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Global patterns of leaf nutrient resorption in herbaceous plants

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Abstract. Nutrient resorption plays an important role in plant ecology because it plays a key role in nutrient conservation strategies of plants. However, our current knowledge about the patterns of nutrient resorption among herbaceous species at a global scale is still inadequate. Here, we present a meta-analysis using a global dataset of nitrogen (N) and phosphorus (P) resorption efficiency spanning 521 observations and 248 herbaceous species. This analysis shows that the N resorption efficiency (NRE) and P resorption efficiency (PRE) across all herbaceous plant groups are 54.7% and 64.5%, respectively. Across all species, NRE, PRE and N:P resorption ratios (NRE:PRE) vary statistically significantly at a global scale, i.e., NRE, PRE and NRE:PRE increase with increasing latitude but decrease with increasing mean annual temperature (MAT) and mean annual precipitation (MAP). For different functional groups, similar patterns of NRE, PRE and NRE:PRE with respect to latitude, MAT and MAP are observed. Our study are very important complementary to global-scale studies of nutrient resorption and also can inform attempts to model biogeochemical cycling at a global scale.

Key words: global scale, nutrient resorption, latitude, temperature and precipitation, herbaceous species

1 Introduction

Nutrient resorption, that is, internal nutrient recycling is recognized as most important mechanisms of nutrient conservation that permits plants to re-use nutrients directly and reduces a dependence on external nutrient supplies especially in nutrient-poor environment (Aerts, 1996; Aerts and Chapin, 1999). This conservation mechanism can affect many ecosystem processes such as plant competition, nutrient uptake, reproduction, and carbon cycling (Killingbeck, 1996; Berg and McClaugherty, 2008; Richardson et al., 2008; Zhang et al., 2013). Thus, a quantitative understanding the nutrient resorption patterns of plants would offer insights into plant nutrient limitations (Güsewell, 2004; Richardson et al., 2008), possibly the different response of plants to multiple global changes (Yuan and Chen, 2009a; Reed et al., 2012) and nutrient cycling (Aerts and Chapin, 1999; Chapin et al., 2011).

Nutrients such as nitrogen (N) and phosphorus (P) are the main nutrients most frequently restricting plant growth and production globally (Chapin, 1980; Güsewell, 2004), the resorption of N and P are paramount importance to plant nutrient conservation (Killingbeck, 1996; Kobe et al., 2005). N and P resorption are often presented as two important indices of internal nutrient recycling in plants, resorption efficiency of N (NRE) and P (PRE), which defined as the proportional resorbed of N and P during leaves senescence: NRE or PRE = [(N or P in green leaves – N or P in senesced leaves) / N or P in green leaves] × 100% (Killingbeck, 1996; Kobe et al., 2005; Yuan and Chen, 2009a).

Significant increase in atmospheric greenhouse gases levels contribute to global warming with significant local and regional changes in precipitation regimes (IPCC, 2007). Such great changes in temperature and precipitation have a significant impact not only on nutrient element cycling in those regions where plant growth and development tend to be limited by nutrient availability (Hungate et al., 2003; Austin et al., 2004; Nelson et al., 2004), but also on soil nutrient availability and plant nutrient status (Vitousek, 2004; Yuan et al., 2006; Yuan and Chen, 2009a). Given that changes in these climatic factors can influence the N and P in green (Reich and Oleksyn, 2004; Wright et al., 2004; Chen et al., 2013) and senesced leaves (Read et al., 2003; Parton et al., 2007; Ge et al., 2016), the NRE and PRE may also change with these climatic factors. It is therefore imperative to acquire more information about the NRE and PRE responses to global environmental factors and to predict these responses in light of future climate changes (Gordon and Jackson, 2000; De Frenne et al., 2013; Brant and Chen, 2015).

Currently, it is well known that the N and P contents of leaves also exhibit distinct biogeographic patterns (Han et al., 2005; Niklas et al., 2007; Yuan and Chen., 2009b; Vergutz et al., 2012; Kang et al., 2010; Ge et al., 2016). Indeed, there is sufficient evidence to conclude that NRE and PRE also differ in response to ecological variables such as mean annual temperature and rainfall (Richardson et al., 2005; Yuan and Chen, 2009a; Vergutz et al., 2012; Tang et al., 2013). In particular, most meta-analyses at a global and regional level have shown that NRE and PRE are related to latitude, mean annual temperature (MAT), and mean annual precipitation (MAP)(Yuan and Chen, 2009a; Vergutz et al., 2012; Tang et al., 2013). For example, Yuan and Chen (2009a) found that within different plant functional groups (trees, shrubs, broadleaf species, and conifers), NRE and PRE have opposite trends with respect to MAT and MAP and with latitude, i.e., NRE decreases with increasing MAT and MAP but increases with respect to latitude, whereas PRE increases with respect to MAT and MAP but decreases with latitude. These trends are consistent with the results reported by Tang et al., (2013) in Eastern China for woody plants. In contrast, Vergutz et al., (2012) reveal that both NRE and PRE decrease with MAT and MAP and increase with respect to latitude at a global level. Although great progress has been made on the relationships between NRE and PRE and ambient climatic factors at the local (Wright and Westoby, 2003; Tully et al., 2013; Zhao et al., 2017), regional (Tang et al., 2013; Kang et al., 2015; Sun et al., 2016) and global scales (Kobe et al., 2005; Yuan et al., 2009b; Vergutz et al., 2012), such mixed findings present an obstacle to modelling global biogeochemical cycling. In particular, most meta-analyses have reported global trends of nutrient resorption for woody plants, with little data pertaining to herbaceous plants (Vergutz et al., 2012). This gap in our knowledge is particularly important because perennial grasses also play a substantial role in a range of global-scale processes, including productivity and nutrient cycling and limitation, and an understanding nutrient-resorption characteristics of these species has significant global change implication (Hobbie, 1992; Knops et al., 2002; Zhou et al., 2006). Therefore, additional studies of herbaceous plants on the global scale are badly needed.

For this purpose, we assembled a global database from published studies to explore

(1) variations in NRE and PRE across a diverse spectrum herbaceous species, and (2) identify how NRE, PRE and N:P ratios of resorption efficiency (NRE:PRE) vary as a function of latitude, MAT, and MAP. We also investigated whether there is a global pattern of NRE, PRE and NRE:PRE with respect to latitude, MAT, and MAP and, if so, whether it differed between different functional species groups (i.e., graminoids vs. forbs and monocots vs. eudicots).

2 Materials and Methods

2.1 Data collection

A global meta-analysis was conducted using published data for NRE and PRE (see Appendix S1 in Supporting Information). To ensure data comparability, we used data from papers in which the authors specifically indicated that leaf litter samples came from newly fallen leaves that fell naturally or from freshly filled litter-traps. Further, we excluded data from leguminous plants (N-fixing species), plants grown under greenhouse conditions, and from fertilized plants. We used the Global Gazetteer Version 2.2 (http://www.fallingrain.com/world/) and WorldClim 1.4 database (http://www.worldclim.org/) to determine latitude, longitude, altitude, temperature and precipitation data (a global dataset with spatial resolution of *c.* 1 km^2) if this information was missing in the original paper. In total, 521 observations were collected encompassing 248 herbaceous species from 55 studies. Across this global data set, sites ranged from 0 to 4756m in altitude, from -9 to 27°C in MAT, and from 7.3 to 4000 mm $year^{-1}$ in MAP. Accordingly, the dataset broadly covered most of the range of MAT and MAP occupied by the majority of herbaceous species and thus permitted a detailed global level of analysis not previously possible.

2.2 Data analysis

The mean values of NRE and PRE between functional species groups (i.e., graminoids vs. forbs and monocots vs. eudicots) were assessed using one-way analysis of variance (ANOVA) and least-significant difference (LSD) *post-hoc* analyses when effects were significant. Data for NRE, PRE, and NRE:PRE ratios were $\log_{10}$-transformed before analysis in order to meet assumptions of normality and homogeneity of variances. Multiple regression analysis was used to identify the effects of latitude, MAT, and MAP on NRE, PRE and NRE:PRE. The combined effects of functional type, phylogeny (monocots versus eudicots), and MAT and MAP on NRE, PRE, and NRE:PRE were determined using analysis of variance. General linear model (GLM) was also used to examine if the responses of NRE, PRE, and NRE:PRE to MAT and MAP differed between different functional species groups. All statistical analyses were performed using R for Window version 3.1.0 statistical software (R Core Team 2014).

3 Results

For the pooled data, the mean NRE and PRE were 54.7% (n = 521, SD = 0.73%) and 64.5% (n = 360, SD = 0.79%), respectively. NRE and PRE differed significantly between the two functional groups. Forbs had lower NRE and PRE (52.8% and 61.2%) than graminoids (57.3% and 68.4%) ($P < 0.05$), whereas monocots had higher NRE and PRE (55.8% and 67%) than eudicots (52.9% and 61.3%) ($P < 0.05$) (Fig. 1).

NRE, PRE, and NRE:PRE manifested statistically significant trends with altitude, MAT, and MAP. For the pooled data, NRE, PRE, and NRE:PRE were positively correlated with latitude and negatively correlated with both MAT and MAP ($P <$

0.0001) (Table S1). Latitude, MAT, and MAP respectively accounted for 6%, 4%, and 5% of the variation observed in NRE, 8%, 6%, and 6% of variation observed in PRE, and 4%, 4% and 2% of variation observed in NRE:PRE. MAT, MAP, and latitude collectively explained 11-19% of the variation observed in NRE, PRE, and NRE:PRE (Table 1). Functional type and climatic data collectively explained 10%, 16% and 7% of global variation observed in NRE, PRE, and NRE:PRE (Table 2).

Similar patterns of NRE, PRE, and NRE:PRE with respect to latitude, MAT, and MAP were observed for the two life-form groups (forbs vs. graminoids) and for the two phylogenetic groups (monocots vs. eudicots) (Fig. 2 and Fig. 3). Although there were differences between regression slopes between forbs and graminoids and between monocots and eudicots (Table 3), the responses of NRE, PRE, and NRE:PRE to MAT and MAP were qualitatively similar.

4 Discussion

4.1 Functional traits and differences in NRE and PRE at the global level

We evaluated leaf NRE and PRE in herbaceous species using a global dataset. The mean values of NRE and PRE across all the herbaceous species are 54.7% and 64.5%, respectively. These values are only slightly higher than values reported by Aerts, (1996) based on a comparatively few data for only herbaceous species at a global scale (i.e., 50% and 57%, respectively), but lower than values reported by Jiang et al., (2012) for 18 herbaceous species in the Qinghai-Tibetan Plateau (i.e., 65.2% and 67.4%). However, these values are markedly higher than those reported for woody plants by Yuan et al., (2009a) (i.e., 47% and 54%, respectively, at a global level) or by Tang et al., (2013) (i.e., 49% and 51%, respectively, at the regional scale). Nutrient resorption efficiency of herbaceous species show obviously higher values than the values of woody species. The relatively higher nutrient resorption efficiency has been interpreted to indicate that non-woody species are more well adapted to nutrient stress through high internal N and P recycling (Norris and Reich, 2009; Freschet et al., 2010).

Additionally, NRE and PRE differ significantly between graminoids and forbs at a global scale. Both NRE and PRE are significantly higher in the former functional type compared to forbs (Fig. 1). This finding is consistent with previous observations (Aerts, 1996; Jiang et al., 2012) and has been interpeted to indicate that graminoids have a competitive advantage over forbs, which provides additional evidence that productivity, foliar nutrient allocation, and leaf biomass may lead to the higher nutrient reabsorption in graminoids compared to forbs (Aerts and Berendse, 1989). Likewise, monocots have higher NRE and PRE compared to eudicots (Fig. 1). However, in this context, it is important to note that the data for monocots are biased because approximately one half of all of the monocots in our data set are graminoids, further investigations are warranted to be conclusive.

4.2 Climatic variations in NRE and PRE at the global level

This study presents the first global-scale analyses on how nutrient resorption of N and P differentially vary with environmental variables across a broad spectrum of herbaceous species. Based on this worldwide level of analysis, both NRE and PRE increase with latitude and decrease with MAT and MAP across all herbaceous species. Plants from tropical habitats (higher temperatures) have lower NRE and PRE, whereas plants from high-latitude habitats (lower-temperatures) have higher NRE and

PRE. These trends hold true for each of the two functional types as well as when the data are pooled (Fig. 2 and Fig. 3).

In terms of NRE, the trends reported here are similar to those of Yuan and Chen, (2009a) and Tang et al., (2013) who found that NRE increased with increasing latitude but decreased with increasing MAT and MAP across woody species. Collectively, these findings support the idea that plants growing at low latitudes, or in areas with high precipitation or temperature are on average more P-limited and would be expected to have lower NRE (Austin and Vitousek, 1998; Aerts and Chapin, 1999; Sterner and Elser, 2002; Reich and Oleksyn, 2004; Santiago et al., 2005). Our results are also supported by findings from common-garden experiments (Oyarzabal et al., 2007), which report a negative relationship between NRE and both MAT and MAP. However, the trends we observed differ from those reported by Aerts et al., (2007), who found that controlled temperature and precipitation treatment had little or no effect on NRE in a high-latitude subarctic peatland. This inconsistency can be attributed to the fact that Aerts et al., (2007) used short-term temperature and precipitation manipulations on a single plant community, whereas our study examined different plant communities across large environmental gradients.

Regarding the NRE pattern reported here, our results are in accordance with the global patterns observed across species by Vergutz et al., (2012) and the regional patterns observed for a single species by Sun et al., (2015). In turn, it is the opposite of that reported by Yuan and Chen, (2009a) and by Tang et al., (2013), who observed that PRE is negatively correlated with latitude and positively correlated with MAT and MAP for woody species. The opposite patterns of PRE in woody and herbaceous species could reflect different plant growth form conservation strategies in responses to climatic differences. It is generally agreed that NRE and PRE patterns are influenced significantly by soil nutrient availability, which can affect plant conservation strategies including nutrient resorption (Oleksyn et al., 2003, Yuan et al., 2005). Previous studies have shown that the effects of temperature and precipitation can lead to limited P in tropical soils, which are generally regarded as older and offering low P availability (Reich and Oleksyn, 2004; Vitousek, 2004). Consequently, it is generally believed that plants growing in tropical soils are more likely to have higher PRE than plants growing in temperate soils (Vitousek, 1984; Aerts, 1996; Yuan and Chen, 2015). However, the climatic patterns of PRE reported here do not manifest this trend. We attribute this to the considerable heterogeneity in tropical soil nutrient conditions and availability (Richter and Babbar, 1991; Reed et al., 2012) that vary across large temporal and spatial scales (Hedin et al., 2009). Unfortunately, data recording this variability are currently unavailable. Further studies are required to resolve this apparent paradox.

The NRE and PRE reported here may also reflect the nutrient conservation strategies of herbaceous species growing at high latitudes with low MAT and MAP. Cold temperatures and drought are known to inhibit the nutrient uptake of roots and thus constrain the metabolic activity of herbaceous plants (Sun et al., 2015). Herbaceous species require some adaptive nutrient conservation strategies to reduce their dependence on the supply of soil nutrients (e.g., rapid growth, high leaf nutrient

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contents, and an accelerated life history, Adler et al., 2014) that can collectively reduce N and P acquisition by roots and their associated ectomycorrhiza (Lambers et al., 2008). In turn, the relatively high degradation capacity of nutrient (Tsujii et al., 2017) would encourage high NRE and PRE as an adaptation.

4.3 Climatic variations in NRE:PRE at the global level

The patterns of NRE:PRE reported here differs from those reported by Sun et al., (2015), who found that NRE : PRE has no significant correlation with either latitude or MAP and only a very weak statistical relationship with MAT. The difference between the findings of Sun et al., (2015) and ours may be explained by the fact that Sun et al., (2015) focused on only a single species at a regional scale, whereas our results reflect interspecific variation at a global scale. In contrast, our findings are consistent with the global patterns observed for woody species by Reed et al., (2012) and by Han et al., (2013), who report that NRE:PRE increases with latitude and decreases with MAT and MAP. The NRE:PRE pattern we observe provides indirect evidence indicating that plants growing in the tropics with higher MAT and MAP are more frequently P limited, whereas plants growing in higher latitudes with lower MAT and MAP are often N limited (Austin and Vitousek, 1998; Sterner and Elser, 2002; Reich and Oleksyn, 2004). Because nutrient availability can strongly influence nutrient resorption (Pugnaire and Chapin, 1993). NRE is generally expected to be higher (and PRE lower) at higher latitude compared to the tropics. However, the PRE pattern reported here is not consistent with this expectation. As noted, we speculate that the acclimation responses of herbaceous species to soil nutrient availability and the heterogeneity of tropical soil nutrient content help to explain this apparent contradiction.

5 Conclusion

Our analyses indicate that, when viewed at a worldwide level, more than half of all leaf N and P is resorbed during senescence in herbaceous species at a global level. Nevertheless, N and P resorption efficiencies and their ratios manifest discernable significant biogeographic patterns. Specifically, NRE, PRE, and NRE:PRE are positively correlated with latitude and negatively correlated with MAT and MAP. These patterns hold for two functional types (graminoids and forbs) and for phylogenetic groups (monocots and eudicots), indicating that they are sensitive to functional or phylogenetic traits. These trends can inform attempts to model potential changes in ecosystem dynamics in response to changing climate and attempts to model biogeochemical cycling at a global scale.

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Author contributions

The authors declare that they have no conflict of interest.

Competing interests

The authors declare that they have no conflict of interest.

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Figure Legends

Fig. 1. Mean nitrogen resorption efficiency (NRE) and phosphorus resorption efficiency (PRE) for functional types (forbs, F versus graminoids, G) and phylogenetic groups (monocots, M versus eudicots, E). Different letters (a and b) indicate significant differences at the 0.05 level. Error bas are standard errors. The number of observations is given within each bar.

Fig. 2. Nutrient resorption efficiencies (NRE and PRE) and nutrient resorption efficiency ratio (NRE:PRE) in relation to latitude (°), mean annual temperature (MAT, °C), and mean annual precipitation (MAP, mm). Red and blue circles represent data points for graminoids and forbs, respectively. The coefficients of determination (r^2) and P are provided in each panel for graminoids (the first line) and forbs (the second line).

Fig. 3. Nutrient resorption efficiencies (NRE and PRE) and nutrient resorption efficiency ratio (NRE:PRE) in relation to latitude (°), mean annual temperature (MAT, °C), and mean annual precipitation (MAP, mm). Red and blue circles represent data points for monocots and eudicots, respectively. The coefficients of determination (r^2) and P are shown in each panel for eudicots (the first line) and monocots (the second line).

Table 1 Multiple regression analyses of nitrogen resorption efficiency (NRE), phosphorus resorption efficiency (PRE), and their ratio (NRE:PRE) in relation to latitude, mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm).

Trait	*n*	R^2	Latitude ***F***	MAT *F*	MAP *F*	MAT×MAP *F*	Latitude×MAT×MAP *F*
NRE	521	0.106	42.22***	1.28^{ns}	3.15*	0.33^{ns}	4.46*
PRE	360	0.189	39.49***	1.63^{ns}	0.25^{ns}	10.86**	26.60***
NRE:PRE	357	0.124	11.92***	0.96^{ns}	4.00*	2.07^{ns}	0.01^{ns}

n is sample number. *F* ratios and significance are shown for each of the dependent variables (ns, $P > 0.05$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

Table 2 Results of general linear models of nitrogen resorption efficiency (NRE), phosphorus resorption efficiency (PRE), and their ratio (NRE:PRE) in relation to functional type, latitude, mean annual temperature (MAT, °C), and mean annual precipitation (MAP, mm).

Trait	*n*	R^2	Phylogeny ***F***	Life-form *F*	Latitude *F*	MAT *F*	MAP *F*
NRE	521	0.100	5.48^{*}	5.10^{***}	26.67^{***}	0.95^{ns}	3.61^{*}
PRE	360	0.161	0.21^{ns}	8.50^{***}	30.92^{***}	1.84^{ns}	0.37^{ns}
NRE:PRE	357	0.073	3.73^{*}	2.12^{*}	10.43^{**}	1.16^{ns}	3.70^{*}

n is sample number. *F* ratios and significance are shown for each of the dependent variables (ns, $P > 0.05$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

Table 3 Results of general linear models (*F*-values for model terms and model R^2) of nitrogen resorption efficiency (NRE), phosphorus resorption efficiency (PRE), and N:P ratio of resorption efficiency (NRE:PRE) using functional group (FG, life-form) and phylogeny (ME) as factors and mean annual temperature (MAT) and mean annual precipitation (MAP) as continuous variables.

Trait	NRE	PRE	NRE:PRE
FG	3.45^{**}	6.13^{***}	2.71^{*}
MAT	22.46^{***}	31.92^{***}	10.27^{**}
MAP	12.01^{***}	1.92^{ns}	2.08^{ns}
MAT × MAP	1.20^{ns}	12.19^{***}	1.85^{ns}
FG × MAT	3.99^{**}	0.75^{ns}	1.66^{ns}
FG × MAP	2.13^{ns}	3.07^{*}	2.18^{ns}
FG × MAT × MAP	0.35^{ns}	5.62^{**}	3.57^{*}
Model R^2	0.12	0.21	0.11
ME	6.38^{*}	20.75^{***}	5.54^{*}
MAT	22.27^{***}	33.01^{***}	10.00^{**}
MAP	11.90^{***}	1.98^{ns}	2.03^{ns}
MAT × MAP	0.61	9.27^{**}	1.35^{ns}
ME × MAT	6.49^{*}	2.50^{ns}	3.72^{*}
ME × MAP	4.79^{*}	13.37^{***}	0.92^{ns}
ME × MAT × MAP	2.45^{ns}	19.22^{***}	1.76^{ns}
Model R^2	0.10	0.22	0.08

ns, $P > 0.05$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

Fig. 1

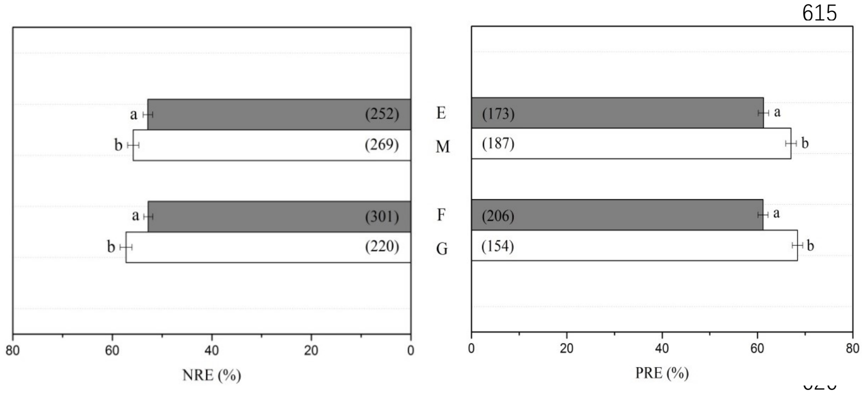

a
(252)
E
(173)
a
b
(269)
M
(187)
b
a
(301)
F
(206)
a
b
(220)
G
(154)
b
80
60
40
20
0
NRE (%)
0
20
40
60
80
PRE (%)

Fig. 2

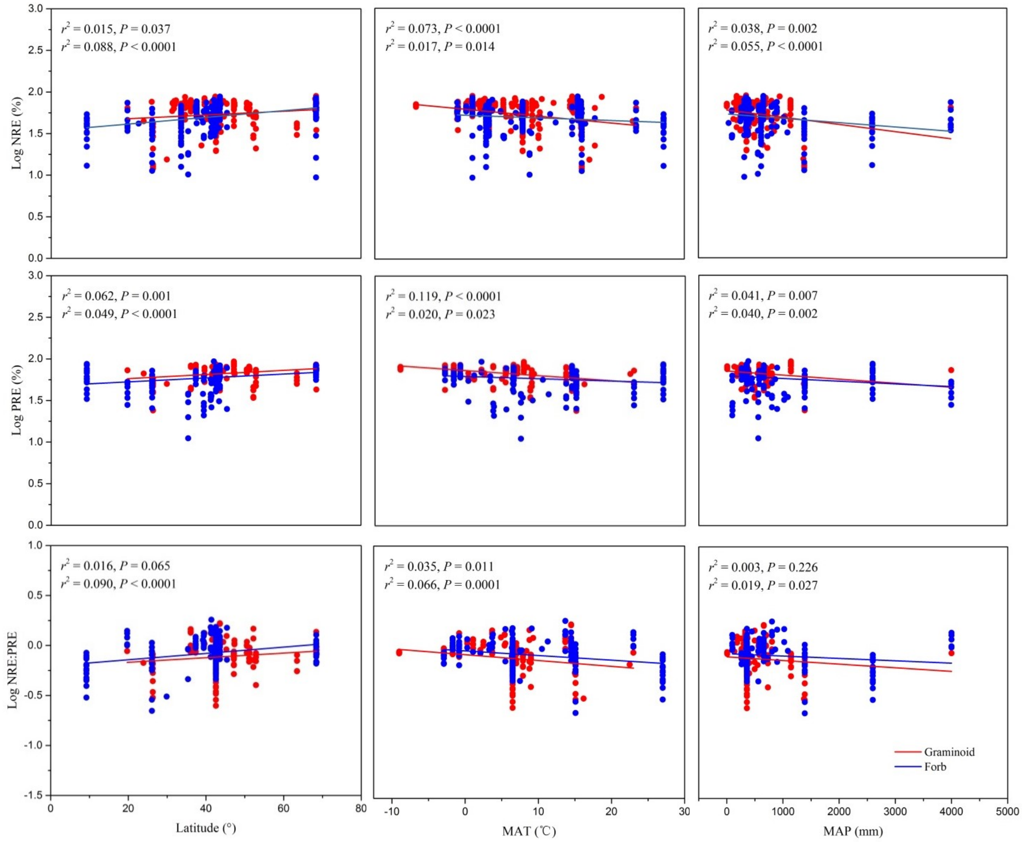
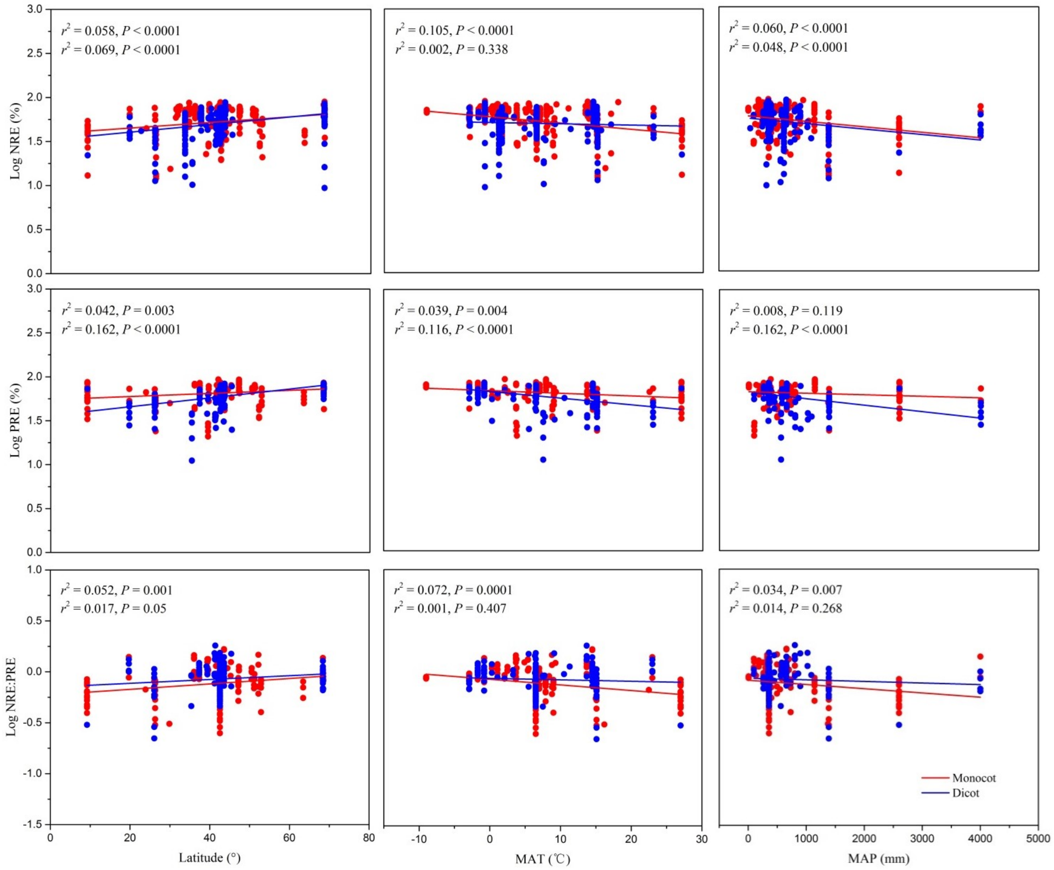

$r^2 = 0.015$, $P = 0.037$
$r^2 = 0.088$, $P < 0.0001$
$r^2 = 0.073$, $P < 0.0001$
$r^2 = 0.017$, $P = 0.014$
$r^2 = 0.038$, $P = 0.002$
$r^2 = 0.055$, $P < 0.0001$
$r^2 = 0.062$, $P = 0.001$
$r^2 = 0.049$, $P < 0.0001$
$r^2 = 0.119$, $P < 0.0001$
$r^2 = 0.020$, $P = 0.023$
$r^2 = 0.041$, $P = 0.007$
$r^2 = 0.040$, $P = 0.002$
$r^2 = 0.016$, $P = 0.065$
$r^2 = 0.090$, $P < 0.0001$
$r^2 = 0.035$, $P = 0.011$
$r^2 = 0.066$, $P = 0.0001$
$r^2 = 0.003$, $P = 0.226$
$r^2 = 0.019$, $P = 0.027$
Log NRE (%)
Log PRE (%)
Log NRE:PRE
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
0
20
40
60
80
Latitude (°)
-10
0
10
20
30
MAT (℃)
0
1000
2000
3000
4000
5000
MAP (mm)
Graminoid
Forb

Fig. 3


$r^2 = 0.058, P < 0.0001$
$r^2 = 0.069, P < 0.0001$
$r^2 = 0.105, P < 0.0001$
$r^2 = 0.002, P = 0.338$
$r^2 = 0.060, P < 0.0001$
$r^2 = 0.048, P < 0.0001$
$r^2 = 0.042, P = 0.003$
$r^2 = 0.162, P < 0.0001$
$r^2 = 0.039, P = 0.004$
$r^2 = 0.116, P < 0.0001$
$r^2 = 0.008, P = 0.119$
$r^2 = 0.162, P < 0.0001$
$r^2 = 0.052, P = 0.001$
$r^2 = 0.017, P = 0.05$
$r^2 = 0.072, P = 0.0001$
$r^2 = 0.001, P = 0.407$
$r^2 = 0.034, P = 0.007$
$r^2 = 0.014, P = 0.268$
Log NRE (%)
Log PRE (%)
Log NRE:PRE
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1.0
0.5
0.0
-0.5
-1.0
-1.5
0
20
40
60
80
-10
0
10
20
30
0
1000
2000
3000
4000
5000
Latitude (°)
MAT (℃)
MAP (mm)
Monocot
Dicot