Changes in individual plant traits and biomass allocation in alpine meadow with elevation variation on the Qinghai-Tibetan Plateau

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Plant traits and individual plant biomass allocation of 57 perennial herbaceous species, belonging to three common functional groups (forbs, grasses and sedges) at subalpine (3700 m ASL), alpine (4300 m ASL) and subnival (≥5000 m ASL) sites were examined to test the hypothesis that at high altitudes, plants reduce the proportion of aboveground parts and allocate more biomass to belowground parts, especially storage organs, as altitude increases, so as to geminate and resist environmental stress. However, results indicate that some divergence in biomass allocation exists among organs. With increasing altitude, the mean fractions of total biomass allocated to aboveground parts decreased. The mean fractions of total biomass allocation to storage organs at the subalpine site (7%±2% S.E.) were distinct from those at the alpine (23%±6%) and subnival (21%±6%) sites, while the proportions of green leaves at all altitudes remained almost constant. At 4300 m and 5000 m, the mean fractions of flower stems decreased by 45% and 41%, respectively, while fine roots increased by 86% and 102%, respectively. Specific leaf areas and leaf areas of forbs and grasses deceased with rising elevation, while sedges showed opposite trends. For all three functional groups, leaf area ratio and leaf area root mass ratio decreased, while fine root biomass increased at higher altitudes. Biomass allocation patterns of alpine plants were characterized by a reduction in aboveground reproductive organs and enlargement of fine roots, while the proportion of leaves remained stable. It was beneficial for high altitude plants to compensate carbon gain and nutrient uptake under low temperature and limited nutrients by stabilizing biomass investment to photosynthetic structures and increasing the absorption surface area of fine roots. In contrast to forbs and grasses that had high mycorrhizal infection, sedges had higher single leaf area and more root fraction, especially fine roots.

Qinghai-Tibetan Plateau, climate stress, biomass allocation, shoot/root ratio, plant traits, fine roots

The Qinghai-Tibetan Plateau, known as the world's "third pole", is a vast and high plateau with an average elevation of over 4000 m. Alpine meadows dominated by herbaceous perennial plants are spread throughout and rolling mountains have a frigid climate and thin, nutrient-poor soil [1]. Due to a strong Massenerhebung effect, alpine vegetation on the plateau is distributed at a much higher altitude than in any other part of the world. Moreover, to a great extent, elevation determines variation in environmental factors and combinations of those factors. In addition, the response and adaptation of individual plant traits and physiological processes to climate change is the basis of understanding vegetation-climate relationships. Therefore, alpine plants are shaped by altitude and form special evolutionary features in

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terms of morphology, physiological characteristics and biomass allocation.

Plant traits and biomass allocation strategies at high altitudes have attracted widespread attention in ecology. In recent years, related studies have focused on alpine forests. In northern Hessen, Germany, four alpine tree species had reduced height and leaf area index (LAI) but increased stomatal density (SD) with increasing elevation [2]. Also, 54 populations of *Picea abies* at eight altitudes in southern Poland showed nonlinear responses of root length, canopy, needles and biomass of stems, roots and their fractions to elevation [3]. High altitude populations of *Pinus sylvestris* L. growing between 50° and 60° north latitudes grew a large number of fine roots and higher belowground biomass compared with low altitude populations [4,5]. Grime [6] and Bloom *et al.* [7] concluded that plants in cold habitats tend to allocate more assimilates to belowground organs, which results in a tradeoff between growth and investment so that individuals have a large root to shoot (R/S) ratio.

Plant traits and biomass allocation of herbaceous perennials along elevations have mostly been assessed at the community level. However, little information exists on individual plants. Previous studies have also been concerned with the relationship between aboveground biomass and soil nutrients at different altitudes [8–10]. Fabbro and Körner [11] found a change in function from plant support for photosynthesis in leaves at low altitudes to support for flowers at high altitudes. Shoot mass was also significantly reduced at high altitudes, as were the proportion of stem biomass and plant height. These led to an increase in self-shading, which likely caused reductions in carbon gain in alpine plants. Sizes of perennial herbs have been found to be negatively correlated with altitude. This indicates that with increasing altitude, plants have reduced growth and energy consumption so as to allocation maximum nutrients to reproduction organs to complete their life history and increase population survival [12]. In addition, on Changbai Mountain, eastern China, the total biomass and leaf biomass ratio of alpine tundra plants have been found to gradually decrease with elevation, while root biomass, R/S ratio and belowground biomass have gradually increased; although responses vary among species [13].

Studies on Qinghai-Tibetan Plateau meadow have mainly concentrated on biomass allocation at the whole community level. Yang *et al.* [14] found that the R/S ratio of 5.8 in alpine grasslands on the plateau was higher than the ratio of 4.2 in global temperate grasslands. This might correlate with low root turnover and low carbohydrate consumption in alpine regions. Li *et al.* [15] proposed that in non-degraded alpine meadow the maximum height of plants and the R/S ratio were highly correlated with altitude and climatic and soil variables. Likewise, R/S ratio increased linearly with increasing altitude, and plant height decreased.

To date, only Körner *et al.* [16] have surveyed biomass allocation of individual alpine plants at two sites at 600 m and 2600–3200 m ASL in the Alps. They found that high altitude plants allocated more biomass to belowground parts, which directly led to lower stem biomass but higher root biomass than in plants at low altitude. The experiment also found that fine root biomass at high altitude is 50% longer than, and average root density increased three times more than those of plants at lower altitude. However, there is no report of biomass fraction in individual plants of common alpine species on the Qinghai-Tibetan Plateau with average altitudes higher than 4000 m ASL. The objective of the present study was to examine plant traits and individual plant biomass fractions of functional groups along an altitudinal gradient to explain the resource acquisition strategies of different functional groups in the unique environment of the Qinghai-Tibetan Plateau.

1 Materials and methods

1.1 Study region

To analyze the biomass distribution of individual plants in *Kobresia pygmaea* meadow, we established three experiment sites at subalpine, alpine and subnival sites. The sites were located on the south slope of Nyainqentanglha Mountain Range. The research sites are characterized by a continental monsoon climate with intense solar radiation, low temperature, small annual temperature range and high daily temperature variation. The alpine meadow soil has a depth of 10–30 cm and a sand-loam texture. Typical vegetation includes alpine *Kobresia* meadow, with dominant species such as *Kobresia pygmaea*, *Kobresia humilis* and *Stipa capillacea*.

The subalpine site was located at 3700 m ASL near Lhasa Municipality, Tibetan Autonomous Region. The plateau monsoon temperate climate has an annual temperature of 4–8°C. Annual precipitation is 450–550 mm with a rainy season concentrated from June to September. The growing season at this site (150 d) is longer than that at the other two sites. At this site, *Kobresia pygmaea* and *Astragalus strictus* are dominant species. The alpine site was established at 4300 m ASL near Damxung County. *Kobresia pygmaea* and *Stipa capillacea* are the dominant species here. The growing season is about 100 d, the mean annual temperature is 1.3°C and annual precipitation is 470 mm. The subnival site was located at and above 5000 m ASL on the upper mountain of the alpine site. Dominant vegetation in this scree field includes *Kobresia pygmaea*, forbs and cushion plants. The growing season is nearly 60–80 d. The average annual temperature is below −0.4°C, and annual precipitation is about 550 mm. Although the subalpine meadow site is nearly 180 km from the alpine meadow and subnival sites, all have similar vegetation types and are representative of each altitude.

1.2   Sampling criteria

In August 2008, we investigated 57 common plant species, including 23 species at the subalpine site, 15 at the alpine site and 19 at the subnival site on the south slope of Nyain-qentanglha Mountains. Plants were selected based on the following criteria [16]: (i) individual plants in natural habitats; (ii) adult individuals at maximum vegetative development (usually onset of flowering except for those few alpine species that flowered before leaf expansion immediately following snow melt); (iii) plants growing in full sunlight (minimum mutual shading) and under moderate to high soil moisture; (iv) well-developed (but not necessarily equal sized), visually-healthy, representative individuals.

1.3   Sample treatment

Plant samples, including roots systems, were carefully located, selected and excavated. Individuals (a total of 150 composed of 23 species at 3700 m, 84 composed of 15 species at 4300 m and 73 composed of 19 species at 5000 m) were carefully excavated from different soil micro-sites following the criteria above and separated from symbiotic species. Root branching patterns were used to locate the whole plant root system. Soil that was dug out was kept intact to minimize loss of fine roots to ensure accurate measurements.

Fresh samples were separated into leaves, stems, reproductive organs, special storage organs (rhizomes, rootstocks, corms, tap roots and all roots exceeding 2 mm in diameter) and the living fine root fraction (<2 mm). An AM200-001 portable type leaf area meter (ACD BioScientific Ltd., UK) was used to measure leaf area. All plant fractions were then dried in an oven at 65°C for 48 h and weighed (accurate to 0.001 g).

1.4   Data analysis

We calculated specific leaf area (SLA, total leaf area/total leaf weight, $cm^2 \ g^{-1}$), leaf area ratio (LAR, total leaf area/total plant weight, $cm^2 \ g^{-1}$), average single leaf area (measured leaf area/leaf number, cm^2), leaf area root mass ratio (LARMR, total leaf area/total root weight, $cm^2 \ g^{-1}$), root mass ratio (RMR, root weight/total plant weight), leaf mass ratio (LMR, leaf weight/total plant weight), supporting organs biomass ratio (SBR, stem weight/total plant weight), underground storage organ biomass ratio (underground storage organ weight/total plant weight), leaf mass fraction (LMF, leaf weight/plant shoot weight) and aboveground biomass ratio (shoot weight /total plant weight). Based on the characteristics of alpine meadow communities and plant traits, we classified all plants into three functional types: grasses, sedges and forbs. An arc-sin transformation of the square roots of the discrete biomass fractions was applied to normalize the datasets before ANOVA tests [17,18]. Origin

7.5 was used to test for normal distribution, and the transformed datasets were analyzed using a one-way ANOVA to unveil differences among populations.

2   Results

2.1   Biomass allocation

2.1.1   Plant organ biomass partitioning

Mean individual biomass at the subalpine, alpine and subnival sites was (3.02±0.39) g, (3.94±1.22) g and (4.69±1.75) g, respectively. There was no significant difference in individual biomass among altitudes (P>0.05). However, there was a small difference in mean individual biomass among the three altitudes if the cushion plant *Arenaria kansuensis* was removed from the subnival site (Appendix Table 1). Leaf mass ratios were relatively steady above the alpine site and were 28%±2%, 23%±4% and 20%±2% at the subalpine, alpine and subnival sites, respectively. There were no differences among the three sites (P>0.05). The biomass fraction to storage organs at the subalpine area (7%±2%) was lower than that at the alpine (23%±6%) and subnival (21%±6%) sites, with no significant difference among the three sites (P>0.05). Biomass partitioning in stems and flowers (setting the subalpine average as 100%) declined with increasing elevation. Biomass partitioning decreased by 45% at the alpine site and by 41% at the subnival site. There were significant differences between the subalpine and alpine sites (P=0.003) and between the alpine and subnival sites (P=0.002). In contrast with the proportion of biomass in stems and flowers, root mass ratio (setting the subalpine average as 100%) increased with elevation. Root mass ratio at the alpine and subnival sites increased by 86% and 102%, respectively, which were not significantly different (P>0.05), while significant differences occurred between the subalpine and subnival sites (P=0.006) and between the alpine and subnival sites (P=0.028).

2.1.2   Above/belowground dry matter ratios in species at different altitudes

Deviation in the above/belowground biomass ratio (*A/B*) of different species along an altitudinal gradient is shown in Figure 1. Generally, *A/B* rapidly declined with increasing elevation from 7.9±1.9 and 2.4±0.9 to 1.7±0.4. However, *Carex atrofusca* in the subalpine area allocated most biomass belowground and had the smallest *A/B* of 0.4. A creeping plant, *Tribulus terrestris,* partitioned the least biomass belowground, with an *A/B* of 47.3 (not shown in Figure 1). At the alpine site, *Carex atrofusca* and *Anaphalis xylorhiza* had the same *A/B* of 0.4. The lowest *A/B* of 0.1 was present in *Poa pratensis*, while *Microula sikkimensis* had the highest *A/B* of 11.7. At the subnival site, *Rhodiola*
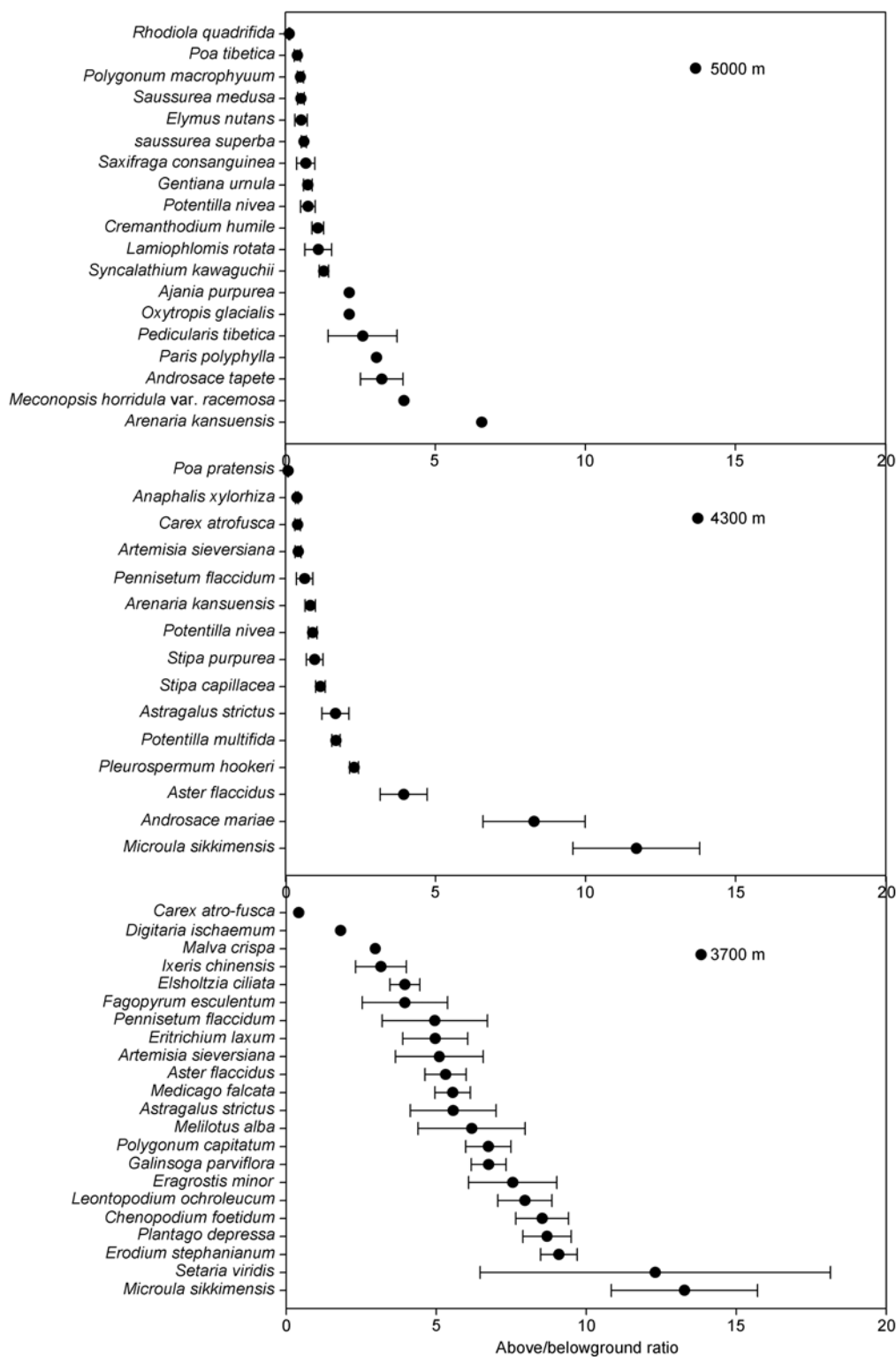
Figure 1   Above/belowground biomass ratios of herbaceous perennials at different altitudes.

quadrifida had the lowest *A/B* of 0.1, and the cushion plant *Arenaria kansuensis* had the highest ratio of 6.5. In brief, the A/B exhibited large variations among species at each altitude, but a pattern of increasing plant biomass partitioned belowground with increasing elevation is evident.

2.1.3   Aboveground biomass partitioning

Mean aboveground biomass ratios decreased from subalpine, alpine to subnival sites with means of 79%±3%, 51%±6% and 50%±5%, respectively. The histogram in Figure 2
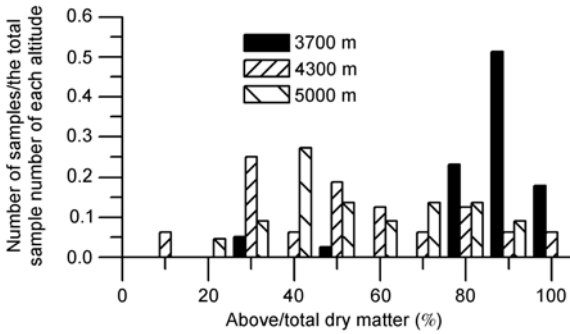
Figure 2   Frequency distribution of the aboveground biomass fraction as a percentage of total plant biomass for all altitudes.

shows a unimodal frequency distribution of individual aboveground biomass ratios. The frequency peaked at 90% at the subalpine site, 30% at the alpine site and 40% at the subnival site. This indicates that the percentage of stem and flower biomass declined, in contrast to increasing fine root fraction with increasing altitude.

2.2 Comparison of different functional groups

Single leaf area of forbs decreased from 185 mm^2 at the subalpine site to 48 mm^2 at the alpine site and then increased to 164 mm^2 at the subnival site. Significant differences existed between the subalpine and alpine sites and the alpine and subnival sites ($P<0.05$); however, there was no significant difference between the subalpine and subnival sites ($P>0.05$). The single leaf area of grasses was similar to that of forbs. It declined from 123 mm^2 to 33 mm^2 from the subalpine to alpine sites, respectively, and then increased to 45 mm^2 at the subnival site. Statistical differences existed among the three sites, but in contrast to that of forbs and grasses, single leaf area of sedges at the subalpine site was only 5 mm^2 higher than that at the alpine site and was not significantly different ($P>0.05$) (Figure 3A).

Total leaf areas per plant for forbs and grasses decreased from the subalpine to subnival sites. Total leaf areas per forb dropped from 11762 mm^2 to 8894 mm^2 and those of grasses declined from 11342 mm^2 to 2865 mm^2. There was

no significant difference among the three sites for forbs ($P>0.05$). A significant difference existed for grasses between subalpine and alpine sites ($P<0.05$), but there was no difference between alpine and subnival sites ($P>0.05$). Total leaf areas per plant for sedges went up from 1869 mm^2 at the subalpine site to 5425 mm^2 at the alpine site, which were significantly different ($P<0.05$) (Figure 3B).

The LARs of grasses decreased by 77.5% with increasing altitude. LARs of grasses at the subalpine site were significantly different from those at the alpine and subnival sites ($P<0.05$), but there was no significant difference between alpine and subnival sites ($P>0.05$). From subalpine to alpine and subnival sites, the LARs of sedges and forbs decreased by 11.6% and 25.7%, respectively. There were no significant differences for sedges between the subalpine and alpine sites or forbs among the three altitudes ($P>0.05$) (Figure 4A).

SLAs of forbs and grasses declined from 172.54 cm^2 g^{-1} and 137.21 cm^2 g^{-1}, respectively, to 142.34 cm^2 g^{-1} and 84.07 cm^2 g^{-1}, respectively, with increasing elevation. Significant differences existed in SLAs of forbs and grasses between subalpine and alpine sites and between subalpine and subnival sites ($P<0.05$), but there was no difference between alpine and subnival sites ($P>0.05$). The SLA of sedges increased from 73.87 cm^2 g^{-1} at the subalpine site to 99.19 cm^2 g^{-1} at the alpine site ($P<0.05$) (Figure 4B).

LARMR of the three functional groups had the same trend as SLA. LARMRs of forbs, grasses and sedges decreased by 68.7%, 97.7% and 13.3%, respectively, with increasing altitude. LARMR in the subalpine area was significantly different from that at the alpine and subnival sites ($P<0.05$), but there was no difference between the alpine and subnival sites ($P>0.05$). There was also no difference in sedges among the subalpine and alpine sites ($P>0.05$) (Figure 4C).

LARMRs of grasses and sedges appeared to decrease with increasing elevation. Those of grasses were significantly different between subalpine and alpine sites and between subalpine and subnival sites ($P=0.05$), but no difference existed between alpine and subnival sites ($P>0.05$). There was also no difference for sedges between altitudes.
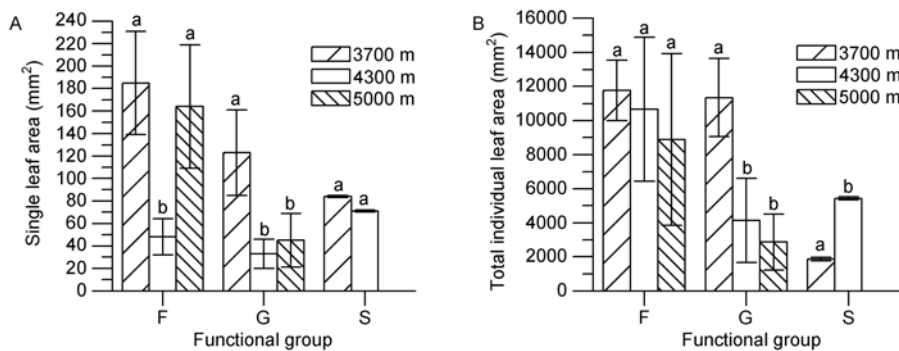

Figure 3   Single leaf areas (A) and total individual leaf areas (B) of the three functional groups at different altitudes. Different letters stand for significant differences. F, forbs; G, grasses; S, sedges.

However, a significant increase in LARMR occurred in forbs from subalpine to subnival sites ($P<0.05$), while there was no difference between subalpine and alpine sites ($P>0.05$) (Figure 4D).

The aboveground biomass of grasses decreased with increasing elevation; however, there was no difference in aboveground biomass of forbs and sedges among altitudes ($P>0.05$). For grasses, significant differences occurred between the subalpine site and alpine site ($P=0.014$) and between the subalpine site and subnival site ($P=0.021$), but there was no difference between the alpine site and subnival site ($P>0.05$) (Figure 5A).

The fine root biomass of grasses and sedges increased with elevation but those of forbs did not differ. The fine root biomass of grasses was significantly different between the subalpine site and the upper two sites ($P=0.030$ for alpine and $P=0.042$ for subnival), but no difference occurred between the higher two sites ($P>0.05$). The fine root biomass of sedges increased from the subalpine site to the alpine site ($P<0.05$) (Figure 5B).

The R/S ratios of forbs and grasses increased with increasing elevation, while those of sedges did not change. For forbs, there was no difference between R/S ratios at the subalpine and alpine sites, but they were both significantly different from that at the subnival site ($P=0.019$ and $P=0.049$, respectively). For grasses, there was no difference between the R/S ratio at the subalpine site and the subnival site, but they were both significantly different from the alpine site ($P=0.041$ and $P=0.050$, respectively) (Figure 5C).

3 Discussion

3.1 Influence of altitude on plant biomass allocation

In the alpine altitudinal belt, altitude fundamentally controls the combination of and variations in environmental factors. The responses of plants along altitudinal gradients provide models of "experiments by nature". Variations in individual biomass of different herbaceous species within the same elevation or vegetation zone reflect convergent adaptations of different functional groups. Therefore, understanding biomass allocation patterns of different groups along an altitudinal gradient is one of the keys to understanding the response of individuals or populations to climate change. The influence of altitude on plant ecophysiology is becoming a hotspot of alpine plant ecology [19]. From the subalpine to subnival sites, the above/belowground ratio and aboveground biomass ratio decreased along with individuals becoming shorter (Figures 1 and 2). The aboveground stem and flowering fraction also decreased. The importance of clonal reproduction has been found to increase over sexual reproduction, which is consistent with the reproduction of *Oxyria sinensis* at five altitudes [20]. While the partitioning of biomass to reproduction organs decreased (Appendix Table 1), fine root biomass increased dramatically with rising altitude (Figure 5B). Plants put more investment into fine roots to enlarge root surface area so as to enhance limited nutrient (e.g., N and P) absorption in harsh alpine environments. Furthermore, in-
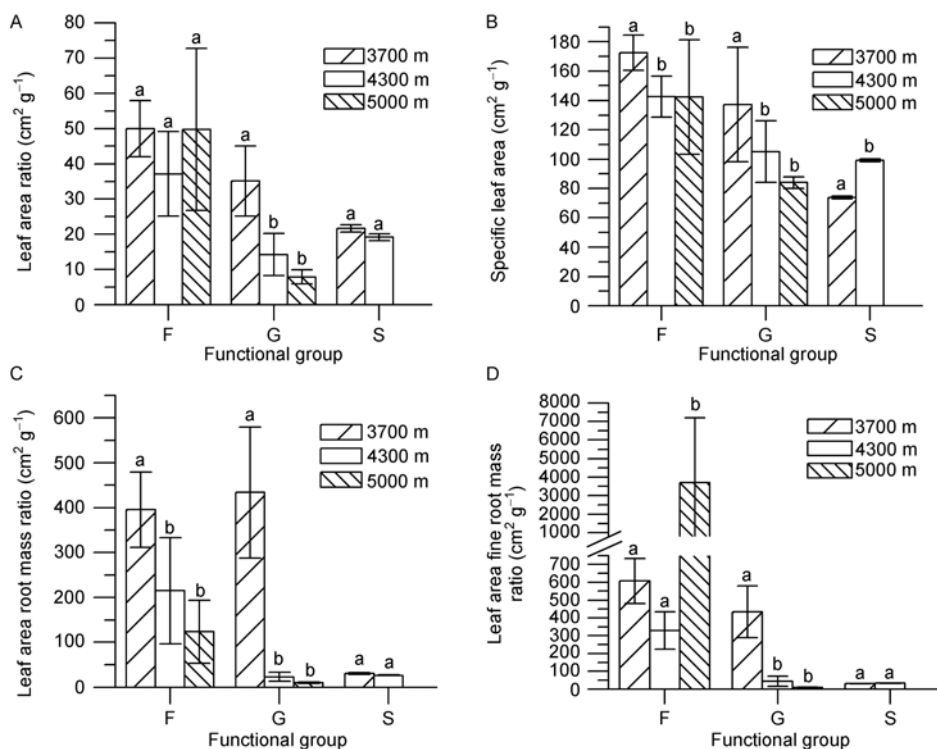

Figure 4 Variation in the three functional groups in leaf area ratio (A), specific leaf area (B), leaf area root mass ratio (C) and leaf area fine root mass ratio (D) among altitudes. F, forbs; G, grasses; S, sedges.
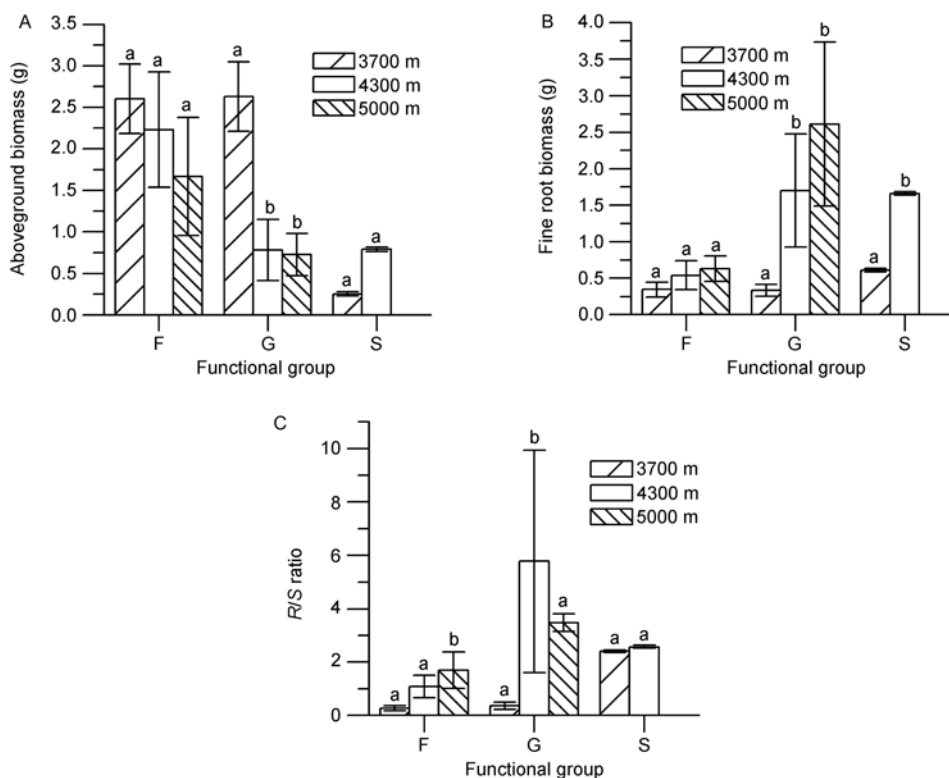
Figure 5   Variation in the three functional groups in aboveground biomass (A), fine root biomass (B) and R/S ratio (C) among altitudes. F, forbs; G, grasses; S, sedges.

vesting less in stems and more in roots (especially <2 mm fine roots) and amplifying the R/S ratio improves belowground nutrient uptake and raises root-zone temperature so as to survive in a windy, cold and barren alpine soil environment [19]. Previous studies also show that alpine plants store substantially more carbohydrates in root systems than in aboveground parts [21–25]. The trends in biomass change with altitudes in alpine plants indicate the existence of possible patterns of overall plant biomass partitioning which can be further supported by observing the allocation of carbohydrates [16]. In the present study, leaf mass ratio (LMR) remained relatively stable in the process of biomass distribution and changed little from 20% to 28% with various altitudes. This variation was similar to the mean of 24% that Körner reached in scree vegetation in the Alps [19]. This indicates that alpine plants are not likely to reduce the investment of carbohydrates to photosynthetic organs. For alpine plants, steady nutrient investment in photosynthetic organs is beneficial to compensate the slow photosynthetic rate found in low CO_2 partial pressure and low temperature in high alpine environments. As a result, through steady investment of biomass to photosynthetic organs and augmentation of root absorbing surfaces, alpine plants fortify capacities of carbon supply and resource absorption in a cold and nutrient-limited environment.

3.2   Integration of traits and functional groups of alpine plants to adapt to altitude variation

Plant traits, also called functional traits, including the physiological and morphological characteristics of adaptation, are the results of long-term interactions between plants and their environment to minimize the negative influence of harsh environments [26]. Altitude has broad effects on plant species and environmental factors. Plants have adapted to climate and environmental changes in that leaves, as photosynthetic organs, and roots (especially fine roots), as absorption organs, change most notably. Different plant functional groups evolve different functional traits due to genetic and physiological variations [16,19,27,28]. As one of these traits, SLA is closely associated with photosynthesis and the production strategy of plants, and in some degree, it reflects a plant's ability to acquire resources and adapt to varied habitats [29–32]. Generally speaking, SLA changes with changes in the environment [27,33–36]. In the current study, the SLA of forbs and grasses decreased with increasing elevation, while the SLA of sedges increased. The incremental trend of SLA with elevation is mainly caused by incrassation of leaf and epidermal cell wall, which is an adaption to the cold climate in alpine areas [19]. The present study showed that although low temperature and low nutrient availability at a higher altitude led to the reduction

of nutrient acquisition of forbs and grasses, they did not influence sedges. LAR, a product of LMR and SLA, increased with elevation in each of the three functional groups. From the viewpoint of plant carbon economy, given the same morphological characteristics, alpine plants tend to produce thicker leaves, live longer, decrease SLA (more carbon investment per leaf area) and LAR, have similar LMR and reduce LAR to better survive an alpine environment [19]. In summary, total leaf area per individual forb and grass decreased with increasing altitude, while total leaf area per individual sedge increased (Figure 3B). The R/S ratio and the fine root biomass of the three functional groups increased with altitude. The advantage of absorptive capacity was especially reflected in the significant increase in fine root mass in grasses and sedges (Figures 5B and C). This is more important for sedges because sedges are not infected with mycorrhizal fungi. Increased fine root mass of sedges could enhance nutrient absorption abilities. The leaf area fine root mass ratio, an important index reflecting carbon supply and nutrient absorption, showed two kinds of adaptive strategies and contrasted between forbs and sedges (Figure 4D). Forbs tended to have increases in leaf area with elevation to enhance carbon gain, while grasses and sedges increased fine root biomass to improve nutrient uptake in the alpine environment. Comparing the three functional groups, sedges have a competitive advantage in terms of both leaf and root traits, explaining why sedges are dominant in alpine meadow on the Qinghai-Tibetan Plateau.

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Appendix Table 1   Relative portion of dry matter allocated to different plant organs (% of total dry matter)[a]

Plant species	Sample number	Fine roots	Storage organs	Flowers stems	Leaves	Total biomass (g)	Se (g)
3700 m subalpine site							
Erodium stephanianum Willd.	6	5.63	4.35	67.10	22.92	3.24	0.16
Microula sikkimensis (C. B. Clarke) Hemsl.	8	7.00	0.82	77.73	14.45	2.73	0.35
Eritrichium laxum Johnst.	8	5.32	11.53	69.66	13.48	1.85	0.45
Setaria viridis (L.) Beauv.	8	9.53	–	42.38	48.09	2.76	0.74
Eragrostis minor Host	6	13.66	–	56.05	30.30	3.99	1.64
Pennisetum flaccidum Griseb.	8	14.87	24.04	25.89	35.20	2.49	0.79
Digitaria ischaemum (Schreb.) Schreb. ex Muhl. Schreb. ex Muhl.	6	[*]3.47	32.05	54.65	9.83	4.73	0.00
Artemisia sieversiana Ehrhart ex Willd.	6	[*]38.31	14.52	25.22	21.95	5.09	3.05
Ixeris chinensis (Thunb.) Nakai	6	14.72	11.68	36.36	37.24	1.44	0.49
Aster flaccidus Bunge	6	11.54	5.59	62.48	20.40	3.63	0.98
Galinsoga parviflora Cav.	6	11.05	2.70	42.18	44.07	1.76	0.54
Leontopodium ochroleucum Beauv.	6	10.91	–	78.25	10.85	1.19	0.28
Carex atrofusca Schkuhr subsp. *minor* (Boott) T. Koyama	6	[*]70.62	–	–	29.38	0.86	0.00
Fagopyrum esculentum Moench	6	23.45	–	38.30	38.24	0.83	0.19
Polygonum capitatum Buch. -Ham. ex D. Don	6	8.55	1.72	57.97	31.77	1.98	0.94
Chenopodium foetidum Schrad.	6	12.21	3.96	70.74	13.09	2.15	0.32
Melilotus alba Desr.	6	[*]3.81	5.75	69.16	21.28	5.93	2.53
Medicago falcata Linn.	6	16.64	–	36.43	46.93	1.02	0.22
Astragalus strictus Grah. ex Benth.	6	10.85	10.25	42.52	36.38	7.01	1.75
Plantago depressa Willd.	6	5.30	5.50	60.43	28.78	1.80	0.24
Malva crispa Linn.	6	12.77	12.44	51.03	23.76	4.23	0.00
Tribulus terrestris Linn.	8	[*]1.95	0.69	68.68	28.68	7.01	1.19
Elsholtzia ciliata (Thunb.) Hyland.	8	14.45	5.59	38.88	41.08	1.77	0.72
Mean (*n*=23)		14.20	6.66	50.96	28.18	3.02	
Standard error		3.02	1.72	4.04	2.41	0.39	
4300 m alpine site							
Carex atrofusca Schkuhr subsp. *minor* (Boott) T. Koyama	6	[*]58.75	13.28	10.49	17.47	2.83	0.55
Pennisetum flaccidum Griseb.	6	22.77	46.31	12.67	18.25	2.09	0.38
Poa pratensis Linn.	6	[*]93.35	–	4.21	2.43	3.37	1.02
Stipa capillacea Keng	3	[*]47.17	–	34.06	18.76	7.47	1.08
Stipa purpurea Griseb.	3	[*]55.50	–	24.53	20.00	0.65	0.17
Potentilla multifida Linn.	6	9.90	17.33	36.84	35.92	0.74	0.16
Potentilla nivea Linn.	6	10.06	43.31	35.91	10.71	1.49	0.48
Astragalus strictus Grah. ex Benth.	6	11.45	35.45	11.32	41.78	8.10	1.86
Anaphalis xylorhiza Sch.-Bip.	6	8.64	61.69	16.63	13.03	18.22	3.72
Aster flaccidus Bunge	6	19.66	2.25	35.75	42.31	1.61	0.51
Artemisia sieversiana Ehrhart ex Willd.	6	17.16	53.48	18.30	11.05	5.52	0.88
Pleurospermum hookeri C. B. Clarke var. *thomsonii* C.B.Clarke	6	6.28	24.56	61.80	7.35	5.46	0.99
Microula sikkimensis (C. B. Clarke) Hemsl.	6	9.81	–	40.00	50.14	0.36	0.09
Androsace mariae var. *tibetica* (Maxim) Hand.-Mazz.	6	10.24	–	49.81	40.00	0.63	0.19

(Continued)

Plant species	Sample number	Fine roots	Storage organs	Flowers stems	Leaves	Total biomass (g)	Se (g)
Arenaria kansuensis Maxim.	6	14.99	41.19	25.82	18.06	0.54	0.13
Mean (*n*=15)		26.38	22.59	27.88	23.15	3.94	
Standard error		6.58	5.80	4.15	3.83	1.22	
>5000 m subnival site							
Oxytropis glacialis Benth. ex Bge.	3	5.57	26.36	57.70	10.36	2.67	0.00
Potentilla nivea Linn.	6	43.16	17.74	13.16	25.93	0.89	0.15
Elymus nutans Griseb.	3	79.23	–	10.08	10.69	4.71	2.04
Poa tibetica Munro ex Stapf	6	75.89	–	16.32	7.79	1.96	0.29
Rhodiola quadrifida (Pall.) Fisch. et Mey.	6	16.82	74.41	4.41	4.36	4.33	1.74
Gentiana urnula H. Smith	4	56.07	3.30	8.13	32.50	1.76	0.67
Saxifraga consanguinea W. W. Smith	3	59.00	–	22.27	18.73	2.83	0.60
Androsace tapete Maxim.	3	23.79	3.20	42.96	30.06	5.81	3.65
Paris polyphylla Smith	3	24.75	–	64.36	10.89	0.10	0.00
Meconopsis horridula var. *racemosa* (Maxim.) Prain	3	13.45	6.74	69.91	9.90	12.84	0.00
Ajania purpurea Shih	3	0.66	31.30	43.55	24.50	2.44	0.00
Syncalathium kawaguchii (Kitam.) Ling	3	23.10	21.44	25.00	30.46	7.09	0.99
Saussurea superba Anth.	3	18.15	44.96	3.28	33.62	2.78	0.75
Saussurea medusa Maxim.	6	20.98	38.04	11.31	29.67	0.40	0.15
Cremanthodium humile Maxim.	3	44.45	1.84	31.74	21.97	1.74	0.80
Arenaria kansuensis Maxim.	3	6.76	6.49	63.77	22.98	*33.67	0.00
Polygonum macrophyllum D. Don	3	1.07	66.82	21.02	11.08	0.99	0.23
Lamiophlomis rotata (Benth.) Kudo	3	5.29	55.08	7.55	32.07	1.46	0.36
Pedicularis tibetica Franch.	6	27.57	6.78	53.53	12.12	0.56	0.15
Mean (*n*=19)		28.72	21.29	30.00	19.98	4.69	
Standard error		5.58	5.54	5.22	2.27	1.75	

a) For the comparison of dry matter fractionation, an arc-sin transformation of the square roots of relative portions was applied to normalize the dataset. Values marked with * were removed.