Plant nutrients do not covary with soil nutrients under changing climatic conditions

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Abstract

Nitrogen (N) and phosphorus (P) play vital roles in plant growth and development. Yet how climate regimes and soil fertility influence plant N and P stoichiometry is not well understood, especially in the belowground plant parts. Here we investigated plant aboveground and belowground N and P concentrations ([N] and [P]) and their stoichiometry in three dominant genera along a 2200 km long climatic gradient in northern China. Results showed that temperature explained more variation of [N] and [P] in C4 plants, whereas precipitation exerted a stronger influence on [N] and [P] in C3 plants. Both plant aboveground and belowground [N] and [P] increased with decreasing precipitation, and increasing temperatures yet were negatively correlated with soil [N] and [P]. Plant N:P ratios were unrelated with all climate and soil variables. Plant aboveground and belowground [N] followed an allometric scaling relationship, but the allocation of [P] was isometric. These results imply that internal processes stabilize plant N:P ratios and hence tissue N:P ratios may not be an effective parameter for predicting plant nutrient limitation. Our results also imply that past positive relationships between plant and nutrient stocks may be challenged under changing climatic conditions. While any modeling would need to be able to replicate currently observed relationships, it is conceivable that some relationships, such as those between temperature or rainfall and carbon:nutrient ratios, should be different under changing climatic conditions.

1. Introduction

Nitrogen (N) and phosphorus (P) are the two most important essential nutrients that limit plant growth, maintenance, and reproduction in terrestrial ecosystems [Reich and Oleksyn, 2004; Elser et al., 2007]. Plant N is tightly linked to photosynthesis, litter decomposition, and plant productivity [LeBauer and Treseder, 2008]. Plant P is a vital component of genetic processing, energy storage, and membrane structure [Elser et al., 2007; Reich et al., 2009; Elser et al., 2010]. Diverse evidence suggests that plant N and P stoichiometry can be a focal indicator of ecosystem function and nutrient limitation [Güsewell, 2004; Elser et al., 2007]. Therefore, understanding variation of plant N and P concentrations (hereafter [N] and [P]) and their stoichiometry has been a key issue for both plant physiologists and ecologists [Güsewell, 2004; Reich and Oleksyn, 2004].

Geographical gradients provide an exceptional opportunity to study factors affecting variations of nutrients in plant tissues, which is important for understanding the underlying patterns of nutrient fluxes and the biogeochemical mechanisms of the response of vegetation to climate changes. Factors along a geographical gradient that may potentially affect plant [N] and [P] and their stoichiometry include temperature, precipitation, soil fertility, and human disturbance such as grazing and atmospheric N deposition [Hungate et al., 2003; Dai, 2013; Delgado-Baquerizo et al., 2013b; Liu et al., 2013; Wardle, 2013]. All plant metabolic processes are temperature dependent, and plants generally increase [N] and [P] in their cells to compensate for the reduced rate of metabolism at low temperature [Reich and Oleksyn, 2004; Sanaullah et al., 2014]. Precipitation can directly affect plant nutritional status by influencing plant phenology [Peñuelas et al., 2009] and photosynthesis [Patrick et al., 2007] and indirectly by affecting soil N and P availability through impacts on decomposition and mineralization [Schuur and Matson, 2001]. Additionally, plant [N] and [P] and their stoichiometry might themselves be dependent on soil fertility [Reich and Oleksyn, 2004; Han et al., 2005; Townsend et al., 2007; Richardson et al., 2008].

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Recent attempts have been made to study spatial patterns of plant [N] and [P] along large-scale gradients of temperature [Reich and Oleksyn, 2004], precipitation [Townsend et al., 2007; Yuan et al., 2011], and soil fertility [Ordoñez et al., 2009; He et al., 2010; Zhang et al., 2012]. However, most of these gradient studies used nutrient data from published literature, in which temperature and precipitation were often measured or reported separately, hence overlooking their interactions. In addition, most studies focused on aboveground parts, but plant belowground biomass serves as an important reservoir for nutrients in terrestrial ecosystems and should be studied more [Jackson et al., 1996; Gordon and Jackson, 2000]. Study at the genus or species level is necessary because different genera or species may respond idiosyncratically to environmental factors [Geng et al., 2012]. However, previous studies have mostly focused on the family or functional group level [Han et al., 2005]. Therefore, more information on the N:P stoichiometry, particularly for plant belowground parts at the genus or species level, is needed for better understanding potential responses and feedback of terrestrial nutrient cycling to climate change [Craine and Lee, 2003; Craine et al., 2005; Liu et al., 2010; Yuan et al., 2011].

To better understand how climate regimes and soil fertility influence plant N and P stoichiometry, especially in the belowground plant parts, we investigated plant aboveground and belowground [N] and [P] and their stoichiometry in three dominant genera along a 2200 km long climatic gradient in northern China, a suitable study region because the impact of climatic factors and soil fertility on plant nutrients is particularly strong in dry and cold grasslands as plant growth and microbial activity are mainly determined by precipitation, temperature, and N availability in these areas [Austin et al., 2004; Lü et al., 2012]. The three grass genera (Stipa, Cleistogenes, and Agropyron) are dominant and widely distributed across an ~2200 km transect in longitudinal space in dry and cold grasslands in northern China. The unique features of this transect include a continuum of mesic to xeric grassland types, relatively gentle geographical relief, distinct patterns of precipitation and temperature (i.e., descending precipitation and ascending temperature from the east to the west), complete meteorological records, and relatively light human disturbance. We aimed to address three main questions: (1) How do [N] and [P] and N:P stoichiometry in aboveground and belowground biomass of the three dominant coexisting plants change along the transect? (2) How are climatic factors and soil fertility associated with these patterns? and (3) Are there differences in tissue N and P stoichiometry between aboveground and belowground plant parts?

2. Material and Methods

2.1. Study Area and Sampling Sites

In early August 2012, we established an east-west transect across the arid and semiarid grasslands in northern China (see Figure 1). The transect is approximately 2200 km long and covers approximately 9° latitude and 15° longitude (40.7–50.1°N and 105.6–120.4°E). The topography of the study area consists of gently rolling hills and tablelands, with elevations ranging from 700 m in the east to 1500 m above sea level in the west. This region has a dry, continental climate with marked annual variation in both temperature and precipitation. Mean annual temperature (MAT) varies from –2°C (east) to 7°C (west), and mean annual precipitation (MAP) ranges from 436 mm (east) to 99 mm (west). Across the broad geographical regions and environmental gradients along the east-west transect, there are three natural vegetation types (i.e., meadow steppe, typical steppe, and desert steppe from east to west). Soil types are predominantly arid, sandy, brown loessials that are rich in calcium and classified in the Kastanozem group according to the Food and Agriculture Organization soil taxonomy system [Gerasimova, 2010]. The sampling sites were selected 500–1000 m away from major roads and >50 km from human settlements, subjected to minimal animal grazing and other anthropogenic disturbances. A total of 37 sampling sites were investigated along the transect. Sampling locations were GPS referenced with latitude, longitude, and elevation (eTreX Venture, Garmin, USA). More details are referred to in Luo et al. [2013] and Wang et al. [2014].

2.2. Plant Materials

Stipa, Cleistogenes, and Agropyron are three widely distributed and dominant genera in the dry and cold grasslands in northern China. Both Stipa spp. and Agropyron spp. are perennial C3 bunchgrasses, while Cleistogenes spp. are perennial C4 bunchgrasses. In our study areas, Stipa spp. mainly include S. krylovii, S. breviflora, S. grandis, and S. baikalensis; Cleistogenes spp. include C. squarrosa, C. songorica, and C. caespitosa; and Agropyron spp. include A. cristatum, A. mongolicum, and A. desertorum. We conducted our study at the genus level since none of those species occurs along the entire transect.
2.3. Sampling

At each site, two 50 m × 50 m main plots were selected, and five 1 m × 1 m sampling subplots were placed within each main plot at the four corners and the center (Figure 1). The maximum plant height (MPH) of the three dominant genera in each subplot was measured with a ruler. Five to ten mature and healthy individuals of the dominant plant species belonging to each of the three target genera (Stipa, Cleistogenes, and Agropyron) in each subplot were selected and excavated [Luo et al., 2013]. Aboveground and belowground tissues of the target plants were carefully separated and then stored in separate paper bags separately. Plant materials were dried at 105°C for 30 min in a portable drying oven to minimize respiration and decomposition and were later completely oven dried at 80°C to constant weight in the laboratory. More details are referred to in Luo et al. [2013] and Wang et al. [2014].

After removing the litter layer, one composite soil core (0–10 cm depth) was obtained from five randomly selected locations in each of the 10 subplots, using a soil gauge (2.5 cm diameter). Subsamples of each soil sample were stored at 4°C immediately after collection for initial gravimetric moisture content and soil available N (NH₄⁺-N plus NO₃⁻-N) measurements. Gravimetric moisture content was measured by drying at 105°C for 48 h. Fresh soil samples were extracted with 50 mL of 2 M KCl, and the filtered soil extract was used to determine soil available [N] with a continuous flow spectrophotometer (FIAstar 5000; Foss Tecator, Denmark).

Figure 1. Sampling sites and plots. A 2200 km long transect in Inner Mongolia grasslands of northern China was sampled. A total of 37 sampling sites were selected along this gradient. Two 50 m × 50 m plots were selected at each site, and five 1 m × 1 m sampling subplots were placed within each plot.
Dried plant and soil materials were ground to pass through a 1 mm sieve (NM200, Retsch, Haan, Germany). Soil available [P] were determined by extracting the soil with 0.5 M NaHCO₃ (pH = 8.5) and analyzed using the molybdenum blue-ascorbic acid method [Olsen, 1954]. Soil total [P] and plant [P] were measured by inductively coupled plasma emission spectroscopy (Perkin Elmer, OPTIMA 3000 DV) after H₂SO₄-H₂O₂ digestion [Bowman, 1988].

2.4. Climate and Soil Fertility

Four climate variables were used to analyze the climatic controls on spatial patterns of plant aboveground and belowground Na and P, i.e., MAT (°C), MAP (mm), annual potential evapotranspiration (PET, mm), and an aridity index (AI). MAT, MAP, and PET were extracted from the global Worldclim data set with a resolution of 0.0083° × 0.0083° (http://www.worldclim.org). AI was defined as 1 MAP/PET [Delgado-Baquerizo et al., 2013a].

A variety of indices can be used as surrogates of soil fertility. We selected four of the most commonly used soil nutrient variables to explore the soil fertility controls on spatial patterns of plant aboveground and belowground N and P: soil total and available N and P.

2.5. Data Analysis

Spatial autocorrelation of our sampling sites was checked using semivariogram analysis, and the results indicated that our sample points had no significant spatial autocorrelation [Luo et al., 2013]. Before numerical and statistical analyses, all variables in each genus were averaged at the subplot level. Plant chemistry data were log₁₀ transformed to obtain a normal distribution. Plant [N] and [P] in aboveground and belowground biomass and the corresponding environmental variables are attached as supporting information (Table S1 in the supporting information).

Ordinary least squares (OLS) regression was used to analyze the responses of plant [N] and [P] and N:P ratio to climate factors (MAT, MAP, and AI) as well as to fertility variables (soil total and available [N] and [P]). To further analyze patterns of plant nutrients, OLS regression was also used to examine the relationships between plant nutrient concentrations and MPH.

The significant correlation between MAP and MAT (P < 0.001; Table S2) could potentially obscure their true roles, so we conducted path analyses to test the independent contributions of temperature and precipitation to plant nutrients. Likewise, path analysis was conducted to compare the relative contributions of all environmental variables to plant nutrients.

We used reduced major axis regression developed by Falster et al. [2003] to describe joint variation between plant belowground and aboveground [N] and [P]. Two-tailed t tests were conducted to determine whether or not...
not the slopes were significantly different from 1.0. A nonsignificant difference from 1.0 indicates an allometric relationship, while a significant difference indicates an isometric relationship [Niklas, 1994].

All statistical analyses were conducted using the statistical package of SPSS 13.0 (SPSS Inc., Chicago, IL, USA, 2004) and the APE packages in R 2.21 [R Development Core Team, 2005].

3. Results

3.1. Plant Nutrients in Relation to Abiotic and Biotic Factors

Path analyses showed that MAT had stronger direct effects than those of MAP on both aboveground and belowground nutrient concentrations in *Cleistogenes* tissues, whereas MAP was dominant for both tissues in *Stipa* and *Agropyron* (Table 1 and Table S3).

Linear regressions showed that [N] and [P] in aboveground and belowground biomass significantly increased with decreasing precipitation (all \( P < 0.05 \); Figure 2) and increasing temperature (all \( P < 0.05 \); Figure 3) and AI (all \( P < 0.05 \); Figure S1 in the supporting information). Plant N:P ratios did not show any clear relationships with both MAT and MAP (all \( P > 0.05 \); Table S4). Plant [N] and [P] in both aboveground and belowground tissues were significantly negatively correlated with MPH (all \( P < 0.05 \); Figure 4). Plant aboveground and belowground [N] and [P] were negatively correlated with all soil variables we measured, including soil total and available [N] and [P] (all \( P < 0.05 \); Table S5) in 15 out of 48 correlations. However, N:P ratios in all three genera were not correlated with any of the soil parameters measured (all \( P > 0.05 \); Table S4).

3.2. Allometric Scaling of Aboveground Versus Belowground Nutrients

Plant [N] and [P] in belowground biomass were significantly positively correlated with those in aboveground tissues for each genus (all \( P < 0.001 \); Figure 5). The slopes of the belowground-aboveground N relationships for each genus were significantly greater than 1.0 (all \( P < 0.05 \); Figure 5), indicating allometric scaling in N allocation. In contrast, the slope of belowground versus aboveground P did not significantly differ from 1.0 for any of the three genera (all \( P > 0.05 \); Figure 5), indicating isometric scaling for P allocation in plants.
4. Discussion

4.1. Climatic Controls on Plant Nutrients

Our results showed that the relative contributions of temperature and precipitation to variation in plant nutrient concentrations were genus dependent (Table 1). Nutrient concentrations were more strongly influenced by precipitation for most tissues in *Stipa* and *Agropyron* but were more associated with temperature for both tissues in *Cleistogenes*. This may be an underlying mechanism contributing to the differential response of biomass allocation to climate change between the C3 plants (*Stipa* and *Agropyron*) and the C4 plant (*Cleistogenes*) [Luo et al., 2013], reflecting the differences in fundamental biochemical pathways and processes between C3 and C4 plants [Taylor et al., 2010; Still et al., 2014].

Although linear regression showed negative relationships between plant [N] and [P] and precipitation for the three dominant genera across the transect (Figure 2), path analyses showed that approximately 50% of the total genus-by-tissue combinations had larger path coefficients for MAP than MAT (Table 1). This was further evidenced by positive relationships between plant nutrient concentrations and AI (Figure S1). Such results clearly indicated that plants maintain higher tissue [N] and [P] in more water-stressed environments. Our findings are consistent with previous reports of higher plant [N] in arid versus semiarid ecosystems in northern China [e.g., Liu et al., 2010]. Similarly, Wright et al. [2001] found that plants growing in dry environments had higher aboveground nutrient concentrations compared to those in humid environments. Generally, low-precipitation and dry environments can limit plant photosynthesis, mainly by stomatal closure and reduced carbon dioxide assimilation [Chaves et al., 2003]. In order to maintain photosynthetic rates in these dry areas, cellular N is increasingly allocated to enzymatic proteins [Reich and Oleksyn, 2004; Hikosaka and Shigeno, 2009; Reich et al., 2009]. [N] and [P] are positively correlated with leaf area-based photosynthetic rates in arid and semiarid grassland plants [Wright and Westoby, 2002; Liu et al., 2010; Gong et al., 2011]. Hence, we infer that increased nutrient concentrations can help plants to opportunistically maximize photosynthesis in the harsh and varying dryland environments [Gong et al., 2011; Ye et al., 2013; Prentice et al., 2014]. In addition, increased plant nutrient concentrations with increasing aridity perhaps reflect plant accumulation of nutrient-rich soluble compounds.

Figure 3. Effects of mean annual temperature (MAT) on plant aboveground and belowground [N] and [P]. Data for the three graminoid genera sampled are distinguished by color and symbol. Regression $R^2$ values are given in the figure. All the regression results are referred to Table S6.
such as proline to overcome damage caused by osmotic stress [Malinowski and Belesky, 2000; Wright and Westoby, 2002; Chaves et al., 2003; Xoconostle-Cazares et al., 2010; Sanaullah et al., 2014]. Such accumulation of nutrient-rich soluble compounds in dryland plants has been interpreted as a functional adaptation to water stress, providing these plants with higher plasticity in the face risks of water deficit.

Linear regression showed that plant [N] and [P] significantly increased with increasing temperature for the three dominant genera (Figure 2), but path analyses showed that approximately only one thirds of the total genus-by-tissue combinations were mainly controlled by temperature (Table 1). The positive relationships between plant [N] and [P] and temperature indicated that plants in warmer environments tended to accumulate more N and P than those growing in cold environments along the transect. These results are contrary to findings of Chapin and Oechel [1983], who reported that alpine and arctic herbaceous plant species had higher [N] and [P] in colder habitats as well as to previous studies arguments that low temperature can reduce rates of biochemical reactions catalyzed by N-rich enzymes and P-rich RNA contents in plant tissues; hence, plants usually allocate more nutrients to these molecules to offset such reduced rates under lower temperature environments [Reich and Oleksyn, 2004]. However, these physiological arguments may not be manifested due to temperature-induced changes in nutrient availability at the ecosystems level. In the cold ecosystems in our study, warmer temperatures may have resulted in increases in microbial activity, decomposition and mineralization rates, and soil N and P availability, and plants take up more N and P as a result.

4.2. Relationship Between Plant Nutrients and Soil Fertility

Plant nutrient concentrations often reflect soil substrata and fertility [Craine et al., 2001; Ordoñez et al., 2009; Orwin et al., 2010; Han et al., 2011; Geng et al., 2012]. However, inconsistent with this widely acknowledged
general pattern, our results showed no positive relationship between soil fertility (i.e., soil total and available [N] and [P]) and plant [N] and [P] for the three dominant genera across the transect (see Table S5). Several other studies have also observed elevated plant nutrients under infertile growth conditions [Wright et al., 2001; Ye et al., 2013]. One potential reason for the failure to find a positive relationship between plant nutrient concentrations and soil fertility may be the “dilution effect” of plant size [Jarrell and Beverly, 1981; Elser et al., 2010]. Both higher soil fertility and higher precipitation increase plant C uptake, growth rate, and plant size [Luo et al., 2013], which, in turn, could dilute plant nutrient concentrations. This hypothesis is supported by our observation of significantly negative relationships between plant [N] and [P] and MPH (Figure 4). In our study region, water availability is the most important factor limiting plant growth [Bai et al., 2004; Han et al., 2011] and plays an important role in controlling and modulating soil nutrient status and plant physiological processes [Lü et al., 2012]. Our previous findings suggest relatively higher nutrient acquisition but lower resource consumption or utilization for plants in more arid grasslands relative to less arid grasslands along the same transect [Luo et al., 2013]. The second potential reason may be that plant nutrient concentrations are driven by demand, instead of supply. That is, plants growing in nutrient-rich soils with optimal growth conditions may only take up nutrients as are needed to match the demand of plant growth instead of matching the ambient nutrient supply [Prentice et al., 2014]. This interpretation is further supported by the consistent N:P ratios in plant tissues across the broad gradient in our study (Figure 3 and Table S4).

Our results gained from this dry and cold transect indicated that soil nutrients were unrelated to plant growth and climate, which is inconsistent with findings from studies in more moderate temperatures in mesic environments [Schuur, 2001; Schuur and Matson, 2001]. For example, in Hawaiian forests, plant N nutrients and soil N availability increased with decreasing precipitation, corresponding with an increase in plant growth, and this negative correlation of plant nutrients with precipitation appeared to be most directly associated with decreased N availability in that warm and wet area [Austin and Vitousek, 1998; Schuur, 2001; Schuur and Matson, 2001]. In such mesic ecosystems with moderate temperature, water supply in excess of plant demand generally does not act as a limiting resource for biotic processes but instead may influence plant growth, maintenance, and reproduction through a variety of abiotic processes such as soil leaching and resupply of oxygen [Austin and Vitousek, 1998; Schuur, 2001]. However, in the dry and cold landscape encompassed by our study area, productivity of plant biomass is likely colimited by precipitation and temperature; thus, precipitation or temperature can directly influence biotic processes and thereby alter soil nutrient availability and plant growth [Wang et al., 2006; Lü et al., 2012]. In sum, the different controlling

Figure 5. (a–f) Allometric relationships between plant aboveground and belowground [N] and [P]. The dashed lines represent isometry, with a slope equal to 1.0 and a y intercept equal to that of the corresponding solid lines. All aboveground relationships differ significantly from the 1:1 line (P < 0.05), while all belowground relationships do not (P > 0.05). N_A, aboveground [N]; N_B, belowground [N]; P_A, aboveground [P]; P_B, belowground [P].
mechanisms in different climatic zones may at least partially explain the discrepancy between our findings in these dry and cold ecosystems and those from more moderate temperatures in mesic environments.

4.3. Invariant N:P Ratios

Plant N:P ratios were insensitive (P > 0.05) to variations in climate factors (MAP and MAT) and soil fertility (soil total and available [N] and [P]) (Table S4). This lack of a clear relationship between plant N:P ratios and climate or soil variables agrees with previous findings that showed that climate factors and soil fertility had little direct effect on plant N:P stoichiometry across nearly 800 species of terrestrial plants in China [Han et al., 2005; Zhang et al., 2012] and across 47 evergreen tropical forest sites in Costa Rica and Brazil [Townsend et al., 2007]. The modest effect of climate and soil factors on plant N:P ratios suggests that intrinsic factors might be more important than extrinsic factors in affecting N:P ratios in natural ecosystems. For example, fast growing cells usually have low N:P ratios [Sterner and Elser, 2002]; processes of cross-tissue regulation and shifts in biomass allocation may maintain characteristic growth rates and thus maintain relatively constant plant N:P ratios.

4.4. Relationships Between Aboveground and Belowground Plant Nutrients

Plant aboveground and belowground nutrient concentrations were significantly correlated for each genus across the transect (Figure 5), in line with previous findings [Craine and Lee, 2003; Tjoelker et al., 2005; Liu et al., 2010]. Plant [N] and [P] in aboveground tissues were higher than those in belowground biomass for all genera (Table S1), which is consistent with the findings of Yuan et al. (2011). This difference in nutrients between aboveground and belowground tissue may be explained by large investments in N-rich enzymes and P-rich RNA for protein synthesis machinery in aboveground tissues to maximize capture of light and carbon dioxide for photosynthesis and its conversion into new cellular biomass [Sterner and Elser, 2002].

The aboveground and belowground [P] showed isometric scaling, while an allometric scaling held true for N (Figure 5). The most plausible explanation for such a nutrient-specific relationship is their different functions within plants. Such different allocation patterns may imply that plant growth in dry environments is N rather than P limited [Reich and Oleksyn, 2004; Reed et al., 2012; Lü et al., 2013]. That is, P is not limiting and thus is allocated isometrically to different tissues, while most of the N absorbed from soil is likely immediately transported to the green tissues (i.e., aboveground tissues) for photosynthetic processes to drive growth, resulting in higher [N] in aboveground than belowground plant tissues.

5. Conclusion

Plant tissue [N] and [P] increased with decreasing precipitation and increasing temperature but were negatively correlated with soil nutrient availability. Such results may have resulted from a dilution effect in cooler, wetter areas or from a demand-regulated plant nutrient system. Plant and soil conditions, such as N stocks in particular, co-develop over extended time periods. Thus, nutrient stocks likely have interacted with plant-driven processes to generate the nutrient patterns we observed in our study. However, previously reported positive relationship of nutrients between soil and plants may be challenged under changing climatic conditions.

Plant N:P stoichiometry was not dependent on soil fertility or climatic variation, which may be because factors intrinsic to each plant species play a more important role in controlling and regulating N:P ratios than extrinsic factors in the dry and cold grasslands we studied. Thus, we would not be able to predict plant nutrient limitation using plant tissue N:P ratios.

Plant [N] and [P] in aboveground and belowground biomass were strongly correlated and showed similar relationships with climatic factors and soil fertility. Plant aboveground and belowground N appeared to follow an allometric scaling relationship, while the allocation of P in plants was isometric, perhaps due to the differences in their acquisition and function. Overall, our findings provide potentially valuable information nutrient cycling in soil-plant system in dry and cold grasslands under changing climatic conditions.

References


