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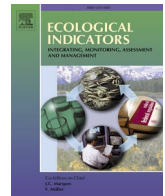
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Variation in biomass and nutrients allocation of *Corydalis hendersonii* on the Tibetan Plateau with increasing rainfall continentality and altitude

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ABSTRACT

The Tibetan Plateau is considered as one of most sensitive region to global change. Nutrient (N and P) availability is an important limiting ecological factor in cold terrestrial ecosystems such as the alpine belt of the Tibetan Plateau. We focused on *Corydalis hendersonii*, an endemic alpine species of the Tibetan Plateau. Exploring the N and P below- and above-ground responses of *C. hendersonii* to climatic factors is crucial for biodiversity conservation of the alpine Tibetan plateau under global change. We used the Outlying Mean Index and regression analyses to assess N and P stoichiometry and biomass responses in leaves and roots of *C. hendersonii* along climatic gradients. We found that investment and allocation of nutrient and biomass in *C. hendersonii* were mainly driven by rainfall continentality. In the eastern less-continental wet area of the Tibetan plateau, *C. hendersonii* had higher biomass in leaf, and lower N and P investment in roots than in the western more continental dry part. Specifically, 300 mm year⁻¹ Mean annual precipitation (MAP) and ca. 80° Rainfall continentality index (GAMS) were threshold values of climate stress inducing strong nutrient limitation for *C. hendersonii* across the Tibetan Plateau. Our results suggest that rainfall continentality is the primary climatic driver of variation in biomass and nutrients allocation of *C. hendersonii* on the Tibetan Plateau. Thus, global warming and drying should induce a decrease in total biomass, a reduction in leaf N and P concentrations and an increase in root/shoot ratio in the alpine region of the Tibetan Plateau.

1. Introduction

The Tibetan Plateau is the largest Alpine plateau of the world, called “the Roof of the World”, and also considered as a “sensor” of climate change in Asia and the northern hemisphere (Zhang et al., 1988; Zheng, 1996). This as a unique region in the world for assessing the responses of plants to climatic factors due to few human disturbances (Zhuang et al., 2010; Jin et al., 2013) and multiple direct climatic gradients related to changes in altitude, latitude and continentality. The Tibetan Plateau vegetation is highly sensitive and vulnerable to global climate change (Zheng, 1996; Piao et al., 2011; Jin et al., 2013), in particular warming and drying (Xie et al., 2009).

Nitrogen (N) and phosphorus (P) are important resources that may limit terrestrial vegetation growth (Reich and Oleksyn, 2004; Jaroslaw

et al., 2021), and their stoichiometry provides an accurate tool for assessing the dynamic equilibrium of elements in the plant-soil system. Ecological factors such as climate (Reich and Oleksyn, 2004; Yuan et al., 2011; Chen et al., 2013), soil fertility (Ordoñez et al., 2009), plant ontogeny (Nielsen et al., 1996; Elser et al., 2000; Jeyasingh et al., 2009), functional groups and species stress-tolerance abilities (Chapin and Oechel, 1983; Geng et al., 2014) and phylogeny (Kerkhoff et al., 2006; Stock and Verboom, 2012) are regulating N, P concentrations and N:P ratio in plants. The assessment of the dynamic of leaf N, P concentrations and N:P ratio at large regional scale has been shown to be likely confounded by phylogenetic constraints when using different species across spatial gradients (He et al., 2010; Stock and Verboom, 2012). Thus, Kerkhoff et al. (2006) and Stock and Verboom (2012) proposed to use a single species to address the ecological driving factors at large

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regional scale.

Climatic factors are key for explaining plant dominance, distribution, growth and nutrient allocation (Welker et al., 2005; Sardans et al., 2011, 2012). Drought and cold are considered as the main factors limiting plant growth and controlling nutrient allocation in natural environments (Elser et al., 2010; He et al., 2015). Meanwhile, plant leaf N concentration rises with decreasing mean annual temperature (MAT), whereas leaf P concentration increases (Reich and Oleksyn, 2004). Besides, temperature-induced relative growth rates of plants shift N:P of leaf and root at large scale (Elser et al., 2003; Reich and Oleksyn, 2004; Kerkhoff et al., 2005). Furthermore, plant root P increases but N:P decreases exponentially with latitude at global-scale (Yuan et al., 2011).

However, most studies assessing changes in plant biomass and N and P allocation at regional scales have focused on temperature and rainfall gradients along latitudinal and altitudinal gradients, neglecting the effect of rainfall continentality, although it has been shown to be a key complex factor driving temperature and drought gradients and thus species distribution at regional scale (Ozenda, 1985). For example, Michalet et al. (2021) have shown that tree and shrub species distribution in western USA was primarily driven by rainfall continentality (increasing with increasing distance from the Pacific Ocean) before the length of the growing season and the importance of the summer dry season (varying with latitude and altitude). This may be explained by the increase in both vapor pressure deficit (hereafter, VPD) and cold stresses induced by increasing rainfall continentality (Michalet et al., 2003; Simonin et al., 2009; Muhamed et al., 2013; Novick et al., 2016).

Corydalis hendersonii Hemsl. (Papaveraceae) is an alpine perennial

herb endemic to the Tibetan Plateau, which distribution is limited to the high mountain areas at an altitude of 4,200–5,900 m (Zhang et al., 2008; Li et al., 2020). *C. hendersonii* is a pioneer plant growing on sandy soils, stony screes throughout the plateau (Fig. 1a-b). It plays an important role on the Tibetan Plateau's alpine ecosystem as ecological indicator of health and environmental changes (Zhang et al., 1988; Li et al., 2020).

We selected *C. hendersonii* as model species for assessing the effect of varying environmental conditions including climate on plant stoichiometry for two reasons. First, *C. hendersonii* had a wide geographical range across the high alpine Tibetan Plateau region (Fig. 1; Table A1). Second, *C. hendersonii* has formed some successful strategies under long-term experiencing of cold and cold-induced water and nutrient stresses (Chapin and Körner, 1995). We focused on two main questions: (1) How does *C. hendersonii* adapt to rainfall and temperature changes by shifting biomass, N, P concentrations and N:P ratios in leaves and roots? (2) What are the most important complex drivers of these changes across the Tibetan Plateau, latitude, altitude or rainfall continentality?

2. Materials and methods

2.1. Site selection and sampling

Our field observations and samplings were conducted in July and August of 2012 and 2013. According to altitude, latitude and longitude gradients, 29 sites of the natural distribution of *C. hendersonii* in flowering were selected (Fig. 1) (He et al., 2006a). At each site, altitude, latitude and longitude were measured *in situ* in a GPS receiver (eXplorist

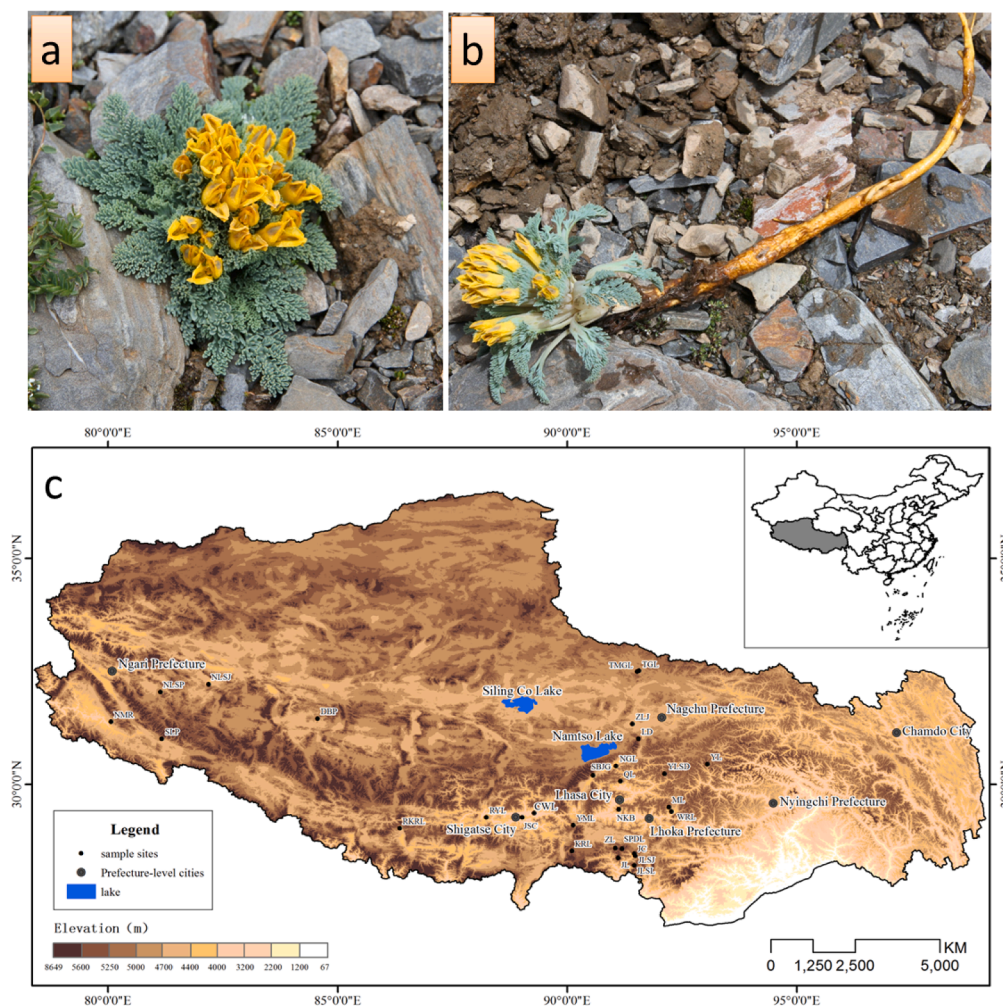


Fig. 1. Morphological characteristics of *C. hendersonii* in its natural habitat and the location of the 29 sites on the Tibetan Plateau.

500, MAGELLAN, USA) and an altimeter (44ST, BARIGO, Germany). Each site included three quadrats, each 1 m × 1 m. At each quadrat, we recorded the number of *C. hendersonii* and harvested all *C. hendersonii*. Tissues of *C. hendersonii* were classified into two groups: aboveground (leaves, *C. hendersonii* has no stem) and belowground (roots) (Fig. 1a-b), placed in envelopes and brought back to the laboratory. The total dry biomass (TDM), total aboveground dry biomass (TADM) and total belowground dry biomass (TBDM) of each quadrat were weighed in the laboratory after oven-drying at 60 °C for 72 h. Formula was as follows:

ADM (or BDM) = TADM (or TBDM) per quadrat/total number of *C. hendersonii* individuals per quadrat.

For each quadrat, five rhizosphere soil samples were collected using a soil auger and an aluminum specimen box; each soil sample was collected from the surface to the depth of 15 cm and then five samples were fully mixed into one composite sample.

2.2. Measurement of N and P

The plant samples were dried for 72 h at 60 °C and grounded using a ball mill (MM400, Retsch, Haan, Germany). Soil samples for analyzing elements were air-dried and grounded to pass through a 100 μ -mesh sieve. N concentrations of plant and soil samples were measured with an elemental analyzer (2400 II CHNS/O Elemental Analyzer, Perkin-Elmer, USA). P concentrations were measured by using the molybdate/ascorbic acid method (John, 1970) after H₂SO₄-HClO₄ digestion.

2.3. Climate data collection

The climate data used in this study were obtained from 30-year average temperature and precipitation records (1981–2010) from 13 well-distributed climate stations across the Tibetan Plateau (data supplied by Tuo Chen, State Key Laboratory of Cryospheric Sciences of CAS). We calculated MAT and Mean annual precipitation (MAP) for each site using a linear model in which altitude, latitude and longitude were explanatory variables (Fang et al., 2001; Piao et al., 2003; Geng et al., 2012). To quantify rainshadow effects, a crucial climate factor in large mountain ranges (Ozenda, 1985; Michalet, 1991; Michalet et al., 2003; Michalet et al., 2021), we used the rainfall continentality index (GAMS) proposed by Gams (1932) in the European Alps and modified by Michalet (1991) in Morocco and Pache et al. (1996) in the Alps. This index is an angle varying between 0 and 90°, with low values for oceanic external climates and high values for rainshadowed continental climates (Cotangent(G) = P/A, where P is annual precipitation in mm and A is the elevation in m, Gams, 1932). The main interest of this index is that it calculates the rainfall continentality independently on the effect of elevation on rainfall, due to the use of the ratio between precipitation and elevation. We applied here the modified formula proposed by Pache et al. (1996) for high elevation sites (above 1600 m).

2.4. Data analysis

The relationships between plant traits and environmental variables were explored in three steps. First, the leaf, root and soil N and P concentrations and their ratios for each site were calculated as the average of three samples from the same site and, then, statistically summarized to show the mean, range and coefficient of variation (CV) for the N and P concentrations and the N:P ratio in the leaves, roots and soils. The significance of the differences in N and P concentrations and N:P ratios among leaves, roots and soils across all sites were tested using a one-way analysis of variance (ANOVA) and a Tukey post hoc test (McGroddy et al., 2004; He et al., 2008). Second, we used the Outlying Mean Index (OMI) analysis proposed by Dolédec et al. (2000) to assess the relationships existing between environmental variables and trait measurements. The trait table included the 9 traits (ADM, BDM, BDM:ADM ratio, N and P concentrations and their ratios in leaves and roots) and the environmental table included the 8 variables (MAP, MAT, longitude,

latitude, altitude, GAMS, STN, STP) measured or calculated at the same 29 sites (Table A2). Finally, we used linear regression for visually assessing changes in plant traits along a continuous gradient of temperature, precipitation, soil fertility or a combined climatic factor (GAMS, latitude) across all sites. Relationships between geographic variables (altitude latitude, longitude), climatic variables (MAT, MAP, GAMS) and soil nutrients (STN, STP) were expressed with Pearson correlation coefficients (*r*), and all tests were treated as two-tailed (Elser et al., 2010; He et al., 2010; Ma et al., 2010a,b). Data on plant traits were log₁₀-transformed to normalize statistical distributions and minimize deviations in the residuals (Reich and Oleksyn, 2004; Ordoñez et al., 2009). The ANOVA, regression and correlation analyses were conducted using IBM SPSS statistics 21.0 (SPSS Inc., Chicago, USA) for Windows and the OMI was conducted using the *ade4* package (Dray and Dufour, 2007) for R.

3. Results

3.1. N:P stoichiometry in leaves, roots and soils

Across all sites, the mean value of N and P concentrations in leaves were 19.94 mg.g⁻¹ and 1.71 mg.g⁻¹, respectively, while those in roots were 11.46 mg.g⁻¹ and 1.38 mg.g⁻¹ and those in soils were 0.73 mg.g⁻¹ and 0.53 mg.g⁻¹ and N:P ratio of foliage, root and soils were 11.76, 8.44 and 1.34, respectively (Table 1). Significant differences in N, P concentrations and N:P were found between leaves, roots and soils (Table 1, *p* < 0.05). There were significant differences between soil N, P concentrations and N:P ratios and both N, P concentrations and N:P ratios in leaves and roots. N and P concentrations and N:P ratios of leaves were always higher than those in roots (Table 1).

3.2. Trait-environment relationships

The first OMI axis was explained by GAMS, MAP and longitude, opposing eastern less continental sites with relatively high precipitation in its negative part to western highly continental sites with very low precipitation in its positive part. The continental sites had also lower soil nutrient content than less-continental sites (Fig. 1; Fig. 2a-b). Plants were characterized by high biomass, high ADM, low BDM:ADM ratio, and low root P and N concentrations in less-continental sites (Fig. 2a-b). Plants of western continental dry sites were characterized by high N and P investment in roots. Axis 2 was mainly explained by latitude, MAT and STN, opposing colder northern sites in its positive part to warmer southern sites with high STN in its negative part (Fig. 1c; Fig. 2a-b). Plants from northern sites had high leaf N and P concentrations and N:P ratio in opposition to those from southern sites (Fig. 1c; Fig. 2a-b). Axis 3 was mainly explained by altitude, MAT and STP, opposing colder sites from high altitudes with higher STP in its positive part to warmer sites from relatively low altitudes in its negative part (Fig. 2c, d). Plants from cold high sites had high leaf P concentrations and low N:P ratios, whereas those from lower elevations had high root N:P ratios and N concentrations (Fig. 2c, d).

Regression analyses supported the results of OMI (Fig. 3d-e; Fig. 4a-d). Root N and P concentrations were significantly negatively correlated with MAP (Fig. 3d-e, *P* < 0.001, *R*² = 0.36 and 0.36, respectively), consistent with their positive correlation with GAMS (Fig. 2a); both TDM and ADM increased but BDM:ADM ratio decreased dramatically with increasing MAP (Fig. 4a-b, d, *P* < 0.05, *R*² = 1.5, 2.1 and 2.5, respectively), consistent with their variation with GAMS (Fig. 2a). Leaf N and P concentrations and N:P ratios in both leaves and roots were quadratically correlated with MAP, with the lowest values of these traits occurring at approximately 300 mm year⁻¹ for MAP (Fig. 3a-c, *f*, *P* < 0.05, *R*² = 0.21, 0.16, 0.24 and 0.15, respectively) or approximately 80° for GAMS (Table A2). The TDM and ADM decreased but BDM:ADM ratio increased with increasing altitude (Fig. 4e-f, *h*; *P* < 0.05, *R*² = 0.14, 0.16 and 0.14, respectively).

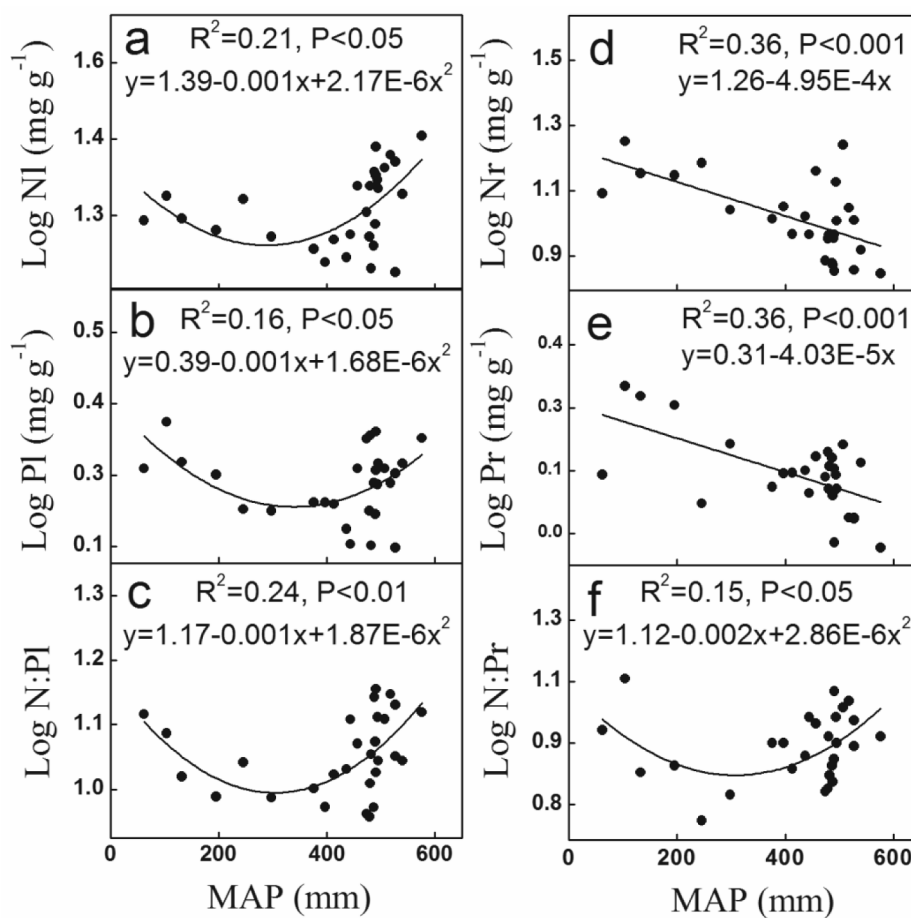


Fig. 3. N and P concentrations and N:P ratios in leaves (NI, PI and N:PI) and roots (Nr, Pr and N:Pr) in relation to mean annual precipitation (MAP).

continentality (decreasing MAP and soil nutrient), because of the importance of N for growth and of P for the formation of new roots (Elser and Hamilton, 2007; Geng et al., 2014; Jarosław et al., 2021) (Figs. 2-4). Moreover, due to the fundamental trade-off in biomass and nutrient allocation (Chapin, 1980, 1990; Koch et al., 1988; Sterner and Elser, 2002), the proportion of total biomass allocated to belowground biomass increased with increasing rainfall continentality, shifting N and P investment towards roots where photosynthates can be used to increase water and nutrient uptake (Sardans et al., 2008a,b, 2012; Ma et al., 2010a,b; Montagnoli et al., 2012; Renton and Poot, 2014). In contrast, the eastern less continental wet sites had high biomass, particularly with high ADM, and low BDM:ADM ratio and root N and P concentrations (Figs. 2-4). Such shifts might be particularly important for alpine plants in the alpine region of the Tibetan Plateau, because inherent developmental growth constraints inhibit nutrient dilution in the plant tissue (e.g., leaf or root) in infertile conditions (Körner, 1989; Chapin et al., 1990).

Our results suggest that ca. 300 mm year⁻¹ MAP (ca. 80° GAMS) was a threshold value of drought combined with nutrient limitation for *C. hendersonii* across the Tibetan Plateau, because MAP and soil nutrient were positively correlated with each other in our study (Table 2). As a result, increases in both N and P concentrations in leaves and N:P ratios in both leaves and roots with decreasing MAP occurred if *C. hendersonii* was subjected to drought and nutrition stress (MAP < 300 mm year⁻¹ or GAMS > 80°) (Fig. 3a-c, f). These results are consistent with those of Huang et al. (2009) who found that leaf N decreased with increasing water supply at lower level [< 9000 ml year⁻¹ (amount of equivalent precipitation 286.6 mm year⁻¹)] in *Leymus chinensis*. Zheng and Shangguan (2007) also found that leaf N:P ratios increased as MAP decreased in the Loess Plateau of China. In contrast, if these conditions

of drought and nutrition stresses were removed (MAP > 300 mm year⁻¹ or GAMS < 80°), N and P concentrations and N:P ratios in leaves increased markedly with increasing MAP (decreasing GAMS), whereas N and P concentrations in roots decreased with increasing MAP (Fig. 3). These changes occurred also due to the fundamental trade-off in both biomass and nutrient investment and allocation (Sardans et al., 2008a; Peñuelas and Sardans, 2009; Sardans et al., 2011). Indeed, these contrasting responses of N and P in leaves and roots when MAP > 300 mm year⁻¹ is likely the result of the effect of MAP on leaf and root growth rate and nutrient (N and P) retranslocation in response to a shift in the BDM:ADM ratio (Sardans et al., 2008a). Enhancing N and P proportionally transfers them from the roots to the leaves for biomass growth and accumulation (Elser et al., 2010; Sardans et al., 2011) with increasing ADM and decreasing BDM:ADM ratio (Figs. 3-4). Meanwhile, retranslocation from root to leaves was stronger for P than N and, thus, root N:P ratio also increased with MAP when MAP > 300 mm year⁻¹ (Fig. 3f). This also suggests varying resource uptake strategies across different habitats rather than consistent selection for coordinated above- and belowground traits (Kembel and Cahill, 2011; Geng et al., 2014; Zheng et al., 2020).

Warming seemed to decrease leaf N and P concentrations and N:P ratios (axis 2 of the OMI in Fig. 2), which supports both the temperature plant physiological hypothesis (TPPH) (Reich and Oleksyn, 2004) and the growth-rate hypothesis (GRH) (Elser et al., 2003; Woods et al., 2003). TPPH predicts that high leaf N may compensate for the low efficiency of physiological processes at low temperatures and, thus, that leaf N should rise with decreasing temperature. GRH assumes that an increase in the growth rate of an organism will reduce its N:P ratio, resulting in a decrease in N:P with a decrease in temperature. However, the modulation of plant traits by MAT was weak in the current study

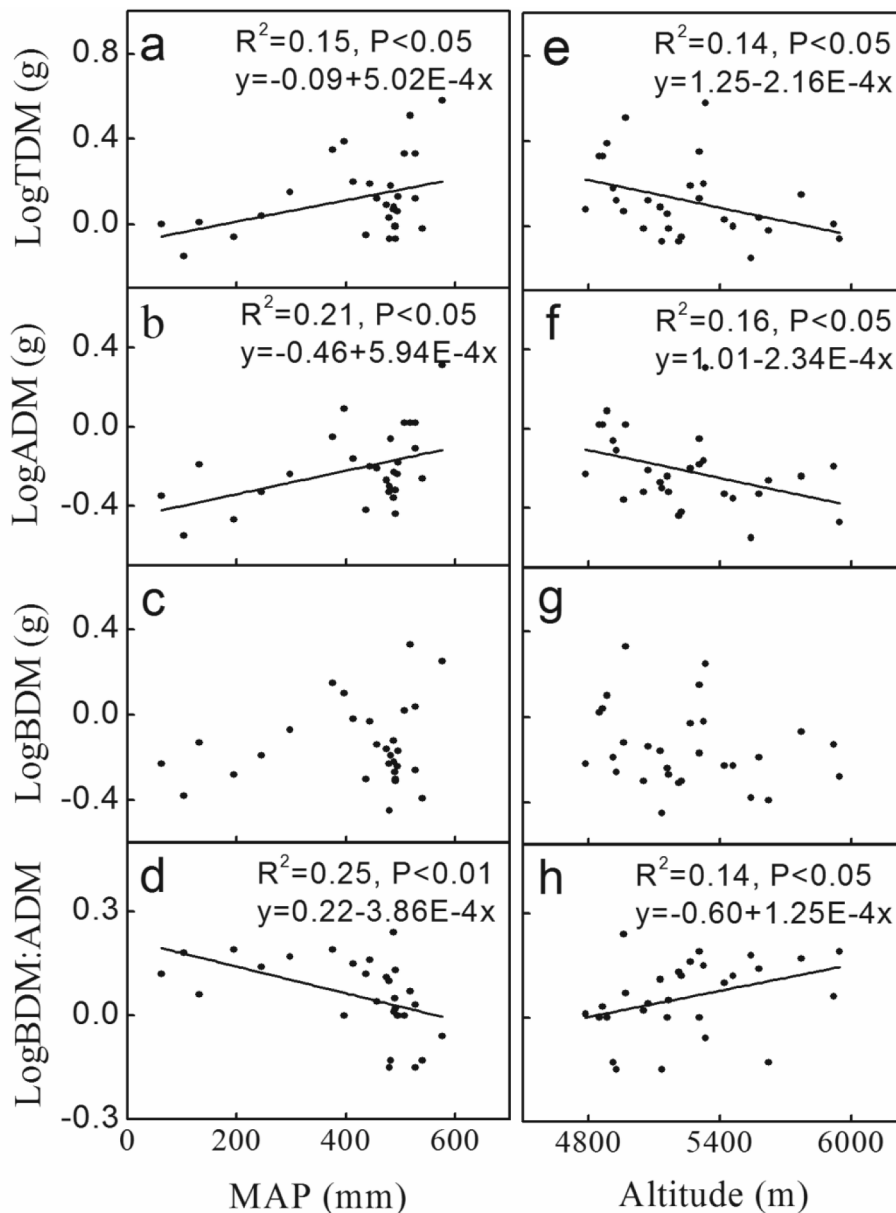


Fig. 4. Relationships between total dry biomass (TDM), aboveground dry biomass (ADM), belowground dry biomass (BDM), below- and above-ground dry biomass ratio (BDM:ADM), and mean annual precipitation (MAP) and altitude (ALT). Regression lines are shown only for relationships that were significant at $P < 0.05$.

Table 2
Correlation matrix for environmental variables.

	LAT	LON	MAT	MAP	GAMS	STN	STP
ALT	0.46*	-0.70**	-0.58**	-0.67**	0.68***	-0.34	-0.29
LAT		-0.42*	-0.96***	-0.37*	0.38*	-0.73***	-0.70***
LON			0.39*	0.99***	-0.99***	0.44*	0.46*
MAT				0.35	-0.35	0.71***	0.64***
MAP					-1.00***	0.43*	0.45*
GAMS						0.44*	0.46*
STN							0.77***

Pearson's correlation coefficients (r) and P values are shown in the upper right and lower left sections, respectively. Abbreviations: ALT, altitude; LAT, latitude; LON, longitude; MAT, mean annual temperature; MAP, Mean annual precipitation; GAMS, the rainfall continentality index; STN, soil total nitrogen concentration; STP, soil total phosphorus concentration. Correlations with ***, $P \leq 0.001$, **, $P \leq 0.01$, *, $P \leq 0.05$; those without, $P > 0.05$.

(Fig. 2), likely because of the overwhelming effect of precipitation on them. Note that in our study many sites have similar temperatures but important differences in precipitation because of the much important variation in longitude and, thus, rainfall continentality, as compared to

latitude (Fig. 1; Table 2). Thus, standardized data collection over a broad MAT range with identical MAP was crucial for detecting these patterns.

Leaf P concentrations increased and both leaf N concentrations and N:P ratios decreased with increasing altitude (Fig. 2; Fig. 4). This pattern

is not consistent with what observed along an altitudinal transect on the northern slope of Changbai Mountain, China (Zhao et al., 2014), but in agreement with the results observed for *Picea abies* with increasing altitude in the temperate climate of Europe (Kang et al., 2011) and those for *Waldheimia tridactylites* under the extreme environmental conditions of Ladakh, NW Himalaya (Macek et al., 2012). This indicates that nitrogen uptake decreases with elevation and might limit plant growth, as we found that TDM and ADM dramatically decreased with increasing altitude (Fig. 4e-f). In addition, the Tibetan Plateau is not only typically characterized by both high altitude and low MAT, but also low air pressure, high wind speed and high UV-B radiation (He et al., 2006b). All these parallel variations are considered to lower photosynthetic rates (Chapin et al., 1993). Thus, we argue that plants growing at very high elevations tend to be limited by a combination of lower nutrient uptake, possibly because of lower photosynthetic rates, poorly developed soils, and scarcity of water (He et al., 2006b; Macek et al., 2012; Yang et al., 2021). Thus, alpine plants have to reduce aboveground- and total-biomass production (Fig. 4e-f) and enhance nutrient and biomass investment and allocation from above- to below-ground (Fig. 4h) to survive in such extreme environment.

4.2. Implications in a changing climate

Global change may contribute to an upwards shift of climatic environments (Parmesan and Yohe, 2003). The Tibetan Plateau is considered as one of most sensitive region to global change and as an amplifier of global climate change (Xie et al., 2009). Thus, the plateau is a well-suited system to study the responses of natural ecosystems and plant acclimation and adaptation to climate change (He et al., 2006b). In light of our findings, increase in drought with increasing rainfall continentality was correlated to a decrease in total biomass and an increase in belowground nutrient and biomass allocation (Figs. 2–4). In addition, warming was related to a decrease in leaf N and P concentrations and N:P ratios in *C. hendersonii* across the Tibetan Plateau (Fig. 2). Considering the warming and drying trends predicted for the Tibetan Plateau (Xie et al., 2009), we argue that global warming should reduce leaf N and P concentrations but increase root N and P concentrations in the future, and these change should be associated with a decrease in total biomass and an increase in BDM:ADM ratios.

5. Conclusion

Ecological stoichiometry is an effective tool for explaining changes in plant traits along environmental gradients. N, P and their stoichiometry for a single species, *C. hendersonii*, highlighted the main climatic constraints occurring in the high altitudes of the Tibetan Plateau. Rainfall continentality was the most significantly correlated climate factor to plant traits and in particular to the allocation of biomass and N and P towards belowground components in *C. hendersonii* across the Tibetan Plateau. Additionally, plants growing at very high elevations tended to be limited by a combination of lower nutrient uptake, and in particular N limitation. Therefore, our results suggest that global warming and drying will reduce leaf N and P concentrations but increase root N and P concentrations in the Tibetan Plateau in the future, at least in *C. hendersonii*, and these shifts should occur in parallel to an increase in biomass allocation to roots. This increasing knowledge on the trait plasticity of *C. hendersonii* with increasing rainfall continentality and altitude is crucial for the conservation of this endemic species under global change in the alpine belt of the Tibetan Plateau. However, in order to assess the likely generalization of our results, such study should be conducted on other alpine species of the Tibetan Plateau.

CRedit authorship contribution statement

Qien Li: Funding acquisition, Conceptualization, Data curation, Formal analysis, Writing - review & editing. **Michalet Richard:**

Methodology, Software, Writing - review & editing. **Xiao Guo:** Investigation, Project administration, Resources, Validation, Writing - original draft. **Huichun Xie:** Resources, Writing - review & editing. **Mingzhu He:** Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.108244>.

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