



Abiotic and biotic factors modulate plant biomass and root/shoot (R/S) ratios in grassland on the Loess Plateau, China



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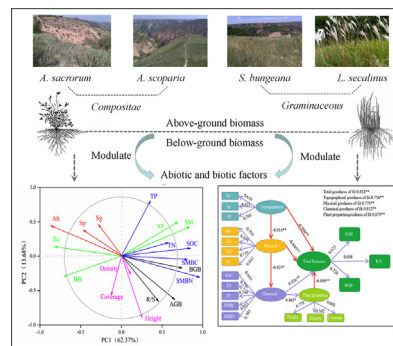
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HIGHLIGHTS

- AGB, BGB, R/S varied greatly and widely across natural grassland.
- There was a strong positively linear relationship between AGB and BGB.
- R/S was indirectly driven by plant properties, and determined by soil properties.
- The data provides an indication for quantifying C stocks on the Loess Plateau.

GRAPHICAL ABSTRACT



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ABSTRACT

Plant biomass and the root/shoot ratio (R/S) are key parameters for estimating terrestrial ecosystem carbon (C) stocks. However, how environmental driving factors (abiotic and biotic factors) modulate plant biomass and R/S has not been well investigated on the Loess Plateau. Here, we tested the impacts of abiotic and biotic driving factors on plant biomass and R/S and whether they are in accordance with optimal partitioning theory in natural grassland in this region. The results showed that above-ground biomass (AGB) and below-ground biomass (BGB) were $63.96 \text{ g} \cdot \text{m}^{-2}$ and $311.18 \text{ g} \cdot \text{m}^{-2}$, respectively, and that R/S ranged from 0.13 to 0.46, with high spatial heterogeneity. There was a strong positive linear relationship between AGB and BGB ($p < 0.05$) in accordance with optimal partitioning theory. A principal component analysis (PCA) indicated that the topographic properties (Slope position, Slope gradient and Altitude) were negatively correlated with the soil physical properties (Ec, Electric conductivity; BD, Bulk density; ST, Soil temperature; and SM, Soil moisture) and positively correlated with the soil chemical properties (SOC, Soil organic carbon; TN, Total nitrogen; SMBC, Soil microbial biomass carbon and SMBN, Soil microbial biomass nitrogen), while soil total phosphorus (TP) was not correlated with the soil physical properties ($p > 0.05$). Structural equation modeling (SEM) suggested that R/S is indirectly driven by plant properties (Height, Density, Coverage), which are determined by soil and topographic properties. However, only 5% of R/S was explained by the soil physical properties and topographic properties, suggesting that these factors had no significant effect on R/S. The data do, however, provide information for quantifying C stocks in natural grassland on the Loess Plateau. Further, ecologists should focus on mechanistic and fresh approaches to understanding the abiotic and biotic factors influencing plant biomass and R/S.

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1. Introduction

Plant species have evolved specialized strategies to regulate their above-ground biomass (AGB) and below-ground biomass (BGB) and consequently affect carbon (C) inputs and cycling (Adler et al., 2011; Doetterl et al., 2016; Said-Pullicino et al., 2016; Sierra et al., 2017). The root:shoot ratio (R/S) has been used to calibrate and estimate C stocks, and it has been incorporated into terrestrial ecosystem C modeling (Poeplau, 2016; Baskaran et al., 2017; Waring and Powers, 2017). In a review of R/S estimates in terrestrial biomes worldwide, Mokany and Shine (2003) found that 62% of R/S observations were unreliable, resulting in dramatic uncertainty in the estimation of C stocks around the world. Several studies in China's grasslands have estimated the community-level R/S and have indicated a higher R/S than the global average (Yang et al., 2004; Yang et al., 2010; Bai et al., 2012; Peng et al., 2013). In addition, an isometric relationship between AGB and BGB was suggested, and R/S for China's grasslands did not show significant trends with either the mean annual temperature (MAT) or mean annual precipitation (MAP) (Yang et al., 2004; Jia et al., 2016; Liu et al., 2017; Yang et al., 2017). Due to the sampling difficulties, large uncertainties remain in the estimation of R/S, and the general patterns in plant biomass are still controversial (IBáñez et al., 2016; Pellegrini et al., 2017; Thomas et al., 2017; Fotis et al., 2018). Although previous studies have demonstrated that R/S is influenced by specific environmental conditions (biotic and abiotic factors), less is known about the interactive effects of these environmental driving factors on R/S.

Optimal partitioning theory (OPT), which is based on the assumption that there are trade-offs in biomass allocation between AGB and BGB, suggests that plants allocate biomass to acquire the most limiting resource (Kobe et al., 2010; Hertel et al., 2013; Tredennick et al., 2015; Ledo et al., 2018). Until now, the results of many works on plant biomass allocation patterns have all been consistent with optimal partitioning theory in terms of biomass, while some findings have indicated that variation in R/S may be driven by plant size (Enquist and Niklas, 2002; Shipley and Meziane, 2002; McCarthy and Enquist, 2007; Ma et al., 2017). For instance, previous studies have demonstrated that various factors influence R/S, including stand development, species characteristics (e.g., life form and leaf traits), soil properties, and topographical factors (Poorter et al., 2012; Reich et al., 2014; Yang et al., 2017; Sun et al., 2018). These debates suggest an urgent need to examine the contributions of environmental variables to R/S (Sande et al., 2017; Sanaei et al., 2018; van der Sande et al., 2018). Owing to the varying effects of these environmental factors on R/S, many studies have sought to quantify plant biomass by focusing on the effect of a single driving factor (Chave et al., 2014; Hiiesalu et al., 2014; Prober et al., 2015; Shen et al., 2015). However, little attention has been paid to the interactions among multiple driving factors on R/S. It is therefore crucial to estimate the abiotic and biotic factors affecting plant biomass and R/S.

Natural grassland, one of the most widespread natural ecosystems on the Loess Plateau, plays a key role in global C cycling under complex environmental conditions (Deng et al., 2014; Feng et al., 2016; Fu et al., 2017). In this region, with a remarkable diversity of soil properties, plant traits, topographic properties, and biogeochemical cycling (An et al., 2013), multiple combinations of grassland characteristics, as well as variable environmental factors, offer a unique opportunity to examine patterns of plant biomass and R/S (Wang et al., 2017). Thus, obtaining a better understanding of the influence that these factors on plant biomass and R/S is fundamentally important for developing ecosystem C management practices in this region.

Here, we investigated plant biomass (AGB and BGB) and R/S in natural grassland (*Artemisia sacrorum*, *Artemisia scoparia*, *Stipa bungeana*, *Leymus secalinus*) on the Loess Plateau. First, we hypothesized that plant species in natural grassland do not experience limitations as a result of the abundant resources. Second, we hypothesized that R/S is well adapted to the environmental conditions. Third, we hypothesized that R/S is strongly influenced by environmental driving factors. To test

these hypotheses, we investigated the AGB, BGB, R/S, abiotic factors (soil and topographic properties) and biotic factors (plant traits) across four natural grasslands on the Loess Plateau. We aimed to (1) document the general patterns in R/S across these four grasslands, (2) examine the effects of abiotic factors and biotic factors on R/S, and (3) illustrate the relative contribution of abiotic and biotic factors to the variation in R/S.

2. Materials and methods

2.1. Sampling areas

We conducted this study in the Zhifanggou watershed in Ansai County (36°46'28''–36°46'42''N, 109°13'03''–109°16'46''E) (Yanhe catchment), located in the middle of the Yellow River on the Loess Plateau. The study site occupies a total area of approximately 8.72 km², has a semiarid climate and a deeply incised hilly gully Loess landscape, and experiences heavy seasonal rainfall and periodic flooding. Hills cover 90% of the region, and with the steep slopes (40%) associated with cliffs, only 7% of this area can be considered useful for agriculture. The average annual rainfall between 1970 and 2000 was approximately 497 mm, and there are distinct rainy and dry seasons. The rainy season occurs from July to October, with August rainfalls amounting for >20% of the annual total. The average annual temperature is 9.1 °C along the elevation gradient. Most of the area lies at an altitude of between 900 m and 1500 m and has loessal soil, according to the Chinese Soil Taxonomy.

The study area is a natural grassland ecosystem. The loess is perfectly arable due to its fine grains, loose texture and high content of mineral nutrients. In fact, this area is the cradle of the ancient Chinese civilization, with a long agricultural history (over 6000 years) in its basins and river valleys. The only major extrinsic influencing factor from humans is the Grain for Green Project, which was implemented in 1978 and has resulted in high canopy cover and biomass. As a result, the vegetation types have substantially varied over time and space since the recent implementation of the Grain for Green Project (Deng et al., 2014).

2.2. Sampling design

A field survey was undertaken in 2016 between July and August, when biomass had reached its peak. We focused on four dominant plant species, i.e., *A. sacrorum*, *A. scoparia*, *S. bungeana*, *L. secalinus*, because each typical species constitutes over half of the biomass or net primary productivity in the natural grassland on the Loess Plateau. Moreover, plant species play an important role in ecosystem functioning. The overstory vegetation of the plant community was dominated by *A. sacrorum*, *A. scoparia*, *S. bungeana*, *L.* and *secalinus*, which had the greatest relative biomass, with coverage >80%.

For all sample collection and vegetation (biomass) investigation, one 50 × 50 m plot was randomly established, within which five 1 × 1 m quadrats along a diagonal line were surveyed (Fig. 1). The number of plant species and coverage in each quadrat were recorded. All quadrats were located at a similar distance from the quadrat edge regardless of the size and edge of the grassland, and microclimatic variables, including soil moisture (SM) and soil temperature (ST) (0–20 cm), were measured three times under the roots of these plants. In each quadrat, the plant species were recorded, and AGB was harvested. The whole plant was removed from the soil, and BGB was harvested, respectively. The roots were found in these soil samples and isolated using a 2-mm sieve, and the remaining fine roots were removed by spreading the samples in shallow trays, and each sample was air dried and stored at room temperature until its physical and chemical properties could be determined. Each tray was overfilled with water, and the outflow was allowed to pass through a 0.5-mm mesh sieve. No attempts were made to distinguish between living and dead roots. All of the litter in each quadrat was also collected, placed into envelopes and labeled. R/S was calculated as the ratio of AGB to BGB, and the species were

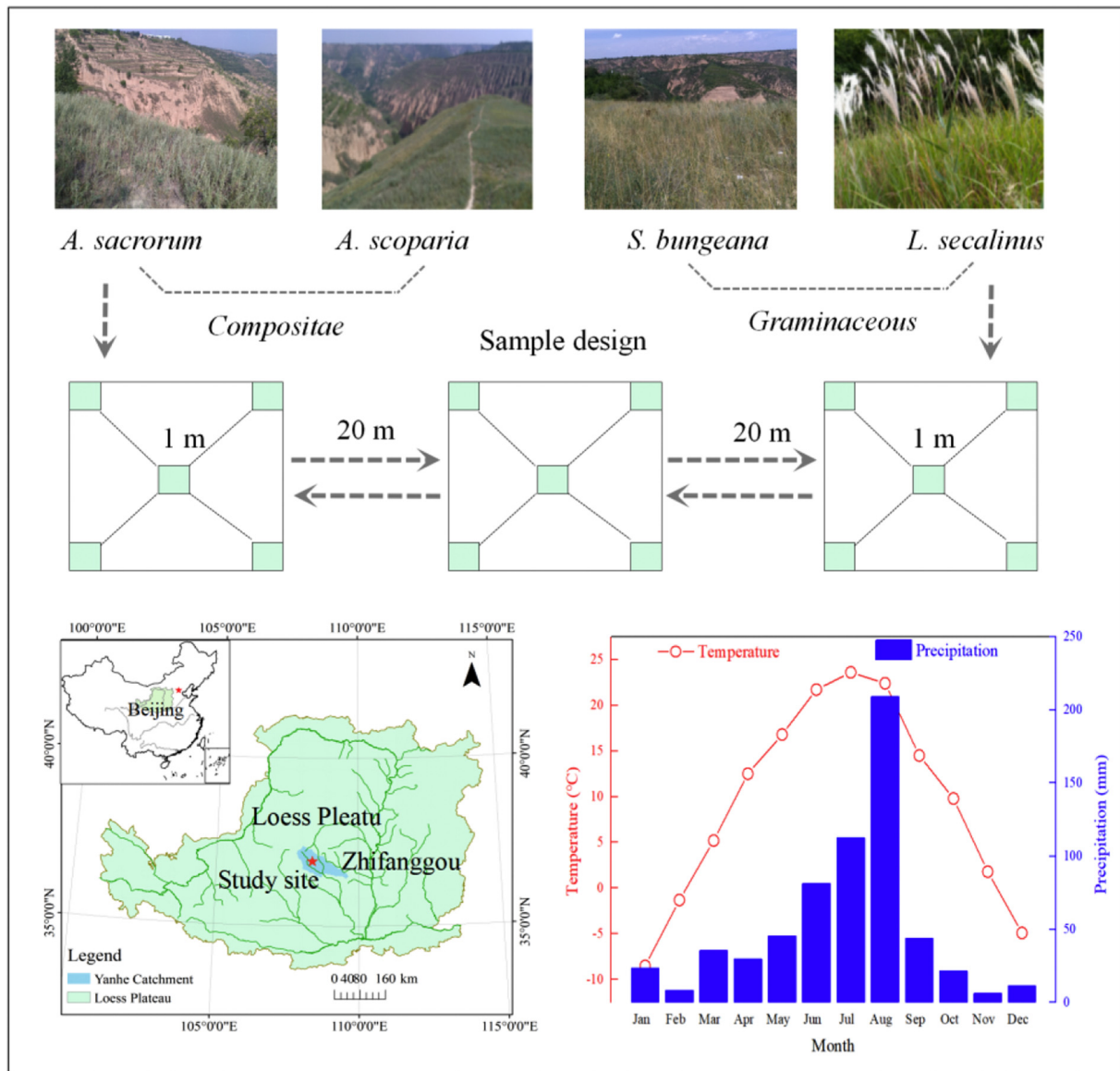


Fig. 1. Sampling site locations in the study area on the Loess Plateau. The green shading indicates the location of the study sites and samples. Precipitation (blue bar) and temperatures (red line) in 2015–2016 at the experimental site. The images were generated in ArcMap version 10.2 (<http://www.esri.com/>). The photographs were taken by the author (Yanxing Dou) in Zhifanggou in July 2016.

separated into two categories: Compositae and Gramineae. All of the above-ground parts of the green plants were immediately dried for 30 min at 105 °C and then transferred to the laboratory, where they were oven dried at 65 °C and weighed to the nearest milligram. Together, these biomass from the quadrats provided accurate data for the proportion of the allocation model to AGB, BGB and R/S. Further, we investigated and recorded the plant species richness, plant height and coverage. The data for each site were averaged across the three quadrats. In addition, the slope, aspect, longitude, latitude and altitude were recorded using a GPS receiver (LT500T, Beijing) (Table 1).

2.3. Data collection

The soil samples were passed through a 2-mm sieve to remove plant parts and other debris. The soil cores were oven dried to determine the soil bulk density (BD, $g \cdot cm^{-3}$) and soil moisture (SM, %). Soil composite samples were air dried for four days until they reached a steady weight. Soil electrical conductivity (Ec, $\mu s \cdot cm^{-2}$) was determined in a 1:1 (v/v) soil water solution and in a 1:1.5 (v/v) soil water aqueous extract. Soil organic carbon (SOC, $g \cdot kg^{-1}$) was measured using the $K_2Cr_2O_7-H_2SO_4$

oxidation method, and soil total nitrogen (TN, $g \cdot kg^{-1}$) was measured using the Kjeldahl procedure (UDK 140 Automatic Steam Distilling Unit, Automatic Titroline 96, Italy). Total phosphorus (TP, $g \cdot kg^{-1}$) was measured using the molybdenum antimony colorimetric method. Soil microbial biomass C and N (SMBC and SMBN, respectively, $mg \cdot kg^{-1}$) were measured using the fumigation-extraction method (Vance et al., 1987). Finally, each of the analyses was performed in triplicate.

Table 1

The definitions and quantifications of topographic properties in grassland on the Loess Plateau.

Shape	Position				
	Ridge	Side of ridge	Middle	Side of valley	Bottom
	5	4	3	2	1
Convex	3	8	7	6	5
Plain	2	7	6	5	4
Concave	1	6	5	4	3

2.4. Statistical analysis

All the variables in this paper are described as the mean \pm standard deviation (SD) and were analyzed using the SAS 9.3 software (SAS Institute Inc., Cary, NC, USA). We tested the normality and homogeneity of the variance and analyzed the data using Fisher's least significant difference (LSD) parametric test at $p < 0.05$ and $p < 0.01$. Pearson's coefficients were used to examine the relationships between AGB and BGB. The explanatory power of the model was assessed based on the significance (p -value) and the coefficient of determination (R^2). Moreover, the interactions among AGB, BGB and driving factors were tested and plotted using the path coefficients. Given the strong correlations between several driving factors, we conducted a principal component analysis (PCA) of the standardized values of those parameters to identify the primary axes of covariation among the driving factors. Then, we used a Monte Carlo permutation test to determine the significance of PCA effects. Prior to this analysis, forward selection was performed for four explanatory variable groups: soil physical properties (BD, Ec, SM, ST), chemical properties (SOC, TN, TP, SMBC, SMBN), plant traits (Height, Coverage, Density), and topographic properties (Altitude, Slope position, Slope gradient). These variable groups were treated as independent variables in the final model to explain AGB and BGB. Finally, structural equation modeling (SEM), a technique well suited for assessing relationships among networks of variables that are able to act simultaneously as both predictors and responses, was used to investigate the direct and indirect effects of the combination of factors on the AGB, BGB and R/S, including all the significances of the regression weights from the plausible interaction pathways. In addition, we removed nonsignificant variables with the lowest Akaike information criterion (AIC) and assessed the regression model fit using chi-squared tests and the root mean square error of approximation (RMSEA, $p < 0.05$). Origin 9.2 was used for plotting.

3. Results

3.1. Abiotic and biotic factors

Table 2 provides the basic information about plant species and ecological characteristics in four natural grasslands. The coverage varied largely and ranged from 66% to 95%, and the mean coverage values for Compositae and Gramineae plants were 75% and 88%, respectively. The plant density showed much variation and a high coefficient of variation (CV), ranging from 8.2 to 113.5 individuals \cdot m $^{-2}$, and the mean values for Compositae and Gramineae plants were 40.9 and 62.9 individuals \cdot m $^{-2}$, respectively. The mean values were 8.1 and 9.9 for Compositae and Gramineae plants, respectively. Gramineae

plants also varied markedly compared to the Compositae plants; in terms of plant height, the observed values ranged from 62.3 to 105.1 cm, and the mean values for Compositae and Gramineae plants were 79.8 and 83.7 cm, respectively. Overall, the plant coverage, density and height of Gramineae plants were higher than those for Compositae plants.

The BD, Ec, SW, ST, SOC, TN, SMBC and SMBN differed among the four grasslands (Table 3, all $p < 0.05$) but not the TP ($p > 0.05$). The SOC, TN, SMBC, and SMBN showed Compositae plants < Gramineae plants, and there were no significant differences between *S. bungeana* and *L. secalinus* in terms of SOC, SMBC or SMBN ($p > 0.05$), while a significant difference between *A. sacrorum* and *A. scoparia* was found for SMBC and SMBN ($p < 0.05$). The SW and ST showed the same variation trend, with the order of Compositae plants < Gramineae plants, and there were no significant differences among *S. bungeana*, *L. secalinus*, *A. sacrorum*, and *A. scoparia* for SW or ST ($p < 0.05$). However, the BD and Ec presented the opposite trend, with the order of Compositae plants > Gramineae plants, and we found a significant difference between *S. bungeana* and *L. secalinus* ($p < 0.05$). In addition, soil properties had a higher CV, indicating that the spatial distribution of soil properties is highly variable in the study area.

3.2. AGB, BGB and R/S

Across all sites, the AGB ranged from 123.58 to 412.35 g \cdot m $^{-2}$, the BGB ranged from 51.01 to 83.45 g \cdot m $^{-2}$, and the R/S ranged from 0.13 to 0.46 (Fig. 2). Further, the AGB and BGB showed similar variation trends, while the R/S showed the opposite trend. Plant biomass in Compositae plants showed the order of AGB > BGB, and Gramineae plants presented the order AGB < BGB. Moreover, the AGB, BGB and R/S significantly varied among plant species. Gramineae plants had a significantly higher AGB than that of Compositae plants ($p < 0.05$). While the BGB and R/S of Compositae plants were significantly higher than those of Gramineae plants ($p < 0.05$), *A. sacrorum* had the highest BGB, and *A. scoparia* had the highest R/S. We found that BGB was nearly two times greater than AGB. This finding was related to the high amount of underground root biomass being the most important source of SOC input. Therefore, the accurate estimation of the BGB was the basis for understanding the processes of the terrestrial C cycle (Hedlund et al., 2003; Tilman et al., 2006).

Moreover, on the basis of the AGB and BGB data for the plant species, we calculated R/S for each plant species and plotted its frequency distribution (Fig. 2). The R/S ranged from 0.3 to 6.8, with high spatial heterogeneity. There was no significant difference ($p > 0.05$) in terms of R/S for *S. bungeana* and *L. secalinus* (Gramineae plants), and there was no significant difference ($p > 0.05$) in terms of R/S for *A. sacrorum* and

Table 2

The basic ecological statistical characteristics of grassland on the Loess Plateau.

Family	Plant species	Plant properties			Topographic properties			Main species
		Coverage (%)	Density (Number \cdot m $^{-2}$)	Height (cm)	Alt (m)	Sp	Sg	
Compositae	<i>A. sacrorum</i>	83.5 \pm 5.2 ^b	8.2 \pm 2.1 ^c	86.3 \pm 12.5 ^b	1256 \pm 12 ^b	8.5 \pm 0.8 ^a	23.7 \pm 2.3 ^b	<i>Stipa bungeana</i> , <i>Lespedeza</i> , <i>Potentilla bifurca</i> , <i>Vetch</i> , <i>Heteropappus altaicus</i> <i>Lespedeza</i> , <i>Licorice</i> , <i>Agropyron mongolicum</i> , <i>Artemisia giraldii</i>
	<i>A. scoparia</i>	65.9 \pm 4.3 ^c	73.5 \pm 6.9 ^b	73.2 \pm 8.9 ^c	1348 \pm 16 ^a	7.2 \pm 1.6 ^b	28.5 \pm 1.9 ^a	
Gramineae	<i>S. bungeana</i>	95.4 \pm 6.1 ^a	12.3 \pm 1.5 ^c	105.1 \pm 16.3 ^a	1142 \pm 8 ^c	5.3 \pm 1.5 ^c	33.4 \pm 2.7 ^a	<i>Artemisia scoparia</i> , <i>Lespedeza</i> , <i>Patrimia scabiosaefolia</i> , <i>Radix bupleuri</i> <i>Calamagrostis brachytricha</i> , <i>Setaria viridis</i> , <i>Artemisia scoparia</i> , <i>Melilotus suaveolens</i>
	<i>L. secalinus</i>	79.8 \pm 7.7 ^b	113.5 \pm 23.2 ^a	62.3 \pm 5.8 ^d	1279 \pm 6 ^b	8.1 \pm 0.7 ^a	18.9 \pm 1.5 ^b	
Coefficient of variation (%)		14.97	97.91	22.53	6.81	19.58	23.87	–
F-value		56.32	72.13	89.74	69.78	65.21	40.57	–
p-value		0.005	0.002	0.000	0.002	0.003	0.019	–

Different letters for vegetation characteristics and environmental factors indicate significant differences among different vegetation types at $p < 0.05$.

Sp-Slope position; Sg-Slope gradient; Alt-Altitude.

Table 3
Descriptive statistics of soil variables in grassland on the Loess Plateau (mean ± SE).

Item		Compositae		Gramineae		Coefficient of variation (%)	F	p
		<i>A. sacrorum</i>	<i>A. scoparia</i>	<i>S. bungeana</i>	<i>L. secalinus</i>			
Soil physical properties	BD(g·cm ⁻³)	1.13 ± 0.19 ^a	1.14 ± 0.21 ^a	0.95 ± 0.13 ^b	0.87 ± 0.25 ^c	13.11	68.77	0.009
	Ec(μm·cm ⁻²)	75.87 ± 5.12 ^a	70.23 ± 4.02 ^b	68.98 ± 3.91 ^b	62.17 ± 5.48 ^c	8.12	72.03	0.005
	SW(%)	8.26 ± 1.78 ^b	8.79 ± 2.07 ^b	9.23 ± 1.03 ^a	10.05 ± 2.15 ^a	8.34	36.94	0.046
	ST(°C)	20.74 ± 3.89 ^b	21.07 ± 1.78 ^b	23.56 ± 2.56 ^a	24.18 ± 2.01 ^a	7.75	51.09	0.025
Soil chemical properties	SOC(g·kg ⁻¹)	9.23 ± 1.56 ^b	10.56 ± 2.01 ^b	13.56 ± 1.37 ^a	14.78 ± 2.48 ^a	21.41	48.12	0.019
	TN(g·kg ⁻¹)	1.26 ± 0.23 ^c	1.24 ± 0.15 ^c	1.56 ± 0.19 ^b	1.75 ± 0.24 ^a	16.97	68.97	0.007
	TP(g·kg ⁻¹)	0.86 ± 0.06 ^a	0.97 ± 0.13 ^a	1.03 ± 0.19 ^a	0.98 ± 0.11 ^a	7.46	24.36	0.123
	SMBC(mg·kg ⁻¹)	263.96 ± 45.03 ^c	298.14 ± 34.18 ^b	356.78 ± 25.61 ^a	361.07 ± 31.02 ^a	14.72	52.19	0.015
	SMBN(mg·kg ⁻¹)	23.65 ± 2.07 ^c	29.48 ± 3.41 ^b	36.07 ± 2.89 ^a	37.12 ± 3.14 ^a	19.87	65.45	0.008

Ec-Electric conductivity; BD-Bulk density; ST-Soil temperature; SM-Soil moisture; SOC-Soil organic carbon; TN-Total nitrogen; TP-Total phosphorus; SMBC-Soil microbial biomass carbon; SMBN-Soil microbial biomass nitrogen.

Different letters for vegetation characteristics and environmental factors indicate significant differences among different vegetation types at $p < 0.05$.

A. scoparia (Compositae plants) ($p > 0.05$). The R/S for Gramineae plants (>40%) ranged from 0 to 1, and that for Gramineae plants (>40%) ranged from 1 to 2. Compared with other grasslands around the world (Table 4), the AGB, BGB and R/S in our study were relatively lower. The reasons for these discrepancies are as follows: (1) There are some differences among plant species, and the natural environments (such as the climate and soil) exhibit marked differences, thus resulting in differences in terms of composition and structure. (2) The data sources were different; our study area cannot reflect the entire plant community as a result of spatial

heterogeneity, which may have led to the subtle differences compared with other grasslands around the world.

To illustrate the contributions to plant species from AGB and BGB, we evaluated the relationship between AGB and BGB using model fitting based on stepwise multiple regression (Fig. 3). A positive linear relationship between AGB and BGB in *A. sacrorum* ($R^2 = 0.458$, $p < 0.05$) and a positive linear relationship in *A. scoparia* ($R^2 = 0.851$, $p < 0.01$) were found. Likewise, there was a positive linear relationship in *S. bungeana* ($R^2 = 0.578$, $p < 0.01$) and a positive linear relationship in

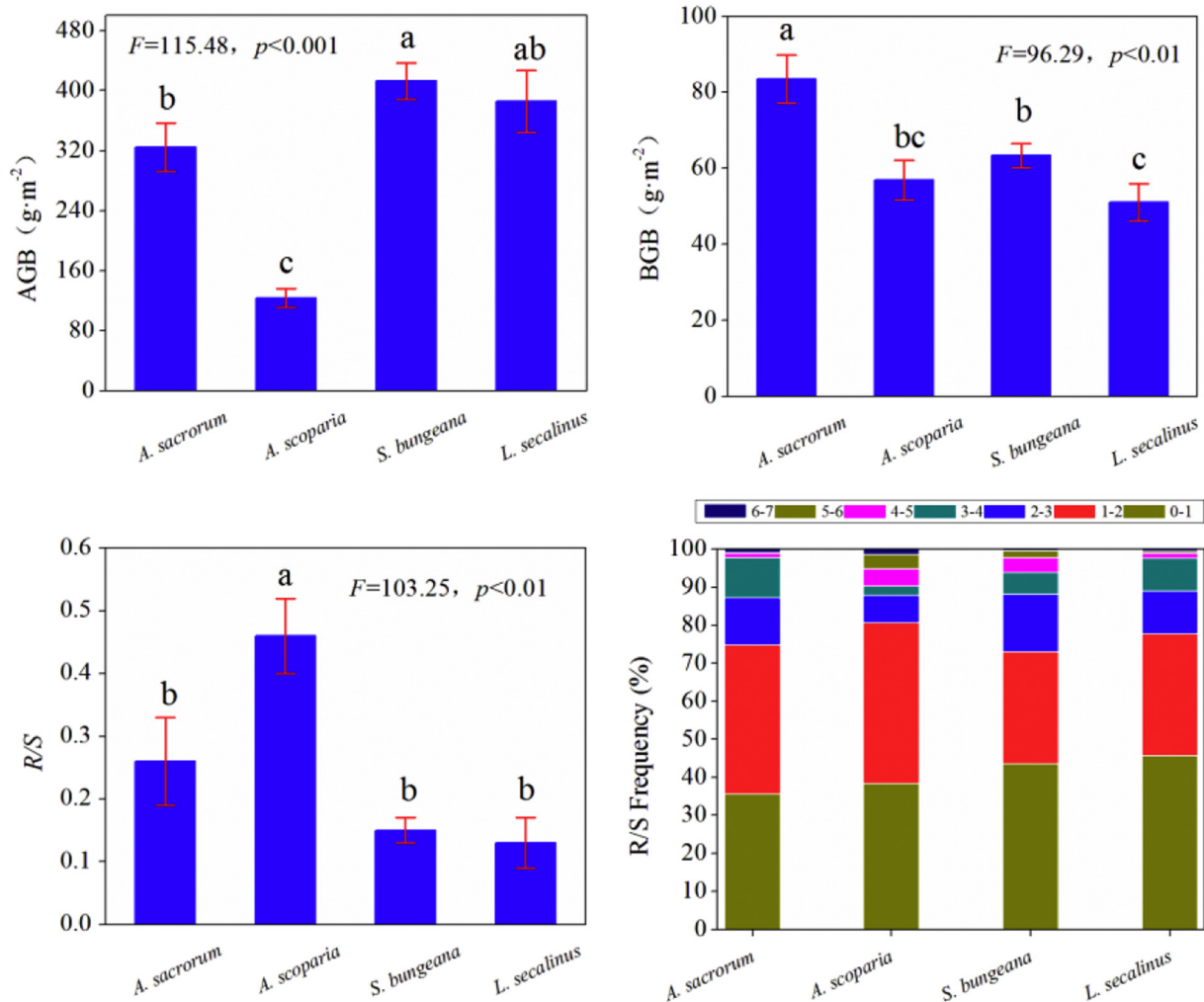


Fig. 2. Mean ± SE of plant biomass, R/S and the frequency distribution of R/S in grassland on the Loess Plateau. Bars with the same letter are not significantly different ($p < 0.05$, Tukey test).

Table 4
Comparison of AGB, BGB and R/S around the world.

Country/temperate grassland	AGB ($\text{g}\cdot\text{m}^{-2}$)	BGB ($\text{g}\cdot\text{m}^{-2}$)	R/S			Reference	
			Mean	Median	Range		
Europe	377.0	1903.8	3.7	3.4	1.1–6.9	Coupland (1979)	
North America	207.8	1469.6	4.4	3.7	1.2–10.3	Coupland (1979)	
Japan	742.0	1415.1	4.3	4.3	1.6–6.9	Coupland (1979)	
World	–	–	–	4.2	–	Mokany et al. (2006)	
China	Meadow steppe	122.4	643.8	5.3	–	–	Fang et al. (1996)
		183.4	1140.7	6.2	–	–	Ma and Fang (2006)
	Typical steppe	135.1	553.9	4.1	–	–	Fang et al. (1996)
		103.4	590.3	5.7	–	–	Ma and Fang (2006)
	Alpine steppe	50.1	277.7	5.5	–	–	Yang et al. (2003)
	Desert steppe Inner Mongolia	153.6	58.01	–	–	–	Ma and Fang (2006)
		94.3	746.3	12.7	6.8	1.2–30	
		182.7	2424.1	13.0	12.6	12.5–13.8	
		135.3	775.2	8.5	6.3	5.2–6.7	
	Grassland	97.0	604.2	–	–	–	Peng et al. (2013)

L. secalinus ($R^2 = 0.568, p < 0.01$), which indicates that the BGB could be accurately estimated based on the biomass.

3.3. Relationships between abiotic and biotic factors and AGB, BGB, and R/S

Based on the ordination analysis of plant biomass, 36 plots could be classified into four vegetation types in order of increasing biomass. The NMDS analysis showed that a two-dimensional solution was sufficient

to achieve low stress values (first axis/dimension = 46.98, $R^2 = 0.53, p = 0.002$; second axis/dimension = 35.78, $R^2 = 0.447, p = 0.004$) to explain biomass (Fig. 4). From the intra-set correlations of the environmental factors with the first two axes of the NMDS analysis (Table 5), the first axis was significantly correlated with BD, SOC, TN, and SMBC ($p < 0.01$), and the second axis was significantly correlated with Alt, SOC, TN, SMBC, SMBN, and Height ($p < 0.01$). The two axes were negatively correlated with Alt, Sp, BD and Ec. These results explained 84% of

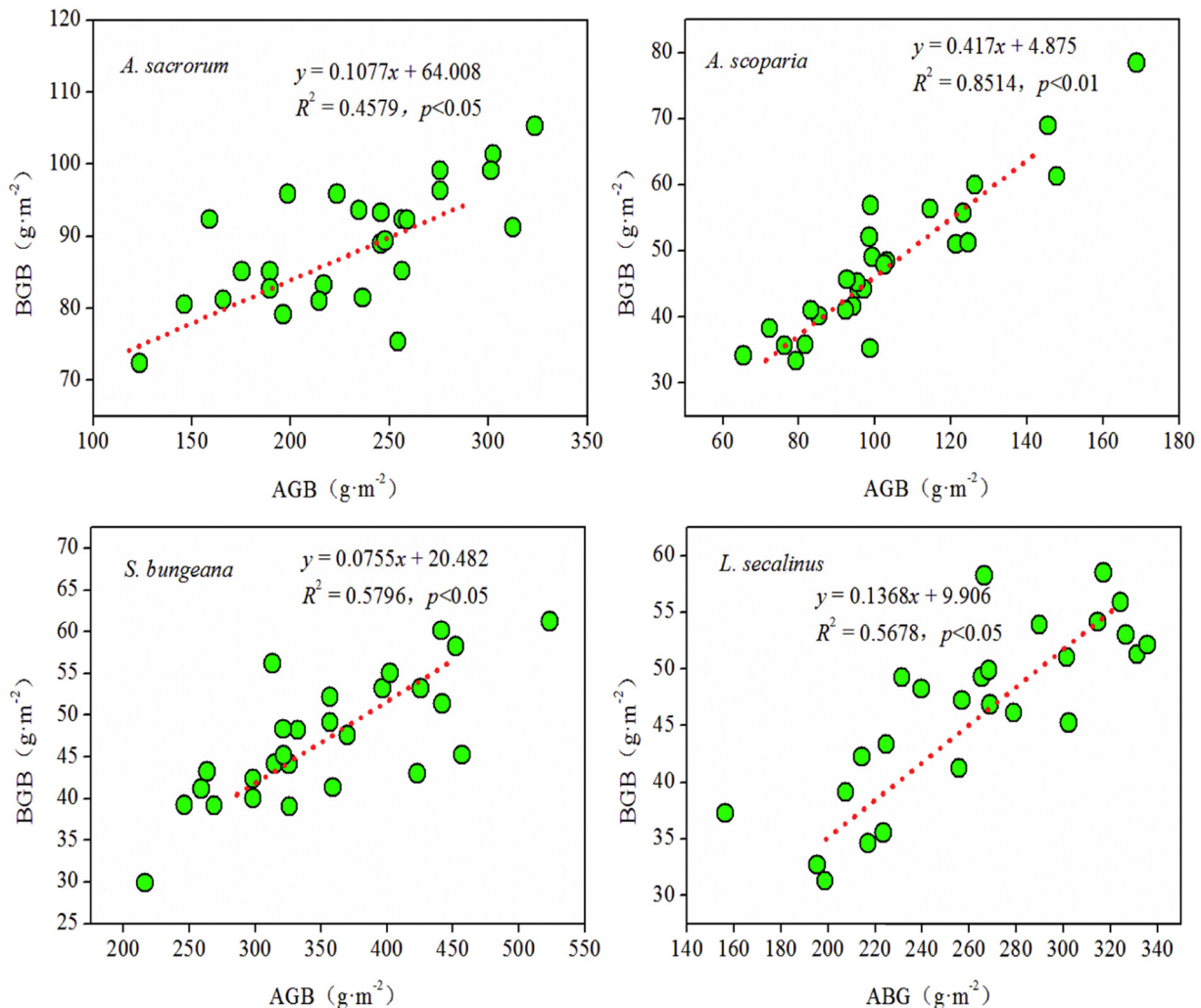


Fig. 3. Relationships between AGB and BGB in natural grassland on the Loess Plateau.

the variation in the plant biomass and environmental conditions, indicating that plant biomass is related to soil and topographic properties and that soil chemical properties (i.e., SOC, TN, SMBC and SMBN) are the key factors affecting plant biomass.

We also analyzed the correlations between AGB, BGB, R/S and topographic properties, soil physical properties, soil chemical properties, plant properties (Table 6). The relationships were significantly different based on 95% confidence intervals, and the total explained variance was 84%. AGB was strongly affected by SOC, TN, SMBC and Height ($p < 0.01$), and BGB was strongly affected by SOC, TN, SMBC and SMBN ($p < 0.01$). Similarly, R/S was strongly affected by the SOC, TN, SMBC and Height ($p < 0.01$). Based on the partial correlation coefficients, Height had the greatest effect on AGB, and SOC had the greatest effect on BGB and R/S. There was little effect of topographic properties and soil physical properties on AGB, BGB and R/S. Overall, Height substantially contributed to AGB and SOC substantially contributed to BGB and R/S in natural grasslands on the Loess Plateau.

3.4. Abiotic and biotic factors modulate the AGB, BGB and R/S

A principal component analysis (PCA) of 15 variables was used to identify the correlations among the variables and AGB, BGB and R/S, which were associated with the first two principal components (Fig. 5). PCA axis 1 primarily reflected the topographic properties and chemical properties of the soil, which accounted for 62% of the overall variance in the standardized soil variables; axis 2 mainly reflected the physical properties of the soil, explaining 14% of the standardized variance. The topographic properties (Slope position, Slope gradient and Altitude) were negatively correlated with the soil physical properties (Ec, BD, ST, SM) and were positively correlated with the soil chemical properties (SOC, TN, SMBC and SMBN), while TP was not correlated with the soil physical properties ($p > 0.05$). A Monte Carlo permutation test was used to test the significance of all of the soil driving factors, and the results showed that all of the soil variables were significant except for TP.

According to the results of PCA, topographic properties (Slope position, Slope gradient, Altitude), soil physical properties (Ec, BD, ST, SM), soil chemical properties (SOC, TN, TP, SMBC, SMBN), and plant properties (Height, Density, Coverage) served as four variables to carry out SEM (Fig. 6). The SEM of the indirect abiotic driving factors showed that both of soil chemical and physical properties affected plant biomass. The goodness of fit index was 0.834, indicating that this model explained the changes in plant productivity well; this result supported the third hypotheses, which indicated that biomass is affected by abiotic

Table 5

Intra-set correlations of the environmental variables and cumulative percentage variance for the first two axes of the NMDS analysis in grassland on the Loess Plateau.

Item		NMDS1	NMDS2
Topographic properties	Alt	-0.05	-0.56**
	Sp	-0.16	-0.49*
	Sg	0.23	0.17
Soil physical properties	BD	-0.56**	-0.41*
	Ec	-0.18	-0.27
	SW	0.21	0.46*
	ST	0.35*	0.19
	SOC	0.87**	0.67**
Soil chemical properties	TN	0.71**	0.54**
	TP	0.06	0.18
	SMBC	0.75**	0.62**
	SMBN	0.50*	0.67**
	Height	0.36	0.57**
Plant properties	Density	0.23	0.48*
	Coverage	0.18	0.32

* $p < 0.05$.
** $p < 0.01$.

factors. The physical and chemical properties accounted for 83% of the variance in biomass. However, the variation in topographic properties appeared to have a much stronger impact on biomass than soil physical properties. The physical properties had a significant negative influence on biomass, and the total effect was -0.846 ($p < 0.01$), of which the direct effect was -0.682 and the indirect effect was -0.164 . The effect of the soil chemical properties on biomass was not significant ($p > 0.05$). The topographic properties had a significant negative effect on soil physical properties, and the direct effect was -0.914 . The soil physical properties also had a significant negative effect on soil chemical properties, and the direct effect was -0.825 ($p < 0.01$). The plant properties had a significant negative effect on biomass, and the direct effect was -0.899 ($p < 0.01$). The physical properties accounted for 75% of the variance in biomass. For our SEM, the loading of all of the variables was > 0.7 .

4. Discussion

In this study, we reported that AGB, BGB and R/S showed great variation among plant species across grasslands on the Loess Plateau (Fig. 2). For example, BGB was significantly higher than AGB ($p < 0.05$), and BGB was nearly two times than AGB among plant species. As a consequence, both AGB and BGB were lower than global values (Fig. 2 and Table 4). In addition, R/S ranged from 1 to 6, and this finding (the lower AGB, BGB and R/S) differed from values found in other grasslands around the world. Specifically, *L. secalinus* had a significantly lower R/S than the other plants (Fig. 2). This could be partly explained by the plant height of *L. secalinus*, since R/S generally decreased with increasing plant height. Furthermore, Gramineaceous plants $>$ Compositae plants in terms of R/S, which indicated that Gramineaceous plants allocated most of their biomass to above-ground parts, whereas Compositae plants allocated the most biomass to below-ground parts. Overall, these four plant species allocated their biomass in order to maximize the capture of light energy in accordance with optimal partitioning theory (Wardle et al., 2004; Pérez-Ramos et al., 2013; Sterck et al., 2014; Barry et al., 2015). Higher biomass allocation to above-ground parts and lower biomass allocation to below-ground parts is a response to nutrient limitation due to morphology and natural selection (Borer et al., 2014; Bracken et al., 2015; Wurzbarger and Wright, 2015; Li et al., 2016; Zhang et al., 2017). During the process of plant growth, more biomass is allocated to vegetative organs, which is an inherent survival strategy to adapt to environmental conditions (Peng et al., 2017; Yang et al., 2017). In addition, the relationship between AGB and BGB was predominantly positive and linear regardless of plant species ($p < 0.05$) (Fig. 3), which was in agreement with other studies and supported the isometric allocation hypothesis (McConnaughay and Coleman, 1999; Shipley and Meziane, 2002; McCarthy and Enquist,

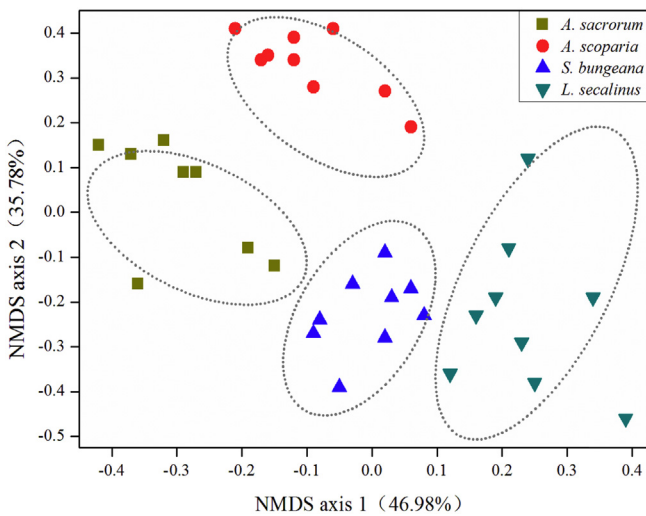


Fig. 4. Nonmetric multidimensional scaling (NMDS) ordination of 36 sites in grassland on the Loess Plateau (first axis/dimension = 46.98, $R^2 = 0.53$, $p = 0.002$; second axis/dimension = 35.78, $R^2 = 0.447$, $p = 0.004$).

Table 6
Partial correlations between plant biomass and abiotic driving factors. The *p* values were calculated on the basis of 999 permutations irrespective of plant species.

Item		Total variance explained (84.36%)	AGB		BGB		R/S	
			Partial correlation coefficient	Sig.	Partial correlation coefficient	Sig.	Partial correlation coefficient	Sig.
Topographic properties	Alt	4.87	0.426	<0.05*	0.413	<0.05*	0.436	<0.05*
	Sp	1.54	0.069	ns	0.105	ns	0.204	ns
	Sg	2.37	0.218	ns	0.423	<0.05*	0.326	ns
Soil physical properties	BD	0.84	0.089	ns	0.203	ns	0.065	ns
	Ec	1.53	0.174	ns	0.165	ns	0.069	ns
	SW	3.58	0.126	ns	0.423	<0.05*	0.563	<0.05*
	ST	2.71	0.185	ns	0.246	ns	0.302	ns
Soil chemical properties	SOC	15.12	0.698	<0.01**	0.723	<0.01**	0.756	<0.01**
	TN	8.12	0.624	<0.01**	0.701	<0.01**	0.687	<0.01**
	TP	0.89	0.054	ns	0.148	ns	0.163	ns
	SMBC	9.98	0.652	<0.01**	0.735	<0.01**	0.652	<0.01**
	SMBN	6.54	0.421	<0.05*	0.621	<0.01**	0.514	<0.05*
Plant properties	Height	16.23	0.703	<0.01**	0.284	ns	0.723	<0.01**
	Density	1.26	0.256	ns	0.307	ns	0.324	ns
	Coverage	8.78	0.532	<0.05*	0.106	ns	0.501	<0.05*

Note: Values in bold indicate a significant difference. * and ** signify $p < 0.05$ and $p < 0.01$, respectively. ns, not significant.

2007). Such an isometric relationship is controlled by both the slope (relative growth rate of AGB and BGB) and the y-intercept (the absolute value of R/S). The y-intercepts for all the plant species were significantly different from zero, indicating that the absolute values of R/S were not consistent. Therefore, our findings indicate that the relationship between AGB and BGB in relation to biotic and abiotic driving factors may be genus specific.

Not surprisingly, we found that AGB, BGB and R/S were strongly affected by biotic and abiotic driving factors (Tables 5 and 6). The NMDS analysis showed that a two-dimensional solution was sufficient to achieve low stress values (Fig. 4). These results explained 84% of the variation in plant biomass and environmental conditions, indicating that plant biomass is related to soil and topographic properties and that soil chemical properties (i.e., SOC, TN, SMBC and SMBN) are the key factors affecting plant biomass. In addition, PCA showed that soil topographic properties (Sp, Sg and Alt) were negatively correlated with soil physical properties (Ec, BD, ST, and SM) and positively correlated

with soil chemical properties (SOC, TN, SMBC and SMBN) (Fig. 5), which supported previous studies (Li et al., 2016; Yang et al., 2017). In this case, there was a strong positive relationship between plant size (Height, Density) and R/S, suggesting that changes in plant size or scale may have a direct or indirect effect on R/S. Numerous studies have demonstrated the relationships between R/S and environmental driving factors (biotic and abiotic driving factors) (Anderson et al., 2004; Díaz et al., 2007; Laliberté et al., 2013; Yang et al., 2017; Yuan et al., 2018). At the local scale, Cairns et al. (1997) demonstrated that there is no relationship between global root biomass and biotic and abiotic factors, e.g., temperature and precipitation. At a large scale, Wang et al. (2013) showed that R/S was negatively related to water availability, shoot biomass, stand age, height and volume, suggesting significant effects of climate and ontogeny on biomass allocation. Falster and Westoby (2003) also indicated that R/S decreased with plant height and increased with latitude but not with longitude or elevation. Bai et al. (2012) found a strong relationship between R/S and biotic and abiotic factors in China's grasslands. However, less is known about the interactions and relative contributions of biotic and abiotic factors driving R/S (Han et al., 2007; Liu et al., 2010; Peña and Duque, 2013; Yang et al., 2017; Wilson et al., 2018). Thus, one of the key issues in this study is that we comprehensively examine the responses of R/S to multiple abiotic and biotic factors. The integrated analysis provided a comprehensive understanding of the variation in R/S and its responses to abiotic and biotic factors. We found that R/S could be significantly impacted by any of the considered abiotic or biotic factors (Table 6). Compared with any single factor, the comprehensive consideration of multiple factors could provide a better explanation for R/S.

In addition, the present study indicated that the variation in soil chemical properties appeared to have a stronger effect than soil physical properties and topographic properties (Fig. 6). Soil physical properties had a significant negative influence on biomass, and the total effect was -0.846 ($p < 0.01$). However, the effect of the soil chemical properties on biomass was not significant ($p > 0.05$). Similarly, the topographic properties had a significant negative effect on the soil physical properties, with a higher direct effect (-0.914). The soil physical properties also had a significant negative effect on the biomass, and the direct effect was -0.899 ($p < 0.01$). In this case, we can conclude that soil chemical properties increased the AGB, BGB and R/S, which have direct effects on topographic properties. Thus, variation in R/S and difference in its responses to individual or combined factors supported the optimal partitioning hypothesis, suggesting that adaptation occurs among plants in varied environments.

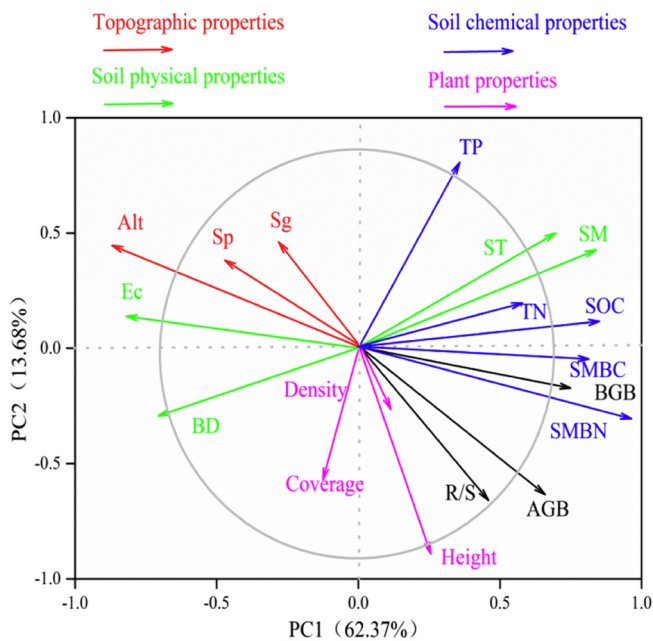


Fig. 5. Principal component analysis of 11 soil variables; each arrow represents the eigenvector corresponding to an individual variable. PC1 accounted for 62.37% of the overall variance, and PC2 accounted for 13.68% of the overall variance.

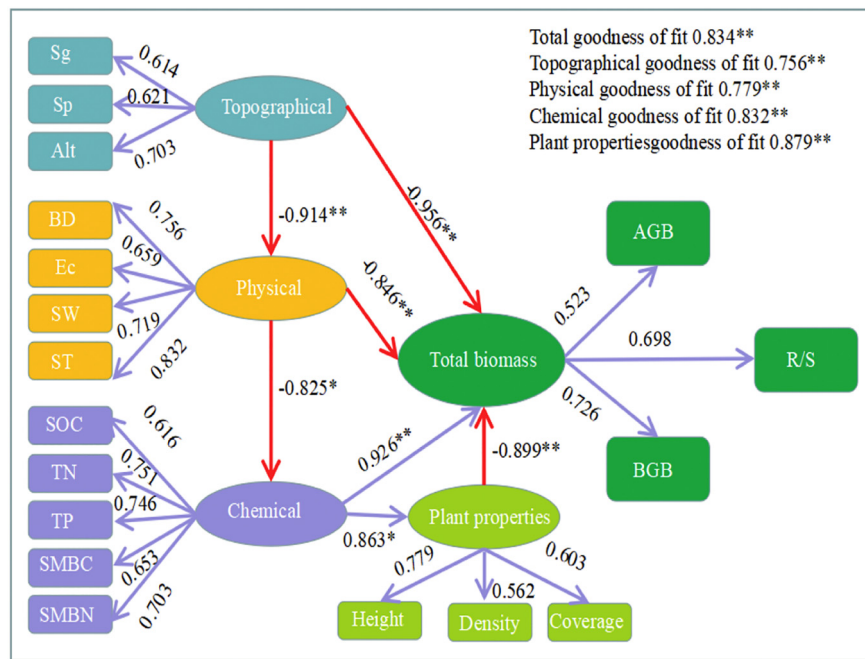


Fig. 6. Structural equation model (SEM) of biomass, topographic properties, soil physical properties, chemical properties and plant properties. The standardized coefficient is given for the SEM. Values in rectangular frames denote the measurable variables. Values in elliptical frames denote the latent variables. The goodness of fit was >0.7 for the SEM. Red arrows denote negative correlations. Blue arrows denote positive correlations.

Overall, R/S is usually thought to reflect the differential investment between AGB and BGB induced by abiotic and biotic factors. For example, plants should allocate relatively more biomass to their roots if their growth is more strongly influenced by below-ground factors, whereas they should allocate relatively more biomass to their shoots if their growth is more strongly influenced by above-ground factors. However, the mechanisms and ecological consequences of such processes remain highly unclear. Is the distribution of biomass an adaptive response to the biotic and abiotic circumstances imposed by nutrient-poor conditions? How phenotypically plastic is new biomass allocation in AGB and BGB? If biomass distribution is adaptive, will plant species modulate biomass through changes in plant traits? We hope that future research will quickly provide answers to these important questions in this region.

5. Conclusions

In summary, we examined biotic and abiotic factors driving AGB, BGB and R/S in natural grasslands on the Loess Plateau, providing important insights and supplementing the current information on biomass allocation patterns for a better understanding of ecosystem productivity and C stocks. We found that AGB, BGB and R/S were strongly affected by biotic and abiotic driving factors. First, AGB and BGB showed the same change trends, and they were positively and significantly correlated with plant height. Second, there was a positive and significant linear relationship between AGB and BGB ($p < 0.05$), in accordance with optimal partitioning theory. The topographic properties (Slope position, Slope gradient and Altitude) were negatively correlated with the soil physical properties (Ec, BD, ST, and SM) and positively correlated with the soil chemical properties (SOC, TN, SMBC and SMBN), while TP was not correlated with the soil physical properties ($p > 0.05$). Finally, SEM suggested that R/S is indirectly driven by plant properties, which are determined by soil and topographic properties. However, only 5% of R/S was explained by the soil physical properties and topographic properties, suggesting that these factors had no significant effect on R/S. This work provides the functional links to understand and establish

relationships between plant biomass and environmental driving factors (biotic and abiotic factors) on the Loess Plateau.

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