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PAPER

# Large-scale pattern of biomass partitioning across China's grasslands

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## ABSTRACT

**Aim** To investigate large-scale patterns of above-ground and below-ground biomass partitioning in grassland ecosystems and to test the isometric theory at the community level.

**Location** Northern China, in diverse grassland types spanning temperate grasslands in arid and semi-arid regions to alpine grasslands on the Tibetan Plateau.

**Methods** We investigated above-ground and below-ground biomass in China's grasslands by conducting five consecutive sampling campaigns across the northern part of the country during 2001–05. We then documented the root : shoot ratio (R/S) and its relationship with climatic factors for China's grasslands. We further explored relationships between above-ground and below-ground biomass across different grassland types.

**Results** Our results indicated that the overall R/S of China's grasslands was larger than the global average (6.3 vs. 3.7). The R/S for China's grasslands did not show any significant trend with either mean annual temperature or mean annual precipitation. Above-ground biomass was nearly proportional to below-ground biomass with a scaling exponent (the slope of log–log linear relationship between above-ground and below-ground biomass) of 1.02 across various grassland types. The slope did not differ significantly between temperate and alpine grasslands or between steppe and meadow.

**Main conclusions** Our findings support the isometric theory of above-ground and below-ground biomass partitioning, and suggest that above-ground biomass scales isometrically with below-ground biomass at the community level.

## Keywords

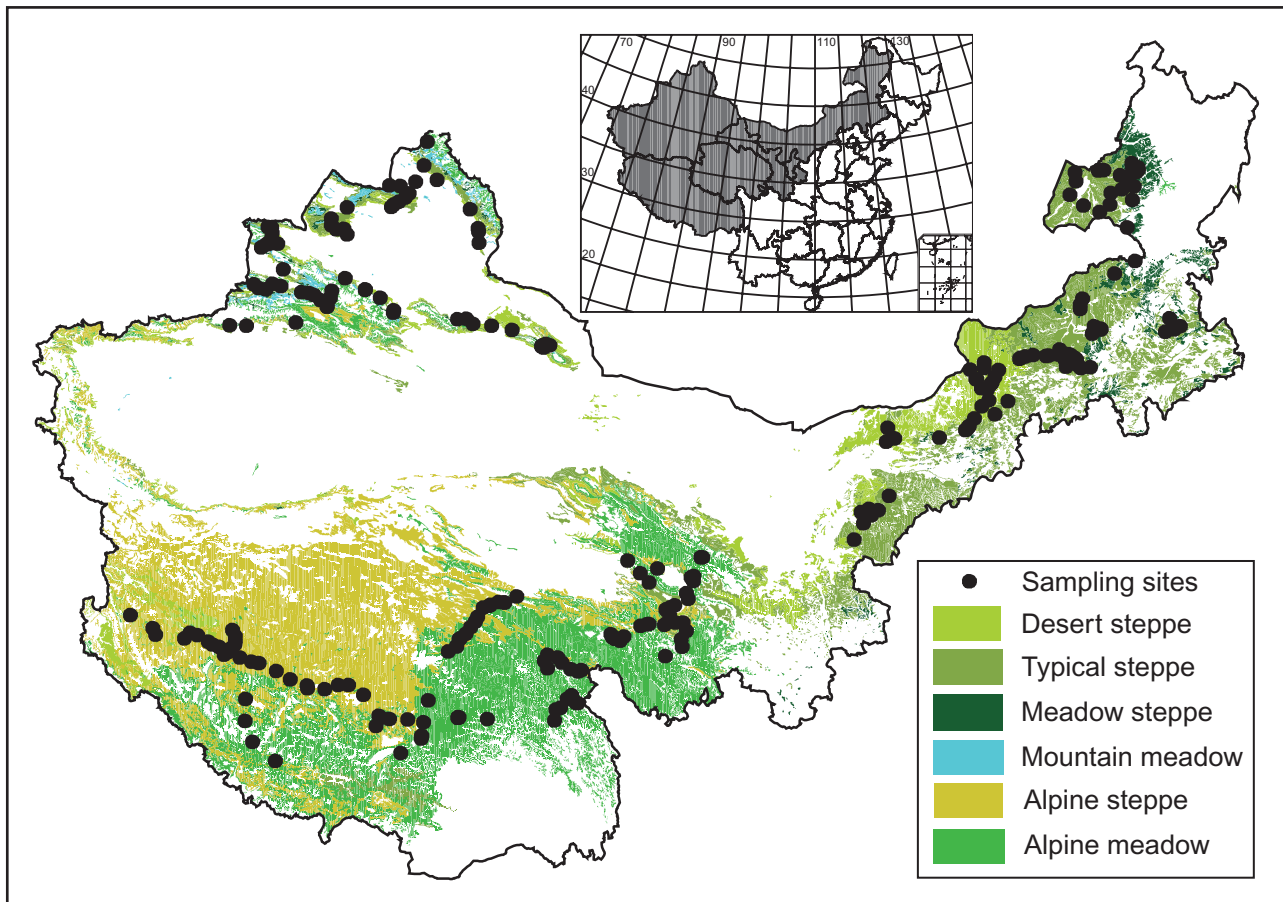
**Above-ground biomass, alpine grasslands, below-ground biomass, China, isometric theory, root : shoot ratio, temperate grasslands.**

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## INTRODUCTION

The partitioning of below- to above-ground biomass, commonly described as root : shoot ratio (R/S), is a key parameter for estimating root biomass from shoot biomass which can be easily measured (Cairns *et al.*, 1997; Mokany *et al.*, 2006). The R/S has been an important input of terrestrial ecosystem carbon modelling (Jackson *et al.*, 1996; Hui & Jackson, 2005). Quantifying this ratio and its relationships with climatic factors is essential to improving our understanding of root biomass distributions, and critical for predicting global carbon cycles in terrestrial ecosystems (Jackson *et al.*, 1996; Titlyanova *et al.*, 1999; Hui & Jackson, 2005; Mokany *et al.*, 2006).

Grasslands account for *c.* 25% of the land surface of the earth and 10% of global carbon stocks, and thus play an important role in global carbon cycling (Scurlock *et al.*, 2002). Compared with forests, grasslands are particularly useful for addressing the questions of biomass partitioning because of the relatively easy sampling of both shoot and root biomass and the larger proportion (*c.* 80%) of total biomass in roots (Hui & Jackson, 2005). However, the R/S reported in previous studies contains considerable errors due to the methodological problems in root sampling and has rendered estimates of root biomass highly unreliable (Jackson *et al.*, 1996). A recent analysis of R/S using a critiquing methodology, in which unreliable R/S estimates were identified and omitted for data analysis, has indicated that 62%



**Figure 1** The locations of 265 sampling sites in northern China's grasslands on the background of a vegetation map of China. The distribution of grassland types is derived from the vegetation map of China at a scale of 1:1,000,000 (Chinese Academy of Sciences, 2001).

of 786 entries of R/S were unreliable; discarding these unreliable data resulted in a dramatic increase in estimated root biomass across global grasslands (Mokany *et al.*, 2006). Therefore, reliable R/S data are urgently needed to obtain a precise estimate of root biomass in grassland ecosystems.

Theoretically, biomass partitioning between root and shoot can be predicted by plant allometric relationships (Enquist & Niklas, 2002; Niklas, 2005, 2006). The allometry theory suggests that above-ground biomass (AGB) scales isometrically with below-ground biomass (BGB) across individual plants, and this isometric relationship is insensitive to phyletic affiliation (conifers versus angiosperms) or variation in environmental conditions (Enquist & Niklas, 2002). The prediction has been validated across a broad spectrum of ecologically diverse vascular plants spanning several orders of magnitude in total body mass (e.g. Enquist & Niklas, 2002; Niklas, 2005). Likewise, the allometry theory also predicts a similar isometric scaling relationship between AGB and BGB at the community level (Cheng & Niklas, 2007), but this has not been adequately tested using field measurements. In particular, it is unknown whether the isometric relationship holds true across diverse grassland types.

China, with diverse grassland types extending from temperate grasslands in arid and semi-arid regions to alpine grasslands on

the Tibetan Plateau (Liao & Jia, 1996), offers a unique opportunity for examining the R/S and the allometric relationship between AGB and BGB across grassland ecosystems. However, only a few studies have been implemented at the local scale (e.g. Li & Zhou, 1998; Yang *et al.*, 2009a) and the large-scale pattern of biomass partitioning in China's grasslands is not well quantified. In this study, we investigated R/S for China's grasslands on the basis of a large-scale biomass survey from 265 sites across the northern part of the country. Our objectives were: (1) to document R/S for various grassland types, (2) to explore the possible effects of climatic factors on the R/S, and (3) to examine the allometric relationships between AGB and BGB.

## MATERIALS AND METHODS

### Large-scale biomass survey

We sampled 265 sites across the northern China during the summers (July to September) of 2001–05 (Fig. 1). At each site (10 m × 10 m), all plants in five plots (1 m × 1 m) were harvested to measure AGB. Either three soil blocks (50 cm × 50 cm × maximum soil depth, depth to bedrock) or nine soil cores with a diameter of 8 cm at depth intervals of 10 cm to maximum soil

depth were sampled to determine BGB. Root samples were immediately placed in a cooler and then transported to the laboratory. In the laboratory, root samples were stored at  $-5^{\circ}\text{C}$  to conduct subsequent processing. Root samples were soaked in deionized water and cleaned from soil residuals using a 0.5-mm sieve. Live roots were distinguished by their colour, resilience and attached fine roots (Vogt & Persson, 1991). Likewise, live and dead shoots were also separated for each sampling site. In this study, live shoot and root biomass were used to explore biomass partitioning patterns and their relationships with climatic variables (e.g. Jackson *et al.*, 1996; Mokany *et al.*, 2006). Finally, biomass samples were oven-dried at  $65^{\circ}\text{C}$  to constant mass, and weighed to the nearest 0.1 g.

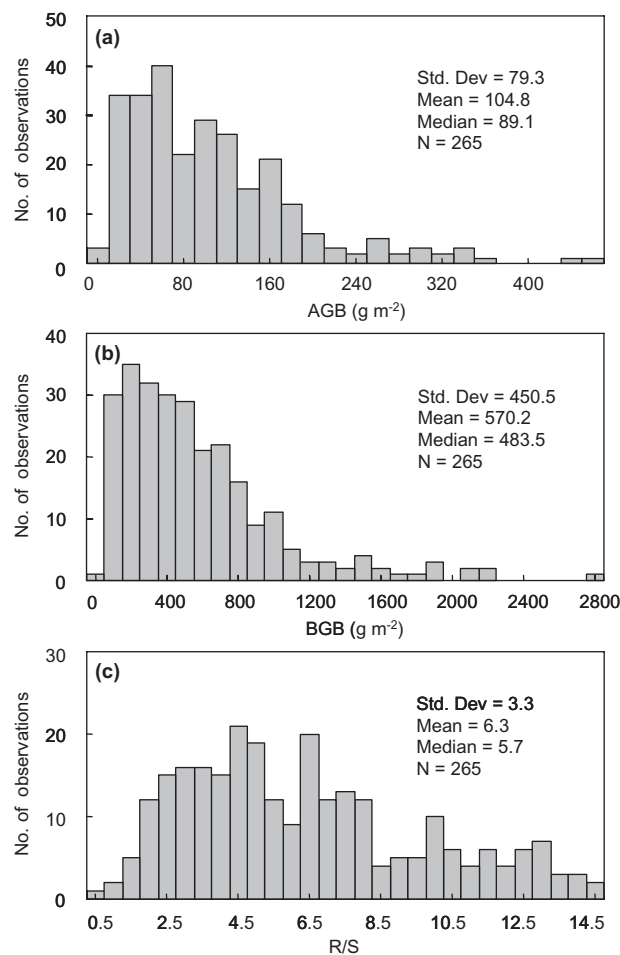
### Climate data and grassland types

Growing season temperature and precipitation are considered to be important factors affecting the large-scale pattern of the R/S. Considering a significant correlation between annual mean and growing season mean climatic variables across China's grasslands and an easy comparison of our data with previous studies, we used mean annual temperature (MAT) and mean annual precipitation (MAP) as indicators of climate variables. Data for MAT and MAP at a resolution of  $0.1^{\circ} \times 0.1^{\circ}$  were compiled from the climate database for China during 1970–99 (Piao *et al.*, 2003). The database was generated from 680 climatic stations across the country.

In order to analyse variations in AGB, BGB and R/S for different grassland types, we adopted China's vegetation classification system (Chinese Academy of Sciences, 2001) to divide northern China's grasslands into six types: desert steppe, typical steppe, meadow steppe, mountain meadow, alpine steppe and alpine meadow. These types are grouped on the basis of climatic zonation, humidity index, vegetation type of grassland and their importance in livestock husbandry (Department of Animal Husbandry and Veterinary, 1996). Of them, desert steppe, typical steppe, meadow steppe and mountain meadow are mainly distributed in arid and semi-arid regions in northern China, while alpine steppe and alpine meadow appear on the Tibetan Plateau. In China's grasslands, forbs accounted for 57–79% of the total number of species (see Appendix S1 in Supporting Information), comparable to the observation in global grasslands (40–80%) (Golluscio & Sala, 1993).

### Statistical analysis

Ordinary least squares (OLS) and reduced major axis (RMA) analyses were applied to the raw and the  $\log_{10}$ -transformed biomass data, respectively (Niklas, 2005; Cheng & Niklas, 2007). OLS analyses were performed to develop regressions with BGB as the dependent variable, while RMA analyses were conducted to establish the allometric relationships between AGB and BGB (Niklas, 2005; Cheng & Niklas, 2007). The slope (scaling exponent) and  $y$ -intercept (allometric constant) of log–log linear functions were determined by the software package 'Standardized major axis tests and routines' (SMATR; Falster *et al.*, 2003).



**Figure 2** Frequency distributions of (a) above-ground biomass (AGB), (b) below-ground biomass (BGB), and (c) root : shoot ratio (R/S) in China's grasslands. Their mean and median values are presented.

## RESULTS

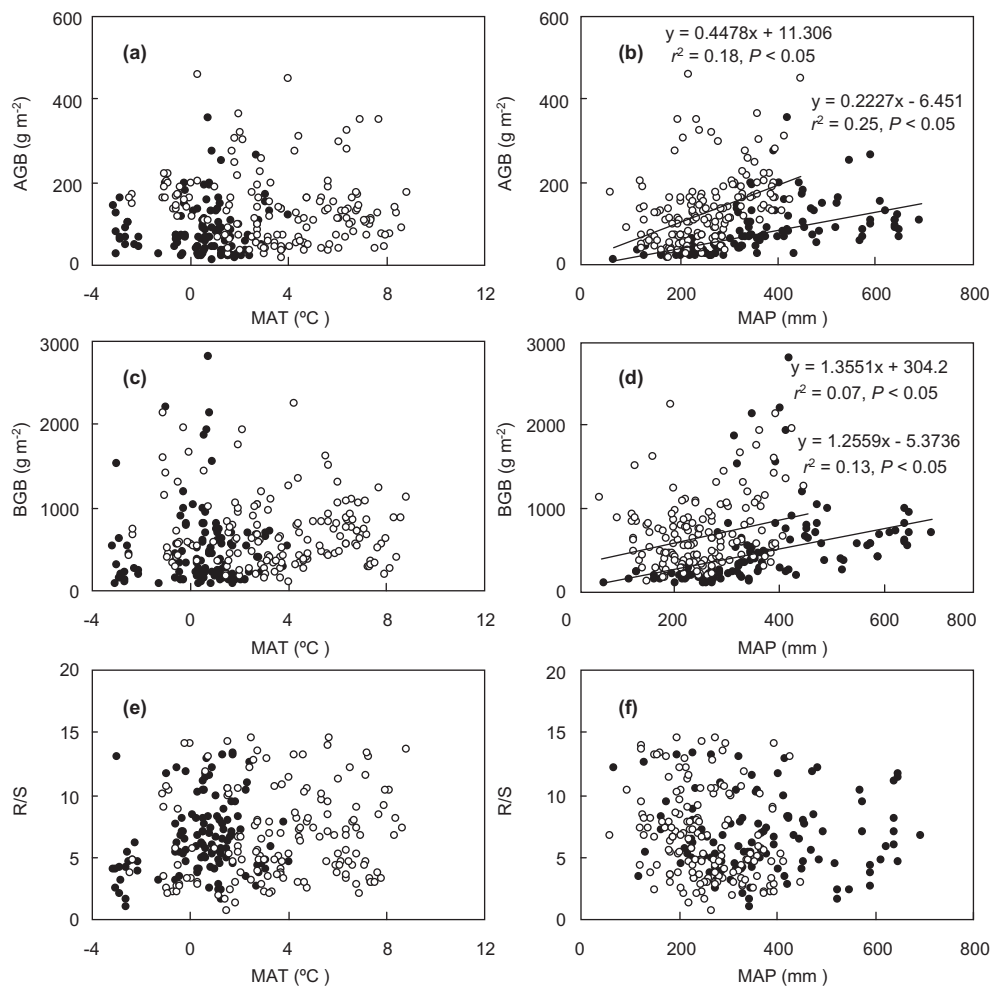
### Variations in AGB, BGB and R/S

AGB, BGB and R/S all exhibited large variations across all the sites, ranging from 4.3 to  $452.1 \text{ g m}^{-2}$  for AGB, 44.6– $2784.8 \text{ g m}^{-2}$  for BGB and 0.4–14.3 for R/S (Fig. 2). The median values were  $89.1 \text{ g m}^{-2}$ ,  $483.5 \text{ g m}^{-2}$  and 5.7 for AGB, BGB and R/S, respectively (detailed data are listed in Appendix S2).

AGB and BGB varied markedly across different grassland types (Table 1). For AGB, the median value ranged from  $40.5 \text{ g m}^{-2}$  (alpine steppe) to  $193.6 \text{ g m}^{-2}$  (meadow steppe), while that of BGB varied from  $201.3 \text{ g m}^{-2}$  (alpine steppe) to  $1254.3 \text{ g m}^{-2}$  (meadow steppe). In contrast, the median value of R/S was less variable, from 3.5 (mountain meadow) to 6.8 (alpine meadow). Further, both AGB and BGB for alpine grasslands ( $59.3$  and  $317.2 \text{ g m}^{-2}$ ) were lower than those for temperate grasslands ( $116.6$  and  $553.3 \text{ g m}^{-2}$ ). However, R/S for alpine grasslands and temperate grasslands showed similar values (5.8 vs. 5.5).

**Table 1** Median values of above-ground biomass (AGB), below-ground biomass (BGB) and root : shoot ratio (R/S) for various grassland types in northern China.

Grassland types	AGB (g m <sup>-2</sup> )	BGB (g m <sup>-2</sup> )	R/S	Range	<i>n</i>
Temperate grasslands	116.6	553.3	5.5	0.4–14.3	151
Desert steppe	60.4	348.3	6.4	2.0–14.3	60
Typical steppe	127.6	640.1	5.6	0.4–14.3	61
Meadow steppe	193.6	1254.3	5.2	1.8–13.8	19
Mountain meadow	155.3	627.6	3.5	1.1–8.2	11
Alpine grasslands	59.3	317.2	5.8	0.8–13.0	114
Alpine steppe	40.5	201.3	5.2	0.8–13.0	75
Alpine meadow	100.4	645.8	6.8	1.4–12.7	39
Overall	89.1	483.5	5.7	0.4–14.3	265

**Figure 3** Relationships of above-ground biomass (AGB), below-ground biomass (BGB) and root : shoot ratio (R/S) with climatic factors for temperate (open circles) and alpine grasslands (closed circles) in northern China: (a, b) AGB, (c, d) BGB, (e, f) R/S. MAT, mean annual temperature, MAP, mean annual precipitation.

### Relationships of AGB, BGB and R/S with climatic factors

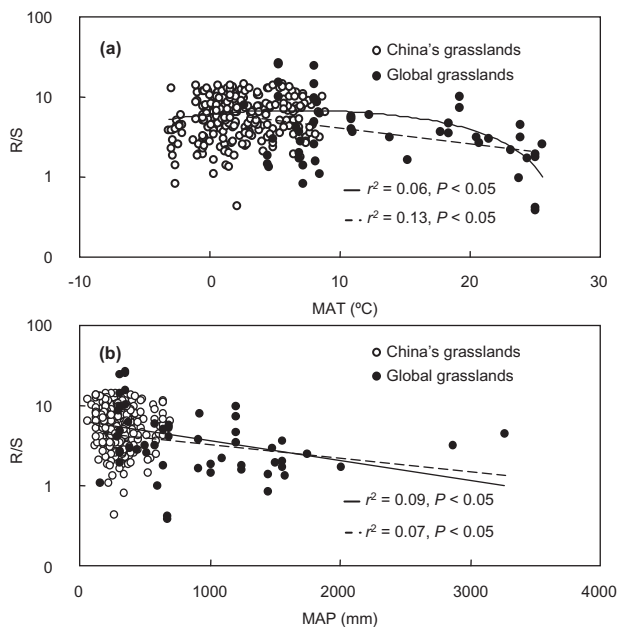
AGB in temperate and alpine grasslands did not exhibit any significant trend with MAT ( $P > 0.05$ ) (Fig. 3a). However, they

significantly increased with MAP (temperate grasslands,  $r^2 = 0.18$ ,  $P < 0.05$ ; alpine grasslands,  $r^2 = 0.25$ ,  $P < 0.05$ ), with a higher slope in temperate grasslands than in alpine grasslands ( $0.45$  vs.  $0.22$  g m<sup>-2</sup> mm<sup>-1</sup>) (Fig. 3b). Likewise, BGB in temperate and alpine grasslands was not correlated with MAT

**Table 2** Reduced major axis (RMA) regression slopes ( $a_{RMA}$ ) and  $y$ -intercepts ( $\log \beta_{RMA}$ ) of the relationships between above-ground biomass (AGB) and below-ground biomass (BGB) for China's grasslands. For comparison, similar analyses were also performed for China's forests. The biomass dataset of China's forests is derived from Cheng & Niklas (2007).

Biome	$a_{RMA}$	95% CI of $a_{RMA}$	$\log \beta_{RMA}$	$r^2$	$n$
Temperate grasslands	1.10	0.96–1.25	−0.99	0.33	151
Alpine grasslands	0.94	0.85–1.05	−0.60	0.68	114
Steppe	1.02	0.94–1.12	−0.80	0.59	215
Meadow	0.93	0.72–1.20	−0.53	0.23	50
Overall grasslands	1.02	0.94–1.10	−0.78	0.56	265
China's forests	1.03	1.01–1.05	0.45	0.88	1534

CI, confidence interval.



**Figure 4** Relationships between root : shoot ratio (R/S) and (a) mean annual temperature (MAT) and (b) mean annual precipitation (MAP). The trend lines for data from Mokany *et al.* (2006) (dashed line) and all data pooled together (solid line) are shown.

( $P > 0.05$ ) (Fig. 3c), but was positively associated with MAP ( $P < 0.05$ ) (Fig. 3d). In addition, R/S in temperate and alpine grasslands did not vary with either MAT or MAP ( $P > 0.05$ ) (Fig. 3e,f).

The R/S of global grasslands dropped significantly with increases in both MAT and MAP (MAT,  $r^2 = 0.13, P < 0.05$ ; MAP,  $r^2 = 0.07, P < 0.05$ ) (Fig. 4a,b). However, the R/S in China's grasslands did not show any significant trend with either MAT or MAP (MAT,  $r^2 = 0.02, P > 0.05$ ; MAP,  $r^2 = 0.01, P > 0.05$ ). Consequently, the decreasing trend of R/S with MAT became weaker for all data combined, especially disappeared under cold environments. By contrast, the R/S still showed a significant decrease with an increase of MAP ( $r^2 = 0.09, P < 0.05$ ).

### Allometric relationships between AGB and BGB

The relationship between BGB and AGB across China's grasslands could be characterized by a power function of  $BGB = 17.13 \times AGB^{0.74}$  ( $r^2 = 0.56, P < 0.001$ ) (Fig. 5a). The slope (scaling exponent) of the allometric relationship across different grassland types was 1.02, with 95% confidence interval (CI) of 0.94–1.10 (Fig. 5b, Table 2). The comparison between temperate and alpine grasslands did not show a significant difference in the scaling exponents for AGB and BGB ( $P > 0.05$ ) (Fig. 5c, Table 2). Similarly, the scaling exponents did not differ significantly between steppe and meadow ( $P > 0.05$ ) (Fig. 5d, Table 2).

## DISCUSSION

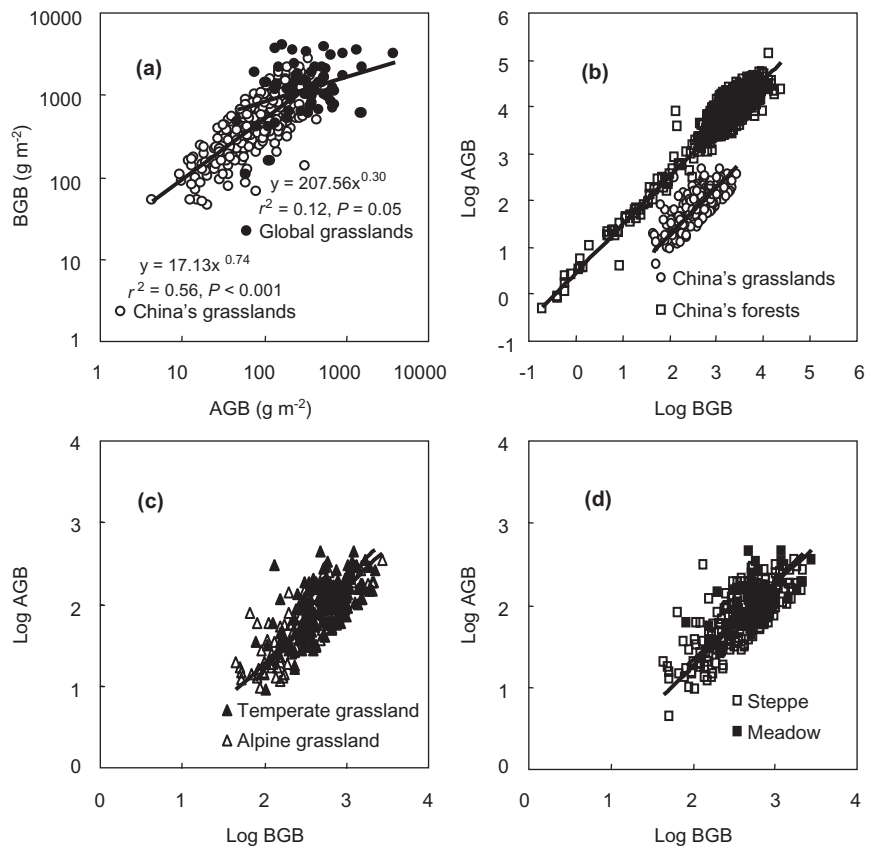
### Size of AGB, BGB and R/S

The overall average of AGB and BGB in China's grasslands was estimated at 104.8 and 570.2 g m<sup>-2</sup>, respectively (Table 3). Our estimates are comparable with a recent satellite-based assessment for China's grasslands (Piao *et al.*, 2007). Using the national grassland resource inventory data and the dataset of normalized difference vegetation index (NDVI), Piao *et al.* (2007) estimated that AGB across all China's grasslands ranged between 91 and 102 g m<sup>-2</sup>, with an average of 97 g m<sup>-2</sup> during 1982–99. They also roughly accounted for BGB for China's grasslands by assuming a constant R/S for each grassland type. They found that BGB for China's grasslands fluctuated from 566–639 g m<sup>-2</sup> during the study period. These estimates were close to those in our study. In addition, both AGB and BGB in China's grasslands are much smaller than the estimates for global grasslands by Jackson *et al.* (1996) (378.4 g m<sup>-2</sup> for AGB and 1400 g m<sup>-2</sup> for BGB) and by Mokany *et al.* (2006) (430.2 g m<sup>-2</sup> for AGB and 1810.9 g m<sup>-2</sup> for BGB) (Table 3).

The average R/S in China's grasslands (6.3, with 95% CIs of 5.9–6.7) is larger than that in global grasslands (3.7 by Jackson *et al.*, 1996, and 4.5 by Mokany *et al.*, 2006), and higher than that of American (4.4) and European grasslands (3.0–4.3) (Table 3). What is responsible for this large difference? According to the optimal partitioning hypothesis, plants respond to variation in environmental conditions by allocating biomass among various organs to capture nutrients, water and light to maximize their

**Table 3** Above-ground biomass (AGB), below-ground biomass (BGB) and root : shoot ratio (R/S) of grasslands for different regions. Arithmetic mean and median values of R/S are presented to facilitate comparisons with other studies.

Region	Biomass ( $\text{g m}^{-2}$ )		R/S		Reference
	AGB	BGB	Mean	Median	
Global	378.4	1400.0	3.7	–	Jackson <i>et al.</i> (1996)
Global	430.2	1810.9	4.5	4.2	Mokany <i>et al.</i> (2006)
North America	207.8	1469.6	4.4	3.7	Coupland (1979)
Central Europe	430.6	1879.1	3.0	2.9	Coupland (1979)
West Europe	382.3	2167.5	4.3	4.3	Coupland (1979)
China	104.8	570.2	6.3	5.7	This study



**Figure 5** Allometric relationships between above-ground biomass (AGB) and below-ground biomass (BGB) for different vegetation types: (a) ordinary least squares (OLS) regression analyses between BGB and AGB; (b–d) reduced major axis (RMA) regression analyses between AGB and BGB. (a) Comparison between China's and global grasslands. (b) Comparison between China's grasslands and forests. (c) Comparison between China's temperate and alpine grasslands. (d) Comparison between China's steppe and meadow. The biomass data for global grasslands and China's forests are provided by Mokany *et al.* (2006) and Cheng & Niklas (2007), respectively.

growth rate (Bloom *et al.*, 1985; Chapin *et al.*, 1987). In general, plants allocate more biomass to shoots in high-nutrient or high-moisture environments and shift more biomass to roots in low-nutrient or low-moisture conditions (McConnaughay & Coleman, 1999). Compared with global grasslands, China's grasslands are distributed in relatively cold and arid regions (Fig. 4). Thus, the combination of lower temperature and less precipitation may make more biomass allocated to roots and lead to a higher R/S for China's grasslands.

To further reveal whether other factors could induce differences in the R/S values between China's and global grasslands, we compared R/S in China's grasslands with that in global

grasslands under similar climatic conditions. Specifically, we extracted sites which having similar climatic conditions to China's grasslands from the global dataset (i.e. MAT  $-3^{\circ}\text{C}$  to  $10^{\circ}\text{C}$  and MAP 0–800 mm), and then compared the R/S between China's and global grasslands. Our results showed that the R/S in global grasslands under cold and dry conditions was estimated at 10.5, greater than that (6.3) in China's grasslands. Considering the skewed distribution of R/S in global grasslands, we further compared the median value of R/S between China's and global datasets. Again, the R/S in global grasslands under cold and dry conditions was higher than that in China's grasslands (8.7 vs. 5.7). These differences suggest that other factors,

such as shoot biomass, soil texture and species composition may also induce variations in the R/S across grassland ecosystems (Mokany *et al.*, 2006).

### Isometric relationships between AGB and BGB

The power function fits well with the relationship between BGB and AGB for China's grasslands ( $r^2 = 0.56$ ,  $P < 0.001$ ), suggesting that root biomass could be reliably estimated by shoot biomass using the allometric relationship (Cairns *et al.*, 1997). Compared to this, Mokany *et al.* (2006) demonstrated that the power function only provided a weak fit to the BGB versus AGB relationship across global grasslands ( $r^2 = 0.12$ ,  $P = 0.05$ ). The much higher explanatory power ( $r^2 = 0.56$ ,  $P < 0.001$ ) of the allometric relationship across China's grasslands may be due to the consistent sampling methodology, large sampling size and broad biomass range in our study. By contrast, the weak BGB–AGB relationship observed in global grasslands may result from the different scaling functions across different biogeographical regions. For instance, in our study, although the scaling exponents were not significantly different between grasslands and forests, there were large differences in the intercepts of the scaling functions between them (Fig. 5b, Table 2). In addition, the allometric relationship observed in grassland ecosystems is also reported in forest ecosystems (Cairns *et al.*, 1997; Fang *et al.*, 2005; Cheng & Niklas, 2007), suggesting the generality of the relationships between AGB and BGB across different biomes.

The scaling exponent of the allometric relationship was 1.02 (Table 2), supporting the isometric prediction across different community types (Enquist & Niklas, 2002; Niklas, 2005, 2006). Moreover, AGB in China's grasslands scales with BGB in a manner strikingly similar to that in China's forests (Cheng & Niklas, 2007). However,  $\gamma$ -intercepts of the allometric relationships for China's grasslands differed remarkably from those for China's forests ( $P < 0.05$ ) (Fig. 5b, Table 2), indicating that absolute values of AGB vary substantially with respect to BGB between grasslands and forests (Cheng & Niklas, 2007). In addition, the lack of significant variation in the scaling exponents for AGB and BGB among different grassland types (temperate grasslands versus alpine grasslands, and steppe versus meadow) ( $P > 0.05$ ) (Table 2) suggests that the isometric relationship is irrespective of grassland types (Enquist & Niklas, 2002).

### Effects of climatic factors on biomass partitioning

The relationships of AGB and BGB to climatic factors observed in China's grasslands were consistent with those reported in other temperate grasslands around the world (e.g. Sala *et al.*, 1988; Epstein *et al.*, 1997; Jobbágy *et al.*, 2002). Neither AGB nor BGB in China's grasslands showed any significant trend along the temperature gradient, suggesting that temperature played a minor role in regulating plant growth in grassland ecosystems (Epstein *et al.*, 1997). However, both AGB and BGB in China's grasslands increased linearly with MAP, largely due

to its limiting effect on the activity of vegetation in arid and semi-arid environments (Sala *et al.*, 1988; Jobbágy *et al.*, 2002; Yang *et al.*, 2009b). Interestingly, a higher slope of the AGB–MAP relationship occurred in temperate grasslands than in alpine grasslands (0.45 vs. 0.22 g m<sup>-2</sup> mm<sup>-1</sup>) (Fig. 3b), reflecting their different water use efficiency which may be derived from the differences in vegetational and biogeochemical constraints between these two grassland types (Lauenroth & Sala, 1992; Paruelo *et al.*, 1999; Huxman *et al.*, 2004). Low temperature may inhibit biogeochemical cycles in alpine grasslands and reduce soil nitrogen availability for plant growth and thus limit the production response of alpine grasslands to precipitation.

The relationships between R/S and climatic factors for China's grasslands were distinctly different from those observed across global grasslands (Fig. 4). It has often been assumed that R/S in terrestrial ecosystems is partly determined by climatic factors (e.g. Klepper, 1991; Cairns *et al.*, 1997; Hui & Jackson, 2005). At the global scale, Mokany *et al.* (2006) demonstrated that R/S in grasslands significantly decreased with increases in both MAT and MAP. However, our data did not show any significant trends in the R/S across China's grasslands along the gradients of temperature and precipitation, possibly due to the following three aspects. First, the large-scale pattern of R/S in China's grasslands along the climatic gradient may be obscured by the interactions between temperature and precipitation. Specifically, MAP was negatively correlated with MAT across China's grasslands ( $r = -0.4$ ,  $P < 0.05$ ). As a result, cold regions are relatively humid, while warm areas have relatively low precipitation. Thus, the interactions between temperature and precipitation may lead to an unclear trend of R/S along the climatic gradient. Second, such a pattern may be associated with the narrow range of climate variables across China's grasslands. To explore whether climatic range affects the relationship of R/S to climatic variables, we extracted sites with MAT of  $-3$  °C to 10 °C or MAP of 0–800 mm from the global dataset (comparable to the climatic range across China's grasslands), and found that R/S in these sites also did not show any significant trend with either MAT or MAP ( $P > 0.05$ ), demonstrating the effect of climatic range on the pattern of R/S along the climatic gradient. Third, the lack of discernible change in R/S along the climatic gradient may also result from similar mechanisms that affect AGB and BGB in grassland ecosystems. As shown in Fig. 3, AGB and BGB in China's grasslands did not show significant change with MAT, but significantly increased with MAP.

### Uncertainties in the R/S estimate

Although our study provides the most comprehensive assessment of R/S for China's grasslands, some uncertainties still exist because of limited sample size and several factors described below. First, grazing activity can modify biomass partitioning patterns through its effects on AGB and BGB in grassland ecosystems. Grazing usually reduces shoot biomass (Johnson & Matchett, 2001), and results in a decrease (Biondini *et al.*, 1998),

increase (Piñeiro *et al.*, 2009) or no change (McNaughton *et al.*, 1998) in root biomass. As a result, a consistent pattern of R/S in grassland ecosystems cannot be observed in response to grazing activity. In this study, the sampling sites were mostly selected in the fence-protected areas, where little human disturbance and few grazing activities occurred. Therefore, grazing activity probably did not have a significant influence on the estimate of the R/S here.

Second, fire disturbance can also be a factor which alters AGB and BGB and thus R/S across grassland ecosystems (Briggs & Knapp, 1995). Above-ground plant production generally increases following a fire due to enhanced soil nitrogen mineralization (Blair, 1997). However, BGB in grassland ecosystems has been shown to increase (Ojima *et al.*, 1994) or remain unchanged (Blair, 1997) after fire disturbance. Thus, the direction of R/S dynamics in response to fire may remain ambiguous. Fire is a frequent natural event in tallgrass prairie of North America and considered as a necessary component for the preservation and maintenance of the tallgrass prairie (Briggs & Knapp, 1995; Knapp *et al.*, 1998). However, for China's grasslands, fire disturbance does not occur widely or frequently because of a strict control by local people due to fire policies (C. Liang, pers. comm.). No fire was recorded in any of our 265 sampling sites. Therefore, fire should not be a significant factor affecting the R/S of China's grasslands.

Third, plant phenology may influence R/S in grassland ecosystems (McConnaughay & Coleman, 1999). To minimize such an influence, we conducted our field investigation at the height of the growing season, which is considered to be the most appropriate time to give the best estimate of the relationship between shoot and root biomass (Scurlock *et al.*, 2002). In order to further evaluate whether sampling time could explain the observed difference in the R/S, we performed an ANOVA analysis using sampling time as a blocking variable. Our results showed that R/S in alpine grasslands did not show any significant changes during the peak of the growing season (July to September), but R/S in temperate grasslands exhibited a significant difference between July and August (Appendix S3), suggesting that sampling time may exert a potential effect on R/S for China's grasslands.

## CONCLUSIONS

To our knowledge, this study provides the first ground-based assessment of geographical variability in R/S and its relationships with climatic variables for China's grasslands. We found that the median values of R/S for China's temperate grasslands (5.5) and alpine grasslands (5.8) were higher than that of global temperate grasslands (4.2) (Mokany *et al.*, 2006), suggesting a *c.* 25% lower estimation for root biomass of China's grasslands if the R/S of global temperate grasslands was applied. Moreover, large-scale observations across China's grasslands could substantially modify the conclusions from previous analyses, especially refuting the decreasing trend of R/S with increasing MAT in cold environments. In addition, our results also indicated that AGB scaled as power function of BGB with an exponent of 1.02

across various grassland types and did not differ significantly between temperate and alpine grasslands, or between steppe and meadow, suggesting the generality of the isometric theory across various grassland types.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Frequency distributions of the proportion of forbs in various grassland types of China.

**Appendix S2** Above-ground biomass, below-ground biomass and root : shoot ratio in China's grasslands, together with

location, climate data, grassland type and dominant species of each site.

**Appendix S3** Changes in root : shoot ratio at different sampling times across China's grasslands.

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## BIOSKETCHES

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