Article:

Ren, Zhuobing, Li, Changjia, Fu, Bojie et al. (3 more authors) (2023) Belowground soil and vegetation components change across the aridity threshold in grasslands. Environmental Research Letters. 094014. ISSN 1748-9326

https://doi.org/10.1088/1748-9326/acec02

ENVIRONMENTAL RESEARCH
LETTERS

LETTER • OPEN ACCESS

Belowground soil and vegetation components change across the aridity threshold in grasslands

To cite this article: Zhuobing Ren *et al* 2023 *Environ. Res. Lett.* **18** 094014

IOP Publishing Environ. Res. Lett. 18 (2023) 094014 https://doi.org/10.1088/1748-9326/acec02

ENVIRONMENTAL RESEARCH
LETTERS

OPEN ACCESS

RECEIVED
16 November 2022

REVISED
2 July 2023

ACCEPTED FOR PUBLICATION
31 July 2023

PUBLISHED
14 August 2023

LETTER

Belowground soil and vegetation components change across the aridity threshold in grasslands

Zhuobing Ren[1,2], Changjia Li[1,2,*], Bojie Fu[1,2], Shuai Wang[1,2], Wenxin Zhou[1,2] and Lindsay C Stringer[3,4]

[1] State Key Laboratory of Earth Surface Processes and Resource Ecology, Faculty of Geographical Science, Beijing Normal University, Beijing 100875, People's Republic of China
[2] Institute of Land Surface System and Sustainable Development, Faculty of Geographical Science, Beijing Normal University, Beijing 100875, People's Republic of China
[3] Department of Environment and Geography, University of York, York YO10 5DD, United Kingdom
[4] York Environmental Sustainability Institute, University of York, York YO10 5DD, United Kingdom
[*] Author to whom any correspondence should be addressed.

E-mail: changjia.li@bnu.edu.cn

Keywords: effect of aridity, belowground components, grassland ecosystem

Supplementary material for this article is available online

Abstract

Grassland ecosystem functions are affected by global climate change and increasing aridity. Belowground components of soil and vegetation, such as specific root length, belowground biomass and soil organic carbon are important for maintaining these functions. However, aridity affects these components in different ways. This research evaluates changes in soil properties and plant attributes with aridity along a 2600 km aridity gradient in the arid and semiarid grasslands of Inner Mongolia. The aridity index was used considering the ratio of precipitation to potential evapotranspiration, where a higher value indicates greater aridity. Results showed an overall aridity threshold for grassland ecosystems of 0.67, where abrupt changes in belowground components were observed. The effect of aridity on specific root length changed from negative (−0.18) below the threshold to positive (0.24) above the threshold, with the emergence of coordination between aboveground and belowground plant characteristics. Aridity exhibited a negative effect on belowground biomass, increasing from −0.24 below the threshold to −0.55 above the threshold as the positive effect of relative grass abundance disappeared. The total effect of aridity on soil organic carbon showed a subtle change, but the driving pathways through which aridity affects changed from soil loss to aridity itself and vegetation cover at plot scale. These findings highlight how aridity affects belowground components in grassland ecosystems above and below the aridity threshold. They provide a basis for better understanding aridity-driven interactions in grassland ecosystems, and can be used to inform actions to protect grasslands under future climate change.

1. Introduction

Grassland covers approximately 35.2% of the Earth's land surface (Bai and Cotrufo 2022), and provides a variety of important ecosystem services such as carbon storage, habitat for biodiversity, and food (White *et al* 2000, Gibson and Newman 2019). However, grasslands are fragile ecosystems and are severely affected by climate change and human activities (Grime *et al* 2008, Gang *et al* 2014, Bai and Cotrufo 2022). Approximately half of the grasslands in the world have been degraded (Bardgett *et al* 2021). Therefore, it is imperative to explore the responses of grassland ecosystems to climate change and increasing aridity, and the pathways that drive these responses, to inform the development of sustainable grassland conservation strategies at regional and global scales.

Belowground components play a key role in maintaining grassland ecosystems, with fine roots effectively protecting the soil from erosion (Wu *et al* 2020). Grasslands store about one third of the terrestrial carbon stock, with approximately 90% of their carbon stored in root biomass and soil organic carbon (Bai and Cotrufo 2022). Effects of aridity on belowground components vary depending on plant characteristics, community structure, and ecosystem function. Specific root length is a classic indicator that reflects the response of plant roots to drought stress, and which characterizes the plant economics spectrum (Ryser 2006, Ostonen *et al* 2007). Some studies have indicated that drought stress reduces specific root length through a conservative resource use strategy (Larson and Funk 2016). Other researchers found that plants increase their specific root length to adapt to increasing aridity by improving water acquisition capacity (Asefa *et al* 2022) by inducing larger root hair density or root surface area (Comas *et al* 2013). Another study reported that aridity does not have a clear positive or negative effect on specific root length, but rather increased the diversity of specific root length (Butterfield *et al* 2017). In terms of community structure, drought stress reduces belowground biomass (Huang and Fu 2000, Sanaullah *et al* 2012, Wang *et al* 2019) by decreasing the allocation of photosynthetic products to the belowground plant system (Huang and Fu 2000, Galvez *et al* 2011). However, some studies revealed that belowground biomass may increase due to a positive root response to aridity (Burri *et al* 2014, Hasibeder *et al* 2015, Liu *et al* 2020), and because aridity induces plants to allocate more resources to the belowground component (Wellstein *et al* 2017). In terms of ecosystem function, aridity modulates soil organic carbon in grasslands by altering productivity (Berdugo *et al* 2020), community composition (Hu *et al* 2021), and the plant parts implicated in carbon input (Hu *et al* 2022). Nevertheless, the pathways that reduce soil organic carbon may shift along the aridity gradient (Hu *et al* 2021). In summary, while existing research has provided some useful insights, the effects of aridity on belowground components have not been fully elucidated.

The aridity threshold refers to the level of aridity at which abrupt changes occur in ecosystem attributes (Berdugo *et al* 2020). Many previous studies have reported that various functions and attributes of ecosystems exhibited abrupt changes with increasing aridity, including nitrogen cycling (Wang *et al* 2014), levels of soil metal elements (Luo *et al* 2016), soil pH (Slessarev *et al* 2016), multifunctionality (Berdugo *et al* 2017), and the ratio between soil carbon, nitrogen and phosphorus (Wang *et al* 2020). Grasslands comprise the largest vegetation cover in dryland regions (FAO 2019), and are expected to experience sudden shifts with changes in aridity level. These shifts may alter the effect of aridity on belowground components in grasslands. However, it is still not known how root traits and belowground biomass change with increasing aridity. In addition, the driving pathways of aridity impacts on belowground components of grasslands (i.e. specific root length, belowground biomass and soil organic carbon) above and below the aridity threshold has not been explored.

The main aim of our study is to: (i) determine the aridity thresholds of different belowground components (specific root length, belowground biomass and soil organic carbon) in semi-arid grasslands; and (ii) examine how aridity drives changes to belowground components above and below the aridity threshold. The hypotheses were that: (i) the belowground components including specific root length, belowground biomass and soil organic carbon show abrupt changes with aridity; and (ii) the underlying driving forces varied below and above the aridity threshold. A systematic transect survey along a 2600 km aridity gradient of the Inner Mongolia grassland was conducted according to BIODESERT guidelines to test the hypotheses. A threshold model and structural equation model were used to explore the effects of aridity on the selected belowground components. Overall, the findings provide a basis for better understanding aridity-driven interactions in grassland ecosystems and can be used to inform development of strategies to protect of grasslands at different aridity levels in the future.

2. Methods

2.1. Study area

This study was conducted along a 2600 km east-west transect (longitude: 109°59′–121°32′E; latitude: 40°19′–50°10′N) in the arid and semiarid grasslands in northern China (figure 1). Mean annual precipitation (MAP) of the region ranged from 161 to 463 mm, and mean annual air temperature (MAT) ranged from −2 to 6 °C. Mean annual potential evapotranspiration (PET) of the west side was approximately 986 mm whereas that at the east side was approximately 735 mm. The aridity of this transect ranged from 0.39 to 0.83 and was calculated using the following equation (Delgado-Baquerizo *et al* 2013):

$$\text{Aridity} = 1 - \frac{\text{MAP}}{\text{PET}}. \tag{1}$$

The higher the value of the aridity, the more arid the region. The ratio of precipitation to potential evapotranspiration (AI) and PET data were obtained from the Global Aridity Index and Potential Evapotranspiration Climate database (https://cgiarcsi.community/). MAP and MAT of each sampling site were calculated from WorldClim (www.worldclim.org/). Soil types varied from southwest to northeast, and included desert, chestnut, and black soil. Chestnut soil was observed in most of the areas. The vegetation type was predominantly perennial clustered gramineous plants, mainly consisting

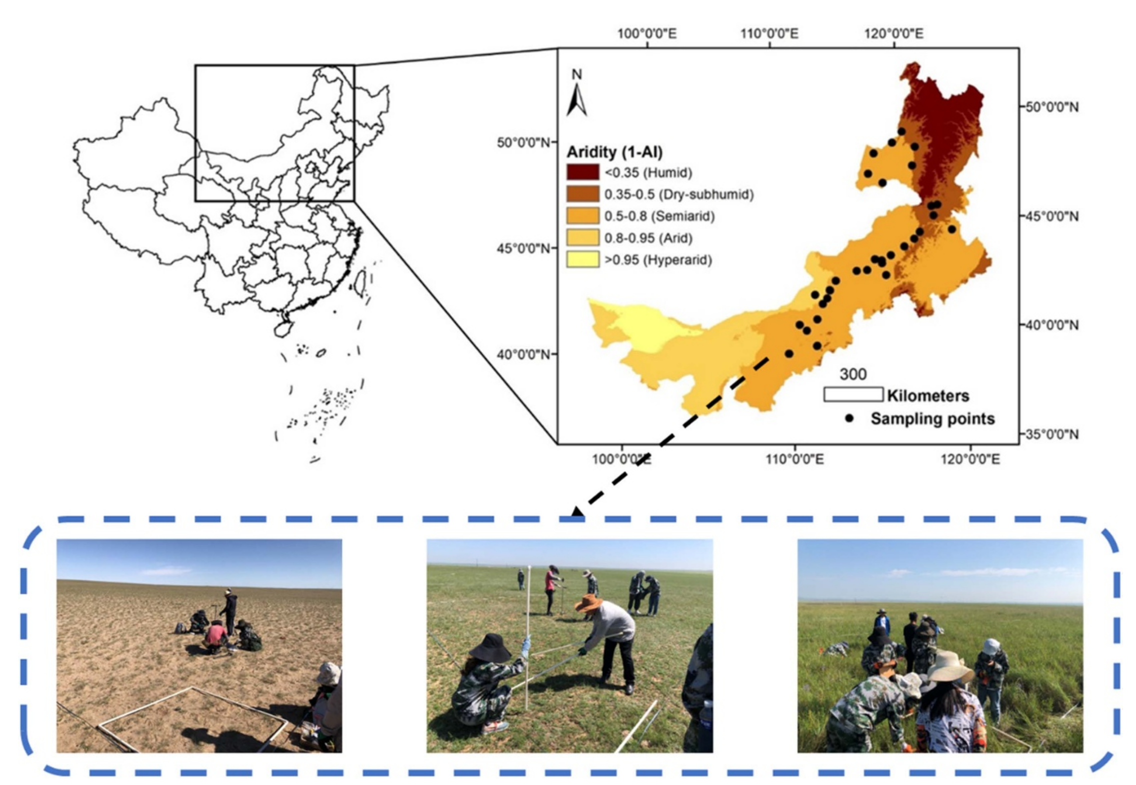

Figure 1. Map of the 40 field sites in grasslands across Inner Mongolia Autonomous Region, northern China. The sites represent the three different dryland subtypes (i.e. dry-subhumid, semiarid, and arid), which are defined with different aridity levels, as demonstrated in the legend. The location of the study area within China is indicated on the left. Photos at the bottom were taken during the field sampling.

of *Leymus chinensis, Stipa capillata*, and *Cleistogenes Keng*.

2.2. Field survey and sampling

Sampling over the entire transect was conducted between July and August 2020. A total of 40 sampling sites were investigated based on a methodology utilized in the BIODESERT survey (Maestre *et al* 2022). A 45 × 45 m plot was set up at each sampling site starting from the upper edge of the hillslope. Subsequently, a 45 m long transect downslope was then located for vegetation and soil surveys. Three parallel transects of the same length, each 10 m apart across the slope, were added. Ground cover was recorded along each of the four transects after every 20 cm. About 20 quadrats (1.5 m × 1.5 m) were arbitrarily selected (4 transects per plot, 5 quadrats per transect) within each plot, thus a total of 800 quadrats were surveyed in the study area. The presence, abundance, coverage and height of all plant species were recorded for each quadrat. A complete herbaceous individual (or five annual branches for shrubs) of dominant species was selected per transect in each plot and collected for determination of plant traits.

Soil samples were collected from each plot using three methods: (i) cutting rings (100 cm^3) were used to collect samples for estimating the soil bulk density at depths of 0–10, 10–20 and 20–30 cm; (ii) soil cores (0–10, 10–20 and 20–30 cm deep) were collected for determination of soil nutrients; and (iii) samples for measuring soil grain size were collected at depths of 0–10, 10–20, 20–40, 40–60, 60–80 and 80–100 cm using U-Tubes sampler. Each sampling method was used to collect samples at three different locations (including bare land, dominant species, and biocrust), which were at least 5 m apart.

2.3. Determination of soil and plant characteristics

Four quadrats were selected (1 quadrat per transect) in each plot and all grasses were harvested for determination of aboveground biomass. The core-break method was used for sampling of roots for belowground biomass determination in the four quadrats under the dominant species (0–10, 10–20, 20–30 cm deep). The belowground biomass samples were fully soaked to remove soil and impurities. Samples were washed repeatedly until the impurities were completely removed. After cleaning, the samples were sent to the laboratory and dried at 65 °C for 48 h to obtain the amount of aboveground and belowground dry biomass.

Plant samples were obtained from each plot to explore the basic characteristics of plant ecological strategies. Leaf dry matter content was evaluated by weighing the fresh and dry material of all leaves of selected plants. Leaf carbon and nitrogen contents were measured at the laboratory using an elemental analyser (Vario MACRO Cube, PerkinElmer, Waltham, Massachusetts, USA), and phosphorus content was determined using ICP−OES (Avio 200, PerkinElmer, Waltham, Massachusetts, USA). The length and diameter of roots were measured with a calliper. Information about the life cycle, life form, seed dispersal, pollination mechanism, photosynthetic pathway, leaf form, and flowering time of all analysed species was obtained from the Flora of China (www.iplant.cn/).

The soil properties measured at the laboratory included soil organic carbon, total nitrogen, total phosphorus, calcium carbonate, pH, grain size, and bulk density. Soil organic carbon content (g/g) and total nitrogen (g/g) were measured using a Vario MACRO Cube Elemental Analyser (PerkinElmer, Waltham, Massachusetts, USA). Soil total phosphorus (mg kg^{-1}) was quantified using ICP−OES (Avio 200, PerkinElmer, Waltham, Massachusetts, USA). Soil calcium carbonate (g kg^{-1}) was determined by the titrimetric method. Soil pH was measured using a pH meter (HQ30d, HACH, Loveland, Colorado, USA). Soil grain size was quantified using a laser particle sizer (Mastersizer 2000, Malvern Panalytical, Malvern, Worcestershire, UK). Soil bulk density (g cm^3) was determined by the clod method and the oven-dry method (at 105 °C for 48 h).

2.4. Calculation of soil and plant attributes

All indicators explored in this study were calculated as shown in table 1. Soil properties in the sampling sites were expressed as the average of the experimental results of all samples for each indicator. Aboveground and belowground biomass were calculated as the total dry weight of aboveground and belowground plant parts divided by the sampling area, respectively. Vegetation coverage was presented as the ratio of vegetation records to the total records along four transects in the sampling sites. The effect of vegetation on soil organic carbon was expressed as the difference between soil organic carbon under vegetation and soil organic carbon in bare land.

Calculation of the plant diversity index and community-weighted mean trait values involved more complex expressions, where the relative abundance of species is a vital parameter. The relative abundance of species was calculated by dividing the number of individuals of a plant species by the total number of plants at the sampling site. The Shannon-Weiner diversity index (Shannon and Weaver 1949), which reflects the plant diversity was calculated using the formula in table 1. The relative abundance of each species was also expressed as a weight to determine various plant functional traits (Garnier *et al* 2004).

2.5. Statistical analysis

Linear and nonlinear (quadratic and general additive models [GAM]) regressions were used to explore the relationships between ecosystem variables and aridity. The Akaike information criterion (AIC) and Bayesian information criterion (BIC) were used to determine the model that exhibited the best fit (Berdugo *et al* 2020). Segmented, step and stegmented regression analyses were conducted and the best model (determined by AIC and BIC) was used to determine the thresholds of variables. The segmented approach was selected to identify the threshold when the quadratic model or GAM was the model with the best fit, considering a continuous trend throughout the aridity gradient in this case. Segmented/stegmented/step and GAM regression analyses were conducted using the chngpt (Fong *et al* 2017) and gam (Hastie and Tibshirani 2017) packages in R 4.0.3 (http://cran.R-project.org/), respectively.

Bootstrap analysis of the linear regressions was conducted at both sides of all the thresholds to determine whether the detected threshold significantly affected the intercepts and slopes of the fitted regressions (Canty and Ripley 2021) using the boot package in R, with each side of the threshold subjected to 200 bootstrap samplings. The bootstrapping results below and above the threshold were compared using the Mann−Whitney U test. The uncertainty of thresholds is presented using confidence intervals and highest density intervals. The threshold values and parameters of the segments for all variables were calculated with a 95% confidence interval. Additionally, the posterior distribution of the aridity threshold for each variable was calculated to test whether the threshold is within the highest density interval.

Distribution of all variables was determined based on the fitting results using MATLAB (table S1). Analysis was conducted to evaluate whether the variables exhibited a unimodal distribution using the gmdistribution.fit function in MATLAB (The MathWorks Inc., Natick, Massachusetts, USA) before fitting threshold regressions. The models used for linear regression were modified when fitting if the data did not exhibit unimodal distribution, by replacing linear regressions with quantile regressions (Berdugo *et al* 2020). The best models for unimodal and bimodal distribution variables were selected (tables S2, 3 and S5, 6).

To examine the influence of inter-annual precipitation variability on aridity thresholds for these variables, a moving-window analysis was used to calculate the aridity threshold values with increasing inter-annual precipitation variability. Threshold models (segmented, step and stegmented) were performed for a subset window of 30 study sites with the lowest inter-annual precipitation variability values, repeating the same calculations as many times as sites remained.

After calculating and validating all thresholds, cluster analysis was used to divide the thresholds into different clusters and then evaluate the overall aridity thresholds. The optimal number of clusters was

Table 1. Variables and their calculations and descriptions used in this study.

Data type	Variable typology	Variable name	Abbreviations	Calculation	Description
Dataset	Climate	Aridity		Aridity = 1—AI, AI = MAP/PET	Aridity calculated as 1—AI, in which resolution is 30 arc-secs
	Climate	Inter-annual precipitation variability	IPV	$\mathrm{IPV} = \frac{\text{SD of annual precipitation}}{\text{MAP}}$	SD refers to standard deviation.
Standardized field sampling	Soil	Soil organic carbon	SOC		Unit: $\mathrm{g\ kg^{-1}}$
	Soil	Soil total nitrogen	STN		Unit: $\mathrm{g\ kg^{-1}}$
	Soil	Soil total phosphorus	STP		Unit: $\mathrm{g\ kg^{-1}}$
	Soil	Soil pH		$\text{Soil indicator} = \frac{\text{Sum of results}}{\text{Number of samples}}$	
	Soil	Sand content			Unit: percentage
	Soil	Soil bulk density	SBD		Unit: $\mathrm{g\ cm^{-3}}$
	Soil	Soil calcium carbonate content	SCC		Unit: $\mathrm{g\ kg^{-1}}$
	Vegetation	Aboveground biomass	AB	$\text{Biomass} = \frac{\text{Total dry weight}}{\text{Sum of sampling area}}$	Unit: $\mathrm{g\ m^{-2}}$
	Vegetation	Belowground biomass	BB		
	Vegetation	Vegetation coverage	VEGCOV	$\mathrm{VEGCOV} = \frac{\text{Vegetation records}}{\text{Total number of records}}$	Unit: percentage
	Vegetation	Shannon's diversity index	SHDI	$\mathrm{SHDI} = -\sum_{i=1}^{S} \frac{N_i}{N} \ln \frac{N_i}{N}$	N_i / N represents the relative abundance of plant species i; N_i represents the number of individuals of plant species i; N represents the total number of individuals of all plant species in one particular quadrat.
	Vegetation	Leaf carbon content	LCC	$\mathrm{CWM}_j = -\sum_{i=1}^{S} \frac{N_i}{N} \cdot X_{ij}$	CWM_j represents community-weighted mean value of plant functional trait j in one particular quadrat, and the unit is same as the original indicator. X_{ij} represents functional trait j of plant species i, N_i / N represents the relative abundance of plant species i.
	Vegetation	Leaf nitrogen content	LNC		
	Vegetation	Leaf phosphorus content	LPC		
	Vegetation	Leaf dry matter content	LDMC		
	Vegetation	Specific root length	SRL		
	Vegetation	Difference between grass and shrub records	DGS	DGS = Grass records − Shrub records	Unit: unitless
	Plant-Soil	Plant effect on soil organic carbon	PESOC	PESOC = SOC under vegetation—SOC in bare land	Unit: $\mathrm{g\ kg^{-1}}$

selected by calculating the within sum of squares and the elbow method (Goutte *et al* 1999). The total within-cluster sum of squares (TWSSs) was calculated for each of the ten cases from 1 to 10 clusters. Subsequently, the trend of TWSS from cluster numbers 1–10 was explored, and the cluster number with the largest change in slope of TWSS was selected as the best cluster number.

Correlation analysis was used to test relationships between belowground components and soil properties, and aboveground vegetation community characteristics, structure, and ecosystem functions mentioned in the hypothesis. False discovery rate (FDR) was applied to correct the significance of these correlations.

Structural equation models were used to infer the hypothesized direct and indirect relationships between aridity and ecosystem attributes. All data were standardized using Z scores. Ecosystem attributes for constructing the model were then selected by considering the different above and belowground components. The lavaan (Rosseel 2012) package in R 4.1.3 was used to construct the structural equation models based on bivariate correlation analysis (Gu *et al* 2014) and theoretical analysis from literature.

3. Results

3.1. Changes in multiple grassland ecosystem attributes with aridity

The aridity thresholds associated with abrupt changes in attributes are shown in figures 2(a), (b) and S1. Results showed that the linear model was more suitable for the soil calcium carbonate content, soil pH, leaf N content, leaf P content, specific root length and Shannon's diversity index (tables S4 and 5), suggesting these variables had no abrupt change with increasing aridity. The nonlinear model was more suitable for the other 12 variables in relation to the aridity gradient, which showed that there were aridity thresholds where abrupt changes occurred. These thresholds were as follows, in ascending order: 0.49 (plant effect on soil organic carbon), 0.52 (soil bulk density), 0.56 (soil total phosphorus), 0.6 (leaf dry matter content), 0.62 (difference between grass and shrub records), 0.63 (belowground biomass and vegetation cover), 0.66 (leaf carbon content), 0.67 (aboveground biomass, soil organic carbon, soil total nitrogen), and 0.69 (soil sand content). Notably, the aridity thresholds of these variables passed the Mann−Whitney test (figures 2(d), (e) and S2). The confidence intervals for these aridity thresholds and their parameters of segments are shown in table S4. Although the posterior distributions of the aridity thresholds for the variables are not Gaussian, the aridity thresholds for all variables are within the highest density intervals (figure S4).

The models using inter-annual precipitation variability show nonlinear changes along the inter-annual variability for plant effect on soil organic carbon, soil bulk density, soil total phosphorus, belowground biomass and sand content. Their thresholds are 20.4, 20.97, 20.97, 20.96 and 20.96, respectively (tables S5 and S6). The aridity thresholds of plant effect on soil organic carbon, belowground biomass, and soil bulk density remained almost unchanged with increasing inter-annual precipitation variability, as shown in table S7.

The bootstrap method was used to calculate aridity thresholds of the variables and to obtain the distribution of the aridity thresholds at different aridity levels (figure S3(c)). The clustering analysis showed that two clusters were established (figure S3(a)), with their centroids at 0.51 and 0.67. Specific root length exhibited significant changes at the overall threshold of 0.67 (figures 2(c) and (f)), and the threshold was within the highest density interval (figure S4(m)).

3.2. Changes in correlations between belowground components and other grassland ecosystem attributes with aridity

Using the FDR correction for correlation analysis between belowground components and other ecosystem structural and functional attributes, our results showed that specific root length had no significant relationships with either soil nutrient or plant community characteristics variables individually (table 2). Below the threshold, belowground biomass had a significant positive correlation with difference between grass and shrub records (0.52, $P < 0.1$) and a significant negative correlation with soil bulk density (−0.46, $P < 0.1$), while above the threshold, these relationships were not significant (table 2). Soil organic carbon had significant positive correlations with vegetation coverage (0.5, $P < 0.1$) and significant negative correlations with pH (−0.73, $P < 0.01$) and sand content (−0.92, $P < 0.01$) below the threshold. However, above the threshold, these relationships were not significant (table 2).

3.3. Changes in effects and pathways of aridity on belowground components in grasslands

Structural equation models were constructed on both sides of the aridity threshold of 0.67 to explore the direct or indirect relationships between aridity and belowground components. Results showed that aridity exhibited a direct negative effect on specific root length, but also had an indirect effect by reducing the soil total nitrogen below the aridity threshold of 0.67 (figure 3(a)). The relationships between aridity, soil total nitrogen and specific root length all became insignificant above the aridity threshold of 0.67 (figure 3(b)). The effect of leaf nitrogen content on specific root length changed from insignificant to significant, with a coefficient of 0.47 (figure 3(b)).

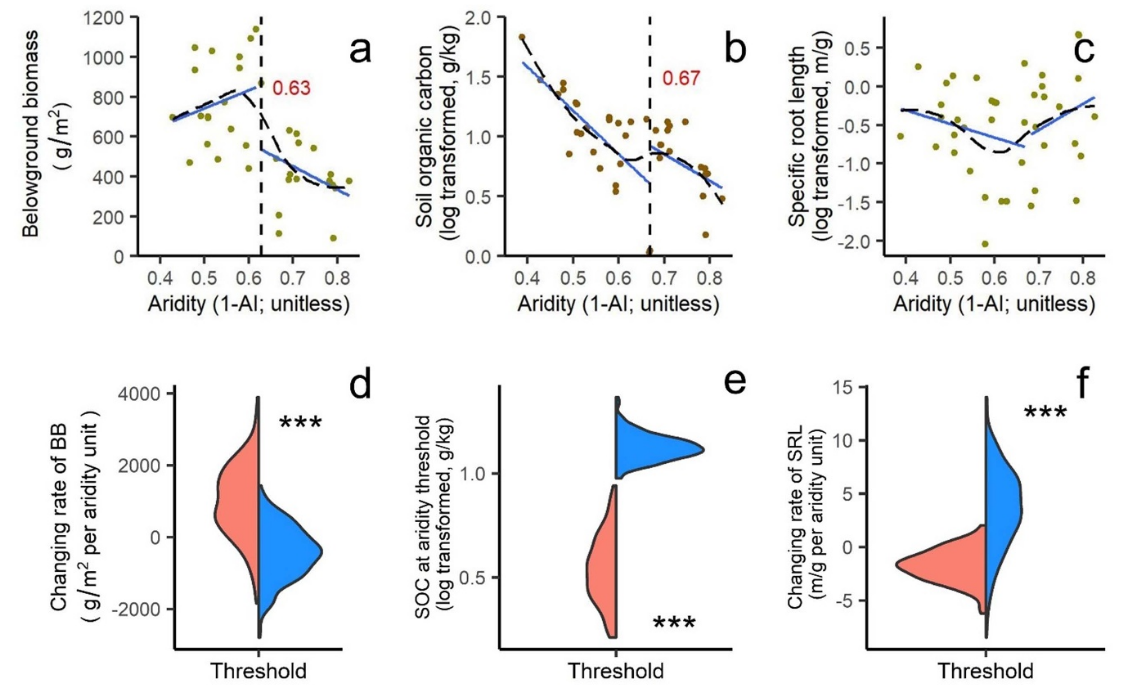

Figure 2. Nonlinear responses of belowground components to increasing aridity. Nonlinear responses observed for belowground biomass (a), soil organic carbon (b), specific root length (c). In (a)–(c), black dashed lines and blue solid lines represent the smoothed trend fitted by a generalized additive model (GAM) and the linear fits at both sides of each threshold, respectively. Inset numbers in red and the vertical dashed lines describe the aridity threshold identified. In (d)–(f), violin diagrams show bootstrapped slopes or values of the predicted fitted trend at the threshold of the two regressions existing at each side of the threshold (red: below the threshold; blue, above the threshold). Asterisks indicate significant differences when conducting a Mann-Whitney U test between slopes or values below and above the threshold where: $^{*}P < 0.1$; $^{**}P < 0.05$; $^{***}P < 0.01$.

Table 2. Corrected correlations between belowground components, soil properties, and aboveground ecosystem attributes.

Variable name		Below the threshold		Above the threshold	
		R	P value	R	P value
SRL	STN	−0.28	0.976	−0.05	0.868
	STP	0.12	0.976	−0.20	0.776
	LCC	−0.01	0.976	0.05	0.868
	LNC	0.10	0.976	0.38	0.615
	LPC	−0.04	0.976	0.24	0.776
	LDMC	0.06	0.976	0.46	0.615
BB	Sand	−0.34	0.209	−0.36	0.278
	SBD	−0.46	0.099	−0.49	0.278
	SHDI	−0.04	0.861	0.34	0.278
	DGS	0.52	0.095	0.33	0.278
SOC	PESOC	−0.06	0.817	−0.27	0.370
	AB	−0.41	0.104	0.34	0.370
	VEGCOV	0.50	0.05	0.62	0.126
	Soil pH	−0.73	0.001	−0.29	0.370
	Sand	−0.92	0.000	−0.42	0.370

The coefficient of the total effect of aridity shifted from −0.18 to 0.24 above the threshold.

The model showed an insignificant effect of aridity and soil bulk density on belowground biomass (figure 3(c)). Difference between grass and shrub records exhibited a positive effect on belowground biomass with a coefficient of 0.44 ($P < 0.05$) below the aridity threshold. A positive effect of aridity on soil bulk density was found (figure 3(c)). The effect of aridity became significant when the level of aridity was >0.67, with a coefficient of −0.44 ($P < 0.1$) (figure 3(d)). Difference between grass

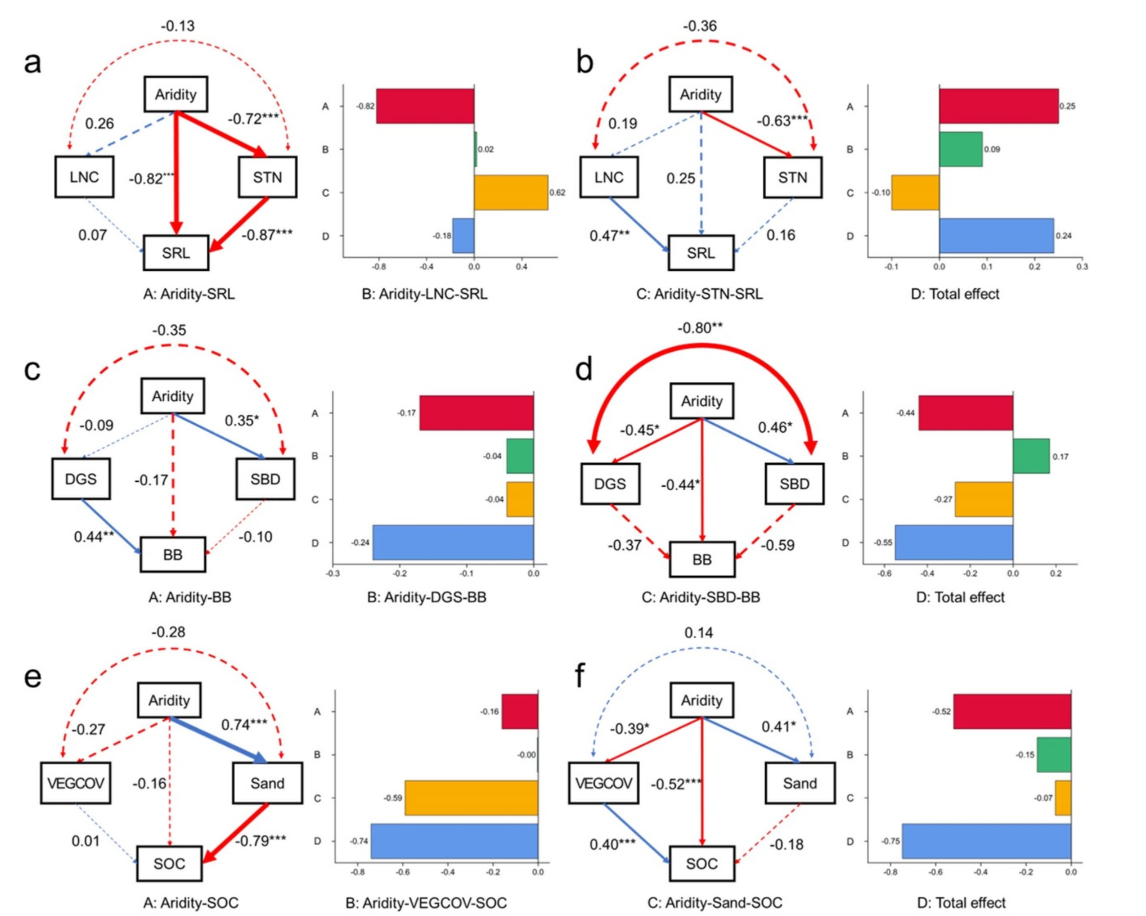

Figure 3. Effects and driving pathways of aridity on specific root length, belowground biomass and soil organic carbon. Structural equation models are shown for sites with aridity <0.67 (a), (c), (e) and >0.67 (b), (d), (f). The numbers in the path diagrams represent the standardized path coefficients, and the colours (negative and positive effects, presented as red and blue arrows, respectively) and widths of the arrows represent the signs and magnitudes of the path coefficients, respectively. Asterisks indicate the significance level of each coefficient: $^*P < 0.1$; $^{**}P < 0.05$; $^{***}P < 0.01$. A, B and C in the bar diagrams on the right of the path diagrams represent the effect of three major paths; D is the total effect. LNC, leaf nitrogen content; STN, soil total nitrogen; SRL, specific root length; DGS, difference between grass and shrub records; SBD, soil bulk density; BB, belowground biomass; VEGCOV, vegetation coverage; Sand, sand content; SOC, soil organic carbon.

and shrub records decreased with increasing aridity (figure 3(d)), but the effect of difference between grass and shrub records on belowground biomass became insignificant. The continuous rise in soil bulk density was negatively correlated with difference between grass and shrub records at a threshold above 0.67 (-0.80, $P < 0.05$). The total effect of aridity was enhanced from -0.24 to -0.55 above the threshold. Unlike belowground biomass, the effect of aridity on the proportion of belowground biomass was always positive and significant above and below the threshold, at 0.52 and 0.45 respectively (figure S5).

Where aridity was below the threshold value of 0.67, soil organic carbon was mainly modulated by the indirect effect of aridity-soil sand content (figure 3(e)). The coefficients between aridity and soil sand content, as well as between soil sand content and soil organic carbon, were 0.74 ($P < 0.01$) and -0.79 ($P < 0.01$), respectively. The negative effect of soil sand content on soil organic carbon was insignificant when the aridity level was above the threshold at 0.67, but aridity showed a negative effect on soil organic carbon with a coefficient of -0.52 ($P < 0.01$) (figure 3(f)). After accounting for the negative effect of aridity on vegetation coverage (-0.39, $P < 0.1$), the effect of vegetation coverage on soil organic carbon is positive with a slope of 0.40 ($P < 0.01$) (figure 3(f)). The total effects of aridity below and above the threshold were similar (-0.74 and -0.75).

4. Discussion

4.1. Aridity thresholds in grassland ecosystems

The results showed abrupt changes in the grassland ecosystem at aridity index levels of 0.51 and 0.67. The threshold changed from negative to positive between plants and soil organic carbon (figure S1(a)). A previous study reported that the input of leaf litter from areas with vegetation increases the organic matter content of the soil compared with bare ground (Kaouthar and Chaieb 2009). Plants can accelerate the decomposition of soil organic carbon by stimulating soil microbial activity through rhizosphere effects (Shahzad *et al* 2015). The aridity threshold obtained for soil total phosphorus was consistent with the results reported by Hu *et al* (2021). However, this value does not indicate a change in the relationship between soil total phosphorus and other ecosystem properties, because soil phosphorus level is mainly modulated by soil type and climate (Wang *et al* 2008) and not the ecosystem. A previous study reported that leaf phosphorus content and soil available and total phosphorus are not significantly correlated (Geng *et al* 2011).

Several ecosystem attributes including difference between grass and shrub records, soil organic carbon, soil total nitrogen, and soil sand content changed abruptly at approximately 0.67 aridity, which corresponds to the 'soil disruption phase' (Berdugo *et al* 2020). Leaf dry matter content firstly increased and then decreased with aridity (figure S1(d)), which reflected a shift in leaf economic spectrum (Blumenthal *et al* 2020). The nonlinear trend of specific root length decreasing first and then increasing with aridity (figure 2(c)), which is contrary to the change in leaf dry matter content, shows the correlation between above and belowground community characteristics. The nonlinear change of belowground biomass with aridity, increasing first and then decreasing, supports our hypothesis (figure 2(a)). Belowground biomass, soil organic carbon, soil sand content, and soil total nitrogen all shifted around 0.67 compared with the aridity threshold of 0.51. Notably, these attributes were markedly correlated with the belowground components. In addition, specific root length shifted from negative to positive at around 0.67 (figures 2(c) and (f)).

Previous studies have shown that inter-annual precipitation variability may affect ecosystem dynamics (D'Odorico and Bhattachan 2012, Berdugo *et al* 2020). However, our results show that several ecosystem attributes (plant effect on soil organic carbon, soil bulk density, belowground biomass, soil total phosphorus, and sand content) have inter-annual variability thresholds, and increasing inter-annual variability does not affect the abrupt changes of plant effect on soil organic carbon, soil bulk density and belowground biomass along the aridity gradient (table S7). This may be because the range of the inter-annual precipitation variability in the surveyed plots was small, ranging from 17.88 to 23.56. In addition, it has been suggested that inter-annual variability exceeding 30% can cause ecosystems to become non-equilibrium (Illius and O'Connor 1999, von Wehrden *et al* 2012), while the inter-annual variability in our study remained below 30%. Therefore, the structural and functional shifts of the ecosystems in this study were mainly driven by aridity, rather than inter-annual variability.

4.2. Effects and driving pathways of aridity on belowground components below and above the threshold

The correlation analysis results showed that the belowground components were only significantly correlated with soil properties and aboveground ecosystem attributes below the aridity threshold. Above the threshold, there was no significant correlation between them (table 2), which presented the need for the involvement of aridity in the analysis. The effects and driving pathways of aridity on belowground components vary below and above the threshold of 0.67.

Aridity exhibited a negative effect on specific root length of plants within communities below the aridity threshold of 0.67 (figure 3(a)). This reduction can be attributed to the reduced soil moisture due to the increased aridity level that hinders root growth (Grzesiak *et al* 2002). As a result, plants have to enhance drought resistance of their roots (by exhibiting a lower specific root length). N content of the soil also reduces with increasing aridity, which could result in increased specific root length (Ostonen *et al* 2007). This implies that aridity indirectly promotes root elongation by affecting the soil nutrient content.

The effect of aridity on specific root length decreased and became insignificant above the aridity threshold of 0.67 (figure 3(b)), indicating the reduced ability of drought stress to limit root growth. The shift in specific root length with increasing aridity is confirmed by the trend of leaf dry matter content increasing first and then decreasing with aridity gradient, and the positive relationship between leaf nitrogen content and specific root length (figure 3(b)). High leaf nitrogen content is associated with high photosynthetic efficiency and increased specific root length corresponds to high water (in shallow soil) (Fort *et al* 2017) and nutrient acquisition capacity (Fort *et al* 2012, Ravenek *et al* 2016). Both high photosynthetic efficiency and resource acquisition capacity are 'fast' economic traits, reflecting coordination between the economic spectrum of above and belowground components. Considering that the correlation analysis did not show any association between specific root length and aboveground community characteristics, the effect of aridity may drive the emergence of this coordination.

Aridity had different driving pathways on belowground biomass above and below the aridity threshold (figures 3(c) and (d)). The increasing aridity level did not significantly increase the belowground biomass before the aridity level reached 0.67, and the total effect was negative. Difference between grass and shrub records exhibited a positive effect on the value of belowground biomass (figure 3(c)), indicating that the relative dominance of herbaceous plants alleviated the negative effect of aridity on belowground biomass in grasslands.

Belowground biomass shifted to be only influenced by aridity above the aridity threshold of 0.67 (figure 3(d)). Several studies report that belowground biomass decreases when aridity increases to a certain level (Wang *et al* 2019, Hu *et al* 2022). Although some findings indicate that the proportion of carbon allocated to the root system increases with aridity (Wellstein *et al* 2017), which is also supported by the effect of aridity on the proportion of belowground biomass (figure S5), the source of allocation, for example, aboveground biomass decreased significantly (figure S1(h)). This finding may explain the negative effect of aridity on belowground biomass. Soil bulk density increased with increasing aridity just below the aridity threshold (figure 3(c)), further increased above the threshold, and ultimately negatively affected difference between grass and shrub records in combination with aridity. Some studies have shown that certain shrub species have more advantages than herbaceous plants to adapt to arid climate (Berdugo *et al* 2020) and compacted soils (Cai *et al* 2020). In addition, the effect of difference between grass and shrub records on belowground biomass was not observed above the threshold (figure 3(d)). This may be because some shrubs have deeper roots to reach the deeper soil water layers (Berdugo *et al* 2022). Therefore, an increase in the relative abundance of shrubs results in a lower distribution of belowground biomass in shallow soils. The total negative effect of aridity on belowground biomass increased without significant effect of difference between grass and shrub records.

The present findings show that soil organic carbon was mainly affected by soil sand content at aridity below 0.67 (figure 3(e)). Aridity can alter soil texture by reducing soil moisture, making soil aggregates more unstable, and increasing the risk of wind erosion (Berdugo *et al* 2022). Aridity exhibited a negative effect on soil sand content (figure 3(e)). Soil texture directly affects soil microbial communities, seed germination and plant growth (Gaines and Gaines 1994, Bach *et al* 2010), which in turn affects the decomposition and input of litter into the soil. Soil clay content declines with an increase in sand content, which directly affects soil organic carbon stocks (O'Brien *et al* 2015).

Aridity showed a direct effect on soil organic carbon at aridity more than 0.67, and the driving pathway through which aridity indirectly affects soil organic carbon changed from sand content to vegetation coverage (figure 3(f)). Plants can effectively protect soils from erosion (Schlesinger *et al* 1990), therefore, when vegetation coverage is reduced, soil resistance to erosion is weakened, resulting in soil organic carbon loss. The reduction in vegetation coverage may be accompanied by a decrease in the amount of litter, which further reduces the input of soil organic carbon. Notably, increasing aridity was associated with small plant effect on soil organic carbon within plots (figure S1(a)). However, vegetation coverage exhibited a significant effect on soil organic carbon between plots, which highlights the ability of vegetation coverage to regulate the effect of aridity on soil organic carbon at a larger spatial scale above the aridity threshold of 0.67.

In summary, the effects and driving pathways of aridity on belowground components in grasslands changed at the aridity threshold of 0.67 (figure 4). The present findings indicate that the effect of aridity on specific root length were consistent with our hypothesis. The negative effects of aridity on belowground biomass and the increase of the proportion of belowground biomass with aridity are consistent with our hypotheses above and below the threshold, respectively. The relative increase in grass no longer alleviates the effects of increases in aridity above the aridity threshold, supporting the hypothesis that the underlying driving forces of belowground biomass changed across the aridity threshold. The effect of aridity on soil organic carbon was not significantly different below and above the threshold. However, the driving pathways showed loss of soil fine particles controlled pre-threshold soil organic carbon and vegetation coverage at plot scale modulated post-threshold soil organic carbon, which confirms our hypothesis that the underlying driving forces of soil organic carbon varied below and above the aridity threshold.

4.3. Limitations and future prospects

This study used threshold models and structural equation models to analyse the effects of aridity on belowground components in grasslands. However, the model did not account for the interactions between multiple factors and ecosystem attributes. A more sophisticated model may be better to illustrate how various soil and climate characteristics affect belowground components in grasslands and reveal their complex interactions. Our current results provide an exploratory analysis for developing such a model. In addition, our study found that certain traits related to plant life history strategies exhibit an aridity threshold, however, the current analytical approach and results are insufficient to explain this phenomenon. Further analysis is required to examine specific plant species and clarify the relationship between individual plant behaviour and community strategies, as well as how their balance changes along the aridity gradient.

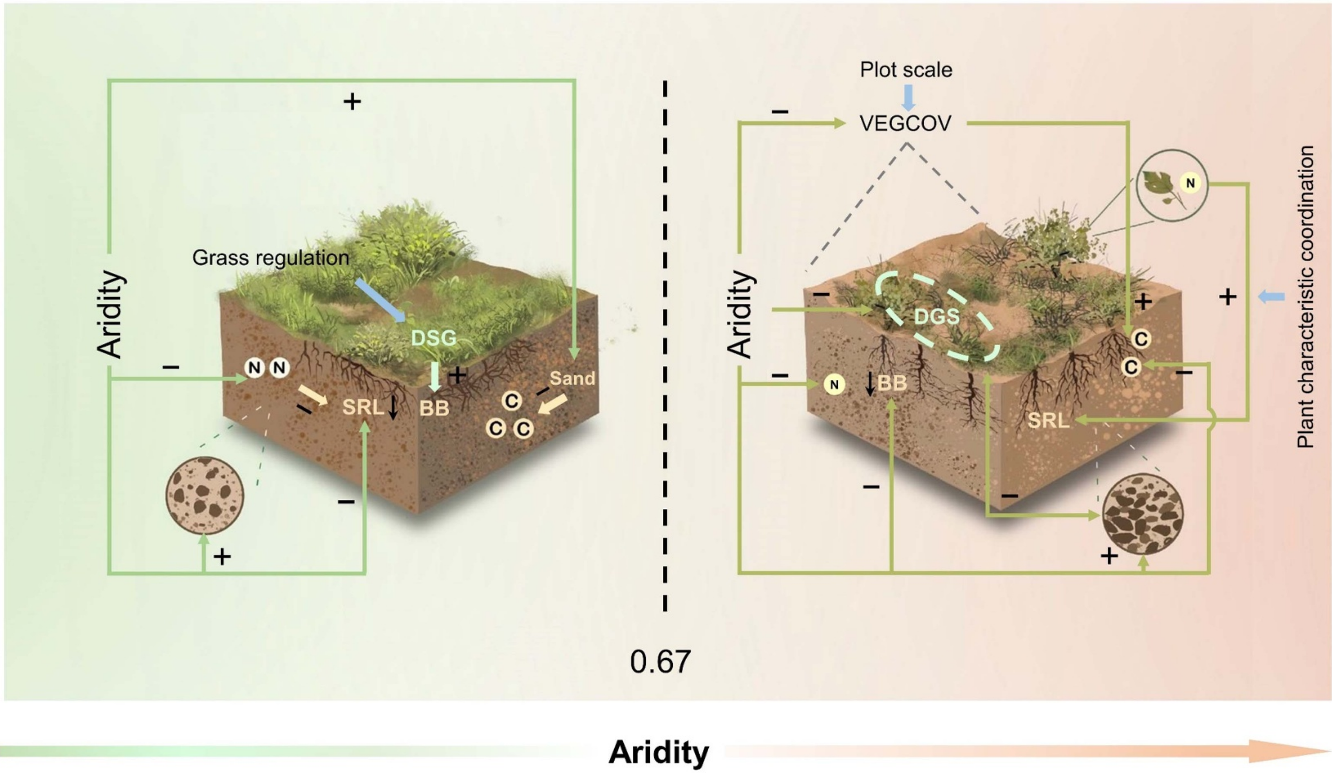

Figure 4. Driving pathways of aridity impacts on belowground components of grassland ecosystems below and above the aridity threshold of 0.67. N, nitrogen content; C, carbon content; SRL, specific root length; DGS, difference between grass and shrub records; BB, belowground biomass; VEGCOV, vegetation coverage.

5. Conclusion

The effects and driving pathways of aridity on belowground components changed at aridity threshold above 0.67 in grasslands. Aridity negatively and positively affects specific root length below and above the threshold, with total effects of −0.18 and 0.24, respectively. This shift is influenced by soil nutrients and indirectly driven by aridity, and is associated with aboveground community characteristics in more arid areas. Influence of aridity on belowground biomass was always negative and was markedly enhanced above the threshold from −0.24 to −0.55. The relative increase in grass contributes to mitigating the effects of increase in aridity below the aridity threshold. Total effects of aridity on soil organic carbon exhibited insignificant change, but the driving pathways through which aridity affects soil organic carbon shifted from soil loss to aridity and vegetation coverage. The findings showed that spatial scale modulated the effect of vegetation coverage on soil organic carbon above the threshold. These findings provide a basis for understanding the mechanisms of how belowground components in grasslands change with aridity and the ways they do this (driving pathways). Findings could inform the protection of grasslands under climate change and future aridification.

Data availability statement

The data cannot be made publicly available upon publication because they are not available in a format that is sufficiently accessible or reusable by other researchers. The data that support the findings of this study are available upon reasonable request from the authors.

Acknowledgments

This research is jointly funded by the National Natural Science Foundation of China Project (Grants 41991235, 42007052), and the Fundamental Research Funds for the Central Universities. The authors have confirmed that any identifiable participants in this study have given their consent for publication.

Author contributions

Z R and C L conceived and designed the study. Z R carried out the calculations, drafted the figures and wrote the first draft of the manuscript. C L, B F, S W and L S reviewed and edited the manuscript before submission. All authors made substantial contributions to the discussion of content.

Conflict of interest

The authors declare no competing interests.

References

Asefa M, Worthy S J, Cao M, Song X, Lozano Y M and Yang J 2022 Above- and below-ground plant traits are not consistent in response to drought and competition treatments *Ann. Bot.* **130** 939–50

Bach E M, Baer S G, Meyer C K and Six J 2010 Soil texture affects soil microbial and structural recovery during grassland restoration *Soil Biol. Biochem.* **42** 2182–91

Bai Y and Cotrufo M F 2022 Grassland soil carbon sequestration: current understanding, challenges, and solutions *Science* **377** 603–8

Bardgett R D *et al* 2021 Combatting global grassland degradation *Nat. Rev. Earth Environ.* **2** 720–35

Berdugo M *et al* 2020 Global ecosystem thresholds driven by aridity *Science* **367** 787–90

Berdugo M, Kefi S, Soliveres S and Maestre F T 2017 Plant spatial patterns identify alternative ecosystem multifunctionality states in global drylands *Nat. Ecol. Evol.* **1** 1–10

Berdugo M, Vidiella B, Sole R V and Maestre F T 2022 Ecological mechanisms underlying aridity thresholds in global drylands *Funct. Ecol.* **36** 4–23

Blumenthal D M, Mueller K E, Kray J A, Ocheltree T W, Augustine D J and Wilcox K R 2020 Traits link drought resistance with herbivore defence and plant economics in semi-arid grasslands: the central roles of phenology and leaf dry matter content *J. Ecol.* **108** 2336–51

Burri S, Sturm P, Prechsl U E, Knohl A and Buchmann N 2014 The impact of extreme summer drought on the short-term carbon coupling of photosynthesis to soil CO_2 efflux in a temperate grassland *Biogeosciences* **11** 961–75

Butterfield B J, Bradford J B, Munson S M and Gremer J R 2017 Aridity increases below-ground niche breadth in grass communities *Plant Ecol.* **218** 385–94

Cai Y, Yan Y, Xu D, Xu X, Wang C, Wang X, Chen J, Xin X and Eldridge D J 2020 The fertile island effect collapses under extreme overgrazing: evidence from a shrub-encroached grassland *Plant Soil* **448** 201–12

Canty A and Ripley B 2021 Package 'boot'. Reference manual available at R-CRAN (available at: https://cran.r-project.org/web/packages/boot/boot.pdf)

Comas L H, Becker S R, Cruz V V, Byrne P F and Dierig D A 2013 Root traits contributing to plant productivity under drought *Front. Plant Sci.* **4** 442

D'Odorico P and Bhattachan A 2012 Hydrologic variability in dryland regions: impacts on ecosystem dynamics and food security *Phil. Trans. R. Soc.* B **367** 3145–57

Delgado-Baquerizo M *et al* 2013 Decoupling of soil nutrient cycles as a function of aridity in global drylands *Nature* **502** 672–6

FAO 2019 Trees, forests and land use in drylands: the first global assessment—Full report *FAO Forestry Paper No. 184*

Fong Y, Huang Y, Gilbert P B and Permar S R 2017 chngpt: threshold regression model estimation and inference *BMC Bioinform.* **18** 1–7

Fort F, Jouany C and Cruz P 2012 Root and leaf functional trait relations in Poaceae species: implications of differing resource-acquisition strategies *J. Plant Ecol.* **6** 211–9

Fort F, Volaire F, Guilioni L, Barkaoui K, Navas M L and Roumet C 2017 Root traits are related to plant water-use among rangeland Mediterranean species *Funct. Ecol.* **31** 1700–9

Gaines T P and Gaines S T 1994 Soil texture effect on nitrate leaching in soil percolates *Commun. Soil Sci. Plant Anal.* **25** 2561–70

Galvez D A, Landhausser S M and Tyree M T 2011 Root carbon reserve dynamics in aspen seedlings: does simulated drought induce reserve limitation? *Tree Physiol.* **31** 250–7

Gang C, Zhou W, Chen Y, Wang Z, Sun Z, Li J, Qi J and Odeh I 2014 Quantitative assessment of the contributions of climate change and human activities on global grassland degradation *Environ. Earth Sci.* **72** 4273–82

Garnier E *et al* 2004 Plant functional markers capture ecosystem properties during secondary succession *Ecology* **85** 2630–7

Geng Y, Wu Y and He J 2011 Relationship between leaf phosphorus concentration and soil phosphorus availability across Inner Mongolia grassland *Chin. J. Plant Ecol.* **35** 1–8
Gibson D J and Newman J A 2019 Grasslands and climate change: an overview *Grasslands and Climate Change* ed D J Gibson and J A Newman (Cambridge University Press) pp 3–18
Goutte C, Toft P, Rostrup E, Nielsen F A and Hansen L K 1999 On clustering fMRI time series *NeuroImage* **9** 298–310
Grime J P, Fridley J D, Askew A P, Thompson K, Hodgson J G and Bennett C R 2008 Long-term resistance to simulated climate change in an infertile grassland *Proc. Natl Acad. Sci. USA* **105** 10028–32
Grzesiak S, Grzesiak M T, Felek W, Hura T and Stabryla J 2002 The impact of different soil moisture and soil compaction on the growth of triticale root system *Acta Physiol. Plant.* **24** 331–42
Gu Z, Gu L, Eils R, Schlesner M and Brors B 2014 circlize implements and enhances circular visualization in R *Bioinformatics* **30** 2811–2
Hasibeder R, Fuchslueger L, Richter A and Bahn M 2015 Summer drought alters carbon allocation to roots and root respiration in mountain grassland *New Phytol.* **205** 1117–27
Hastie T J and Tibshirani R J 2017 *Generalized Additive Models* (Routledge)
Hu W *et al* 2021 Aridity-driven shift in biodiversity-soil multifunctionality relationships *Nat. Commun.* **12** 5350
Hu Z *et al* 2022 Aridity influences root versus shoot contributions to steppe grassland soil carbon stock and its stability *Geoderma* **413** 115744
Huang B and Fu J 2000 Photosynthesis, respiration, and carbon allocation of two cool-season perennial grasses in response to surface soil drying *Plant Soil* **227** 17–26
Illius A W and O'Connor T G 1999 On the relevance of nonequilibrium concepts to arid and semiarid grazing systems *Ecol. Appl.* **9** 798–813
Kaouthar J and Chaieb M 2009 The effect of Stipa tenacissima tussocks on some soil surface properties under arid bioclimate in the southern Tunisia *Acta Bot. Gall.* **156** 173–81
Larson J E and Funk J L 2016 Seedling root responses to soil moisture and the identification of a belowground trait spectrum across three growth forms *New Phytol.* **210** 827–38
Liu Y, Li P, Wang T, Liu Q and Wang W 2020 Root respiration and belowground carbon allocation respond to drought stress in a perennial grass (Bothriochloa ischaemum) *Catena* **188** 104449
Luo W *et al* 2016 Thresholds in decoupled soil-plant elements under changing climatic conditions *Plant Soil* **409** 159–73
Maestre F T, Eldridge D J, Gross N, Le Bagousse-Pinguet Y, Saiz H, Gozalo B, Ochoa V and Gaitán J J 2022 The BIODESERT survey: assessing the impacts of grazing on the structure and functioning of global drylands *Web. Ecol.* **22** 75–96
O'Brien S L, Jastrow J D, Grimley D A and Gonzalez-Meler M A 2015 Edaphic controls on soil organic carbon stocks in restored grasslands *Geoderma* **251–252** 117–23
Ostonen I *et al* 2007 Specific root length as an indicator of environmental change *Plant Biosyst.* **141** 426–42
Ravenek J M, Mommer L, Visser E J W, van Ruijven J, van der Paauw J W, Smit-Tiekstra A, de Caluwe H and de Kroon H 2016 Linking root traits and competitive success in grassland species *Plant Soil* **407** 39–53
Rosseel Y 2012 lavaan: an R package for structural equation modeling *J. Stat. Softw.* **48** 1–36
Ryser P 2006 The mysterious root length *Plant Soil* **286** 1–6
Sanaullah M, Chabbi A, Rumpel C and Kuzyakov Y 2012 Carbon allocation in grassland communities under drought stress followed by C-14 pulse labeling *Soil Biol. Biochem.* **55** 132–9
Schlesinger W H, Reynolds J F, Cunningham G L, Huenneke L F, Jarrell W M, Virginia R A and Whitford W G 1990 Biological feedbacks in global desertification *Science* **247** 1043–8
Shahzad T, Chenu C, Genet P, Barot S, Perveen N, Mougin C and Fontaine S 2015 Contribution of exudates, arbuscular mycorrhizal fungi and litter depositions to the rhizosphere priming effect induced by grassland species *Soil Biol. Biochem.* **80** 146–55
Shannon C E and Weaver W 1949 The mathematical theory of communication *Philosophical Review*
Slessarev E W, Lin Y, Bingham N L, Johnson J E, Dai Y, Schimel J P and Chadwick O A 2016 Water balance creates a threshold in soil pH at the global scale *Nature* **540** 567–9
von Wehrden H, Hanspach J, Kaczensky P, Fischer J and Wesche K 2012 Global assessment of the non-equilibrium concept in rangelands *Ecol. Appl.* **22** 393–9
Wang C *et al* 2014 Aridity threshold in controlling ecosystem nitrogen cycling in arid and semi-arid grasslands *Nat. Commun.* **5** 1–8
Wang J, Shi Y, Ao Y, Yu D, Wang J, Gao S, Knops J M H, Mu C and Li Z 2019 Summer drought decreases Leymus chinensis productivity through constraining the bud, tiller and shoot production *J. Agron. Crop Sci.* **205** 554–61
Wang T, Yang Y and Ma W 2008 Storage, patterns and environmental controls of soil phosphorus in China *Acta Sci. Nat. Univ. Pekin.* **44** 945–52
Wang X, Lu X, Zhang H, Dijkstra F A, Jiang Y, Wang X, Lu J, Wu Y, Wang Z and Han X 2020 Changes in soil C:N:P stoichiometry along an aridity gradient in drylands of northern China *Geoderma* **361** 114087
Wellstein C, Poschlod P, Gohlke A, Chelli S, Campetella G, Rosbakh S, Canullo R, Kreyling J, Jentsch A and Beierkuhnlein C 2017 Effects of extreme drought on specific leaf area of grassland species: a meta-analysis of experimental studies in temperate and sub-Mediterranean systems *Glob. Change Biol.* **23** 2473–81
White R P, Murray S and Rohweder M 2000 *Pilot Analysis of Global Ecosystems: Grassland Ecosystems* (World Resources Institute)
Wu G, Liu Y, Cui Z, Liu Y, Shi Z, Yin R and Kardol P 2020 Trade-off between vegetation type, soil erosion control and surface water in global semi-arid regions: a meta-analysis *J. Appl. Ecol.* **57** 875–85