Leaf nitrogen and phosphorus stoichiometry of plant communities in geochemically phosphorus-enriched soils in a subtropical mountainous region, SW China

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Abstract Leaf nitrogen (N) and phosphorus (P) stoichiometry might reflect the biogeochemical features of ecosystems, yet the potential range of stoichiometric flexibility under geochemically P-enriched soils (GPES) is still unclear. Leaf N and P of 126 plant species in 70 vegetation plots in GPES were investigated in central Yunnan, southwestern China, and leaf P fractions (i.e., inorganic vs. organic P) of the dominant species were examined. Our objectives were to improve the understanding of the role of soil N and P variability in controlling leaf N and P stoichiometry of plant communities in GPES. We found that plants in GPES had higher mean leaf P (4.07 mg/g) and lower N:P ratios (4.94) than average plant values that have been recorded in other parts of the world so far. Some fast-growing plants had extremely high leaf P (>10 mg/g).

Community leaf N and P contents increased as soil N availability increased, but soil N variability was unrelated to community leaf N:P. Instead, community leaf P and N:P ratios were primarily determined by soil P; as soil P availability increased, leaf P increased and leaf N:P significantly decreased. Greater accumulation of inorganic P relative to organic P in leaf was the direct driving factor for community leaf P and N:P ratio patterns in GPES. Although soil P availability was the main controlling factor of leaf N:P patterns, community composition could be manipulated to restore the balance of N and P stoichiometry based on the different responses across species and plant types.

Keywords Species-specific responses · Leaf inorganic phosphorus · Leaf organic phosphorus · Geochemically P-enriched soils (GEES) · Central Yunnan

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Introduction

Leaf nitrogen (L_N), phosphorus (L_P), and nitrogen:phosphorus ratios ($L_{N:P}$) (i.e., N:P stoichiometry) reflect general ecological characteristics of plants, plant-soil feedbacks, and ecosystem function (Chapin et al. 2011). Leaf N:P stoichiometry is a good indicator of biogeochemical features and is a fundamental component in the accurate prediction of ecological responses to global change (Qin et al. 2014; Sistla and Schimel 2012; Sterner and Elser 2002).

Several studies indicated that, moving from cool and temperate to tropical climates, terrestrial ecosystems generally increase in plant $L_{N:P}$ and decrease in L_P contents (Reich and Oleksyn 2004; Townsend et al. 2007). Lower L_P and higher $L_{N:P}$ were found in China compared with

global averages (Han et al. 2005). These observations are thought to be the result of phosphorus (P) limitations in terrestrial productivity at low latitudes, especially in China (Han et al. 2005; Reich and Oleksyn 2004; Vitousek et al. 2010). Many P-enriched soils exist around the world, which have been neglected by eco-stoichiometry research. Since the end of the 20th century, human activities have resulted in a rapid increase in P-enriched soil regions and the P limitation pattern has gradually changed in some regions (Elser 2012; Zapata and Roy 2004). In those regions, water safety is seriously threatened and the fitness and growth of plants are facing a new pressure from these altered conditions (Beavers et al. 2013; Bennett and Elser 2011; Wang et al. 2015). Understanding the potential range and mechanisms controlling plant leaf N and P stoichiometric variation in P-enriched regions is indispensable to help predict nutrient balance patterns in ecosystem processes using a stoichiometric framework and enhance vegetation management (Sistla and Schimel 2012; Sterner and Elser 2002).

Enormous sedimentary phosphate deposits exist in tropical and subtropical regions, in particular in the Northern Hemisphere, which has led to the development of geochemically P-enriched soils (GPES) regions (Zapata and Roy 2004). Central Yunnan in China is a typical representative GPES region. Previous studies of L_P in GPES found conflicting results, with some studies finding forbs with high L_P contents in GPES regions (Xiao et al. 2009; Yan et al. 2011). Other studies found that some plants resisted accumulating high P in leaves, because high internal P concentrations could cause symptoms of P toxicity (Hawkins et al. 2008; Silber et al. 2002). The situation for nitrogen (N) was complex, as although a large number studies found that the correlations between L_N , $L_{N:P}$, and soil N availability were weak (Kozovits et al. 2007; Mayor et al. 2014; Novotny et al. 2007), some studies reported positive effects of N addition on L_N , L_P , and $L_{N:P}$ in N-limited regions (Lü et al. 2012; Perring et al. 2008). Little is known about the effect of N addition in GPES regions. In short, our understanding of leaf N and P stoichiometry of plant communities in GPES is lacking, with such knowledge reflecting the potential range of stoichiometric flexibility related to extreme nutrient conditions.

To answer the above questions, this paper described a study of 70 sample plots in GPES in central Yunnan, China. L_N and L_P of 126 plant species, and soil N and P availability were investigated. Considering invasive plants leading to the degeneration and N_2 -fixing plants were dominant in early succession in GPES mountain, we focused on six plant types, e.g., invasive plants, forbs, N_2 -fixing plants, shrubs, trees, and grasses (Yan et al. 2011). Additionally, Species-specific responses, including leaf P

fractions (i.e., inorganic vs. organic P), were observed for 10 dominant species to further understand community responses.

Our objectives were to (1) assess the L_N , L_P , and $L_{N:P}$ stoichiometry of plant communities in GPES; and (2) understand the roles of soil N and P variability in controlling leaf N and P stoichiometry of plant communities in GPES. To our knowledge, this is the first study of leaf N and P stoichiometry in GPES regions. Our findings will improve the understanding of variations in N and P stoichiometry and their responses to global P change, and facilitate the incorporation of these data into future global biogeochemical models.

Materials and methods

Study area

Central Yunnan, China is one of the four largest sedimentary phosphate deposits in the world, along with Khouribga, Morocco, Florida, USA, and Kola, Russia (Zapata and Roy 2004). Most of the GPES and vegetation in this region are located in the mountainous area around the Dianchi and Fuxian Lakes (Li et al. 2015) (Fig. 1). In the study area, the annual mean temperature is 14.6 °C and the annual mean rainfall is 925.4 mm. Under the subtropical semi-humid monsoon, the rainy season lasts from May to October. The zonal vegetation of the study areas is subtropical semi-humid evergreen broad-leaved forest (Tang et al. 2010), and the secondary plant communities around GPES land are dominated by *Ageratina adenophora*, *Chenopodium ambrosioides*, *Erianthus rufipilus*, *Themeda hookeri*, *Coriaria nepalensis*, *Fragaria nilgerrensis*, *Ficus tikoua*, *Rumex hastatus*, *Cotoneaster microphyllus*, and *Pinus yunnanensis*.

The research region (24°1′–25°3′N, 102°23′–103°09′E) was constrained within a narrow elevation range (1980–2210 m) and the main soil types were Ferralsols and Cambisols. The range of soil total P and N was 1.47–87.38 and 0.06–2.66 mg/g, respectively. Soil P concentrations were generally high and variable, whereas other soil chemical properties were relatively stable, as shown in Table 1.

Sample collection

Field work was conducted during July and August in 2011. Sampling plots were located in plant communities around GPES. The species richness to area relationship was studied to determine the minimum plot area, which was 25 m² (Buys et al. 1994). The plots were located at least 1 km away from residential areas,

Fig. 1 The research area and the distribution of geochemically phosphorus-enriched regions

and the distance between plots was greater than 100 m. Plant community composition was described using a relevé plot method, recording species name, number and percent coverage of each species, and growth form of each species.

For leaf sampling, fresh mature leaves were collected for each species (percent coverage >1 %) from each plot. For each tree and large shrub species, 10 leaves were sampled from five random individual plants that were exposed to the most direct sunlight (Cornelissen et al.

2003; Richardson et al. 2008). For herbaceous and small shrub species, five whole plants were collected for each species from the most light-exposed locations. Leaf samples were preserved and transported on ice. Leaf samples were collected from a total of 126 plant species (coverage >1 %) in 40 families, and most species occurred in multiple plots (mean = 6 plots, median = 4 plots, range = 1–55 plots).

Soils were sampled from the upper 100 mm of the mineral horizon to measure soil fertility properties. A mix

Table 1 Arithmetic mean and coefficient of variation for each of the eight topsoil properties

Topsoil properties	Mean	CV (%)
Soil total N (mg/kg)	0.78×10^3	67.42
Soil available N (mg/kg)	87.4	79.41
Soil total P (mg/kg)	6.57×10^3	144.1
Soil available P (mg/kg)	381.54	152.99
Soil total K (mg/kg)	3.36×10^3	11.61
Soil available K (mg/kg)	70.67	43.26
Soil organic matter (%)	3.21	40.50
Soil pH	6.23	19.40

Soil total N, P, available N, and available P were measured across 70 plots in this paper, and the other indexes were measured by the earlier work (Yan et al. 2011)

of five soil subsamples collected from each plot was used as the plot samples.

Chemical analysis

Total N and P of all leaf samples were measured on ground, oven-dried (60 °C for 48 h) materials after acid digestion. N contents were measured using the Kjeldahl method (Ryan et al. 2007). For leaf P, the total P concentration was measured colorimetrically at 700 nm after reaction with molybdenum blue; inorganic P (P_i) was extracted by shaking 0.2 g of leaf tissue for 30 min in 10 mL of 0.25 M H_2SO_4 . Organic P (P_o) was calculated as the difference between total P and P_i (Mayor et al. 2014).

Soil available P was determined after extraction with 0.5 M bicarbonate and measured with a spectrophotometer. Soil available N was analyzed by the alkali-hydro diffusion method using 1 M NaOH. Results were expressed on an oven-dry (105 °C) soil basis (Ryan et al. 2007).

Statistical analysis

Normality tests were first conducted for the calculated values, and the results that did not show normal distributions were log transformed before further analyses. Cover-weighted mean L_N and L_P for each plot were calculated. Both the cover-weighted and species-specific data were directly comparable with assembled data from published results (latitude range from 23 to 25, reference data) (Han et al. 2005; Reich and Oleksyn 2004; Zhang et al. 2011). The differences in N and P stoichiometry among different plant types were compared using one-way analysis of variance.

Regression analysis was used to assess how the total plant community L_N , L_P , and $L_{N:P}$ stoichiometry (mass

ratio) responded to soil N and P availability. The total variation explained was the r^2 for the model using both variables. All values were reported as a percentage of the total variation explained (Richardson et al. 2008). Species-specific responses were assessed for those 10 species that were present in at least 15 plots. Regression analysis was used for the interpretation of leaf total P variation of each dominant species affected by P_o and P_i ; the variation explained was r^2 and reported as a percentage.

Results

Patterns of leaf N, P and N:P ratio across all species and plant types

Plants (species-specific data) in GPES had high L_P contents (mean 4.07 mg/g) and low $L_{N:P}$ (mean 4.94). No difference was found between species-specific and cover-weighted data (Fig. 2). L_P contents had the highest variation (coefficient of variation = 67.25 %), ranging from 1.33 to 16.14 mg/g. Positive correlations were found between L_N and L_P contents ($p = 0.001$). Most plants, especially dominant plants, had a medium L_P content (Fig. 3; Table 3). Invasive plants and forbs had the highest L_N and L_P contents across plant types, and among them, the L_P contents of *Polygonum hydropiper* (16.23 mg/g), *Epilobium fangii* (13.44 mg/g), *Erigeron acer* (12.23 mg/g), and four other species were larger than 10 mg/g. Shrubs, trees, and grasses had low L_N and L_P contents (Fig. 3). The variation in $L_{N:P}$ across plant types was smaller than that of L_N and L_P , and $L_{N:P}$ was primarily controlled by the variation in L_P rather than L_N (Fig. 3).

Leaf N, P, and N:P ratio responses to soil N and P variability

With increasing soil N availability, L_N of the most species increased except for some N_2 -fixing plants (e.g., *C. nepalensis* and *F. nilgerrensis*) and the L_P of *C. ambrosioides* and five other species increased (Table 3). Soil N availability was important for driving both community L_N (36.0 %) and L_P (13.9 %). The response of L_N to soil N availability was greater than that of L_P (Table 2). Low correlations ($p = 0.102$) were found between soil N variability and community $L_{N:P}$.

Soil P was the key factor influencing community L_P (29.8 %), and $L_{N:P}$ ratios (43.0 %), but no significant correlations were found between soil P and community L_N (0.06 %; Table 2). For the dominant species, increasing soil P availability led to increased L_P and decreased $L_{N:P}$ for most species (Table 3). Within-species

Fig. 2 Comparisons of leaf N, P, and N:P in GPES and reference data. See “Statistical analysis” section for details of the reference data

Fig. 3 Histograms showing the distribution of leaf N (a), leaf P (b), and leaf N:P ratios (c); solid curves in (a–c) indicate fitted log-normal curves. Leaf N, P, and ratios among different plant types, *I* invasive

plants, *F* forbs, *N* N_2 -fixing plants, *S* shrubs, *T* trees, *G* grasses; a–d significantly different $p < 0.05$

variations were greater in L_P than in L_N (Table 3). L_P varied 3.5-fold on average in the dominant species examined, and L_N varied 1.7-fold. Leaf P_i increased several times from 8.94 fold to 30.88-fold for different species. On average, leaf P_i accounted for approximately

50 % of leaf total P. P_i relative to P_o was the primary factor driving community L_P and $L_{N:P}$ ratios in GPES, as more than 70 % of the variation in leaf total P was explained by the increase in P_i for all the dominant plants (Table 3).

Table 2 The proportion of explained variation in leaf nutrient concentrations attributable to soil available N and P in GPES

	Community leaf P (%)	Community leaf N (%)	Community leaf N:P (%)
Variation explained by soil P alone	29.8	0.06	43.0
Variation explained by soil N alone	13.9	36.0	6.7
Variation explained by soil N and P	48.3	36.1	46.7

The proportion of explained variation was calculated from model coefficients of determination (r^2) using soil available N and P or both. See “Statistical analysis” section for a description of how the proportion of variation was calculated. The number of replicates is 70

Discussion

The characteristics of leaf N, P, and N:P ratios in the GPES

Our results showed that plants in the GPES region had high L_P content and low $L_{N:P}$. L_P content (4.07 mg/g) was 1.88–3.87 times greater than the reference data (Fig. 2), the average in China, and global averages (Table 4). The mean $L_{N:P}$ was 4.96 at our study site, compared with data from all previous studies that yielded a mean $L_{N:P}$ higher than 10. In particular, $L_{N:P}$ in the GPES region was 23.82 % of the reference data value (19.69). Plant L_N content (17.25 mg/g) in this study was less than the average in China, but greater than the other reference data (Table 4).

According to the temperature–plant physiological and soil age hypotheses (Reich and Oleksyn 2004; Lambers et al. 2008; Han et al. 2011), L_N and L_P decrease and the $L_{N:P}$ increases towards the equator which is why plant L_N at our study site and reference data were less than China’s and global averages. For the same reason, the L_P content was smaller and $L_{N:P}$ was larger in the reference data than in China’s and global averages, respectively. The above rationale could not explain the extreme high L_P content and low $L_{N:P}$ found in our study site in Central Yunnan, China, and the high soil P situation could be a key factor controlling those patterns.

The differences in L_N and L_P occurred across plant types, as more ruderal species and fewer stress-tolerant species in the community (with different metabolism) had high L_N and L_P contents (Güsewell 2004; Ratnam et al. 2008). For instance, trees (i.e., *P. yunnanensis*) and grasses (i.e., *E. rufipilus* and *T. hookeri*) had lower L_N and L_P contents; invasive plants and forbs had the highest L_N and L_P contents across plant types (Fig. 3; Table 3). Some invasive plants and forbs with extremely high L_P content, e.g., *P. hydropiper*, *E. fangii*, and *E. acer*, were previously found by Xiao et al. (2009) in another GPES region in southwest China.

$L_{N:P}$ was significantly higher in trees and shrubs than in forbs at our study site, consistent with higher $L_{N:P}$ in long-lived, slow-growing species than in short-lived, fast-

growing species, as previously identified (Güsewell 2004). Although previous studies found more grasses and fewer forbs in vegetation with a high $L_{N:P}$ ratio (Güsewell 2004; Han et al. 2005; Ratnam et al. 2008), no significant difference was found between the $L_{N:P}$ ratio in these plant types in GPES (Fig. 3), which could be explained if the $L_{N:P}$ ratio in GPES was primarily constrained by soil P availability compared to phylogeny (Ågren and Weih 2012). $L_{N:P}$ ratios across different plant types varied less than N or P alone because of the highly positive correlations between L_N and L_P (Fig. 3), which reflected a fundamental feature of the plant kingdom with respect to leaf N and P stoichiometry in GPES (Han et al. 2005; McGroddy et al. 2004).

By comparing the reference data and previous results from Central Yunnan (Hou et al. 2010) with results obtained in this study, it was determined that geochemical features of GPES were the most important drivers of leaf N and P stoichiometry at this site, rather than other factors such as longitude and latitude, climate, and plant type.

The role of soil P in controlling N and P stoichiometry of plant communities

The variation in soil P availability could affect P use and the nutrient allometric accumulation of plants, and thus affect the leaf N and P stoichiometry patterns and ecological strategy (Mayor et al. 2014). Our results showed that soil in the GPES region had extremely high total P (6.57×10^3 mg/kg) and available P content (381.54 mg/kg), which were significantly higher than the results obtained by Hou et al. (2010) from non-GPES regions in Central Yunnan. The soil P level in GPES in Central Yunnan was significantly higher than the P-enriched threshold identified by Delorme et al. (2000), where GPES had higher soil P content and variability, and was very different from other P-enriched regions identified in earlier studies, e.g., pasture and farmland (Delorme et al. 2000; Read 2012; Sharma and Sahi 2005).

P forms in leaves were relatively variable, as plants could store not only P_o but also P_i in leaves. The P_o – P_i pattern reflected the soil nutrient availability and the

Table 3 Regression results for within-species shifts in leaf nutrient concentrations in GPES

Species	<i>A. adenophora</i>	<i>C. ambrosioides</i>	<i>C. microphyllus</i>	<i>C. nepalensis</i>	<i>E. rufipilus</i>	<i>F. nilgerrensis</i>	<i>F. tikoua</i>	<i>P. yunnanensis</i>	<i>R. hastatus</i>	<i>T. hookeri</i>
Growth form	Invasive forb	Invasive forb	Shrub	N ₂ -fixing shrub	Grass	N ₂ -fixing herb	Woody vines	Conifer	Shrub	Grass
Number	42	16	20	31	21	21	15	19	17	18
Leaf N (mg/g)	23.43	25.5	14.26	22.4	8.67	14.61	13.46	11.63	16.94	10.19
Leaf P (mg/g)	3.87	6.08	2.67	3.24	2.83	3.85	3.72	2.79	4.71	4.14
Inorganic P (mg/g)	1.33 [80.4 %]	3.33 [90.4 %]	1.20 [90.4 %]	1.41 [85.8 %]	1.42 [88.4 %]	2.11 [76.9 %]	2.19 [79.6 %]	1.64 [78.2 %]	2.64 [75.4 %]	2.52 [70.4 %]
Organic P (mg/g)	2.54 [44.4 %]	2.75 [26.8 %]	1.47 [34.7 %]	1.83 [30.5 %]	1.41 [24.8 %]	1.74 [30.8 %]	1.53 [35.8 %]	1.15 [9.7 %]	2.07 [29.8 %]	1.62 [37.8 %]
Leaf N: P	6.05	4.19	5.34	6.91	3.06	3.79	3.62	4.17	3.60	2.46
SN leaf N	(3.02)*	(5.46)*	(10.45)**	(0.92)	(25.78)***	(1.24)	(10.01)**	(5.26)*	(12.42)**	(6.47)*
SP leaf N	(0.73)	(0.10)	(0.75)	(0.45)	(0.91)	(0.58)	(0.02)	(0.79)	(0.11)	(0.06)
SN-leaf P	(1.32)	(5.29)*	(6.44)**	(3.16)	(0.07)	(0.12)	(7.30)*	(5.05)*	(6.08)**	(10.32)**
SP-leaf P	(5.35)*	(17.18)***	(46.89)***	(10.73)**	(10.99)**	(39.57)***	(12.12)**	(15.99)**	(5.08)*	(9.57)**
SN-leaf N:P	(0.07)	(0.48)	(1.21)	(2.46)	(5.66)*	(0.02)	(0.03)	(0.18)	(0.03)	(0.92)
SP-leaf N:P	(4.50)*	(19.27)***	(37.62)***	(1.62)	(3.24)	(23.71)***	(10.77)**	(7.62)*	(11.27)**	(5.37)*

We present the mean value of leaf N, leaf P (total P, inorganic and organic P) and leaf N:P. Regression analyses' results for leaf total P variation with leaf inorganic or organic P are also provided in square brackets; r^2 indicates the variation explained and the percentages indicate contribution of these variables. SN or SP-leaf N, P or N: P: the regression mode among soil nutrient availability and leaf nutrient concentrations. The F statistic from each regression model is given in parentheses

SV soil N availability, SP soil P availability, *Number* number of observations from 70 plots

* $p \leq 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 4 Comparisons of leaf nitrogen (N), phosphorus (P) and N:P among studies

Study region	Latitude	Leaf N		Leaf P		Leaf N:P ratios		Date source
		A.M.	CV	A.M.	CV	A.M.	CV	
Central Yunnan of China (Phosphorus-enriched soils regions)	24	17.25	42.31	4.07	67.25	4.96	48.13	This study (species-specific data)
Reference data (Tropical and subtropical regions)	23–25	14.24	37.85	0.97	121.65	19.69	56.83	Han et al. (2005); Reich and Oleksyn (2004); Zhang et al. (2011)
China 1	18–49	20.20	41.63	1.46	67.81	16.30	57.18	Han et al. (2005)
China 2	18–52	19.96	41.38	1.41	79.43	17.00	53.47	Zhang et al. (2011)
Global 1	–	20.60	59.37	1.99	74.87	12.70	53.70	Elser et al. (2000)
Global 2	1–68	20.10	43.33	1.77	63.28	13.80	68.62	Reich and Oleksyn (2004)

AM arithmetic mean (mg/g), CV coefficient of variation (%)

nutrient use strategy of plants, thus further affecting the biogeochemical cycles of plant communities (Ågren and Weih, 2012; Mayor et al. 2014).

Our results showed that soil P availability was the main driver of L_P (29.8 %, $p = 0.000$) and $L_{N:P}$ (43.0 %, $p = 0.000$). Additionally, the variations in leaf total P were explained primarily by the increase in P_i relative to P_o (Table 3). We found that both the content and proportion of P_i in leaves were higher in the GPES region (content: from 1.22 to 3.33 mg/g; proportion: approximately 50 %) than previous results (content: less than 0.5 mg/g; proportion: less than 30 %) (Close and Beadle 2004; Mayor et al. 2014). Under high soil P conditions, plants could store higher levels of P_i in leaf cytoplasm and vacuoles as storage materials from luxury P accumulation (Close and Beadle 2004; Mayor et al. 2014).

Various studies found that the increase in soil P availability could lead to an increase in community L_P , and a decrease in community $L_{N:P}$ (Reich and Oleksyn 2004; Richardson et al. 2008). Some other studies indicated that plants could reject accumulating high P in leaves to prevent P toxicity in P-enriched situations and alter the pattern described above (Hawkins et al. 2008; Silber et al. 2002). Our results for plant communities in GPES support the above pattern, that with increased soil P, L_P increased and $L_{N:P}$ decreased, which could be explained as follows: (1) plants living in this area are adapted to high soil P through evolution and long-term selective processes; (2) most plants, especially dominant plants, had a medium L_P content, at which P level the symptoms of P toxicity might not be serious.

The relationship between soil N and N and P stoichiometry of plant communities

N in soil was the other key factor besides P affecting the leaf N and P stoichiometry patterns and ecological strategy.

On a global and continental scale, increasing soil N availability could lead to an increase in community L_N . On a regional and local scale, however, this situation has become more complex. A large number of studies found that the correlations between L_N , $L_{N:P}$, and soil N availability could be weakened by physiological limitations in N storage (as structural compounds) in leaves (Kozovits et al. 2007; Mayor et al. 2014; Novotny et al. 2007), but some studies reported positive effects of N addition on L_N , L_P , and $L_{N:P}$ in N-limited regions (Lü et al. 2012; Perring et al. 2008).

Our results showed that soil N in the GPES region was not high (total N: 0.78×10^3 mg/kg; available N: 87.4 mg/kg), similar to results obtained by Hou et al. (2010) from non-GPES in Central Yunnan. It is hard to identify nutrient limitation from the mean soil N contents (Han et al. 2011); the mean $L_{N:P}$ found in GPES was just 4.96; therefore, according to the eco-stoichiometry theory, N was limited at our study site (Güsewell 2004).

In the GPES region, we found that community L_N increased (36.0 %) following an increase in soil N availability. Specifically, we found that any increase in soil N availability would promote the accumulation of L_N directly by individual plants (Table 3). Additionally, we found that N could increase the efficiency of P use and concentration in the plant community, and community L_P increased following an increase in soil N availability. A synergistic effect was found between soil N and P availability in driving the community L_P pattern, as variation explained by both soil N and P (48.3 %) was significantly higher than that by soil N (13.9 %) or soil P (29.8 %) alone (Table 2). Especially under nutrient limitation, both N and P can stimulate growth or other processes because N supply often influences how efficiently P is acquired and used, and vice versa (Güsewell et al. 2003; Güsewell 2004), and the above results further support that N was limited in GPES.

The increase in soil N availability led to increased community L_N ($p = 0.001$) and L_P contents ($p = 0.017$) in GPES. However, low correlations were found between soil N availability and community $L_{N:P}$ because of the stability of L_N with physiological limitation of N storage (as structural compounds) in leaves and the great variability of L_P in response to soil P availability (Fig. 3; Table 3). This result was similar to results obtained from empirical studies of N and P stoichiometry (Güsewell 2004; Richardson et al. 2008). Considering the large variation in soil N availability, perhaps soil N could also alter community composition to indirectly drive community N and P stoichiometry, but further study is necessary to confirm this hypothesis.

N limitation to plant growth and other ecosystem processes, e.g., biogeochemical cycles, is widespread in GPES. In contrast, N_2 -fixing plants (e.g. *C. nepalensis*) had high L_N contents, and L_N contents were less affected by soil N availability, which could stimulate N cycling (Chaer et al. 2011; Walker et al. 2003). Some N_2 -fixing plants could accumulate P (Sharma et al. 2007), but could also enhance soil quality (soil C and N, infiltration, and soil particles) (Chaer et al. 2011), and thus coordinate the balance of N and P stoichiometry. These plants might be potential candidates for promoting succession and enhancing ecological function of GPES ecosystems, but further long-term field experiments are required.

Conclusion

Plants in GPES had much higher L_P and lower $L_{N:P}$ ratios than tropical and subtropical reference data, China's averages, and global averages. Because of high soil P availability in GPES, a large amount of P_i accumulation in leaves was the key reason for those patterns. Community L_N and L_P contents increased following the increase in soil N availability. Community leaf P and N:P was primarily determined by soil P availability because of the stability of L_N and a large amount of P could accumulate in leaves as inorganic forms responding to elevated soil P availability. Although community N and P stoichiometry was mainly driven by the special geochemical features in GPES, plant type and nutrient strategy were contributing factors. Regulating community composition is suggested as a promising approach to restore the balance of N and P stoichiometry and to promote biogeochemical cycles in GPES, especially using N_2 -fixing plants.

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