

Patterns of above- and belowground biomass allocation in China's grasslands: Evidence from individual-level observations

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Above- and belowground biomass allocation not only influences growth of individual plants, but also influences vegetation structures and functions, and consequently impacts soil carbon input as well as terrestrial ecosystem carbon cycling. However, due to sampling difficulties, a considerable amount of uncertainty remains about the root: shoot ratio (R/S), a key parameter for models of terrestrial ecosystem carbon cycling. We investigated biomass allocation patterns across a broad spatial scale. We collected data on individual plant biomass and systematically sampled along a transect across the temperate grasslands in Inner Mongolia as well as in the alpine grasslands on the Tibetan Plateau. Our results indicated that the median of R/S for herbaceous species was 0.78 in China's grasslands as a whole. R/S was significantly higher in temperate grasslands than in alpine grasslands (0.84 vs. 0.65). The slope of the allometric relationship between above- and belowground biomass was steeper for temperate grasslands than for alpine. Our results did not support the hypothesis that aboveground biomass scales isometrically with belowground biomass. The R/S in China's grasslands was not significantly correlated with mean annual temperature (MAT) or mean annual precipitation (MAP). Moreover, comparisons of our results with previous findings indicated a large difference between R/S data from individual plants and communities. This might be mainly caused by the underestimation of R/S at the individual level as a result of an inevitable loss of fine roots and the overestimation of R/S in community-level surveys due to grazing and difficulties in identifying dead roots. Our findings suggest that root biomass in grasslands tended to have been overestimated in previous reports of R/S.

aboveground biomass, allometry, alpine grassland, belowground biomass, Inner Mongolia, isometric relationship, root: shoot ratio, temperate grassland, Tibetan Plateau

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1 Introduction

Plant species have evolved specialized strategies to regulate their above- and belowground biomass allocation. This influences not only the performance of the individual, but also vegetation structures and functions, consequently affecting soil carbon input and the terrestrial ecosystem carbon cycling. Hypotheses regarding different strategies of biomass allocation are among the most important theories in plant

ecology and evolution [1–3]. However, the general patterns in the biomass allocation of plants are still controversial.

West, Brown and Enquist [4–6] developed an integrated model to identify and quantify various allometric relationships in plants, based on the fractal-like branching networks of vascular plants and the efficiency of resource use. Enquist and Niklas [7] extended the allometry theory using three assumptions: (1) tissue densities of stem and root are approximately constant during ontogeny, (2) the total effective hydraulic cross-sectional areas of stems and roots are equivalent, and (3) stem length scales roughly isometrically

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with respect to root length. They argued that above- and belowground biomass will scale in a nearly isometric manner both within and across clades and habitats. However, many herbaceous plants do not have typical hierarchical branching structures and the stem length may not scale isometrically with root length. Therefore, further tests using field observations across a broad range of species and habitats are necessary to validate their theory for herbaceous plants.

Previous studies of terrestrial ecosystem carbon cycling have indicated that root: shoot ratio (R/S) is a key parameter in many global terrestrial carbon cycling models, especially in models based on plant and vegetation growth[11–14]. However, due to sampling difficulties, large uncertainties remain in the estimations of the root: shoot ratio (R/S) [10,15–17]. In a review of R/S estimates in terrestrial biomes worldwide, Mokany *et al.* [18] found that 62% of 786 R/S observations were unreliable, resulting in a dramatic uncertainty in the estimation of root carbon storage in global grasslands. Moreover, the root and shoot biomass in previous studies has mostly been estimated for communities as a whole by sampling soil cores or soil blocks and harvesting all shoots during the growing season [10]. This yielded only part of the roots and measurements were not reported for individual plants. For example, several studies in China's grasslands [19–21] have estimated the community-level root: shoot ratio, and indicated a higher R/S than the global average [10,15,22]. Moreover, an isometric relationship between above- and belowground biomass was suggested [15]. The R/S for China's grasslands did not show significant trends with either mean annual temperature or mean annual precipitation [10,17,22]. However, there have been few comparisons conducted between the community sampling method and individual plant sampling.

We initiated a new investigation of R/S at the individual

level over a wide spatial scale using a systematic biomass survey across the Inner Mongolian and Tibetan grasslands. First, we estimated the individual-level R/S for different grassland types. Then, the results were compared with R/S values estimated at community level. Next, we examined the allometric relationship between above- and below-ground biomass of China's herbaceous species in a global context. Finally, we evaluated effects of climate on R/S.

2 Materials and methods

2.1 Study area

The study area encompassed temperate grasslands on the Mongolian Plateau and alpine grasslands on the Tibetan Plateau (Figure 1). The natural grassland zones in these regions include five main types: meadow steppe, typical steppe, desert steppe, alpine steppe and alpine meadow [23].

Sample sites in inner Mongolia range from latitude 41.76–49.89 °N/longitude 112.82–102.12 °E; and altitudes of 669–1435 m. Growing season temperature (GST) and growing season precipitation (GSP) of the sample sites range from 8.7–14.8°C and from 133–448 mm, respectively. Sample sites on the Tibetan Plateau range from latitudes 30.47–37.78 °N/longitudes from 92.35–102.31 °E, and altitudes of 3196–4964 m. Across these sites, GST ranged from 3.2–8.5°C, and GSP ranged from 184–361 mm. Figure 1 shows the site locations.

2.2 Site selection and plant sampling

In total, we selected 35 sites along a transect, 18 in Inner Mongolia (6 of meadow steppe, 7 of typical steppe and 5

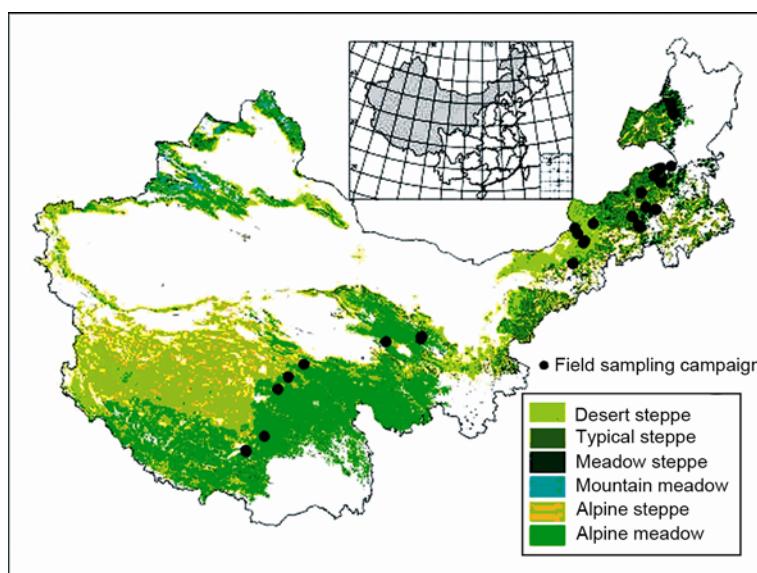


Figure 1 Vegetation map of the China's grasslands [23], showing the sample sites

of desert steppe) and 16 on the Tibetan Plateau (6 of alpine steppe and 10 of alpine meadow) (Figure 1). The sites were selected from areas of minimal anthropogenic disturbance. At each site the dominant species were sampled, 42 species from 27 genera in 13 families in Inner Mongolia, and 53 species from 30 genera in 12 families on the Tibetan Plateau.

At each site, 5–10 mature and healthy individuals for each species were collected [24]. A patch containing the whole or overwhelming majority of the root system was excavated by spade. Patch size and shape was determined by the root morphology of each species. Usually a 10–20 cm diameter patch of the grass was excavated to a depth of 20–30 cm. Roots of each sample were carefully separated from soil and other belowground material. Dead roots were removed. Then roots and shoots were separated. Roots were placed in a car freezer or on ice in a cooler until they could be cleaned. Shoot samples were further divided into stems, leaves and reproductive structures and put into separate paper envelopes. Afterwards, the roots were washed free of soil under running water (<5°C) before all plant samples were oven-dried at 65°C to a constant mass in the laboratory.

2.3 Climate data

To investigate the potential effects of climatic factors on R/S, mean annual temperature (MAT) and mean annual precipitation (MAP) were extracted for each site from the WorldClim database (<http://www.worldclim.org/>) with a spatial resolution of 0.0083° (approximately 1 km² at the equator) [25,26].

2.4 Data analysis

Individual measurements of above- and belowground biomass were averaged for each species at each site. The relationship between log-transformed above- and belowground biomass was determined with both ordinary least square (OLS) regression and standardized major axis (SMA) regression [8,9]. SMA slopes and intercepts were obtained using the SMART software package developed by Falster *et al.* [27]. The SMA slopes were tested against 1.0; non-significant difference from 1.0 in the slopes indicates an isometric relationship exists between roots and shoots [28].

3 Results

3.1 General pattern of R/S

R/S varied substantially across biogeographic regions, veg-

itation types and plant species at both the individual and community levels. Individual species R/S ranged from 0.2–17.7 while community R/S ranged from 0.4–32.2 (Figure 2 and Table 1). In the study area, temperate grassland plants show a tendency toward having a larger R/S compared with plants in the alpine grasslands. At the individual level, median R/S for species in temperate grasslands is higher than in alpine grasslands (0.84 vs. 0.65). This is consistent with previous observations at community level (6.3 vs. 5.8, respectively).

3.2 Allometric relationships between above- and belowground biomass

At the individual level, the relationship between above- and belowground biomass can be expressed using an exponential function, $S=1.1465R^{0.5302}$ ($r^2 = 0.47$, $P < 0.001$), where S is the above-ground biomass and R represents the below

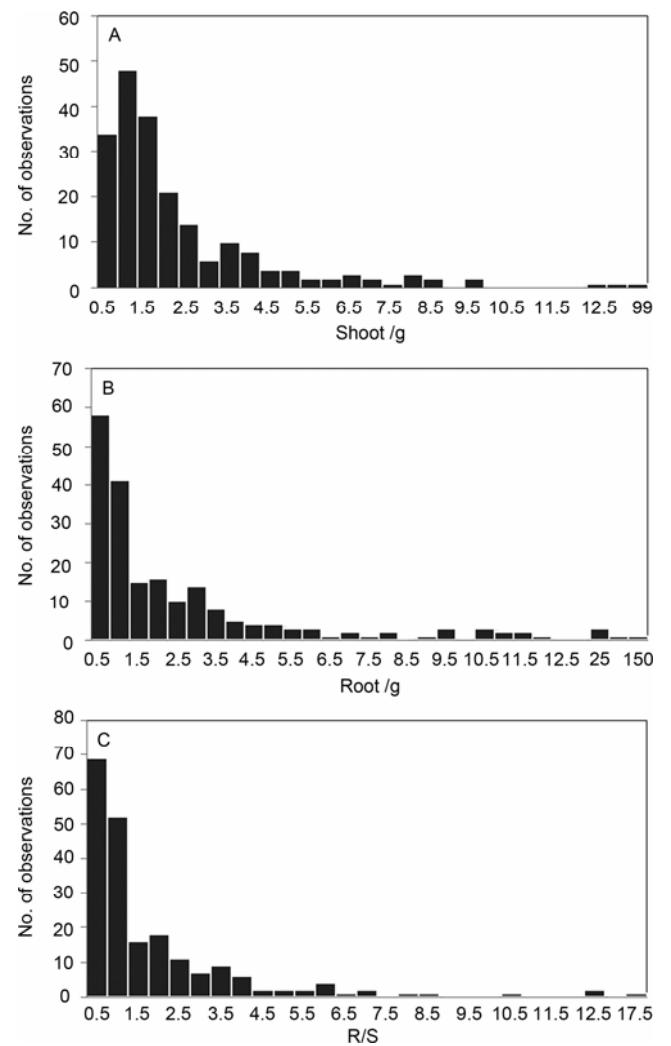


Figure 2 Frequency distributions of above-ground biomass (Shoot) (A), belowground biomass (Root) (B), and root:shoot ratio (R/S) (C) for herbaceous species in China's grasslands. No. of observations represents the number of replicates (species × site)

ground biomass. The allometric slope which is obtained by the SMA regression for Chinese grasslands species is 0.78 showing a 95% confidence interval of 0.70–0.86 (Table 2). More specifically, the allometric slope of alpine grasslands on the Tibetan Plateau is significantly different from temperate grasslands in Inner Mongolia (0.71 vs. 0.84, $P < 0.05$). Compared with the globally averaged values, species on the Tibetan Plateau have a significantly lower allometric

slope. Contrarily, the allometric slope of species in Inner Mongolia is not significantly different from the global value (Table 2 and Figure 3).

3.3 Relationships between R/S and climate

For all sampling sites as a whole, the individual R/S was not significantly correlated with AT, whereas it was signifi-

Table 1 Root:shoot ratios for different grassland types at individual and community levels in China. Median (Med.), Minimum value (Min.), Maximum value (Max.) and number of replicates (species \times site, n) are reported. The global data at individual level were extracted from the database provided by Enquist [7] (shoot biomass ranges from 0.18–15.64g). R/S ratios for temperate (Temp) and alpine grasslands at community level were reported previously by Ma & Fang [22] and Yang *et al.* [15], respectively.

Grassland Type	Individual R/S				Community R/S			
	n	Med.	Min.	Max.	n	Med.	Min.	Max.
Temp Grassland	106	0.84	0.25	12.48	101	6.3	0.4	32.2
Desert steppe	25	1.40	0.25	12.48	44	6.7	2.0	32.2
Typical steppe	47	0.67	0.29	8.16	54	5.3	0.4	19.9
Meadow steppe	34	1.11	0.30	5.36	18	5.2	1.9	14.7
Alpine grassland	101	0.65	0.21	17.72	112	5.8	0.8	13.0
Alpine meadow	65	0.47	0.21	17.72	73	5.2	0.8	13.0
Alpine steppe	36	1.68	0.26	10.23	39	6.8	1.4	12.7
Global	324	0.59	0.05	7.33	46	4.5	0.8	26.0

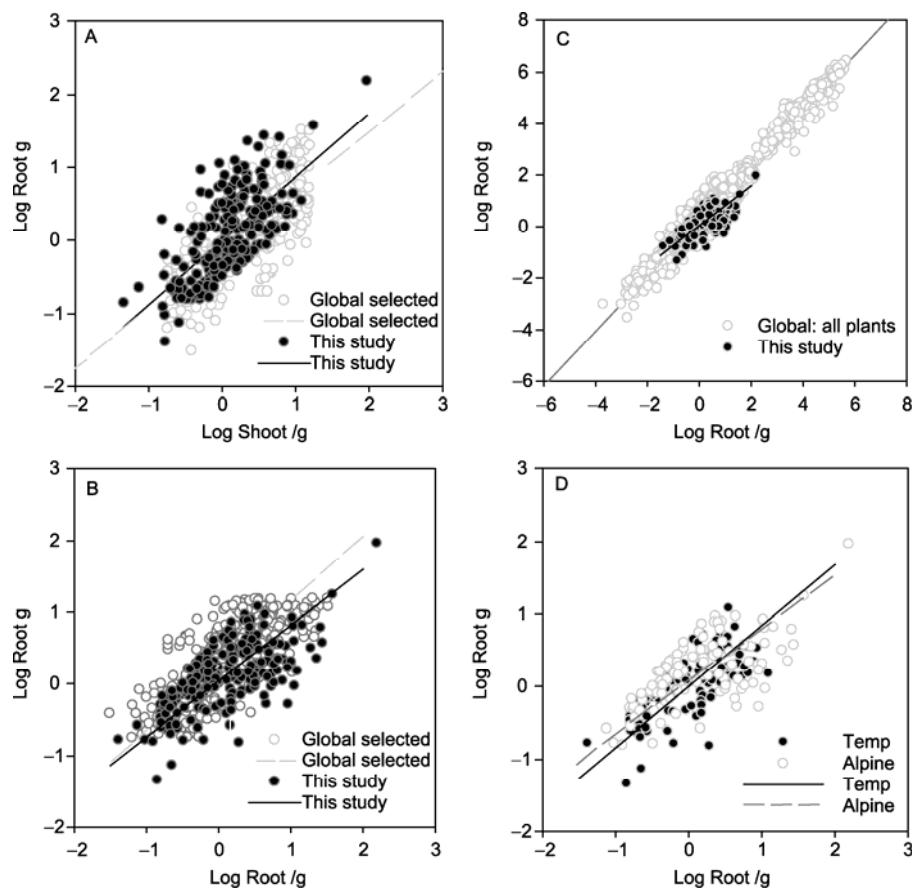


Figure 3 Relationships between shoot and root biomass for herbaceous species in China's grasslands (black dots in A, B, and C) and species obtained from the global database of plant biomass provided by Enquist *et al.* [7] (gray circles in a, b and c). In (A) and (B), the relationship of China's herbaceous species (This study) was compared with species of similar size obtained from Enquist et al.'s database (Global selected), while in (C), the data of China's herbaceous species (This study) were compared with those of all plants in Enquist *et al.*'s database (Global: all plants). (D) shows the relationships for herbaceous species in temperate (Temp) and alpine grasslands (Alpine); OLS regression was used for (A), while reduced major axis regression was used for (B), (C), (D). Root and shoot biomass were all \log_{10} -transformed.

Table 2 Regression results for the relationships between above- and belowground biomass for herbaceous species in China's grasslands and species obtained from a global database provided by Enquist *et al.*[7] using a standardized major axis (SMA) method. For the global dataset, only species with shoot biomass ranging from 0.18–15.64 g were used. Both above- and belowground biomass was log10-transformed. P is significance level at which the estimated slopes are different from 1.0.

	n	r^2	slope (95% CI)	intercept	P (H_0 : slope = 1.0)
Temperate Grasslands	106	0.50	0.84 (0.74–0.97)	0.00	0.016
Alpine Grasslands	101	0.43	0.71 (0.61–0.83)	0.09	0.000
Grasslands in China	207	0.46	0.78 (0.70–0.86)	0.04	0.000
Global	324	0.55	0.90 (0.83–0.96)	0.26	0.003
All data combined	531	0.50	0.89 (0.84–0.95)	0.17	0.000

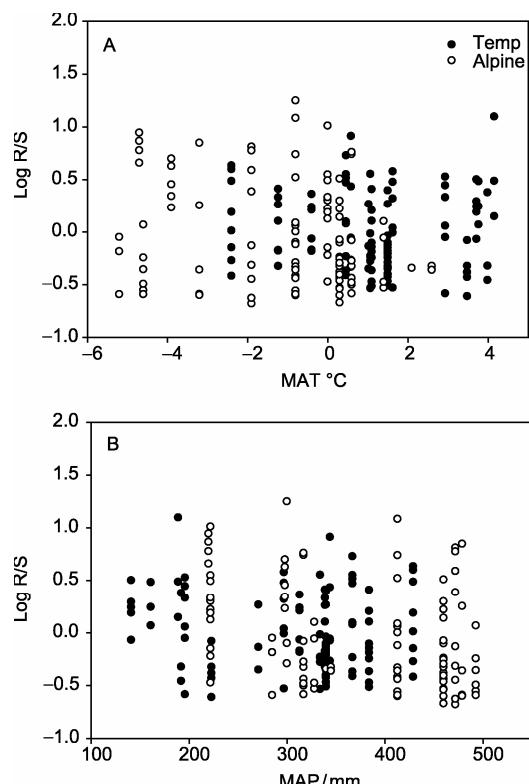


Figure 4 Changes in root:shoot ratios with mean annual temperature (MAT) (A) and mean annual precipitation (MAP) (B). Solid dots and open circles represented species in temperate (Temp) and alpine grasslands (Alpine), respectively.

cantly, but weakly correlated with MAP (MAT: $r^2=0.02$, $P>0.05$; MAP, $r^2=0.03$, $P<0.05$). In temperate grasslands, R/S was not significantly correlated with both MAT and MAP (MAT: $r^2=0.02$, $P>0.05$; MAP, $r^2=0.02$, $P>0.05$). By contrast, R/S of alpine grasslands declined significantly with increasing MAP, but was not significantly correlated with MAT (MAT: $r^2=0.03$, $P>0.05$; MAP, $r^2=0.06$, $P<0.05$).

4 Discussion

4.1 Root:shoot ratios in China's grasslands

At the level of the individual plant, temperate grasslands in

Inner Mongolia exhibited larger R/S values than Tibetan grasslands. These results are consistent with previous observations at community level [15, 22]. The community level R/S of China's entire temperate grassland system did not differ significantly from the R/S of alpine grasslands, because of the smaller R/S in Xinjiang grasslands at community level [10]. Moreover, at the individual level, species in both the Inner Mongolian and Tibetan grasslands showed larger R/S than species with comparable shoot biomass (0.18–15.64 g) in Enquist's global dataset. The higher R/S in China's grasslands in this study might be ascribed to the lower temperature and precipitation in China's grasslands. Additionally, other factors, such as shoot biomass, soil texture and species composition play an important role. More detailed information for sites and climate of the species in Enquist's global dataset will be required to further explore the reasons for the higher R/S in China when compared with the global average.

Although patterns of biomass allocation were similar at individual and community levels, the absolute R/S values were significantly different between these two levels. This difference could be caused by climatological factors.

Data related to local environmental conditions might be different between sites to some degree because the timing of data collection was not exactly the same at all sites. However, we sampled all sites during the same season and sampling sites were all typical vegetation types along a climate transect both in the Inner Mongolian and the Tibetan Plateau. Moreover, environmental factors are weakly or non-significantly correlated with R/S, suggesting that climate might not be the major cause for the large difference in R/S across China's grasslands. Fundamentally, the R/S at the community level is the average of below- and aboveground biomass ratios for all species occurring at each site. In contrast, many species with low coverage were ignored for the estimation of the R/S at individual level. This omission of non-dominant species in sampling and unweighted average could be another reason for the difference between R/S at the community and individual levels.

However, the above-mentioned reasons are insufficient to explain such big differences. While sampling errors might be the most important cause, no single cause

would result in such differences. The R/S at community level is especially comparable with other studies using the same method. Similarly, our R/S at individual level is at the same order of magnitude with those obtained using similar methods in previous studies [29–32].

We believe sampling errors at both individual and community levels might be the most likely reason for the R/S difference between our study and previous ones. We believe our data of sampling individual shoot biomass was accurate as only healthy and mature individuals were selected. At the same time, root biomass was probably underestimated in our study due to unavoidable loss of fine roots while sampling. As a result, R/S at the individual level was underestimated. However, it is not possible to give an accurate estimation for the fraction of roots lost during sampling processes. Several factors probably resulted in sampling errors at the community sampling level: (1) shoot biomass could be underestimated due to grazing by herbivores, (2) a small part of the above-ground biomass could be lost during shoot biomass collection, (3) root biomass could be overestimated because it is very difficult to separate dead roots from living ones by color [33].

The extent of the overall underestimation or overestimation of R/S is still unclear for any particular grassland type at both individual and community levels. Intensive and systematic studies at the same sites looking at both the individual and community levels are still needed.

4.2 Allometric relationship between above- and belowground biomass

For the species in China's grasslands, the slope of the allometric regression between above- and belowground biomass was significantly different from 1.0 (Figure 3), indicating grass species in China's grasslands did not support the isometric prediction. This could be caused by (1) the relatively narrow variation in plant size, and (2) many of our species, especially those from the Tibetan alpine grasslands, do not have typical hierarchical branching structures. Regarding the narrow variation in plant size, the species with similar size (shoot biomass ranged from 0.18–15.64 g) from the database provided by Enquist did not show isometric relationships either. Besides, the r^2 for the allometric relationship was much smaller than the overall r^2 (0.55 vs. 0.97). Related to the second cause, some of these species are perennial rosette plants whose stems are for supporting the reproductive organs rather than transporting nutrients to leaves. Additionally, some of the plant's' belowground parts are not used for water and nutrient uptake from soil. Many organs are specialized into tuberous roots, rhizomes, tubers

for nutrient storage or other functions. These findings suggest that many species do not meet the assumptions proposed by Enquist *et al.* [7], especially the assumption that stem length scales isometrically with respect to the root length.

In terms of the slope of the allometric regressions between above- and belowground biomass, the alpine grasslands on the Tibetan Plateau were significantly different from Inner Mongolian temperate grasslands as well as the global dataset ($P < 0.01$). In the same way, the measurement for grass species was significantly smaller than for herb species, (0.63 (95% CI: 0.50–0.80, $r^2 = 0.393$, $n = 46$) vs. 0.89 (95% CI: 0.78–1.028, $r^2 = 0.75$, $n = 55$), respectively. Some previous studies indicated the allometric relationship was not altered by species composition or environmental parameters [7,34] in contrast with our results. The ecological strategies of the grass species responding to the extreme environmental conditions on the Tibetan Plateau may account for these differences.

4.3 Effects of climatic factors on biomass partitioning

Biomass partitioning in various ecosystems is strongly influenced by climate [35]. To maximize the ability to capture nutrients, plants often change their biomass allocation patterns under different environmental conditions. However, most evidence of plasticity in biomass allocation is based on short-term experiments [36]. In contrast, above- and belowground biomass allocation patterns in field observations at a regional scale indicate the long-term adaptation of species. Mokany *et al.* [18] demonstrated that R/S in grasslands significantly decreased with increasing MAT and MAP. However, the species in China's grasslands did not show significant changes of the R/S in response to the variation of temperature and precipitation. This could be caused by: (1) the large-scale pattern of R/S in China's grasslands along the climatic gradient may be complex because of the negative correlation between MAP and MAT across sites, (2) the pattern of R/S may be related to the relatively narrow range of climate variables across China's grasslands, and (3) the lack of discernible change in R/S along the climatic gradient.

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