

The stoichiometric traits and biogeochemical niches of four alpine herbs along elevation gradient in southeastern Tibet

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Research Article

Keywords: Ecological stoichiometry, biogeochemical niche, elemental phenotype, adaptive strategy, intraspecific and interspecific variation

Posted Date: December 12th, 2025

DOI: <https://doi.org/10.21203/rs.3.rs-8303088/v1>

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Additional Declarations: No competing interests reported.

Abstract

Ecological stoichiometry is a fundamental concept for understanding nutrient allocation strategies and ecosystem functioning. However, the spatial and elevational variability of stoichiometric traits across different plant species and their organs remains poorly understood, particularly in high-altitude ecosystems. This study systematically investigated the C:N:P ecological stoichiometry of four alpine herbaceous species—*Potentilla saundersiana*, *Carex moorcroftii*, *Kobresia humilis*, and *Leontopodium leontopodioides*—across an elevation gradient ranging from 2,647 to 4,898 meters in the alpine grasslands of southeastern Tibet. A total of 433 samples were collected from 34 distinct sites to assess the influence of elevation gradient on plant stoichiometry. Our results revealed significant intra- and interspecific variations in stoichiometric traits among organs and species. *Carex moorcroftii* exhibited the largest biogeochemical niche size, while *L. leontopodioides* showed the smallest. Leaves generally exhibiting higher biogeochemical niche size than stems and roots. Elevation significantly influenced plant nitrogen and phosphorus concentrations, with species-specific responses. Climatic factors explained most of the variance in carbon-related stoichiometric traits, while soil nutrients primarily affected phosphorus-related traits. These results highlight the complex interactions among climatic, soil, and biological factors in shaping plant stoichiometry along elevation gradients. This study confirms the intraspecific and interspecific variations in plant stoichiometry and altitudinal heterogeneity in alpine grassland ecosystem, offering valuable insights for future ecological modeling and conservation efforts.

INTRODUCTION

Ecological stoichiometry considers the balance of multiple chemical elements—such as carbon (C), nitrogen (N), and phosphorus (P)—in organisms and ecosystems. This balance is crucial for understanding plant nutrient dynamics, ecosystem functioning, and biogeochemical cycles (Elser et al. 2000). Plant stoichiometric traits, which include the concentrations and ratios of C, N, and P, serve as indicators of nutrient use efficiency, growth strategies, and responses to environmental changes (Feng et al. 2024; Liu and Wang 2021; Reich and Oleksyn 2004). Specifically, leaf N and P concentrations can reveal information about the leaf economic spectrum and resource acquisition strategies (Leal et al. 2017; Wright et al. 2005). These traits are essential for predicting how plants adapt to varying environmental conditions and how ecosystems respond to global changes, including climate change and nutrient deposition (He et al. 2006; Moody et al. 2025; Zhang et al. 2023). Consequently, investigating the plasticity and drivers of inter- and intraspecific variation in stoichiometric traits will enhance our understanding of plant resource utilization strategies and the mechanisms underlying plant adaptation to environmental conditions (Elser et al. 2010; Leal et al. 2017; Liu and Wang 2021; López-Sepulcre et al. 2024; Qin et al. 2022a).

Plant stoichiometric traits are regulated by a suite of abiotic and biotic factors, including soil nutrient availability, climatic conditions, plant functional types, tissue-specific allocation patterns, and biotic stress (Reich and Oleksyn 2004; Yu et al. 2011). Notably, elevation gradients in alpine ecosystems have received considerable scientific interest because they drive pronounced variations in temperature,

precipitation, and soil nutrient distribution across limited spatial scales (Körner 2007; Yang et al. 2015). Elevation gradients represent valuable natural laboratories for studying ecological responses to global change, effectively addressing the spatial and temporal limitations of traditional manipulative experiments (Binter et al. 2025; Sundqvist et al. 2013).

Empirical studies consistently demonstrate significant variation in plant C:N:P stoichiometric ratios along elevation gradients, with foliar N and P concentrations showing particularly strong elevational dependence (Körner 1989; Gong et al. 2020; Qin et al. 2022b). However, these stoichiometric responses display significant species-specific variation (Minden and Kleyer 2014; Reich and Oleksyn 2004). The literature reveals divergent patterns: while some studies report positive correlations between elevation and both leaf N and P concentrations (Cao et al. 2020; Gong et al. 2020; Han et al. 2005), others observe inverse relationships, with leaf N content and N:P ratios decreasing with elevation (Macek et al. 2012; Tong et al. 2021; Zhang et al. 2019).

While early research predominantly focused on whole-plant and foliar stoichiometric characteristics (Han et al. 2005; Reich and Oleksyn 2004), recent advances have revealed critical functional divergence among plant organs (Yang et al. 2015). This organ-specific stoichiometry reflects differential resource allocation strategies, with leaves typically exhibiting 20–30% higher nitrogen concentrations than stems and roots due to their photosynthetic specialization (Körner 1989; Qin et al. 2022b; Schreeg et al. 2014). Such patterns are particularly pronounced along elevation gradients, where foliar N and P concentrations demonstrate non-linear responses to environmental covariates (Gong et al. 2020; Tong et al. 2021; Zhang et al. 2019).

The Biogeochemical Niche (BN) hypothesis provides a unifying framework for these observations, proposing that each species occupies a unique position in elemental composition space as an adaptive strategy (Peñuelas et al. 2019). The plasticity of a species' biogeochemical niche manifests as positional shifts within a multidimensional elemental space (Fernández-Martínez et al., 2022), which can be quantified through multivariate analyses (Yang et al. 2015). The BN framework thus provides a powerful approach for examining both intraspecific and interspecific variability in elemental composition, while elucidating the dynamic interplay between stoichiometric homeostasis and plasticity (Sardans et al. 2015; Wang et al. 2023).

The Qinghai-Tibet Plateau, recognized as the world's "Third Pole", hosts the highest-altitude grassland ecosystem globally, with mean elevations exceeding 4,500 m (Dong et al. 2023). This unique ecoregion, where alpine grasslands cover > 60% of the land area (Wei et al. 2023), exhibits characteristic nutrient limitations - particularly low soil nitrogen availability resulting from cold-temperature constraints on decomposition (Müller et al. 2017). While previous studies have documented elevational patterns in foliar stoichiometry (Gong et al. 2020; Qin et al. 2022b), critical knowledge gaps remain regarding: (1) whole-plant stoichiometric strategies across organs (Wang et al. 2022), (2) interspecific comparisons along elevation gradients (Tong et al. 2021), and (3) the integration of stoichiometry theory with high-altitude plant adaptations (Sundqvist et al. 2014). To address these gaps, we conducted a

comprehensive field study across a 2,251 m elevation gradient (2,647–4,898 m) on the southeastern Tibetan Plateau, analyzing C:N:P stoichiometry in four organs (leaves, stems, roots, flowers) of four alpine herbs. Specifically, we hypothesized that: (1) Spatial heterogeneity in stoichiometric traits along elevation will reveal species-specific BN optimization (Peñuelas et al. 2019). (2) Climatic factors will dominate over edaphic factors in governing elevational stoichiometric pattern.

MATERIALS AND METHODS

Description of study area

Field investigations were conducted along a 1,300-km transect in the southeastern Tibetan Plateau during July and August 2020. The study area spanned latitudes of 29°20'N to 29°53'N and longitudes of 91°00'E to 95°46'E, with elevations ranging from 2,647 to 4,898 meters above sea level. Climatic data were obtained from the Xizang Meteorological Stations via the China Meteorological Network, covering the period from 1990 to 2020. Based on these data, we calculated the mean annual temperature (MAT), mean annual precipitation (MAP), and mean annual sunshine hours for each sampling site. Across all sites, the average MAT was 5.03°C, the average MAP was 647.78 mm, and the mean annual sunshine duration totaled 2,556.52 hours.

The Qinghai-Tibet Plateau is dominated by alpine meadows and alpine steppes, with temperate grasslands occurring at lower elevations. Due to the harsh climatic conditions, the plant growing season is notably short. Dominant species in the study area include *Kobresia* spp., *Potentilla* spp., and *Poa* spp.

Field transect survey and sampling methodology

We established 34 sampling sites along the transect, with geographic coordinates (latitude, longitude) and elevation recorded at each site using a GPS device (eTrex Venture, Garmin, USA). To ensure spatial independence, sites were spaced more than 50 km apart. Within each site, we systematically placed five quadrats (1m×1m) with a 100m interval between different quadrats. We conducted comprehensive vegetation surveys in each quadrat, measuring community and species-level parameters. We recorded the plant density, mean height, coverage, and aboveground biomass of each plant species. Based on their widespread distribution across sampling sites, we selected four plant species for stoichiometric analysis: *Potentilla saundersiana* (PS), *Carex moorcroftii* (CM), *Kobresia humilis* (KH), and *Leontopodium leontopodioides* (LL).

When the four target species did not co-occur at a site, we collected only the available species, and stoichiometric traits were analyzed for each species across sites. Overall, we gathered data from 14 sites for PS, 17 sites for CM, 13 sites for KH, and four sites for LL (Fig. 1). At each study site, we collected 30 intact specimens per target species for stoichiometric characterization. This sampling design provided three biological replicates per species per site, with each replicate consisting of ten individual plants. Following plant collection, we extracted soil samples (0–15 cm depth) from the rhizosphere of each species. Soil from 10 individuals was composited per replicate. In total, we analyzed

three elements across 138 individuals, yielding 433 samples (site locations and climatic data are detailed in Table S1).

Laboratory analysis

All plant samples were oven-dried at 65°C for 48 hr until reaching constant weight, then finely ground using a ball mill (Retsch MM 400, Germany). Soil samples were air-dried, homogenized, and sieved (2.0 mm mesh) to remove coarse debris. The N concentrations in leaves, stems, roots, and soil were quantified via the Kjeldahl digestion-distillation method. For total P concentrations, plant and soil samples underwent persulfate-mediated oxidative digestion, followed by ammonium molybdate spectrophotometric detection. The organic carbon contents were determined using the Springer-Klee wet oxidation method, involving dichromate ($K_2Cr_2O_7$)-sulfuric acid (H_2SO_4) digestion under controlled heating.

Data calculation and statistical analysis

Data normality was assessed using the Kolmogorov-Smirnov test before conducting statistical analyses. When required, log-transformation was applied to normalize the data distribution. We initially conducted Pearson's correlation analysis to examine the influence of elevation gradients on the stoichiometric traits of four plant species. Subsequently, a two-way ANOVA was performed to assess the effects of species and organs on these stoichiometric traits. Additionally, multiple comparisons of means were performed using Tukey's HSD test for roots and soil stoichiometric traits, while paired t-tests were applied to assess stoichiometric traits of shoots for KH and LL, and stem and leaves for CM and PS. Significance levels were set at $P < 0.05$, $P < 0.01$, and $P < 0.001$. We performed the principal component analysis (PCA) to quantify the biogeochemical niche of four plant species based on three elemental traits. The first three principal components (PC1, PC2, and PC3) were extracted using the *stats* package in R. Biogeochemical niche differentiation was further assessed by calculating hypervolumes from the PCA scores using the *hypervolume* package. To examine how climatic factors (MAT and MAP), soil properties (C, N, and P concentrations), and biological factors (species and organ type) influenced stoichiometric variation along the elevation gradient, we employed both Generalized Linear Mixed Models (GLMMs) and Linear Mixed Effects Models (LMEMs), with elevation included as a random effect. Because of missing soil phosphorus data for LL, the GLMM and LMEM analyses were restricted to PS, CM, and KH. All statistical analyses were performed in R version 4.1.1 (R Core Team, 2015), using the *lmer* package for LMEMs and *glmm.hp* for GLMMs. All the graphs were generated using OriginPro 2024 (Education Edition) or ArcGIS (version 10.8, ESRI, Redlands, CA).

RESULTS

Overall evaluation of stoichiometric traits of four alpine herbs

For PS, the C:N:P ratios were as follows: root (263:9:1), stem (318:9:1), leaf (250:14:1), flower (481:23:1), soil (176:12:1). For CM, the C:N:P ratios were: root (357:11:1), stem (288:9:1), leaf (214:10:1), soil (137:10:1). In the case of KH, the measured ratios were: root (866:13:1), shoot (783:20:1), soil (171:12:1). Finally, for LL, the observed C:N:P ratios were: root (1296:22:1) and shoot (1312:25:1). A comprehensive evaluation of these stoichiometric traits across the organs of the four species was presented in Table S2.

The impact of elevation gradient on stoichiometric traits of four plant species

Along the elevation gradient, C concentrations decreased significantly for both CM ($P = 0.016$) and KH ($P = 0.014$) (Fig. 2a), whereas N concentrations increased significantly for PS ($P = 0.014$) (Fig. 2b). P concentrations increased significantly in PS and KH ($P < 0.001$ for both) but decreased significantly in CM ($P < 0.001$) (Fig. 2c). Regarding stoichiometric ratios, the C:N ratio of PS decreased significantly with elevation ($P < 0.001$; Fig. 2d), while the C:P ratio increased significantly in CM ($P < 0.001$) but decreased in PS and KH ($P < 0.001$; Fig. 2e). Finally, the N:P ratio increased significantly in CM ($P < 0.001$) and decreased in KH ($P < 0.001$; Fig. 2f).

The intraspecific and interspecific difference in stoichiometric traits

Soil substrates displayed uniformly significantly lower C, N, and P concentrations along with reduced C:N and C:P ratios compared to plant tissues across all four species ($P < 0.01$). For PS, the highest C and N concentrations, along with C:P and N:P ratios, were all found in flowers ($P < 0.01$). For CM, leaves showed significantly higher N and P concentrations, along with lower C:N, C:P, and N:P ratios compared to roots and stems ($P < 0.05$). As for KH, shoots showed significantly higher N concentrations and N:P ratios, coupled with lower C:N ratios than roots ($P < 0.05$). While LL did not show significant differences in stoichiometric traits between shoots and roots.

When comparing stoichiometric traits across different species, both PS and CM had considerably higher root N and P concentrations, and had significantly lower root C:N and C:P ratios compared to KH and LL ($P < 0.01$). PS exhibited significantly higher leaf C concentrations, stem C:N ratios, and leaf N:P ratios, alongside lower stem N:P ratios than CM ($P < 0.05$). KH had significantly lower shoot C:N and C:P ratios in comparison to LL ($P < 0.05$). The soil stoichiometric traits did not reveal significant differences among four plant species.

The first three components explained 93.7% of the total variations of the elemental contents for all the four species in our study region (PC1, PC2 and PC3 explained 52.7%, 28.4% and 12.6% of the variation, respectively). PC1 was most positively influenced by soil N concentration, while negatively influenced by soil C concentration; PC2 was most positively driven by soil P concentration. While CM displayed the largest niche sizes and LL displayed the least niche sizes. Leaf occupied the largest niche size compared with other organs for PS and CM.

Driving factors of plant stoichiometric traits along elevation gradients

The results from LMEMs indicate that MAT and MAP had no significant effect on plant stoichiometric traits (Fig. 5). However, species (PS, CM, KH, and LL) showed a significant negative effect on N concentrations (Effect Value [EV]: -2.94, $P < 0.001$) and P concentrations (EV: -0.34, $P < 0.001$), while showed a significantly positive impact on plant C:N ratios (EV: 7.79, $P < 0.001$) and C:P ratios (EV: 177.12, $P < 0.001$). Organs (root, stem, leaf, and flower) exhibited a significant positive effect on plant N concentrations (EV: 4.01, $P < 0.001$), P concentrations (EV: 0.23, $P < 0.001$) and C:P ratios (EV: -65.23, $P < 0.001$). Soil P concentrations had a significant positive impact on both plant N concentrations (EV: 7.39, $P = 0.03$) and P concentrations (EV: 1.72, $P = 0.002$). Soil C concentrations positively influenced plant C:N ratios (EV: 0.41, $P = 0.02$) and C:P ratios (EV: 10.97, $P < 0.001$), while soil N concentrations had a negative impact on plant C:N ratios (EV: -6.46, $P = 0.02$) and C:P ratios (EV: -137.52, $P = 0.002$).

As for the driving factors of plant stoichiometric traits along elevation gradients, climatic factors (MAT and MAP) could explain 87.90% and 62.67% of variances for plant C concentrations and C:N ratios. Biotic factors (species and organ), climatic factors, and soil nutrition explained 46.68%, 30.66%, and 22.66% of variances for plant N concentrations, respectively. Soil nutrition explained 60.31%, 47.86% and 59.17% of variances for P concentrations, C:P and N:P ratios, respectively.

DISCUSSION

Intraspecific and interspecific variation in stoichiometric traits along elevation gradients

This study found that, except for C and N:P ratio, the stoichiometric traits varied significantly among species and organs, indicating a high level of specificity in these traits in the QTP. The differential stoichiometric regulation among plant organs represents a fundamental strategy for optimizing resource acquisition, metabolic efficiency, and environmental adaptation (Wang et al. 2023; Zhang et al. 2020a). Flowers consistently demonstrating the highest C and N concentrations for PS, and this result is consistent with another alpine herb (*Gentiana rigescens*) conducted in Southwest China (Zhang et al. 2020b). The results indicate that flowers serve as the primary nutrient sink, necessitating greater allocations of carbon and nitrogen (Wang et al. 2023). Nutrient deficiencies trigger organ-dependent C reallocation strategies (Liu et al. 2024). Such trade-offs highlight why whole-plant biogeochemical models must resolve organ-specific stoichiometric responses rather than averaging across tissues (Leroux et al. 2017). Organ-specific stoichiometry is not merely a passive outcome of nutrient availability but an active modulator of plant adaptation (Leal et al. 2017; Lemmen et al. 2019). Therefore, embedding these organ-resolved dynamics into ecological models will be pivotal for predicting biogeochemical cycles (El-Sabaawi et al. 2023).

The observed stoichiometric plasticity across four alpine herbs demonstrated the dynamic adjustments in C:N:P ratios among organs and species, which is aligned with the concept of the elemental phenotype

(El-Sabaawi *et al.* 2023; Leal *et al.* 2017; Lemmen *et al.* 2019). In alpine ecosystems, where nutrient availability is limited by low temperatures, short growing seasons, and heterogeneous soils, such plasticity enables plants to reallocate elements to prioritize growth or stress defense (Zhang *et al.* 2020a). PS shifting N to leaves for photosynthesis and plant growth along elevation gradient (Fig. 2 and Fig. 3). While LL adapted to stressful environment by maintain stoichiometric homeostasis in our study site (Table S2). The variation in leaf N:P ratios among four alpine herbs highlights the species-specific nutrient utilization strategies in spite of relatively constant soil N:P ratios (Fig. 3).

Our results confirm the biogeochemical niche (BN) hypothesis, with four alpine herbs exhibit distinct elemental phenotypes reflecting evolutionary strategies for resource acquisition and utilization along elevation gradient, which support our first hypothesis (He *et al.* 2025; Peñuelas *et al.* 2019). The coexistence of four tested species exemplifies biogeochemical niche partitioning, such BN differentiation in alpine communities result in reduce competition in community and buffer metabolic disruptions caused by stoichiometric mismatches (Zhang *et al.* 2024). The divergent elemental acquisition and utilization strategies mark the potential strategies for species in faced with biotic and abiotic stresses (Fahimipour and Gross 2020; Sardans *et al.* 2015). LL's high N:P (> 16) and low P content reflect preferential N allocation in alpine area (Wang *et al.* 2022). In contrast, high N and P contents in PS and CM support ATP-intensive growth and competitive biomass accumulation (Hüseyinoğlu and Yalcin 2017).

Following the C-S-R (Competitor-Stressor-Ruderal) strategies theory, species with low N and P contents, high N:P ratios and low stoichiometry flexibility are classified as stress-tolerator, while species with high N and P contents are classified as competitor, and species with high stoichiometry flexibility are classified as ruderal (Grime, 2001; Güsewell, 2004; Peñuelas *et al.* 2019). Based on this theory, LL exhibit S (stressor) strategy, whereas PS and CM are categorized under CR (Competitor-Ruderal) strategies due to their high concentrations of both N and P (Table S2). The elevated N:P ratios observed in LL (Fig. 2) may partially explain its adaptability to stressful environments and the bimodal distribution of LL in degraded grasslands of the QTP (Wang *et al.* 2022). KH can be classified as a CS strategy for its competitive nutrient acquisition strategy (microbial symbiosis) and tolerance to P limitation (high N:P ratios). Previous studies have indicated that KH can recruit rhizosphere growth-promoting bacteria, thereby enhancing soil nutrient utilization despite low mineralization rates in alpine soils (Li *et al.* 2024). Given the harshness of their habitat, none of the four herbs demonstrated ruderal (R-selected) traits typically associated with rapid nutrient acquisition (Gibson 2008). Such CSR framework reveals divergent vulnerabilities among keystone alpine species under anthropogenic change. For LL would face high extinction risks from nitrogen deposition due to narrow biogeochemical niches and limited plasticity (Fig. 4). Meanwhile, CR-strategists such as PS and CM would eroding niche complementarity through competitive exclusion (Fig. 4).

Driving factors of stoichiometric traits along elevation gradients

Given the pronounced geographic gradients in climate, altitude, and soil conditions across the eastern Tibetan Plateau, we expected to detect the biogeographic pattern of stoichiometry of four alpine herbs along elevation gradients. Our findings of elevated N and P concentrations at higher elevations is consistent with observations in northern China's *Artemisia* species (Yang et al. 2015), which demonstrate the operation of the Growth Rate Hypothesis in alpine ecosystems (Elser et al. 2000). While C concentrations remained stable due to their fundamental structural role and metabolic processes (Gong et al. 2020; Qin et al. 2022b).

Notably, MAT emerged as the dominant climatic driver of stoichiometric variation, exerting positive effects on plant C content and C:N, C:P, and N:P ratios (Fig. 5). This aligns with global meta-analyses demonstrating that temperature gradients strongly regulate plant nutrient allocation strategies by modulating microbial activity, soil mineralization rates, and growth-resource trade-offs (Körner 2007; Reich and Oleksyn 2004). The pronounced MAT variability across our study sites (range: -2.97 to 10.32°C ; CV = 90.71%) likely amplified these thermal effects, low-temperature in alpine ecosystem would constraint the N and P cycling along elevation gradients (Sundqvist et al. 2013; Wang et al. 2022). In contrast, the limited impact of MAP (range: 537.09–769.09 mm; CV = 10.48%) on stoichiometric traits may be due to insufficient variation in precipitation. Together, these results advance our mechanistic understanding of how alpine plants reconcile the fundamental trade-off between growth and stress resistance through stoichiometric adjustments.

Our results demonstrated that phosphorus-related stoichiometric traits, including plant P content, N:P, and C:P ratios, were predominantly regulated by soil nutrient availability, particularly soil phosphorus concentrations. In contrast, carbon-related metrics, including C content and C:N ratios, were strongly driven by climatic factors, especially MAT, partially supporting our second hypothesis. These findings align with global-scale studies on plant stoichiometry (Du et al. 2020), suggesting that carbon-related traits are more indicative of the climatic regulation of plant growth and metabolism (Elser et al. 2000; Reich and Oleksyn 2004). On the other hand, nitrogen-related stoichiometric traits were influenced by a combination of climatic factors, soil nutrients, and species interactions, highlighting the greater complexity of nitrogen allocation strategies (Yu et al. 2011; Wang et al. 2019). The decoupled drivers of C-, N-, and P-related stoichiometry suggest that climate change will have asymmetric effects on plant elemental composition in QTP, where rising temperature may enhance C assimilation, reducing foliar C:N ratios due to increased N demand for growth (Reich and Oleksyn 2004).

CONCLUSIONS

Our study revealed pronounced intraspecific and interspecific variability in stoichiometric traits, with organs exhibiting greater heterogeneity in stoichiometric ratios. The four studied species demonstrate biogeochemical niche partitioning, particularly through LL's elevated N:P ratios - an adaptive strategy that maximizes phosphorus use efficiency in the P-limited alpine ecosystem, thereby reducing interspecific competition for this critical resource. Using the C-S-R framework, we identified CM as high-homeostasis species with competitive (CR) strategies, while LL's high N:P ratios suggest stress-tolerator

(SR) strategies. Climatic factors account for most of the variance in carbon-related stoichiometric traits along elevation gradient, and soil-available nutrients predominantly influenced phosphorus-related stoichiometric traits. These findings highlight the necessity of considering organ-specific and species-specific responses when investigating plant stoichiometry in alpine ecosystems. Ultimately, this research could enhance our understanding of nutrient cycling and plant adaptation strategies in high-altitude environments.

A key strength of this study lies in its systematic evaluation of multi-organ stoichiometric traits across four dominant QTP species, advancing beyond the common leaf-centric approach in alpine plant stoichiometry. Particularly, this research highlights the stoichiometric traits of flowers for PS, an aspect often overlooked in other studies. However, it is important to note that only PS sampled flowers in this research, and the stoichiometric traits of LL (4 sites) were relatively limited. Thus, we recommend a more comprehensive comparison of stoichiometric traits among different plant organs, not only focus on the commonly used three elements (C, N and P), but also concern with other elements such as K, Mg, Fe, Cu etc. This may enhance our understanding of stoichiometric theory related to plant adaptation in stressful environments within the QTP. Future studies should expand sampling of reproductive organs (flowers, seeds) to test their role in stoichiometric fitness trade-offs. Meanwhile, linking stoichiometric traits with functional traits (e.g., specific leaf area, root morphology) to decode the biogeochemical niche partitioning would enhance our understanding of elemental strategies in stressful condition.

Declarations

Authors' Contributions

Tudi Yimiti (Data curation, Formal analysis, Software, Visualization, Writing - Original Draft), Ziwei Zhang (Conceptualization, Data curation, Investigation, Methodology, Resources), Yiqian Du (Resources, Validation. Derong Su: Data curation, Resources), Xiaoyan Ping (Conceptualization, Funding acquisition, Supervision, Writing - Original Draft, Writing - Review & Editing).

Conflict of interest statement.

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.

Funding

This work was supported by the Second Tibetan Plateau Scientific Expedition and Research (Grant 2019QZKK0302-02) and Open bidding for selecting the best candidates for National Forestry and Grassland Administration (202401-06-04).

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Figures

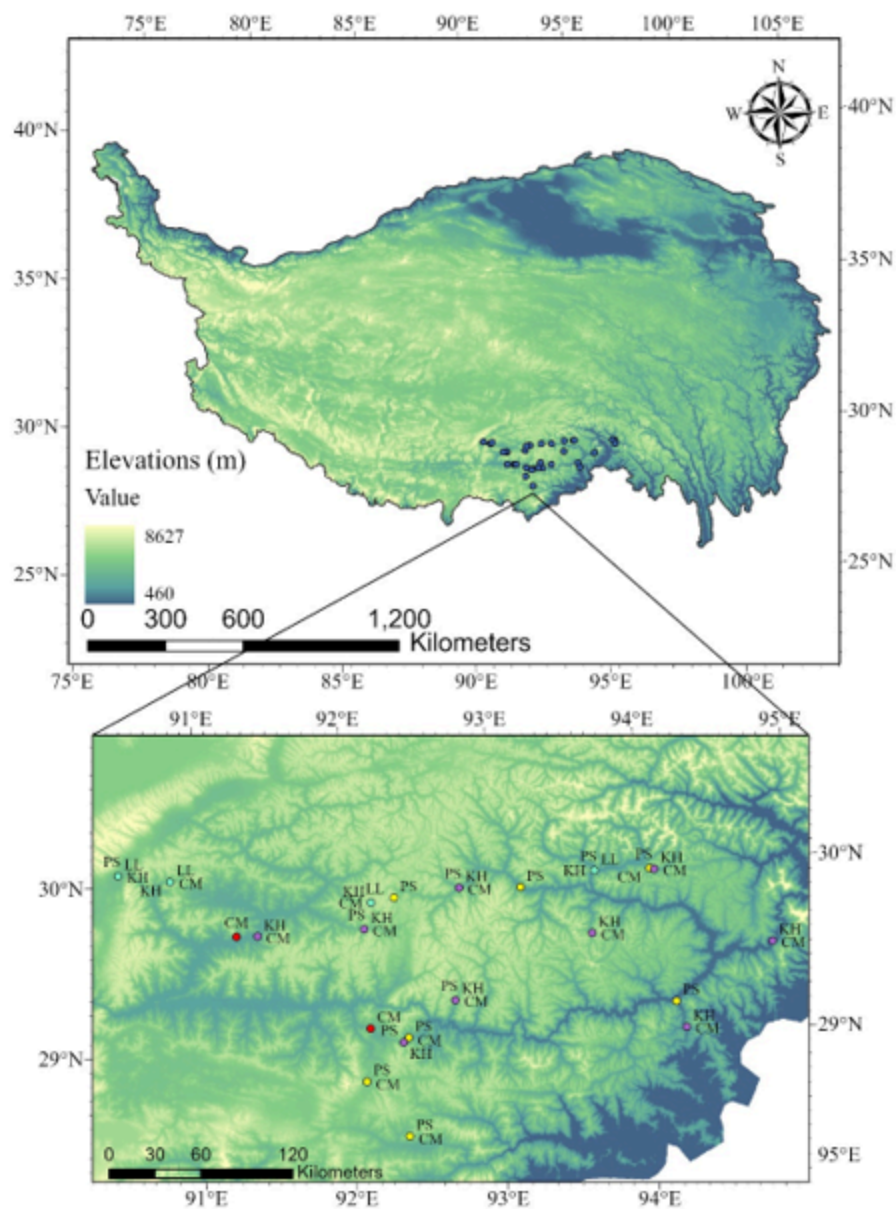


Figure 1

Sampling sites for assessing stoichiometric traits of four alpine herbs in the Qinghai-Tibet Plateau. CM represents *Carex moorcroftii*, PS represents *Potentilla saundersiana*, LL represents *Leontopodium leontopodioides* and KH represents *Kobresia humilis*.

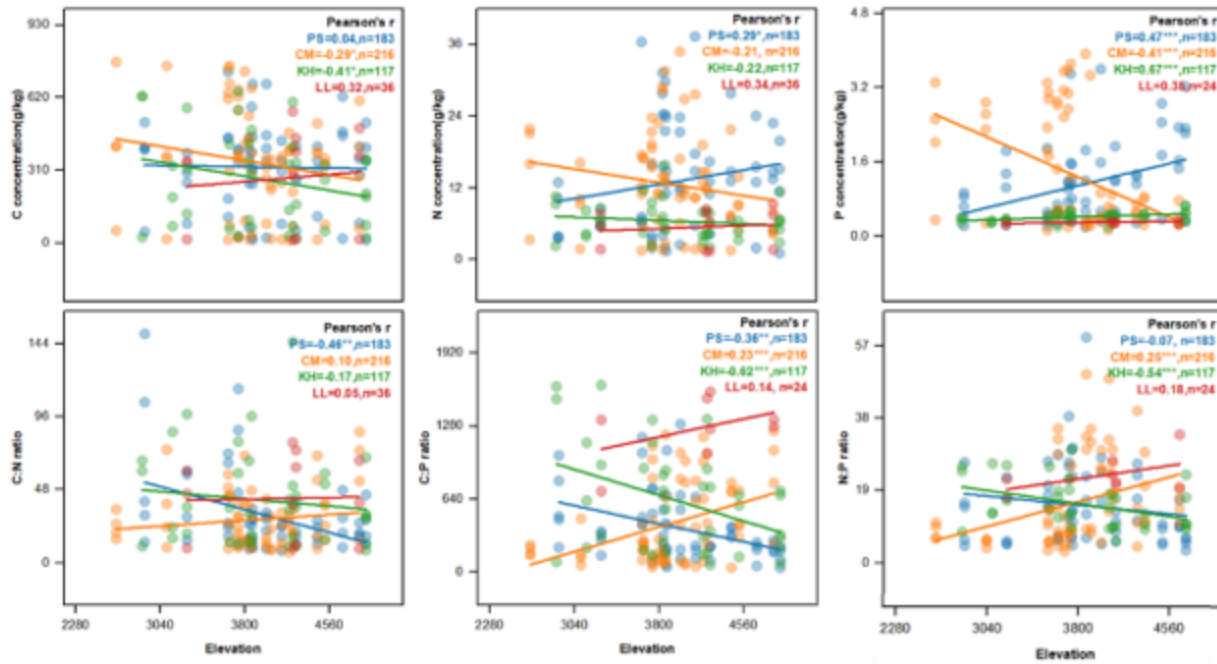


Figure 2

The stoichiometric traits of four alpine herbs along an elevation gradient. Pearson's correlation analysis assessed elevation effects on stoichiometric traits. PS: *Potentilla saundersiana*, CM: *Carex moorcroftii*, KH: *Kobresia humilis*, LL: *Leontopodium leontopodioides*. Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ (two-tailed test).

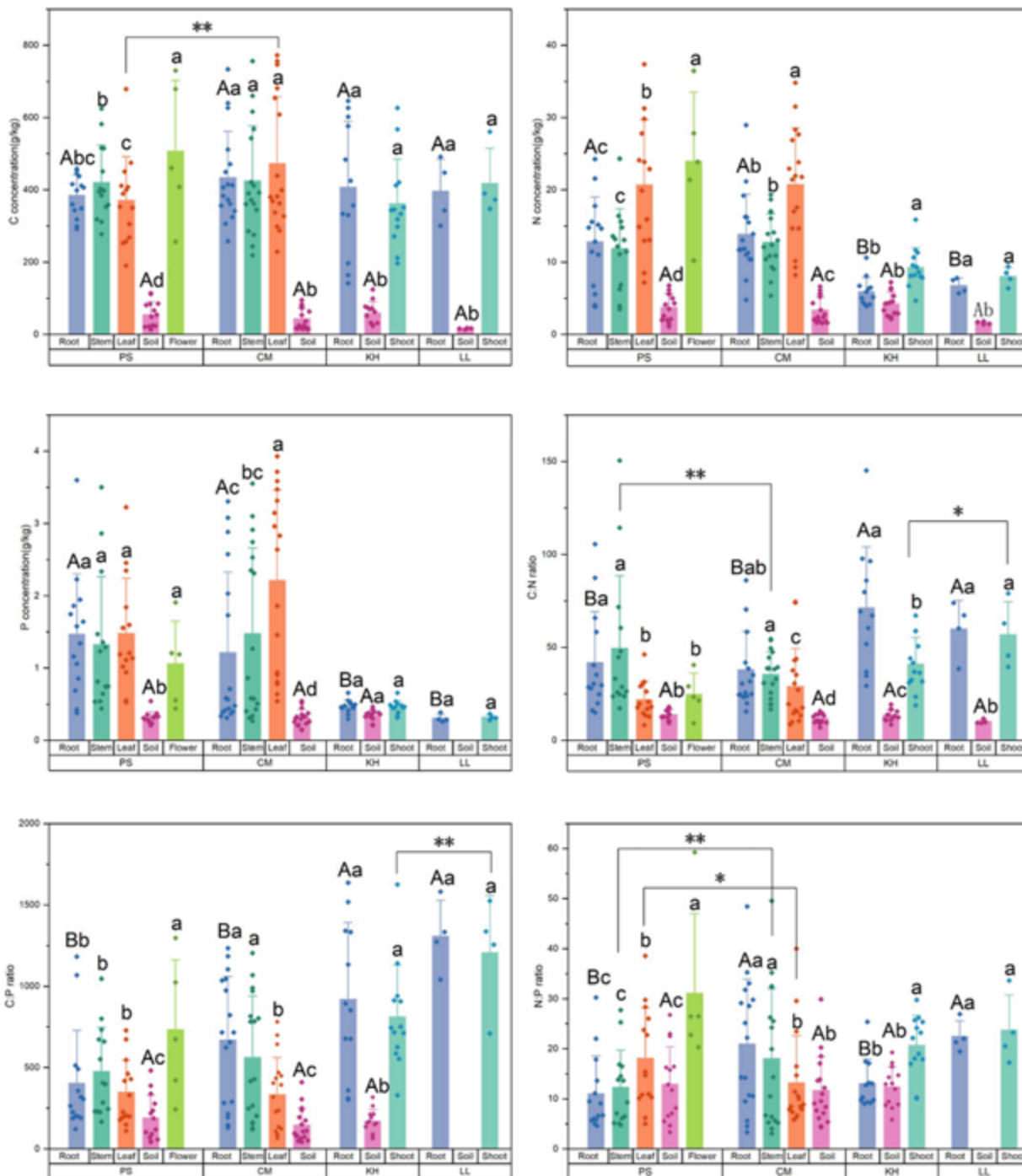


Figure 3

The intraspecific and interspecific difference in stoichiometric traits. Different lowercase letters indicate significant differences in stoichiometric traits among different organs within the same plant species ($P < 0.05$). Different uppercase letters signify significant differences in stoichiometric traits of roots and soil among various species ($P < 0.05$). * and ** indicate significant differences in stoichiometric traits of stem and leaf between PS and CM, and in shoot stoichiometric traits between KH and LL at the 0.05 and 0.01 levels, respectively.

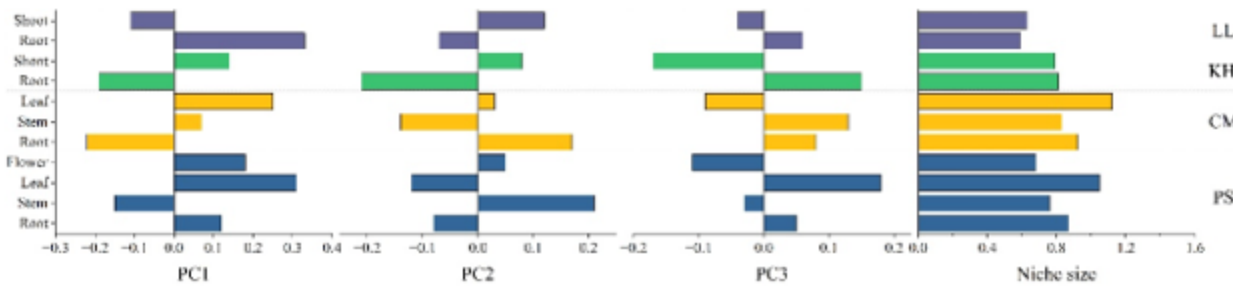


Figure 4

The loading scores of each plant organ of four plant species for the first three PCA components and hypervolume niche size

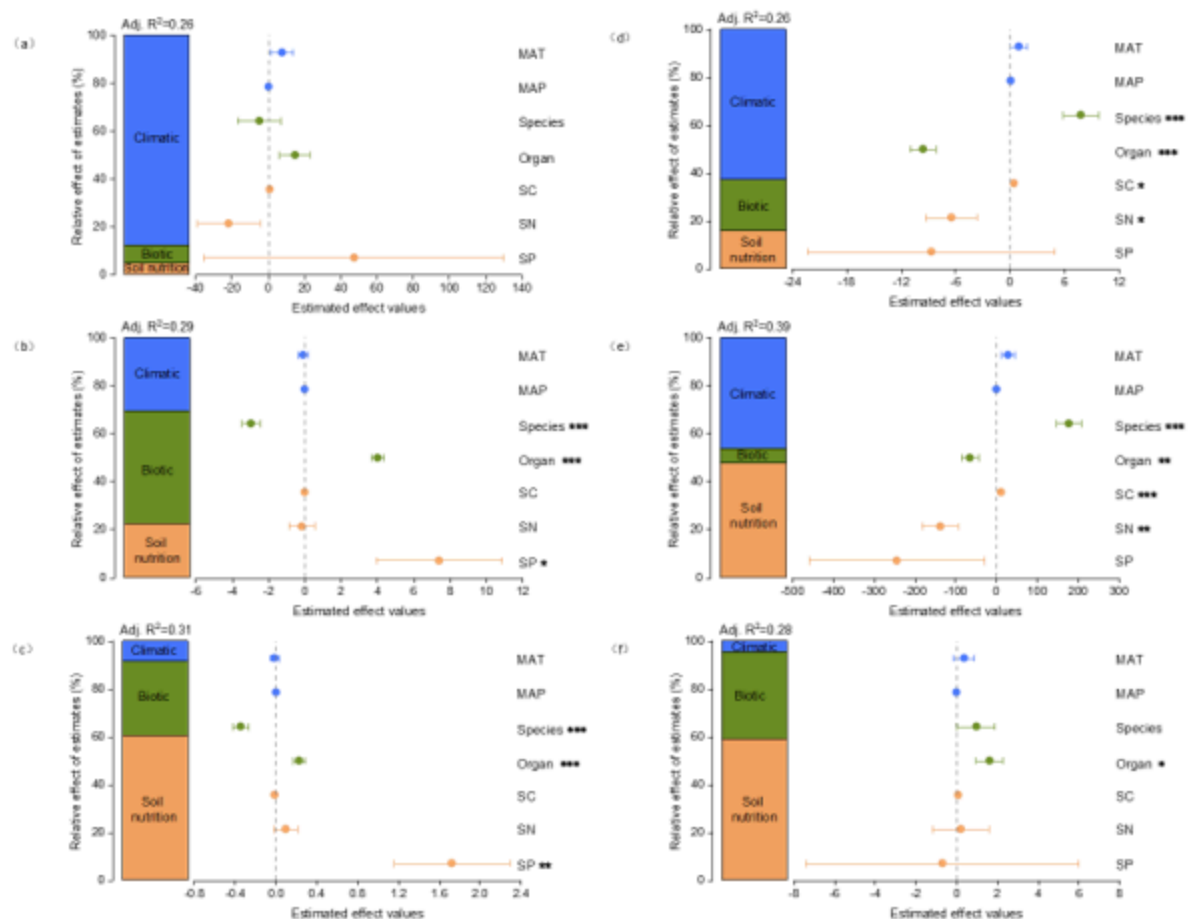


Figure 5

The estimated effect values and relative importance of climatic factors, soil nutrition, and biotic factors for the plant stoichiometric traits along elevation gradient. (a), (b), (c), (d), (e), and (f) represent plant C, N, and P concentrations, and C:N, C:P and N:P ratios, respectively. SC, SN, and SP represent soil organic carbon, soil total nitrogen, and soil total phosphorus contents, respectively. Species refer to PS, CM, KH,

and LL, and organs refer to root, stem, leaf, and flower, respectively. The relative importance of climatic factors, soil nutrition, and biotic factors were calculated based on GLMMs analysis, and the estimated effect values were calculated based on LMEMs analysis. *, **, and *** indicate significant differences at the 0.05, 0.01, and 0.001 levels, respectively.