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Community Structure of Alpine Peat Swamps and the Soil Environment Jointly Regulate the Biomass Distribution and Carbon Storage Pattern

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Abstract

Elevation drives soil environmental heterogeneity, modifying plant species composition, morphological traits, biomass and carbon sequestration capacity. The peat bogs at 3400~3800 m in the first meander of the Yellow River National Nature Reserve were assessed. Using variance analysis and path analysis, the characteristics of plant biomass allocation and carbon storage and their main influencing factors at the elevation gradient were assessed. The distribution ratio of plant biomass in alpine peat bogs was in the order of root > leaf > stem, and the belowground biomass was higher than the aboveground biomass. AS the elevation increased, the aboveground biomass decreased, the total biomass and belowground biomass initially increased and then decreased, and the root-shoot ratio increased. Additionally, the organic carbon content of plant organs in peat bog was in the order of stem > leaf > root. The belowground carbon storage of plants was higher than the aboveground carbon storage, and the total carbon storage increased first and then decreased. Path analysis showed that average density and soil temperature had direct positive effects on plant biomass and carbon storage, whereas soil bulk density and pH had direct negative effects on plant biomass and carbon storage. Soil hydrothermal heterogeneity along elevation gradients shapes the species composition and spatial distribution of peatland plant communities, further regulating organ-level biomass allocation patterns and carbon storage of marsh plants. This study carries important theoretical and practical implications for elucidating the environmental response mechanisms of peat bog plants under global climate change and assessing carbon sinks of wetland vegetation.

Keywords: Peat bog plants; Biomass allocation; Plant organic carbon content; Plant carbon storage; Alpine peat bogs

1 Introduction

Terrestrial ecosystems are earth's important carbon sinks; hence, their carbon cycle has become the central topic and research priority of global change and ecology research (Keenan *et al*., 2018; Wang e*t al*., 2020). Wetlands, as a component of the carbon pool in terrestrial ecosystems, play irreplaceable roles in regulating climate change and mitigating greenhouse effects (Bao *et al*., 2023). Peat bog wetlands are wetlands with a peat thickness greater than 30 cm and a soil organic matter content exceeding 30% (Chai *et al*., 1990). Alpine peat bogs are peat-rich bogs formed by the gradual accumulation of a large number of organic residues of wet plants growing on poorly drained surfaces that cannot be decomposed under cold and wet climate conditions in high-altitude areas (Cui *et al*., 2017). Due to their long-term exposure to a water-saturated anaerobic environment, it is difficult to release nutrients, forming a special nutritive poor environment, and plants show different diverging adaptability, forming a unique alpine peat bog plant community (AminiTabrizi *et al*., 2022). Plants in the peat swamp wetland of the first meander of the Yellow River National Nature Reserve are mainly perennials of the sedge family, such as *Blysmus sinocompressu*s, *Kobresia tibetica*, *Carex muliensis*, and *Carex kansuensis*. Through photosynthesis, plants in alpine peat bogs convert atmospheric carbon dioxide into organic carbon, which they then store in their biomass or release into the soil (Korrensalo *et al*., 2017). Carbon sequestration by plants effectively reduces the atmospheric concentration of greenhouse gases and plays a crucial role in stabilizing the global climate and mitigating greenhouse effects (Mitsch *et al*., 2013). Current studies have extensively focused on the carbon sequestration capacity of peat swamp wetlands, particularly the soil carbon storage. However, the spatial distribution patterns of plant biomass allocation, organ carbon content, and carbon storage along the elevation gradient of peat swamps remain unclear. Moreover, systematic analyses of the intrinsic mechanism by which the plant community structure and soil environment jointly regulate the carbon storage pattern of vegetation are limited. This study aims to analyze the distribution patterns of biomass allocation and carbon storage of peat swamp plants along the elevation gradient and combines the plant community structure and soil environment to clarify the driving factors. Our findings will provide a scientific basis for accurately elucidating the carbon cycling process of high-altitude peat wetlands.

Plant biomass can reflect the production level and nutrient storage capacity of wetland ecosystems and is the basis for studying the material circulation and energy flow of wetland ecosystems (Hendrik *et al*., 2011). The variability in the partitioning of plant organ biomass arises from intrinsic trade-offs in allocating and utilizing limited carbon assimilation products, reflecting the adaptation of plants to their external environment over extended periods (Poorter *et al*., 2012). Both aboveground and belowground plant components are intricately interconnected, forming a balanced organic entity. Biomass partitioning serves as a valuable indicator of resource allocation patterns for photosynthetic products between aboveground and belowground biomass (Liu *et al*., 2021). The variation in the ratio of root to crown represents a fundamental aspect of plant configuration (Ahirwal *et al*., 2021). Extensive research on plant biomass provides foundational knowledge for investigating carbon stocks (Tian *et al*., 2020). Importantly, different plant species exhibit significant disparities in the carbon sequestration capacity of aboveground and belowground plant biomass (Bagdonaite,*et al*., 2026). Hence, it is vital for the conservation and management of plant resources in alpine peat bogs to study the biomass distribution and distribution characteristics of plants in alpine peat bogs and understand the life history strategies of plants in alpine peat bogs.

Plant biomass is the primary precursor for peat formation and plays a fundamental role in the storage and dynamics of organic carbon (Kuptsova *et al*., 2022). Plant organic carbon concentration acts as a critical proxy for carbon-fixation and carbon-storage capacity, reflecting how plants assimilate and retain carbon elements (Tomimatsu *et al*., 2016). Carbon fixed via photosynthesis is allocated across functionally distinct plant organs for synthesis, translocation, and storage (Poorter *et al*., 2012). Plant biomass, acting as the primary pathway for organic carbon input into peat bog wetland ecosystems, provides insights into the carbon sequestration capacity of these ecosystems (Tian e*t al*., 2020). Currently, most researchers calculate vegetation carbon storage based on biomass data and carbon content coefficient. Generally, grassland vegetation biomass is multiplied by 0.45 (Chapungu *et al*., 2020), and the forest vegetation carbon content coefficient is 0.5 or 0.45 (Zhou *et al*., 2022). However, due to vegetation diversity and interspecific differences, the carbon content of plants in the same type of vegetation or in the same region is different. Therefore, the estimate of plant carbon storage based on the uniform plant carbon content coefficient has a large error, which is inconsistent with the actual situation (Thomas *et al*., 2012). By combining historical data, vegetation index, and carbon conversion factors to estimate wetland ecosystem biomass and carbon stocks in specific regions, this approach may introduce bias in estimating plant carbon stocks. In contrast, studies on carbon stocks in peat bogs have predominantly focused on soil organic carbon response to environmental factors (Doetterl *et al*., 2016), with relatively limited investigation into carbon stocks and organic carbon content of individual plant organs within peat bog ecosystems. Specialized studies focusing on organ-scale organic carbon concentration and organ carbon storage in peat marsh ecosystems remain relatively scarce. To fill this research gap, this study quantitatively analyzed organ-scale carbon allocation and carbon-storage characteristics of alpine peat marsh plants using field-measured organic carbon concentration of individual plant organs combined with organ biomass data. Therefore, our study of the organic carbon content and carbon storage characteristics of plant organs in alpine peat marshes provides data that support the accurate estimation of the ecosystem carbon pool in alpine peat marsh.

The hydrological regime is the primary determinant shaping the formation and development of peat bogs. Cold temperatures, high humidity, prolonged water accumulation, and limited water mobility are the key factors that determine the plant community structure within peat bog ecosystems (Liu *et al*., 2019). Elevation creates heterogeneous habitats by regulating water availability, temperature, and soil properties. These factors influence species composition and resource competition (Ratier Backes *et al*., 2021). Abiotic factors, such as soil temperature, moisture, and nutrient content, exhibit notable spatial heterogeneity along the elevation gradient, influencing plant growth and the distribution of biomass (Xia *et al*., 2025). Several researchers have conducted comprehensive studies on the species composition of plant communities (Tendar *et al*., 2020), the fractal structure of dominant plant roots (Wang *et al*., 2023), and leaf surface absorption efficiency (Kucerova *et al*., 2022) in alpine peat bogs at an elevation gradient. Previous studies have also reported that variations in biomass and carbon stocks of plant communities along elevation gradients can be characterized by negative correlations (Suarez *et al*., 2023), positive correlations (Blume-Werry *et al*., 2018), or follow a "single peak" curve (Liu *et al*., 2022). Existing studies have focused on the changes in biomass and carbon storage of peat swamp plants with altitude. However, further analyses are needed to determine how the composition of plant communities and the soil environment jointly regulate the differential patterns of plant biomass and carbon storage along the altitude gradient, as well as underlying coupling mechanisms. The spatial and biomass distribution patterns of peat bog plants have evolved over extended periods and play crucial roles as internal drivers in the formation of alpine peat bog carbon pools (Chen *et al*., 2014). In this study, we quantified the distribution of plant biomass and carbon stocks in peat bogs along an elevational gradient to identify the principal factors controlling these

patterns. Our findings will provide the theoretical basis and data support for ecological environment protection and accurate estimation of carbon storage in alpine peat bogs.

The first meander of the Yellow River National Nature Reserve is an outstanding example of a primitive and representative alpine peat bog wetland located in the Gannan Plateau. The study area harbors diverse flora with abundant species, and its natural vegetation remains well-preserved, which is typical and representative of China's alpine areas (Xue *et al*., 2021). Peat bog wetlands within nature reserves provide ideal research sites for investigating plant biomass characteristics, carbon storage, and associated environmental response mechanisms of peat-bog ecosystems. As highlighted in previous studies, their primary advantage lies in minimal direct human disturbance. Current research on peat bogs in the first meander of the Yellow River National Nature Reserve, both domestically and internationally, has primarily focused on wetland area and land cover conversion (Jiang *et al*., 2023), wetland landscape evolution (Xue *et al*., 2021), plant community structure, and species diversity (Ma *et al*., 2011). However, the distribution patterns of biomass and carbon storage of peat swamp plants along the elevation gradient remain unclear; thus, it is impossible to elucidate the environmental adaptation mechanisms of peat swamp plants and their carbon sequestration capabilities. Therefore, we selected the peat bog of the Yellow River National Nature Reserve at an elevation of 3400~3800 m as the experimental sample point. The biomass allocation and carbon storage characteristics of plants in alpine peat bogs under different altitude gradients were studied, and the main factors affecting plant biomass and carbon storage were discussed. The primary objectives of our study were as follows: (1) To assess the allocation strategies of plant organ biomass at different altitude gradients in alpine peat swamps; (2) To clarify the spatial distribution patterns of organic carbon content and carbon storage in plant organs along the altitude gradient; (3) To analyze the synergistic regulatory mechanisms of plant community structure and soil environment on the distribution patterns of plant biomass and carbon storage. This study aimed to reveal the altitudinal variation of biomass distribution, organic carbon content, and carbon storage of plants in alpine peat bogs. Our results will clarify the effects of soil environment and community characteristics on plant biomass and carbon storage in alpine peat bogs. Our findings will also provide a theoretical basis and scientific guidance for the government's wetland management and protection and provide a data basis for an accurate assessment of the carbon pool accounting of the high peat bog ecosystem.

2 Methods

2.1 Study Area

The study area covers the First Meander of the Yellow River National Nature Reserve, situated in the southwest of Maqu County, Gannan Tibetan Autonomous Prefecture, Gansu Province, with a total reserve area of 203,400 hectares. This region features a typical plateau continental climate characterized by long, cold winters and brief, cool summers. It is marked by a small annual temperature amplitude yet pronounced diurnal temperature fluctuations. The mean annual temperature varies between 1.1°C and 1.5°C; the extreme maximum temperature reaches 23.6 °C, while the extreme minimum temperature drops to −29.6°C. The annual precipitation ranges from 635 mm to 655 mm, contrasting with an annual evaporation of 1,353.4 mm. The average annual sunshine duration is about 2,580 hours. Meadow soil, swamp soil and peat soil constitute the major soil types across the study area. The bog communities are dominated by herbaceous cyperaceous species, including *Blysmus sinocompressus*, *Ranunculus hirtellus*, *Kobresia tibetica*, and *Carex muliensis*. Other common vascular plants include *Potentilla anserina*, *Carex kansuensis*, *Sanguisorba filiformis*, *Koeleria cristata*, *Heleocharis dulcis*, *Pedicularis kansuensis*, and *Polygonum viviparum*.

2.2 Experimental Design

First, the location of peat bogs was identified using Google Maps in conjunction with remote sensing image data from Gaofen-1. Subsequently, multiple field investigations were conducted on the peat bogs located in the First Bend of the Yellow River Nature Reserve. Considering accessibility, areas exhibiting typical development and minimal disturbance were selected as research subjects. Field plot investigation experiments were conducted in July, 2021, and from July to August, 2022, respectively. Overall, 189 sample plots were collected, encompassing various topographic conditions such as wetland type, plant type, geomorphic type, and altitude within the study area (Figure.1). The primary land use in this region was winter pasture. During the experimental period, plant growth was robust enough to mitigate factors related to grazing interference and ensure comparability among experimental data.

ALOS DEM data (https://search.asf.alaska.edu/) sourced from Japan's ALOS satellite was utilized for this study; it has a resolution of 12.5 meters. ArcGIS version 10.8 was employed to extract altitude values for all 189 sample points based on the digital elevation model (DEM) of the study area. In this study, we set up 189 sampling points, and the sample size met the requirements for large sample statistical analysis (Figure.1). This ensured that the statistical analysis had a high degree of freedom and test efficacy and was suitable for statistical models such as variance analysis, correlation analysis, and regression fitting. The peat bog sampling points at an altitude of 3400–3800 in the study area were divided into five gradients of 3400, 3500, 3600, 3700, and 3800 m at an altitude interval of 100 m. The sampling points of peat bogs in different altitude ranges were counted. The number of sampling points was 38, 41, 37, 40, and 33, respectively.

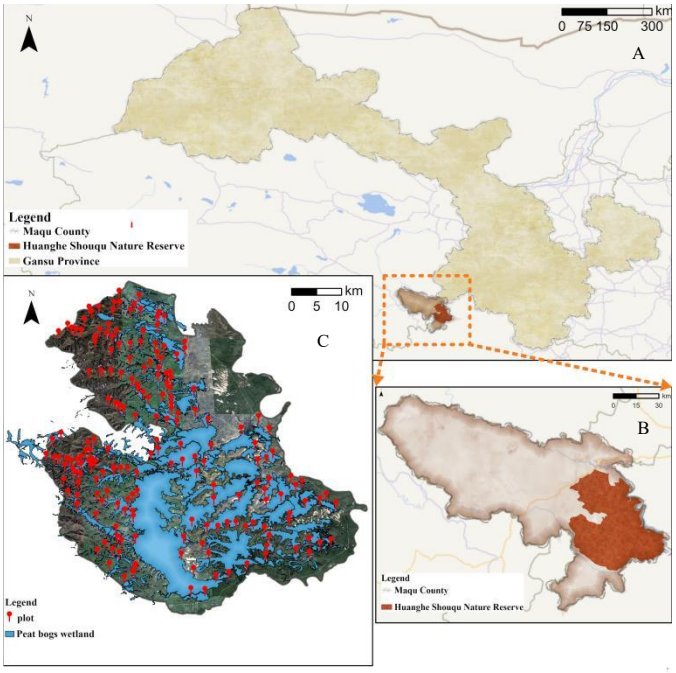


Fig. 1 Location and setting of the experimental plots in the first meander of the Yellow River National Nature Reserve of Maqu County. (A) Location of Maqu in Gansu Province; (B) The Huanghe Shouqu Nature Reserve in Maqu; (C) 189 sampling points set up along the Huanghe Shouqu.

2.3 Field Sampling

The sampling process was as follows: (1) Community survey: Based on the Flora of China "and" the plant list "(http://www.theplantlist.org/), species names were confirmed for each sample, and statistical data was collected on plant coverage, height, and density. (2) Collection of plant samples: After the community survey was complete, the aboveground portion of plants in the sample site was harvested using a cutting method. Thereafter, surface-adhered soil, gravel, and other impurities were removed and sealed into envelopes to be brought back to the laboratory. A soil block measuring 30 cm (length) × 30 cm (width) × 50 cm (height) was dug in each sample plot, as almost all plant roots of the wetland community were distributed within this layer of soil. Soil attached to the plant roots was rinsed at the river's edge with a 0.25 mm pore size sieve. All plant roots were placed in envelopes to be transported back to the laboratory. (3) Collection of soil samples: A 200-g sample of 0–50 cm soil was obtained from the center of each sample plot for the determination of soil physical and chemical properties in the laboratory. Soil samples (0–50 cm) were collected using a ring knife (100 cm^3) and weighed on site for recording data. Soil temperature was determined in situ in layers using a soil three-parameter meter (Moisture MeterHH2, Delta-T Devices Ltd, Britain). When the water table stabilized, the groundwater level was recorded ("+" indicates water table above ground surface, "-" indicates water table below ground surface"). At the end of soil sampling, the field soil profile was restored to its original state.

2.4 Laboratory Analysis

At the ecohydrology laboratory of Northwest Normal University, the aboveground portion (divided into stems and leaves) and the belowground portion (root system) of the plant community were collected in the field and placed into numbered envelopes; afterward, they dried and weighed. Specifically, they were put into the oven at 105 ℃ for killing for 30 min, and then dried at 85 ℃ until a constant weight was obtained. The stem, leaf, and root biomass of the plant community were then recorded using an electronic balance (0.0001 g) and used to determine the aboveground and belowground biomass, as well as the total biomass of the plant community. The weighed plants underwent grinding and sieving (40 mesh) using a plant crusher, and the carbon content of the roots, stems, and leaves was analyzed using a carbon/nitrogen analyzer (Vario EL III, Germany).

The soil sample contained excess moisture; therefore, impurities were removed by drying the soil indoors in cool and ventilated conditions for 1 week. The samples were then dried in an oven at a constant temperature of 70 °C for 48 h until reaching a constant weight. The soil was finally physically ground, sieved through a 60-mesh sieve, and packaged in sealed bags for index determination. Soil pH value was measured using a PHS-3 pH meter (ELTA32, Mettler-Toledo, Germany), while soil total nitrogen content was determined using the semi-micro Kjeldahl method. Soil total phosphorus content was determined using sulfuric acid-perchloric acid decoction and the molybdenum antimony colorimetric method. Additionally, soil samples collected with a ring knife were dried and weighed at 105 ℃ to determine dry soil weight, from which soil bulk weight and moisture content were calculated using the volume of the ring knife.

Table1 Common parameters and their abbreviations

Parameter	Abbreviations	Units	Parameter	Abbreviations	Units
Leaf biomass	LB	g/m^2	Leaf organic carbon	LCC	g/kg
Stem biomass	SB	g/m^2	Stem organic carbon	SCC	g/kg
Root biomass	RB	g/m^2	Root organic carbon	RCC	g/kg
Litter biomass	DB	g/m^2	Litter organic carbon	DCC	g/kg

Aboveground biomass	AB	g/m^2	Aboveground carbon storage	ACS	$gC•m^{-2}$
Underground biomass	UB	g/m^2	Underground carbon storage	UCS	$gC•m^{-2}$
Total biomass	TB	g/m^2	Total carbon storage	TC	$gC•m^{-2}$
Root-shoot ratio	RST	No	Vegetation coverage	FVC	%
Average height	AH	cm	Average density	AD	$branch/m^2$
Soil bulk density	SBD	g/cm^3	Soil moisture	SWC	%
Soil total nitrogen	TN	%	Soil temperature	TS	℃
Soil total phosphorus	TP	%	Soil total potassium	TK	%

2.5 Data analysis methods

The height, coverage, density, and biomass were processed to calculate the important values of each plant species in the plot. Important value (IV) is a comprehensive quantitative measure of the importance of a species in its community. Significance values for each species are calculated using the average of relative height (RH), relative coverage (RC) and relative density (RD) (Guo *et al*., 2020). Important value (IV) is calculated as follows:

$$\boldsymbol{IV = \frac{RH + RC + RD}{3}} \quad (1)$$

RH = (Average height of a species in the quadrat / Sum of the average height of all species in the quadrat) × 100;

RC= (Coverage of a species in the quadrat/Sum of coverage of all species in the quadrat) × 100%;

RD = density of a species in the quadrat/Sum of the densities of all species in the quadrat) × 100%;

Excel 2019 software was used to pre-process the data, while SPSS version 22.0 (IBM Corp., Armonk, NY, USA) was applied to analyze the data statistically. Pearson correlation analysis was used to analyze the relationships between total plant biomass and total carbon storage, soil parameters, and community characteristics at different elevation gradients.

Path analysis is a statistical technique based on multiple regression to decompose correlation coefficients into direct and indirect effects. Multivariate stepwise regression analysis of the data set was performed and the dependent variables were required to follow a normal distribution. The leading factors affecting total plant biomass and total carbon storage were screened out using path analysis and compared with their influence degree by building a model, which was based on correlation analysis. Factors were decomposed into independent and dependent variables, and then the relationship between them was analyzed to obtain the direct and indirect path coefficients, which were calculated to obtain decision coefficients (Du *et al*., 2010). The specific formula for the path analysis was as follows:

$$r_{iy}P_{jy} = r_{ij} \times P_{jy} \quad \textbf{(2)}$$

$$r_{iy} = P_{iy} \times r_{iy} P_{jy} \quad \textbf{(3)}$$

Where: $r_{iy}P_{jy}$ is the indirect pathway coefficient between the independent variable x_i and the dependent variable y. r_{ij} is the correlation coefficient between two independent variables. r_{iy} is the path coefficient between the independent variable x_i and the dependent variable y. r_{iy} is the simple correlation coefficient between the independent variable x_i and dependent variable y. P_{jy} is the direct path coefficient between the independent variable xi and the dependent variable y.

3 Results

3.1 Vegetation community and soil characteristics

3.1.1 Alpine peat bog plant species community composition across an elevation gradient

Fig. 2 shows that the important value of plant species varies significantly over the elevation gradient. The dominant species at the sample site at an elevation of 3400 m was *Blysmus sinocompressus*, with an important value of 0.47, followed by companion species such as *Carex muliensis* (0.29) and *Kobresia tibetica* (0.10). At 3500 m above sea level, *Blysmus sinocompressus* and *Kobresia tibetica* had the highest important values of 0.49 and 0.30, respectively. The important values of *Carex muliensis* (0.07) and *Potentilla anserina* (0.04) were relatively lower. At an elevation of 3600 m, *Kobresia tibetica* was the dominant species with the highest important value of 0.47, followed by *Blysmus sinocompressus* (0.20) and *Carex muliensis* (0.18) as companion species. At an elevation of 3700 m, *Carex muliensis* and *Kobresia tibetica* had important values of 0.37 and 0.18, respectively, followed by *Blysmus sinocompressus* (0.11) and *Carex kansuensis* (0.10) as associated species. At an elevation of 3800 m, *Carex kansuensis* had the largest important value of 0.47, followed by companion species such as *Kobresia tibetica* (0.29), *Carex muliensis* (0.10), *Heleocharis dulcis* (0.08), and *Pedicularis kansuensis* (0.07).

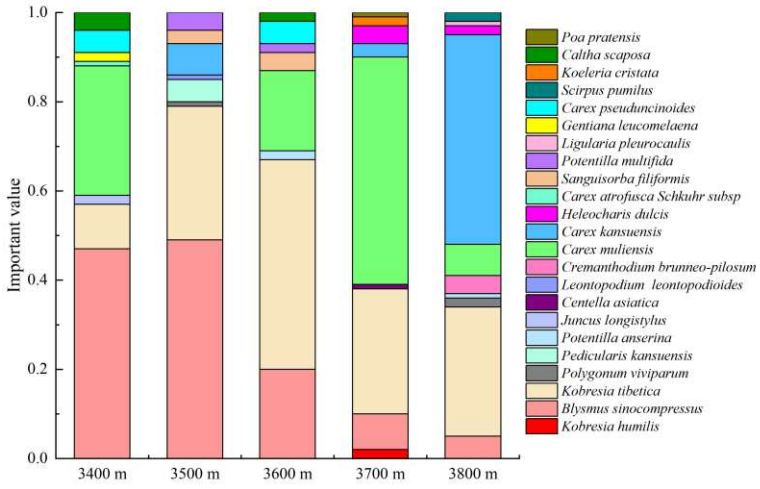


Fig. 2 Plant species composition and importance in alpine peat bogs at an elevation gradient

3.1.2 Characteristics of plant communities in alpine peat bogs

The average height (AH), average density (AD), and average coverage (FVC) of plant communities in alpine peat bogs at different elevations are shown in Fig 3. At 3400 m above sea level, the plant communities exhibited the highest values for AH, FVC, and AD, measuring 35.89±0.53 cm,

97.55±0.87%, and 1233.50±21.70 branch·m^{-2}, respectively. Conversely, the lowest values were observed at an elevation of 3800 m, with AH, FVC, and AD measuring 18.06±0.31 cm, 75±0.69%, and 939.52±23.25 branch·m^{-2}, respectively. As the elevation increased, the AH, FVC, and AD of the plant community decreased by 49.67%, 23.46%, and 23.78%, respectively.

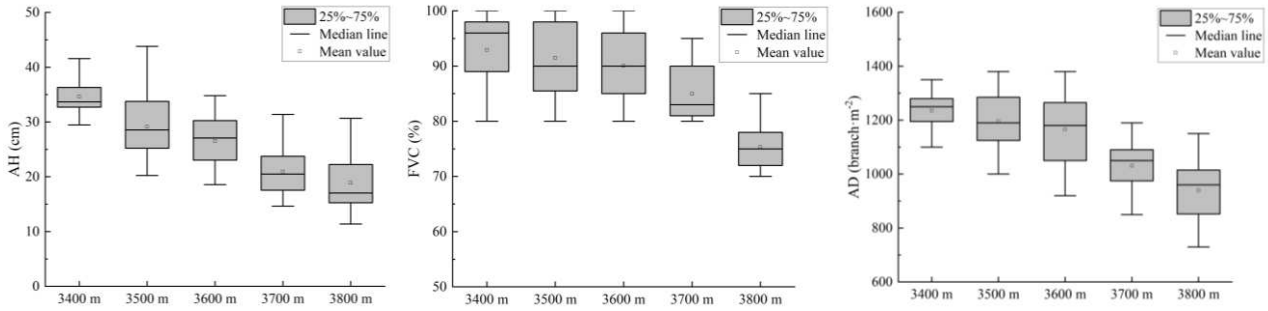


Fig. 3 Plant community characteristics in alpine peat bogs

Note:*AD*, average density;*AH*, average height; *FVC,* Vegetation coverage.

3.1.3 Physical and chemical soil properties

Table 2 shows the physical properties of alpine peat bogs at different elevations. The pH of the peat bog soils ranged from 5.93 to 6.50, indicating a neutral to acidic nature. With increasing elevation, both soil pH and temperature (TS) exhibited a decreasing trend, declining by 8.77% and 27.47%, respectively. Soil moisture (SWC), total phosphorus (TP), and total nitrogen (TN) initially increased and then decreased with elevation, showing changes of 35.63%, 8.43%, and 13.28%, respectively. Additionally, the soil bulk density (SBD) followed a pattern of decreasing first and then increasing, with a variation range of 10.25%.

Table 2. Soil physical properties in alpine peat bogs across the elevation gradients

Elevation	SWC(%)	SBD(g/cm^3)	pH	TS (℃)	TN (%)	TP (%)	TK(%)
3400 m	51.84±3.94b	0.40±0.03a	6.50±0.09a	15.14±0.64a	1.27±0.02c	0.78±0.02c	1.14±0.01b
3500 m	55.57±3.82a	0.39±0.002b	6.18±0.05b	14.14±0.43b	1.37±0.02b	0.80±0.02b	1.21±0.02a
3600 m	52.25±2.78b	0.36±0.02d	6.14±0.03b	12.74±0.33c	1.43±0.01a	0.83±0.01a	1.09±0.02b
3700 m	43.62±3.83c	0.37±0.02c	6.01±0.06c	11.63±0.37d	1.34±0.03b	0.79±0.01b	0.99±0.02c
3800 m	35.77±4.47d	0.39±0.004b	5.93±0.04d	10.98±0.35d	1.24±0.02c	0.76±0.02d	0.95±0.03d

Note: Different lowercase letters in the same column indicate significant differences among plots ($p < 0.05$). see Table 1 for abbreviations.

3.2 Plant biomass characteristics of alpine peat bogs across an elevation gradient

3.2.1 Biomass distribution characteristics of rhizomes and leaves

Fig. 4 shows the biomass distribution characteristics of plants in alpine peat bogs under elevation gradient among various organs (roots, stems, and leaves). Plant biomass allocation followed the order of roots > leaves > stems, with the percentage of biomass allocated to the root system being highest, ranging from 78.69 % to 83.44%, and exhibiting an increasing trend with elevation. In contrast, the biomass of leaves ranged from 10.85% to 15.04%, whereas that of stems was the lowest, ranging from 5.71% to 7.11%. Furthermore, both leaves and stems showed a decreasing trend in biomass allocation with increasing elevation.

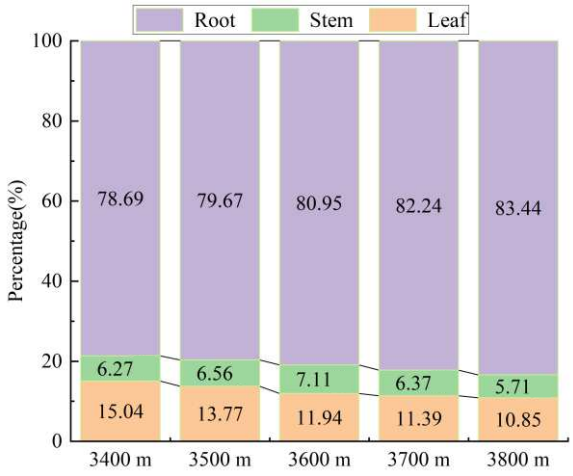
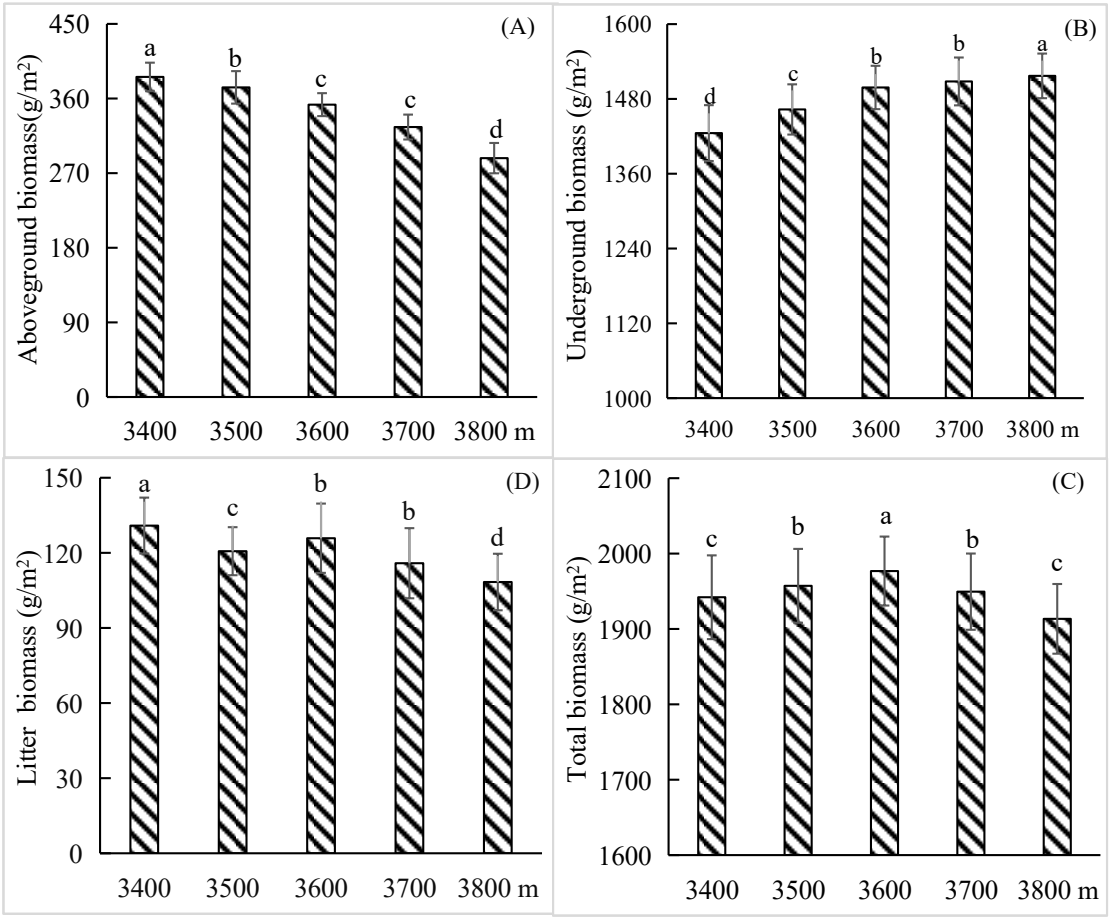


Fig. 4 Ratio of root, stem, and leaf biomass of plants in alpine peat bogs across elevation gradients

3.2.2 Aboveground and belowground biomass characteristics

Fig. 5 Aboveground and belowground biomass characteristics of plants in alpine peat bogs at different elevations (Figs. 5A, B, C, and D). With the increase in elevation, the total plant biomass increased first and then decreased. The total plant biomass was highest at 3600 m (1976.82 g/m^2) and lowest at 3800 m (1913.41 g/m^2) (Fig.5C). Plant aboveground biomass decreased with increasing elevation. Plant aboveground biomass was highest at 3400 m (386.06 g/m^2) and lowest at 3800 m (288.11 g/m^2) (Fig. 5A). The belowground biomass of plants increased with increasing elevation (Fig.5B). The litter biomass was highest at 3400 m (130.87 g/m^2) and lowest at 3800 m (108.35 g/m^2) (Fig.5D). The root-shoot ratio was minimum (3.69) at 3400 m above sea level and maximum (5.27) at 3800 m above sea level. The root-shoot ratio showed an increasing trend with an increase of 42.81% (Fig.6).



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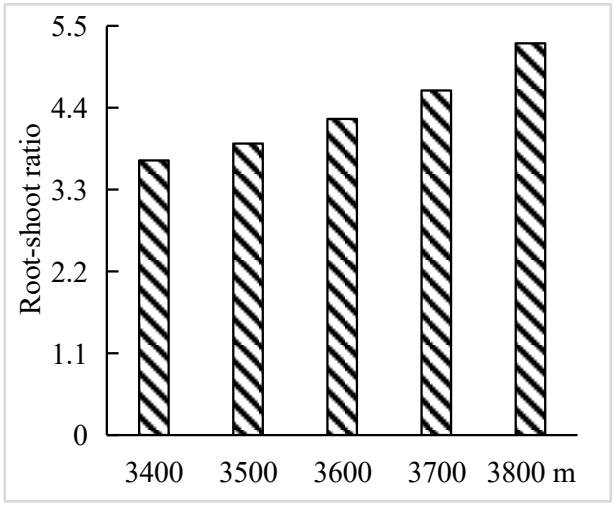
326 **Fig. 5** Characteristics of plant biomass in alpine peat bogs across elevation gradients



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328 **Fig. 6** Characteristics of plant root-to-shoot ratio in alpine peat bogs across elevation gradients

329 **3.3 Carbon storage characteristics of plants in alpine peat bogs across various elevation**
330 **gradients**

3.3.1 Plant organic carbon content

Fig. 7 shows the characteristics of the organic carbon content in the roots, stems, and leaves of plants in alpine peat bogs at different elevations. The organic carbon content of plant organs was in the order of stem > leaf > root > litter. At an elevation of 3800 m, the highest organic carbon content was found in the stems and leaves, which were 440.68 g/kg and 432.40 g/kg, respectively. At an elevation of 3400 m, the lowest content was found in the stems and leaves of peat bog plants, which were 420.99 and 410.94 g/kg, respectively. With the increase in elevation, the stem and leaf organic carbon content increased by 4.67% and 5.22%, respectively. The organic carbon content of plant roots was relatively low, with the lowest (363.69 g/kg) at 3800 m above sea level and the highest (380.12 g/kg) at 3400 m above sea level. The organic carbon content of plant litter was relatively low, with the lowest (341.08 g/kg) at 3400 m above sea level and the highest (365.75 g/kg) at 3700 m above sea level. With the increase in elevation, the litter organic carbon content increased by 7.23%.

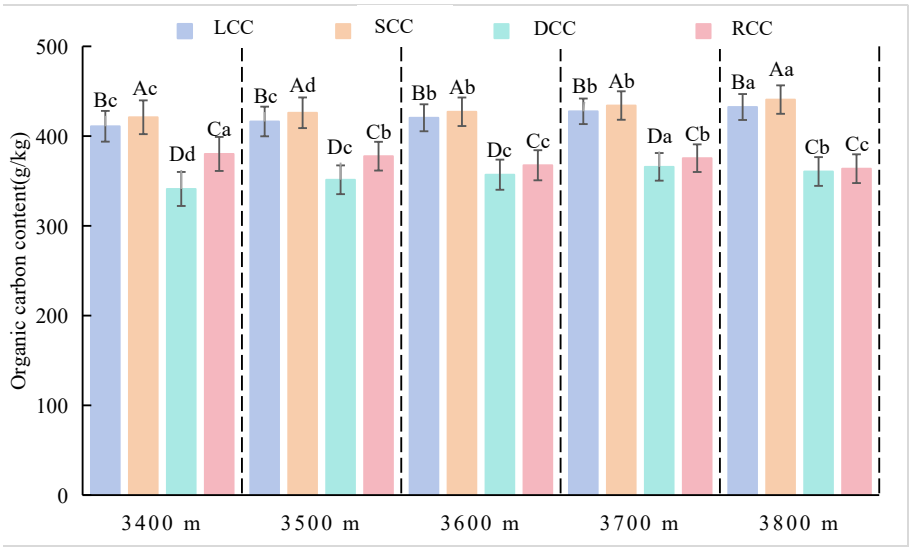

Fig. 7 Characteristics of the organic carbon content in the roots, stems, and leaves of alpine peat bogs across an elevation gradient.

Note: LCC, Leaf organic carbon. SCC, stem organic carbon. RCC, Root organic carbon. DCC, Litter organic carbon. Lowercase letters indicate that plant organs show significant differences at different elevations. The capital letters indicate differences in organic carbon content between plant organs at the same elevation.

3.3.2 Aboveground and subsurface carbon storage

Fig. 8 shows the carbon storage characteristics of plants in alpine peat bogs at different elevations. The total plant carbon storage was highest at 3600 m (743.21 $gC•m^{-2}$) and lowest at 3800 m (723.53 $gC•m^{-2}$). With the increase in elevation, plant carbon storage showed a trend of first increasing and then decreasing, with a change range of 5.94%. Belowground carbon storage of plants in peat bogs was higher than aboveground carbon storage at each elevation gradient. The plant belowground carbon stock was highest at 3600 m (551.16 $gC•m^{-2}$) and lowest at 3400 m (524.97 $gC•m^{-2}$). The belowground carbon stock of plants increased and then decreased with increasing elevation with a variation of 4.98%. The average aboveground carbon stock of plants was highest at 3400 m (158.79 $gC•m^{-2}$) and lowest at 3800 m (123.23 $gC•m^{-2}$). The aboveground carbon stocks of plants showed a decreasing trend with

increasing elevation, with a decrease of 22.39%. The litter plant carbon stock was maximum at 3600 m (44.92 gC•m^{-2}) and minimum at 3800 m (42.16 gC•m^{-2}).

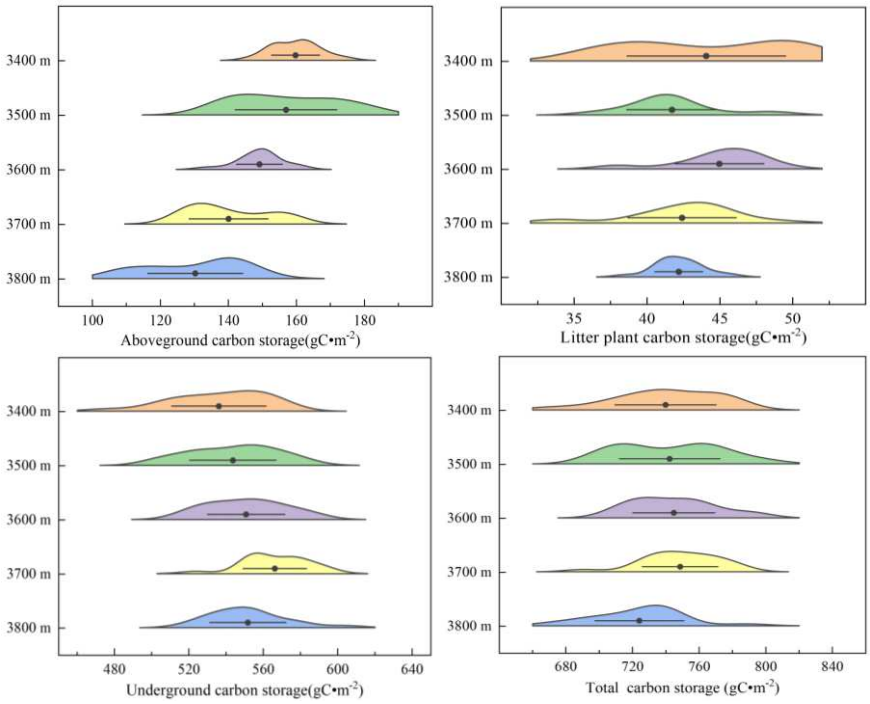

Fig. 8 Carbon storage characteristics of plants in alpine peat bogs across an elevation gradient

3.4 Analysis of the influencing factors of plant biomass and carbon storage in alpine peat bogs

3.4.1 Correlation analysis of plant biomass and carbon storage with environmental factors under elevation gradients

Fig. 9 Pearson correlation between plant biomass, carbon storage, soil physicochemical properties, and community characteristics in alpine peat bogs. The characteristics of the plant community (AH, FVC, and AD) were positively correlated with total biomass (TM) and total carbon storage (TC). In particular, the highest correlation coefficients were found between plant density and biomass and carbon stock (R^2=0.52, P≤0.01). There were highly significant positive correlations (P≤0.01) between soil temperature (TS), soil total nitrogen (TN), soil total phosphorus (TP), and soil water (SWC) with plant biomass (TM) and carbon stock (TCS). A highly significant negative correlation (P≤0.01) was found between soil bulk weight, pH, and plant biomass and plant carbon stock.

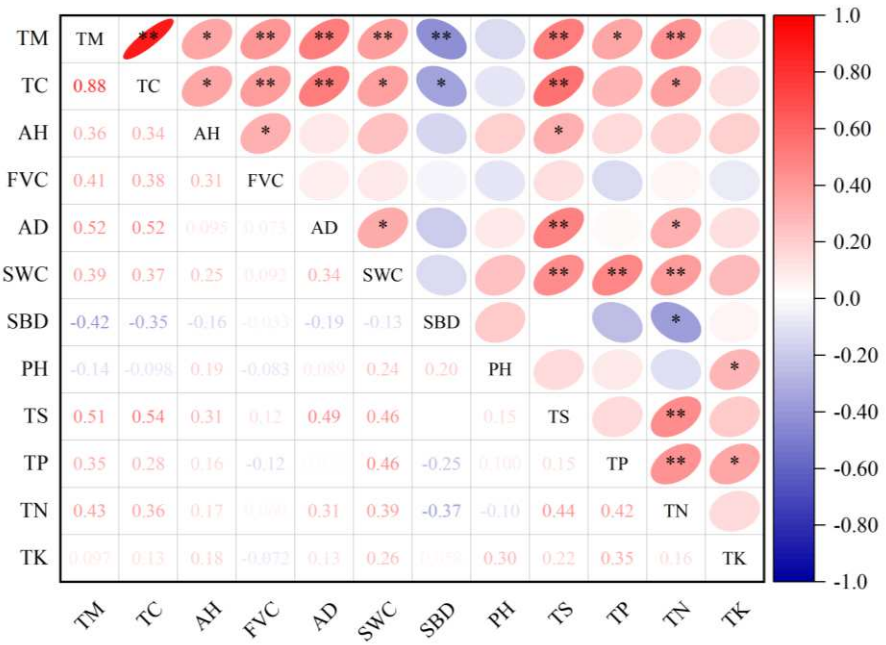

Fig. 9 Analysis of the influencing factors of plant biomass and carbon storage.

Note: see Table 1 for abbreviations. * $p < 0.05$ (bilateral); ** $p < 0.01$ (bilateral).

3.4.2 Path analysis of environmental factors and plant biomass and carbon storage at different elevation gradients

Table 3 shows the normality test of total plant biomass and total carbon storage in alpine peat bogs. The Shapiro-Wilk statistics of the dependent variables total plant biomass and total carbon storage were 0.984 and 0.989, respectively, with a significance level of Sig = 0.200> 0.05 (Table 3), indicating that the data were did not significantly deviate from a normal distribution and was suitable for regression analysis.

Table 3. Normality tests of total plant biomass and total carbon storage in alpine peat bogs

Item	Kolmogorov-Smirnova			Shapiro-Wilk		
	Statistics	df	significance	Statistics	df	significance
TM	0.051	189	0.200*	0.984	189	0.25
TC	0.07	189	0.200*	0.989	189	0.609

The multiple stepwise regression equations for the influencing factors, plant biomass, and carbon stock were established by regression analysis as follows.

TM=0.04+0.46TS-0.48SBD+0.50AD+0.38FVC+0.28TP

TC=0.03+0.73TM+0.42TS-0.02SBD+0.31AD+0.32FVC

As shown in Table 4, the independent variables TS, SBD, AD, FVC, and TP had significant (P<0.05) effects on the dependent variable TM, and other environmental factors that did not have significant ($P > 0.05$) *effects* on TM were excluded from the stepwise regression. The independent variables TM, TS, SBD, AD, and FVC had significant (P<0.05) effects on the dependent variable

TC, and other environmental factors that did not have significant (*P > 0.05) effects* on TC were excluded from the stepwise regression.

Since there were strong correlations among environmental factors, potential multicollinearity issues may arise during the regression analysis. To diagnose multicollinearity, we calculated the variance inflation factor (VIF) and tolerance (Tol). A VIF value greater than 10 and a Tol value less than 0.10 suggest the presence of severe multicollinearity among independent variables. However, in this study, the VIF values were less than 10 and the Tol values were greater than 0.10 (Table 4), indicating no significant multicollinearity problems among the environmental factors.

Table 4. Output results of the regression coefficients of total plant biomass and total carbon storage

Item	index	Unnormalized coefficient		Standardization coefficient			Collinearity statistics	
		B	Std	Beta	t	P	allowance	VIF
TM	Constant	0.04	0.10		0.38	0.71		
	FVC	0.38	0.14	0.29	2.68	0.01	0.71	1.40
	AD	0.50	0.12	0.38	4.06	0.00	0.96	1.04
	TP	0.28	0.10	0.27	2.73	0.01	0.88	1.14
	SBD	-0.48	0.16	-0.29	-2.93	0.01	0.87	1.15
	TS	0.46	0.18	0.28	2.59	0.01	0.71	1.41
TC	Constant	0.03	0.06		0.42	0.68		
	TM	0.73	0.08	0.73	9.40	0.00	0.60	1.67
	TS	0.42	0.04	0.35	3.16	0.00	0.43	1.37
	SBD	-0.02	0.01	-0.20	-3.02	0.00	0.81	1.24
	AD	0.31	0.02	0.19	2.73	0.01	0.63	1.21
	FVC	0.32	0.13	0.18	2.38	0.02	0.64	1.57

Note: B represents the regression coefficient; Std is a significance test for regression coefficients ($p < 0.05$). see Table 1 for abbreviations.

Stepwise regression analysis could not visualize the contribution of each environmental factor to plant biomass and carbon stocks. The path coefficients were calculated using the standardized regression coefficient method, where the correlation coefficients were decomposed into the algebraic sum of the direct path coefficients and the indirect path coefficients. This can directly reflect the effects of various environmental factors on plant biomass and carbon stock. As can be seen from Table 5, the main contributions of AD, FVC, TN, and TS to plant biomass were direct positive effects (the direct pathway coefficients were greater than the indirect pathway coefficients and the direct pathway coefficients were all greater than 0), and the main contributions of SBD and pH to plant biomass were direct negative effects. From the calculation results of decision coefficients (Table 5), it can be seen that the combined order of influencing plant biomass was: AD >TS> SBD > TP > FVC, which indicated that soil temperature and plant density had significant effects on plant biomass. The direct contribution of AD, SWC, and TS to the plant carbon stock was positive, whereas the main contribution of SBD to the plant biomass was negative. Based on the results of the decision coefficient calculation, the combined order of influencing plant carbon stock was TM > TS > AD >SBD> FVC.

Table 5. Correlation coefficients between plant biomass, carbon storage, and environmental factors in alpine peat bogs

Item	index	Correlation coefficient	Direct path coefficient	Indirect path coefficient							Decision coefficient
				TM	FVC	AD	TS	TP	SBD	total	
TM	FVC	0.42	0.29			0.03	0.03	-0.03	0.01	0.04	0.11
	AD	0.52	0.38		0.02		0.14	0.01	0.05	0.22	0.31
	SBD	-0.42	-0.29		-0.01	-0.07	0	-0.07		-0.15	0.17
	TS	0.51	0.28		0.04	0.19		0.04	0	0.26	0.23
	TP	0.35	0.27		-0.04	0.01	0.04		0.07	0.09	0.12
TC	TM	0.88	0.73		0.07	0.1	0.18		0.08	0.44	1.17
	FVC	0.38	0.18	0.3		0.01	0.04		0.01	0.37	0.16
	AD	0.52	0.19	0.38	0.01		0.17		0.04	0.6	0.26
	SBD	-0.35	-0.2	-0.31	-0.01	-0.04	0.01			-0.34	0.18
	TS	0.54	0.35	0.37	0.02	0.09			0	0.48	0.46

Note: See Table 1 for abbreviations

4 Discussion

The environmental characteristics of cold temperatures, high humidity, long-term water accumulation, and poor local water mobility play a crucial role in shaping the structure of plant communities in alpine peat bog ecosystems (Chai *et al*., 1990； Canedoli *et al*., 2024). To maintain necessary physiological activities and ensure normal growth, plants must effectively allocate biomass to their roots, stems, and leaves, optimizing resource allocation for improved environmental adaptability (Liu *et al*., 2022; McCarthy *et al*., 2007). Our findings revealed that the biomass distribution ratio of plants in peat bogs was in the order of root > leaf > stem. As elevation increased, the root-matter ratio increased, the leaf matter ratio decreased, and the stem-matter ratio initially increased and then decreased. These patterns can be attributed to the dominant plant species in the study area, namely, *Blysmus sinocompressus*, *Kobresia tibetica*, *Carex muliensis*, and *Carex kansuensis* (Fig. 2). These perennial plants belong to the Sedge family and possess dense clusters and well-developed roots, which enhance their nutrition and reproductive capabilities. Furthermore, to access oxygen from the surface, these plants grow new branches upward and adventitious roots downward, resulting in a higher biomass allocation to roots, thereby supporting the optimal allocation hypothesis (Colmer *et al*., 2009).

The aboveground and subterranean parts are fundamental components of plants. Plant roots absorb nutrients from the soil and transport them via physiological processes, indicating a close relationship between these belowground components and the aboveground parts (Bania *et al*., 2025) . Our study identified that the subterranean biomass of vegetation exceeded the aboveground biomass. As elevation increased, there was a decrease in aboveground biomass, an increase in subterranean biomass, and an increase in the root-shoot ratio, with total plant biomass initially increasing and then decreasing. This pattern can be mainly attributed to the following: (1) The proximity of peat bogs' water level to the surface, as well as the presence of undecomposed or semi-decomposed organic residues in the soil due to prolonged anaerobic decomposition, contributing to a significant amount of subterranean biomass. (2) The hydrothermal conditions of the peat bog at an elevation of 3400 m were relatively favorable (Table 2), which promoted the growth and development of the peat bog plants. These plants are distributed in clusters, forming a plant community with *Blysmus sinocompressus* as the dominant species (Fig. 2). Plants are highly nutritious and competitive, with intense neighbor disturbances and interspecific competition forcing more resources into stems and leaves. Plants

perform photosynthesis by increasing plant height and leaf area, and plant leaf biomass is higher (Figs. 3 and 4). (3) As the elevation increased, there was a decrease in soil temperature and available resources, such as soil nutrients and water. This resulted in a greater allocation of biomass to the belowground, leading to a decrease in plant height and aboveground biomass and a significant increase in the root-shoot ratio. (4) The low temperatures and nutrient deficiency in the peat bog at an elevation of 3800 m limited the growth of aerial components (leaves and stems) in *Carex kansuensis* and other plant species, resulting in low aboveground biomass (Figs. 3 and 5). However, *Carex kansuensis* and other clump-forming plants possess lateral extension of root systems, strong infiltration capabilities, and the self-reproduction ability of root tips and root caps, leading to a large subterranean biomass. Additionally, to withstand the environmental stress of low temperatures, plants enhance their photosynthetic capacity and maintain water balance by optimizing the allocation of aboveground and belowground biomass, ensuring their own growth and development (Ma *et al*., 2017) . This strategy represents an important manifestation of plant ecological adaptation to environmental heterogeneity stress, which is consistent with the research results of Du *et al*. (2026).

Plant organic carbon content reflects the ability of plants to fix and store carbon during photosynthesis. The difference in organic carbon content in plant organs stems from their own functions, physiological characteristics, and environmental heterogeneity. Our study revealed that in peat bogs, the organic carbon content of plant organs followed the order of stem > leaf > root > litter. As elevation increased, plant leaves and stems exhibited an increasing trend in organic carbon content, whereas plant roots showed a decreasing trend in carbon content (Fig.7). This is mainly because of the following factors: (1) The primary plants in peat bogs are sedges such as *Blysmus sinocompressus*, *Kobresia tibetica*, *Carex muliensis*, and *Carex kansuensis* (Fig. 2). Plant reproductive organs (flower spikes) contain several nutrients, such as protein, carotene, and pastrin, resulting in high carbon content. Additionally, the plant stem contains a higher proportion of lignin, contributing to higher carbon content. Therefore, the upper stem (inflorescence) exhibits the highest carbon content. Leaf litter, fruit litter, and thin stem litter of plants in peat bogs are the main litter, and their main components are soluble organic compounds such as protein, amino acids, and simple sugars. Soil organic matter derived from these litter types is easily decomposed by microorganisms (Cornelissen *et al*., 1999). However, a small amount of aboveground stem and fine root litter is composed of difficult-to-decompose organic components such as lignin, cellulose, and polyphenols (Ma *et al*., 2025); therefore, the content of plant litter is relatively low. (2) The Gannan Plateau has intense solar radiation and abundant light resources, providing sufficient energy sources for plant photosynthesis in the context of high-altitude and low-temperature environments. Adequate light is beneficial for plant carbon fixation through photosynthesis and promotes the formation of higher leaf dry weight and leaf area index in the community, resulting in overall strong photosynthetic activity. The aboveground stems and leaves are the main functional organs for plant photosynthetic carbon assimilation and serve as mechanical supports and ventilation structures (Tian *et al*., 2020). The cellulose and lignin components in the tissues account for a high proportion of carbon-rich structural components; therefore, the organic carbon content of the aboveground stem and leaf organs of plants is relatively high. Consequently, the organic carbon content in the aboveground parts (stems and leaves) of wetland plants exceeds that in the belowground parts (roots), aligning with the findings of zhao *et al(2019)*. (3) As elevation increases, plant leaves need to thicken to withstand adverse weather conditions such as radiation, cold, and wind (leading to an increase in leaf mass per area). As the optimal photosynthesis temperature decreases, chlorophyll content also decreases, while carotenoid content and UV radiation absorption increase. Moreover, plant leaves are rich in fibrous material and silica, with well-developed cuticle membranes and strong metabolic activity, promoting photosynthesis and biomass accumulation. The stem adapts and balances between support and conduction functions, tending to become lignified and robust above

ground, leading to an increasing trend in the organic carbon content of plant leaves and stems with rising elevation.

During plant growth, leaf pores absorb carbon dioxide through photosynthesis and fix it into organic compounds, achieving the carbon sequestration process. Studies have shown that the belowground carbon storage of plants was higher than their aboveground carbon storage at an elevation gradient. With the elevation increase, plant total carbon storage and belowground carbon storage increased first and then decreased, and aboveground carbon storage decreased. This can be attributed to several factors: (1) The prolonged presence of stagnant water and low-temperature conditions in peat bog wetlands leads to the accumulation of a significant amount of undecomposed or partially decomposed organic residues in the soil, resulting in a high belowground biomass. Additionally, the rate of belowground biomass loss is relatively low, facilitating the accumulation of root carbon sequestration. Therefore, the belowground carbon storage of plants surpasses the aboveground carbon storage, consistent with the conclusion drawn by Ma *et al*. (2017). (2) At an elevation of 3400 m, the water and heat conditions of the alpine peat bogs are relatively good, and the aboveground part of the community grows strongly. Plants continue to use CO_2 to synthesize photosynthetic products as organic carbon is fixed, and the carbon storage of plant stems and leaves continues to increase. Therefore, the abovementioned carbon storage of peat bogs at 3400 m was relatively high (158.79±6.44 $gC•m^{-2}$) (Fig. 8). However, the substantial vegetation coverage in this region intensifies the competition for light and other resources among plants. In response, plants allocate more biomass resources to the aboveground portion, resulting in lower root biomass and a decline in belowground carbon sequestration and the overall carbon sequestration capacity of the plant community (Fig. 7). (3) At an elevation of 3600 m, the soil moisture content (SWC) was 52.25%, the soil temperature (TS) was 12.74 ℃, and the total nitrogen and phosphorus nutrient contents in the soil were relatively high, creating a relatively suitable combination of water and heat conditions (Table 2). Lower vegetation coverage reduces the shading effect among populations, which is conducive to better photosynthesis of plants, thus effectively improving plant biomass and carbon storage. Therefore, the carbon storage of plants at 3600 m above sea level is the largest (743.21±18.56 $gC•m^{-2}$) (Fig. 8). (4) With the elevation increase, soil moisture, soil temperature, and soil nutrients decreased, leading to decreased plant height, density, and cover. This reduction in plant photosynthesis, biomass, and carbon sequestration capacity results in the lowest level of carbon storage in alpine peat bogs at an elevation of 3800 m (Fig. 2 and Fig. 3). Thus, with increasing elevation, plant carbon storage in peat bogs follows a "low-high-low" pattern, consistent with the findings of Mou *et al* (2026).

5 Conclusion

Under the climatic background of global warming, the unique topographic and hydrological conditions of the Maqu alpine peat bogs play important roles in regional climate regulation and ecological diversity conservation. With the increase in soil temperature and the decrease in nutrients, the dominant species of the plant community changed from *Blysmus sinocompressus* and *Kobresia tibetica* to *Carex muliensis* and *Carex kansuensis*. Plants occupy living space and obtain environmental resources by regulating photosynthetic products to their roots. The root-matter ratio of plants increases and changes, while the leaf matter ratio and stem matter ratio decrease with elevation, reflecting the adaptability of plant organs in peat bogs to alpine environments. On the elevation gradient, plant biomass and carbon storage in alpine peat bogs increased first and then decreased. By regulating the local hydrothermal conditions, altitude creates a heterogeneous soil environment and affects the accumulation of plant biomass and carbon storage by influencing the species composition and morphological characteristics of plants in peat bogs, as well as the distribution pattern of biomass and carbon resources in each organ. The responses of plant biomass and carbon storage allocation patterns

to altitude were analyzed only at the community scale. Plant morphological characteristics, biomass allocation, and carbon sequestration capacity have not been studied from the perspective of plant species and will be the focus of subsequent research

6 Conflicts of Interest

The authors declare no conflicts of interest.

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8 Author Contributions

Man P Kang (MPK) , Cheng Z Zhao (CZZ),and Wen T Xu (XWT) conceived and designed the experiments. MPK performed the experiments, analyzed the data, and drafted the manuscript. CZZ support in the funding acquisition, resources, and critical revision of the article. MPK and XWT undertook the investigation and contributed the methodology. All authors reviewed and approved the final manuscript.

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10 Data Availability Statement

Due to our lab's policies or confidentiality agreements, we cannot provide raw data. We have fully described the process of experimental design, analysis, and results, as well as data analysis and processing. If editors and reviewers have questions about specific data, we will try to provide more detailed explanations

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