

RESEARCH PAPER

Biogeographic patterns of nutrient resorption from *Quercus variabilis* Blume leaves across China

X. Sun^{1,2}, H. Kang¹, H. Y. H. Chen³, B. Björn⁴, B. F. Samuel³ & C. Liu^{1,5}¹ School of Agriculture and Biology, Shanghai Jiao Tong University, Shanghai, China² College of Agro-grassland Science, Nanjing Agricultural University, Nanjing, China³ Faculty of Natural Resources Management, Lakehead University, Thunder Bay, ON, Canada⁴ Department of Forest Sciences, University of Helsinki, Helsinki, Finland⁵ Research Centre for Low Carbon Agriculture, Shanghai Jiao Tong University, Shanghai, China**Keywords**

Climate; intraspecific variation; latitudinal pattern; nutrient resorption; soil and green leaf characteristics.

Correspondence

Chunjiang Liu, School of Agriculture and Biology, Shanghai Jiao Tong University, Dongchuan Road 800, Shanghai 200240, China.

E-mail: chjliu@sjtu.edu.cn

Editor

D. Byers

Received: 12 May 2015; Accepted: 16 November 2015

doi:10.1111/plb.12420

ABSTRACT

The variation in nutrient resorption has been studied at different taxonomic levels and geographic ranges. However, the variable traits of nutrient resorption at the individual species level across its distribution are poorly understood. We examined the variability and environmental controls of leaf nutrient resorption of *Quercus variabilis*, a widely distributed species of important ecological and economic value in China. The mean resorption efficiency was highest for phosphorus (P), followed by potassium (K), nitrogen (N), sulphur (S), magnesium (Mg) and carbon (C). Resorption efficiencies and proficiencies were strongly affected by climate and respective nutrients concentrations in soils and green leaves, but had little association with leaf mass per area. Climate factors, especially growing season length, were dominant drivers of nutrient resorption efficiencies, except for C, which was strongly related to green leaf C status. In contrast, green leaf nutritional status was the primary controlling factor of leaf nutrient proficiencies, except for C. Resorption efficiencies of N, P, K and S increased significantly with latitude, and were negatively related to growing season length and mean annual temperature. In turn, N, P, K and S in senesced leaves decreased with latitude, likely due to their efficient resorption response to variation in climate, but increased for Mg and did not change for C. Our results indicate that the nutrient resorption efficiency and proficiency of *Q. variabilis* differed strongly among nutrients, as well as growing environments. Our findings provide important insights into understanding the nutrient conservation strategy at the individual species level and its possible influence on nutrient cycling.

INTRODUCTION

Understanding the nutrient resorption of plants may provide insights into plant nutrient limitations (Güsewell 2004, 2005; Richardson *et al.* 2008; Reed *et al.* 2012), plant responses to global climate changes (Yuan & Chen 2009a; Reed *et al.* 2012) and nutrient cycling (Vitousek 1982; Vitousek & Sanford 1986; Attiwill & Adams 1993; Aerts & Chapin 2000; Rejmánková 2005; Chapin *et al.* 2011). The variabilities in leaf nutrient resorption and their possible controlling factors have been investigated at the global (Kobe *et al.* 2005; Yuan & Chen 2009a; Vergutz *et al.* 2012), regional (Tang *et al.* 2013) and local scales (Aerts 1996; Wright & Westoby 2003; Richardson *et al.* 2005; Lü *et al.* 2012; Tully *et al.* 2013). However, across large geographic scales, surprisingly little is known about the intraspecific variability of nutrient resorption and its controls. A study of the intraspecific variation of widely distributed species can provide more details of environmental controls on nutrient resorption by eliminating the confounding effects of interspecific variation, and may also improve our understanding of the nutrient resorption of plants in response to changes in the global climate (De Frenne *et al.* 2013).

Many studies have explored the intraspecific variability of leaf nutrient resorption responses to soil fertility at local or site scales. In some studies, plants that grew in infertile soils were more efficient at resorption (Aerts 1996; Killingbeck 1996; Rejmánková 2005; Lü *et al.* 2012), whereas other studies have found positive or no resorption efficiency response to increased nutrient supplies (Chapin & Moilanen 1991; Aerts 1996). However, a recent meta-analysis of fertilisation experiments showed that nutrient fertilisation may reduce plant nutrient resorption across a wide range of global terrestrial biomes (Yuan & Chen 2015). The inconsistent results among individual studies may be due to differences in experimental environments, such as temperature, as well as variations in plant phenology, the timing of periods of strong nutrient demand and methodological issues. Furthermore, green leaf nutrient status has a significant effect on nutrient resorption (Kobe *et al.* 2005). Climate may also influence nutrient resorption directly by impacting hydrolysis and phloem transport, and indirectly by affecting the soluble compounds and enzymolysis in senescing leaves, the availability of soil nutrients and root nutrient uptake (Chapin & Oechel 1983; Pugnaire & Chapin 1992). Yet, the effects of climate factors on nutrient resorption is surprisingly unclear,

although a few studies have shown that water deficiencies and elevated temperatures can result in low nitrogen (N) and phosphorus (P) resorption efficiencies (hereafter RE-N and RE-P, respectively) (Pugnaire & Chapin 1992; Norby *et al.* 2000). Further, leaf structures, such as leaf mass per area (LMA), may vary along environmental gradients, which can affect leaf nutrient resorption (Renteria & Jaramillo 2011).

Emerging meta-analyses suggest that RE-N decreases with mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm) at the global (Yuan & Chen 2009a; Vergutz *et al.* 2012) and regional scales (Tang *et al.* 2013), resulting in a positive relationship between RE-N and latitude. On the other hand, leaf RE-P has been reported as positively (Yuan & Chen 2009a; Tang *et al.* 2013) and negatively (Vergutz *et al.* 2012) related to MAT and MAP, suggesting that the relationships between leaf RE-P and climate factors were not clear. This inconsistent relationship may arise from biological factors (*e.g.* interspecific variations in nutrient resorption) and methodological sources (*e.g.* sample size, community assembly, resorption calculations and geographic distributions) of investigations. The latitudinal patterns of RE-N:RE-P have also been documented as decreasing with MAT and MAP, and increasing with latitude (Reed *et al.* 2012). As yet, no study has investigated the variable patterns of leaf nutrient resorption of a widely distributed species across a broad geographic area while simultaneously accounting for the contributions of soil fertility and leaf traits.

Previous work has focused primarily on the N and P resorption of leaves; however, potassium (K), magnesium (Mg) and sulphur (S) are also essential for ecosystem processes (Tripler *et al.* 2006; Maathuis & Diatloff 2013). For instance, K plays a critical role in a number of plant physiological activities (*e.g.* phloem transport, osmotic balance and photosynthesis; Maathuis & Diatloff 2013), and Mg plays a role in phloem loading, the transport of photoassimilates into sink organs, photosynthesis, enzyme activation and the formation and utilisation of ATP within plants (Cakmak & Yazici 2010). As such, K and Mg are typically in high demand for plants. However, there are substantially fewer data available to quantify their latitudinal patterns (Vergutz *et al.* 2012). Additionally, carbon (C) can also resorb from non-structural carbohydrates in senescing leaves (Vergutz *et al.* 2012) to be invested in regrowth or other nutrients resorption. Thus, knowledge about the resorption efficiencies of these elements is essential for a better understanding of nutrient resorption in plants.

Nutrient resorption can be measured as efficiency or proficiency. Nutrient resorption efficiency is defined as the ability of a plant to resorb nutrients, expressed as a percentage value (Aerts 1996). Nutrient resorption proficiency is determined based on the absolute level to which a nutrient is reduced during leaf senescence, and can be measured as the nutrient concentrations in senesced leaves (Killingbeck 1996). Nutrient resorption efficiency measures the percentage of a nutrient that is withdrawn from senescing leaves prior to their abscission. Resorption proficiency, on the other hand, measures how much of a nutrient is retained in senesced leaves, *i.e.* low nutrient concentrations in senesced leaves indicate high nutrient proficiencies (Killingbeck 1996).

In this study, we evaluated variations in nutrient (C, N, P, K, Mg and S) resorption efficiency and proficiency for a widely distributed, ecologically and economically important tree spe-

cies, *Quercus variabilis* Blume, in China. We collected *Q. variabilis* leaves from the northern temperate regions to the southern subtropical regions of China in order to evaluate how climate, soil nutrient availability, green leaf nutritional status and leaf traits affected nutrient resorption efficiencies and proficiencies.

MATERIAL AND METHODS

Study sites

The study area encompassed the temperate northern, warm temperate central and subtropical southern regions of China (24–41°N and 99–123°E; Fig. 1, Table S1). We collected leaf samples from 22 stands in 2007, 24 stands in 2008 and 16 stands in 2009 (Table S1). The MAT and MAP across the region ranged from 4.4 to 20 °C and from 511 to 2029 mm, respectively. The vegetation of the northern portion of the study area comprises temperate deciduous broadleaf forests dominated by *Q. variabilis*, the typical soil types being Entisols (US Soil Survey Staff 2010). In the central study area, the climate transitions from temperate to subtropical, with the typical vegetation comprising mixed deciduous and evergreen broadleaf forests dominated by *Q. variabilis*, growing in Inceptisols. In the south, the zonal vegetation is subtropical evergreen and broadleaved with *Q. variabilis* as a companion species, and the soils are typically Ultisols. All of the sampled stands were located in remote, protected mountain forests.

Leaf and soil sampling

At each site, we choose a stand where *Q. variabilis* is the dominant or co-dominant species, and set up a sampling plot (20 m × 20 m) in the southerly, mid-slope position of the mountain for surveying the tree height and DBH (1.3 m) of all *Q. variabilis* trees in the plot (*Q. variabilis* tree height varied from 8 to 22 m and DBH from 10.3 to 28.1 cm; Table S1). Five canopy trees were randomly selected (>20 cm in diameter with distance between sampled trees >20 m) within each site. In obtaining the green leaves, we selected eight to ten sunlit branches from each sample tree when the leaves were fully flushed, harvested them from the middle branch, and subsequently composited them to yield one sample per tree. For the senesced leaves, at the end of the growing season, we shook the sunlit branches of each sample tree gently using a long stick and collected the fresh senesced leaves on the ground. We used this collection method consistently to minimise possible influences of variation in leaf traits among trees. For each sample tree, ten green leaves were randomly selected for leaf area measurement using a scanning planimeter (SHY-150, China) in the field and bagged separately from other leaves. All leaves were stored in an ice-filled cooler immediately after collection and transported to the laboratory within 2 days for pretreatment.

Five plots (5 m × 5 m) were randomly selected within each sampling area for soil samples. Within each subplot, five surface soil cores (0–10-cm depth) were collected using a 2.5-cm diameter soil auger, and pooled to form a composite soil sample. In total, five soil samples were extracted from each sample plot.

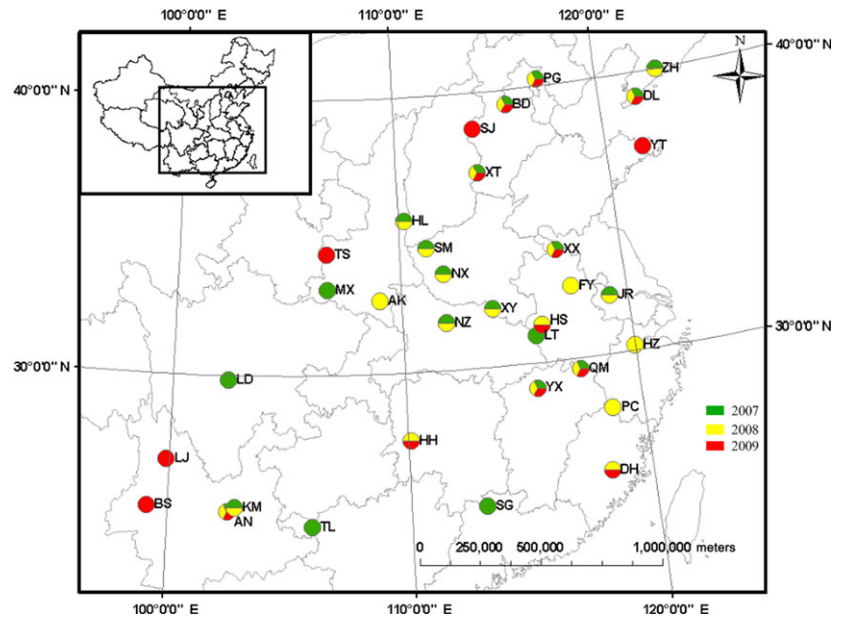


Fig. 1. Distribution of *Quercus variabilis* stands sampled across eastern China. Abbreviations and descriptions of the locations are found in the Table S1.

Sample preparation and analysis

In the laboratory, all leaves were wiped clean with wet absorbent cotton (wetted with double distilled water) to remove dirt particles on the leaf surfaces, and then dried at 65 °C for 72 h (Markert 2008). The leaf samples used for leaf area measurements were separately dried, and their dry masses were weighed to the nearest 0.001 mg. Leaf mass per area (LMA) was calculated as the leaf dry mass per one-sided leaf area. The soil samples were air-dried in a shaded and ventilated environment for ~1 month to a constant weight. Soil and leaf samples were subsequently ground in a 20-inch mesh in a Wiley Mill and kept cool and dry for chemical analysis.

Soil and leaf samples were analysed for total C and N ($\text{mg}\cdot\text{g}^{-1}$) using an elemental analyser (Vario EL III, Elementar, Germany). The quantification of P, K, Ca, Mg and S were analysed by employing an inductively coupled plasma emission spectrometer ICP (Iris Advantage 1000, Thermo Jarrel Ash, Franklin, MA, USA) after the samples were digested using trace metal-grade nitric and perchloric acid, and diluted in 100 ml distilled water (Dahlquist & Knoll 1978). The subsamples of soil were oven dried at 65 °C in order to obtain air- to oven-dried conversion, and elemental concentrations within the oven-dried soils were calculated according to the transformation factor.

Calculation of leaf resorption efficiency and proficiency

A typical issue associated with the calculation of leaf resorption efficiency is leaf mass loss or leaf area shrinkage during senescence, which may result in an underestimation of leaf resorption efficiency (van Heerwaarden *et al.* 2003; Vergutz *et al.* 2012). Here, we used the mass loss correction factor for deciduous broadleaved species (MLCF = 0.784) according to Vergutz *et al.* (2012) to quantify the nutrient resorption efficiencies as follows:

$$\text{Resorption efficiency} = \left(1 - \frac{X_{\text{sen}}}{X_{\text{gr}}} \text{MLCF} \right) \times 100$$

where X_{gr} and X_{sen} are concentrations of C, N, P, K, Mg or S in green and senesced leaves, respectively. The nutrient resorption proficiency was expressed as nutrient concentration in senesced leaves (Killingbeck 1996).

Site-specific climate data

Geographic positions and altitudes were obtained using a global positioning system (Thales, USA). We entered the GPS data into a global climate database (<http://www.worldclim.org/>) to obtain MAT (°C), MAP (mm), average diurnal range of temperature (DRT, °C) and annual precipitation seasonality (coefficient of variation in monthly mean precipitation, APS, %) with a resolution of 1 km × 1 km. Average growing season length (GSL, days), defined as the number of days with diurnal mean temperature >5 °C, was estimated from records of 756 climate stations in China, spanning 1954–2007, using a kriging extrapolation method (Han *et al.* 2011).

Statistical analyses

Five sample trees were selected as replicates at each site for 1 year, whereas some sites were sampled across multiple years. In statistical analyses, the mean value of the five trees for each element was employed as a data point for 1 year. Nutrient resorption efficiencies and proficiencies were log-transformed when necessary to meet the parametric test assumptions of normality and homogenous variances. Linear regression was used to describe the relationships between leaf resorption (efficiency and proficiency) and environmental factors (MAP, MAT, GSL and green leaf and soil element concentrations), as well as latitude. We assessed C, N, P, K, Mg and S resorption efficiencies (hereafter RE-C, RE-N, RE-P, RE-K, RE-Mg and

RE-S, respectively) and proficiencies (hereafter RP-C, RP-N, RP-P, RP-K, RP-Mg and RP-S, respectively) and their correlations with the climate factors and latitude using bivariate Reduced Major Axis regression models (Bohonak & van der Linde 2004). To examine whether the sensitivity of resorption efficiency to climate factors differed among nutrients, we tested the regression slopes.

The hierarchical partitioning (HP) method can reduce collinearity problems among explanatory variables by disentangling the independent contribution and joint contribution of explanatory variables to the response variable (Heikkinen *et al.* 2004; Olea *et al.* 2010). HP analysis allows reliable ranking of the explanatory variables where the data set consists of no more than nine explanatory variables (Olea *et al.* 2010). There were eight explanatory variables in our study, and these variables showed significant collinearity. Therefore, we used the HP method to explore the contribution of each explanatory variable to the variability of leaf resorption efficiencies and proficiencies. HP was conducted using the 'hier.part package' version 0.5–1 (Mac Nally & Walsh 2004). All statistical analyses were performed using R version 2.15.3 (R Development Core Team, available from www.r-project.org/, accessed 2013).

RESULTS

Variations in nutrient resorption and latitudinal patterns

Mean resorption efficiency was highest for P, followed by RE-K, RE-N, RE-S, RE-Mg and RE-C; RE-P was three times more efficient than RE-C (Table 1). There were considerable variations in nutrient resorption efficiencies across their distribution, from 4.8 to 73.2% for Mg with the highest coefficient of variation (CV = 42%), and from 60.6 to 81.6% for N with the lowest CV (16%; Table 1). Additionally, the nutrient resorption efficiencies of *Q. variabilis*, except for RE-Mg, showed significant interrelationships (Figure S1).

Table 1. Summary statistics of leaf nutrient resorption efficiencies (%) and proficiencies (mg·g⁻¹) in *Q. variabilis* across China.

nutrient resorption	mean	maximum	minimum	SE	CV %
resorption efficiencies					
RE-C	20.1	36.0	5.5	0.9	33.0
RE-N	60.6	81.6	33.9	1.2	16.0
RE-P	68.5	89.9	2.1	2.7	30.0
RE-K	65.6	85.8	14.8	2.1	24.0
RE-Mg	28.6	73.2	4.8	1.6	42.0
RE-S	49.8	63.8	16.4	2.0	27.0
RE-N: RE-P	1.1	2.1	0.6	0.4	23.0
resorption proficiencies					
RP-C	488.3	539.3	391.3	2.9	5.0
RP-N	9.2	17.6	4.7	0.3	27.0
RP-P	0.5	2.6	0.1	0.1	108.0
RP-K	3.0	11.3	1.1	0.2	54.0
RP-Mg	2.1	3.5	1.0	0.1	30.0
RP-S	1.1	2.1	0.8	0.0	27.0

CV % = coefficient of variation × 100%, RE-C, RE-N, RE-P, RE-K, RE-Mg and RE-S are resorption efficiencies for C, N, P, K, Mg and S, respectively. RP-C, RP-N, RP-P, RP-Mg, RP-K and RP-S are resorption proficiencies for C, N, P, K, Mg and S, respectively.

The mean nutrient concentrations of senesced leaves were lowest for P, followed by S, Mg, K, N and C (Table 1). There were large variations in nutrient concentrations of senesced leaves across the gradient. For example, it varied by 20.3-fold for P with the highest coefficient of variation (CV = 108%) compared with 1.4-fold for C with the lowest CV (5%).

The RE-N, RE-P, RE-K and RE-S increased significantly with latitude ($P = 0.001–0.022$), whereas RE-C and RE-Mg showed no significant trends with latitude (Fig. 2). There was no significant relationship between RE-N:RE-P and latitude (Fig. 3). Furthermore, N, P, K and S in senesced leaves displayed significant negative trends with latitude ($P = 0.0018–0.029$), whereas Mg was positively related to latitude ($P < 0.0001$; Fig. 4).

Climate and nutritional influence on leaf nutrient resorption

Hierarchical partitioning indicated that a substantial fraction of variation in elemental resorption efficiencies and proficiencies could be explained MAT, MAP, DRT, APS and GSL, green leaves and soil nutrients (from 26% for RE-Mg to 79% for RE-C, and from 28% for RP-N to 76% for MgR-P), whereas little explanatory information was contributed by LMA (Tables 2 and 3). Most notably, RE-N and RE-K responded strongly to climate factors, particularly GSL; RE-P, RE-Mg and RE-S responded strongly to soil P, Mg and S, respectively; whereas RE-C and RE-Mg responded strongly to green leaf C and Mg, respectively (Table 2). The resorption proficiencies were controlled largely by green leaf nutrient status, except for leaf C proficiency, (Table 3).

Due to the relatively strong influence of MAT, MAP and GSL on nutrient resorption in comparison with the other factors (DRT and APS), and the close relationships and multicollinearity among the five climate factors considered in this study (Tables 2, 3 and S2), we focused our analysis on MAT, MAP and GSL. RE-N decreased significantly with GSL, MAT and MAP ($P < 0.05$). Similarly, RE-P and RE-S decreased significantly with GSL ($P < 0.001$ for RE-P and $P = 0.017$ for RE-S) and MAT ($P = 0.031$ for RE-P and $P = 0.014$ for RE-S), while RE-K only showed a negative relationship with GSL ($P = 0.0023$; Fig. 2). RE-N:RE-P was weakly correlated (negative) with MAT ($P = 0.04$; Fig. 3). Furthermore, the leaf Mg proficiency decreased significantly with MAT ($P = 0.0002$), MAP ($P = 0.0009$) and GSL ($P = 0.0001$), and N proficiency increased significantly with MAT ($P = 0.024$) and MAP ($P = 0.024$), while P and K proficiencies showed positive relationship with GSL ($P = 0.0001$ for P, and $P = 0.0071$ for K; Fig. 4).

Leaf RE-C and RE-S showed positive relationships with the corresponding elements in green leaves, whereas leaf RE-P, RE-Mg and RE-S decreased with the corresponding elements in soils ($P < 0.05$; Figure S2).

Differences in sensitivity of nutrient resorption efficiencies to climate factors

The resorption of the studied elements differed in their sensitivities to the gradients in climate factors, as determined by the slope of responses to environmental gradients (Table S3, Fig. 2). The resorption of N, P, K and S responded to shifts in MAT with similar RMA slopes (Fig. 2). The element resorption efficiencies also showed a similar sensitivity to shifts in MAP

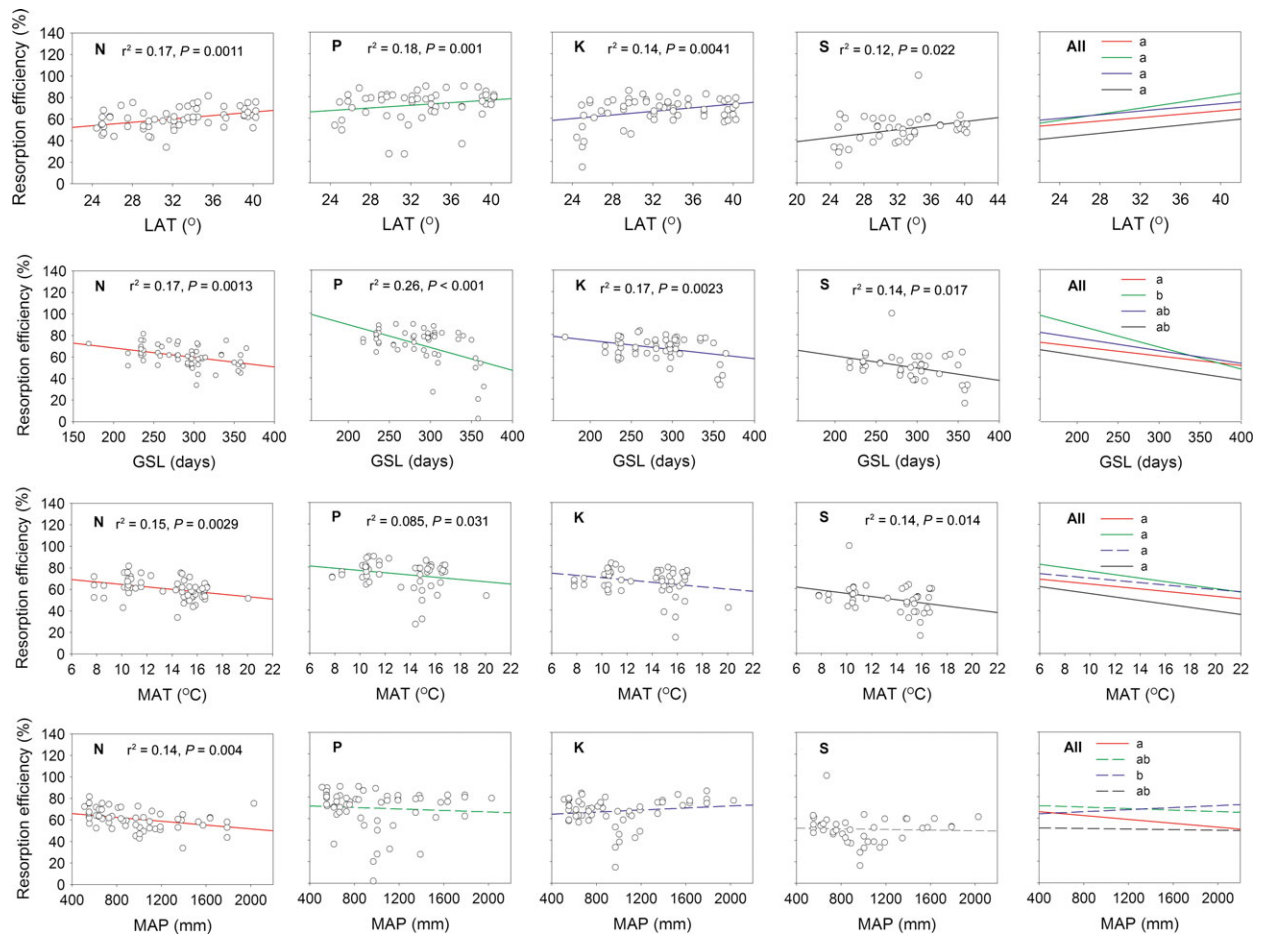


Fig. 2. Trends in leaf element resorption efficiencies for *Quercus variabilis* with latitude (LAT) and climatic variables (mean annual temperature; MAT, mean annual precipitation; MAP, and growing season length; GSL) in China. Broken lines indicate insignificant relationship ($P > 0.05$), and the lower-case letters in the panel 'All' indicate significant differences between slopes.

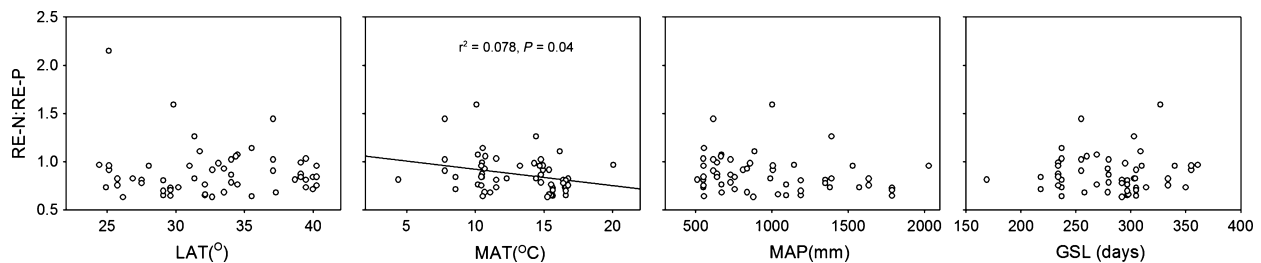


Fig. 3. Trends in leaf N and P resorption efficiency ratio (RE-N: RE-P) of *Quercus variabilis* with latitude (LAT) and climatic variables (mean annual temperature, MAT, mean annual precipitation, MAP, and growing season length, GSL) gradients at a regional scale.

and GSL, except for a flatter slope in RE-K than RE-N, and RE-N than RE-P, respectively (Fig 2). Compared with leaf nutrient resorption efficiencies in response to MAP, the leaf nutrient resorption efficiencies were more sensitive to MAT and GSL (Table S3).

DISCUSSION

The resorption of nutrients from senescing leaves is a critical physiological process for plant nutrient conservation, which

is important for the survival, growth and competition of plants in communities (Aerts 1996). This physiological process is controlled by a variety of biological and environmental factors (Killingbeck 1996), but little is known in regard to how a widespread species regulates its internal nutrient conservation in different environments. Using *Q. variabilis*, a temperate–subtropical distributed species as our focal species, we showed for the first time how nutrient resorption of multiple elements differentially vary with environmental variables at a species level across its distribution, and the possible

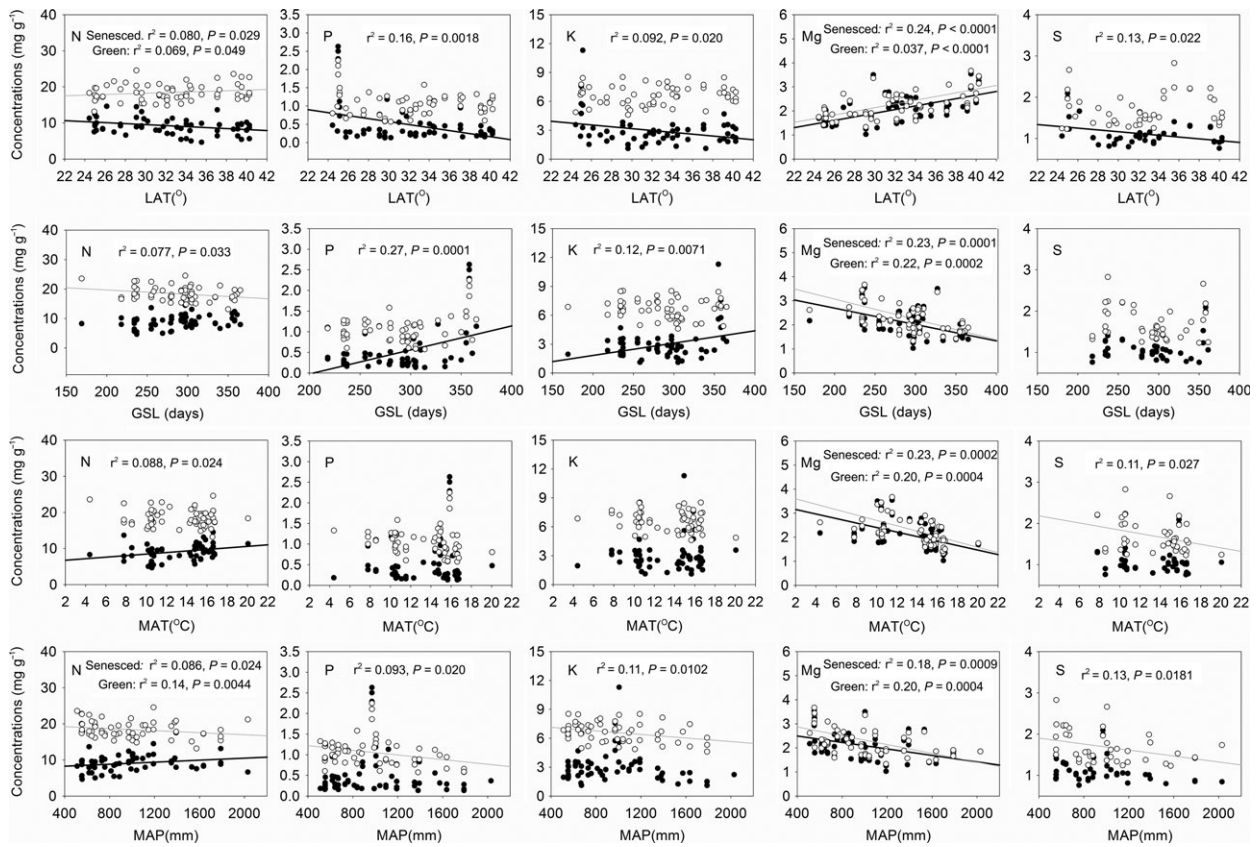


Fig. 4. Trends in leaf element resorption proficiency (defined as the nutrients concentrations in litter) for *Quercus variabilis* with latitude (LAT) and climatic variables (mean annual temperature, MAT and mean annual precipitation, MAP) in China.

Table 2. Results of hierarchical partitioning for the effects of climate factors, green leaves and soil nutritional status on leaf element resorption efficiencies of *Q. variabilis* in China.

element resorption efficiency	full model (r^2)	contribution of the individual predictor (%)					soil nutrients	leaf traits	
		climate factors						nutrients	LMA
		MAT	DRT	MAP	APS	GSL			
RE-C	0.79	0.35	0.55	0.90	0.56	1.23		96.58 ^a	0.00
RE-N	0.39	12.50	8.91	11.54	9.35	34.31 ^a	13.71	3.99	5.70
RE-P	0.69	5.82	1.33	2.74	1.82	28.38 ^a	42.74 ^a	13.25 ^a	3.92
RE-K	0.48	9.68	5.77	13.68 ^a	9.95	50.47 ^a	3.55	0.42	6.48
RE-Mg	0.26	1.83	2.63	20.52 ^a	22.58 ^a	4.35	38.96 ^a	4.26	4.87
RE-S	0.59	10.20	2.95	11.33	2.81	24.51 ^a	34.86 ^a	13.82	1.14
RE-N:RE-P	0.46	25.48 ^a	8.70	6.03	3.36	34.89 ^a	12.36	6.97	2.19

Fraction of variance is explained by the full model (r^2) and the respective contributions of the individual predictors to the overall model. RE-C, RE-N, RE-P, RE-K, RE-Mg and RE-S represent the resorption efficiencies of C, N, P, K, Mg and S, respectively, REN:REP is the ratio of REN and REP, MAT is mean annual temperature, DRT is average diurnal range of temperature, MAP is mean annual precipitation, APS is annual precipitation seasonality, GSL is average growing season length and LMA is leaf mass per area.

^aIndicates significance ($P < 0.05$).

mechanisms involved. Our results contribute new insights to understand the variable traits of nutrient resorption and the influential factors for a widely distributed species, and exemplify how this species has adapted across a broad environmental range.

Leaf nutrient resorption of *Q. variabilis* and biogeographic patterns

The RE-N and RE-K of *Q. variabilis* were within 10% of the global average reported for global flora, deciduous plants and

Table 3. Results of hierarchical partitioning for the effects of climate factors, leaf and soil elements on leaf element resorption proficiencies in *Q. variabilis* in China.

element resorption proficiency	full model (r^2)	contribution of the individual predictor (%)							
		climate factors					leaf traits		
		MAT	DRT	MAP	APS	GSL	soil nutrients	nutrients	LMA
RP-C	0.07	3.98	8.76	46.03	4.97	22.50		12.11	1.65
RP-N	0.28	6.57	5.75	5.88	4.22	15.88	6.27	46.75 ^a	8.69
RP-P	0.70	3.20	2.55	3.93	1.96	25.37 ^a	16.13 ^a	45.03 ^a	1.82
RP-K	0.63	3.82	3.08	15.06 ^a	8.42	29.87 ^a	4.60	31.84 ^a	3.32
RP-Mg	0.76	7.51	1.84	5.47	16.07 ^a	8.57	15.25 ^a	41.61 ^a	3.68
RP-S	0.67	2.79	6.28	26.36 ^a	4.60	13.94	1.27	39.15 ^a	5.61

Fraction of variance is explained by the full model (r^2) and the respective contributions of the individual predictors to the overall model. RP-C, RP-N, RP-P, RP-K, RP-Mg, and RP-S represent the resorption proficiencies of C, N, P, K, Mg and S, MAT is mean annual temperature, DRT is average diurnal range of temperature, MAP is mean annual precipitation, APS is annual precipitation seasonality, GSL is average growing season length and LMA is leaf mass per area.

^aIndicates significance ($P < 0.05$).

Quercus spp, whereas RE-C was 22–27% lower, and RE-P was 10–20% higher than that reported for global and China-specific cases (Table S4). The high RE-P likely reflected a possible P limitation for plants in Chinese *Q. variabilis*-dominated ecosystems, as highlighted in previous studies (Han *et al.* 2005; Wu *et al.* 2012; Tang *et al.* 2013). It may also be due to the different RE-P measurement techniques, such as different mass loss correction factors for deciduous and evergreen plants, or various internal nutrient conservation strategies (Vergutz *et al.* 2012). The N and P concentrations in senesced leaves ranged from 4.7 to 17.6 mg·g⁻¹ and 0.13 to 1.2 mg·g⁻¹ (except for high P at three sites in Yunnan province due to the presence of phosphorite at these sites), respectively, which were almost identical to the range of N (4.5–12.3 mg·g⁻¹) and P (0.1–1.5 mg·g⁻¹) concentrations of *Quercus* spp., but some of the values were even lower than the ‘complete’ resorption of N (7.0 mg·g⁻¹) and P (0.5 mg·g⁻¹) for deciduous species reported in Killingbeck (1996). This result suggests that the complete resorption may be dependent on soil nutrient availability.

The nutrient resorption efficiencies of *Q. variabilis* showed a 2.5- to 15.0-fold variation across the sampling areas, which suggested that this widely distributed tree species had some degree of flexibility in nutrient resorption so as to acclimate or adapt to environmental changes along specific latitudes. However, we could not exclude the fact that the variations could also be influenced by leaching; neither could we solely attribute these variations to species acclimation. The variabilities of RE-N, RE-K, RE-Mg and RE-N:RE-P of *Q. variabilis* were 25.00–80.99% lower than the global estimates for *Quercus* spp. (Table S5). This was likely due to coupled biochemical relationships among leaf elements, which was supported by the strong correlations between the resorption efficiencies of elements.

The N and P resorption efficiency of *Q. variabilis* leaves were positively correlated with latitude, but negatively correlated with MAT and MAP, which is in agreement with global patterns observed across species (Vergutz *et al.* 2012), but in contrast to some of the conclusions of Yuan & Chen (2009a) and Tang *et al.* (2013), who found that RE-P decreased significantly with increasing latitude. Similar to the positive relationships between senesced leaf N, MAT and MAP observed by Yuan & Chen (2009b), the leaf RP-N increased with MAT and MAP. In

contrast, there was no relationship between RP-P and these two climate factors. These inconsistent results for RE-P and RP-P may be due to the fact that we studied a single species at a regional scale, while the previous studies (Yuan & Chen 2009a,b; Tang *et al.* 2013) coupled interspecific variation and latitudes at a global scale. Alternatively, low P availability in soils or high P homeostasis in a species relative to the community resulted in different strengths between P resorption, latitudinal and climatic relationships. In the study of Reed *et al.* (2012), RE-N:RE-P increased significantly with latitude and declined with MAT and MAP at a global scale; however, we did not find a significant relationship between RE-N:RE-P and latitude, although we observed a significantly weak relationship between RE-N:RE-P and MAT, likely caused by coupled biochemical relationships between N and P, such as the synthesis of protein.

In agreement with the global patterns observed by Vergutz *et al.* (2012), we found that K resorption efficiency increased with latitude. However, the Mg resorption efficiency in our study had no significant relationship with latitude or climate factors, unlike the observations of Vergutz *et al.* (2012). One possible explanation for these contrasting results was the relatively narrow latitudinal scale of this study in contrast with the global scale studied by Vergutz *et al.* (2012). This is supported by the fact that when our data are integrated with the global data set compiled by Vergutz *et al.* (2012), the Mg resorption efficiencies also displayed significant trends. The similar patterns implied that plants at high latitudes have similar strategies for reducing nutrient loss associated with leaf turnover and increasing internal nutrient cycling. Since trends at the global scale reflect both changes in community composition and physiological regulations, and those for a given species are primarily a result of physiological regulation in response to environmental changes, which are narrower due to the limited distribution range, it is not surprising that the variation in RE-Mg at the global scale was 64% higher than that for *Q. variabilis*.

Potential causes of biogeographic patterns

Our results indicated that temperature-related factors, such as MAT and GSL, are critical factors that shape the evolution of

plant nutrient conservation strategies, especially at the high latitude regions with lower MAT and GSL. The nutrient resorption efficiencies were high and nutrient concentrations in senesced leaves were low. Cold temperatures not only suppress the nutrient release and root N or P uptake, but also inhibit the metabolic activity of a plant, whereas plants at high latitude with a short growing season tend to grow quickly to complete development. Therefore, plants at high latitude with cold temperatures and short growing seasons tend to have high nutrient retrieval strategies to enhance metabolic activity and growth rates, and reduce their dependence on the supply of soil nutrients, resulting in low nutrient concentrations in senesced leaves. This explanation is supported by results from a global meta-analysis (Yuan & Chen 2009a,b; Vergutz *et al.* 2012) and a common garden study (Wright & Westoby 2003).

Previous studies have shown that low nutrient availability in soils, especially P, generally leads to high leaf resorption (Vitousek 1982; Güsewell 2005; Rejmánková 2005; Yuan & Chen 2015). We also found high leaf P and S resorption efficiencies at high latitude with low soil-resident P and S (Figure S3), which suggested that soil P and S contribute significantly to the positive trends of latitudinal patterns. Although RE-Mg decreased with soil Mg, there was no trend of RE-Mg with latitude, which was likely due to the complex impact of climate factors and available Mg in soils. In contrast, soil N and K did not vary with latitude. Thus, the observed latitudinal gradients in N and K resorption, together with no relationships between the resorption and concentrations of these elements in soils further suggested that leaf N and K resorption are largely caused by differences in climate along latitude.

Some studies have demonstrated leaf nutritional controls on element resorption (Wright & Westoby 2003; Güsewell 2005; Kobe *et al.* 2005). Herein, we found that higher green leaf C and S were correlated with higher C and S resorption efficiencies across the sampling sites. The leaf nutrient proficiencies were, however, largely controlled by green leaf nutritional status, which was consistent with the results at global (Kobe *et al.* 2005; Vergutz *et al.* 2012) and regional scales (Ratnam *et al.* 2008; Mayor *et al.* 2014). All studies revealed that senesced leaf nutrients are positively correlated with the status of green leaf nutrition. The latitudinal and climate variations of nutrient resorption observed here were also likely caused by leaf nutrient loss *via* leaching, variabilities of leaf traits such as leaf specific strength (Wood *et al.* 2011) and leaf C sink strength, or genetic differentiation (Oleksyn *et al.* 2003). However, further experiments are required in order to explore the influence of these factors on variations in nutrient resorption.

The sensitivity of elements to climate factors

The element resorption efficiencies measured here were almost similar in their sensitivity to shifts in climate factors, except for RE-N, which was more sensitive to MAP than RE-N, and RE-P, which was more sensitive to GSL than RE-P. Additionally, Mg resorption efficiency showed no significant sensitivity to the climate factors measured here. The high sensitivity of N resorption efficiencies to MAP were likely caused by leaf amino acid responses to shifts in drought conditions (Barnett & Naylor 1966; Good & Zaplachinski 1994), because free amino acids usually increase with drought. These free amino acids break

down easily, potentially facilitating plant leaf N resorption. P resorption efficiency was more sensitive to the variability of growing season length across the geographic range, which may be caused by growth rate, as accelerated growth requires larger amounts of P. The high sensitivity of leaf nutrient resorption efficiencies to MAT and GSL, in comparison to MAP, in this study is likely because temperature influences virtually all physiological rate processes, including hydrolysis and phloem transport. Future investigations are required to explore the underlying mechanisms of climate factors on nutrient resorption.

CONCLUSIONS

To our knowledge, this is the first study to evaluate variations in nutrient resorption and potential environmental controls for a given widespread species across its geographic distribution. Our results show that the observed global and regional biogeographic patterns observed via meta-analyses, to some extent, also exist for *Q. variabilis* at regional scales. This suggests a fundamental feature of plant nutrient conservation strategies in response to the prevailing variabilities in environmental factors induced by large latitudinal gradients. Additionally, our findings offer a finer resolution of how nutrient retrieval in plants responds to changes in climate, and also provides insights into nutrient cycling and limitation in *Q. variabilis*-dominated ecosystems.

ACKNOWLEDGEMENTS

We are grateful to Leonardus Vergutz for valuable comments on an earlier version of the manuscript. This work was financially supported by National Natural Science Foundation of China (NSFC 31270640, 31270491, 31070532 and 71333010).

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of geographic location (latitude; longitude, altitude), site code for sample sites and information on stand growth *in situ* mature *Q. variabilis* populations across eastern China.

Table S2. Correlation between five climate variables based on climate data for all sites in this study. Values are correlation coefficient (*R*).

Table S3. Reduced major axis slopes of the resorption efficiencies of the studied elements in *Q. variabilis*.

Table S4. Comparison of global carbon (RE-C), nitrogen (RE-N), phosphorus (RE-P), potassium (RE-K) and magnesium resorption efficiency (RE-Mg) in the present study and previous findings (compiled for global flora, deciduous trees and *Quercus* spp.).

Table S5. Comparison of the variation (measured as coefficient of variation, CV) in resorption efficiency in the present study (*Q. variabilis*) and that of Vergutz *et al.* (2012) (compiled for global data, deciduous trees and *Quercus* spp.). The range (minimum–maximum) of values observed in this study is given in parentheses.

Figure S1. The relationships among element resorption efficiencies in *Q. variabilis* leaves.

Figure S2. Relationships between element resorption efficiencies and corresponding elements in green leaves of *Q. variabilis* (a) and soil (b). Significant relationships between RE-P and RE-S with respective elements in soil were driven by extreme points.

Figure S3. Trends in soil nutrient concentration ($\text{mg}\cdot\text{g}^{-1}$) for *Q. variabilis* stands with climate factors (mean annual tem-

perature, MAT; mean annual precipitation, MAP; growing season length, GSL) and latitude (LAT) in China. The significant relationships between soil P with LAT and GSL were driven by extreme points (Anning, Yunnan).

REFERENCES

- Aerts R. (1996) Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology*, **84**, 597–608.
- Aerts R., Chapin F.S. (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. In: Fitter A.H., Raffaelli D.G. (Eds), *Advances in ecological research*, Vol. 30. Elsevier Academic Press, San Diego, CA, USA, pp 1–67.
- Attwill P.M., Adams M.A. (1993) Nutrient cycling in forests. *New Phytologist*, **124**, 561–582.
- Barnett N.M., Naylor A.W. (1966) Amino acid and protein metabolism in bermuda grass during water stress. *Plant Physiology*, **41**, 1222–1230.
- Bohonak A.J., van der Linde K. (2004) RMA: software for reduced major axis regression. Java version. Available from <http://www.kimvdlinde.com/> (accessed 25 January 2009).
- Cakmak I., Yazici A.M. (2010) Magnesium: a forgotten element in crop production. *Better Crops*, **94**, 23–25.
- Chapin F.S., Moilanen L. (1991) Nutritional controls over nitrogen and phosphorus resorption from Alaskan birch leaves. *Ecology*, **72**, 709–715.
- Chapin F.S., Oechel W.C. (1983) Photosynthesis, respiration, and phosphate absorption by *Carex aquatilis* ecotypes along latitudinal and local environmental gradients. *Ecology*, **64**, 743–751.
- Chapin F.S. III, Chapin M.C., Matson P.A., Vitousek P. (2011) *Principles of terrestrial ecosystem ecology*. Springer, New York, NY, USA.
- Dahlquist R.L., Knoll J.W. (1978) Inductively coupled plasma-atomic emission spectrometry – analysis of biological-materials and soils for major, trace, and ultra-trace elements. *Applied Spectroscopy*, **32**, 1–29.
- De Frenne P., Graae B.J., Rodriguez-Sanchez F., Kolb A., Chabrierie O., Decocq G., De Kort H., De Schrijver A., Diekmann M., Eriksson O., Gruwez R., Hermy M., Lenoir J., Plue J., Coomes D.A., Verheyen K. (2013) Latitudinal gradients as natural laboratories to infer species' responses to temperature. *Journal of Ecology*, **101**, 784–795.
- Good A.G., Zaplachinski S.T. (1994) The effects of drought stress on free amino-acid accumulation and protein-synthesis in *Brassica napus*. *Physiologia Plantarum*, **90**, 9–14.
- Güsewell S. (2004) N:P ratios in terrestrial plants: variation and functional significance. *New Phytologist*, **164**, 243–266.
- Güsewell S. (2005) Nutrient resorption of wetland graminoids is related to the type of nutrient limitation. *Functional Ecology*, **19**, 344–354.
- Han W.X., Fang J.Y., Guo D.L., Zhang Y. (2005) Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. *New Phytologist*, **168**, 377–385.
- Han W.X., Fang J.Y., Reich P.B., Ian Woodward F., Wang Z.H. (2011) Biogeography and variability of eleven mineral elements in plant leaves across gradients of climate, soil and plant functional type in China. *Ecology Letters*, **14**, 788–796.
- van Heerwaarden L.M., Toet S., Aerts R. (2003) Current measures of nutrient resorption efficiency lead to a substantial underestimation of real resorption efficiency: facts and solutions. *Oikos*, **101**, 664–669.
- Heikkinen R.K., Luoto M., Virkkala R., Rainio K. (2004) Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural-forest mosaic. *Journal of Applied Ecology*, **41**, 824–835.
- Killingbeck K.T. (1996) Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. *Ecology*, **77**, 1716–1727.
- Kobe R.K., Lepczyk C.A., Iyer M. (2005) Resorption efficiency decreases with increasing green leaf nutrients in a global data set. *Ecology*, **86**, 2780–2792.
- Lü X.T., Freschet G.T., Flynn D.F.B., Han X.G. (2012) Plasticity in leaf and stem nutrient resorption proficiency potentially reinforces plant–soil feedbacks and microscale heterogeneity in a semi-arid grassland. *Journal of Ecology*, **100**, 144–150.
- Maathuis F.J., Diatloff E. (2013) Roles and functions of plant mineral nutrients. *Methods in Molecular Biology*, **953**, 1–21.
- Mac Nally R., Walsh C.J. (2004) Hierarchical partitioning public-domain software. *Biodiversity and Conservation*, **13**, 659–660.
- Markert B. (2008) *Environmental sampling for trace analysis*. John Wiley & Sons, Chichester, UK.
- Mayor J.R., Wright S.J., Turner B.L. (2014) Species-specific responses of foliar nutrients to long-term nitrogen and phosphorus additions in a lowland tropical forest. *Journal of Ecology*, **102**, 36–44.
- Norby R.J., Long T.M., Hartz-Rubin J.S., O'Neill E.G. (2000) Nitrogen resorption in senescing tree leaves in a warmer, CO₂-enriched atmosphere. *Plant and Soil*, **224**, 15–29.
- Olea P.P., Mateo-Tomás P., De Frutos Á. (2010) Estimating and modelling bias of the hierarchical partitioning public-domain software: implications in environmental management and conservation. *PLoS One*, **5**, e11698.
- Oleksyn J., Reich P.B., Zytkowski R., Karolewski P., Tjoelker M.G. (2003) Nutrient conservation increases with latitude of origin in European *Pinus sylvestris* populations. *Oecologia*, **136**, 220–235.
- Pugnaire F.I., Chapin F.S. (1992) Environmental and physiological factors governing nutrient resorption efficiency in barley. *Oecologia*, **90**, 120–126.
- Ratnam J., Sankaran M., Hanan N.P., Grant R.C., Zambatis N. (2008) Nutrient resorption patterns of plant functional groups in a tropical savanna: variation and functional significance. *Oecologia*, **157**, 141–151.
- Reed S.C., Townsend A.R., Davidson E.A., Cleveland C.C. (2012) Stoichiometric patterns in foliar nutrient resorption across multiple scales. *New Phytologist*, **196**, 173–180.
- Rejmánková E. (2005) Nutrient resorption in wetland macrophytes: comparison across several regions of different nutrient status. *New Phytologist*, **167**, 471–482.
- Renteria L.Y., Jaramillo V.J. (2011) Rainfall drives leaf traits and leaf nutrient resorption in a tropical dry forest in Mexico. *Oecologia*, **165**, 201–211.
- Richardson S.J., Peltzer D.A., Allen R.B., McGlone M.S. (2005) Resorption proficiency along a chronosequence: responses among communities and within species. *Ecology*, **86**, 20–25.
- Richardson S.J., Allen R.B., Doherty J.E. (2008) Shifts in leaf N:P ratio during resorption reflect soil P in temperate rainforest. *Functional Ecology*, **22**, 738–745.
- Tang L.Y., Han W.X., Chen Y.H., Fang J.Y. (2013) Resorption proficiency and efficiency of leaf nutrients in woody plants in eastern China. *Journal of Plant Ecology*, **6**, 408–417.
- Tripler C.E., Kaushal S.S., Likens G.E., Walter M.T. (2006) Patterns in potassium dynamics in forest ecosystems. *Ecology Letters*, **9**, 451–466.
- Tully K.L., Wood T.E., Schwantes A.M., Lawrence D. (2013) Soil nutrient availability and reproductive effort drive patterns in nutrient resorption in *Pentaclethra maculosa*. *Ecology*, **94**, 930–940.
- US Soil Survey Staff (2010) *Keys to soil taxonomy*, 11th edition. Natural Resource Conservation Service, United States Department of Agriculture, Washington, DC, USA.
- Vergutz L., Manzoni S., Porporato A., Novais R.F., Jackson R.B. (2012) Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. *Ecological Monographs*, **82**, 205–220.
- Vitousek P. (1982) Nutrient cycling and nutrient use efficiency. *American Naturalist*, **119**, 553–572.
- Vitousek P.M., Sanford R.L. (1986) Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics*, **17**, 137–167.
- Wood T.E., Lawrence D., Wells J.A. (2011) Inter-specific variation in foliar nutrients and resorption of nine canopy-tree species in a secondary neotropical rain forest. *Biotropica*, **43**, 544–551.
- Wright I.J., Westoby M. (2003) Nutrient concentration, resorption and lifespan: leaf traits of Australian sclerophyll species. *Functional Ecology*, **17**, 10–19.
- Wu T.G., Yu M.K., Wang G.G., Dong Y., Cheng X.R. (2012) Leaf nitrogen and phosphorus stoichiometry across forty-two woody species in Southeast China. *Biochemical Systematics and Ecology*, **44**, 255–263.
- Yuan Z.Y., Chen H.Y.H. (2009a) Global-scale patterns of nutrient resorption associated with latitude, temperature and precipitation. *Global Ecology and Biogeography*, **18**, 11–18.
- Yuan Z.Y., Chen H.Y.H. (2009b) Global trends in senesced-leaf nitrogen and phosphorus. *Global Ecology and Biogeography*, **18**, 532–542.
- Yuan Z.Y., Chen H.Y.H. (2015) Negative effects of fertilization on plant nutrient resorption. *Ecology*, **96**, 373–380.