, plants need to extract additional N to enhance metabolic activity and growth rates, while reducing their dependence on available soil nutrients. This result also signified the interesting finding that temperature had a consistent influence on NRE regardless of spatial or temporal scales. However, precipitation had more complex influence on nutrient resorption. For instance, NRE and PRE initially decreased and then increased with MAP (Fig. 4). Comparatively, Yuan and Chen (2009) found that P resorption increased with higher precipitation, while Vergutz et al. (2012) reported that N and P resorption decreased with precipitation on a global scale. Moreover, Du et al. (2017) found that N and P resorption was enhanced with precipitation along an altitude gradient of the same area. Our study indicated that excessive or low precipitation may restrict the growth of plants, which resulted in high N and P resorption. The results indicated that precipitation may play a predominant role in the determination of nutrient demands and plant growth in local ecosystems.

In the drought year (2014), CRE was significantly enhanced in the plants (Fig. 1), which suggested that plants may store additional energy for reproduction under drought conditions. Correspondingly, the concentrations of C in the litter of the forest floor were reduced, as was demonstrated by Sardans et al. (2008). This could influence litter quality and decomposition, and even ecosystem C cycling downstream. Based on the predicted changes in local temperature and precipitation (0.9°C higher annual mean

temperature and 6.4 mm lower total precipitation, see Zhao et al. (2012)), the resorption efficiency of C, N, and P will likely, to some extent, decrease over the next twenty years (Table S6), as demonstrated by Prieto and Querejeta (2020). This decrease likely reduced nutrient demands and plant growth and may have some influence on litter quality and decomposition (Prescott 2010; Prieto et al. 2019).

NuRE was also associated with the elemental concentrations of fresh leaves. Surprisingly, there were positive relationships between leaf element concentrations and NuREs (except for P) (Fig. S3). Our results were unlike most previous studies, in which the high nutrient content of fresh leaves typically led to low nutrient resorption (Kobe et al. 2005; Ratnam et al. 2008; Vergutz et al. 2012), or there was no significant relationship between them (Aerts 1996; Chapin and Moilanen 1991). For our study, the relationships between the elemental concentrations of fresh leaves and climatic factors were also analyzed, which revealed that they were quite consistent with that which existed between NuRE and climatic factors. This revealed that both the elemental concentrations of fresh leaves and the resorption of nutrients were impacted by climatic factors, which may form coupling relationships. When plants possessed high nutrient concentrations during the growing season, increased nutrient resorption was likely to occur at the end of the growing season to maintain a source-sink balance. Furthermore, we found that soil had no influence on NuRE between years (Table S2), which agreed with the findings of Aerts (1996) and Aerts and Chapin (2000). This was likely caused by the low fluctuation of available soil nutrients between years and low sensitivity to changes in the soil due to long-term adaptation.

Regulation pattern of nutrient resorption of multiple elements

The elemental CVs between different years generally decreased with higher NuREs in all three oak species (Fig. 6). This was because high concentrations with low variability benefitted plants by maintaining their homeostasis, which was in alignment with the stability of limiting elements hypothesis (Han et al. 2011). Meanwhile, this was also supported by the study of Karimi and Folt (2006), who found a strong regulation of macronutrients, and weak regulation of micronutrients and non-essential elements in organisms. The exception was Al that appeared to have both low variation and resorption, which was likely due to the avoidance of phytotoxic effects by plants (Brunner and Sperisen 2013). These results suggested that nutrient resorption, akin to leaf stoichiometry, had a similar regulation pattern in homeostasis, i.e. higher nutrient concentrations or resorption efficiencies, with lower variability in plants.

Our results exhibited that nucleic acid-protein and photosynthesis-enzyme elements had higher resorption efficiency compared to structural and toxic elements (Figs. 1, 5). This is because nucleic acid-protein elements are generally limited in supply (Elser et al., 2007; Du et al. 2020), and therefore have a high resorption efficiency. Further, although photosynthesis-enzyme elements are required in low quantities, they are essential for new growth (Marschner and Marschner 2012) and may therefore, to some extent, re-absorbed (Son et al. 2000). The negative resorption efficiencies of structural and toxic nutrients have also been previously reported (Killingbeck 1993; Liu et al. 2014; Du et al. 2017). This is likely due to these nutrients are freely loaded into xylem but highly restricted in phloem (Bukovac and Wittwer 1957; Hill 1980), which limits their inputs into perennial tissues. Therefore, they attain high levels at end of the

growing season, in contrast to nucleic acid-protein nutrient elements (Saur et al. 2000; Andivia et al. 2010). The accretion of these nutrients from leaf shedding may assist with amplifying the reserves of other required nutrients, such as nucleic acid-protein and photosynthesis-enzyme elements, while concurrently playing a critical role in detoxification. This was also reflected through seasonal variations in the elements of *Q. variabilis* at the same sites, which revealed low structural and toxic nutrients and high nucleic acid-protein and photosynthesis-enzyme nutrient elements at the onset of the growing season (Du et al. 2021). These results revealed that plants engaged in resorption trade-offs as the end of the growing season approached. Generally, nucleic acid-protein and photosynthesis-enzyme elements were positively re-absorbed, with structural and toxic nutrients expelled in a trade-off manner between multiple elements at the conclusion of the growing season (Fig. 7). To facilitate this trade-off process, interannual climate and fresh leaf nutrient status may be referenced by plants.

Furthermore, Ca served not only as a structural element (Marschner and Marschner 2012) as was typically thought, but also the key regulator of plant growth and development (Hepler 2005). We found that Ca resorption was significantly correlated with multiple elements (Fig. S2). For instance, Ca could negatively regulate the resorption of C and N in *Q. glandulifera* and *Q. variabilis*, and this process could be coupled by N to influence the resorption of P and S (Fig. S2). Since leaf senescence is a genetically programmed process, Ca could act as a second messenger and involve a specific Ca^{2+} -dependent protein kinase to regulate the process (Gepstein et al. 2003; Wang et al. 2019). Poovaiah and Leopold (1973) also demonstrated that due to the addition of Ca, the senescence of corn leaves was deferred. Therefore, we inferred that Ca might play a critical role in regulating the NuRE of plants, which needs to be further investigated.

Conclusions

Our study described a comprehensive representation relating to the interannual patterns of nutrient resorption of multiple elements in three oak species. Our conclusions were that (1) different plants growing under the same conditions may have analogous nutrient conservation strategies in response to interannual climate change; (2) interannual climate variation strongly impacted plant nutrient resorption, particularly, N, P, S, Ca, and Mg, which can play important roles toward adapting to interannual climate variability and reproduction; (3) to maintain the stability of nutrient supplies, NuRE also supports the stability of the limiting elements hypothesis, and in terms of the regulation of multiple elements, deciduous plants at the conclusion of growing season may establish a trade-off mechanism to rebalance nutrients for regrowth. Our findings have clear implications for understanding localized plant adaptation strategies and biogeochemical cycling processes under global climate changes.

Abbreviations

NuRE: nutrient resorption efficiency; NRE: nitrogen resorption efficiency; MAT: mean annual temperature; MAP: mean annual precipitation; CV: coefficient variation.

Declarations

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Author contributions

CL designed the study; SL provided climatic data; BD, and HJ conducted field studies and chemical analyses. BD, SY, and HK wrote the manuscript. All authors approve the paper.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

This research is not considered to involve ethical problems.

Consent for publication

Not applicable.

Competing interests

There are no competing interests

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Tables

Table 1 Analysis of variance for nutrition resorption efficiencies (F statistics) by tree species and year. Asterisks indicate probability level at $p < 0.05$.

Element	Plant species	Year	Plant species × Year
C	0.10	57.52*	3.30*
N	3.26	39.86*	2.67
P	1.41	369.31*	2.21
S	1.31	12.07*	1.03
K	2.62	2.47	1.32
Na	0.07	6.69*	0.85
Ca	0.58	59.11*	4.65*
Mg	0.78	3.06*	1.02
Al	0.58	40.20*	1.97
Fe	1.49	59.62*	3.60*
Mn	1.16	6.91	0.65
Zn	13.35*	2.66*	1.64
Cu	0.54	48.95*	1.86
Ba	0.90	4.08	1.05

Figures

Figure 1

Nutrient resorption efficiency (NuRE) (Mean $\pm$ SE) of three oak species, *Q. aliena* var. *acuteserrata*, *Q. glandulifera*, and *Q. variabilis* over five years. Letters above bars represent significant difference ($p < 0.05$) by Duncan test.

Figure 2

Plant species (a) and year (b) differences defined by the first two canonical variables extracted from canonical discriminant analyses, based on multi-element nutrient resorption efficiencies.

Figure 3

Relationships between element resorption efficiencies and mean annual temperature.

Figure 4

Relationships between element resorption efficiencies and mean annual precipitation.

Figure 5

Element classification by nutrient resorption efficiency and species using cluster analysis, *Q. aliena* var. *acuteserrata* (a), *Q. glandulifera* (b), and *Q. variabilis* (c) as well as element classification by biological functions (d). Blue circles represent the results of principal component analysis (PCA) by Zhang et al. (2012) on green leaves; pink circles represent the PCA results by Garten (1978) on green leaves; green circles represent the PCA results by Ågren and Weih (2012) on green leaves; yellow circles represent the

Euclidian distances of nutrient resorption efficiency by Du et al. (2017); and red circles represent the Euclidian distances of nutrient resorption efficiencies from this study.

Figure 6

Relationships between mean nutrient resorption efficiencies and coefficient of variations (CV). Ca, Na, and Mn are showed in Table S4.

Figure 7

Conceptual model for trade-off regulation of nutrient resorption. Element classification is grouped by biological functions in Fig. 5.

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