Journal of
Water & Climate Change

Journal of Water and Climate Change Vol 14 No 7, 2465 doi: 10.2166/wcc.2023.146

Asymmetric response of above- and below ground biomass of C_3- and C_4-dominated grasslands to aridity

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ABSTRACT

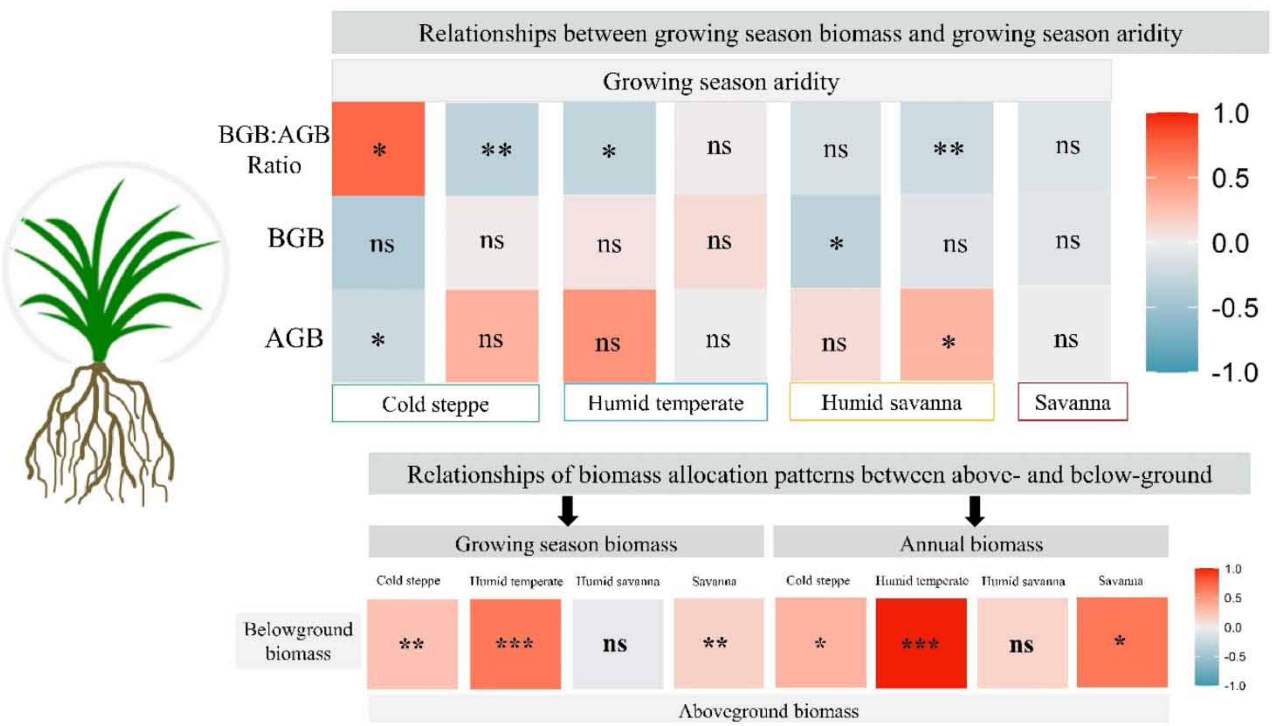
Assessing the dynamics of grassland functioning is critical for gaining an understanding of their feedback on rising aridity. In attempting to understand the response of grassland ecosystem functioning to aridity, the (i) relationships between biomass productivity (above- and below-ground biomass: AGB and BGB, and their partitioning: BGB:AGB) and seasonal and annual aridity, and (ii) biomass allocation pattern between the AGB and BGB of C_3- and C_4-dominated grasslands in humid temperate, humid savanna, cold steppe, and savanna ecoregions were assessed. Results reveal that biomass productivity and its partitioning responded significantly to differences in growing season aridity, but the response patterns were not consistent for ecoregions. The decreased annual and seasonal biomass partitioning in humid savanna and cold steppe was associated with increased AGB and decreased BGB with accelerated aridity. There was a significant positive correlation in the biomass allocation pattern between the AGB and BGB of plants in three ecoregions, which supports the optimal partitioning theory. This study reveals that growing season aridity, rather than annual aridity, is the primary factor of biomass productivity and partitioning in the studied grasslands. These findings have significant repercussions for predicting ecosystem functioning and stability, restoring degraded ecosystems, and ensuring the sustainable management of grassland biodiversity.

Key words: aridity, biomass allocation, C_3 and C_4 grasslands, climatic variability, ecoregion, ecosystem productivity

HIGHLIGHTS

- Ecosystem functioning under aridity has been assessed for four grassland ecoregions.
- Significant changes in growing season biomass resulted from increasing growing season aridity.
- Above- and belowground biomass showed a positive correlation and supported optimal partitioning theory.

GRAPHICAL ABSTRACT



1. INTRODUCTION

Aboveground biomass (AGB) and belowground biomass (BGB) productivity are significant determinants of ecosystem health and are used to assess the functionality and predictability of grassland ecosystems (Isbell *et al.* 2015; Hossain & Li 2021a). Over the past few decades, one of the most important topics of investigation in the field of plant ecology has been the impact of climate change on AGB and BGB productivity in grassland ecosystems (Jentsch *et al.* 2011; Luo *et al.* 2017; Zhang *et al.* 2017a; Hossain & Li 2021b). In ecological research, there has been a discussion going on for over three decades about the factors that drive grassland AGB productivity (Craine *et al.* 2012; Kreyling *et al.* 2017; Hossain & Li 2020) and BGB productivity (Wu *et al.* 2011; Luo *et al.* 2017; Zhang *et al.* 2019) and their partitioning (BGB:AGB ratio) (Yang *et al.* 2010; Qi *et al.* 2019).

The sensitivity of grasslands' AGB and BGB to climatic variability (e.g., temperature and precipitation) has been documented in several empirical investigations (Huxman *et al.* 2004; Wilcox *et al.* 2014; La Pierre *et al.* 2016; Guo *et al.* 2017). Despite much progress in climate–ecosystem relationships, there is still debate over whether the growing season or annual climatic variability affects the productivity of AGB and BGB (Figure 1). For example, numerous studies have shown that climatic variability during the growing season (e.g., April–October in Chinese grasslands and mid-March–mid-September in Central European grasslands) is the primary factor in determining both AGB and BGB productivity (Sala *et al.* 1988; Winslow *et al.* 2003; Niu *et al.* 2005; Xia *et al.* 2010; La Pierre *et al.* 2011; Hossain 2022). While growing evidence reports that the annual, but not the seasonal temperature and precipitation are better predictors of AGB and BGB productivity at large spatial scales (Knapp & Smith 2001; Hsu *et al.* 2012; Sala *et al.* 2012; Wilcox *et al.* 2017; Su *et al.* 2020). Even more, studies have demonstrated that the interactions between BGB and precipitation are positive (Byrne *et al.* 2013; Wilcox *et al.* 2014), negative (Byrne *et al.* 2013; Xu *et al.* 2013), and inconsistent (Hui & Jackson 2006; Zhang *et al.* 2017b, 2019).

The observed discrepancies in previous studies could result from multiple factors, including (i) the variations in spatial scales of the study (e.g., single or multiple sites; Hossain *et al.* 2021; Zhang *et al.* 2021), (ii) the differences in experimental duration (e.g., short or long term; Niu *et al.* 2005; Hossain *et al.* 2022), (iii) the differences in vegetation types (e.g., C_3 or C_4 plants; Winslow *et al.* 2003; Niu *et al.* 2005; Hossain *et al.* 2023a), and (iv) consideration of either AGB or BGB without considering biomass allocation pattern (Hossain & Li 2021b). Since a large percentage of grasslands' coverage is

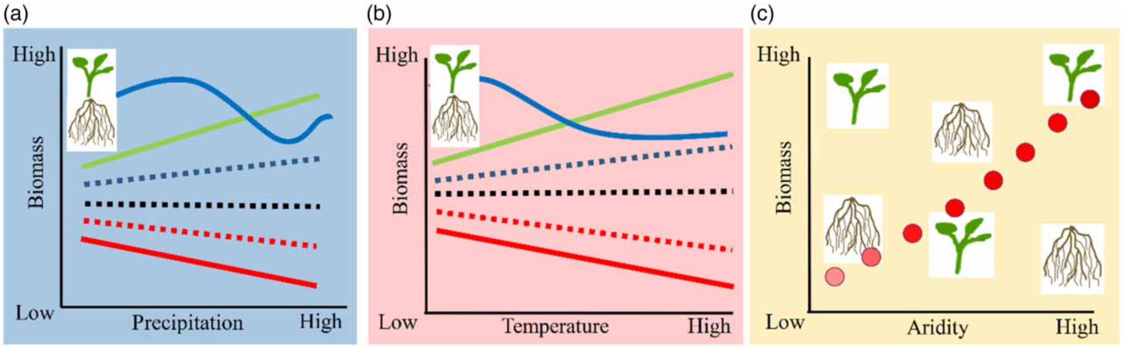


Figure 1 | Mixed understanding of responses of AGB and BGB to climatic variability (precipitation (a) and temperature (b)) and climatic condition (aridity (c)) observed in previous studies across various grassland ecosystems.

water-limited, aridity can play a great role in the functioning and stability of these ecosystems (Harpole *et al.* 2011). In order to advance our understanding of the interactions of ecosystems with climatic conditions, considerations of several biophysical properties, such as plant functional types, multiple ecoregions, several climatic variables (growing season and annual aridity), and the long-run datasets of AGB and BGB, are of great importance (Li *et al.* 2013a, 2013b; Aleksanyan *et al.* 2020; Cui *et al.* 2021). The aforementioned recurring debates highlight the importance of gaining a comprehensive understanding of the functioning of C_3- and C_4-dominated grasslands at larger scales in relation to temporal patterns of aridity.

Aridity is the most influential abiotic factor in grassland ecosystems because the majority of grasslands have limited water resources (Merbold *et al.* 2009; Harpole *et al.* 2011). The global area of drylands is projected to rise by 11–23% by 2100 (Huang *et al.* 2015), accompanied by decreased soil moisture and increased aridity (Fu & Feng 2014; Zhang *et al.* 2014, 2015). The expected rises in aridity would reduce the capability of global grasslands to supply the valuable services of ecosystems that sustain life (Li *et al.* 2013b; Trenberth *et al.* 2014; Berdugo *et al.* 2020). It has been claimed that aridity reduces the number of plant species and their functioning and alters the organization of above- and belowground communities across grassland types (e.g., meadow, alpine, and temperate grasslands) (Maestre *et al.* 2015; Berdugo *et al.* 2020). There is mounting evidence that the productivity of grasslands has been affected by altered precipitation patterns, increased growing season temperature, more frequent extreme weather events, and increased aridity across grassland-dominated ecosystems (Huang *et al.* 2015; Hossain & Li 2021a). Approximately 250 million people in lower and developing nations are being impacted by desertification and land degradation resulting from these climate-induced stresses (Reynolds *et al.* 2007). Because ecosystem services, including nutrient cycling, carbon storage in plants and soil, and the breakdown of organic matter, are influenced by these abiotic factors, ecosystem stability is predicted to diminish with rising aridity (Maestre *et al.* 2012; Durán *et al.* 2018; Hossain *et al.* 2023b). Exploring the relationships between aridity and the biomass productivity of grasslands across ecoregions will advance our understanding of how aridity impacts grassland performance. Our ability to forecast the future productive capacity of grasslands and to plan for future sustainable grassland management will improve our understanding of the effects of aridity on annual and seasonal biomass productivity across ecoregions.

The study of the influence of aridity on grassland productivity is important because it helps us understand how climate-induced stresses affect the functioning and stability of grassland ecosystems (Hossain *et al.* 2023b). Aridity is increasing in many parts of the world due to climate change (Li *et al.* 2016, 2017), and this has significant implications for the productivity and biodiversity of grasslands (Maestre *et al.* 2015; Berdugo *et al.* 2020). As grasslands are one of the largest ecosystems on Earth, providing important ecosystem services such as carbon sequestration and habitat for wildlife (Trenberth *et al.* 2014), understanding their sensitivity to aridity is critical for predicting and mitigating the impacts of climate change (Li *et al.* 2015). By studying the relationship between aridity and grassland productivity, we can develop effective strategies to manage and conserve these important ecosystems in the face of climate change. One important area of research is to identify the threshold of aridity beyond which grasslands become unproductive or converted to other land uses. This is important because it can help inform land-use planning and management decisions. For example, if the threshold of aridity is known, land managers can develop strategies to maintain soil moisture levels above this threshold, such as implementing sustainable irrigation practices. Irrigation practices are again dependent on river networks. River networks provide a source of water for ecosystems and can influence nutrient availability in grasslands. River corridors can act as wildlife corridors, providing habitat and connectivity for a range of species. River networks can influence the frequency and intensity of disturbances in grasslands (Sarker *et al.* 2019, 2023; Sarker 2021; Gao *et al.* 2022).

In addition to the ecological impact, the study of aridity and grassland productivity also has important social and economic implications. Grasslands are used for livestock grazing, hay meadow production, agriculture, and biodiversity conservation, and changes in productivity and biodiversity can have significant impacts on local economies and livelihoods. Understanding how grasslands respond to changes in soil moisture levels can help inform decisions about land-use and management practices that support sustainable production systems and rural livelihoods.

Plant ecologists have long believed that the allocation of biomass between BGB and AGB is highly idiosyncratic, which is consistent with two well-established hypotheses (isometric partitioning and optimal partitioning). The optimal partitioning theory suggests that vegetation distributes proportionally greater energy to structures with a greater capacity to absorb the scarcest nutrients (Mao *et al.* 2012). Thus, it is anticipated that plants will devote higher biomass belowground in arid conditions and aboveground in wetter settings (Villar *et al.* 1998). The isometric partitioning theory argues that AGB and BGB maintain an isometric arrangement (Enquist & Niklas 2002; Wang *et al.* 2014), suggesting that there is not an absolute exchange between AGB and BGB (Enquist & Niklas 2002; Wang *et al.* 2014). Large numbers of empirical studies that refute isometric partitioning (Enquist & Niklas 2002; Wang *et al.* 2014) have produced contradictory findings (Chen *et al.* 2016; Ma & Wang 2021). A better understanding of how biomass is distributed between the root and shoot in plants would expand our ability to forecast how grasslands will function in the future.

In an attempt to better understand how grassland ecosystems respond to gradients of aridity and how plant biomass is allocated into root and shoot in two plant types at seven sites belonging to four grassland ecoregions (savanna, humid temperate, cold steppe, and humid savanna), this study assessed (i) the relationships of annual and seasonal biomass and their partitioning with annual and growing season aridity and (ii) the biomass allocation pattern between AGB and BGB across four ecoregions belonging to C_3- and C_4-dominated grasslands.

2. METHODOLOGY

2.1. Study area

The current study encompasses seven study locations spread over four ecoregions (Figure 2, Hossain & Li 2021c). Ecoregions are distinguished from one another by the presence of a greater number of smaller ecosystems that are dispersed all over the geographical area (Bailey 1998). Ecoregions are a reflection of the distribution of communities and species based on various

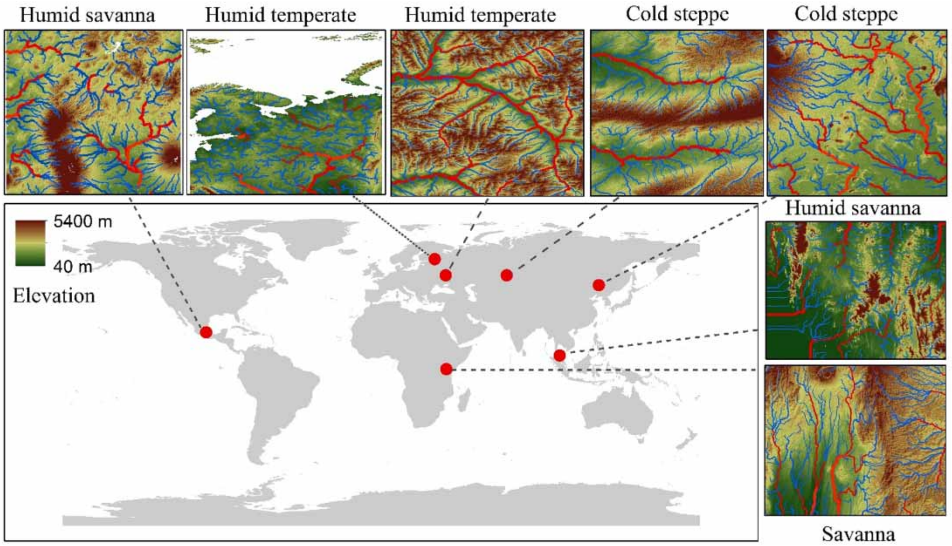


Figure 2 | The study sites are dispersed across four ecoregions. The C_3 grasslands predominate in humid temperate and cold steppe ecoregions, while C_4 grasslands prevail in humid savanna and savanna ecoregions.

biophysical parameters such as plant types (e.g., C_3 and C_4 plants), functional groups (e.g., herbs, legumes, and grasses), species dominance patterns, climatic conditions, species composition, and the geological history of an area (Bailey 1998; Olson *et al.* 2001). Among the four selected ecoregions (cold steppe, humid temperate, humid savanna, and savanna) in our study, the grasslands of the humid temperate and cold steppe ecoregions are dominated by plants belonging to the C_3 grasslands, whereas the grasslands in the other two ecoregions (i.e., savanna and humid savanna) are dominated by plants belonging to the C_4 grasslands. The grasslands in the cold steppe ecoregion are characterized by hot summers and extremely cold winters. A humid savanna is a broad, open grassland that was produced as a consequence of anthropogenic disruptions (e.g., inappropriate forest logging and farmland extension and intensification) and natural perturbations (e.g., fire). These human and natural disturbances led to the formation of the humid savanna (Pandey & Singh 1992). In the humid temperate ecoregion, grasslands are dominated by grasses with deep roots, which enable the plants in these areas to better tolerate the effects of extreme climate and fire (Nunez 2019). Savanna grasslands are disturbed habitats that are distinguished by the significant spatial variety and contain the most expansive vegetation types (Veldhuis *et al.* 2016; Sankaran 2019). Savanna grasses are highly specialized to flourish during extended periods of drought and have adapted defense mechanisms to protect themselves from being eaten by grazing animals.

2.2. Data sources

In this paper, we utilized climate and grassland AGB and BGB data for the period 1969–1994 to assess the effect of aridity on grassland functioning. All AGB and BGB data were extracted from the global Net Primary Productivity (NPP) database at the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC) (Scurlock *et al.* 2015). Climate data include annual and monthly precipitation and temperature. These climate data were extracted from the ORNL DAAC (Scurlock *et al.* 2015) and the Climate Research Unit (Harris *et al.* 2014). We extracted the Digital Elevation Model (DEM) raster files from the United States Geological Survey (USGS) (Farr *et al.* 2007). For this, the study sites were selected using known latitudes and longitudes. Raster images (30 m resolution) from 'SRTM 1 Arc-Second Global' were used in preparing the study map.

2.3. Data processing

We used spatial analyst tools in the Arc Toolbox to process the study sites. First, the images were processed by several tools (fill, flow direction, and flow accumulation) in the Hydrology toolbox. Second, the raster calculator in the map algebra toolbox was used for raster calculation. Finally, the stream order and stream-to-feature tools were applied for producing the final maps of the study sites, which represent the river networks and elevation in the respective sites in the ecoregions (Figure 3).

Biomass data were arranged by growing season harvest and site (Figure 4). For example, the growing season in a humid temperate ecoregion ranges from April to September. In this case, we considered the (i) aridity of April–June and correlated the aridity index (AI) with summer harvest (i.e., June) and (ii) the aridity of July–September and correlated the AI with autumn harvest (i.e., September). Biomass was collected by the original authors of the respective experiments following a standard protocol. For example, shoots were harvested in the peak growing season within the central part of the quadrat. The harvested shoots were then sorted, oven-dried, and measured for dry weight. Similarly, roots were collected using soil cores. Then, the roots were sorted, washed, oven-dried, and measured for dry weight.

The growing season AGB and BGB in a given year were summed up to get the annual AGB and BGB in their respective sites. The ratios BGB:AGB were obtained by dividing the growing season and annual BGB by their respective growing season

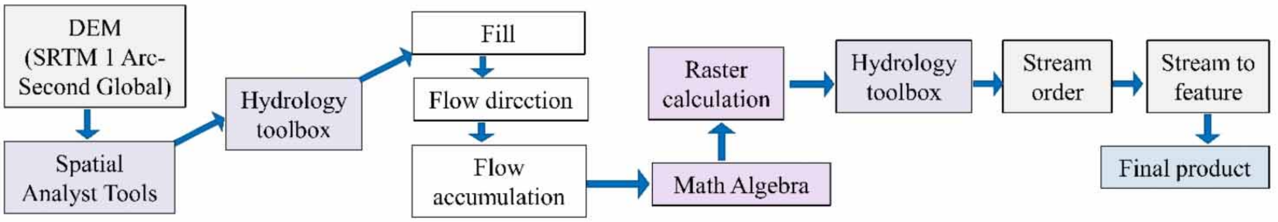


Figure 3 | Flow diagram of the methodology adopted for the processing of DEM images derived from the Shuttle Rada Topography Mission (STRM) in the USGS.

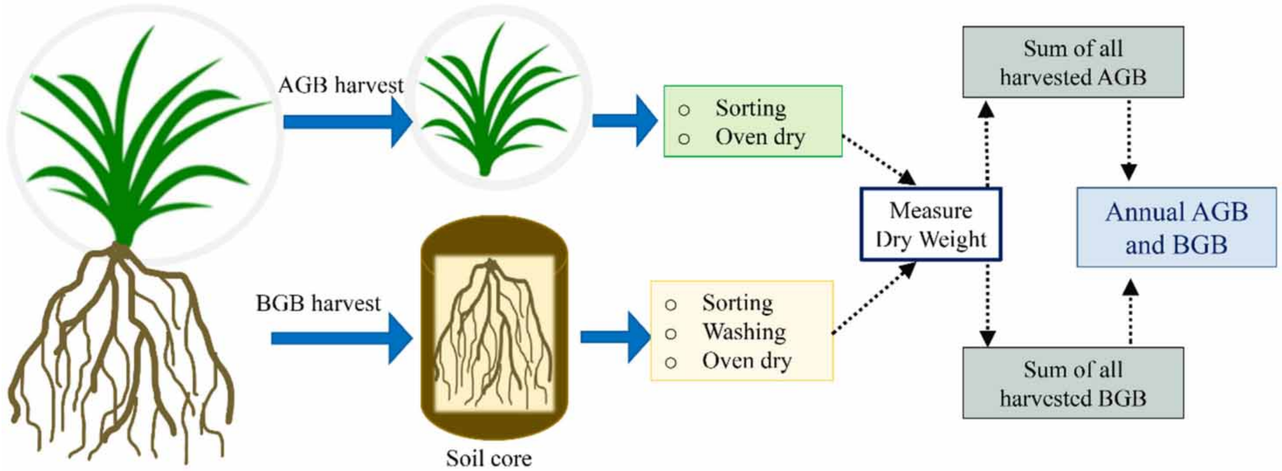


Figure 4 | Biomass harvesting and processing for seven study sites.

and annual AGB. Biomass data from these seven sites were then assembled into four ecoregions and two functional types (C_3 and C_4) (Scurlock *et al.* 2002).

The growing season and annual AI (De Martonne 1926; Sun *et al.* 2013) were calculated using temperature and precipitation data according to Martonne's formula (Equation (1))

$$AI = \frac{P}{(T + 10)} \tag{1}$$

where P and T refer to precipitation (mm) and average temperature (°C), respectively.

2.4. Data analysis

The relationships between (i) growing season biomass (AGB and BGB, BGB:AGB ratio) and growing season aridity, and (ii) annual biomass and annual aridity at the site level were assessed using Pearson correlation analysis (Sun *et al.* 2021). We used a heat map and correlation matrix to display the strength and direction of the relationships between biomass and aridity. For example, dark colors (blue and red) represent the stronger relationships (negative and positive) between biomass and aridity. Similarly, the relationships between the growing season and annual AGB and BGB across ecoregions were assessed by the Pearson correlation. The level of significance of biomass allocation between BGB and AGB was detected at $p < 0.05$. All statistical analysis was performed in the statistical package R version 4.0.3 (R Core Team 2020).

3. RESULTS

3.1. Biomass response to aridity

The response of growing season AGB, BGB, and BGB:AGB ratio to growing season aridity exhibited large variations across ecoregions and plant types (Figure 5). Growing season aridity influenced the growing season AGB of C_3-dominated grassland at one site in cold steppe (Figure 5(a), $p < 0.01$, $R = 0.35$) and C_4-dominated grasslands at a site in humid savanna ecoregions (Figure 5(f), $p < 0.01$, Table 1, $R = 0.33$). Growing season aridity had no effects on the growing season BGB of grasslands in all ecoregions, except for significant negative effects on growing season BGB at a site in the humid savanna ecoregion (Figure 5(e), $p < 0.05$, Table 1, $R = -0.30$). The relationships between growing season aridity and the BGB:AGB ratio were significantly positive for two sites in C_3-dominated grasslands (one site in cold steppe: Figure 5(a), $p < 0.05$, $R = 0.54$, one site in humid temperate: Figure 5(c), $p < 0.05$, $R = 0.51$), significant negative for one site in cold steppe (Figure 5(b), $p < 0.001$, $R = -0.41$), and one site in humid savanna (Figure 5(f), $p < 0.01$, $R = -0.36$) and insignificant for the other three sites (Figure 5). When annual aridity was considered, only one site in the cold steppe ecoregion showed a significant positive interaction between annual aridity and annual AGB (Figure 6(b), $p < 0.01$, Table 1, $R = 0.76$) and a significant

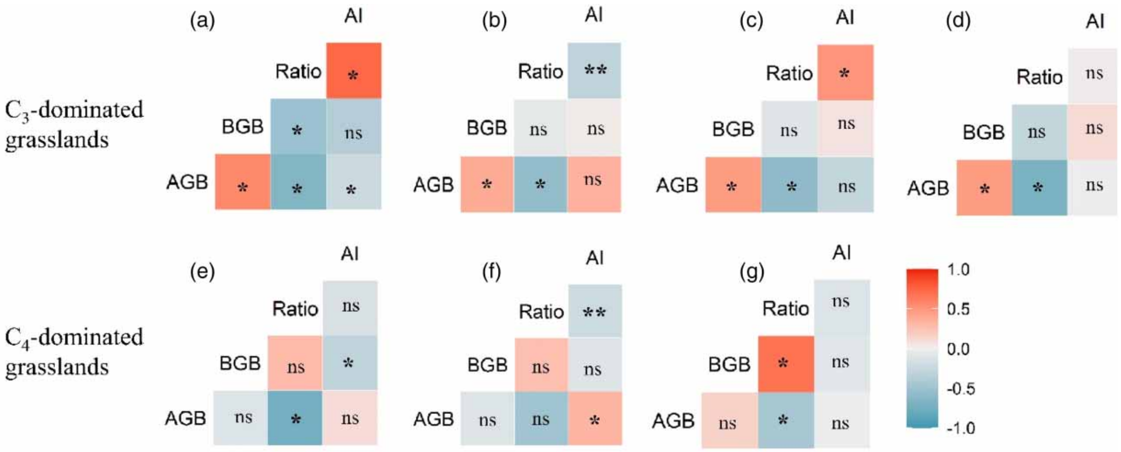


Figure 5 | Response of growing season AGB and BGB productivity and their partitioning (BGB:AGB ratio) in C_3-dominated grasslands at two sites (a and b) in cold steppe and two sites (c and d) in humid temperate and C_4-dominated grasslands at two sites (e and f) in humid savanna and one site (g) in savanna ecoregions to the growing season aridity (AI). Asterisks (* and **) indicate the relationships between growing season biomass and growing season aridity are significant at $p < 0.05$ and $p < 0.01$. The symbol 'ns' indicates that the relationships between growing season biomass and growing season aridity are not significant. The relationships between growing season biomass and growing season aridity for C_3-dominated grasslands (a–d) are shown in the upper panel and for C_4-dominated grasslands (e–g) are shown in the lower panel of the figure. The *r* values (Pearson correlation) of the relationships between growing season biomass and growing season aridity are shown in Table 1.

Table 1 | The *r* values of the relationships between biomass and aridity at respective sites across four ecoregions belonging to C_3- and C_4-dominated grasslands obtained using the Pearson correlation. The heat maps of the correlation and the level of significance have been shown in (i) Figure 5 for the relationships between growing season biomass and growing season aridity, and (ii) Figure 6 for the relationships between annual biomass and annual aridity

		C_3-dominated grasslands				**C_4-dominated grasslands**		
Biomass	**Seasonal/ annual**	**Cold steppe (shr)**	**Cold steppe (tmg)**	**Humid temperate (krs)**	**Humid temperate (otr)**	**Humid savanna (kln)**	**Humid savanna (mnt)**	**Savanna (nrb)**
AGB	Growing season	−0.23	0.35	−0.28	−0.01	0.10	0.33	−0.01
	Annual	−0.46	0.77	0.87	−0.15	−0.18	0.50	0.09
BGB	Growing season	−0.37	0.02	0.07	0.11	−0.30	−0.10	−0.09
	Annual	−0.34	−0.10	0.95	0.55	−0.39	−0.14	0.13
Ratio	Growing season	0.54	−0.38	0.51	−0.03	−0.20	−0.36	−0.10
	Annual	−0.11	−0.92	0.81	0.39	−0.09	−0.55	0.13

Abbreviations: kln, Klong Hoi Khong; krs, Kursk; mnt, Montecillo; nrb, Nairobi; otr, Otradnoe; shr, Shortandy; tmg, Tumugi.

negative interaction between annual aridity and the annual BGB:AGB ratio (Figure 6(b); $p < 0.01$, Table 1, $R = -0.90$). Biomass productivity at other sites in the ecoregions did not display a significant change with increasing aridity (Figure 6; all $p > 0.05$).

3.2. Mechanism of biomass allocation

Biomass allocation for both the annual and growing season BGB and AGB was examined for assessing the allocation pattern of biomass across ecoregions (Figure 7). Vegetation in three ecoregions showed a significant positive correlation between AGB and BGB, regardless of the growing season and annual biomass (Figure 7). For example, positive interactions between AGB and BGB were observed in the cold steppe (growing season biomass: $p < 0.01$, annual biomass: $p < 0.05$), humid temperate

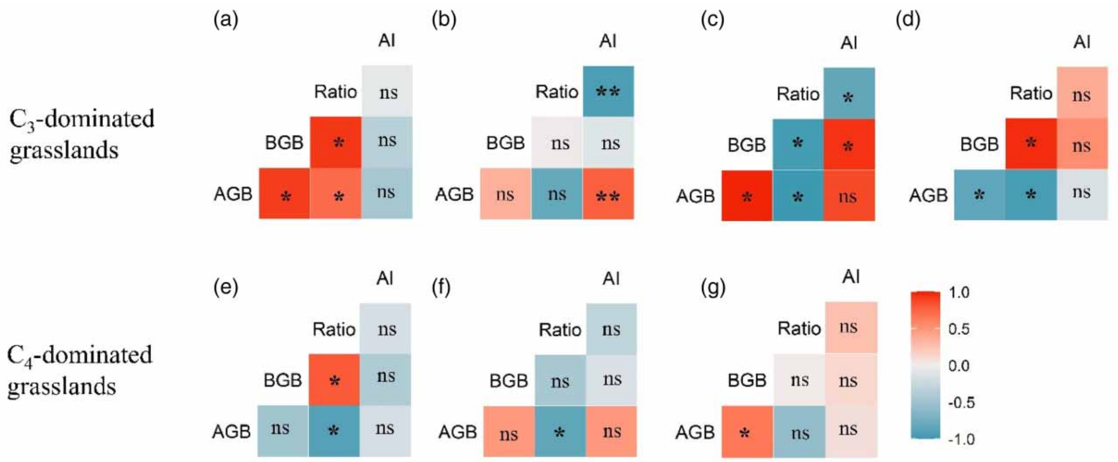


Figure 6 | Response of annual AGB and BGB productivity and their partitioning (BGB:AGB ratio) in C_3-dominated grasslands at two sites (a and b) in cold steppe and two sites (c and d) in humid temperate and C_4-dominated grasslands at two sites (e and f) in humid savanna and at one site (g) in savanna ecoregions to the annual aridity. Asterisks (* and **) indicate that the relationships between annual biomass and annual aridity are significant at $p < 0.05$, and $p < 0.01$. The symbol 'ns' indicates that the relationships between annual biomass and annual aridity are not significant. The relationships between annual biomass and annual aridity for C_3-dominated grasslands (a–d) are shown in the upper panel, and for C_4-dominated grasslands (e–g) are shown in the lower panel of the figure. The *r* values (Pearson correlation) of the relationships between annual biomass and annual aridity are shown in Table 1.

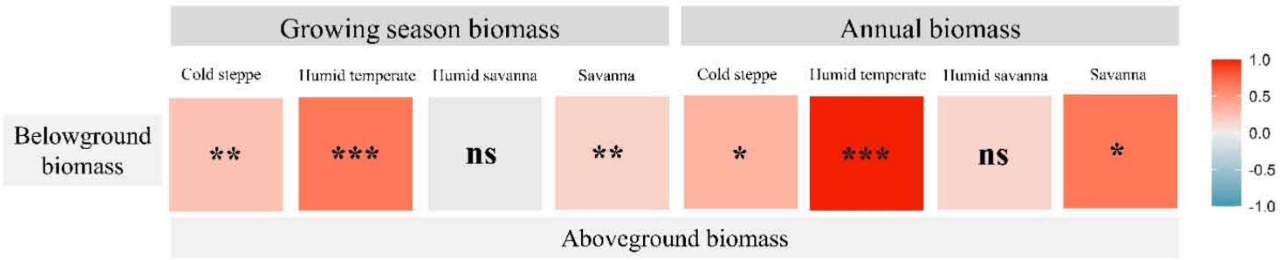


Figure 7 | Relationships between the allocation of biomass of grasslands in four ecoregions (cold steppe, humid temperate, humid savanna, and savanna) for both growing season harvests and their annual sum. Asterisks (*, **, and ***) denote the significance ($p < 0.05$, $p < 0.01$, and $p < 0.001$) of the correlation between AGB and BGB. The symbol 'ns' indicates that the relationships between AGB and BGB are not significant.

(growing season biomass: $p < 0.001$, annual biomass: $p < 0.001$), and savanna (growing season biomass: $p < 0.01$, annual biomass: $p < 0.05$). The biomass allocation pattern in these three ecoregions supports the optimal partitioning theory for both the growing season and annual biomass (Figure 7). That is, plants in humid temperate, savanna, and cold steppe ecoregions made greater efforts to extract the most scarce resources, depending on the abiotic conditions. No detectable pattern (i.e., neither optimal partitioning nor isometric partitioning) was observed for the biomass allocation in C_4-dominated grasslands in the humid savanna ecoregion (Figure 7, $p > 0.05$ for both the growing season and annual biomass).

4. DISCUSSION

Under an altered precipitation pattern, growing temperature, and aridity, grasslands are likely to modify their functioning by altering root and shoot productivity. Uncovering the essential attributes controlling grassland productivity in multiple ecoregions over the long term is a significant challenge in plant ecology. In this study, we investigated (i) how growing season and annual aridity affect seasonal and annual AGB, BGB, and BGB:AGB ratio, and (ii) how the biomass of these ecoregions is allocated into AGB and BGB.

The impact of aridity on AGB, BGB, and BGB:AGB ratio differed between plant types, ecoregions, and the duration of aridity (i.e., growing season and annual). The rise in growing season aridity in this study enhanced the growing season

AGB of grasslands at one site in cold steppe and one site in humid savanna ecoregions and did not affect the growing season AGB of other sites in all ecoregions. The observed positive associations between growing season aridity and AGB in C_4 plants in humid savanna and C_3 plants in the cold steppe suggest that rising aridity enhances AGB by increasing photosynthesis. It is expected that in arid conditions, plants exert more effort aboveground and are capable of coordinating the association between the assimilation of carbon and the usage of water for transpiration (Paoletti *et al.* 1998). In this way, plants can maintain high water-use efficiency and a stable photosynthetic rate and promote the production of shoots (Chengjiang & Qingliang 2002).

Grasslands in different ecoregions respond inversely to aridity in order to adapt to changing conditions. This is done by regulating the supply of photosynthate to shoots and roots, and as a result, the BGB:AGB changes with the fluctuations in aridity (Qi *et al.* 2019). There was a large amount of variation in the ways in which the BGB:AGB ratio responded to aridity across ecoregions. The different ways in which the BGB:AGB ratio reacts to changes in the environment can be clarified by the various functional types of plants. The fact that the ratio of BGB to AGB has decreased in C_3 plants in the cold steppe ecoregion as aridity has increased suggests that C_3 plants devote more efforts aboveground to optimize shoot growth and capture more sunlight than they do belowground to obtain soil resources in arid conditions (Angelo & Pau 2015). The positive associations of the seasonal BGB and AGB with the growing season aridity in C_3-dominated grasslands in our study were in accordance with those confirmed in C_3 grasslands in steppe and temperate ecoregions (Chen *et al.* 2017; Guo *et al.* 2018; Hossain & Beierkuhnlein 2018).

Grasslands in ecoregions with warmer temperatures have developed adaptive strategies for dealing with the stresses caused by higher aridity (Volder *et al.* 2010). However, elevated stress is shown to inhibit the capacity of grasslands to partition their biomass, which we observed for C_4-dominated grasslands. The observation of a decreasing BGB:AGB ratio in C_4-dominated grasslands with increasing aridity demonstrates that C_4 plants adapt to arid conditions by either lowering the AGB or increasing the BGB. The loosening of plant photosynthesis because of a reduction in soil moisture and a rise in evapotranspiration during increasing aridity can explain the decreased AGB of C_4 plants during the growing season aridity (De Boeck *et al.* 2011). This finding is in line with an experiment by Kahmen *et al.* (2005), which revealed that in semi-arid grasslands, arid conditions reduced the AGB. Similarly, the stable BGB of C_4 plants with rising growing season aridity suggests that under arid conditions, plants can sustain BGB productivity by enhancing fine root systems to draw out more water (Luo *et al.* 2013; Dai *et al.* 2019).

According to two well-established hypotheses, biomass allocation between AGB and BGB is greatly distinctive, which is what plant ecologists have long believed (isometric partitioning and optimal partitioning). Based on the theory of optimal partitioning, vegetation should distribute more energy proportionally to structures that have a higher capacity for absorbing the most limited substances (Bloom *et al.* 1985; Gedroc *et al.* 1996; Mao *et al.* 2012). Therefore, it is expected that plants will allocate more biomass aboveground in wetter environments and belowground in arid environments (Villar *et al.* 1998). Our findings of the distribution of biomass across three ecoregions – cold steppe, humid temperate, and savanna – confirm the theory of optimal partitioning for both the growing season and annual biomass. In other words, plants in these three ecoregions distributed their greater efforts more evenly in response to the abiotic conditions to extract the scarcest resources. The optimal partitioning of AGB and BGB in these three ecoregions is consistent with several other studies across different grassland types. For example, Mao *et al.* (2012) reported that two grass species exhibit optimal partitioning for allocating biomass between roots and shoots.

Aridity influences ecosystem productivity and stability. Understanding how different grasslands across ecoregions respond to the growing season and annual aridity is critical to the sustainable management of grassland biodiversity and to the stable delivery of ecosystem goods and services to mankind. This study's findings provide empirical evidence of the stronger effects of growing season aridity on growing season AGB and BGB, which is of practical importance for pastoralists and herders in biomass and hay meadow production. As the empirical evidence of how BGB changes with the changes in AGB is limited, the optimal partitioning pattern of biomass allocation in our three ecoregions (i.e., cold steppe, humid temperate, and savanna) has important implications in decision-making for selecting species dominance and composition across various grasslands, including C_3- and C_4-dominated grasslands.

5. CONCLUSION

This paper demonstrates the evidence of the influence of aridity on biomass productivity (AGB and BGB) and their partitioning of two distinct grasslands in four ecoregions. Results exhibited that seasonal and annual AGB, BGB, and BGB:AGB ratio of C_3 and C_4 plants were influenced by the gradients of the growing season and annual aridity, but the interactions were not consistent for all ecoregions. The study findings emphasize that growing season aridity is a stronger controlling determinant of seasonal and annual biomass productivity and their partitioning in C_3 and C_4 plants in cold steppe and humid savanna ecoregions, respectively. This result suggests that enhanced aridity may enhance AGB in these two ecoregions, but a substantial decrease in BGB is likely to decrease the functioning of ecosystems. The theory of optimal partitioning for both seasonal and annual biomass is supported by our findings of the distribution of biomass between aboveground and belowground for the cold steppe, humid temperate, and savanna ecoregions. The relationships described here provide a foundation for further long-term coordinated research in grasslands across wider spatial scales with respect to the increasing severity and recurrence of extreme climatic events and aridity. These findings have significant implications for predicting the functioning of ecosystems across arid, semi-arid, and temperate grasslands.

FUNDING

This work was supported by the research grants from the Guangdong-Hong Kong Joint Laboratory for Water Security (project no. 2020B1212030005) and the Research Grants Council of the Hong Kong Special Administrative Region, China (project no. HKBU12302518).

AUTHORS’ CONTRIBUTIONS

M.L.H. conceptualized the work, carried out methodology, software, and formal analysis, wrote, reviewed, and edited the original draft. **J.L.** performed methodology, wrote, reviewed, and edited the original draft, supervised the work, did funding acquisition, and administered the project.

ACKNOWLEDGEMENT

We have obtained the freely available data of grassland biomass productivity as well as monthly precipitation data from the global NPP database that was housed at the Oak Ridge National Laboratory Distributed Active Archive Center (Scurlock *et al.* 2015). Climate Research Unit provided data on monthly temperatures (Harris *et al.* 2014).

DATA AVAILABILITY STATEMENT

All relevant data are available from an online repository or repositories https://doi.org/10.3334/ORNLDAAC/654, https://catalogue.ceda.ac.uk/uuid/10d3e3640f004c578403419aac167d82.

CONFLICT OF INTEREST

The authors declare there is no conflict.

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First received 15 March 2023; accepted in revised form 10 June 2023. Available online 23 June 2023