

Shrubland biomass and root-shoot allocation along a climate gradient in China

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Background – Shrublands are receiving increasing attention because of climate change. However, knowledge about biomass allocation of shrublands at the community level and how this is regulated by climate is of limited availability but critical for accurately estimating carbon stocks and predicting global carbon cycles.

Methods – We sampled 50 typical shrublands along a climate gradient in China and investigated the biomass allocation of shrubland at the community level and the effect of climate on biomass allocation. Shrub biomass was estimated using species-specific allometric relationships and the biomass of understory herbs was collected by excavating the whole plant. Regression analysis was used to examine the relationships between the biomass and the climate factors. RMA were conducted to establish the allometric relationships between the root and the shoot biomass at the community level.

Key results – Shoot, root, and total biomass of shrub communities across different sites were estimated with median values of 206.5, 145.8, and 344.5 g/m², respectively. Shoot, root, and total biomass of herb communities were estimated at 68.2, 58.9, and 117.2 g/m², respectively. The median value of the R/S ratio of shrub communities was 0.58 and that of herb communities was 0.84. The R/S ratio of the shrub community showed a negative relationship with mean annual temperature and mean annual precipitation and a positive relationship with total annual sunshine and the aridity index. The R/S ratio of the herb community however showed a weak relationship with climate factors. Shoot biomass of the shrub community was nearly proportional to root biomass with a scaling exponent of 1.17, whereas shoot biomass of the herb community was disproportional to root biomass with a scaling exponent of 2.1.

Conclusions – In shrublands, root biomass was more affected than shoot biomass by climate factors and this is related to water availability as a result of biomass allocation change of the shrub community. The understory herb community was less affected by climate due to the modification of the overstory–understory interaction to the climate-induced biomass allocation pattern. Shoot biomass of shrubs scales isometrically with root biomass at the community level, which supports the isometric theory of above-ground and below-ground biomass partitioning.

Keywords – Allometric relationship; biomass allocation; China; climate; shrublands.

INTRODUCTION

Terrestrial vegetations in middle and high latitudes act as major stocks for atmospheric CO₂ (Schimel et al. 2001; Goodale et al. 2002; Scurlock et al. 2002) and are receiving increasing attention because of climate change (Serreze et

al. 2000; IPCC 2007). A deep understanding of the biomass patterns and the determinants of these vegetations at the community level is critical for accurately estimating carbon stocks and predicting global carbon cycles (Jackson et al. 1996; Houghton 2005; Hui & Jackson 2006; Mokany et al. 2006).

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Most previous studies on biomass patterns in middle and high latitudes focused more on forests (Mokany et al. 2006; Cheng & Niklas 2006; Wang et al. 2008; Cahoon et al. 2012) and grasslands (Johnson & Matchett 2001; Hui & Jackson 2006; Yang et al. 2009, 2010) given the importance of forests and grasslands in the terrestrial carbon sink, whereas shrublands, also an important type of terrestrial ecosystem, received less attention (He et al. 1997; Mokany et al. 2006; Cahoon et al. 2012). Reports indicated that shrubby vegetation has increased in the middle and high latitudes compared to low latitudes possibly because of increased warming in that region (Sturm et al. 2001; Goodale & Davidson 2002; Cahoon et al. 2012; Throop et al. 2012), which suggests that shrublands may become important in accumulating carbon with climatic change. Recently, some studies investigated the shrub biomass at the local scale (Návar et al. 2004; Li & Xiao 2007; Castro & Freitas 2009; Li et al. 2010; Corona et al. 2012), but these studies are conducted at the individual or species level in a homogeneous climate. Limited knowledge is available on the biomass pattern of shrublands at the community level and its climatic determinants.

In biomass estimation, root biomass is a major source of uncertainty because it is difficult and costly to measure, and has therefore become a research focus in recent years (Brown 2002; Mokany et al. 2006; Yang et al. 2010). Practically, the root biomass can be predicted by the plant allometric relationships between root and shoot both at the individual and community level (Enquist & Niklas 2002; Niklas 2005; Cheng & Niklas 2006). The allometry theory suggests that root biomass scales isometrically with shoot biomass, and this relationship is insensitive to the phyletic affiliation or variation in environmental conditions (Enquist & Niklas 2002). The prediction has been validated at the individual level (Enquist & Niklas 2002; Niklas 2005). However, the allometry prediction has not been adequately tested at the community level using field measurements (Yang et al. 2010; Poorter et al. 2012; Poorter et al. 2015). Especially, whether the isometric relationship holds true across shrublands is unknown. Therefore, quantifying the biomass pattern of shrublands at the community level and its relationships with climatic factors is essential to improve our understanding of the allometry theory and precisely estimating the belowground biomass.

Shrubland is one of the major types of terrestrial vegetations in the middle and high latitudes of China (30°–53.5°N), covering over 20% of the terrestrial land area of China (Hu et al. 2006; Wang et al. 2014). The widely distributed shrublands have sustained drastic climatic changes over the past decades (Ding & Dai 1994; Ren et al. 2005; Piao et al. 2006) and have consequently experienced significant changes in biomass and productivity (Hu et al. 2006; Li et al. 2010). These significant changes suggest the urgent examination of biomass distribution and its relationship with climate. Therefore, we attempted to accomplish three objectives using field measurements of shrubland biomass along a climatic gradient in the Shaanxi Province of central and northern China: (1) documentation of the regional biomass of shrublands, (2) exploration of the effect of climate factors on the biomass allocation of

shrublands at community level, and (3) examination of the shoot-root allometric relationship of shrublands at the community level.

MATERIAL AND METHODS

Study area

The study was conducted in the Shaanxi Province of China (105°29'–111°15'E, 31°42'–39°35'N, fig. 1), which is the most important shrubland area between the middle and high latitudes of China. The large latitudinal span and the additional segmentation by the Qinling Mountains leads to a distinct climatic gradient in hydrothermal conditions from southern Shaanxi close to the subtropics with wet and warm climates to northern Shaanxi characterized by a dry and cold temperate climate. Along the hydrothermal gradient, Shaanxi is divided into five climate regions from south to north, including the north slope of the Bashan Mountains (NB), the south slope of the Qinling Mountains (SQ), the north slope of the Qinling Mountains (NQ), the Loess Plateau (LP), and the Mu Us desert (MD) (table 1), which offer a natural opportunity to examine the biomass pattern of shrublands along a climatic gradient.

Biomass survey

We sampled 50 typical shrublands in the five climate regions to collect biomass data (table 1, supplementary file 1). Each shrubland was sampled with five 5 m × 5 m random but minimally disturbed (e.g. by felling or grazing)

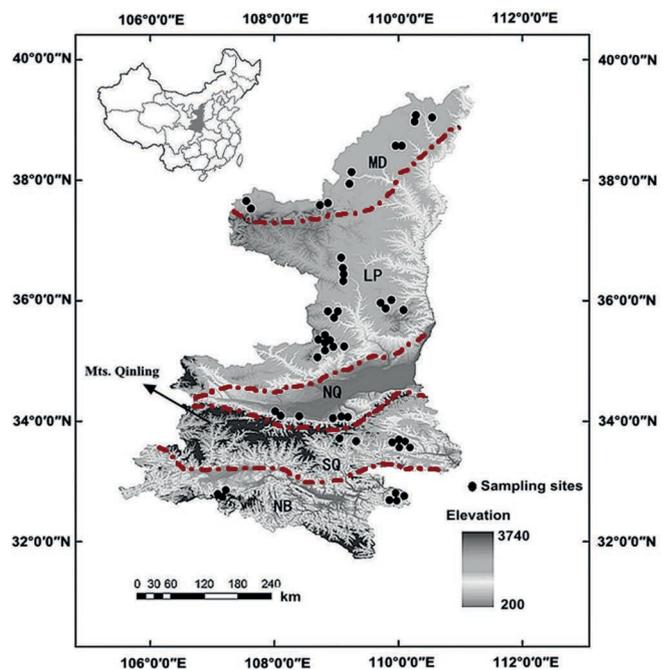


Figure 1 – Locations of the sampling sites in Shaanxi, China. NB, the north slope of the Bashan Mountains; SQ, the south slope of the Qinling Mountains; NQ, the north slope of the Qinling Mountains; LP, Loess Plateau; MD, Mu Us desert. Map created with QGIS version 2.14 (QGIS Development Team 2012).

Table 1 – Climate and sampling information of the five regions in Shaanxi (China). NB, north slope of the Bashan Mountains; SQ, south slope of the Qinling Mountains; NQ, north slope of the Qinling Mountains; LP, Loess Plateau; MD, Mu Us desert; MAT, mean annual temperature; MAP, mean annual precipitation; TAS, total annual sunshine.

Regions	Stand number	Latitudinal span	MAT (°C)	MAP (mm)	TAS (h)
NB	7	32.35–32.51	15	1017	1440
SQ	6	33.31–33.34	13	924	1900
NQ	7	33.50–34.30	11	750	2156
LP	19	35.03–36.26	8.8	549	2415
MD	11	37.37–38.50	6.5	388	2740

plots. The biomass per plot was collected separately for the shrub community and the understory herb community. Shrub biomass was estimated using species-specific allometric relationships. The “standard tree” method was used to establish the species-specific allometric relationships between the measured morphometric attributes and the biomass fractions. The basal diameter, the number of stems, the maximum height, and the crown area were measured as the morphometric attributes of the shrubby species. The crown area was assumed an elliptical shape and calculated as $CA = \pi \times CL/2 \times CW/2$, where CL is the crown length at its widest point and CW is the crown width perpendicular to the crown length (Sah et al. 2004). For each common shrub species in the stand, 5–7 adult individuals with different diameter of the same species outside of the plot were measured and harvested as “standard trees” to develop the species-specific allometric relationships. The rare shrub species in the stand, that is individuals < 5, were merged to develop a multispecies allometric relationship.

We harvested the whole plant of each “standard tree”, including the shoot and root biomass, to obtain an accurate estimation of the shrub biomass. First, we measured and harvested the shoot part from ground base and then divided them into the leaf and stem fractions. Subsequently, we excavated the root part of each “standard tree.” We measured the root biomass at different depths according to site-specific conditions considering the sampling methods of the root biomass, such as depth of sampling and minimum root size sampled, that influence the accuracy of root biomass estimation (Chew & Chew 1965; Mokany et al. 2006). Mokany et al. (2006) suggested that the maximum depth of root sampling when analyzing the root-shoot ratios should be ≥ 50 cm below ground level for shrublands and ≥ 75 cm for deserts and arid ecosystems. In our study, the depth of root sampling was ≥ 75 cm in arid regions (i.e. LP and MD), whereas in the mountainous regions (i.e. NB and SQ), we excavated to the bedrock to obtain the root biomass. The harvested root samples were cleaned from the soil residuals using a 1-mm sieve after soaking in deionized water. Finally, the biomass samples were oven-dried at 65°C to constant mass and weighed. A total of 288 individuals and 42 shrub species were collected (see supplementary file 2).

The biomass of understory herbs was collected in five 1 m \times 1 m random subplots in each plot by excavating the whole plant. After harvesting, the plants were divided into the shoot and root fractions. The excavated roots were cleaned from

the soil residuals. After that, the shoot and root fractions were oven-dried to calculate the biomass. R/S ratio was defined as the root biomass divided by the shoot biomass.

Climate data

In the present study, we selected mean annual temperature (MAT), mean annual precipitation (MAP), total annual sunshine (TAS), and the aridity index (AI) as indicators of climate factors. The data for MAT and MAP at a resolution of 1 km² were acquired from the Worldclim-Global Climate Data (<http://www.worldclim.org/>). The data for TAS were obtained from 23 climatic stations across the Shaanxi Province. The aridity index was calculated by the reciprocal of de Martonne aridity index ((MAT+10)/MAP) (de Martonne 1926). A higher AI value corresponds to higher climatic aridity and lower water availability to plants.

Statistical analysis

Regression analysis was used to examine the relationships between the biomass and the climate factors. Ordinary least squares (OLS) and reduced major axis (RMA) analyses were applied to the raw and the log₁₀-transformed biomass data, respectively. OLS analyses were performed to develop regressions with root biomass as the dependent variable, while RMA were conducted to establish the allometric relationships between the root and the shoot biomass at the community level (Niklas 2005; Cheng & Niklas 2006). The slope (scaling exponent) and y-intercept (allometric constant) of the log–log linear functions were determined by the standardized major axis test which was performed using the Smatr package of R program (Warton et al. 2012).

RESULTS

Biomass and R/S ratios at the community level

The total, shoot, and root biomass of shrub communities ranged from 52.3–1413.8, 26.1–855.7, and 11.5–600.5 g/m², with the median values of 344.5, 206.5, and 145.8 g/m², respectively. R/S ratio of shrub communities varied from 0.17 to 1.78 with a median value of 0.58. Among the different climate regions, the SQ region showed the highest total, shoot, and root biomass (525.3, 321.1, and 199.6 g/m², respectively), while the NQ region showed the lowest total, shoot, and root biomass (211.1, 140.6, and 73.8 g/m²,

Table 2 – Median values and ranges of total, shoot, and root biomass (g/m²) and R/S ratio of each climatic region. Abbreviations for regions explained in the caption of table 1.

	Total biomass		Shoot biomass		Root biomass		R/S ratio	
	Median	Range	Median	Range	Median	Range	Median	Range
Shrub community								
NB	427.5	164.8–812.6	270.9	107.6–581.8	147.6	38.6–256.0	0.45	0.31–0.81
SQ	525.3	52.4–1297.1	321.1	40.9–855.7	199.6	11.5–441.5	0.58	0.17–1.02
NQ	211.1	81.4–577.1	140.6	57.9–376.2	73.8	23.5–201.8	0.53	0.36–1.78
LP	387.8	115.3–1413.8	208.7	66.1–813.3	178.2	49.3–600.5	0.81	0.66–1.11
MD	364.8	154.6–790.5	223.9	26.1–531.1	169.3	23.5–365.1	0.69	0.42–2.36
Overall	344.5	52.4–1413.8	206.5	26.1–855.7	145.8	11.5–600.5	0.58	0.17–2.36
Herb community								
NB	105.9	36.7–269.8	47.2	21.2–148.1	41.8	15.5–121.7	0.82	0.42–1.91
SQ	129.5	48.6–560.8	69.8	23.3–104.9	59.5	25.2–529.9	1.08	0.47–17.20
NQ	229.9	82.6–547.0	99.8	49.5–247.5	117.6	23.3–475.8	0.73	0.35–12.51
LP	243.4	62.4–755.9	70.4	42.3–141.9	192.6	121.4–685.3	2.78	1.22–9.73
MD	88.8	13.2–516.2	57.1	8.1–174.8	31.1	5.1–363.5	0.58	0.17–2.45
Overall	117.2	13.2–755.9	68.2	8.1–247.5	58.9	5.1–475.8	0.84	0.17–17.20

respectively) (table 2). R/S ratio was highest in the LP region (0.81) and lowest in the NB (0.45) (table 2).

For the herb communities in the shrublands, the total, shoot, and root biomass ranged from 13.2–755.9 g/m², 8.1–247.5 g/m², and 5.1–475.8 g/m², respectively. The median values were 117.2 g/m², 68.2 g/m², and 58.9 g/m² for the total, shoot, and root biomass. R/S ratio of herb communities ranged from 0.17 to 17.20 with a median value of 0.84. Among the different regions, NQ showed the highest shoot biomass (99.8 g/m²) and LP the highest root biomass (192.6 g/m²), while NB showed the lowest shoot biomass (47.2 g/m²) and MD the lowest root biomass (31.1 g/m²) (table 2). In addition, the R/S ratio was highest in the LP region and lowest in the MD region (table 2).

Relationships of biomass and R/S ratio with climate factors

Shoot biomass of the shrub communities did not exhibit any significant trend with climate factors (fig. 2A–D). Root biomass was negatively correlated with MAT and MAP, while positively correlated with TAS and AI (fig. 2E–H). The R/S ratio showed similar but stronger relationships with climate factors compared to root biomass (fig. 2I–L). Particularly, it showed a strong negative correlation with MAP and a positive correlation with AI.

For the herb communities, both the shoot and root biomass did not show any significant trend along the climate gradient (fig. 3A–H). However, the R/S ratio showed weak

relationships with MAP and TAS. It decreased with the increase of MAP and increased with increasing TAS.

Allometric relationships between shoot and root biomass

The relationship between shoot biomass (SB) and root biomass (RB) across different shrub communities was characterized by a power function of $RB = 2.89 \times SB^{0.81}$ ($R^2 = 0.48, P < 0.0001$) (fig. 4A). The scaling exponent (slope) of the allometric relationship was 1.17 with 95% confidence interval (CI) of 0.84–1.42 (fig. 4B). The scaling exponent did not differ significantly among different climate regions (table 3).

The shoot-root relationship for herbaceous communities was characterized by a power function of $RB = 1.67 \times SB^{0.98}$ ($R^2 = 0.23, P < 0.001$) (fig. 4A). The scaling exponent of the allometric relationship across different climate regions was 2.1, with 95% confidence interval (CI) of 1.54–2.51 (fig. 4B). However, the allometric relationship varied significantly among different climate regions, and the function did not fit well except for NB and MD (table 3).

DISCUSSION

Biomass and R/S of shrublands

In the present study, shoot, root, and total biomass of shrub communities across different regions were 26.1–855.7, 11.5–600.5, and 52.4–1413.8 g/m², respectively. Shoot biomass was lower than the estimate of 400–1100 g/m² made by Corona et al. (2012) for the shoot biomass of shrub

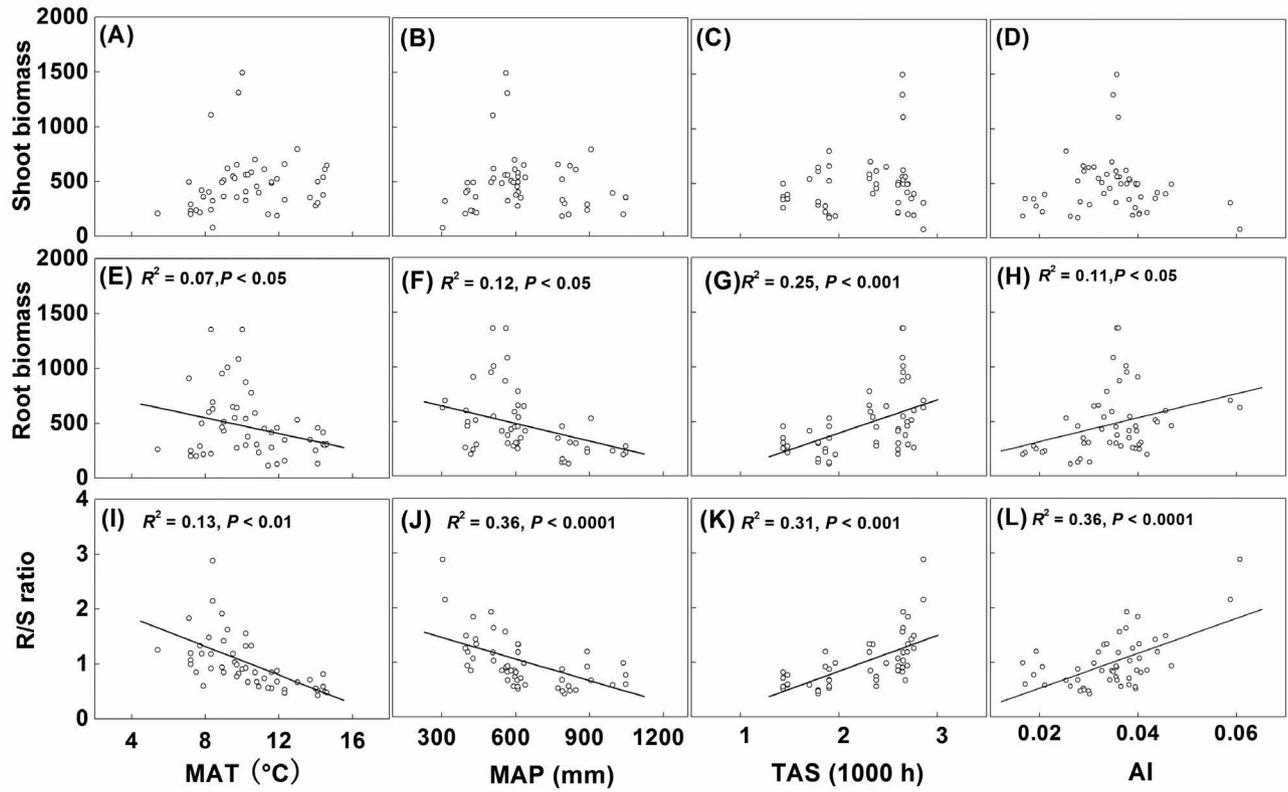


Figure 2 – Changes in the biomass and the R/S ratio of the shrub communities with mean annual temperature (MAT), mean annual precipitation (MAP), total annual sunshine (TAS), and aridity index (AI).

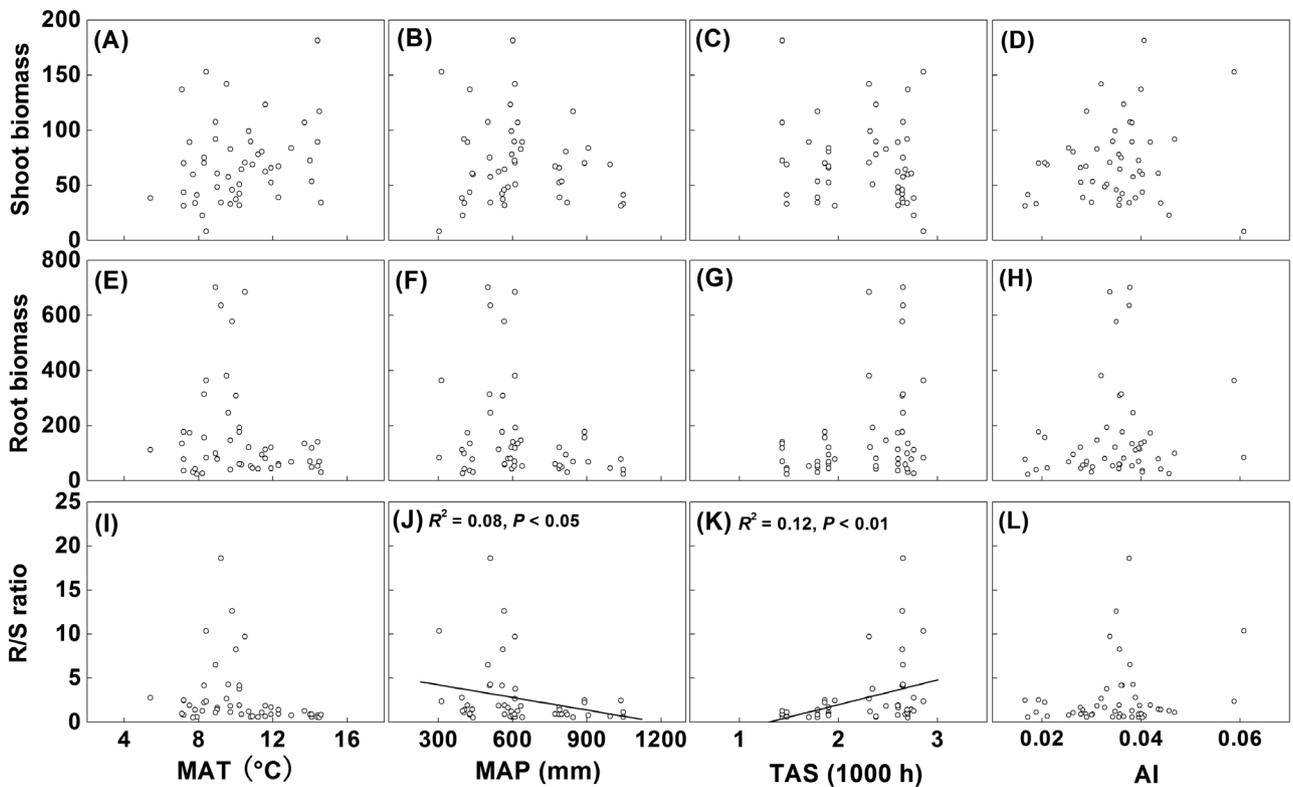


Figure 3 – Changes in the biomass and the R/S ratio of the herb communities with mean annual temperature (MAT), mean annual precipitation (MAP), total annual sunshine (TAS), and aridity index (AI).

Table 3 – RMA regression slopes (α_{RMA}) and y-intercepts ($\log \beta_{RMA}$) of the shoot-root biomass relationships in the shrublands across the different regions. Abbreviations for regions explained in the caption of table 1.

	α_{RMA}	95% CI of α_{RMA}	$\log \beta_{RMA}$	R^2
Shrub community				
NB	1.11	-1.16–1.54	-0.56	0.65
SQ	0.98	0.57–1.31	-0.12	0.86
NQ	0.91	0.64–1.08	0.15	0.92
LP	1.21	0.70–1.38	-0.57	0.68
MD	0.89	0.15–1.08	0.68	0.67
Herb community				
NB	0.71	-4.73–1.78	0.41	0.41
SQ	0.96	-1.16–4.47	0.14	0.02
NQ	1.01	0.43–5.72	0.01	< 0.001
LP	2.22	1.55–7.32	-1.80	< 0.001
MD	1.7	1.04–2.05	-1.38	0.90

communities in the Mediterranean. The total biomass was also much smaller than the estimate for shrub community in the subtropical zone of China made by He et al. (1997) (1360–2250 g/m² for total biomass). These differences support the global distribution of terrestrial vegetation productivity that plant communities at low latitudes have higher biomass production than these at higher latitudes (Nemani et al. 2003; Houghton 2005). In addition, the median value of the R/S ratio in the shrublands of our study was 0.58, which was lower than 1.84 in global shrublands reported by Mokany et al. (2006). The R/S ratio is reported to be related to a wide range of factors, including water availability and disturbance (McConnaughay & Coleman 1999; Mokany et al. 2006; Yang et al. 2010). However, this difference does not seem to be

caused by the difference in climate, since the R/S ratio in the present study was lower than the lowest value of that in the same climate conditions reported by Mokany et al. (2006). This difference may be attributed to disturbance. Most of the data collected for shrublands by Mokany et al. (2006) were from areas that had received disturbance, such as fire and heavy grazing. Disturbance usually reduces shoot biomass (Johnson & Matchett 2001) and increases root biomass (Piñeiro et al. 2009), and results in a higher R/S ratio. In this study, the sampling sites were mostly selected in areas where little human disturbance occurred and thus disturbance did not have a significant influence on the estimate of the R/S here. Therefore, the average R/S in our study was much

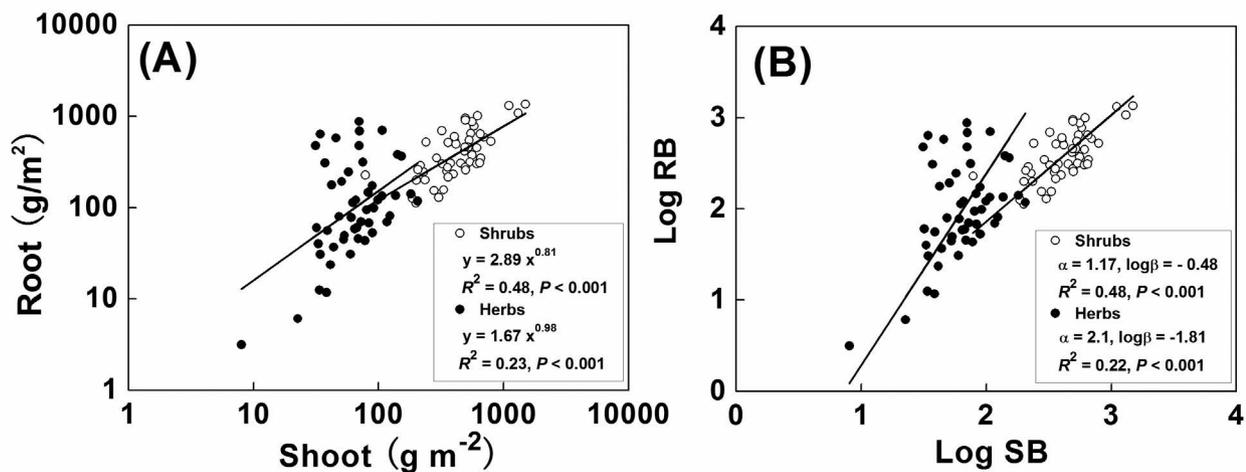


Figure 4 – Allometric relationship between shoot biomass (SB) and root biomass (RB). A. Ordinary least squares (OLS) regression analysis. B. Reduced major axis (RMA) regression analysis.

lower than that in global shrublands reported by Mokany et al. (2006).

The shoot and root biomass of herb communities in our study ranged from 8.1–247.5 and 5.1–475.8 g/m² with the median values of 68.2 and 58.9 g/m², respectively. Although there is no direct study on the biomass of understory herb communities in shrublands, the biomass of herb communities in the grassland has been widely documented around the world. Yang et al. (2010) estimated that the median values of shoot and root biomass of China's grasslands was 89.1 and 483.5 g/m², respectively. At the global scale, Mokany et al. (2006) estimated the shoot and root biomass of grasslands at 430.2 g/m² and 1 810.9 g/m², respectively. Obviously, both the shoot and root biomass in our study were much smaller than the biomass for China's grasslands and global grasslands. It suggests that herb biomass productivity is largely limited in the shrublands compared to grasslands, which supports other reports that woody plant growth is one of the primary factors influencing understory productivity (Lecerf et al. 2016). In addition, the R/S ratio of herb communities in the shrublands (0.84) was also much smaller than that in China's grasslands (5.7, Yang et al. 2010) and global grasslands (4.5, Mokany et al. 2006). This large difference may be partly attributed to the lower temperature and water availability in grasslands compared to shrublands. Compared to China's grasslands, the shrublands in our study are found in lower latitudes with a relatively warmer and moister climate. In these circumstances, plants allocate more biomass to shoots and less biomass to roots (McConnaughay & Coleman 1999). In addition, the lower R/S ratio of the herb community in shrublands than in the grasslands might be partly due to their lower disturbances. Grasslands are typically disturbed ecosystems (such as grazing and frequent rodent activities), while shrublands experience relatively lower levels of these disturbances. Therefore, herbaceous species in shrublands have lower R/S ratios than those in grasslands according to previous reports (Johnson & Matchett 2001; Piñeiro et al. 2009).

Effects of climate on biomass allocation

Plant biomass accumulation and allocation have been reported to change significantly with abiotic factors, such as soil moisture, soil texture, and fertility, in some local-scale studies (Cairns et al. 1997; Mokany et al. 2006; Yang et al. 2009). However, the effect of climate on biomass accumulation and allocation is unclear. In particular, the knowledge on shrublands biomass is of limited availability (Mokany et al. 2006; Shoshany 2012).

Mokany et al. (2006) showed that the R/S ratio is negatively related to precipitation for forests and woodlands around the world, suggesting that woody plants allocate a high proportion of biomass to roots when water availability decreases. The negative relationship between the R/S ratio and precipitation has recently also been found in the forests of northeast China (Wang et al. 2008, 2014) and in the grasslands of northern China (Yang et al. 2010). For the shrub community, our results support the above findings. In our study, the R/S ratio of shrub communities was negatively related to precipitation and positively related to aridity

index (fig. 2). This confirms that water availability is closely related to productivity, a lower proportion of biomass is allocated to roots at wet sites. In addition, the R/S ratio of shrub communities in our study showed weak relationships with temperature and sunshine duration. Temperature and sunshine duration are generally supposed to influence biomass allocation through their effect on the availability of water to plants. High temperature and long sunshine duration can increase soil evapotranspiration, reduce water availability to plants, and cause an increased R/S ratio (Liu et al. 2002; Mokany et al. 2006; Wang et al. 2008). However, our data showed a negative trend in the R/S along the temperature gradient, possibly due to the consistence between temperature and precipitation gradients in our study area. In our study area, the wet region has a relatively higher temperature, while the dry region is relatively colder (table 1). Therefore, temperature may play a minor role in regulating the shoot-root biomass allocation considering the positive correlation between temperature and precipitation in our study area. In addition, we found that the variation in climate affected the root biomass much more than the shoot biomass as a result of allocation change (fig. 2), which is in contrast to the result of Wang et al. (2008) in northeastern China. This difference may be associated with the climatic differentiation and the resulting variation in nutrient supply. Our study area is relatively more arid during the growing season than northeastern China, and the variation of the underground water availability for plants from south to north is more apparent than the other climatic factors of plant growth (Chen 1983; Wang et al. 2008). Thus, plants allocate relatively more biomass to roots while limiting the increase of the shoot biomass if the limiting factor for growth is below the ground (Lambers et al. 2006; Poorter et al. 2012). Therefore, the root biomass is sensitive to the climatic factors related to water and nutrient availability in dry and low fertile conditions.

Compared to shrub communities, herb biomass seems less limited by climatic factors. Shoot and root biomass of herb communities did not show any significant trend along the climate gradients, whereas the R/S ratio showed a weak correlation with precipitation and sunshine duration (fig. 3). It suggests that climate limits the biomass allocation both for woody and understory herb plants. However, the variation of the biomass allocation for herb communities is probably not only due to water availability because the R/S ratio did not show a significant change along the aridity gradient. The different responses to climate gradient between shrubs and understory herbs biomass suggest that other factors, such as overstory-understory interaction, may also induce variations in the R/S of herb communities across shrublands ecosystems (Moreno et al. 2013), which may modify the climate-induced pattern of biomass. In the future, more studies are needed to reveal the effects of shrubs on understory herb biomass production in consideration of its potential application to the precisely estimating of shrublands biomass.

Shoot-root allometric relationship

The shoot-root allometric relationship is used to estimate root biomass from shoot biomass (Cairns et al. 1997; Cheng & Niklas 2006; Poorter et al. 2012). In our study, the power

function between shoot and root biomass fitted well for shrub communities ($R^2 = 0.48$, $P < 0.001$), but provided a weak fit for herbaceous communities ($R^2 = 0.23$, $P < 0.01$), suggesting that root biomass could be reliably estimated by shoot biomass using the allometric relationship for shrub communities but not for understory herbaceous communities in the shrublands. In addition, an allometric relationship is also observed in tree communities of forests (Fang et al. 2005; Cheng & Niklas 2006; Wang et al. 2008) and in herb communities in grasslands (Yang et al. 2009, 2010), suggesting the generality of the shoot-root relationship in dominant communities across different biomes.

The scaling exponent (α) of the allometric relationship for shrubs was 1.17, and all the scaling exponents of the different regions showed no difference, thus supporting the isometric prediction across different community types (Enquist & Niklas 2002; Niklas 2005). This is in line with the report of Wang et al. (2014) that the shoot biomass scales isometrically with the root biomass with a similar isometric scaling of 1.05. Moreover, the shoot biomass in shrublands scaled up with the root biomass in a manner similar to that in the forests (Cheng & Niklas 2006) and grasslands of China (Yang et al. 2010), suggesting that the isometric relationship is applicable to different vegetation types at the community level. In contrast to shrub communities, the scaling exponent of understory herbs in shrublands was 2.1, and most of the scaling exponents among the regions with the different climates were significantly different from 1.0, suggesting an allometric relationship between the shoot and the root. However, the scaling exponent of the understory herbs varied strikingly among the different regions, revealing a lack of consistent allometric relationships for understory plants.

CONCLUSION

This paper examined the effect of climate factors on the biomass allocation of shrublands at community level and the shoot-root allometric relationship. The results have revealed that the R/S ratio of the shrub community showed negative relationships with MAT and MAP and positive relationships with TAS and AI. Especially, root biomass was more affected than shoot biomass by climate factors related to water availability as a result of a biomass allocation change of the shrub community. Compared to the shrub community, the understory herb community was less affected by climate due to the modification of the overstory-understory interaction to the climate-induced biomass allocation pattern. Shoot biomass of shrubs scales isometrically with root biomass at the community level across various shrubland types, support the isometric theory of above-ground and below-ground biomass partitioning.

SUPPLEMENTARY FILES

Supplementary file 1 – Information about the sampled stands across the five climate regions.

<https://doi.org/10.5091/plecevo.2021.1570.2351>

Supplementary file 2 – Species-specific allometric equations between the measured morphometric attributes and biomass fractions.

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