

Divergent drivers govern carbon allocation in the alpine giant herb *Rheum nobile*

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Abstract

The carbon economy of alpine plants, particularly the allocation of non-structural carbohydrates (NSCs), is fundamental to survival in extreme environments. However, how iconic giant herbs partition these resources among organs across steep environmental gradients remains poorly understood. We investigated the giant herb *Rheum nobile* at five sites on the Tibetan Plateau, quantifying NSC concentrations in roots, stems, leaves, and its prominent bracts to elucidate organ-specific allocation patterns and their key drivers. Overall, NSC concentrations were highest in roots (28.5%), followed by stems (25.1%), bracts (23.6%), and leaves (22.9%). Crucially, the drivers of NSC variation differed markedly among organs. Stem, root, and bract NSC concentrations were predominantly shaped by abiotic factors; for example, stem NSCs showed a hump-shaped relationship with elevation and mean annual temperature, while root NSCs displayed a U-shaped response to a soil fertility gradient. In contrast, leaf NSCs were mainly governed by the plant's morphological traits, exhibiting complex nonlinear relationships with plant height and stem diameter. These findings reveal a finely tuned, organ-level carbon allocation strategy in *Rheum nobile*, where investment in storage and support organs is strongly coupled to the external environment, while carbon status in photosynthetic leaves is regulated by plant size and architecture. This provides novel insights into the physiological mechanisms underpinning plant adaptation to high-altitude ecosystems.

1. Introduction

The Tibetan Plateau, known as the “Third Pole” of the Earth, with its extreme habitats characterized by alpine hypoxia, intense radiation, dramatic temperature fluctuations, and nutrient scarcity, provides a natural laboratory for studying plant adaptive evolution (Ren et al., 2023; Deng et al., 2024). Under such rigorous selective pressure, plants have evolved efficient strategies for carbon acquisition and allocation, which are crucial for their survival and reproduction. Non-structural carbohydrates (NSCs), comprising soluble sugars (SS) and starch (ST), serve as temporary storage pools for photosynthetic products and act as central signaling molecules in plants (Andrew et al., 2013; He et al., 2020; Meghan et al., 2022). Their dynamic balance directly determines plant stress resistance and resilience (Leonie et al., 2018). Specifically, SS function as osmoregulatory substances, providing immediate protection against stresses like drought and cold, whereas ST serves as a long-term energy reserve, hydrolyzed to meet demand when necessary (Henry et al., 2013; Michael et al., 2015; Liu et al., 2025). NSCs are thus considered key physiological buffers for plants coping with environmental stress. However, the underlying mechanisms of how NSCs contribute to the adaptation of Tibetan Plateau plants to extreme environments require further in-depth investigation.

A plant's ability to withstand adversity depends not only on its overall NSCs pool but also critically on the allocation strategies among different organs, which is a core manifestation of resource trade-off theory (Dietze et al., 2014). Typically, NSCs are preferentially allocated to organs with the most urgent demand or those critical for survival. Studies have shown that mild drought may promote NSCs accumulation in roots, while severe drought might direct NSCs to meristematic tissues to prepare for recovery (Ngugi et

al., 2003; Liu et al., 2019). As carbon “source” organs, leaves often exhibit significant accumulation of SS under drought stress to maintain physiological functions (Liu et al., 2019), whereas the response of NSCs reserves in stems, which act as conductive hubs, displays high complexity and species specificity (Ido et al., 2024). Research on the Tibetan Plateau has commonly observed NSCs enrichment in below-ground organs (e.g., roots) (Zhu et al., 2012; Zhang et al., 2021), indicating that reserves in persistent tissues are crucial for long-term adaptation. Temperature and moisture are key environmental factors regulating this allocation pattern, driving interspecific and intraspecific differences in NSCs allocation by influencing processes such as photosynthesis, respiratory consumption, and source-sink relationships (Shi et al., 2015; Zhang et al., 2024).

The regulation of plant NSCs allocation by environmental factors is complex and varied. For instance, in alpine meadows on the southeastern margin of the Tibetan Plateau, the NSCs allocation patterns of two *Carex* species showed significant differences along a soil moisture gradient (Li and Zhang, 2025). Furthermore, the effects of hydrothermal factors often exhibit species-specificity and even organ-specificity. Liu et al. (2025) found that NSCs content in *Picea crassifolia* was positively correlated with mean annual temperature but negatively correlated with mean annual precipitation. More complexly, Zhang et al. (2024), in a study on alpine coniferous forests, further revealed that leaf NSCs, including total NSCs and soluble sugars, were coordinated with the leaf economics spectrum, and this coordination itself was driven by local temperature and precipitation patterns. Therefore, leaf functional traits should be regarded as a core dimension for deciphering the environmental responses and adaptation strategies of NSCs dynamics in plants. The coordination between these traits and the leaf economics spectrum is expected to reveal the ecological strategy mechanisms underlying carbon allocation.

However, existing research on plant NSCs allocation on the Tibetan Plateau has predominantly focused on trees and common herbaceous species. Systematic studies at the organ level for endemic flagship species remain poorly understood. *Rheum nobile* Hook. f. & Thomson, a perennial giant herb of the genus *Rheum* (Polygonaceae), is an iconic species of alpine scree slopes at elevations of 4000–4800 m (Zhang et al., 2010). Its tower-like inflorescence, reaching up to 2 meters in height, and translucent bracts form a unique “greenhouse” structure, representing a morphological adaptation to the extreme cold environment (Song et al., 2013, 2024). Current understanding of its adaptation mechanisms, particularly the allocation patterns and regulatory mechanisms of NSCs among different organs (such as the functionally specialized bracts, stems, leaves, and roots), is largely unknown (Li et al., 2023; Wang et al., 2018). Therefore, our study proposes the following hypotheses: (1) NSCs content differs significantly among organs of *Rheum nobile*, with roots, as persistent organs, exhibiting the highest reserves; (2) Compared to the specialized bracts, leaf functional traits, as the primary photosynthetic source, exert a stronger influence on the overall NSCs allocation; (3) Low temperature and drought are the dominant environmental factors driving inter-organ NSCs allocation in *Rheum nobile*, with the specialized bracts showing a unique response in NSCs accumulation to cold stress. To test these hypotheses, we established five sampling sites along an environmental gradient on the Tibetan Plateau, systematically measuring NSCs content in the roots, stems, leaves, and bracts of *Rheum nobile*, while simultaneously

recording plant functional traits and key environmental factors. This study aims to: (1) reveal the distribution patterns of NSCs in different organs of *Rhcom nobile*; and (2) elucidate the relative contributions of environmental factors (moisture, temperature) and plant functional traits to NSCs allocation. The findings will provide deep insights into the intrinsic carbon trade-off strategies employed by *Rhcom nobile* to adapt to the extreme alpine environment, offering new theoretical perspectives for understanding the physiological and ecological adaptation mechanisms of alpine plants.

2. Materials and Methods

2.1 Study Area

This study was conducted along an environmental gradient from the southeastern margin of the Tibetan Plateau to the Hengduan Mountains of China. Five high-altitude sampling sites were selected: Sejila Mountain (Linzhi city, Xizang), Longzi County (Shannan city, Xizang), Yadong County (Rikaze city, Xizang), Lower Yadong (Rikaze, Xizang), and Geza Township (Shangri-La, Yunnan). The elevation range of these sites was 4438–4786 m above sea level. The mean annual temperature (MAT) ranged from – 3.23 to 2.16°C, and the mean annual precipitation (MAP) ranged from 512.5 to 941.5 mm. The habitats encompassed alpine valleys, periglacial landforms, scree slopes, and alpine meadows. The study species, *Rheum nobile*, an endemic plant of this region, was widely distributed on the scree slopes and edges of alpine meadows at the aforementioned sites.

2.2 Sample collection and processing

Field sampling was carried out during the flowering and fruiting period of *Rhcom nobile* (August to September 2024) across the selected geographical regions. Yadong County, Rikaze City, included two independent sampling locations (Yadong and Xiayadong). At each sampling site, ten healthy, flowering/fruiting individuals of *Rhcom nobile* were randomly selected, resulting in a total of 50 plant samples. In Shangri-La, five plants were at the flowering and fruiting stage, and the remaining five were at the vegetative growth stage. The precise geographical coordinates (longitude, latitude) and elevation of each individual were recorded using a GPS device during sampling.

For each plant individual, tissues from roots, stems, leaves, and bracts were collected separately as follows: (1) Roots: The soil around the root zone was carefully excavated, and fine, absorptive roots were clipped. A fresh weight of at least 10 g of root tissue was collected per individual. (2) Stems: An approximately 5 cm long segment was cut from the middle part of the stem. (3) Leaves and Bracts: Two healthy, intact mature leaves and bracts were selected from each plant.

All plant samples were immediately preserved in silica gel for subsequent NSCs analysis. Leaves and bracts intended for functional trait measurements were placed in paper envelopes for transport to the laboratory. Additionally, approximately 500 g of soil was collected from the rhizosphere (0–20 cm) of each *Rhcom nobile* individual. The soil samples were sieved (2 mm mesh) to remove gravel and root

debris, air-dried naturally, and stored for soil physicochemical analysis. Long-term climatic data (MAT, MAP, and climatic moisture deficit (CMD) index) for each site were obtained using the ClimateAP software (Wang et al., 2016) based on the recorded geographic coordinates and elevation.

2.3 Plant non-structural carbohydrates and functional traits

The NSCs content in different organs (roots, stems, leaves, bracts) of *Rhcum nobile* was determined. SS and ST concentrations were measured separately using the anthrone-sulfuric acid colorimetric method. The total NSCs content was calculated as the sum of SS and ST. Concurrently, functional traits of leaves and bracts were measured, including: (1) Morphological traits: Leaf area (LA), bract area (BA), specific leaf area (SLA, calculated as leaf area divided by leaf dry mass), and specific bract area (SBA). (2) Chemical traits: Leaf nitrogen content (LNC), leaf phosphorus content (LPC), bract nitrogen content (BNC), and bract phosphorus content (BPC).

Leaf and bract areas were measured using a Li-3000 leaf area meter. Fresh leaves/bracts were weighed, then oven-dried at 65°C to constant weight (approximately 72 hours), and weighed again to obtain dry mass. The dried samples were ground and passed through a 0.52 mm sieve. Nitrogen content was determined using an elemental analyzer, and phosphorus content was measured using the molybdenum-antimony anti-spectrophotometric method.

2.4 Soil physicochemical properties

Soil physicochemical properties were analyzed following standard methods, primarily referencing “Soil Agricultural Chemistry Analysis (Third Edition)” (Bao, 2000). The specific analyses included: Soil organic carbon (SOC) was measured using the potassium dichromate volumetric method. Total nitrogen (TN) was determined by the Kjeldahl method. Total phosphorus (TP) was measured using the NaOH fusion-Mo-Sb anti-spectrophotometric method. Total potassium (TK) was determined by HF digestion-flame photometry. Available nitrogen (AN) was measured using the alkaline hydrolysis diffusion method. Available phosphorus (AP) was determined by the HCl-H₂SO₄ extraction method. Available potassium (AK) was measured by extraction with 1 mol/L ammonium acetate followed by flame photometry. Soil pH was measured using a pH meter (Thermo Orion-868) at a soil-to-water ratio of 1:2.5. Ammonium nitrogen (NH₄⁺-N) was determined by the indophenol blue colorimetric method, and nitrate nitrogen (NO₃⁻-N) was determined by ultraviolet spectrophotometry.

2.5 Data analysis

To reveal the allocation patterns of NSCs across different organs and geographical populations, one-way analysis of variance (ANOVA) followed by LSD post-hoc tests was performed to examine differences in NSCs (and their components), plant traits, soil properties, and organ-specific (root, stem, leaf, and bract) NSCs concentrations among different geographical distribution areas. Principal Coordinates Analysis (PCoA) was used to visualize the variation in organ-specific NSCs across the geographical distribution. A

Mantel test was employed to analyze the relationship between the Euclidean distance of NSCs composition and geographical distance.

Subsequently, to investigate the effects of various environmental and biological factors on NSCs content:

A Pearson correlation network was constructed to explore relationships between NSCs content and abiotic factors (climatic condition, soil fertility), plant growth (plant height, ground diameter), and functional traits (leaf and bract traits) of *Rhcam nobile*. Principal component analysis (PCA) was performed on soil physicochemical properties. The scores of the first principal component axis, which integrated plant availability of soil resources, were used to represent "soil fertility" (Mayer et al., 2020). To quantify the multidimensional trade-offs among traits of leaf and bract, PCA was also conducted to characterize the leaf economic spectrum and bract economic spectrum based on varimax rotation, showing the "conservation" and "acquisition" with the first principal components. Bivariate linear regression analysis was then performed between these PCA scores and the significantly correlated factors identified. Finally, bidirectional stepwise regression based on the Akaike Information Criterion (AIC) (using the stepAIC function in the MASS package) was used to select key predictor variables from the full set. The stepwise regression aimed to minimize AIC by automatically adding and removing variables to identify the optimal subset. Generalized linear mixed models were fitted using the lme4 package to analyze the data with location as a random factor. To assess the relative importance of biotic and abiotic factors on NSCs content, hierarchical partitioning analysis was performed using the glmm.hp package. This analysis calculated the independent contribution of each predictor variable to the total marginal R^2 , thereby determining the relative importance of each environmental factor (Lai et al., 2022,2023). All statistical analyses were conducted in R 4.5.2, and graphs were plotted using the ggplot2 package.

3.Results

3.1 Variations in soil physicochemical properties, plant traits, and non-structural carbohydrates composition

Significant variations in soil properties, plant traits, and NSCs composition were observed among the five regions (Table 1). Soil pH was highest in Shangri-La and lowest in Xiayadong and Yadong. In contrast, SOC and AN showed the opposite trend. AP was significantly higher in Sejila and Yadong than in Shangri-La and Longzi County. No significant differences in AK were detected among the five regions. TN was highest in Yadong and Xiayadong and lowest in Shangri-La. The highest TP was found in Longzi county, while the lowest was in Sejila. TK in Shangri-La was significantly higher than in the other four regions. $\text{NH}_4^+\text{-N}$ content was lowest in Shangri-La (1.69 ± 1.29), significantly lower than the other four sites ($p < 0.05$). In Longzhi Sejila, Xiayadong, and Yadong, $\text{NH}_4^+\text{-N}$ contents were 15.35 ± 11.81 , 14.77 ± 9.66 , 11.2 ± 7.16 , and 9.99 ± 7.57 , respectively, with no significant differences among them ($p > 0.05$). Soil nitrate nitrogen ($\text{NO}_3^-\text{-N}$) content was highest in Sejila (4.94 ± 2.73), significantly higher than in Shangri-La,

Longzi, Xiayadong, and Yadong ($p < 0.05$). Shangri-La had the lowest NO_3^- -N content (1.56 ± 1.48), significantly lower than the other sites ($p < 0.05$). Regarding plant traits, the ground diameter of *Rheum nobile* individuals was significantly larger in Sejila than in the other four regions, with the smallest ground diameter (4.66 cm) observed in Yadong. Plant height was greatest in Sejila (1.79 m) and lowest in Shangri-La (0.79 m). For NSCs components, stem ST content was highest in Yadong, significantly exceeding that in other regions, and lowest in Longzi county (132.20 mg/g). SS content in roots, leaves, bracts, and stems, as well as the ST content in roots, leaves, and bracts, was highest in Shangri-La and lowest in Lower Yadong. Soluble sugar content in all four organs and starch content in roots and leaves were highest in Shangri-La and lowest in Lower Yadong. Bract starch content was highest in Longzi County and lowest in Lower Yadong. Stem starch content was highest in Yadong and lowest in Longzi County.

LA and BA were the largest in Shangri-La ($1154.3 \pm 316.55 \text{ cm}^2$ and $424.25 \pm 295.27 \text{ cm}^2$, respectively), with LA significantly larger than in other regions, and smallest in Longzi County ($533.66 \pm 223.3 \text{ cm}^2$ and $292.11 \pm 66.53 \text{ cm}^2$, respectively). SLA and SBA were both highest in Yadong and lowest in Sejila and Lower Yadong, respectively. LNC was highest in Shangri-La (23.14%), significantly higher than in Lhünzê and Lower Yadong, and lowest in Lhünzê (15.42%). LPC was relatively high in Longzi and Shangri-La (2.29% and 2.21%, respectively), significantly higher than in Lower Yadong (1.56%), and Lower Yadong was significantly lower than all other regions, while no significant differences were found among Yadong, Sejila, and Shangri-La. BNC was highest in Yadong (19.50%), significantly higher than in Longzi (14.70%), with no significant differences between other regions and Yadong or Lhünzê, although Sejila showed high variation. BPC was highest in Yadong (2.14%) and lowest in Xiayadong (1.48%), with a significant difference between these two, while the other regions fell in between with no significant differences. (Table 1).

Table 1

Soil physicochemical properties, plant traits, and non-structural carbohydrates composition across the different regions. Different lowercase letters within the same row indicate significant differences ($P < 0.05$) based on one-way analysis of variance (ANOVA) followed by LSD post-hoc tests. SOC, soil organic carbon; AN, available nitrogen; AP, available phosphorus; AK, available potassium; TN, total nitrogen; TP, total phosphorus; TK, total potassium; $\text{NH}_4^+\text{-N}$, ammonium nitrogen; $\text{NO}_3^-\text{-N}$, nitrate nitrogen; LA, leaf area; SLA, specific leaf area; LNC, leaf nitrogen content; LPC, leaf phosphorus content; BA, bract area; SBA, specific bract area; BNC, bract nitrogen content; BPC, bract phosphorus content.

Type	Shangri-La city	Longzi county	Sejilashan, Linzhi city	Xiayadong, Rikaza city	Yadong, Rikaza city
Soil pH	5.97 ± 0.94a	5.60 ± 0.18ab	5.39 ± 0.38b	4.80 ± 0.17c	4.82 ± 0.24c
SOC/g·kg ⁻¹	32.94 ± 25.49c	86.84 ± 33.61b	68.09 ± 42.09b	124.68 ± 27.21a	91.50 ± 27.34b
Soil AN/mg·kg ⁻¹	175 ± 108.99c	535.7 ± 168.3ab	435.3 ± 169.77b	569.1 ± 101.85a	568.9 ± 131.12a
Soil AP/mg·kg ⁻¹	8.58 ± 6.02b	8.50 ± 4.04b	18.96 ± 15.16a	12.05 ± 2.87ab	16.93 ± 9.44a
Soil AK/mg·kg ⁻¹	53.60 ± 40.62a	80.40 ± 16.95a	97.40 ± 80.69a	76.50 ± 43.65a	56.60 ± 39.95a
Soil TN/g·kg ⁻¹	2.92 ± 1.86c	5.60 ± 1.39ab	4.26 ± 1.93bc	6.52 ± 1.45a	5.99 ± 2.28a
Soil TP/g·kg ⁻¹	1.04 ± 0.25ab	1.06 ± 0.09a	0.86 ± 0.17c	0.89 ± 0.11bc	1.03 ± 0.24ab
Soil TK/g·kg ⁻¹	22.29 ± 3.3a	17.64 ± 2.37bc	16.92 ± 2.10c	19.32 ± 1.98b	18.06 ± 2.50bc
Soil $\text{NH}_4^+\text{-N}$ /mg·kg ⁻¹	1.69 ± 1.29b	15.35 ± 11.81a	14.77 ± 9.66a	11.2 ± 7.16a	9.99 ± 7.57a
Soil $\text{NO}_3^-\text{-N}$ /mg·kg ⁻¹	1.56 ± 1.48c	2.65 ± 1.82bc	4.94 ± 2.73a	2.92 ± 0.54bc	3.27 ± 1.85b
Ground diameter/cm	4.80 ± 0.76c	6.24 ± 1.41b	7.20 ± 1.02a	5.24 ± 0.75c	4.66 ± 0.98c
Height/m	0.79 ± 0.48d	1.48 ± 0.41b	1.79 ± 0.23a	1.13 ± 0.14c	1.14 ± 0.25c
Root soluble sugar/%	17.24 ± 7.79a	8.66 ± 1.72b	9.09 ± 3.1b	8.51 ± 1.07b	10.5 ± 2.65b
Root starch/%	19.54 ± 5.4a	15.28 ± 1.57b	14.98 ± 2.86b	13.51 ± 2.75b	16.03 ± 3.49b
Leaf soluble sugar/%	9.77 ± 1.71a	9.01 ± 1.11ab	7.61 ± 1.43bc	7.15 ± 2.03c	7.38 ± 1.46c

Type	Shangri-La city	Longzi county	Sejilashan, Linzhi city	Xiayadong, Rikaza city	Yadong, Rikaza city
Leaf starch/%	14.84 ± 2.38a	12.94 ± 2.21ab	12.56 ± 2.84ab	12.06 ± 1.98b	13.74 ± 3.52ab
Bract soluble sugar/%	9.9 ± 1.18a	9.67 ± 2.22a	8.1.6 ± 1.71a	6.26 ± 1.92b	8.37 ± 1.81a
Bract starch/%	13.66 ± 1.67a	15.03 ± 4.07a	13.15 ± 1.93a	12.41 ± 1.87a	14.54 ± 3.86a
Stem soluble sugar/%	10.66 ± 6.29a	8.03 ± 1.5a	10.33 ± 1.62a	7.7 ± 3.25a	10.32 ± 2.46a
Stem starch/%	13.73 ± 1.13b	13.22 ± 1.28b	13.4 ± 1.64b	13.84 ± 1.68b	16.76 ± 3.39a
LA/cm ²	1154.3 ± 316.55a	607.01 ± 226.55b	533.66 ± 223.3b	696.58 ± 164.82b	649.9 ± 257.08b
SLA/cm ² ·g ⁻¹	120.78 ± 10.17cd	162.66 ± 46.55ab	116.28 ± 15.92d	142.33 ± 18.99bc	184.51 ± 35.58a
LNC/g·kg ⁻¹	23.14 ± 5.51a	15.42 ± 2.47c	20.93 ± 3.31ab	18.82 ± 3.91bc	21.98 ± 3.5ab
LPC/g·kg ⁻¹	2.21 ± 0.4a	2.29 ± 1a	1.83 ± 0.27ab	1.56 ± 0.44b	1.94 ± 0.4ab
BA/cm ²	424.25 ± 295.27a	345.54 ± 145.49a	292.11 ± 66.53a	344.67 ± 100.27a	363.44 ± 119.74a
SBA/cm ² ·g ⁻¹	220.49 ± 38ab	242.44 ± 52.39a	215.17 ± 29.09ab	204.32 ± 25.11b	248.34 ± 35.19a
BNC/g·kg ⁻¹	15.43 ± 2.28ab	14.7 ± 2b	17.37 ± 7.95ab	16.1 ± 3.03ab	19.5 ± 4.05a
BPC/g·kg ⁻¹	1.74 ± 0.43ab	2.01 ± 0.38ab	1.89 ± 0.63ab	1.48 ± 0.43b	2.14 ± 0.86a

3.2 Comparison of non-structural carbohydrates across different organs

Among the four organs analyzed, the highest NSCs content in *Rheum nobile* was found in the roots, followed by the stems, bracts, and leaves. The composition of NSCs in *Rheum nobile* varied across the different geographical regions (Fig. 2A). Specifically, leaf and root NSCs contents were significantly higher in the Shangri-La region compared to other regions. The highest bract NSCs content was observed in Longzi County, while the highest stem NSCs content was found in the Yadong region. Conversely, the lowest stem NSCs content was recorded in Longzi County, and the lowest leaf, bract, and root NSCs contents were all observed in the Xiayadong region (Fig. 2B). Significant differences in total NSCs content of *Rheum nobile* were detected among the five locations. PCoA analysis indicated that the variation in NSCs content across different organs was significantly associated with geographical

distance ($P < 0.05$) (Fig. 2C). However, Mantel test results revealed that this variation was not directly caused by geographical distance itself, suggesting that environmental filtering plays a dominant role in driving the allocation of NSCs among different organs (Fig. 2D).

3.3 Correlation among climatic conditions, plant traits, soil fertility, and non-structural carbohydrates

Pearson correlation analysis revealed significant relationships between NSCs content in various organs and environmental/plant traits (Fig. 3). Root NSCs content showed significant positive correlations with MAP, soil pH, TK LA, and LNC. In contrast, it was significantly negatively correlated with SOC, AN, AK, plant height, and ground diameter. Leaf NSCs content was significantly positively correlated with MAP, soil pH, and root NSCs content, but significantly negatively correlated with SOC content, ground diameter, and plant height. Bract NSCs content exhibited a significant negative correlation with MAT and LNC, and a significant positive correlation with SBA and leaf NSCs content. Stem NSCs content showed significant correlations with soil pH and BNC (Fig. 3).

3.4 Bivariate relationship between non-structural carbohydrates and biotic, abiotic factors

Regression analyses examining the effects of climatic and growth factors on NSCs content in different organs revealed distinct patterns (Fig. 4). Leaf NSCs content exhibited a non-linear relationship with growth factors, initially decreasing, then increasing, and finally decreasing again with increasing ground diameter and plant height. Bract NSCs content showed complex responses: it initially decreased and then increased with rising elevation; displayed an initial decrease, followed by an increase and a subsequent decrease with increasing MAT; and initially increased, then decreased, and increased again with increasing climatic moisture deficit index. Stem NSCs content initially increased and then decreased with rising elevation and MAT, while it initially decreased and then increased with increasing MAP. No clear trends were observed between the analyzed climatic/growth factors and root NSCs content (Fig. 4).

Regression analysis indicated that soil fertility had no significant effect on leaf, bract, or stem NSCs content, but it had a significant non-linear effect on root NSCs content, which initially decreased and then increased with increasing soil fertility (Fig. 5). Similarly, PCA on leaf and bract functional traits yielded a principal component (PC1) representing their resource-use strategy. Regression analysis between this PC1 (leaf/bract resource-use strategy) and NSCs content in various organs showed a significant negative correlation with root NSCs content. Bract functional traits (represented by their own PC1) showed no significant correlation with the NSCs content of any organ (Fig. 6).

3.5 Relative importance of biotic and abiotic factors on non-structural carbohydrates in different organs

Hierarchical partitioning analysis quantified the relative contributions of different factor groups to NSCs content in each organ (Fig. 7). Abiotic factors (climate and soil) contributed substantially to the variation in NSCs content across all organs, particularly for roots, where their relative contribution reached 80% (Fig. 7G). Growth factors contributed considerably to leaf NSCs content (Fig. 7A) but had lower contributions to the other organs. Leaf functional traits accounted for approximately 20% of the variation in NSCs content across all four organs. Bract functional traits contributed to the variation in NSCs content in leaves, stems, and bracts (but not roots), with the highest contribution to bract NSCs content (Fig. 7C) and the lowest to leaf NSCs content. Growth factors contributed the most to the stem NSCs content, followed by leaf traits (Fig. 7E).

Among the growth factors, which were the most important for leaf NSCs content, ground diameter had a significant negative effect, while plant height and SLA had significant positive effects (Fig. 7B). For bract NSCs content (Fig. 7D) and stem NSCs content (Fig. 7F), where abiotic factors were most important, MAT and LA had significant negative effects, while MAP and the climatic moisture deficit index had significant positive effects; other factors' effects were non-significant. MAP also exhibited a significant negative effect on root NSCs content (Fig. 7H).

4. Discussion

4.1 Allocation pattern of non-structural carbohydrates in *Rheum nobile*

Consistent with our first hypothesis that carbon allocation prioritizes storage in perennial high-altitude plants, our results demonstrate that NSCs content in *Rheum nobile* was highest in the roots, followed by the stems, bracts, and leaves. This pattern aligns with observations in other woody species from the Tibetan Plateau, such as *Quercus aquifolioides* (Zhu et al., 2012). However, compared with the herbaceous plants *Artemisia gmelinii* and *Hippophae rhamnoides* subsp. *Yunnanensis* in southeastern Tibet, the root NSCs content of *Rheum nobile* was relatively high; the root NSC content in Shangri-La was twice that of *Artemisia gmelinii* (Ai et al., 2024). The differential NSCs allocation across organs reflects their distinct physiological roles: leaves are the primary site of carbon assimilation, stems serve as conduits for transport and short-term storage, and roots act as major long-term carbon reservoirs (Hartmann et al., 2013). The relatively low NSCs content in leaves suggests rapid translocation of photoassimilates to support metabolic demands in other organs rather than accumulation at the source, a strategy potentially crucial for growth in short alpine growing seasons (Asao et al., 2024).

The high root NSCs content underscores the role of roots as a central carbon pool in *Rheum nobile*'s carbon economy. In extreme alpine environments characterized by low temperatures, high radiation, and a short growing season, where photosynthesis is often limited and above-ground tissues are susceptible to damage, substantial starch and soluble sugar reserves in roots are likely indispensable for supporting reproduction and stress resilience (Piper et al., 2020). On this basis, the overwintering root system of *Rheum nobile* also accumulates large quantities of antifreeze proteins (e.g., AFP, LEA), proline, protective

sugars, proanthocyanidins, and other metabolites, further confirming that roots are the core organ for stress resistance (Li et al., 2023). Genomic analysis indicates that, compared to leaves, most photosynthesis-related genes are downregulated in bracts, and photosynthetic pigments are significantly reduced, suggesting that bracts no longer perform photosynthesis. As specialized structures for inflorescence protection and pollination, their lower NSCs content suggests their carbon demand is primarily met through translocation from other organs rather than relying on significant internal reserves (Li et al., 2023; Song et al., 2024). This is consistent with the concept of a reproductive threshold, where resources are allocated to reproduction only after a minimum vegetative biomass is achieved (Lovett Doust & Lovett Doust, 1988).

4.2 Leaf functional traits influence NSCs in *Rheum nobile*

Our study found that the ecological strategy of leaf functional traits has a significant impact on root non-structural carbohydrates. As the strategy shifts from conservative to acquisitive, NSCs show a decreasing trend. Further findings confirmed that SLA promotes the accumulation of NSCs. In this process, bract functional traits have no significant effect on the allocation of NSCs, which supports the second hypothesis that leaf functional traits have a greater influence on the NSCs of *Rheum nobile* than bract functional traits. This finding has been validated in studies on NSCs of *Pinus* species on the Tibetan Plateau (Zhang et al., 2024). As predicted by the leaf economics spectrum, acquisitive plants characterized by high SLA typically prioritize the investment of photoassimilates into rapid growth and tissue construction rather than accumulating large amounts of non-structural carbohydrates in leaves. Our results show that *Rheum nobile* leaves exhibit high SLA and low NSCs storage, consistent with the acquisitive strategy: high SLA typically characterizes an acquisitive resource-use strategy, promoting rapid growth and resource turnover at the expense of long-term carbon retention. Conversely, a low SLA reflects a conservative strategy, often associated with thicker leaves, higher leaf mass per area, greater nitrogen concentration per unit mass, and enhanced potential for carbon storage. From the perspective of the growth-storage trade-off theory, there is a carbon competition relationship between NSCs storage and growth: the acquisitive strategy allocates more carbon to immediate growth and metabolism, while the conservative strategy tends to store carbon in leaves and other organs to enhance tolerance to extreme environments. In *Rheum nobile* leaves, this trade-off manifests as prioritizing the export of photoassimilates to support whole-plant metabolism rather than accumulating them locally as starch or soluble sugars (Signori-Muller et al., 2022). Furthermore, lower sugar accumulation in leaves may alleviate feedback inhibition of photosynthesis, promoting efficient transport of photoassimilates to sink tissues such as roots, thereby achieving rapid resource turnover under short alpine growing season conditions. Although previous evidence for the growth-storage trade-off has largely come from seedlings, woody organs, or limited species, the tight coupling between leaf NSCs storage patterns and the leaf economics spectrum in *Rheum nobile* provides evidence for the existence of an intra-leaf growth-storage trade-off at the population and species levels, revealing the adaptive significance of plant carbon allocation strategies in extreme environments.

4.3 Climatic conditions affected the allocation of more non-structural carbohydrates in the bract, stem, and root of *Rheum nobile*

Supporting our objective to identify key drivers of NSCs variation, our findings indicate that NSCs content in different organs of *Rheum nobile* is primarily influenced by precipitation and temperature. For roots, the major storage organ, NSCs content showed a significant positive correlation with MAP, soil pH, TK, and LNC, but a negative correlation with plant height and AN or AK. The high relative contribution of abiotic factors (80%) to explaining root NSCs variation highlights the strong constraint imposed by soil nutrient availability and water conditions on root carbon storage. Contrary to some studies on drought-tolerant shrubs like *Artemisia* spp. and *Hippophae rhamnoides* subsp. *yunnanensis*, which reports increased root NSCs under drought stress (He et al., 2023; Ai et al., 2024), we found a positive correlation with MAP. This discrepancy may be attributed to the unique phenology of *Rheum nobile*, a monocarpic perennial sampled at its end-of-life flowering stage. During this phase, the plant may not need to conserve carbon for post-reproductive stress survival, allowing NSCs to accumulate under ample water availability. Furthermore, the higher conditional R^2 compared to marginal R^2 for the root NSCs model suggests significant influences from unmeasured local factors, such as soil microbial communities or root symbionts (Zhang et al., 2025). Stem NSCs content was mainly regulated by hydrothermal conditions and appeared independent of leaf economic traits, a pattern also observed in global studies of woody species (Zhang et al., 2024). This supports the role of stems as transport conduits and temporary storage sites, whose carbon dynamics are governed by different principles than leaf resource acquisition strategies. The relatively low explanatory power of the stem NSCs model indicates that other unmeasured factors also contribute to its variation.

For bracts, a less-studied organ, we proposed an analogous "bract resource acquisition strategy." Bract NSCs content was positively correlated with SBA and leaf NSCs, suggesting a resource acquisition strategy similar to leaves, where higher SBA facilitates greater carbon assimilation. The significant negative correlation with MAT indicates increased NSCs accumulation in bracts under colder conditions. This likely represents a cold adaptation mechanism, where soluble sugars act as cryoprotectants to lower freezing points and stabilize membranes (Liu et al., 2025). From a life-history perspective, as structures dedicated to reproduction, bracts may receive prioritized carbon allocation when overall resource availability is high, leading to a distinct regulatory pattern for NSCs allocation compared to vegetative organs.

5. Conclusion

Our study across five regions of the Qinghai-Tibet Plateau reveals a distinct allocation pattern of NSCs in the giant glasshouse plant *Rheum nobile*, characterized by the highest concentration in the roots, followed by the stems, bracts, and leaves. This hierarchical allocation underscores the role of roots as a critical carbon reservoir in this monocarpic perennial. Furthermore, leaf functional traits exerted a significantly stronger influence on NSCs allocation compared to bract functional traits. This finding highlights that the key photosynthetic organ (leaves), through traits such as specific leaf area and leaf

nitrogen content, directly governs carbon acquisition, storage, and transport strategies. In contrast, while bracts are crucial for protecting reproductive structures, their functional traits play a more limited role in regulating NSCs partitioning. The accumulation of NSCs in both leaves and roots was primarily and positively regulated by mean annual precipitation and soil pH. The significant positive correlation between leaf and root NSCs content further indicates a synergistic relationship in resource accumulation between these source and sink organs. Bract NSCs content, however, exhibited a distinct response pattern, showing a significant negative correlation with MAT. This suggests an adaptive accumulation of NSCs in bracts under colder conditions, potentially serving as a cryoprotection mechanism. Additionally, the significant positive correlations of root NSCs content with mean annual precipitation, LA, and LNC content emphasize the combined role of water availability and source-strength traits in facilitating belowground carbon storage. In summary, these results elucidate the adaptive strategies employed by *Rhcom nobile* to manage carbon resources in extremely high-altitude environments. The integrated response of NSCs allocation to climatic factors and organ-specific functional traits provides a mechanistic understanding of the survival strategy of this unique species. This study offers a critical theoretical framework for predicting plant responses to environmental change in alpine ecosystems.

Declarations

Competing Interests

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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Author Contribution

All authors contributed critically to the drafts and gave final approval for publication. [Guosi Zhang] Conceptualization, Methodology, Formal analysis, Writing-original draft; [Shuaifeng Li] Conceptualization, Methodology, Formal analysis, Writing-review & editing; [Jianrong Su] Conceptualization, Writing-review & editing ; [Siju Ma] Investigation,Writing-review & editing; [Zhihong Guo] Investigation,Writing-review & editing; [Jiansheng Wei] Investigation,Writing-review & editing; [Xiaobo Huang] Investigation,Writing-review & editing.

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Figures

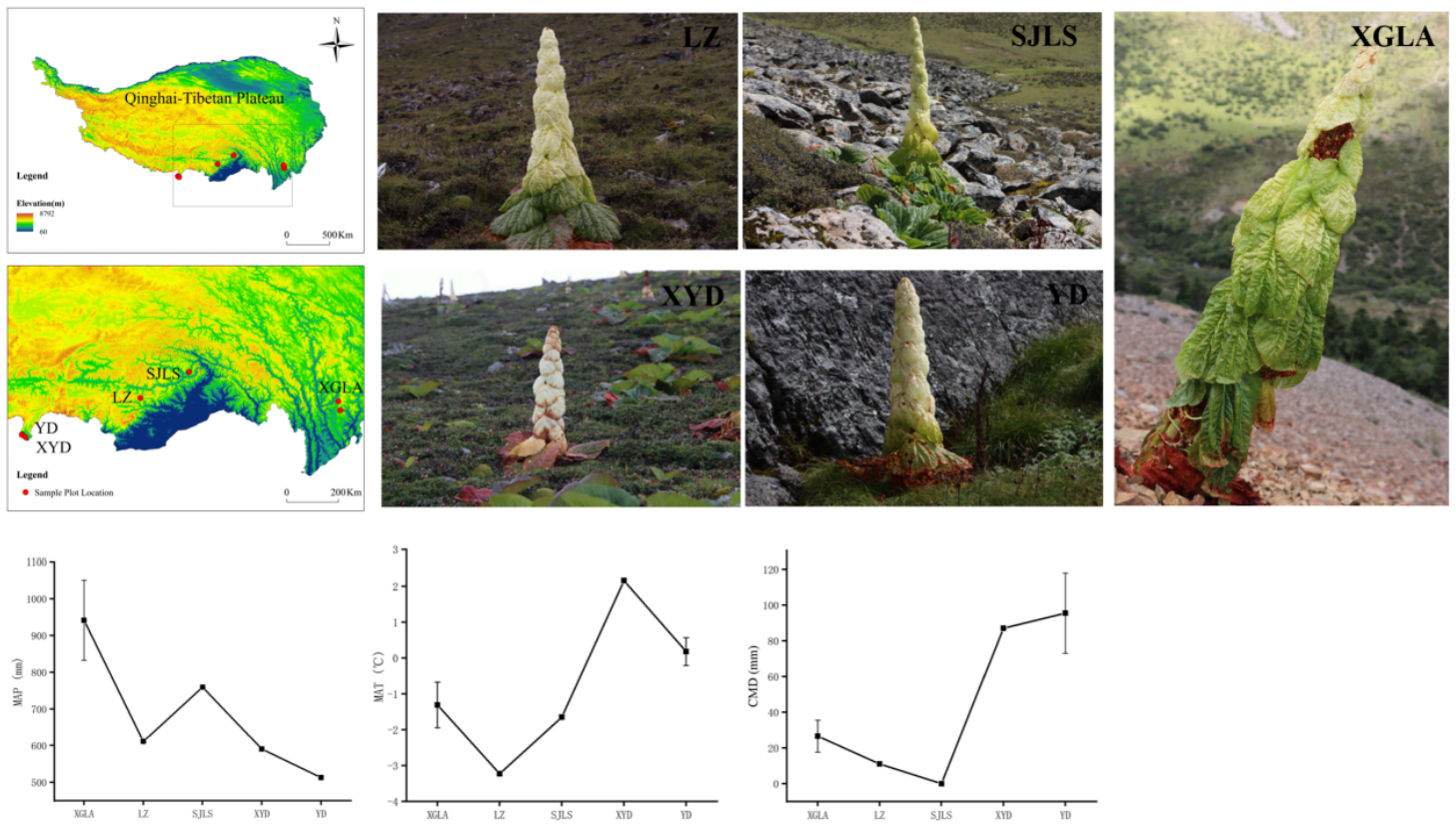


Figure 1

Location of the study sites and morphologies of the research objects. LZ, Longzi; XGLA, Shangri-La; SJLS, Seijilashan; XYD, Xiayadong; YD, Yadong; MAP, mean annual precipitation; MAT, mean annual temperature; CMD, climatic moisture deficit.

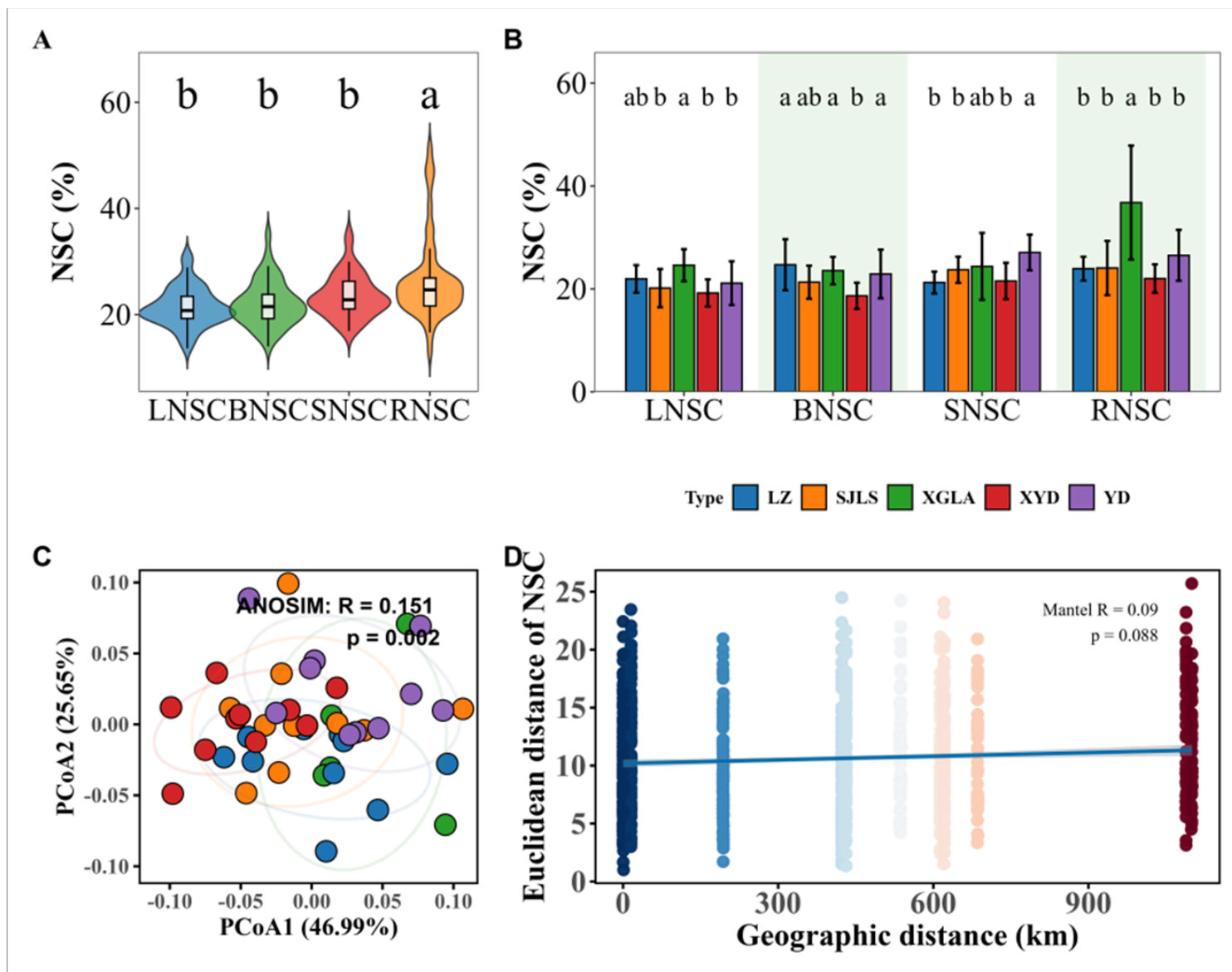


Figure 2

Differences of non-structural carbohydrates (NSC) among different organs and distribution using one-way analysis of variance (ANOVA) followed by LSD post-hoc tests, principal coordinate analysis (PCoA), and Mantel r test. Different lowercase letters above the bars indicate significant differences ($P < 0.05$). LZ, Longzi; SJLS, Sejilashan; XGLA, Shangri-La; XYD, Xiayadong; YD, Yadong; LNSC, leaf NSC; BNSC, bract NSC; SNSC, stem NSC; RNSC, root NSC.

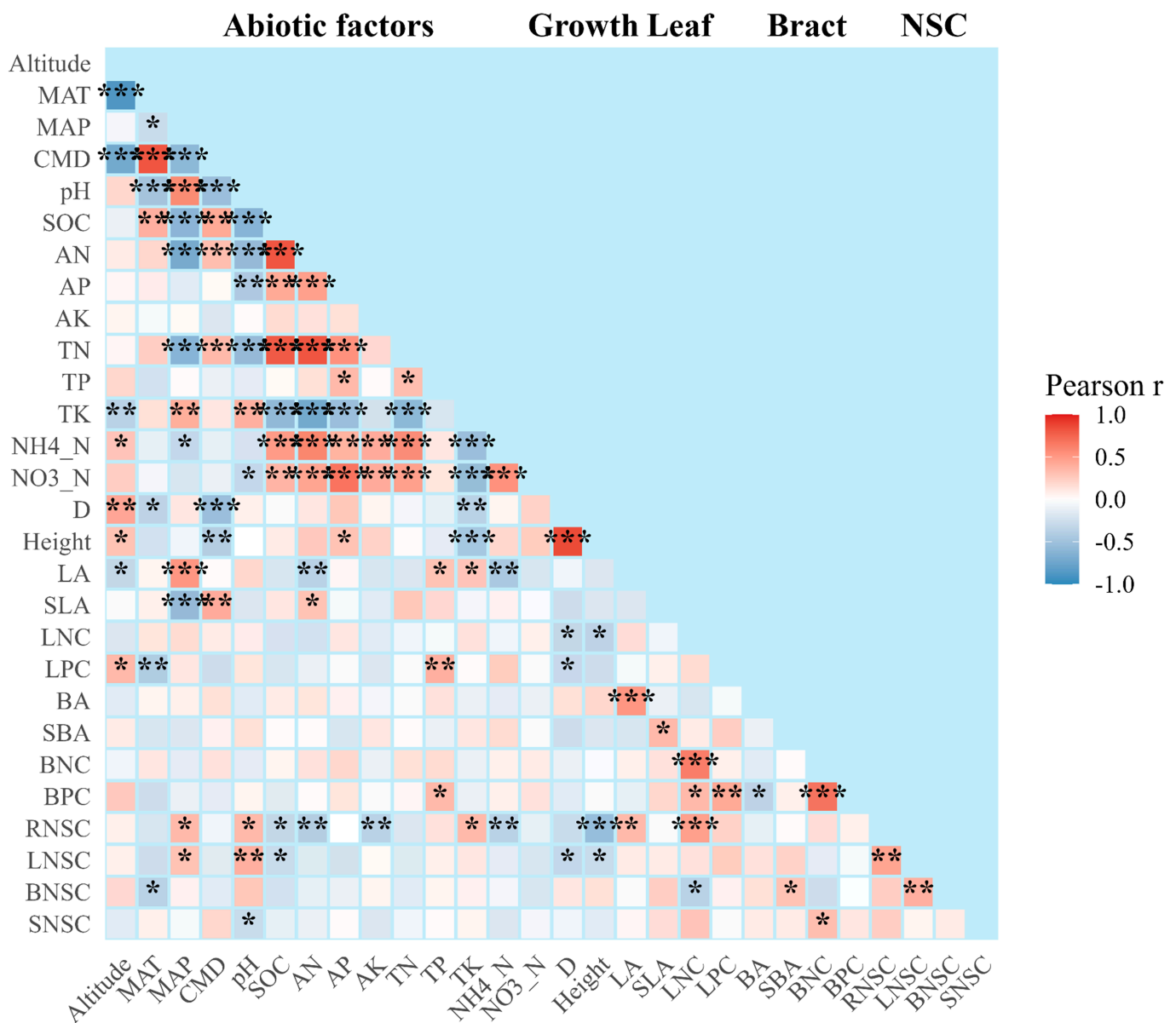


Figure 3

Correlation analysis among **non-structural carbohydrates (NSC)**, biotic and abiotic factors. MAT, mean annual temperature; MAP, mean annual precipitation; CMD, climatic moisture deficit; SOC, soil organic carbon; AN, available nitrogen; AP, available phosphorus; AK, available potassium; TN, total nitrogen; TP, total phosphorus; TK, total potassium; NH₄⁺-N, ammonium nitrogen; NO₃⁻-N, nitrate nitrogen; D, Ground diamete; LA, leaf area; SLA, specific leaf area; LNC, leaf nitrogen content; LPC, leaf phosphorus content; BA, bract area; SBA, specific bract area; BNC, bract nitrogen content; BPC, bract phosphorus content; LNSC, leaf NSC; BNSC, bract NSC; SNSC, stem NSC; RNSC, root NSC.

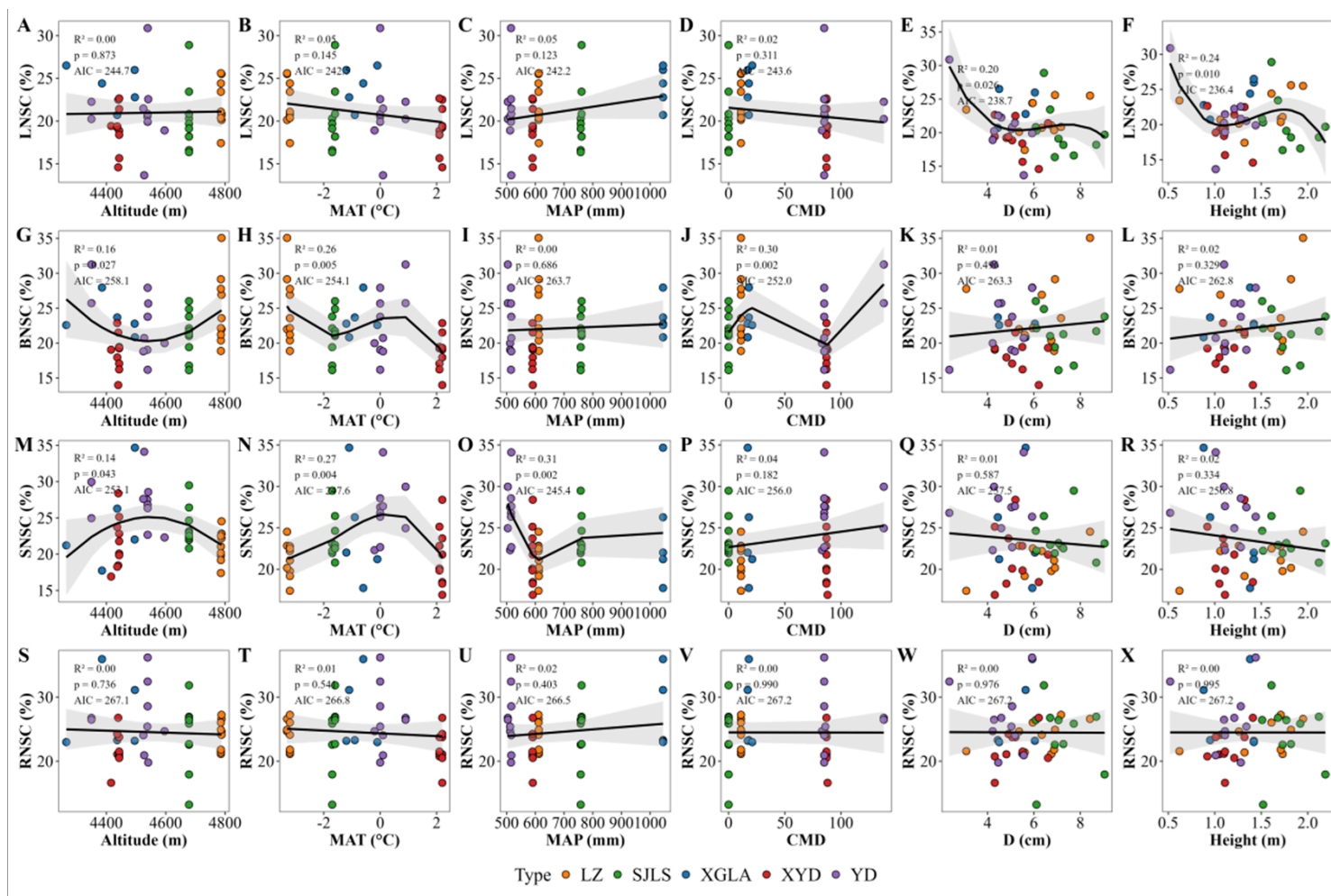


Figure 4

Bivariate linear regression analysis between **non-structural carbohydrates (NSC)** content in different organs of *Rheum nobile* and climatic factors and plant traits. MAT, mean annual temperature; MAP, mean annual precipitation; CMD, climatic moisture deficit; D, Ground diameter; LZ, Longzi; SJLS, Sejilashan; XGLA, Shangri-La; XYD, Xiayadong; YD, Yadong.

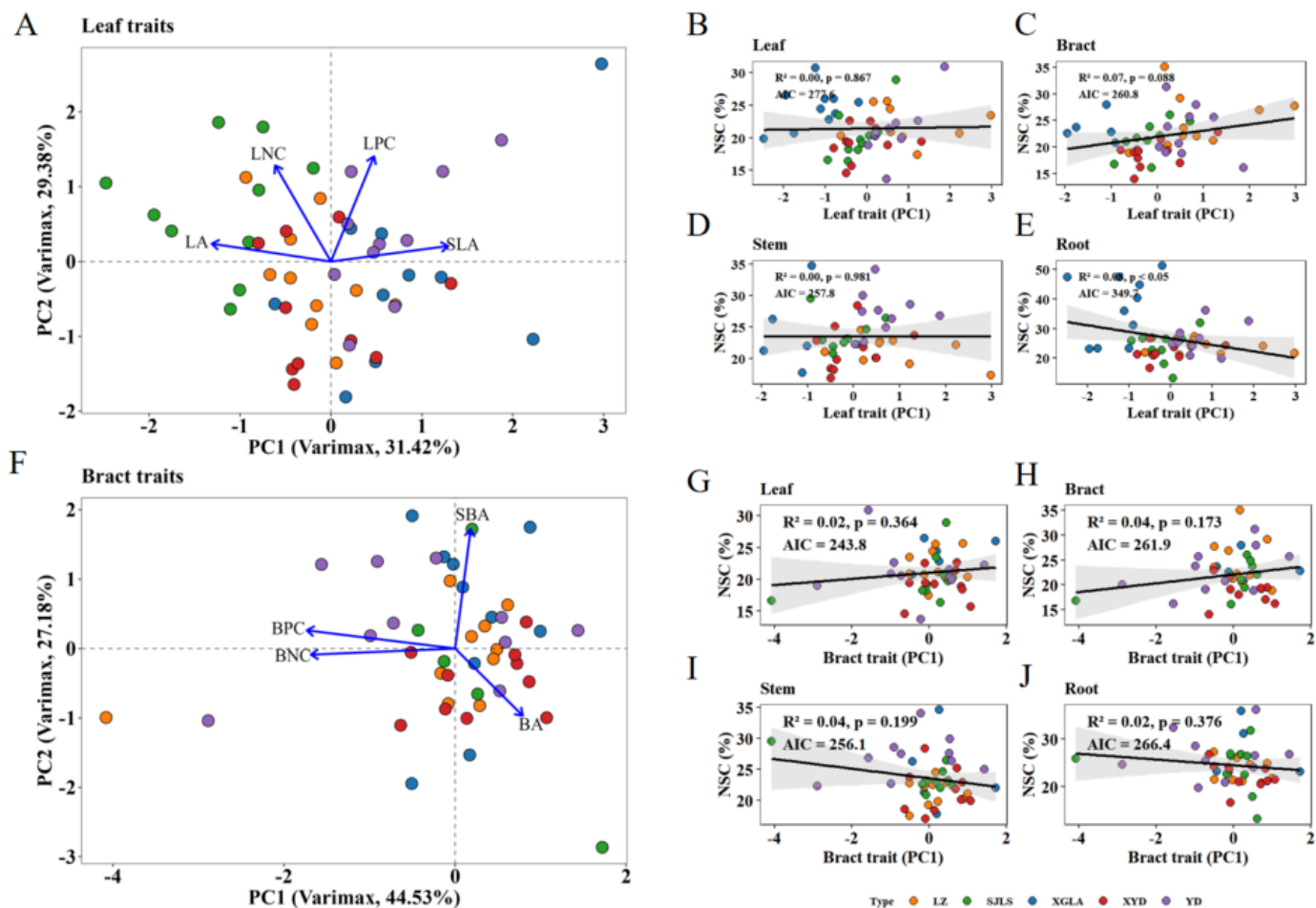


Figure 5

Principal component analysis (PCA) of functional traits of leaves and bracts of *Rheum nobile*, and bivariate linear regression analysis of **non-structural carbohydrates** (NSC) contents in different organs with PC1 of leaves and bracts. LA, leaf area; SLA, specific leaf area; LNC, leaf nitrogen content; LPC, leaf phosphorus content; BA, bract area; SBA, specific bract area; BNC, bract nitrogen content; BPC, bract phosphorus content; LZ, Longzi; SJLS, Sejilashan; XGLA, Shangri-La; XYD, Xiayadong; YD, Yadong.

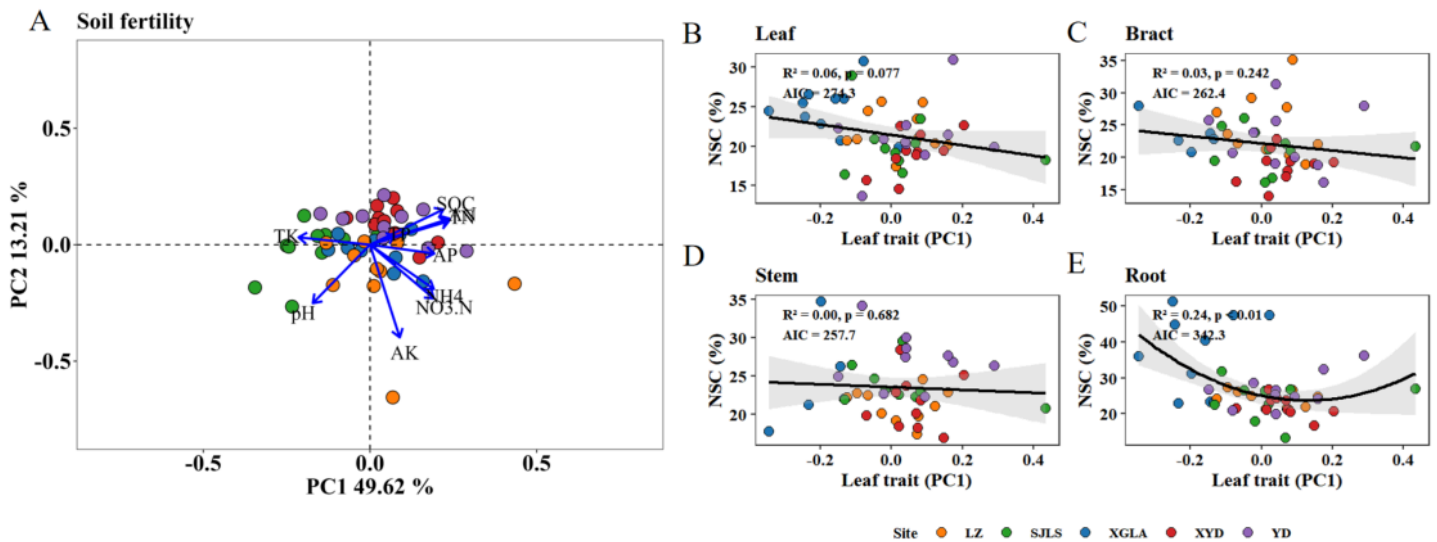


Figure 6

Principal component analysis (PCA) of soil physicochemical properties, and bivariate regression analysis of **non-structural carbohydrates** (NSC) contents in different organs with soil fertility (PC1). SOC, soil organic carbon; AN, available nitrogen; AP, available phosphorus; AK, available potassium; TN, total nitrogen; TP, total phosphorus; TK, total potassium; NH₄⁺-N, ammonium nitrogen; NO₃⁻-N, nitrate nitrogen; LZ, Longzi; SJLS, Sejilashan; XGLA, Shangri-La; XYD, Xiayadong; YD, Yadong.

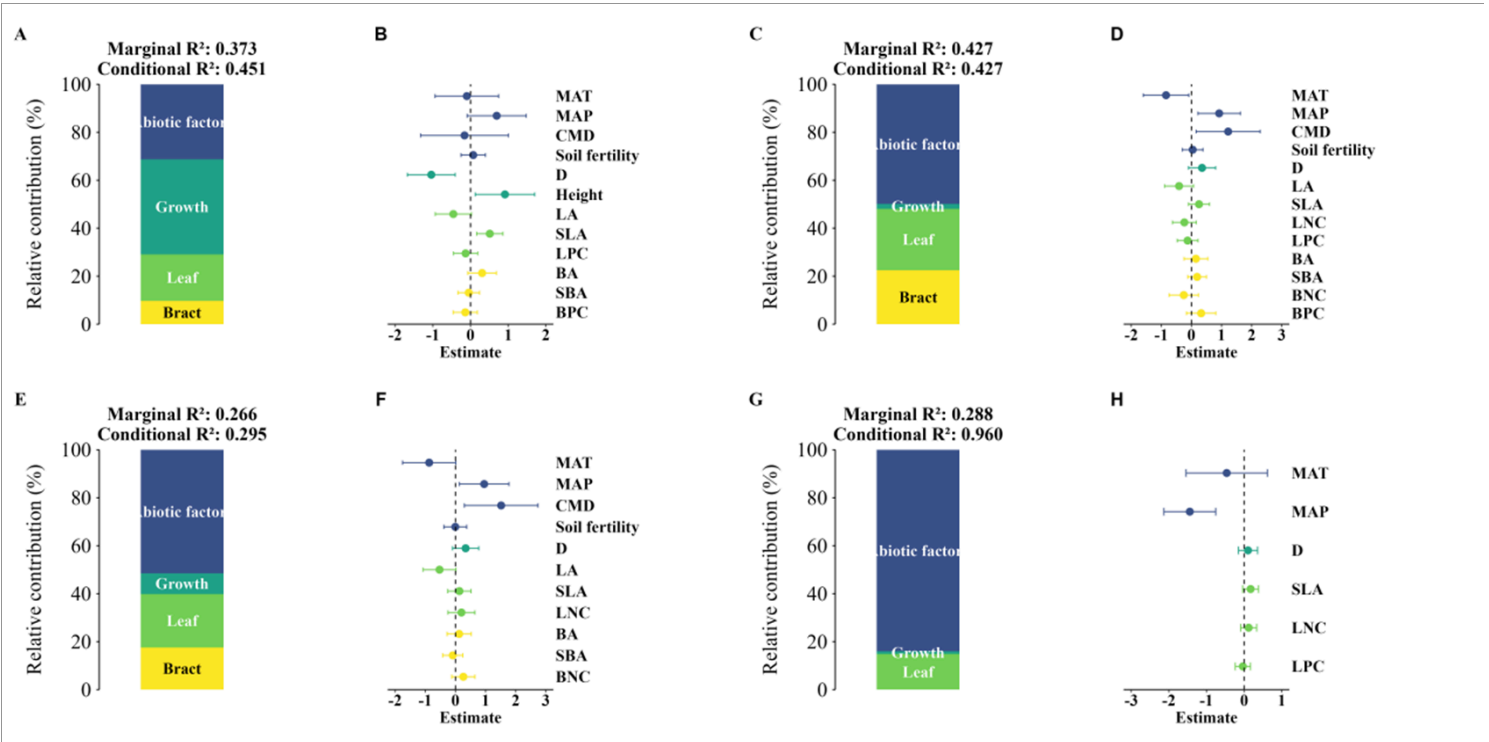


Figure 7

Relative importance of biotic and abiotic factors on **non-structural carbohydrates** content in different organs of *Rheum nobile* based on GLMM. MAT, mean annual temperature; MAP, mean annual precipitation; CMD, climatic moisture deficit; D, Ground diameter; LA, leaf area; SLA, specific leaf area; LNC, leaf nitrogen content; LPC, leaf phosphorus content; BA, bract area; SBA, specific bract area; BNC, bract nitrogen content; BPC, bract phosphorus content.