



Above- and belowground biomass in relation to environmental factors in temperate grasslands, Inner Mongolia

MA WenHong^{1,2†}, YANG YuanHe¹, HE JinSheng¹, ZENG Hui^{1,2} & FANG JingYun¹

¹ Department of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China

² School of Environment & Urban Study, Peking University Shenzhen Graduate School, Shenzhen 518055, China

Above- and belowground biomasses of grasslands are important parameters for characterizing regional and global carbon cycles in grassland ecosystems. Compared with the relatively detailed information for aboveground biomass (AGB), belowground biomass (BGB) is poorly reported at the regional scales. The present study, based on a total of 113 sampling sites in temperate grassland of the Inner Mongolia, investigated regional distribution patterns of AGB, BGB, vertical distribution of roots, and their relationships with environmental factors. AGB and BGB increased from the southwest to the northeast of the study region. The largest biomass occurred in meadow steppe, with mean AGB and BGB of 196.7 and 1385.2 g/m², respectively; while the lowest biomass occurred in desert steppe, with an AGB of 56.6 g/m² and a BGB of 301.0 g/m². In addition, about 47% of root biomass was distributed in the top 10 cm soil. Further statistical analysis indicated that precipitation was the primary determinant factor in shaping these distribution patterns. Vertical distribution of roots was significantly affected by precipitation, while the effects of soil texture and grassland types were weak.

temperate grasslands, aboveground biomass (AGB), belowground biomass (BGB), spatial pattern, vertical distribution, precipitation

Temperate grassland is one of the most widespread biomes on the earth and plays a key role in regional carbon cycles^[1]. Vegetation biomass or production significantly contributes to soil organic matters, particularly in grassland ecosystems with belowground biomass accounting for more than 80% of total biomass^[2,3]. Therefore, accurate estimates of biomass and quantifying its relationships with environment are essential to predict the responses of grasslands to climate change, and to assess forage quality in grassland management^[2–5].

Recently, a number of studies have estimated grassland biomass in China using mean biomass derived from global biomass database^[6,7], inventory data^[8,9], remote sensing model^[10], and field measurements^[11,12]. These estimates provided important information for evaluating the role of grassland biome in terrestrial carbon cycle. However, some uncertainties remain due to the follow-

ing reasons. Firstly, biomass estimates varied greatly by different authors, partly due to different data source or methods. For instance, the inventory-based estimation of grassland biomass^[8] was far smaller than those obtained based on global biomass database^[7] (1.02 vs. 3.06 Pg). Secondly, the lack of systematic and uniform ground observations introduced great uncertainty in estimating biomass at the regional scale. Finally, most previous studies focused on the relationship between aboveground biomass (AGB) and precipitation^[11,13], and only very few studies address how the patterns of belowground biomass (BGB) are shaped in temperate grasslands^[14]. To reduce the uncertainty in biomass estimates

Received September 20, 2007; accepted October 12, 2007

doi: 10.1007/s11427-008-0029-5

[†]Corresponding author (email: mawh@szpku.edu.cn)

Supported by the National Natural Science Foundation of China (Grant Nos. 90211016, 40021101 and 30700090)

for temperate grasslands of China, we launched a four-year-campaign to conduct regional investigation for accurately estimating grassland biomass and evaluating its environmental controls.

The grasslands of China are important components of Eastern Eurasian steppes, extending 4500 km from northeast China to the Loess Plateau, and then to the Tibetan Plateau^[15], with natural grasslands accounting for 40% of the total land area of the nation^[16]. As one of the most widespread vegetation types in China, temperate grasslands in Inner Mongolia are composed of three different grassland types, i.e., meadow steppe, typical steppe and desert steppe, distributed in order from east to west as zonal vegetation types^[17]. It provides an ideal region for examining patterns and controls of above- and belowground biomass. In this study, based on field observations, we aimed to (1) estimate AGB and BGB for different grassland types in Inner Mongolia, (2) explore their spatial patterns, and (3) address the relationships between AGB and BGB and environmental factors.

1 Materials and methods

1.1 Site descriptions

Grasslands cover an area of over 45% of the total area of Inner Mongolia and extend from the northeast China, through the Hulunbeir Plateau, the Xilin Plateau, to the Ordos Plateau^[17]. This region is dominated by temperate continental climate, which is characterized by cold, dry winters and warm, rainy summers. From northeast to southwest, mean annual temperature (MAT) increases from -5 to 9°C , and annual precipitation (AP) decreases from 500 to 150 mm. Meadow steppe in the eastern part of the study area is composed of herbaceous perennial mesophytic and xerophytic species, such as *Stipa baicalensis*, *Filifolium sibiricum*, and *Leymus chinensis*. Typical steppe stretches across the middle part of the region, dominated by typical xerophytic species, such as *S. grandis*, *S. krylovii*, and *Leymus chinensis*. Desert steppe is distributed in the western region, where dry-tolerant, short grasses, e.g., *S. klemenzii* and *S. breviflora* are dominant. Soil types correspond to the grassland types: meadow steppe is mainly associated to chernozem soil, typical steppe to chestnut soil, and desert steppe to brown calcic soil^[17].

1.2 Field sampling

We investigated 113 sites during the growing season

(late July and August) of 2002–2005 (Figure 1). At each site, we selected a $10\times 10\text{ m}^2$ plot in the fenced or light grazing-disturbed grasslands to conduct the field survey. At each site, five quadrates (each with an area of $1\times 1\text{ m}^2$) were sampled for aboveground biomass (AGB), and three of them were selected for belowground biomass (BGB). The plant was clipped to the ground, oven-dried at 65°C and then weighed.

Roots were sampled with a 8-cm-diameter corer at 10-cm intervals to the depth of 50 cm. Belowground materials were washed through a 0.5 mm-sieve, and then refrigerated at 0°C . Live roots and dead ones were separated by color and consistency. Live roots were then oven dried for 24 h at 65°C and weighed. At 16 sampling sites soil monolith with an area of 0.25 m^2 ($50\times 50\text{ cm}^2$) was collected to the depth of 50 cm.

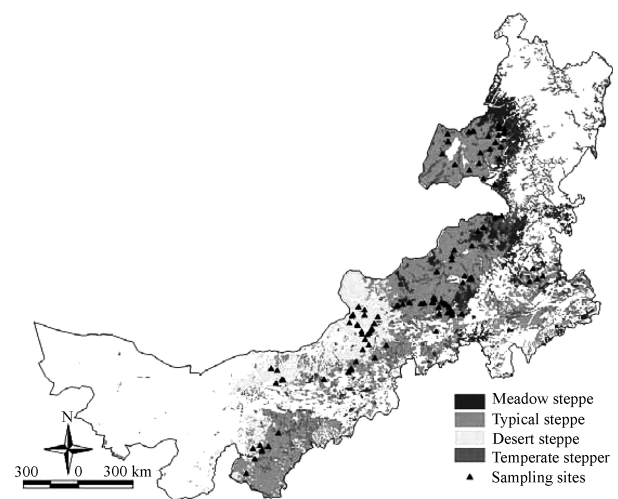


Figure 1 Study area and sampling sites in temperate grasslands, Inner Mongolia.

1.3 Data analyses

All plots were grouped into 15 community types according to the dominant species. AGB and BGB were averaged for each community type and assigned to the Vegetation Map of China with a scale of 1:1000000^[18] to obtain the spatial distribution of biomass.

Analysis of variance (ANOVA) and Kolmogorov-Smirnov method were used to test the differences of AGB and BGB among different grassland types (meadow steppe, typical steppe, and desert steppe). General linear model (GLM) was applied to examine the integrative effects of environmental factors (climate, grassland

types) and soil texture) on AGB and BGB. All analyses were performed by the software package R^[19].

To compare vertical distribution of roots among three grassland types, we calculated the percentage of root biomass in the upper 10 cm to the total of 0–50 cm. A high proportion implies a shallow distributed root system^[20].

Climatic variables used in this study include mean annual temperature (MAT) and annual precipitation (AP). The climate data were derived from grid-formatted climatic maps at a resolution of 0.1×0.1 degrees, which were compiled from the 1970–1999 climatic database of China. A digital map of soil texture of China was aggregated to grid cells at a resolution of 0.1×0.1 degrees^[21].

2 Results

2.1 Above- and belowground biomass in the grasslands of Inner Mongolia

Both AGB and BGB showed large spatial variations (Table 1). Averaged AGB and BGB were 135.3 and 775.2 g/m², respectively, ranging from 9.5 to 358.4 g/m² for AGB and 77.2 to 2727.7 g/m² for BGB. AGB and BGB exhibited significant difference among three grassland types ($P<0.05$). The largest AGB and BGB occurred in meadow steppe (196.7 and 1385.2 g/m², respectively), and the lowest appeared in desert steppe (56.5 and 300.5 g/m², respectively).

2.2 Spatial distribution of AGB and BGB

In the Inner Mongolia, AP increased, while MAT decreased from southwest to northeast parts. Along these gradients, AGB increased from <100 g/m² in the southwestern desert steppe region to >200 g/m² in northeastern meadow steppe (Figure 2(a) and (b)). Similarly, BGB also increased from <500 g/m² in the southwest to

>1000 g/m² in the northeast (Figure 2(c) and (d)).

Three grassland types showed similar rooting profiles (Figure 3), with an overall mean of 47% of roots occurring in the top 10 cm soil.

2.3 Relationships between biomass and environmental factors

The general linear model (GLM) analysis indicated that both AGB and BGB were most closely related to AP, which explained 43.2%–56.6% and 28.2%–44.7% of the variations in AGB and BGB, respectively (Table 2). AP exhibited positive effect on the distribution of AGB and BGB ($AGB = 5.9182e^{0.0094*AP}$ ($R^2=0.57$, $P<0.01$); $BGB = 58.368e^{0.0075*AP}$ ($R^2=0.45$, $P<0.01$)) (Figure 4(a) and (c)). On the contrary, MAT had negative effects on grassland biomass and explained 13.4% and 17.2% of the variations in AGB and BGB, respectively (Figure 4(b) and (d)). In contrast to the strong effect of climate on the distribution of AGB and BGB, grassland types and soil texture played a very weak roles influencing the distribution of AGB and BGB. The proportion of root biomass in the upper 10 cm soil was also positively related to AP, explaining 8.4% of the variation.

3 Discussion

3.1 Comparison with other temperate grasslands around world

Temperate grasslands are distributed widely at the mid latitudes of Asia, North and South America^[22]. Above-, and belowground biomass in Inner Mongolia were approximately less than half of the estimations for other temperate grasslands around world (Table 3). This could result from drier climate and intensive grazing activity in the Inner Mongolia^[15].

Based on inventory data or field measurements, different studies have reported the AGB in temperate grasslands of China^[8,9,12]. However, because of the dif-

Table 1 Aboveground (AGB) and belowground biomass (BGB) in grasslands of Inner Mongolia

Ecosystems	n	AGB (g/m ²)		BGB (g/m ²)	
		mean	range	mean	range
Desert steppe	40	56.6 ^a	9.5–175.1	301.0 ^a	77.2–749.0
Typical steppe	55	133.4 ^b	17.0–310.1	688.9 ^b	134.0–1615.7
Meadow steppe	18	196.7 ^c	68.3–358.4	1385.2 ^c	304.3–2727.7
Total	113	135.3	9.5–358.4	775.2	77.2–2727.7

Differences among grassland types were tested by one-way ANOVA with a Turkey's *post hoc* test of significance. Different letters denote significant difference at $P<0.05$.

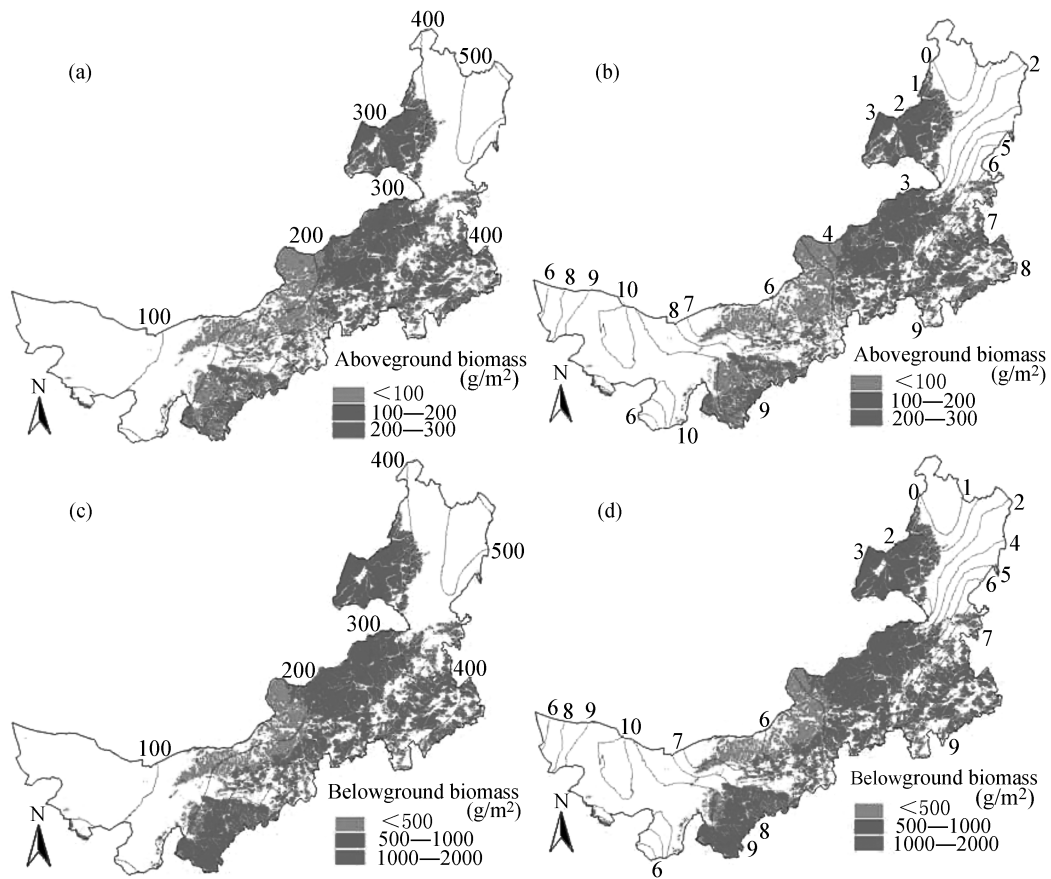


Figure 2 The spatial distribution of aboveground biomass ((a) and (b)) and belowground biomass ((c) and (d)) in the grasslands of Inner Mongolia. The contour line in the background indicates the distribution of annual precipitation ((a) and (c), unit: mm) and mean annual temperature ((b) and (d), unit: °C).

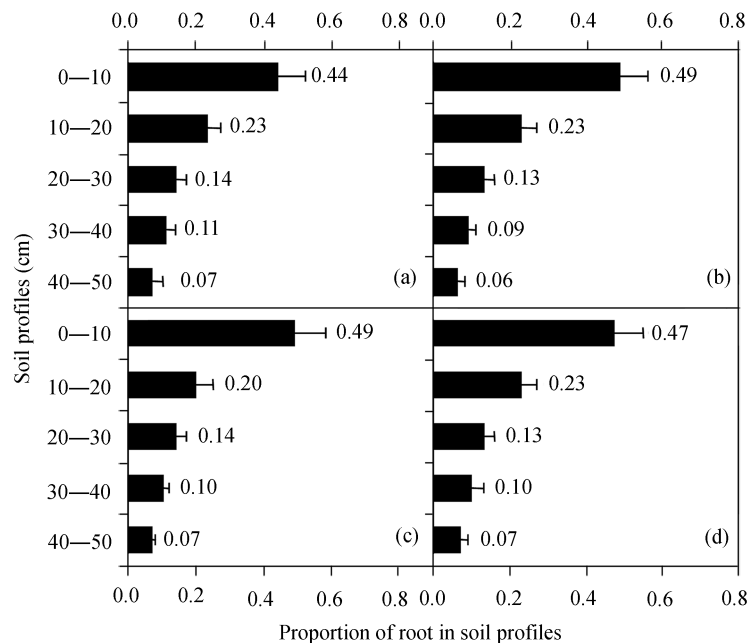


Figure 3 The vertical distribution of belowground biomass for the desert steppe (a), typical steppe (b), meadow steppe (c), and overall grasslands in Inner Mongolia (d).

Table 2 Summary of general linear model (GLM) of AGB, BGB, and the proportion of root biomass in the top 10 cm soil as functions of annual precipitation (AP), mean annual temperature (MAT), soil texture and grassland types. The climatic variables (MAT and AP) entered model with different sequences.

Factor	df	MS	SS (%)	Factor	df	MS	SS (%)
AGB				AGB			
MAT	1	9.9	13.4**	AP	1	42.0	56.6**
AP	1	32.1	43.2**	MAT	1	0.0	0.0
Grassland type	2	0.3	0.8	Grassland type	2	0.3	0.8
Soil texture	1	0.0	0.0	Soil texture	1	0.0	0.0
Residual	107	0.3	42.5	Residual	107	0.3	42.5
BGB				BGB			
MAT	1	9.5	17.2**	AP	1	24.8	44.7**
AP	1	15.6	28.2**	MAT	1	0.4	0.7
Grassland type	2	1.5	5.4**	Grassland type	2	1.5	5.4**
Soil texture	1	0.1	0.3	Soil texture	1	0.1	0.3
Residual	95	0.3	49.0	Residual	95	0.3	49.0
Root distribution ^{a)}				Root distribution ^{a)}			
MAT	1	0.009	2.5	AP	1	0.038	10.9*
AP	1	0.030	8.4*	MAT	1	0.000	0.1
Grassland type	2	0.002	1.0	Grassland type	2	0.002	1.0
Soil texture	1	0.010	2.9	Soil texture	1	0.010	2.9
Residual	54	0.006	85.2	Residual	54	0.006	85.2

** $P < 0.01$; * $P < 0.05$; ^{a)} represented as root proportion of the top 10 cm soil.

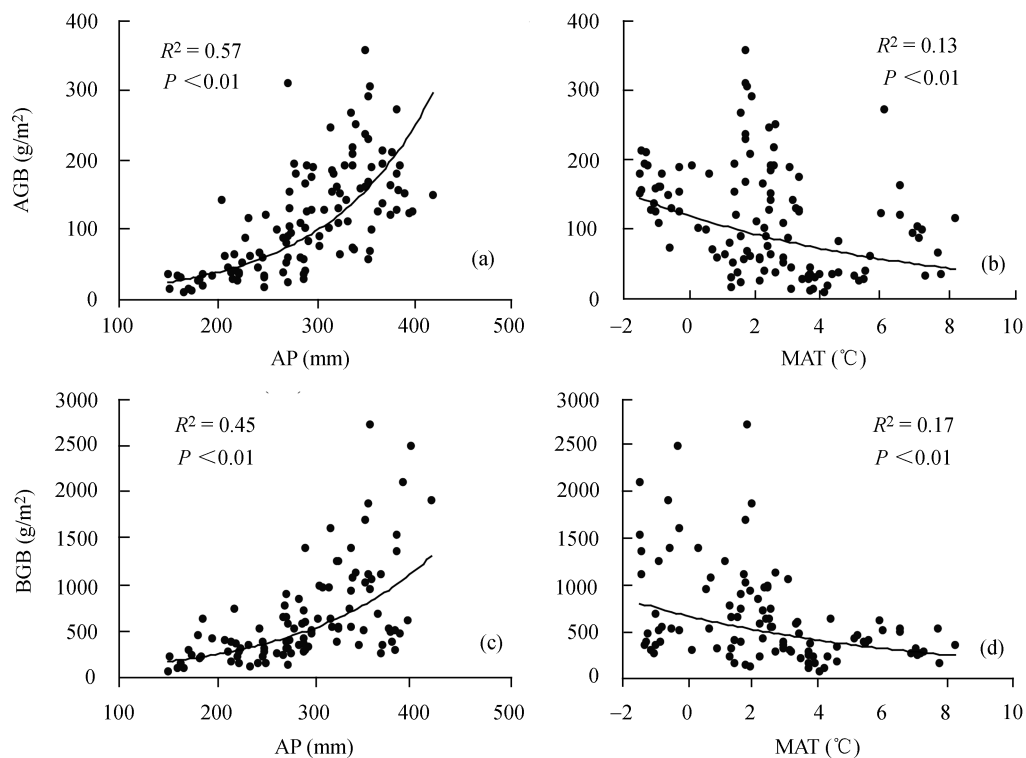


Figure 4 Relationships between AGB, BGB, annual precipitation (AP, mm) ((a) and (c)) and mean annual temperature (MAT, °C) ((b) and (d)) in temperate grasslands of Inner Mongolia.

Table 3 Comparisons of aboveground biomass (AGB), belowground biomass (BGB) and annual precipitation (AP) of Inner Mongolia with other temperate grasslands in the world.

Region	AGB (g/m ²)	BGB (g/m ²)	AP (mm)
Europe ^[23]	377.0	1903.8	629.0
North America ^[23]	207.8	1469.6	488.0
Global average ^[2]	378.4	1400.0	550.0
Inner Mongolia	135.3	775.2	310.2

ferent methods and data sources used in these analyses, the estimations by different authors were inconsistent with each other. For instance, in a recent study, we estimated that the average AGB in temperate grasslands of China was 113.0, 105.3 g/m² for meadow steppe, typical steppe, respectively, which are slightly higher than that reported by a recent study^[12]. One reason to cause this discrepancy was that we excluded grazing disturbed plots from the present study. In addition, previous estimates derived from inventory-based database or literature collections commonly involve more wide grassland regions in China, which would contribute to the differences in biomass estimating.

Compared with the well-developed knowledge of aboveground production in grasslands, relatively few estimates for BGB at the regional scale have been presented for temperate grassland ecosystems of China. Previous studies using *R:S* ratio^[8] or field measuring data at the local scale to estimate BGB may overestimate the BGB due to methodological issues. For example, by collecting data from temperate grasslands of northern China, Ni^[11] estimated a much higher BGB of grassland than the present study (meadow steppe: 2415.7 vs. 1385.2 g/m², typical steppe: 1777.7 vs. 688.9 g/m², and desert steppe: 1038.8 vs. 301.0 g/m²). This large inconsistency may be caused by the difficulties in the root production measurement in the field, especially in root sampling (such as separating live roots from dead ones).

This inconsistency indicates the necessity of accurate BGB data for grassland ecosystems for the study of regional or global carbon budget^[1]. Previously overestimated BGB would challenge current understanding of the role of grassland ecosystems played in the global carbon cycle. Direct field measurements using the systematic method for broad ecosystem types are therefore needed in future.

3.2 Vertical distribution of belowground biomass

Roots play a key role in linking aboveground and belowground ecological processes^[24]. Root distribution is ne-

cessary for understanding ecological processes in various ecosystems^[2]. The root distribution presented in this study showed that 47% of roots were distributed in the upper 10 cm soil, which agreed with globally averaged root proportion in temperate grasslands (with 44% of roots in the top 10 cm)^[2]. Within grassland biome, we found no significant difference in root distributions among three grassland types. Such similar root distribution was also detected within forest ecosystems^[3]. This result may be supported by previous finding of no significant differences in *R:S* ratios between different steppe types^[25]. However, when comparing the root distribution patterns across different ecosystem types (i.e., grassland, shrub and forest), Jackson et al.^[2] found there were significantly different root distributions among them, with the shallowest rooting profile occurring in grasslands, and the deepest rooting profile in shrubs.

3.3 Determining factors for biomass in temperate grasslands

It is widely accepted that increasing precipitation promotes the aboveground production of temperate grasslands in the world^[4,13,26-28] and in China as well^[11,29,30]. Our result from temperate grasslands in Inner Mongolia is consistent with the general patterns. However, a large fraction of variations in AGB could not be explained by the environmental factors involved in this analysis, indicating that other factors (i.e. nutrient use efficiency or human activity) possibly have strong effects on grassland production^[15,31,32].

Although it is widely acknowledged that belowground organs play important roles in ecosystems functioning^[33,34], few studies have explored the relationships between BGB and environmental factors. Sala et al.^[22] found that BGB in temperate grasslands of North and South America was well related to annual temperature. Consistent with their results, we found that precipitation, rather than temperature accounted for a large variation in BGB among sites. Drier climate in Inner Mongolia than that in North and South America may

explain such different correlations with climate factors. In the present study, BGB exhibited similar patterns of climatic variables with AGB, supporting the finding that there is no significant difference in $R:S$ ratios among different grassland types^[25].

Climate, soil conditions, and vegetation types were reported as important factors influencing root distribution^[5,35]. Plants are rooted deeper in arid regions than in humid environments^[35], and deeper in sandy soil than in loamy soil^[35]. In this study, GLM analysis revealed

that root vertical distribution was related to precipitation. However, we detected no significant impacts of soil texture and grassland types on vertical distribution of roots, possibly due to the small range of soil texture or little changes in relation to functional group composition among the three grassland types in Inner Mongolia.

We wish to thank Liu Zhongling, Zhu Zongyuan, Liang Cunzhu, Zhao Liqing, Wang Zhiheng, Ren Yanlin, Lin Xin for their help in field sampling. Tang Zhiyao provided helpful comments on the manuscript.

- 1 Scurlock J M O, Johnson K, Olson R J. Estimating net primary productivity from grassland biomass dynamics measurements. *Global Change Biol*, 2002, 8 (8): 736–753
- 2 Jackson R B, Canadell J, Ehleringer J R, et al. A global analysis of root distributions for terrestrial biomes. *Oecologia*, 1996, 108 (3): 389–411
- 3 Schenk H J, Jackson R B. The biogeography of roots. *Ecol Monogr*, 2002, 72 (3): 311–328
- 4 Jobbágy E G, Sala O E. Controls of grass and shrub aboveground production in the Patagonian steppe. *Ecol Appl*, 2000, 10 (2): 541–549
- 5 Garnett M H, Ineson P, Stevenson A C, et al. Terrestrial organic carbon storage in a British moorland. *Global Change Biol*, 2001, 7(4): 375–388
- 6 Ni J. Carbon storage in terrestrial ecosystems of China: Estimates at different resolutions and their responses to climate change. *Clim Change*, 2001, 49(3): 339–358
- 7 Ni J. Carbon storage in grasslands of China. *J Arid Environ*, 2002, 50(2): 205–218
- 8 Fang J Y, Liu G H, Xu S L. Carbon reservoir of terrestrial ecosystem in Chin. In: Wang G C, Wen Y P, eds. *Monitoring and Relevant Process of Greenhouse Gas Concentration and Emission* (in Chinese). Beijing: China Environmental Science Publishing House, 1996
- 9 Ni J. Forage yield-based carbon storage in grasslands of China. *Clim Change*, 2004, 67(2-3): 237–246
- 10 Piao S L, Fang J Y, He J S, et al. Spatial distribution of grassland biomass in China. *Acta Phytocool Sin* (in Chinese), 2004, 28(4): 491–498
- 11 Ni J. Estimating net primary productivity of grasslands from field biomass measurements in temperate northern China. *Plant Ecol*, 2004, 174(2): 217–234
- 12 Ma W H, Fang J Y. The relationship between species richness and productivity in four typical grasslands of northern China. *Biodivers Sci* (in Chinese), 2006, 14(1): 21–28
- 13 Bai Y F, Han X G, Wu J G, et al. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, 2004, 431(9): 181–184
- 14 Hu Z M, Fan J W, Zhong H P, et al. Progress on grassland underground biomass researches in China. *Chin J Ecol* (in Chinese), 2005, 24(9): 1095–1101
- 15 Chen Z Z, Wang S P. *Typical Steppe Ecosystems of China* (in Chinese). Beijing: Science Press, 2002
- 16 Department of Animal Husbandry and Veterinary Medicine, and General Station of Animal Husbandry and Veterinary Medicine of the Ministry of Agriculture of China. *Rangeland resources of China* (in Chinese). Beijing: China Agriculture Science and Technology Press, 1996
- 17 The Integrated Survey Team to Ning Xia and the Inner Mongolia Autonomous Regions, the Chinese Academy of Sciences. *Inner Mongolia Vegetation* (in Chinese). Beijing: China Science and Technology Press, 1985
- 18 Editorial board of vegetation map of China, Chinese Academy of Sciences. *Vegetation Atlas of China (1:1,000,000)* (in Chinese). Beijing: China Science and Technology Press, 2001
- 19 Development Core Team. *A language and environment for statistical computing*. Foundation for Statistical Computing, 2005, Vienna, Austria. <http://www.R-project.org>
- 20 Jobbágy E G, Jackson R B. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol Appl*, 2000, 10(2): 423–436
- 21 Deng S Q. Map of soil texture of China. In: Institute of Soil Science, Chinese Academy of Sciences, eds. *The Soil Atlas of China* (in Chinese). Beijing: Sinomaps Press, 1986. 23–24
- 22 Sala O E, Lauenroth W K, Burke I C. Carbon budgets of temperate grasslands and the effect of global change. In: Breymer A I, Hall O E, Melillo J M, et al., eds. *Global change: Effects on coniferous forests and grasslands*. New York: John Wiley & Sons Ltd, 1996
- 23 Coupland R T. *Grassland Ecosystems of the World: Analysis of Grasslands and their Uses*. New York: Cambridge University Press, 1979
- 24 Trumbore S E, Grandinski J B. The secret lives of roots. *Science*, 2003, 302(5649): 1344–1345
- 25 Ma W H, Fang J Y. $R:S$ ratio of temperate steppe and the environmental controls in Inner Mongolia. *Acta Sci Nat Uni Pek*, 2006, 42(6): 774–778
- 26 Sala O E, Parton W J, Joyce L A, et al. Primary production of the central grassland region of the United States. *Ecology*, 1988, 69(1): 40–45
- 27 Lauenroth W K, Sala O E. Long-term forage production of north American shortgrass steppe. *Ecol Appl*, 1992, 2(4): 397–403
- 28 Jobbágy E G, Sala O E, Paruelo J M. Patterns and controls of primary production in the Patagonian steppe: A remote sensing approach. *Ecology*, 2002, 83(2): 307–319
- 29 Fang J Y, Piao S L, Zhou L M, et al. Precipitation patterns alter growth

- of temperate vegetation. *Geophys Res Lett*, 2005, 32, L21411
- 30 Bai Y F, Wu J G, Pan Q M, et al. Positive linear relationship between productivity and diversity: Evidence from the Eurasian steppe. *J Appl Ecol*, 2007, 44(5): 1023–1034
- 31 Burke I C, Lauenroth W K, Parton W J. Regional and temporal variation in the primary production and nitrogen mineralization in grasslands. *Ecology*, 1997, 78(5): 1130–1340
- 32 Baer S G, Blair S L, Collins S L, et al. Soil resources regulate productivity and diversity in newly established tallgrass prairie. *Ecology*, 2003, 84(3): 724–735
- 33 Mokany K, Raison R J, Prokushkin A S. Critical analysis of root: shoot ratios in terrestrial biomes. *Global Change Biol*, 2006, 11(1): 84–96
- 34 Scurlock J M O, Hall D O. The global carbon sink: a grassland perspective. *Global Change Biol*, 1998, 4(2): 229–233
- 35 Schenk H J, Jackson R B. Mapping the global distribution of deep roots in relation to climate and soil characteristics. *Geoderma*, 2005, 126(1-2): 129–140