Effects of water availability gradient on biomass allocation of dominant plants in Inner Mongolia steppe

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Abstract

1 Extreme events such as extreme drought and rainfall are predicted to be more frequent under ongoing climate change. Biomass allocation is an important strategy for plants to respond to such changes. However, few studies explored the effects of water availability on biomass allocation of dominant plants in Inner Mongolia steppe in China. 2 A controlled experiment was conducted by treating four perennial plant species (Leymus chinensis, Stipa grandis, Artemisia frigida and Potentilla acaulis) with eight levels of water availability, which was selected based on the local annual mean precipitation, simulating rainfall scenarios facing climate change. 3 Water availability significantly affected the aboveground biomass, belowground biomass, total biomass and the ratio of belowground biomass and aboveground biomass of plants, and these effects were modified by species. Our results indicated that plants could modify their biomass allocation strategies to adapt to the gradient of water availability. 4 Climatic factors such as precipitation and temperature always co-vary, thus responses of plants to more complicated climate change (e.g. the joint variation of temperature and rainfall) should be further explored in order to better understand grassland management and restoration under climate change.

1 Introduction

Climate change, such as extreme drought and rainfall, varies spatially and temporally (IPCC 2007; Benestad et al., 2012). Such changes significantly affect plants. For example, global warming caused substantial damage on plants due to the drought and heat stress (Lipiec et al., 2013; Elst et al., 2017). Rainfall variation impacted terrestrial ecosystems since water limited plant growth, reproduction and productivity (De Boeck et al., 2017). Resource allocation is a vital strategy for plants to respond to the environmental variation (Harper et al., 1970; Mokany et al., 2006). For instance, the energy originated from photosynthesis of a plant can be allocated between aboveground and belowground organs such as leaves and roots. The former enables plants to do photosynthesis, while the latter could store resources for plants to grow. Biomass allocation between aboveground and belowground organs is known as root: shoot ratio (i.e. R: S, Guo et al., 2007). Several studies explored the effects of climate change on plants (Bai et al., 2008; Gonzalez-Dugo et al., 2010; Knapp et al., 2008, 2017). However, contrasting results were found in plant growth and productivity, which merits further research.

Previous studies found that abiotic factors such as temperature and rainfall impacted the R: S (Fay et al., 2003; Yang et al. 2018). For example, rainfall affected the biomass allocation and the belowground ecological processes of plants (Fay et al., 2003), where plants allocated more biomass to roots in order to explore soil water when they growing on dry conditions (Bray 1963), while they allocated more biomass to shoots in order to seize the light when plants growing on wet conditions (Villar et al., 1998). Moreover, higher levels of soil heterogeneity increased R: S (Michael et al., 2004; Wu et al., 2014; Liu et al., 2017a), where plants growing on patches with low quality grew more roots into their neighboring patches with high quality (Liu et al., 2017b, Liu et al., 2019). However, effects of biotic factors on biomass allocation were complicated.

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Some studies found that R: S was not affected by the aboveground competition (Zhang et al., 2014), and belowground competition did not increase the biomass allocation to roots. However, some other studies found that R: S was influenced by the type of grasslands (Coupland 1980) and plant growth (Gedroc et al., 1996; James et al., 2003). Thus, further studies are needed.

Climate changes such as extreme drought are predicted to be more frequency (Benestad et al., 2012; Felton et al., 2019). Thus, it is crucial to explore the effects of such changes on plant productivity and their allocation strategies (Bai et al., 1997; Cai et al., 2005 Lv et al., 2016). Here an experiment was conducted to explore the effects of water availability on biomass allocation of plants at the population scale, where 4 plant species (*Leymus chinensis* , *Stipa grandis* , *Artemisia frigida* , *Potentila acaulis*) that dominant at degraded grasslands in Inner Mongolia steppe were treated with 8 levels of water additions, which was set to simulate the rainfall scenarios in the face of climate change. Note that the degradation of grasslands in Inner Mongolia are caused by activities such as grazing (Liu et al., 2006, 2007), where *L. chinensis* and *S. grandis* are the two dominant species in the lightly degraded grasslands (Li et al., 2005), while *A. frigida* and *P. acaulis* are the dominant species in the heavily degraded grasslands. We expect that species at the lightly degraded grasslands will be more sensitive to the rainfall variation since they grow fast and tend to have relatively larger plant sizes, while species at the heavily degraded grasslands could withstand the water additions as they tend to grow slowly and to have relatively smaller plant sizes (Ma 2015). Specially, the biomass allocation between the aboveground and belowground organs of *L. chinensis* and *S. grandis* are expected to vary with water availability; while water availability is expected to not impact the biomass allocation of *A. frigida* and *P. acaulis* . This study can improve our understanding of grassland management and the restoration of degraded grasslands, especially in the face of climate change.

2 Materials and Methods

2.1 Study field

This study was conducted in Inner Mongolia steppe in China (43°33'N, 116deg40'E). The mean elevation of the location is 1225 m (range: 1200 m–1250 m). This location is characterized by mild humid summer and dry clod winter, which is temperate semi-arid continental monsoon climate. Annual mean temperature is around -1.1 degC–0.2 degC. There is a large temperature difference within a year (-21.4 degC in the coldest month in January, while 18.5 degC in the warmest month in July). The frost-free period is around 100 days in a year. The annual mean precipitation between 1980 and 2000 is 350 mm, where the precipitation mainly occurs in June and August, and the amount of rainfall during this period is around 80% of the amount of rainfall in the whole year. The site is dominated by dark chestnut soil (Jia et al., 2005; Lisetskii and Rodionova 2015). The dominant species are Dauri-Mongolian species such as *L. chinensis* , *S. grandis* , *A. frigida* and *P. acaulis* (Li and Li 2002).

2.2 Experimental design

From May 2000 to October 2001, an experiment was conducted to explore the responses of the 4 target plant populations to 8 levels of water additions, which were set according to the local annual mean precipitation during 1980–2000 (i.e. 350 mm), and they were 170 mm, 250 mm, 300 mm, 350 mm, 525 mm, 595 mm, 665 mm and 700 mm, respectively. This study aims to explore the effect of water amount on plants, not to mimic the local rainfall pattern. Thus, water was added daily to each treatment, and the amount of water was determined by dividing the total amount of rainfall in each pattern by the total growing days. Plants grew in pots with diameter 30 cm. There were three replications of each treatment for each species, ending with 19 pots in total. For *L. chinensis* , seeds were randomly sown in the pots in early May 2000, and four individuals with the similar size in each pot were kept after germination, and the rest were removed manually. For *S. grandis* , four ramets with similar size were transplanted from the nearby field to each pot in later May 2000 (similar sowing was done here in early May 2000, but the germination rate was too low). For *A. frigida* and *P. acaulis* , plants were dug out from the nearby field, and ramets were then separated into similar size. Four of them were transplanted into each pot in early May 2001. All the plants were grown under natural condition before applying treatments, which occurred from 10 June to 10 September 2001.

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At the end of the experiment, all the plants in each pot were washed out from their growing soils, and then separated into aboveground group (AG) and belowground group (BG), where soil surface is the baseline. For *L. chinensis* and *S. grandis*, AG included leaves and stems, while BG included roots and rhizomes. For *A. frigida*, AG included leaves, flowers and stems, while BG included roots. For *P. acaulis*, AG included leaves and stems, while BG included roots. All the biomasses were oven-dried at 65degC to constant weight and weighted.

2.3 Statistical analysis

In each pot: aboveground biomass (or belowground biomass) was calculated by dividing the aboveground biomass (or belowground biomass) of the four individuals by the pot surface area (i.e. 3.14 x 0.3 m x 0.3 m). Total biomass was calculated by adding the aboveground biomass and belowground biomass, converted to g m^{-2} via dividing by pot surface area. Ratio of belowground biomass and aboveground biomass (R: S) was calculated by dividing belowground biomass by aboveground biomass.

Curve estimations were applied to explore the relationship between water availability and total biomass, aboveground biomass, belowground biomass and R: S ratio. Then, linear or non-linear regressions were conducted to test the equations of these relationships, where equation with a larger R^2 and a significant p value is a better one. All statistics were done with SPSS 21.0.

3 Results

Water availability significantly affected total biomass, aboveground biomass, belowground biomass and R: S ratio of plants, which were modified by species (Table 1-4; Fig. 2-5).

(1) For *L. chinensis* : increasing water availability significantly increased its total biomass (Fig. 2a) and R: S ratio (Fig. 5a). The latter mainly derived from the increased belowground biomass (Fig. 4a), and aboveground biomass firstly increased and then decreased after reaching to a peak (Fig. 3a).

(2) For *S. grandis* : increasing water availability increased firstly and then decreased its total biomass (Fig. 2b), forming a unimodal pattern. Similar patterns were found in aboveground biomass (Fig. 3b) and belowground biomass (Fig. 4b). However, increasing water availability did not impact its R: S ratio (Fig. 5b).

(3) For *A. frigida* : increasing water availability increased its total biomass (Fig. 2c) and belowground biomass (Fig. 4c). Aboveground biomass (Fig. 3c) and R: S ratio (Fig. 5c) followed a unimodal pattern.

(4) For *P. acaulis* : increasing water availability increased its total biomass (Fig. 2d), aboveground biomass (Fig. 3d) and belowground biomass (Fig. 4d). However, it decreased the R: S ratio (Fig. 5d).

4 Discussions

In this study, we found that increasing water availability increased the total biomass of three of the four target species. However, the total biomass of *S. grandis* followed a unimodal pattern with increasing water availability. Interestingly, the four target plant species adopted different strategies to deal with water availability, where with increasing water availability, R: S of species *L. chinensis* and *A. frigida* followed an unimodal pattern, where the lowest points were 83 mm and 475 mm, respectively. *L. chinensis* has strong forage ability as a rhizomatous species (Wang et al. 2004), which enables this species to allocate more biomass to its roots when growing on wet conditions (Yang and Yang 1998). R: S of species *P. acaulis* decreased, while R: S of species *S. grandis* was not significantly affected. Our findings are in line with previous studies that plants modified their biomass allocation strategies to adapt to their growing conditions (Schmid 1987; Enquist et al., 2002). We expected that species dominant in lightly and heavily degraded grasslands responded differently to the water availability. In line with our expectation, R: S of *A. frigida* and *P. acauli*decreased, to some extent, with the increasing water availability (Fig. 5c-d). Such findings are also consistent with the results of species such as *Salix psammophila* , *Hedysarum leave* ,*Artemisia ordosica* and *Caragana korshinskii* in the previous studies (Dong et al., 1999; Xiao et al., 2001). However, the responses

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of R: S of *L. chinensis* and *S. grandis* to increasing water availability in this study indicate that some other strategies merit further research.

A unimodal relationship between water availability and total biomass was found in species *S. grandis* and *A. frigida* , where the highest points were 519 mm and 850 mm, respectively. In other words, increasing water availability firstly increased and then decreased their total biomass when the rainfall became detrimental, which might be caused by a lack of oxygen since it is fatal to the root respiration (Lambers and Steingrover 1978). Such result indicates that species *S. grandis* and *A. frigida* could tolerate dry conditions, while the latter species has a much wider range of water availability. Under extreme wet conditions, both *S. grandis* and *A. frigida* decreased their total biomass, while the former reduced both its aboveground biomass (Fig. 3b) and belowground biomass (Fig. 4b), while the latter decreased only its aboveground biomass (Fig. 4c). Such difference could be a key driver of species coexistence (Sanaei et al., 2018). Species adopted different biomass allocation strategies to respond to water availability, suggesting that fitness of some species such as *S. grandis* is not significantly affected by the water availability, and such dominant species could further impact the community structure and ecosystem functioning. However, increasing water availability inhibited the growth and productivity of species such as *A. frigida* and *P. acaulis* , but improved the plant fitness through reducing the availability of the grasslands (Neilson 1995).

5 Conclusions

Water availability significantly increased the total biomass of plant species. Remarkably, water availability affected the biomass allocation of plants, which were modified by species. Generally, increasing water availability did not impact or increased R: S of plant species that dominant in the lightly degraded grasslands, while it decreased R: S of plant species that dominant in the heavily degraded grasslands. Thus, biomass allocation of plants is an important indicator to explore the responses of plants to climate change, which should be further explore by considering more complicated conditions such as jointed effects of temperature and precipitation.

Acknowledgements

Authors' contributions

LZ designed and conducted the study. LY and LZ analysed the data. LY, HF and LZ discussed the data and contributed critically to the drafts.

Data availability statement

Data from this manuscript will be available through Nicholas A. Levis' Dryad account once this manuscript be published.

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Table 1 Results of the curve estimation of the relationship between water additions and total biomass, aboveground biomass, belowground biomass and R: S ratio (i.e. the ratio of aboveground biomass and belowground biomass) of species *Leymus chinensis* with linear, quadratic, power and exponential equations, where R^2, F, Df1, Df2, significance, constant, b1 and b2 were showed. A larger R^2 with a significant value is a better estimation, which is marked in red

Leymus chinensis Equation	Total biomass	Total biomass	Total biomass	Total biomass	Total biomass	Total biomass	Total biomass	Total biomass	Abovegro biomass	Abovegro biomass	Abovegro biomass	Abovegro biomass	Abov biom
	R^2	F	Df1	Df2	Sig.	Constant	b1	b2	R^2	F	Df1	Df2	Sig.
Linear	0.601	33.178	1	22	**<0.001**	26.031	0.198		0.674	45.522	1	22	**<0.0**
Quadratic	0.615	16.744	2	21	**<0.001**	-11.359	0.404		0.675	21.813	2	21	**<0.0**
Power	0.624	36.437	1	22	**<0.001**	0.925	0.786		0.655	41.853	1	22	**<0.0**
Exponential	0.587	31.257	1	22	**<0.001**	43.239	0.002		0.633	37.963	1	22	**<0.0**
Leymus chinensis Equation	Belowgro biomass	Belowgro biomass	Belowgro biomass	Belowgro biomass	Belowgro biomass	Belowgro biomass	Belowgro biomass	Belowgro biomass	R: S	R: S	R: S	R: S	R: S
	R^2	F	Df1	Df2	Sig.	Constant	b1	b2	R^2	F	Df1	Df2	Sig.
Linear	0.122	3.060	1	22	0.094	26.704	0.020		0.594	32.240	1	22	**<0.0**
Quadratic	0.277	4.024	2	21	**0.033**	-2.565	0.182		0.613	16.650	2	21	**<0.0**
Power	0.206	5.694	1	22	**0.026**	5.611	0.301		0.545	26.391	1	22	**<0.0**
Exponential	0.150	3.886	1	22	0.061	25.451	0.001		0.582	30.641	1	22	**<0.0**

Table 2 Results of the curve estimation of the relationship between water additions and total biomass, aboveground biomass, belowground biomass and R: S ratio (i.e. the ratio of aboveground biomass and belowground biomass) of species *Stipa grandis* with linear, quadratic, power and exponential equations, where R^2, F, Df1, Df2, significance, constant, b1 and b2 were showed. A larger R^2 with a significant value is a better estimation, which is marked in red

Stipa grandis Equation	Total biomass	Total biomass	Total biomass	Total biomass	Total biomass	Total biomass	Total biomass	Total biomass	Abovegro biomass	Abovegro biomass	Abovegro biomass	Abovegro biomass	Abov biom
	R^2	F	Df1	Df2	Sig.	Constant	b1	b2	R^2	F	Df1	Df2	Sig.
Linear	0.328	10.745	1	22	**0.003**	66.674	0.219		0.377	13.302	1	22	**0.00**

Stipa grandis Equation

Equation	Total biomass R²	Total biomass F	Total biomass Df1	Total biomass Df2	Total biomass Sig.	Total biomass Constant	Total biomass b1	Total biomass b2	Aboveground biomass R2	Aboveground biomass F	Aboveground biomass Df1	Aboveground biomass Df2	Aboveground biomass Sig.
Quadratic	0.617	16.889	2	21	**<0.001**	-194.739	1.660	-0.002	0.522	11.463	2	21	**<0.0**
Power	0.387	13.880	1	22	**0.001**	2.768	0.662		0.522	24.039	1	22	**<0.0**
Exponential	0.282	8.650	1	22	**0.008**	76.948	0.001		0.433	16.777	1	22	**<0.0**

Stipa grandis Equation (Belowground biomass / R: T)

Equation	R²	F	Df1	Df2	Sig.	Constant	b1	b2	R2	F	Df1	Df2	Sig.
Linear	0.227	6.444	1	22	**0.019**	46.417	0.110		0.126	3.172	1	22	0.089
Quadratic	0.582	14.629	2	21	**<0.001**	-129.035	1.075	-0.001	0.243	3.362	2	21	0.054
Power	0.170	4.520	1	22	**0.045**	3.463	0.528		0.070	1.660	1	22	0.211
Exponential	0.100	2.442	1	22	0.132	51.786	0.001		0.108	2.673	1	22	0.116

Table 3 Results of the curve estimation of the relationship between water additions and total biomass, aboveground biomass, belowground biomass and R: S ratio (i.e. the ratio of aboveground biomass and belowground biomass) of species *Artemisia frigida* with linear, quadratic, power and exponential equations, where R^2, F, Df1, Df2, significance, constant, b1 and b2 were showed. A larger R^2 with a significant value is a better estimation, which is marked in red

Artemisia frigida Equation

Equation	Total biomass R2	Total biomass F	Total biomass Df1	Total biomass Df2	Total biomass Sig.	Total biomass Constant	Total biomass b1	Total biomass b2	Aboveground biomass R2	Aboveground biomass F	Aboveground biomass Df1	Aboveground biomass Df2	Aboveground biomass Sig.
Linear	0.806	91.404	1	22	**<0.001**	71.905	0.224		0.692	49.425	1	22	**<0.0**
Quadratic	0.833	52.219	2	21	**<0.001**	20.145	0.509		0.696	23.999	2	21	**<0.0**
Power	0.827	104.893	1	22	**<0.001**	5.230	0.575		0.688	48.440	1	22	**<0.0**
Exponential	0.772	74.647	1	22	**<0.001**	87.474	0.001		0.710	53.906	1	22	**<0.0**

Atemisia frigida Equation (Belowground biomass / R: S)

Equation	R2	F	Df1	Df2	Sig.	Constant	b1	b2	R2	F	Df1	Df2	Sig.
Linear	0.688	48.505	1	22	**<0.001**	38.747	0.145		0.122	3.049	1	22	0.095
Quadratic	0.758	32.9	1	21	**<0.001**	-20.289	0.471		0.359	5.888	2	21	**0.00**
Power	0.734	60.71	1	22	**<0.001**	1.739	0.671		0.162	4.259	1	22	0.051
Exponential	0.653	41.371	1	22	**<0.001**	47.348	0.002		0.103	2.514	1	22	0.127

Table 4 Results of the curve estimation of the relationship between water additions and total biomass, aboveground biomass, belowground biomass and R: S ratio (i.e. the ratio of aboveground biomass and belowground biomass) of species *Potentila acaulis* with linear, quadratic, power and exponential equations, where R^2, F, Df1, Df2, significance, constant, b1 and b2 were showed. A larger R^2 with a significant value is a better estimation, which is marked in red

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Potentila acaulis Equation	Total biomass	Total biomass	Total biomass	Total biomass	Total biomass	Total biomass	Total biomass	Total biomass	Aboveground biomass	Aboveground biomass	Aboveground biomass	Aboveground biomass	Aboveground biomass
	R2	F	Df1	Df2	Sig.	Constant	b1	b2	R2	F	Df1	Df2	Sig.
Linear	0.797	86.135	1	22	**<0.001**	10.186	0.128		0.653	41.314	1	22	**<0.0**
Quadratic	0.807	43.794	2	21	**<0.001**	-8.067	0.228		0.708	25.432	2	21	**<0.0**
Power	0.829	106.501	1	22	**<0.001**	0.256	0.912		0.717	55.705	1	22	**<0.0**
Exponential	0.756	68.272	1	22	**<0.001**	22.529	0.002		0.619	35.779	1	22	**<0.0**

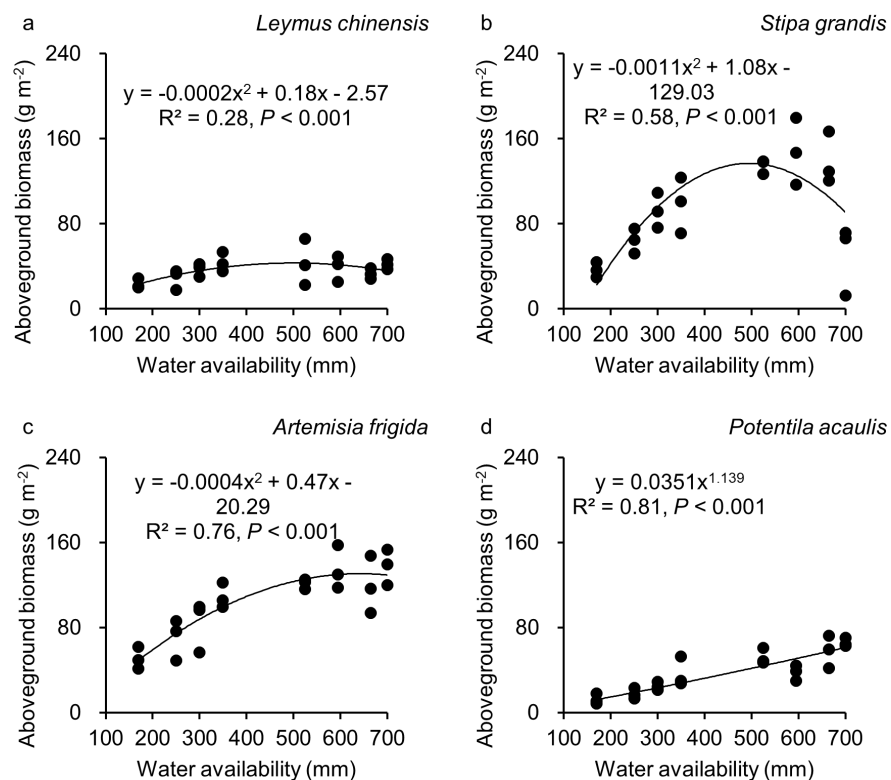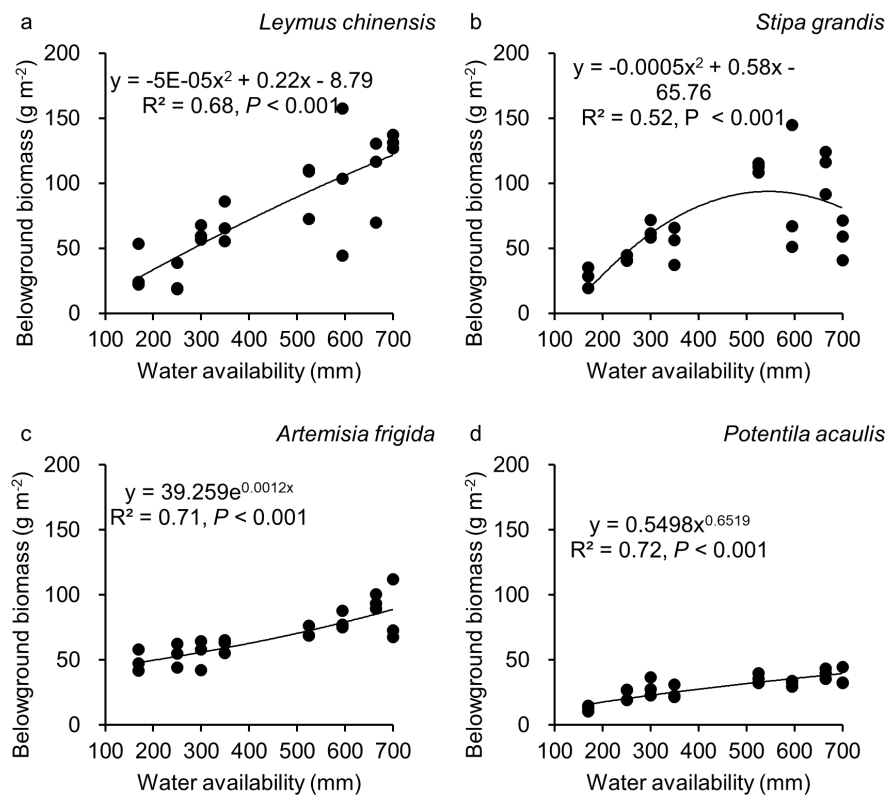| *Potentila acaulis* Equation	Belowground biomass	Belowground biomass	Belowground biomass	Belowground biomass	Belowground biomass	Belowground biomass	Belowground biomass	Belowground biomass	R: S	R: S	R: S	R: S	R: S
	R2	F	Df1	Df2	Sig.	Constant	b1	b2	R2	F	Df1	Df2	Sig.
Linear	0.758	68.894	1	22	**<0.001**	-1.816	0.089		0.473	19.721	1	22	**<0.0**
Quadratic	0.759	33.060	2	21	**<0.001**	-5.934	0.112		0.476	9.546	2	21	**<0.0**
Power	0.814	96.177	1	22	**<0.001**	0.036	1.139		0.464	19.081	1	22	**<0.0**
Exponential	0.761	69.935	1	22	**<0.001**	9.273	0.003		0.481	20.357	1	22	**<0.0**

Figure 1 The experimental field

Figure 2 Non-liner regressions between water additions and total biomass, separately for *Leymus chinensis* (a), *Stipa grandis* (b), *Artemisia frigida* (c) and *Potentila acaulis*(d), where estimation equation, R^2 and the significance are given

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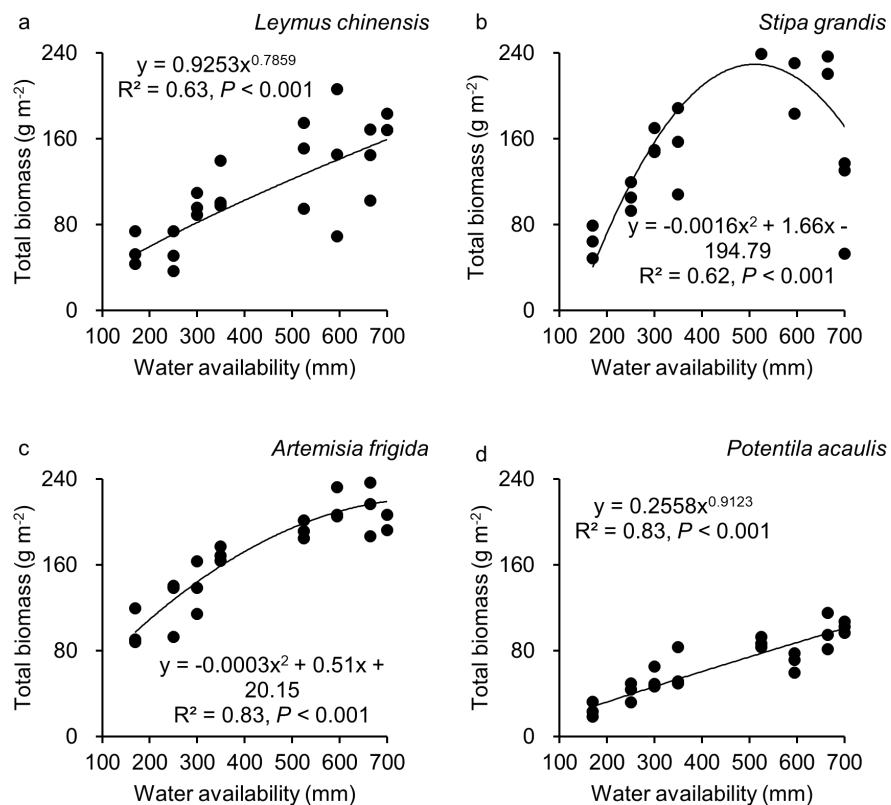
Figure 3 Non-linear regressions between water additions and aboveground biomass, separately for *Leymus chinensis* (a),*Stipa grandis* (b), *Artemisia frigida* (c) and*Potentila acaulis* (d), where estimation equation, R^2 and the significance are given

Figure 4 Non-linear regressions between water availability and belowground biomass, separately for *Leymus chinensis* (a), *Stipa grandis* (b), *Artemisia frigida* (c) and *Potentila acaulis* (d), where estimation equation, R^2 and the significance are given

Figure 5 Non-linear regressions between water availability and R: S (i.e. the ratio of belowground biomass and aboveground biomass), separately for *Leymus chinensis* (a), *Stipa grandis* (b),*Artemisia frigida* (c) and *Potentila acaulis* (d), where estimation equation, R^2 and the significance are given

a   *Leymus chinensis*

$y = 6E\text{-}06x^2 - 0.001x + 1.31$
$R^2 = 0.61, P < 0.001$

b   *Stipa grandis*

c   *Artemisia frigida*

$y = 4E\text{-}06x^2 - 0.0038x + 1.49$
$R^2 = 0.36, P < 0.001$

d   *Potentila acaulis*

$y = 1.4825e^{-0.001x}$
$R^2 = 0.48, P < 0.001$

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