Biomass partitioning of C₃- and C₄-dominated grasslands in response to climatic variability and climate extremes

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Abstract
The rising temperature, altering precipitation, and increasing extreme events under climate warming affect the stability and sustainability of grassland ecosystems. The dynamics of above-ground biomass (AGB), below-ground biomass (BGB), and biomass partitioning (BGB:AGB ratio) of grasslands are of fundamental importance to understand their feedback to climate change. In this study, we used grassland productivity data extracted from the Oak Ridge National Laboratory Distributed Active Archive Center, Tennessee, USA, in which the AGB was collected within a 1.0 m × 0.25 m quadrat and the BGB was sampled within the center of the quadrat. Using multiple pairwise tests and Pearson’s correlation analysis, we assessed the variations of grassland productivity and examined the response of single-harvest and annual biomass partitioning of C₃- and C₄-dominated grasslands to the growing-season and annual climatic variability and climate extremes in seven sites belonging to four ecoregions (i.e. cold steppe, humid temperate, humid savanna, and savanna). The results show that the annual and single-harvest BGB:AGB ratio varied significantly across the plant types and ecoregions. Overall, the C₃-dominated grasslands exhibited a higher BGB:AGB ratio than that of C₄-dominated grasslands. Growing-season temperatures (GSTs) were found to be the key determinants in explaining the single-harvest BGB:AGB ratio rather than growing-season precipitation. For instance, the single-harvest BGB:AGB ratio of C₄-dominated grasslands increased, while that of C₃-dominated grasslands decreased with elevated GSTs. The growing-season extreme dry climates significantly increased the single-harvest BGB:AGB ratio of C₄ plants by a large reduction of AGB, potentially affecting the ecosystem functioning and stability. The C₃-dominated grasslands in the cold steppe ecoregion are at great threat of drought-induced stress, as we observed that growing-season extreme dry climates reduced, albeit insignificantly, both the single-harvest AGB and BGB. This study provides key insights into factors influencing the biomass partitioning of C₃- and C₄-dominated grasslands and has important implications for assessing the grassland functioning and stability under increasing climate extremes.

1. Introduction
The grassland ecosystem, covering over 30% of the terrestrial surface [1] and accounting for nearly 10% of global carbon storage [2], provides numerous ecosystem goods and services [3]. The above-ground biomass (AGB) and below-ground biomass (BGB) productivities are important and commonly used indicators to evaluate the functioning and stability of the grassland ecosystem [4, 5]. Global climate change is propelling a rapid decline in grassland biodiversity and threatening their productivity [6]. The projected changes in global climates are expected to exert profound effects on grassland biodiversity [7], affecting the functioning [8] and stability [9] of the grassland ecosystem, especially in C₃-dominated grasslands in

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humid temperate and cold steppe ecoregions as well as C₃-dominated grasslands in humid savanna and savanna ecoregions [10, 11]. Given the likely threat of global change to the grassland ecosystem, it is essential to understand the interactions of the functioning of C₃- and C₄-dominated grasslands with the rising climate extremes and climatic variability. Biomass partitioning (i.e. the BGB:AGB ratio) is a key parameter reflecting the plant-adaptive strategy to maintain their functioning in a changing climate [12]. The BGB:AGB ratio explains the functioning of the ecosystems and biogeochemical cycles, and thus a change of this ratio would greatly affect the global carbon balance as well as the ecosystem stability and biodiversity [13]. Although many empirical studies have documented that temperature and precipitation are the key determinants of grassland AGB [11, 14] and BGB [15, 16] productivity across different grassland types, the search for the key climate predictor in controlling the grassland BGB:AGB ratio has been challenging for plant community ecologists [5, 17]. For more than two decades, there has been a debate in plant ecology research about the key determinants of grassland biomass partitioning [18–20]. For example, certain previous studies have reported that the BGB:AGB ratio increases [5, 21], while other studies have demonstrated that it decreases [22, 23] with the increasing temperature. No significant correlation between the BGB:AGB ratio and temperature was observed in other studies [17, 24]. Meanwhile, a substantial body of evidence has demonstrated negative [13, 21], positive [23], and insignificant [17, 25] correlations between biomass partitioning and precipitation. These disparate findings may be due to the differences in study duration, grassland ecoregions, plant functional types (C₃ or C₄ plant), climatic variability (growing-season or annual climates), and harvest frequency [18, 19, 26]. Every harvest of biomass is regarded as a single harvest. There may be several harvests in a season or a year depending on the length of the growing season, plant functional types, and ecoregion [10]. Therefore, the biomass in every harvest is considered as the single-harvest biomass, and the sum of all single harvests in a year is the annual biomass. In order to provide compelling evidence of this debated issue, an advance understanding of the correlation between biomass partitioning of C₃- and C₄-dominated grasslands and climatic variability at broad spatial scales is required.

The increasing trends in the frequency and magnitude of climate extremes (e.g. floods and droughts) in recent decades have had profound effects on grassland ecosystems [27]. In recent years, a growing number of studies have investigated the response of grassland productivity to climate extremes and found that the effects of climate extremes on AGB and BGB vary greatly [28, 29]. Plenty of empirical evidence has demonstrated that the effects of extreme dry events on the BGB are negative [30], positive [29], and insignificant [31], and the effects of extreme wet events on the AGB are negative [32], positive [27], and insignificant [15]; however, the effects of climate extremes on the BGB:AGB ratio remain largely unknown. Despite the great efforts that have been made in recent years to explore the effects of extreme events on the BGB:AGB ratio in different grasslands, no consensus has been made, since some studies reported that the response of the BGB:AGB ratio to extreme dry climates was either positive [5] or negative [33], and other studies found an increased [26] and decreased [34] BGB:AGB ratio caused by extreme wet events. These differential findings may result from (a) the differences in plant functional types [18], study duration [19], and experiments [5], (b) consideration of either annual or growing-season extremes in different climate settings [25, 28], and (c) methodological difficulties in classifying climate extremes [35]. For instance, extreme dry events were defined in various ways in previous studies, such as (a) a 30-day rain-free period [35], (b) 100% rainfall reduction for specific periods during the growing season [36], and (c) a temperature increase of 2.5 °C [5] across different grasslands. In addition, the response of one plant type to climate extremes may differ from another, since C₃ plants are dominant in humid temperate and cold steppe ecoregions, while C₄ plants are dominant in humid savanna and savanna ecoregions. Thus, an examination of the effects of extreme events on the grassland BGB:AGB ratio focusing on both C₃- and C₄-dominated grasslands based on a widely used drought index classification is critically important to provide new insights into grassland productivity with the growing risk of climate warming.

Exploring the effects of climate extremes and climatic variability on the BGB:AGB ratio and biomass productivity (i.e. AGB and BGB) of C₃- and C₄-dominated grasslands across ecoregions is helpful to advance our understanding of the response of grassland biomass partitioning to the changing climate. In attempting to understand how climate extremes and climatic variability affect the BGB:AGB ratio, and which plant type suffers from and which responds well to climatic variability and perturbations across four ecoregions (cold steppe, savanna, humid savanna, and humid temperate), the following three objectives have been established:

(a) To assess the spatial variation in the single-harvest and annual BGB:AGB ratio and biomass productivity in the four ecoregions, and in C₃ and C₄ plants;
(b) To evaluate the correlation of the single-harvest and annual BGB:AGB ratio and biomass productivity with the growing-season and annual climatic variables; and
(c) To examine the effects of growing-season and annual climate extremes on the single-harvest
Figure 1. Locations of the seven study sites across four ecoregions (adapted from Scurlock et al [39]). Grasslands in cold steppe and humid temperate ecoregions are dominated by C\textsubscript{3} plants, and grasslands in savanna and humid savanna ecoregions are dominated by C\textsubscript{4} plants.

and annual BGB:AGB ratio and biomass productivity of C\textsubscript{3} and C\textsubscript{4} plants.

2. Materials and methods

2.1. Description of the study area

The present study comprises seven study sites across four ecoregions (figure 1) [37]. Ecoregions represent the habitat of species based on biophysical characteristics, such as distinct species assemblage, structure of vegetation, climatic settings, and geology [38]. The seven sites in this study are located in China, Russia, Kazakhstan, Thailand, Kenya, and Mexico, and belongs to the humid savanna, humid temperate, savanna, and cold steppe ecoregions (figure 1). The grasslands in the humid savanna and savanna regions are dominated by C\textsubscript{4} plants, and the grasslands in the humid temperate and cold steppe regions are dominated by C\textsubscript{3} plants (see table S1 of supplementary material, available online at stacks.iop.org/ERL/16/074016/mmedia) [16, 39]. The humid temperate and cold steppe regions are characterized by a very cold winter and a warm summer, and the vegetation is dominated by deep-rooted grasses. The deep rooting profile helps this vegetation to withstand climatic disturbances [40]. Grasslands in humid savanna and savanna are able to grow in arid climates, and are distributed widely in the tropics and sub-tropics [41].

The profile of the ecoregions is given in section 1.1 of the supplementary material, and the characteristics of the study sites are given in table S1 of the supplementary material.

2.2. Data sources

The grasslands’ AGB and BGB and all climatological data except the monthly average temperature of the seven study sites were extracted from the global net primary productivity (NPP) database at the Oak Ridge National Laboratory Distributed Active Archive Center, Tennessee, USA [39]. Harvests of AGB were made within a 1.0 m × 0.25 m quadrat, and the BGB was sampled within the center of the quadrat. AGB and BGB harvest frequency vary among the sites and ecoregions. For example, in the cold steppe ecoregion, a harvest was made every month during April–September (i.e. six times) at a site in Kazakhstan and every month during April–November (i.e. eight times) at a site in China. In the humid savanna and savanna ecoregions, the biomass was harvested every month (i.e. 12 times in a year). The monthly average temperature and missing values of other climate variables in the NPP database were obtained from the Climatic Research Unit (CRU v.4.03) database [42]. Growing-season climate variables include the growing-season temperature (GST), growing-season precipitation (GSP), growing-season maximum temperature (GST\textsubscript{max}), growing-season minimum temperature (GST\textsubscript{min}), and cumulative growing-season precipitation (GSP\textsubscript{cum}). Annual climate variables include the mean annual temperature (MAT), annual precipitation (AP), mean annual maximum temperature (MAT\textsubscript{max}), and mean annual minimum temperature (MAT\textsubscript{min}). Detailed definitions of these variables are given in table S2 of the supplementary material.

2.3. Data pre-processing

The AGB and BGB data were sorted by the respective harvest (hereafter single-harvest AGB and BGB) and site. The single-harvest AGB and BGB in a particular year at a site were summed up to obtain the annual AGB and BGB of that site. The BGB:AGB ratio was obtained by dividing the single-harvest/annual BGB by the respective single-harvest/annual AGB. The biomass data of seven sites were grouped into four ecoregions and two plant types as defined by
Figure 2. Boxplots of single-harvest and annual BGB:AGB ratio across four ecoregions (a) and (b) and two plant types (c) and (d). One-way ANOVA was used to test the significance of the differences of biomass partitioning among the ecoregions and plant types. Asterisks (∗∗∗) on horizontal solid lines denote the significance of the differences (p < 0.001) between two ecoregions, and the ‘NS’ indicates that the differences biomass partitioning between the ecoregions were not significant. Whiskers indicate the 95% confidence intervals. Solid lines in boxplots indicate medians and dashed lines denote the mean values of all ecoregions and plant types. The p values on the boxplots represent the significance of the differences of biomass partitioning among the plant types and ecoregions.

Scurlock et al [10] (table S1). In order to pair the growing-season climate variables with the single-harvest biomass, the growing-season climate of a harvest was defined based on the harvest interval between two harvests, as shown in table S2 [16]. Climate extremes were categorized based on the commonly used drought classification index (Standardized Precipitation Evapotranspiration Index (SPEI)) [43]. SPEI values were calculated using the monthly precipitation and maximum and minimum temperatures from NPP. The 12-month and 3-month SPEI values were used to indicate the annual and growing-season climate extremes, respectively. SPEI values ≥1.28 indicate extreme wet and ≤−1.28 represent extreme dry events (see table S3 of supplementary material for drought classification [44]).

2.4. Data analysis
First, using one-way analysis of variance (ANOVA), the significance of the differences in the mean single-harvest and annual biomass among the plant types and ecoregions was tested [45]. If the difference in the mean values of the BGB:AGB ratio among the four ecoregions was significant, a two-sample t-test was used for pairwise comparisons of the mean BGB:AGB ratio between ecoregions. Second, we conducted a Pearson’s correlation analysis in order to examine the relationship between the BGB:AGB
ratio and respective climate variables. Finally, using multiple pairwise tests, we explored the effects of annual and growing-season climate extremes on the annual and single-harvest BGB:AGB ratio in the respective ecoregions. A one-way ANOVA test explained the significance of the differences in the mean BGB:AGB ratio among climate extremes and normal climates at the respective sites. The two-sample t-test exhibited whether the BGB:AGB ratio of a particular climate event was significantly higher or lower than the BGB:AGB ratio of another climate event. Likewise, the annual and single-harvest AGB and BGB were analyzed separately in order to examine the underlying reasons for the differential response of the BGB:AGB ratio to the respective climate variables and extremes. All statistical analysis was done in the statistical package R, version 4.0.3 [46].

3. Results

3.1. Variations in BGB:AGB ratio across ecoregions and plant types

The single-harvest BGB:AGB ratio exhibited large variations among the four ecoregions and two plant types (figures 2(a) and (c)). Significant differences in the single-harvest BGB:AGB ratio among the ecoregions were observed (figure 2(a), ANOVA \( p < 0.001 \)), with the highest single-harvest BGB:AGB ratio in the cold steppe (86) and the lowest in the savanna regions (0.93). The highest single-harvest BGB:AGB ratio in the cold steppe was attributed to the lowest AGB (73 gm\(^{-2}\) harvest\(^{-1}\)) and the highest BGB (1097 gm\(^{-2}\) harvest\(^{-1}\)) among the ecoregions. The single-harvest AGB (BGB) in the humid temperate, humid savanna, and savanna regions were 206 (703), 200 (477), and 144 (112) gm\(^{-2}\) harvest\(^{-1}\), respectively (figures S1(a) and (b)). The lowest single-harvest BGB:AGB ratio in the savanna was caused by the lower single-harvest AGB and BGB than those of other ecoregions (figures S1(a) and (b)). Correspondingly, the BGB:AGB ratio of \( C_3 \)-dominated grasslands was higher (61) compared to \( C_4 \)-dominated grasslands (4.6) (figure 1(c)). The higher single-harvest BGB:AGB ratio of \( C_3 \)-dominated grasslands resulted from the lower single-harvest AGB but higher BGB of this plant type (figures S1(c) and (d)).

Similarly, the annual BGB:AGB ratio varied markedly across the ecoregions and plant types (figures 2(b) and (d), all ANOVA \( p < 0.001 \)). The annual BGB:AGB ratio decreased in the order of cold steppe > humid temperate > humid savanna > savanna (figure 2(b)). The annual BGB:AGB ratio between ecoregions differed significantly (all \( p < 0.001 \)), except between humid temperate and humid savanna ecoregions (figure 2(b), \( p > 0.05 \)). The highest annual BGB:AGB ratio in the cold steppe (16) was associated with the lowest annual AGB (514 gm\(^{-2}\) yr\(^{-1}\)) and highest annual BGB (7681 gm\(^{-2}\) yr\(^{-1}\)) compared to other ecoregions (figures S2(a) and (b)). Like the single-harvest BGB:AGB ratio, \( C_3 \)-dominated grasslands exhibited a higher annual BGB:AGB ratio (12.2) than \( C_4 \)-dominated grasslands (2.3) (figure 2(d)).

3.2. Response of BGB:AGB ratio to climatic variability

Pearson’s correlation analysis showed that the single-harvest BGB:AGB ratio of \( C_3 \)-dominated grasslands was significantly negatively correlated with GST, GST\(_{\text{max}}\), and GST\(_{\text{min}}\) (figures 3(a), S3(a), and S4(a); all \( p < 0.01 \)). These temperature variables had significant positive effects on the single-harvest AGB at all sites and on the single-harvest BGB at two sites (shr and otr) in \( C_3 \)-dominated grasslands (figures 3(b) and (c), S3(b) and (c), and S4(b) and (c); all \( p < 0.05 \)). On the contrary, the annual BGB:AGB ratio of \( C_3 \)-dominated grasslands did not show any significant correlation with MAT, MAT\(_{\text{max}}\), and MAT\(_{\text{min}}\) (figures S5(a), S6(a), and S7(a); all \( p > 0.05 \)). These insignificant correlations between the annual BGB:AGB ratio of \( C_3 \)-dominated grasslands and annual temperatures were because neither the annual AGB (figures S5(c), S6(c), and S7(c)) nor the annual BGB (figures S5(e), S6(e), and S7(e)) exhibited a significant response to these temperature variables (all \( p > 0.05 \)), with the exception of a significant increase in annual BGB at a site in the cold steppe region (figures S5(e), S6(e), and S7(e); all \( p < 0.05 \)).

Unlike the \( C_3 \)-dominated grasslands, the single-harvest BGB:AGB ratio of \( C_4 \)-dominated grasslands was significantly positively correlated with GST\(_{\text{max}}\) (figure S3(a), \( p < 0.05 \)). The increase in the single-harvest BGB:AGB ratio of the \( C_4 \) plant with GST\(_{\text{max}}\) was due to the decrease in single-harvest AGB (figure S3(b), all \( p < 0.05 \)) but the insensitive response of BGB (figure S3(c), all \( p > 0.05 \)). No significant effects of GST and GST\(_{\text{min}}\) on the single-harvest BGB:AGB ratio of \( C_4 \)-dominated grasslands were observed (figures 3(a) and S4(a); all \( p > 0.05 \)), except a significant positive effect of GST on the BGB:AGB ratio of this plant type at a site in the humid savanna ecoregion (figure 3(a), \( p < 0.001 \)). Like \( C_3 \)-dominated grasslands, no detectable correlations were observed between annual temperature variables and the annual BGB:AGB ratio of \( C_4 \)-dominated grasslands (figures S5(b), S6(b), and S7(b)). The only significant positive effects of MAT\(_{\text{max}}\) on the annual BGB:AGB ratio of this plant type were detected at a site in the humid savanna ecoregion (figure S6(b), \( p < 0.05 \)).

As shown in figure 4, irrespective of sites, the responses of the single-harvest BGB:AGB ratio of \( C_3 \)-dominated grasslands to GST and the annual BGB:AGB ratio of \( C_4 \)-dominated grasslands to GST\(_{\text{cum}}\) were different. For instance, the single-harvest BGB:AGB ratio of the \( C_3 \) plant at a site in the cold steppe and the \( C_4 \) plant at a site in the humid savanna declined with the rising GST (figure 4(a),
both $p < 0.01$), while the single-harvest BGB:AGB ratio of both categories of plants at other sites across the ecoregions did not show a significant response to the GSP (figure 4(a), all $p > 0.05$). Likewise, for $C_3$-dominated grasslands in the cold steppe ecoregion, the annual BGB:AGB ratio at one site increased while at another site it decreased with the rising GSP$_{cum}$ (figure 4(b), both $p < 0.05$). In the savanna and humid savanna ecoregions, the GSP$_{cum}$ had significant negative effects on the annual BGB:AGB ratio of $C_4$-dominated grasslands (figure 4(b), $p < 0.05$). The decreasing trends of the annual BGB:AGB ratio of $C_4$-dominated grasslands were caused by the significantly positive response of the annual AGB but the insignificant response of the annual BGB to the increasing GSP$_{cum}$ (figures S8(c) and (d)). Neither $C_3$- nor $C_4$-dominated grasslands in the humid temperate, humid savanna, or savanna ecoregions exhibited significant interactions between the annual BGB:AGB ratio and AP (figure S9(a), all $p > 0.05$), which was due to the insignificant correlation of AP with the annual AGB and BGB of these plant types (figures S9(b) and (c), all $p > 0.05$).

### 3.3. Climate extremes effects on BGB:AGB ratio

Irrespective of plant types and ecoregions, the effects of growing-season climate events (i.e. extreme wet, normal, and extreme dry) on the single-harvest BGB:AGB ratio, AGB, and BGB were different. The most pronounced differences in single-harvest biomass were observed in $C_3$-dominated grasslands in the cold steppe (figure 5) and $C_4$-dominated grasslands in the savanna and humid savanna ecoregions (figure 6). For example, the single-harvest BGB:AGB of $C_4$-dominated grasslands significantly varied among the climate events (figures 6(a), (d), and (g); all ANOVA $p < 0.01$). Compared to normal growing-season climates, extreme dry events resulted in a significantly higher single-harvest BGB:AGB ratio of $C_4$-dominated grasslands (figures 6(a), (d), and (g); all $p < 0.05$). Meanwhile, for $C_4$-dominated grasslands, extreme dry climates reduced the single-harvest AGB and increased the single-harvest BGB (figure 6). Notably, $C_4$-dominated grasslands also exhibited a significantly higher single-harvest BGB:AGB ratio during the growing-season extreme dry climates compared to the BGB:AGB ratio base-mean (figures 6(a), (d), and (g)).
The same as figure 3, but for the association of single-harvest BGB:AGB ratio of C3- and C4-dominated grasslands with the GSP (a), and the association of annual BGB:AGB ratio of C3- and C4-dominated grasslands with the GSP\textsubscript{cum} (b).

For C3-dominated grasslands, no significant differences were observed in the variations of the single-harvest BGB:AGB ratio among the growing-season climate events (figures 5 and S10, all ANOVA $p > 0.05$), although extreme dry events exhibited a higher single-harvest BGB:AGB ratio in the cold steppe (figures 5(a) and (d)) and at a site in the humid temperate ecoregions (figure S10(d)). Neither extreme dry nor extreme wet events had significant effects on the single-harvest AGB and BGB of C3-dominated grasslands (figures 5 and S10), except for a significant reduction of the AGB in extreme dry climates at a cold steppe site (figure 5(e), $p < 0.05$).

The annual BGB:AGB ratio, AGB, and BGB of C3-dominated grasslands did not show any consistent patterns with annual climate events (figures S11(a), (d), (g), and (j)), except for significant differences of the annual AGB at a site in the cold steppe ecoregion (figure S11(e)), ANOVA $p = 0.004$). At this site, the annual AGB in wet events was significantly higher than that in normal and dry events (figure S11(e), both $p < 0.05$). The effects of annual climate events on the annual BGB:AGB ratio of C3-dominated grasslands were insignificant (figure S12).

The annual BGB:AGB ratio, AGB, and BGB of C4-dominated grasslands did not show any consistent patterns with annual climate events (figures S11(a), (d), (g), and (j)), except for significant differences of the annual AGB at a site in the cold steppe ecoregion (figure S11(e)), ANOVA $p = 0.004$). At this site, the annual AGB in wet events was significantly higher than that in normal and dry events (figure S11(e), both $p < 0.05$). The effects of annual climate events on the annual BGB:AGB ratio of C4-dominated grasslands were insignificant (figure S12).

4. Discussion

With increasing temperature and altered precipitation intensity and timing, global climate change is projected to affect grassland AGB and BGB productivity [5], which may affect the BGB:AGB ratio [12]. Exploring the critical factors regulating grassland biomass partitioning across ecoregions is a
Figure 5. Effects of growing-season climate events (i.e. extreme wet, normal, and extreme dry) on single-harvest BGB:AGB ratio, AGB, and BGB of C₃-dominated grasslands at SHR (a)–(c) and TMG (d)–(f) sites in cold steppe ecoregion. Significance difference of the single-harvest BGB:AGB ratio, AGB, and BGB between climate events was examined by the t test. The values on horizontal solid lines denote the significance of the difference between climate events (e.g. extreme wet and extreme dry). Asterisks (*p < 0.05, **p < 0.01, ***p < 0.001) on top of the box represent significant differences of biomass compared to their base-mean, and the abbreviation 'ns' indicates a non-significant effect. Horizontal dashed lines indicate the biomass base-mean (i.e. mean of extreme and normal climates). The boxes indicate the first and third quartiles, and whiskers denote the 95% confidence intervals. The circles and solid lines in the box represent the mean and median, respectively.

4.1. Variations in BGB:AGB ratio

Our results show that the annual and single-harvest BGB:AGB ratio varies significantly across the four ecoregions (figure 2). Similar results were also reported for six grassland types in northern China [17], for four grassland ecoregions in the Northern Tibetan Plateau [47], and for four grassland types on the Qinghai–Tibetan Plateau [48]. For both the single-harvest and annual biomass, the highest BGB:AGB ratio of C₃-dominated grasslands in the cold steppe was attributed to a significantly lower AGB but higher BGB than other ecoregions. This is because C₃ plants in the cold steppe are slow-growing and low-productive in their shoots, while the low respiration rate of roots accumulates a higher BGB [18]. Like our study findings, similar evidence was also observed in the northern Qinghai–Tibet Plateau [19], where the BGB in the colder alpine and meadow steppe was reported to be higher than the AGB, implying a higher BGB:AGB ratio. The lowest BGB:AGB ratio in the savanna was the consequence of the production of almost equal amounts of biomass above and below ground. The differences in the BGB:AGB ratio across ecoregions and plant types could be explained by the differences in climate. For example, C₃-dominated grasslands are limited by precipitation and low temperatures, while C₄-dominated grasslands are regulated by higher temperatures. In general, C₃ plants allocate more photosynthates to roots than shoots [49], and thus exhibited a higher BGB:AGB ratio. Another possible interpretation is that in limited precipitation, using the deep rooting profile and three-directional expansion of roots (e.g. horizontal, lateral, and at an angle to the surface),
Figure 6. The same as figure 5, but for the effects of growing-season climate events on the single-harvest BGB:AGB ratio, AGB, and BGB of C₃-dominated grasslands in humid savanna (KLN site (a)–(c) and MNT site (d)–(f)) and savanna (NRB site (g)–(i)) ecoregions.

C₃-dominated grasslands may uptake the required water for maintaining their growth and development [50]. Furthermore, the higher BGB:AGB ratio of C₃-dominated grasslands could be partially attributed to the comparatively slow decomposition of roots because of the cold climate condition [51], while the lower BGB:AGB ratio of C₄-dominated grasslands may be associated with the higher mineralization and decomposition of roots [52] and higher evapotranspiration [52].
4.2. Response of BGB:AGB ratio to climatic variability
In order to adapt to the local climate, grasslands in different regions respond differently to climatic variability by adjusting the distribution of photosynthate to roots and shoots, and thus the biomass partitioning alters with the changes of temperature and precipitation [12]. The responses of the BGB:AGB ratio to temperature and precipitation across ecoregions were mixed. These differential responses of the BGB:AGB ratio to climatic variables can be explained by the plant functional types. The decreased BGB:AGB ratio of C₃-dominated grasslands in the humid temperate and cold steppe ecoregions with rising temperatures suggests that the C₃ plants invest more resources above ground to capture more sunlight to optimize shoot growth than below ground to extract water and nutrients in a warm climate [53]. In our study, the positive correlations of the single-harvest AGB and BGB with the GST, GSTmax, and GSTmin in C₃-dominated grasslands were consistent with those demonstrated in C₃-dominated grasslands in temperate and cold steppe ecoregions [54–56]. Although temperature promoted both the AGB and BGB of C₃-dominated grasslands, the allocation of AGB was much higher than that of BGB, and thus the BGB:AGB ratio of C₃ plants decreased with elevated temperatures. Unlike C₃-dominated grasslands, the increased BGB:AGB ratio of C₄ plants in humid savanna and savanna ecoregions with elevated temperature indicates that the BGB in these ecoregions would benefit from the increasing temperature [57] at the cost of AGB [35]. The decreased single-harvest AGB and enhanced single-harvest BGB of C₄-dominated grasslands with increasing GST and GSTmax suggest that the reduced AGB may be attributed to the heat stress caused by GST and GSTmax [58], and the increased BGB may be caused by the plant’s allocation of more resources for the production of fine roots in order to reduce temperature-induced stress [59].

The negative correlations of the BGB:AGB ratio with GSP and GSPcum observed in C₄-dominated grasslands might be caused by the increased photosynthesize allocated to AGB or the faster decomposition of BGB with increasing precipitation [13]. This evidence supports our findings of positive correlations of AGB and of negative or no correlations of BGB with precipitation in C₄-dominated grasslands. The increased AGB of C₄-dominated grasslands with increasing GSP and GSPcum suggests that growing-season precipitation can explain AGB changes better than AP [60], as C₄ plants require water at different growing stages [61]. The correlation between AP and the annual AGB of C₄ plants was insignificant, because late precipitation in plant growth stages delays plant senescence and thus has no effect on the annual AGB [62].

4.3. Effects of climate extremes on BGB:AGB ratio
The differential effects of climate extremes on biomass partitioning were not only caused by the differences in sites, ecoregions, and plant types, but can also be ascribed to the direction (e.g. dry or wet) and timescale of climate extremes (e.g. growing-season or annual climate events). In our study, the growing-season climate extremes explained the variable responses of the single-harvest BGB:AGB ratio across ecoregions and plant types (figures 5 and 6). The observed positive effects of growing-season extreme dry climates on the single-harvest BGB:AGB of C₃-dominated grasslands in the cold steppe ecoregion might be caused by an increase in evapotranspiration, weakening of photosynthesis, and reduction in soil moisture under extreme dry conditions [63, 64]. Conversely, although the growing-season extreme wet climates reduced the single-harvest BGB:AGB ratio of C₃ plants in the cold steppe ecoregion, both the single-harvest AGB and BGB of these grasslands tended to rise during the extreme wet conditions. These results suggest that extreme wet events would have positive effects on grassland carbon stocks in C₃-dominated grasslands, which is in accordance with previous studies in alpine and temperate grasslands [65].

The grasslands in warmer ecoregions have adaptive strategies to address environmental stresses [66]. However, excessive stress impairs the ability of grassland biomass partitioning, which we observed in our study for C₄-dominated grasslands. The observed higher single-harvest BGB:AGB ratio of C₄-dominated grasslands during extreme dry events highlights that C₄ plants either reduce the AGB or enhance the BGB to cope with extreme dry conditions. The decreased single-harvest AGB of C₄ plants during the growing-season extreme dry climates can be explained by the weakening plant photosynthesis due to a decrease in soil water and increase in evapotranspiration during extreme dry events [64], and is in accordance with a study by Kahmen et al [67], which reported that drought decreased the AGB in semiarid grasslands. Likewise, the enhanced single-harvest BGB of C₄ plants during the growing-season extreme dry climates supports the notion that plants allocate more photosynthesize below ground to extract more water and maintain BGB productivity [68] by stimulating fine roots [18]. Compared with extreme wet or normal climates, the significantly higher single-harvest BGB:AGB ratio during the growing-season extreme dry climates suggests that droughts would enhance the BGB of C₄ plants, which may potentially make a contribution to the global soil carbon stocks in the savanna and humid savanna grasslands at the expense of AGB, and lowering the above-ground functioning [19].
Last but not least, caveats shall be made to interpret the results and implications in practice. First, this study comprises four ecoregions, but the study sites may be limited for individual ecoregions. The findings of biomass partitioning based on a small number of sites in an ecoregion may not sufficiently represent the entire ecoregion, as species composition, richness, and functional groups (e.g. grasses, herbs, legumes, etc) may differ among the sites/experiments within an ecoregion [10]. Given the variability in species composition and the differences in the gradient of species richness and functional groups among sites, future studies should consider the observations of AGB and BGB data in multiple sites in an ecoregion in order to have a better representation of the correlations of biomass partitioning with climatic variability and climate extremes in that ecoregion. Second, the harvest frequency also differed among the sites and ecoregions due to the length of the plants’ growing season. For example, in the cold steppe and humid temperate ecoregion, harvest frequency ranges between six and eight times a year, while in the savanna and humid savanna ecoregion the biomass was harvested every month of the year. Moreover, the temporal scale of the study varied widely, ranging from 3 years at a site in the humid temperate ecoregion to 10 years in the savanna and cold steppe ecoregions. Furthermore, our study focused on C3- and C4-dominated grasslands separately, but the cultivation of a mixture of C3 and C4 plant types in meadow production (e.g. smallholder farming systems) can have complementary effects with each other and buffer the grasslands from climate extremes [69]. Our study demonstrated that the growing-season climate extremes reduce the AGB in both C3- and C4-dominated grasslands. A higher cut may be an option in smallholder farming systems in order to minimize the loss of biomass productivity under extreme climate conditions. Although plenty of experiments are being conducted across different biomes in order to explain the debated issue of climate-productivity relationships [28, 29], long-term AGB and BGB observations across multiple sites in different ecoregions are important to advance our study understanding. In a long-running experiment, plants will experience more climate events and may have adaptive response mechanisms in their biomass partitioning. For short-term observations (e.g. 1–2 years), there are less likely to be annual extreme events, and thus one cannot apply our study methodology to assess the relationship between annual productivity and annual climate events. However, our methodology can be applied for the examination of the effects of growing-season climate events on the respective harvest, as the occurrence of growing-season extreme events is highly likely in short-running experiments [44].

5. Conclusion

Variations in biomass partitioning in C3- and C4-dominated grasslands and their response to climatic variability and climate extremes were evaluated using grassland biomass data from seven study sites in humid temperate, cold steppe, savanna, and humid savanna ecoregions. The single-harvest and annual BGB:AGB ratio varied significantly across ecoregions, with the lowest values of BGB:AGB ratio in savanna and the highest in cold steppe. C3-dominated grasslands exhibited a higher BGB:AGB ratio than C4-dominated grasslands. The biomass of these grasslands responded significantly to variations in growing-season and annual climate variables and climate extremes, but the responses were different for the two plant types in four ecoregions. Specifically, the increased single-harvest BGB:AGB ratio of C4 plants and reduced BGB:AGB ratio of C3 plants with the increasing GST and GSTmax suggest that C4 plants lose and C3 plants gain AGB with increased growing-season warming. In C4-dominated grasslands, precipitation had greater effects than the temperature on the annual biomass partitioning, where the decreased annual BGB:AGB ratio of C4 plants mostly resulted from the positive associations between annual AGB and GSPcum. The single-harvest BGB:AGB ratio of C4-dominated grasslands varied significantly among the growing-season climate extremes. Compared to normal climates, extreme dry climates increased the BGB:AGB ratio of C4 plants. This result can be explained by the increase in BGB and decrease in AGB in C4-dominated grasslands in extreme dry events. The large reduction of AGB is likely to reduce ecosystem functioning and stability in C4-dominated grasslands. But, for C3-dominated grasslands in the cold steppe, the higher single-harvest BGB:AGB ratio during the growing-season extreme dry climate resulted from the drought-induced loss of both AGB and BGB, suggesting that the grasslands in this ecoregion are potentially under threat from the increasing climate extremes, particularly under extreme droughts. This study helps us to better understand the plants’ responses to climate extremes and their adaptive strategies in biomass partitioning. These results have important implications for sustainable grassland management in relation to current climatic variability and for predicting the response of biomass partitioning to frequent climate extremes across C3- and C4-dominated grasslands in different ecoregions.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://doi.org/10.3334/ORNLDAAC/654.
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We gratefully acknowledge two data sources. We retrieved the open access grassland data and all climate data from the global NPP database at the Oak Ridge National Laboratory Distributed Active Archive Center, Tennessee, USA [39]: https://doi.org/10.3334/ORNLDAAC/654, with the exception of the monthly mean temperature and some missing values of monthly precipitation and maximum and minimum temperature at some sites. The monthly mean temperature and missing values were extracted from the Climatic Research Unit (CRU) [42], https://catalogue.ceda.ac.uk/uuid/10d3e3640f004c578403419aac167d82]. The Hong Kong PhD Fellowship (Fellowship Application Reference Number PF17-08241) was awarded to M L H by the Research Grants Council (RGC) of the Hong Kong Special Administrative Region, China. This work was supported by research grants from the RGC (Project No. HKBU12302518) and National Key R&D Program of China (Project No. 2019YFC1510400).

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