

Changes in plant biomass and species composition of alpine *Kobresia* meadows along altitudinal gradient on the Qinghai-Tibetan Plateau

WANG ChangTing^{1,3†}, CAO GuangMin¹, WANG QiLan¹, JING ZengChun¹, DING LuMing¹ & LONG RuiJun²

¹ Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810001, China;

² College of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou 730070, China;

³ Graduate University of the Chinese Academy of Sciences, Beijing 100039, China

Alpine *Kobresia* meadows are major vegetation types on the Qinghai-Tibetan Plateau. There is growing concern over their relationships among biodiversity, productivity and environments. Despite the importance of species composition, species richness, the type of different growth forms, and plant biomass structure for *Kobresia* meadow ecosystems, few studies have been focused on the relationship between biomass and environmental gradient in the *Kobresia* meadow plant communities, particularly in relation to soil moisture and edaphic gradients. We measured the plant species composition, herbaceous litter, aboveground and belowground biomass in three *Kobresia* meadow plant communities in Haibei Alpine Meadow Ecosystem Research Station from 2001 to 2004. Community differences in plant species composition were reflected in biomass distribution. The total biomass showed a decrease from 13196.96 ± 719.69 g/m² in the sedge-dominated *K. tibetica* swamp to 2869.58 ± 147.52 g/m² in the forb and sedge dominated *K. pygmaea* meadow, and to 2153.08 ± 141.95 g/m² in the forbs and grasses dominated *K. humilis* along with the increase of altitude. The vertical distribution of belowground biomass is distinct in the three meadow communities, and the belowground biomass at the depth of 0–10 cm in *K. tibetica* swamp meadow was significantly higher than that in *K. humilis* and *K. pygmaea* meadows ($P < 0.01$). The herbaceous litter in *K. tibetica* swamp was significantly higher than those in *K. pygnaeca* and *K. humilis* meadows. The effects of plant litter are enhanced when ground water and soil moisture levels are raised. The relative importance of litter and vegetation may vary with soil water availability. In the *K. tibetica* swamp, total biomass was negatively correlated to species richness ($P < 0.05$); aboveground biomass was positively correlated to soil organic matter, soil moisture, and plant cover ($P < 0.05$); belowground biomass was positively correlated with soil moisture ($P < 0.05$). However, in the *K. pygnaeca* and *K. humilis* meadow communities, aboveground biomass was positively correlated to soil organic matter and soil total nitrogen ($P < 0.05$). This suggests that the distribution of biomass coincided with soil moisture and edaphic gradient in alpine meadows.

plant species richness, plant litter, aboveground biomass, belowground biomass, soil moisture, alpine meadow

Distinctive features of plant communities that reflect responses to strong environmental gradients include species composition, species richness, growth forms, and plant biomass structure (i.e. the distribution of biomass among the above- and belowground components)^[1]. Previous studies on biomass totals for the common streamside sedge species have been focused on

carbon sequestration, and have been conducted in wetlands, primarily marshes and fens, where these species

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[†]Corresponding author (email: wcht6@hotmail.com or wct@nwipb.ac.cn)

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occur in extensive, nearly monospecific stands, and have high productivity^[2]. Belowground biomass affects sub-surface biogeochemical processes^[3] and floodplain soil development, and provides habitat for aquatic organism. The distribution of vegetation type correlated with soil humidity and soil temperature obviously in alpine meadow. With respect to the general biogeography of the region, the *Kobresia humilis* meadows, typical alpine meadow dominated by *K. humilis* and accompanied with *Elymus mutans*, are widely distributed along the valley floor and on the northern slopes. The *Kobresia pygmaea* meadow is distributed on the northern slopes with lower soil moisture. The *Kobresia tibetica* of swamp meadow is found in the humidity zone where it is dominated by *K. tibetica*. Despite the importance of these functions for *Kobresia* meadow ecosystems, few studies have been carried out on the biomass structure of dominant *Kobresia* meadow plant communities, particularly in relation to soil moisture and edaphic gradients.

The Qinghai-Tibetan Plateau is the unique largest and highest plateau in the world, covering an area of nearly 2.5×10^6 km². *Kobresia*, as one of the dominant genera of alpine meadows, is a typical vegetation on the Qinghai-Tibetan Plateau^[4]. Given the high altitude and extreme harsh environment, this high elevation grazing land ecosystem might, up to date, be among the least affected zones by human activities. The alpine meadows range from 2000 to 5000 m with cold and semi-humid climate. Grassland resources are vital for the livelihood of the people and their livestock. The available alpine rangelands of the plateau cover about 128.2×10^6 hm², approximately accounting for 30.7% of China's total rangelands area. These alpine rangelands mainly consist of alpine meadow (49.3%) and alpine steppe (44.9%)^[5]. Thus it will be important to develop animal husbandry in Qinghai-Tibetan Plateau. The grassland, however, is characterized by the long cold and dry, short warm seasons, with the growing season of 90–150 days, resulting in lower primary productivity in alpine *Kobresia* meadow^[6]. It has long been known that the productivity of cold ecosystems is limited by short growing season^[7] and reduced soil nutrient availability^[8,9]. Plant growth in cold ecosystems might also be influenced by soil moisture, especially in alpine regions where sharp differences in soil water availability are associated with microtopography^[10].

The change of the above- and belowground biomass

of alpine meadow was particularly studied and reported^[11–14]. The results showed that the seasonal changes of aboveground biomass and biomass composition of different vegetation types are different in plant growing season, and the belowground biomass is distributed mainly at 0–10 cm soil level and has vertical distributive characteristics. In this study, we experimentally examined the relative importance of vegetation canopy and leaf litter. Special attention was given to community differences in biomass components and the vertical belowground biomass along soil moisture gradients.

We investigated the relationships among plant richness, above- and belowground biomass, soil moisture, and soil resources in the three *Kobresia* meadow plant communities. The three communities—referred to as *K. tibetica* of swamp meadow, *K. humilis* meadow and *K. pygmaea* meadow—occurred along an altitudinal gradient. The objectives of the present study are: (1) to compare amounts and distribution of above- and belowground biomass in the three meadow communities; (2) to examine relations among plant species richness, biomass, soil moisture and soil resources along the environmental gradients.

1 Materials and methods

1.1 Study sites

The study was conducted at Haibei Research Station, the Chinese Academy of Sciences in August from 2001 through 2004. The station is located in northeast of the Qinghai-Tibetan Plateau (N 37°37', E 101°18') with an altitude of 3240 m a.s.l. The average annual precipitation recorded at the station from 1976 to 2001 was 560 mm, with 85% of rainfall concentrated in the growing season from May to September. The average annual air temperature for the 25 years from 1976 to 2001 was -1.7°C . The mean, maximum and minimum of air temperature from 1980 to 1990 were 8.7°C , 15.6°C , and 2.5°C , respectively, in summer and -13.2°C , -2.2°C and -22.1°C , respectively in winter^[15]. The soils at the study site are classified as swamp meadow soil, alpine shrub soil and alpine meadow soil. There were various types of vegetation dominated by alpine *Kobresia* species.

1.2 Plant composition and biomass

One experimental site with 50 m×50 m was established in each of the three alpine communities: *K. pygnaeca*

meadow, *K. humilis* meadow, and *K. tibetica* swamp meadow. Plant species composition and cover were sampled in ten 1 m×1 m quadrats. Data were collected and samples cut in mid to late August each year. Plant species were identified and recorded, and percent cover and height for each recorded plant species were measured.

Aboveground biomass was harvested from 10 quadrats, each with an area of 1 m×1 m. All litter and vegetation rooted within the quadrats were clipped at the ground level. Aboveground biomass samples were air-dried, sorted into 5 categories — graminoids, sedges, legumes, forbs, and litter, dried at 65°C for 48 h, and then weighed.

Belowground biomass samples were collected by soil cores to a depth of 30 cm at 5 quadrats, each with an area of 25 cm×25 cm, after aboveground biomass harvest. After extraction, each core was sliced into 10 cm segments, yielding samples were from the following depths: 0–10, 10–20, 20–30 cm. Belowground biomass samples were washed using an elutriation system with 0.5 mm-mesh screens, dried at 65°C for 48 h, and then weighed.

1.3 Soil moisture and soil properties

Soil moisture was measured gravimetrically at 105°C for 24 h. Soils of each plot were sampled by aggregating five soil cores (5 cm in diameter and 10 cm in depth) in a V-shaped pattern and split into 0–10, 10–20, 20–30 sections. Organic matter contents of the soil samples were determined by the method reported by FAO^[16]. The contents of total N and total P in the soil samples were measured by the methods described by Bremner et al.^[17] and Olsen and Sommers^[18] respectively.

1.4 Data analysis

Mean soil moisture ($n=10$ replicates) was calculated for each plot, depth, and date of sampling. Biomass values were averaged for each plot (10 for aboveground biomasses, 5 for belowground biomasses). For each site, one-way ANOVA was used to detect community differences in soil moisture, soil properties, total plant cover, and total biomass. Belowground biomass data were analyzed using one-way ANOVA with different depth within plant community. Data for species richness, graminoids (grasses), sedges, legumes, and forbs were analyzed using Kruskal-Wallis tests^[1]. For each site, soil resources, ratios of belowground-to-aboveground bio-

mass, community differences in components of above- and belowground biomass and community differences in total belowground biomass were tested using Kruskal-Wallis tests. Statistical analyses were performed in SPSS version 10.0^[19]. Species richness was the total number of vascular plant species within the five plots per site. Spearman rank correlations among total biomass, species richness, plant cover, soil moisture were conducted for each site.

2 Results

2.1 Above-, belowground biomass and plant litter

Total aboveground biomass differed significantly among *K. tibetica* swamp and *K. pygnaeca* and *K. humilis* meadow communities (Table 1). Moreover, the relative contribution of individual biomass components indicates community differences in species composition (Table 2, Figure 1). *K. tibetica* swamp meadow communities were mainly dominated by *K. tibetica* which had the lowest coverage (Table 2). *K. humilis* meadow communities, with the highest coverage, were composed of a mixture of forbs and graminoids, with the dominating forbs *Gentiana straminea*, *Leontopodium nanum*, and *Potentilla anserine*, with the graminoids dominated by *Stipa aliena* and *Elymus natans*. The *K. pygnaeca* meadow communities, intermediate in coverage, are composed of a mixture of forbs dominated by *Potentilla nivea*, *Thalictrum alpinum*, and the sedges dominated by *K. pygnaeca*. However, *K. tibetica* swamp meadow communities had the lowest species richness. The *K. pygnaeca* meadow communities were intermediate in species richness. *K. humilis* meadow communities were the highest in species richness. In the *K. tibetica* swamp meadow communities, aboveground biomass was dominated by sedge species (~70%–80% of the aboveground biomass). In the *K. pygnaeca* and *K. humilis* meadow communities, aboveground biomass was composed of a mixture of forbs, graminoids and sedges. Forbs comprised about 38%–42% of the aboveground biomass in the *K. pygnaeca* meadow communities and 21%–26% of the aboveground biomass in the *K. humilis* meadow communities. Grass comprised about 20%–24% of the aboveground biomass in the *K. pygnaeca* meadow communities and 42%–46% of the aboveground biomass in the *K. humilis* meadow communities.

Table 1 Species richness, aboveground, belowground biomass and ratios for *K. pygmaea* meadows, *K. humilis* meadow, and *K. tibetica* swamp meadow (Mean±SD)

Item	Year	Species richness	Biomass totals (g·m ⁻²)		BG biomass/AG biomass	Total biomass (AG+BG) (g·m ⁻²)	Plant litter (g·m ⁻²)
			Aboveground (AG)	Belowground (BG)			
<i>Kobresia pygnaea</i> meadow	2001	21±3 ^b	283.61±9.28 ^b	2790.24±171.50 ^b	9.84±0.62 ^b	3073.85±200.04 ^b	38.06±1.89 ^b
	2002	25±3 ^b	283.88±33.06 ^b	3055.34±140.14 ^b	10.85±0.96 ^b	3339.22±188.08 ^b	37.75±1.58 ^b
	2003	24±3 ^b	280.89±28.23 ^b	2744.16±137.44 ^b	9.87±1.40 ^b	3025.05±126.22 ^b	38.90±2.30 ^b
	2004	23±4 ^b	283.39±14.66 ^b	3023.68±204.32 ^b	10.68±1.40 ^b	3307.07±407.88 ^b	41.94±3.25 ^b
<i>Kobresia humilis</i> meadow	2001	22±3 ^a	326.00±29.72 ^{ab}	2245.92±80.96 ^c	6.93±0.58 ^c	2571.92±95.57 ^c	37.63±2.13 ^b
	2002	31±2 ^a	315.44±20.75 ^{ab}	2232.16±159.52 ^c	7.08±0.37 ^c	2547.60±175.06 ^c	45.67±4.09 ^b
	2003	30±4 ^a	289.21±37.34 ^{ab}	1911.68±114.08 ^c	6.67±0.96 ^c	2200.89±229.54 ^c	43.11±2.14 ^b
<i>Kobresia tibetica</i> swamp meadow	2004	30±2 ^a	303.09±23.76 ^{ab}	2139.68±153.28 ^c	7.09±0.72 ^c	2442.77±157.85 ^c	48.21±3.20 ^b
	2001	17±2 ^c	365.51±29.25 ^a	12605.56±537.12 ^a	34.41±1.56 ^a	12971.07±548.60 ^a	99.66±5.43 ^a
	2002	18±2 ^c	393.22±66.69 ^a	13090.24±338.88 ^a	34.22±6.86 ^a	13483.46±279.62 ^a	99.79±7.48 ^a
	2003	18±1 ^c	357.48±15.81 ^a	12856.16±795.84 ^a	36.04±3.04 ^a	13213.64±792.41 ^a	99.80±9.08 ^a
	2004	18±2 ^c	379.76±80.48 ^a	13915.04±652.00 ^a	36.55±8.62 ^a	14294.80±136.74 ^a	100.55±9.51 ^a

For each vegetation type, different superscript letters indicate a significant difference among community means (one-way ANOVA for litter and biomass; Kruskal-Wallis test for species, $P=0.05$). BG, belowground; AG, aboveground.

Table 2 Dominant species cover and distribution of different functional group biomass for *K. pygmaea* meadows, *K. humilis* meadow, and *K. tibetica* swamp meadow (Mean±SD)

Items	Year	Plant cover (%)	Dominant species cover (%)	Grasses biomass (g·m ⁻²)	Legumes biomass (g·m ⁻²)	Sedges biomass (g·m ⁻²)	Forbs biomass (g·m ⁻²)	Aboveground (AG) (g·m ⁻²)
<i>Kobresia pygnaea</i> meadow	2001	156±4 ^b	63.20±2.58 ^b	72.11±12.33 ^b	40.17±5.96 ^b	62.77±10.85 ^b	108.56±14.33 ^a	283.61±9.28 ^b
	2002	157±14 ^b	66.90±3.29 ^b	70.69±19.95 ^b	39.00±6.68 ^b	61.94±12.42 ^b	112.25±14.84 ^a	283.88±33.06 ^b
	2003	152±11 ^b	56.60±2.91 ^b	87.33±28.18 ^b	37.85±12.34 ^b	51.12±12.75 ^b	104.59±19.84 ^a	280.89±28.23 ^b
	2004	155±6 ^b	65.60±3.61 ^b	74.29±21.03 ^b	36.60±5.20 ^b	61.06±12.28 ^b	111.45±13.72 ^a	283.39±14.66 ^b
<i>Kobresia humilis</i> meadow	2001	189±5 ^a	55.30±2.27 ^c	122.55±16.22 ^a	68.21±6.74 ^a	46.78±11.56 ^c	88.46±15.28 ^b	326.00±29.72 ^{ab}
	2002	183±13 ^a	55.50±1.93 ^c	125.86±16.41 ^a	54.31±4.55 ^a	47.00±6.73 ^c	88.28±10.16 ^b	315.44±20.75 ^{ab}
	2003	186±12 ^a	56.20±2.35 ^c	121.83±23.98 ^a	50.21±6.62 ^a	42.81±9.57 ^c	74.36±19.00 ^b	289.21±37.34 ^{ab}
<i>Kobresia tibetica</i> swamp meadow	2004	185±7 ^a	50.20±1.39 ^c	123.27±26.85 ^a	61.85±13.07 ^a	37.26±19.33 ^c	80.71±12.31 ^b	303.09±23.76 ^{ab}
	2001	104±4 ^c	87.52±1.54 ^a	11.88±3.35 ^c		311.50±35.26 ^a	42.13±14.31 ^c	365.51±29.25 ^a
	2002	105±5 ^c	88.60±2.04 ^a	8.06±1.41 ^c		340.85±71.14 ^a	44.47±17.03 ^c	393.22±66.69 ^a
	2003	107±3 ^c	87.40±0.61 ^a	13.26±7.35 ^c		304.84±16.60 ^a	39.38±10.60 ^c	357.48±15.81 ^a
	2004	104±6 ^c	88.20±2.20 ^a	7.90±1.42 ^c		328.34±83.59 ^a	43.52±15.61 ^c	379.76±80.48 ^a

For each vegetation type, different superscript letters indicate a significant difference among community means (one-way ANOVA for dominant species cover, plant cover, and biomass). BG, belowground; AG, aboveground.

Total belowground biomass was significantly higher than total aboveground biomass in each meadow community (Table 1), and differed among the three meadow communities ($P<0.0001$). In the *K. tibetica* swamp, *K. pygnaea* meadow and *K. humilis* meadow communities, belowground biomass comprised about 96%, 90% and 87% of the total biomass, respectively, and belowground biomass-to-aboveground biomass ratios were 35.31, 10.31 and 6.94, respectively (Table 1).

The vertical distribution of belowground biomass was distinctive in three meadow communities (Figure 2), and

significant differences in belowground biomass were observed in 0–10 cm depth for the three sites ($P<0.01$). In the *K. tibetica* swamp meadow community, 52%–57% of the belowground biomass occurred in the 0–10 cm depth, 22%–30% in the 10–20 cm depth, and 15%–21% in the 20–30 cm depth. In contrast, 86%–88%, 8%–10%, and 3%–4% of the belowground biomass occurred in the 0–10, 10–20, and 20–30 cm depth in the *K. pygnaea* community, 88%–91%, 6%–8%, and 2%–4% of the belowground biomass occurred in the

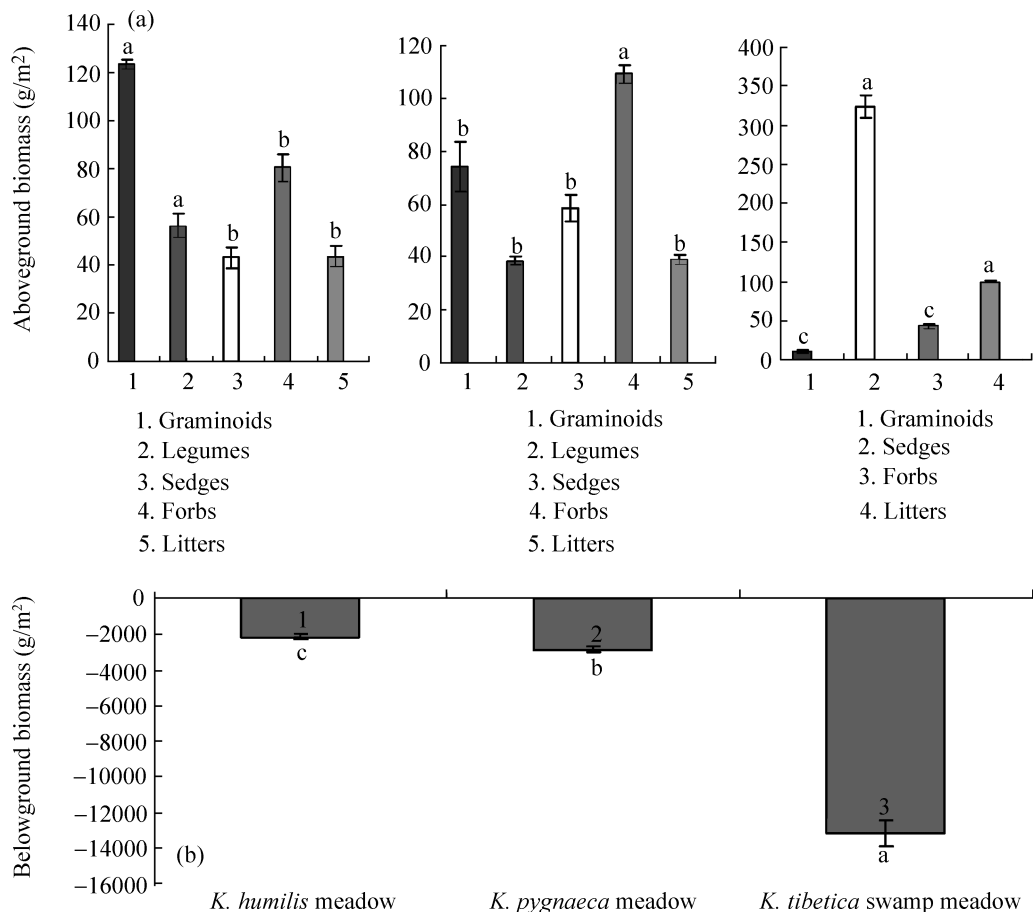


Figure 1 Distribution of biomass (Mean±SD (g/m²)) in the *K. pygnaeca*, *K. humilis*, *K. tibetica* swamp meadow communities. Components of aboveground biomass are indicated above the x-axis, belowground biomass is shown below the x-axis. At the same component biomass for each community, different letters denote a significant difference between means (Kruskal-Wallis test for forbs, graminoids, sedges, herbaceous litters and belowground biomass).

0–10, 10–20, and 20–30 cm depth in the *K. humilis* community, and no significant differences in belowground biomass were observed between the 10–20 and 20–30 cm depth in the *K. humilis* and *K. pygnaeca* communities (Figure 2).

The herbaceous litter was significantly different among *K. tibetica* swamp meadow, *K. pygnaeca* and *K. humilis* meadows ($P < 0.0001$). It is the highest in the *K. tibetica* swamp meadow community (18%–21% of the total aboveground biomass) (Table 1).

2.2 Soil moisture and soil properties

Water availability is important in affecting plant colonization and distribution in wetland^[20,21] and the number of plant niches^[22]. Mean soil moisture and soil resources differed significantly among the three alpine meadow communities (Table 3). Soil moisture at 0–30 cm depth was significantly higher in *K. tibetica* swamp meadow

than in *K. pygnaeca* and *K. humilis* meadows. The same tendency was shown in soil organic matter and soil total N. However, there was less difference in contents of the soil total P for the three different alpine meadows (Table 3).

2.3 Relationship between biomass and species richness as well as soil characteristic

In the *K. tibetica* swamp meadow community, aboveground biomass was negatively correlated to species richness ($r_s = -0.900$, $P = 0.037$); aboveground biomass was positively correlated to soil organic matter ($r_s = 0.982$, $P = 0.003$), soil moisture ($r_s = 0.921$, $P = 0.026$), and plant cover ($r_s = 0.882$, $P = 0.048$). In the *K. pygnaeca* and *K. humilis* meadow communities, aboveground biomass was positively correlated to soil organic matter ($r_s = 1.000$, $P = 0.000$; $r_s = 0.900$, $P = 0.037$) and soil total nitrogen ($r_s = 0.975$, $P = 0.005$, $r_s = 0.900$, $P = 0.037$).

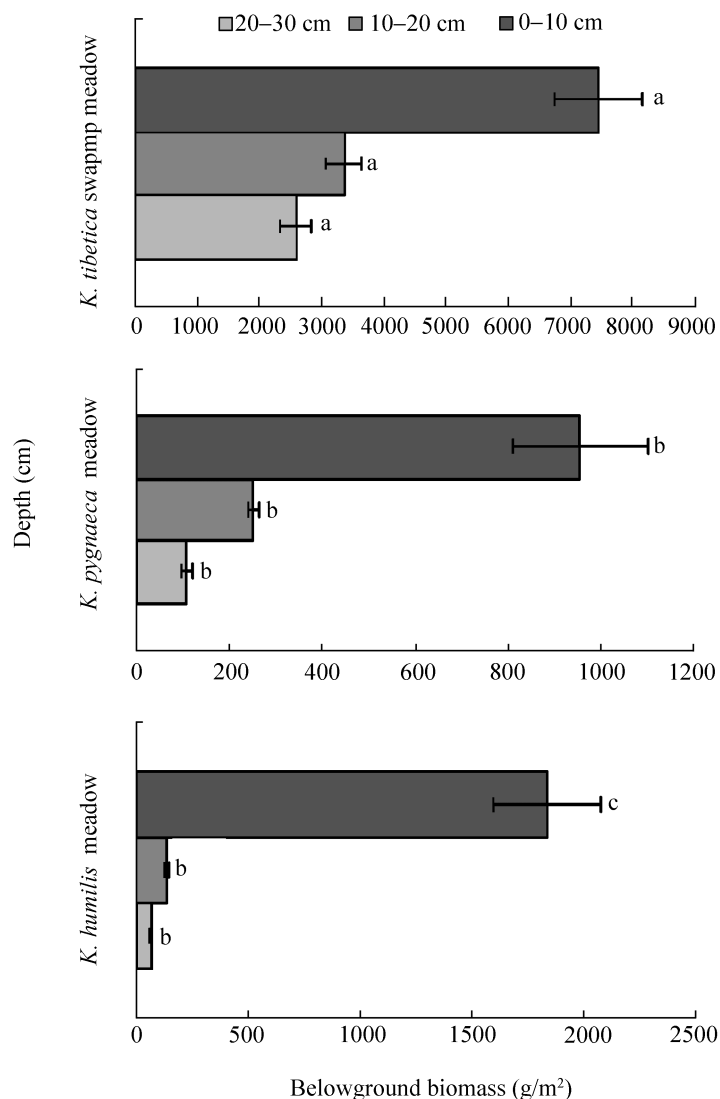


Figure 2 Vertical distribution of belowground biomass for the *K. pygnaecea* meadow, *K. humilis* meadow, and *K. tibetica* swamp meadow plant communities (Mean±SD). Within each community, different letters indicate a significant difference in belowground biomass between depths.

Table 3 Annual means of soil moisture and soil properties at 0–30 cm in three alpine meadow plant communities (Mean±SD)

Community type	Year	Moisture (%)	Organic matter (%)	Total N (%)	Total P (%)
<i>Kobresia pygnaecea</i> meadow	2001	32.03±0.04 ^b	11.49±0.60 ^b	0.57±0.02 ^b	0.08±0.01 ^a
	2002	33.09±0.04 ^b	10.76±0.75 ^b	0.53±0.03 ^b	0.06±0.01 ^a
	2003	35.24±0.03 ^b	11.56±0.99 ^b	0.58±0.06 ^b	0.06±0.01 ^a
	2004	36.97±0.04 ^b	11.80±0.73 ^b	0.53±0.03 ^b	0.06±0.01 ^a
<i>Kobresia humilis</i> meadow	2001	34.85±0.05 ^b	9.88±0.64 ^b	0.51±0.05 ^b	0.08±0.01 ^a
	2002	35.57±0.10 ^b	10.03±0.38 ^b	0.53±0.02 ^b	0.07±0.02 ^a
	2003	37.82±0.04 ^b	10.95±0.27 ^b	0.55±0.04 ^b	0.07±0.01 ^a
	2004	39.33±0.06 ^b	10.42±0.56 ^b	0.54±0.02 ^b	0.06±0.02 ^a
<i>Kobresia tibetica</i> swamp meadow	2001	67.09±0.02 ^a	25.29±0.83 ^a	1.31±0.06 ^a	0.08±0.01 ^a
	2002	71.57±0.04 ^a	24.77±1.22 ^a	1.24±0.06 ^a	0.06±0.01 ^a
	2003	72.84±0.05 ^a	25.34±1.13 ^a	1.28±0.03 ^a	0.06±0.01 ^a
	2004	75.91±0.06 ^a	24.76±1.22 ^a	1.34±0.04 ^a	0.07±0.01 ^a

For each vegetation type, different superscript letters indicate a significant difference between community means ($P < 0.05$).

Meanwhile, aboveground biomass was not significantly correlated to species richness. However, species richness was positively correlated to soil moisture ($r_s = 0.895$, $P = 0.040$) in the *K. humilis* meadow community.

Belowground biomass was negatively correlated with plant species richness ($r_s = -0.907$, $P = 0.034$), and positively correlated with soil moisture ($r_s = 0.900$, $P = 0.037$) in the *K. tibetica* swamp meadow community. In contrast, belowground biomass was not significantly correlated with both plant species richness and soil moisture in the *K. humilis* and *K. pygnaecea* communities.

3 Discussion

The distribution of plant biomass differed markedly among the three meadow plant communities, particularly belowground biomass (Figures 1 and 2). Significant differences in soil moisture and soil organic matter, resources total N and total P among the communities indicated the environmental gradient that occurred along the sampling transects. Strong correlations among soil moisture and soil organic matter, resources total N and total P revealed that the distribution of biomass corresponded to the environmental gradient (Table 2). The highest total biomass occurred in the sedge-dominated, *K. tibetica* swamp meadow community and lowest biomass was observed in the more diverse *K. humilis* meadow communities, dominated by a mixture of forbs and graminoids. The ratios of belowground-to-aboveground biomass, which is as much as 4–6 times higher in the wet meadow communities than in the dry meadow communities, were also indicative of community differences in plant species composition. Moreover, the distinctive vertical profile of belowground biomass within each community (Figure 2) also reflected the different characteristics of plant species composition.

In the dominant sedges of the wet meadow community, these sedges species form well-developed aerenchyma and are capable of extensively increasing the production of the belowground biomass in low oxygen and anoxic environments^[23,24], as indicated by the occurrence of considerable biomass throughout the 30 cm profile in this study (Figure 2). In contrast, belowground biomass in the *K. humilis* and *K. pygnaecea* communities was concentrated within 10 cm of the soil surface (Figure 2). These distribution characteristics may be due to dominant graminoid in the dry meadows, which is shal-

lowly rooted and produces short rhizomes that extend horizontally near the soil surface^[25]. In addition, the forbs species occurring in the dry meadow communities do not have extensive belowground structures^[26]. To sufficiently utilize advantageous condition of synchronous season temperature and precipitation in alpine meadow, most of the rhizomes intersperse at 0–10 cm top soil surface to absorb more heat, water, and mineral. Moreover, with soil depth increasing, the soil temperature, soil moisture and aeration would be gradually reduced, thus the roots which distributed in deep soil layer were reduced. The amount and vertical distribution of belowground biomass components may greatly contribute to stabilization of alpine *Kobresia* meadow. Maybe this is a adaptive strategy for ecological environment where plants live in alpine meadow.

Community differences in species composition and growth forms were evident in the various components of aboveground biomass (Figure 1). In the *K. tibetica* swamp meadow community, sedges aboveground biomass ($324.13 \pm 14.97 \text{ g/m}^2$) was more than 4–6 times that in the *K. humilis* ($43.23 \pm 4.36 \text{ g/m}^2$) and *K. pygnaecea* community ($58.49 \pm 4.99 \text{ g/m}^2$). Forbs aboveground biomass was 109.21 ± 3.46 and $80.45 \pm 5.84 \text{ g/m}^2$ in the *K. pygnaecea* and *K. humilis* communities, respectively. Grasses aboveground biomass was 74.10 ± 9.16 and $122.38 \pm 1.75 \text{ g/m}^2$ in the *K. pygnaecea* and *K. humilis* communities, respectively. The relationship between plant species richness and biomass is a topic of considerable study and discussion in the terrestrial ecosystem^[27]. One cornerstone of ecological theory is that nutrient availability limits the number of species that can inhabit a community. However, the relationship between the spatial distribution of limiting nutrients and species diversity is not well established because there is no single scale appropriate for measuring variation in resource distribution^[28]. The relationship between the spatial distribution of limiting resources and patterns of plant diversity is a central component of community ecology. On small scales, plants extracting nutrients from the same patch may partition the soil profile with different rooting strategies, such as tap versus fibrous root systems, or by employing rapid morphological plasticity in root uptake and growth^[29]. In some meadows, the highest number of species was associated with the lowest community biomass, which is consistent with patterns observed in other herbaceous plant communities along strong environmental gradients^[30,31]. The higher species richness in the

K. pygnaeica and *K. humilis* meadow communities was primarily due to the occurrence of diverse forbs. Although forbs enhance the number of species and coverage in *K. pygnaeica* and *K. humilis* meadow communities, they do not contribute obviously to aboveground or belowground biomass. Up to now, sampling belowground biomass has been limited and field studies of the relationships between biodiversity and ecosystem function have been focused mainly on aboveground productivity or aboveground biomass. Therefore, we may extrapolate the importance of biomass (including belowground biomass) to explain plant species diversity-productivity relationships for alpine meadow communities.

Even a small difference in soil moisture may result in a significant difference in seed germination and thus in floristic diversity of a wetland community^[32]. Morse et al.^[33] suggested that species diversity was expected to change with variation in resource distribution in a manner that depends on organism size and resource or habitat requirements. Significant correlations of biomass (aboveground and belowground biomass) with soil moisture (0–30 cm) and soil resources (soil organic matter and soil total nitrogen) suggested that fluctuations in soil moisture and soil resources (near the soil surface) influenced biomass distribution. In most ecosystems it is assumed that dominant plant species control ecosystem processes such as productivity, decomposition and nutrient cycling^[34]. Different species may have different rooting depths^[35], and vary in their ability to exploit high nutrient patches^[36] or in their relative uptake rates of different types of N^[37]. In the alpine meadow, particularly *K. tibetica* swamp meadow belowground mostly concentrated at 0–10 cm soil surface, soil nutrients also interspersed at 0–10 cm soil surface^[5,38], which in turn could result in a much more soil carbon, soil total nitrogen to the plant community, thus increasing the productivity of plant community. In the other words, in poor-species nature plant communities, species traits (such as ability to respond to higher nutrient levels) as well as competitive interaction may determine the ecosystem processes (e.g. productivity) by which dominant species (*Kobresia*) affect relationships between diversity and productivity. Also in single-dominant species plant communities, the ability for dominant species to capture another different limiting resource (e.g. light, water, or other nutrients) strengthens, resulting in plant fast growth with root biomass absorbing more C and N.

Previous studies have shown that accumulation of plant litter generally reduces species richness in most plant communities^[39]. In general, the effect of plant litter by itself was more important than that of vegetation canopy in affecting total species richness and seedling species richness. This perhaps reflects a major difference in that the added litter might act as a filter by allowing only certain species to germinate and emerge through the litter layer^[40], whereas canopy shade, which also affects both germination and seedling survival, may discriminate less between species^[41,42]. This study found that significant differences in herbaceous litters were observed between the *K. tibetica* swamp meadow community ($99.95 \pm 0.41 \text{ g/m}^2$) and the *K. pygnaeica* ($39.17 \pm 1.91 \text{ g/m}^2$), *K. humilis* meadow communities ($43.65 \pm 4.52 \text{ g/m}^2$), and the change of alpine meadow plant community was consistent with soil moisture conditions. It is possible that the effects of plant litter are enhanced where ground water and soil moisture levels are elevated and the rate of litter decomposition is increased. Therefore, the relative importance of litter and vegetation may vary with soil water availability. In the *K. tibetica* swamp meadow community, dominant *Kobresia* plant species may be tolerant to water, anaerobic soil conditions that likely restricted the occurrence of other alpine meadow species to increase competition between plant species (interspecific and intraspecific). As a result the species diversity decreases gradually and community productivity increases slowly; the *K. pygnaeica* and *K. humilis* meadow communities were composed of a greater diversity of plant species and life forms, which were generally less tolerant to water (soil moisture) conditions. Species richness in these communities has been suggested to be locally determined largely by biotic interactions, primary competition^[43]. One fascinating aspect of communities is that many seemingly functionally redundant organisms coexist while competing for the same resources^[44].

The distribution of aboveground and belowground biomass is largely influenced by the plant species and growth forms within spatial gradients in soil moisture and edaphic conditions. It will be important to well understand how the spatial distribution of resources influences the number and type of species that can coexist, colonize, and persist within a community.

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