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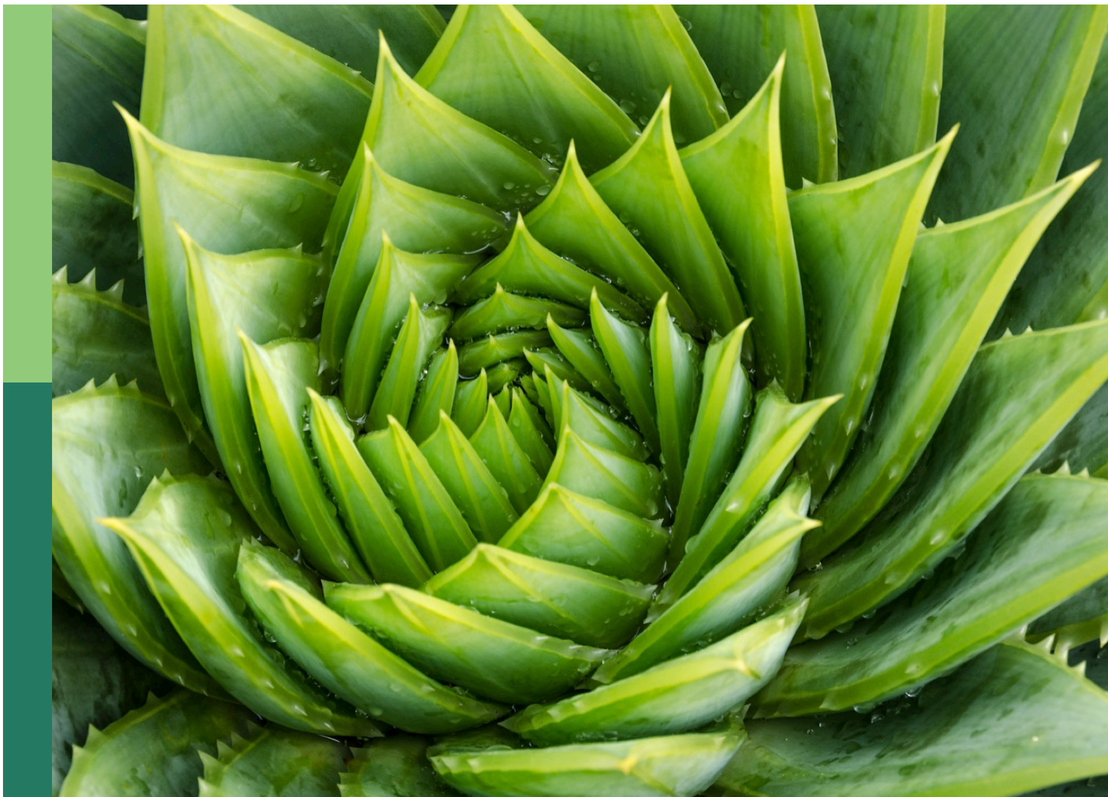
Plant diversity and biomass dynamics under environmental variation

Edited by
Arshad Ali

Published in
Frontiers in Plant Science



ISSN 1664-8714
ISBN 978-2-83252-078-9
DOI 10.3389/978-2-83252-078-9

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Plant diversity and biomass dynamics under environmental variation

Topic editor
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Citation
Ali, A., ed. (2023). *Plant diversity and biomass dynamics under environmental variation*. Lausanne: Frontiers Media SA. doi: 10.3389/978-2-83252-078-9

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Frontiers in Plant Science

TYPE Editorial
PUBLISHED 20 March 2023
DOI 10.3389/fpls.2023.1159695

OPEN ACCESS

EDITED AND REVIEWED BY
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SPECIALTY SECTION
This article was submitted to
Functional Plant Ecology,
a section of the journal
Frontiers in Plant Science

RECEIVED 06 February 2023
ACCEPTED 10 March 2023
PUBLISHED 20 March 2023

CITATION
Ali A (2023) Editorial: Plant diversity
and biomass dynamics under
environmental variation.
Front. Plant Sci. 14:1159695.
doi: 10.3389/fpls.2023.1159695

Editorial: Plant diversity and biomass dynamics under environmental variation

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KEYWORDS

aboveground biomass, biodiversity, belowground biomass, ecological mechanisms, environmental factors, forests, grasslands

Editorial on the Research Topic
Plant diversity and biomass dynamics under environmental variation

Background and aims of the research topic

For assessing the long-term viability of grasslands and forests, it is essential to decipher the effects of environmental drivers (including climate and soil) on plant diversity and biomass dynamics (including above-ground and below-ground parts) and their interconnections in both natural and experimental conditions (van der Plas, 2019; Wang et al., 2019; Ma et al., 2021; Cabon et al., 2022). Although plant diversity and composition (including functional traits) are the main biotic drivers of plant biomass dynamics, environmental factors could have significant impacts on both plant diversity and biomass (Díaz et al., 2007; Chu et al., 2016; Poorter et al., 2017; Abbasi et al., 2022). Over the last few decades, most research on plant diversity and biomass has been focused on how niche complementarity, mass ratio, and selection effects play a role in understanding how biodiversity and ecosystem functioning can be connected in natural and experimental plant communities (van der Plas, 2019; Abbasi et al., 2022). Yet, exploring the pathways by which plants interact with their environment is important in understanding how they grow and produce energy which in turn can affect plant diversity and biomass (Chu et al., 2016; Poorter et al., 2017; Michaletz et al., 2018).

Understanding the environmental effects on biotic processes is essential for predicting how climate change will affect ecological processes that have feedback on the plant's physiological processes (Figure 1; left side) (Chu et al., 2016; Michaletz et al., 2018; Cabon et al., 2022). The plant physiology and ecology concepts suggest that climate factors, such as temperature and precipitation, have several divergent and convergent influences on the productivity and functioning of ecosystems (Corlett, 2016). The photosynthetic rates, respiration rates, and the distribution of plant biomass are the key physiological processes that determine plant development and are directly influenced by temperature and water availability (Brown et al., 2004; Huxman et al., 2004; Chu et al., 2016; Abbasi et al., 2022). Also, climate can influence plant biomass indirectly *via* adjusting the biodiversity and structure of a community or ecosystem (Poorter et al., 2017; Michaletz et al., 2018; Ma et al., 2021). Many studies have shown that plants suffer more from climate change because of drought and heat which govern the diversity and distribution of plants and the dynamics of their biomass (Corlett, 2016; Bennett et al., 2021; Abbasi et al., 2022). However, it is generally suggested that advancement in research occurs when theoretical and natural observational studies coincide with experimental studies (such as environmental manipulation) (Loreau et al., 2001; Díaz et al., 2007). While researching from both natural observational and experimental viewpoints, we are still not sure if the effects of the environment on plant diversity and biomass are the same for every ecosystem. Furthermore, there is little research on these consequences on a worldwide level.

Our understanding is still limited, thereby demanding additional research across ecosystems and biomes to investigate how environmental factors affect plant diversity and biomass dynamics in natural and experimental plant communities. This Research Topic provided a platform to collect papers on linking the environment, biodiversity and plant above- and below-ground biomass in grasslands and forests through experimental and natural observational approaches. In doing so, I bring together eight theoretical, observational, and experimental studies in China's grasslands and forests with two global meta-analyses (see general map in Figure 1). The ten published papers have tested the research questions using advanced statistical models to demonstrate and discuss the drivers and mechanisms of plant diversity and biomass dynamics under experimental environment control and natural conditions.

Contributions of the research topic

Ten publications make up this Research Topic (e-book), including eight original studies from China and two global meta-analyses (see general map in Figure 1), thereby encompassing both forests and grasslands (see Figure 2). The authors of eight original studies evaluated the effects of environmental conditions on plant diversity and biomass as well as their interrelationships through statistical modellings, using original data from control experiments in grassland (Cheng et al.; Liu et al.; Li et al.) and young tree seedling in a greenhouse (Yang et al.), and natural observations in grasslands (Yao et al.; Wang et al.) and forests (Yang et al.; Liang et al.). The two global meta-analyses (Zhang and Xi; Xie et al.) have studied the terrestrial ecosystems in five continents to explore the effects of precipitation on above- and below-ground biomass as well as biodiversity. For a better understanding of the research findings, this e-book can be divided into three main sections, i.e., experimental and natural studies on grasslands (Section 1; Cheng et al.; Liu et al.; Li et al.; Yao et al.; Wang et al.), studies on forests (Section 2; Yang et al.; Yang et al.; Liang et al.), and global meta-analyses on terrestrial ecosystems (Section 3; Zhang and Xi; Xie et al.) (Figure 2). Although the specific research questions of the ten studies included in this Research Topic have investigated the connections between plant diversity and biomass under environmental variation, the broad contributions can be summarized and discussed in the following main points: 1) biotic drivers (e.g., plant traits, coverage, tree sizes and species diversity) of China's grasslands and forests under environmental controls; 2) effects of precipitation and warming on plant diversity and biomass; and 3) the effects of precipitation on global ecosystem productivity.

Biotic drivers of China's vegetation biomass under environmental controls

Although several studies have examined the biotic drivers of above-ground biomass in natural forest and grassland ecosystems, further research is needed to improve our understanding of these relationships in grasslands subjected to either environmental manipulation or covering large-scale, and in the tree communities of arid regions (van der Plas, 2019). In this Research Topic, Cheng et al. show that the community-weighted mean (CWM) of plant height and leaf dry matter content promoted whereas leaf area declined above-ground biomass directly under the precipitation manipulation experiments in the desert steppe of Inner Mongolia, indicating that plant functional trait composition rather than species diversity is the major biotic driver of ecosystem functioning (Díaz et al., 2007; van der Plas, 2019). Moreover, Liu et al. show that, under the growing season precipitation manipulation experiments in the Inner Mongolia steppe, patterns of plant biomass allocation varied significantly between the four dominant grassland species, pointing to morphological differences between plant species, which may explain how biomass is allocated through physiological processes, rates, and scaling rules (Brown et al., 2004; Ma et al., 2021). Interestingly, Li et al. show that, under 9-year soil warming experimental conditions in the Qinghai–Tibetan Plateau, the temporal biomass stability of sedges, which decreased with warming, explained more than two-thirds of the variance in the temporal stability of the entire plant community, indicating that dominant plants better control ecosystem functions than species richness (Díaz et al., 2007; van der Plas, 2019). These experimental studies in Research Topic (Cheng et al.; Liu et al.; Li et al.) show that, under various environmental conditions in grasslands, plant functional traits and dominant functional groups are better predictors of above-ground biomass and even temporal stability than species richness (Díaz et al., 2007; Isbell et al., 2009).

By using the observation data from 123 grassland meta-sites dominated by *Leymus chinensis*, Yao et al. show that while species richness had negligible effects on above-ground biomass across topographical and climatic gradients, plant coverage promoted and species evenness restricted above-ground biomass (Chu et al., 2016; Grace et al., 2016; Sanaei et al., 2019). However, Wang et al. show that the above- and below-ground biomass of the alpine meadows decreased when plateau pika was present, indicating that herbivore disturbance declines biomass probably due to directly altering plant coverage and species diversity (Archibald et al., 2019; Sanaei et al., 2019). By using the greenhouse experiment on two tree species under well-watered and waterlogging treatments, Yang et al. indicate that biotic interactions shape tree diversity and functioning, thus suggesting that suitable plant species should be selected for plantation and revegetation activities in wetland zones (Paquette and Messier, 2010). In natural forest and planted tree ecosystems in the northwest arid region of China, Yang et al.

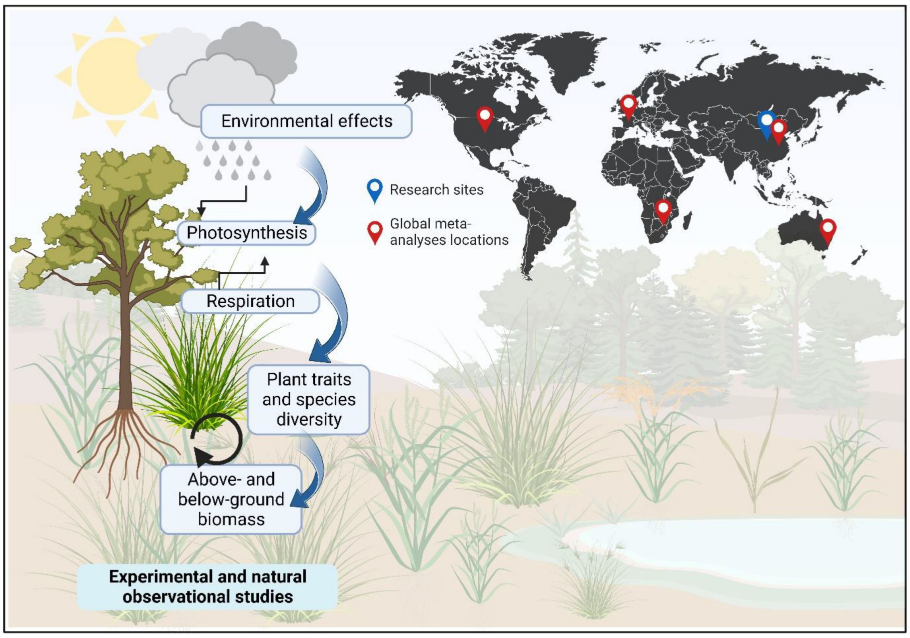

FIGURE 1
Conceptual framework showing the scientific scope of this Research Topic (e-book).

demonstrate that large plants, species diversity, and tree stand density all increased above-ground biomass in the arid region, which shows that the big-sized trees effect and scaling theory are generalizable to arid regions (Lutz et al., 2018; Ali et al., 2019). These observational studies show that the potential biotic driver of above-ground biomass is plant coverage in grasslands, whereas, in tree ecosystems, large plants do so, indicating that the effects of species richness on ecosystem functioning are overridden by dominant species and functional groups (Díaz et al., 2007; Ali et al., 2019; Sanaei et al., 2019).

Precipitation regulates China's vegetation directly and indirectly

Although the primary biotic drivers of plant biomass dynamics are plant diversity and composition (including their functional traits), both plant diversity and biomass depend heavily on environmental factors (van der Plas, 2019). In this Research Topic, using the precipitation manipulation experiments in the desert steppe of Inner Mongolia in Northern China, Cheng et al. show that plant functional traits (plant height, leaf area, and leaf dry matter content) rather than species diversity regulated variation in above-ground biomass through direct and indirect pathways, thereby suggesting that plant functional traits are mechanistically linking the responses of ecosystem functioning to changing patterns in precipitation (van der Plas, 2019). As such, another study by Liu et al. in Inner Mongolia steppe shows that, by using manipulation experiments based on growing season precipitation, increased growing season precipitation led to a rise in the above-ground, below-ground, and total biomass of four main grassland species, thereby also showing that biomass allocation patterns between species are dependent on the amount of precipitation (Brown et al., 2004; Ma et al., 2021). Interestingly, Li et al. show that under 9-year soil warming experimental conditions in the Qinghai–Tibetan Plateau, the relative AGB of grasses and forbs significantly increased and that of sedges decreased irrespective of the soil moisture effects but depended on annual precipitation, indicating that the temporal stability of plant community is largely governed by the few dominant plant functional groups which mediate the responses of ecosystem functioning and stability to environmental conditions (Isbell et al., 2009; Wang et al., 2019). By using the greenhouse experiment on two tree species under well-watered and waterlogging treatments, Yang et al. show that plant competitive interactions that occur in well-watered environments changed to mutualistic interactions in waterlogged environments, indicating that harsh environmental conditions lead to niche facilitation between tree species for high productivity and functioning (Brooker et al., 2008).

By using the observation data from 123 grassland meta-sites dominated by *Leymus chinensis*, Yao et al. show that the above-ground biomass was influenced by precipitation and temperature in several ways, both directly and indirectly *via* the coverage and diversity of plants, indicating that the grasslands of northern China are sensitive to climate change, meaning that an increase in atmospheric heat and a decrease in climatic moisture may decline above-ground biomass (Chu et al., 2016; Grace et al., 2016; Ma et al., 2021). However, Wang et al. show that the above- and below-ground biomass of alpine meadows in the eastern Tibetan Plateau's responded differently to soil variables at sites with and without plateau pika disturbances, suggesting that grazing and herbivore disturbances in grasslands and meadows should be well-controlled

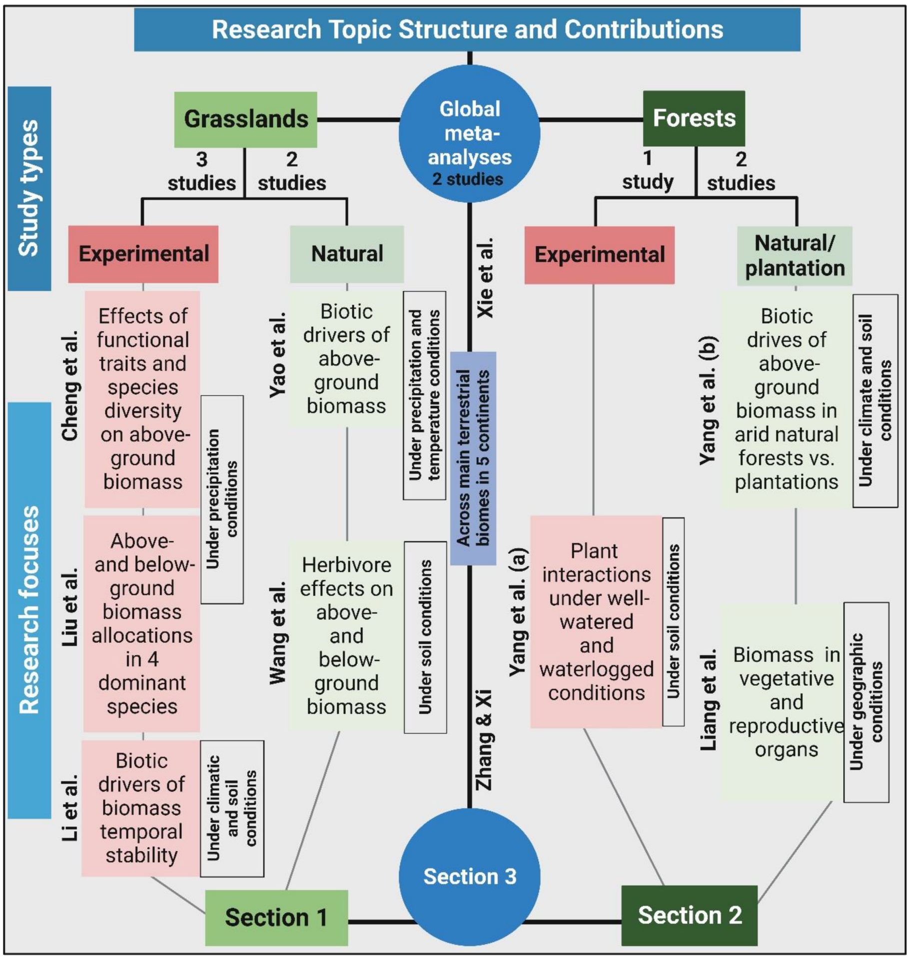

FIGURE 2
Flowchart diagram showing the structure and contributions of this Research Topic (e-book).

and managed to preserve biodiversity over time (Grace et al., 2016; Archibald et al., 2019; Sanaei et al., 2019). In tree ecosystems of China's northwest arid region, Yang et al. show that big-sized plants respond differently to climatic humidity and soil fertility, and even to species diversity, thereby highlighting the distinct roles that different environmental factors play in shaping the physiological processes of natural and planted large plants, which control plant diversity and above-ground biomass in arid regions (Lutz et al., 2018; Ali et al., 2019). Moreover, Liang et al. show that dove trees at high latitudes tend to have smaller twigs, and they use more resources for stems and leaves but less for flowers, indicating that dove trees adjust their growth and the distribution of twig biomass in response to environmental changes along a latitudinal gradient (Salazar et al., 2019; Ma et al., 2021).

Precipitation regulates global ecosystem productivity

The above- and below-ground biodiversity and ecosystem productivity are regulated by environmental factors such as precipitation and temperature, which provide feedback to climate change (Trenberth et al., 2014). However, it has been increasingly recognized that precipitation patterns can have a big impact on ecosystem biodiversity, structure, and functions as it affects climatic and edaphic water availability (Chu et al., 2016; van der Plas, 2019; Abbasi et al., 2022). However, several issues, including (1) assessing patterns of combined responses of soils and plants to climatic conditions, and (2) intra-annual rainfall patterns and their influence on the biodiversity and productivity of terrestrial ecosystems, remain unresolved at a wide geographical scale. In this Research Topic, by using meta-data from 32 global sites, located in Asia, North America, Africa and Oceania, Zhang and Xi show that both above- and below-ground plant biomass as well as soil microbial biomass can react asynchronously to changes in precipitation, thus it is crucial to investigate the plant-soil feedback to comprehend how environmental changes affect grassland ecosystems. In addition, by using meta-data from 19 global sites across 6 major biomes, located in Asia, North America and Oceania, Xie et al. show that the above-ground plant production was enhanced by the regularity of precipitation, while below-ground plant growth was promoted by the varying patterns of precipitation, thus suggesting the importance of precipitation event timing uniformity and heterogeneity on ecosystem functioning.

The two global or large-scale meta-analyses (Zhang and Xi; Xie et al.) included in this Research Topic, contribute several important findings and cover the knowledge gaps for linking above- and below-ground biomass with environmental factors across terrestrial ecosystems. Both meta-analyses agree with the key finding that precipitation is an important environmental factor to regulate the responses of biodiversity and ecosystem productivity to drought and heat, i.e., climate change. Also, Zhang and Xi provide evidence that the asynchrony between above-ground and below-ground production, as well as microbial biomass carbon, is mediated by plant biomass allocation, thereby supporting the optimal allocation theory and emphasising that understanding the consequences of precipitation changes on grassland ecosystems may require understanding the plant-soil feedback (Brown et al., 2004; van der Plas, 2019; Ma et al., 2021). Also, Xie et al. emphasize that not only ecosystem productivity but also community structure and biodiversity respond to changes in precipitation patterns, thereby indicating that the relationship between biodiversity and ecosystem functioning is context-dependent which should be further studied at large spatial scales under different environmental conditions (Poorter et al., 2017; Ali et al., 2019; van der Plas, 2019; Abbasi et al., 2022). The findings of these meta-analyses also agree with both experimental and observational studies, included in this Research topic, conducted in China's grasslands and forests, thereby supporting the general notion that climatic and soil humidity matter for higher biodiversity and productivity in most cases.

Concluding remarks and future directions

Most of the ten published studies (particularly the original eight studies), in this Research Topic, focused on the effects of species diversity, however, functional trait identity, plant coverage, the existence of a particular functional group, and big-sized plants were often better predictors of ecosystem productivity (i.e., plant biomass). Furthermore, the majority of research suggests that climatic water availability increased but warming restricted plant diversity and ecosystem productivity, and thus ecosystem stability. Conservation should thus not just support plant diversity and biomass in general but also the environmental factors that favor species with optimal functional traits to jointly enhance those ecosystem diversity, structure, functions, and processes that support human well-being.

Studies in this Research Topic explored the effects of environmental factors on plant diversity and the biomass stock of both above- and below-ground portions of an ecosystem. However, future studies should focus on plant diversity- ecosystem multifunctionality which is a less debated topic in the current global ecological literature. Moreover, to better understand the environmental drivers of plant diversity and biomass dynamics, further research is largely needed to clearly consider the plant's physiological and metabolic processes in both experimental and large-scale observational studies. Moreover, it is very important to explore the unexplored forest and grassland ecosystems of the world to better understand the consequences of biodiversity loss on ecosystem functioning and productivity under global climate change. For future research in well-explored ecosystems, it is crucial to address advanced research questions using an interdisciplinary approach by combining plant biology and climatology. This can have significant implications for science, practice, and policy to better understand how global climate change and biodiversity loss affect both people and nature.

Author contributions

The author confirms being the sole contributor of this work and has approved it for publication.

Funding

My research work is supported by Hebei University (Grant No. 521100221033).

Acknowledgments

I appreciate Frontiers in Plant Science's editorial staff for the invitation to lead and edit this Research Topic and for their ongoing support. I am indebted to several handling editors and reviewers who contributed to the successful evaluation of the papers for this Research Topic. My sincere gratitude goes to the authors and my colleagues for their contributions to this Research Topic. The unwavering support of my research team is greatly appreciated. Graphical designs were created in the paid premium version of BioRender by the author of this editorial.

Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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in Plant Science

SYSTEMATIC REVIEW
published: 25 February 2021
doi: 10.3389/fpls.2021.614968

Precipitation Changes Regulate Plant and Soil Microbial Biomass *Via* Plasticity in Plant Biomass Allocation in Grasslands: A Meta-Analysis

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In theory, changes in the amount of rainfall can change plant biomass allocation and subsequently influence coupled plant-soil microbial processes. However, testing patterns of combined responses of plants and soils remains a knowledge gap for terrestrial ecosystems. We carried out a comprehensive review of the available literature and conducted a meta-analysis to explore combined plant and soil microbial responses in grasslands exposed to experimental precipitation changes. We measured the effects of experimental precipitation changes on plant biomass, biomass allocation, and soil microbial biomass and tested for trade-offs between plant and soil responses to altered precipitation. We found that aboveground and belowground plant biomass responded asynchronically to precipitation changes, thereby leading to shifts in plant biomass allocation. Belowground plant biomass did not change under precipitation changes, but aboveground plant biomass decreased in precipitation reduction and increased in precipitation addition. There was a trade-off between responses of aboveground plant biomass and belowground plant biomass to precipitation reduction, but correlation wasn't found for precipitation addition. Microbial biomass carbon (C) did not change under the treatments of precipitation reduction. Increased root allocation may buffer drought stress for soil microbes through root exudations and neutralize microbial responses to precipitation reduction. However, precipitation addition increased microbial biomass C, potentially reflecting the removal of water limitation for soil microbial growth. We found that there were positive correlations between responses of aboveground plant biomass and microbial biomass C to precipitation addition, indicating that increased shoot growth probably promoted microbial responses via litter inputs. In sum, our study suggested that aboveground, belowground plant biomass and soil microbial biomass can respond asynchronically to precipitation changes, and emphasizes that testing the plant-soil system as a whole is necessary for forecasting the effects of precipitation changes on grassland systems.

Keywords: aboveground-belowground interaction, asynchrony, carbon stock, grasslands, optimal biomass allocation, precipitation

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Specialty section:
This article was submitted to Functional Plant Ecology, a section of the journal Frontiers in Plant Science

Received: *07 October 2020*
Accepted: *01 February 2021*
Published: *25 February 2021*

Citation:
Zhang C and Xi N (2021) Precipitation Changes Regulate Plant and Soil Microbial Biomass Via Plasticity in Plant Biomass Allocation in Grasslands: A Meta-Analysis. Front. Plant Sci. 12:614968. doi: 10.3389/fpls.2021.614968

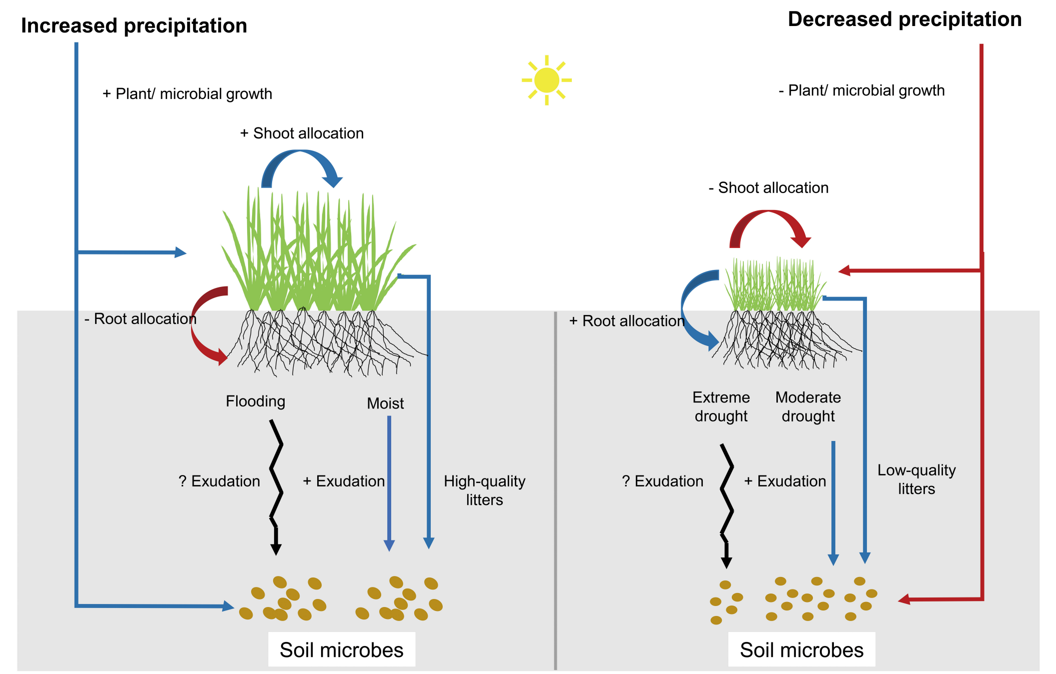

FIGURE 1 | Graphical depiction of how precipitation changes influence aboveground and belowground biomass *via* plasticity in plant biomass allocations. "+" and "–" indicate "increasing" and "decreasing" respectively. Black arrows indicate that there are no consistent conclusions on these ecological processes.

BACKGROUND

Grasslands represent the largest terrestrial biome, playing crucial roles in global carbon (C) cycling because they have higher soil C contents than other vegetation types for a given climate regime (Anderson, 1991). Plant productivity and microbial biomass C are two key factors in determining grassland C cycling. However, grassland C cycling may be largely variable, because of an increased frequency of wetter or drier years in future (Knapp and Smith, 2001). To date, the coupling responses of plants and soil microbes to precipitation changes remain a knowledge gap. There is an urgent need to fill this gap to acquire a comprehensive understanding of grassland ecosystems in the context of climate change.

Previous studies have illustrated that aboveground (APB) and belowground plant biomass (BPB) responded differently to precipitation changes, regulated by shifts in plant biomass allocation patterns (Byrne et al., 2013; Wilcox et al., 2017). Optimal allocation theory asserts that plants should allocate biomass to the organ that acquires the most limiting resource (Bloom et al., 1985; Gleeson and Tilman, 1992; Giardina et al., 2003). Under decreased precipitation (DPPT) conditions, plants may increase the allocation of carbohydrates to roots to maximize soil resource uptake, thus minimizing BPB loss while exacerbating APB loss (**Figure 1**). Under increased precipitation (IPPT) conditions, plants may increase aboveground growth to maximize light capture, resulting in greater aboveground responses than belowground (**Figure 1**). In principle, there are trade-offs between APB and BPB in the responses to either DPPT or IPPT, because in plants allocation of photosynthetic production is a zero-sum dynamic, i.e., increased allocation of production to shoots or roots must be at the expense of other organs (Mccarthy and Enquist, 2007).

Despite an increasing number of studies testing plant above- and belowground responses to altered precipitation, one critical knowledge gap is the combined response of plants and soil microbes to changes in precipitation amount. This lacuna could lead to a biased understanding of grassland function and service under climate change because soil microorganisms play a key role in carbon-cycling processes, such as litter decomposition and greenhouse gas emissions (van der Heijden et al., 2008; Bardgett and van der Putten, 2014). There are many reports showing that rainfall amounts can strongly influence soil microbial growth and community structure by changing soil moisture (Williams, 2007; Hueso et al., 2012; Ochoa-Hueso et al., 2018). Changes in the amount of rainfall also indirectly influence microbial communities by regulating litter inputs and changing root exudations (**Figure 1**) (Nielsen and Ball, 2015; Luo et al., 2017; Williams and de Vries, 2020). For instance, under moderate drought stress, plants may increase allocations of assimilated C into root soluble sugars that can be released as root exudates, thereby influencing soil microbial C uptakes (Preece and Peñuelas, 2016; Karlowsky et al., 2018a). However, root exudations and its consequence on soil microbes can be highly variable during extreme drought stress (Preece and Peñuelas, 2016). Moderate increases in soil moisture may also

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Abbreviations: APB, aboveground plant biomass; BPB, belowground plant biomass; MBC, microbial biomass carbon; DPPT, decreased precipitation; IPPT, increased precipitation.

enhance root exudations, as plants increase root growth and release root exudates that may have enzymatic properties and can enhance degradation of organic matters and microbial activity (Dijkstra and Cheng, 2007; Canarini et al., 2019). However, high soil moisture/flooding may lead to hypoxia and shift root respiration from aerobic to anaerobia, thereby complicating the patterns of root exudations (Badri and Vivanco, 2009). Although there are strong associations between plants and soil microbes via exchanges at root-soil interfaces, plants and microbes may respond asynchronously to soil resource availability due to contrasting life history strategies (Xi et al., 2014). Soil microorganisms can adapt to changes in soil moisture more rapidly than plants due to their fast growth, considerable capacity for osmotic adjustment under fluctuating soil moisture, speedy community composition shifts, and potential for contemporary evolution (Schimel et al., 2007; Lau and Lennon, 2011). The asynchrony between plant and microbial biomass may have significant implications for the competitive balance of plants and soil microbes, as well as for the regulation of biogeochemical cycling (Karlowsky et al., 2018a; Williams and de Vries, 2020).

Recently, a growing number of field grassland experiments have recorded APB, BPB, or MBC responses to precipitation amounts in individual ecosystems, providing a valuable opportunity to test shifts in plant biomass allocation and to compare plant versus soil microbial responses to altered precipitation at grasslands. To achieve a comprehensive understanding of the responses of plant-soil systems to precipitation changes in grassland ecosystems, we synthesized results from 499 experimental observations using a meta-analytical method. We searched for studies that measured plant biomass and microbial biomass carbon (MBC) under different manipulated precipitation amounts. Data were extracted and analyzed to address the following hypotheses: (1) microbial biomass C has greater responses to precipitation increases and decreases than plant biomass; (2) there is a trade-off between plant above- and belowground responses to precipitation increases and decreases; (3) responses of microbial biomass C and plant biomass are positively correlated.

METHODS

Data Collection

We searched the literature using Web of Science (http://isiknowledge.com) on 1st August 2019. Two sets of search terms were used to obtain papers related to primary productivity and soil microbial biomass in response to experimental precipitation manipulations in grassland ecosystems that were published between 1st January 1900 and 1st August 2019. The first set of terms was "('plant growth" OR "primary product*' OR 'plant product*' OR 'ANPP' OR 'BNPP') AND ('altered precipitation' OR 'drought' OR 'decreased precipitation' OR 'increased precipitation' OR 'increased summer precipitation' OR 'decreased summer precipitation' OR 'water addition' OR 'water reduction' OR 'water treatment*') AND ('herbaceous' OR 'grass*') AND ('experiment*' OR 'treatment*')." The second set of terms is "('microbial biomass') AND ('altered precipitation' OR 'drought' OR 'decreased precipitation' OR 'increased precipitation' OR 'increased summer precipitation' OR 'decreased summer precipitation' OR 'water addition' OR 'water reduction' OR 'water treatment*') AND ('herbaceous' OR 'grass*') AND ('experiment*' OR 'treatment*')." We selected papers based on the following criteria: (a) experiment was conducted in the field; (b) the magnitude of precipitation changes was clearly described; (c) studies recorded paired responses to precipitation changes (i.e., APB vs. BPB, or APB vs. MBC, or BPB vs. MBC); (d) no other forcing factors (e.g., nutrient addition, warming) were applied in the precipitation treatments.

Our dataset consisted of experimental studies that are set up across 32 sites which are located in Asia, North America, Africa and Oceania (**Supplementary Figure 1**). For plant biomass, we focused on APB and BPB, and this dataset included 65 published papers (**Supplementary Figure 2** and **Supplementary Appendix 1**). MBC is a commonly used indicator for microbe biomass and is widely measured in studies of grassland ecology (Li et al., 2004; Treseder, 2008; He et al., 2020). Therefore, for soil microbial biomass, we focused on MBC, and this dataset included 30 published papers (**Supplementary Figure 2** and **Supplementary Appendix 2**). Ultimately, there were 33 case studies in which MBC and APB were paired [6 DPPT case studies (11 experimental observations) + 27 IPPT case studies (35 experimental observations)]. There were 19 case studies in which MBC and BPB were paired [(4 DPPT case studies (4 experimental observations) + 15 IPPT case studies (15 experimental observations)], and 60 case studies where APB and BPB were paired [23 DPPT case studies (34 experimental observations) + 37 IPPT case studies (54 experimental observations)].

Effect Sizes

Effect size was calculated using a natural log-transformed response ratio (RR) for each observation (Hedges et al., 1999):

$$RR = \mathrm{Ln}\left(\frac{\overline{X_t}}{\overline{X_c}}\right)$$

where $\overline{X_t}$ and $\overline{X_C}$ are the means of biomass (APB, BPB, or MBC) or soil moisture in changed rainfall (IPPT or DPPT) and ambient treatments, respectively. Its variance (v_{RR}) was calculated as (Hedges et al., 1999):

$$v_{RR} = \frac{s_t^2}{n_t X_t^2} + \frac{s_c^2}{n_c X_c^2}$$

where n_t and n_c are the sample size of the concerned variable in the treatment and control, respectively; s_t and s_c are the standard deviations of the concerned variable in the treatment and control groups, respectively.

We also calculated effect size of aboveground: belowground biomass ratio in responses to DPPT or IPPT (D):

$$D = \ln\left(\frac{\overline{APB_t}}{\overline{BPB_t}}\right) - \ln\left(\frac{\overline{APB_c}}{\overline{BPB_c}}\right) = \ln\left[\frac{\left(\frac{\overline{APB_t}}{\overline{BPB_t}}\right)}{\left(\frac{\overline{APB_c}}{\overline{BPB_c}}\right)}\right]$$

$$= \ln\left[\frac{\left(\frac{\overline{APB_t}}{\overline{APB_c}}\right)}{\left(\frac{\overline{BPB_t}}{\overline{BPB_c}}\right)}\right]$$

$$= \ln\left(\frac{\overline{APB_t}}{\overline{APB_c}}\right) - \ln\left(\frac{\overline{BPB_t}}{\overline{BPB_c}}\right) = RR_{APB} - RR_{BPB}$$

where $\overline{APB_t}$ and $\overline{BPB_t}$ are the means of above- and belowground biomass in changed rainfall treatments (IPPT or DPPT). $\overline{APB_c}$ and $\overline{BPB_C}$ are the means of above- and belowground biomass in ambient rainfall treatments. RR_{APB} and RR_{BPB} are effect sizes for aboveground and belowground biomass respectively. Consequently, the positive/negative sign of D indicates that altered precipitation increases or reduces biomass allocation to aboveground components. Its variance (v_D) was calculated as (Borenstein, 2009):

$$v_D = \frac{v_{RR(APB)}}{n_{RR(APB)}} + \frac{v_{RR(BPB)}}{n_{RR(BPB)}}$$

where $n_{RR(APB)}$ and $n_{RR(BPB)}$are sample sizes of RR_{APB} and RR_{BPB} in altered precipitation and ambient treatments, respectively; $v_{RR(APB)}$ and $v_{RR(BPB)}$ are the variances of RR_{APB} and RR_{BPB} respectively.

Statistical Analyses

We calculated the average response ratio of APB, BPB, MBC, soil moisture, and plant aboveground: belowground biomass ratio using meta-analytic mixed models with case study as a random factor. We performed pairwise comparisons between effect sizes of APB, BPB, and MBC using meta-analytic mixed models with case study as a random factor. We set up linear mixed-effects models, with case study as a random factor, to test correlations between effect sizes of MBC, APB, and BPB. Because of the low number of observations (< 5), we did not test the relationships between effect sizes of MBC and BPB to DPPT. The case study was designated as a random effect within the mixed-effects model to account for pseudo-replication originating from studies spanning multiple years.

We tested publication bias of the sensitivity based on the rank correlation test for funnel plot asymmetry, and did not detect publication bias (**Supplementary Table 1**). All analyses were conducted in R (R Core Team, 2019), and meta-analytic mixed-effects models and linear mixed-effects models were conducted using the *metafor* (Viechtbauer, 2010) and *lme4* (Bates et al., 2015) package, respectively.

RESULTS

Effects of Decreased Precipitation on Plant Biomass, Microbial Biomass C, and Soil Moisture

Effect size of APB to DPPT was significantly negative ($P < 0.05$), and effect sizes of MBC and BPB to DPPT were not different from 0 ($P > 0.05$) (**Figures 2A–C**). There were significant differences between effect sizes of MBC and APB in responses to DPPT ($Q_M = 4.12$, $df = 1$, $P = 0.0423$); effect size of APB to DPPT was negative compared to that of MBC (**Figure 2A**). There were differences between effect sizes of MBC and BPB in responses to DPPT ($Q_M = 4.08$, $df = 1$, $P = 0.0434$); effect size of MBC to DPPT tended to be negative compared to that of BPB (**Figure 2B**). Effect size of APB to DPPT was negative compared to that of BPB ($Q_M = 7.24$, $df = 1$, $P = 0.0071$; **Figure 2C**). Effect size of soil moisture to DPPT was significantly negative ($P < 0.05$; **Supplementary Figure 3**).

Effects of Increased Precipitation on Plant Biomass, Microbial Biomass C, and Soil Moisture

Effect sizes of MBC and APB to IPPT were significantly positive ($P < 0.05$), and effect sizes of BPB to IPPT were not different from 0 ($P > 0.05$) (**Figures 2D–F**). The effect size of APB to IPPT was positive compared to that of BPB ($Q_M = 8.08$, $df = 1$, $P = 0.0045$; **Figure 2F**). There were no differences in effect sizes to IPPT between APB and MBC ($Q_M = 0.66$, $df = 1$, $P = 0.4163$; **Figure 2D**) or between BPB and MBC ($Q_M = 3.36$, $df = 1$, $P = 0.0667$; **Figure 2E**). Effect size of soil moisture to IPPT was significantly positive ($P < 0.05$; **Supplementary Figure 3**).

Shifts in Plant Aboveground: Belowground Biomass Ratio During Altered Precipitation

Effect size of plant aboveground: belowground biomass ratio (i.e., D) to DPPT was significantly negative ($P = 0.0029$), while effect size of its responses to IPPT was positive ($P = 0.0128$) (**Figure 3**).

Correlations Between MBC, APB, and BPB

There was a negative relationship between effect size of APB and BPB to DPPT (slope $= -0.38$, $P = 0.0384$; **Figure 4A**; **Supplementary Table 2**). There was a marginally significant correlation between effect size of APB and BPB to IPPT (slope $= 0.30$, $P = 0.0715$; **Figure 4B**; **Supplementary Table 2**). The effect size of MBC to IPPT was positively correlated with that of APB (slope $= 0.58$, $P = 0.0023$; **Figure 4C**; **Supplementary Table 2**). We did not detect significant correlation between the effect sizes of APB and MBC to DPPT ($P = 0.2983$), or between the effect sizes of BPB and MBC to IPPT ($P = 0.2963$).

Correlations Between Soil Moisture and Precipitation Changes

Precipitation changes were significantly positively related to soil moistures (slope $= 0.69$, $P < 0.0001$; **Supplementary Figure 4**).

DISCUSSION

Plants and soil biota are inter-linked in mediating soil C cycling in grasslands (Bardgett et al., 2008; Ficken and Warren, 2019), but how plant-soil systems respond to altered precipitations has not been clarified. We filled this knowledge gap using a meta-analysis of published experimental studies. This meta-analysis has produced the key finding that plant biomass allocation determines plant-soil systems to precipitation changes, and this can increase our understanding of the likely influences of future climate change on grassland ecosystems.

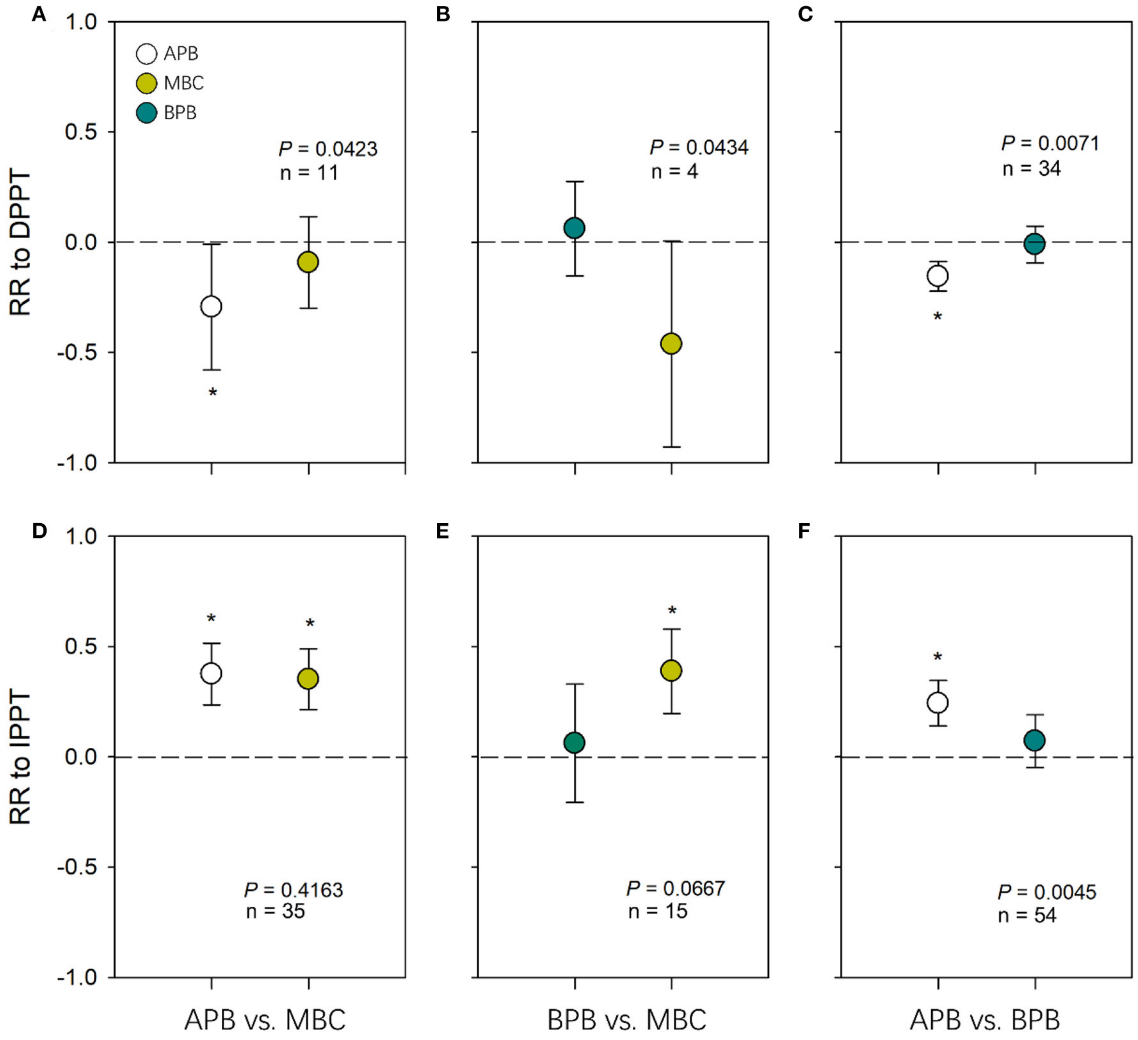

FIGURE 2 | Pairwise comparisons of response ratio between APB, BPB, and MBC in response to DPPT **(A, B, C)** and IPPT **(D, E, F)**. The error bars represent 95% confidence intervals. *P* values are given to show the significance of pairwise comparisons. Asterisks indicate the average effect sizes as they differ from zero ($P < 0.05$). The dotted lines indicate the effect size of zero. DPPT, decreased precipitation; IPPT, increased precipitation.

Effects of Precipitation Reduction on Plants and Soil Microbes

Our results indicated that APB was more sensitive than BPB in response to decreased precipitation (**Figure 2A**). We provided the first evidence that experimental drought manipulations caused greater allocation to roots, while added precipitations increased biomass allocation to shoots (**Figure 3**). This finding was consistent with theoretical prediction (Gleeson and Tilman, 1992) and empirical evidence for global patterns of biomass allocation across environmental gradients (Mccarthy and Enquist, 2007; Poorter et al., 2012). The plasticity in plant biomass allocation probably caused different responses of APB vs. BPB in responses to altered precipitation. Increased root allocation can promote soil water and nutrient capture and, therefore, buffer drought effects on BPB. Therefore, increasing APB responses unavoidably decreased BPB responses due to shifts in biomass allocations between above versus belowground production.

Contrary to what we predicted, we found that MBC tended to be more sensitive to DPPT than BPB but less sensitive than APB (**Figure 2A**). In principle, MBC responses to precipitation changes are directly driven by microbial eco-physiological characters or indirectly by soil conditions (such as available water, substrate, or nutrients for microbes) changes (Schimel et al., 2007). Under DPPT, plants could increase production of soluble root sugars for supporting the survival of roots through providing C for respiration, or for enhancing fine root growth to increase plant access to deep soil water (Karlowsky et al., 2018a,b; Hasibeder et al., 2015). Soluble root sugars may be linked with root exudations (Karlowsky et al., 2018a), thereby increasing the substrate available for soil microbes and buffer environmental stress for the microbial communities (Bloor et al., 2018). We

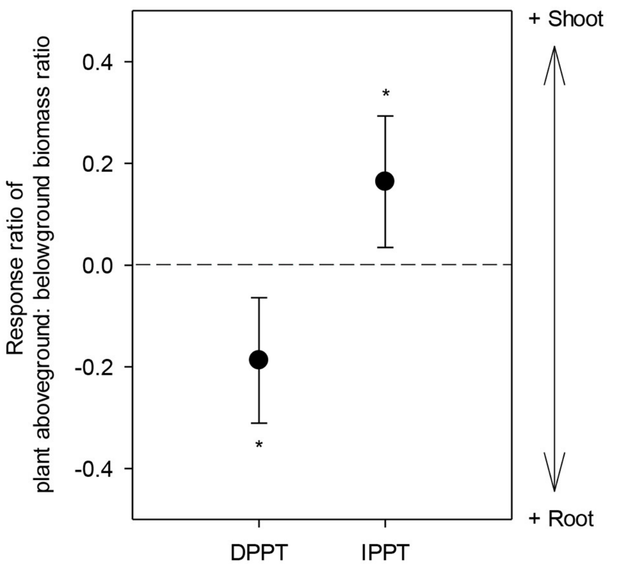

FIGURE 3 | Response ratio of plant aboveground: belowground biomass ratio (i.e., D) in response to DPPT and IPPT. The error bars represent 95% confidence intervals. Asterisks indicate average response ratios as they differ from zero ($P < 0.05$). The dotted line indicates the effect size of zero. DPPT, decreased precipitation; IPPT, increased precipitation.

also cannot rule out the possibility that changes in microbial community composition increase the resistance of whole soil communities to drought, because previous studies have suggested that drought-tolerant taxa, such as fungi or microbes with *K* strategy, increase their relative abundances in drought conditions (Manzoni et al., 2012; de Vries and Shade, 2013; Ren et al., 2018).

Effects of Precipitation Addition on Plants and Soil Microbes

Under IPPT, overall effects of increased precipitation resulted in increased shoot allocation (**Figures 2B**, **3**), reflecting light may be the more limiting factor for plants than soil water. Under wet conditions, the longevity of live roots is typically greater (Facette et al., 1999), reducing the need/ space for increased BPB to renew root systems (Hayes and Seastedt, 1987). Other studies showed that, under wetter conditions, saturated soil moisture conditions might limit root development (Kozlowski, 1997). We did not detect significant correlation between response ratio of APB and BPB to IPPT (**Figure 4B**), mirroring that experimental precipitation addition did not completely remove water limitation for plants. However, we suggest that plasticity in biomass allocation was likely to be the important factor driving different APB vs. BPB responses to IPPT and DPPT, and BPB responses to IPPT may be associated with root physiological changes.

In contrast with DPPT, IPPT stimulated microbial biomass (**Figure 2B**), reflecting the asymmetry of MBC responses to IPPT and DPPT. IPPT could directly increase soluble substrate availability for microbial communities through enhancing soil

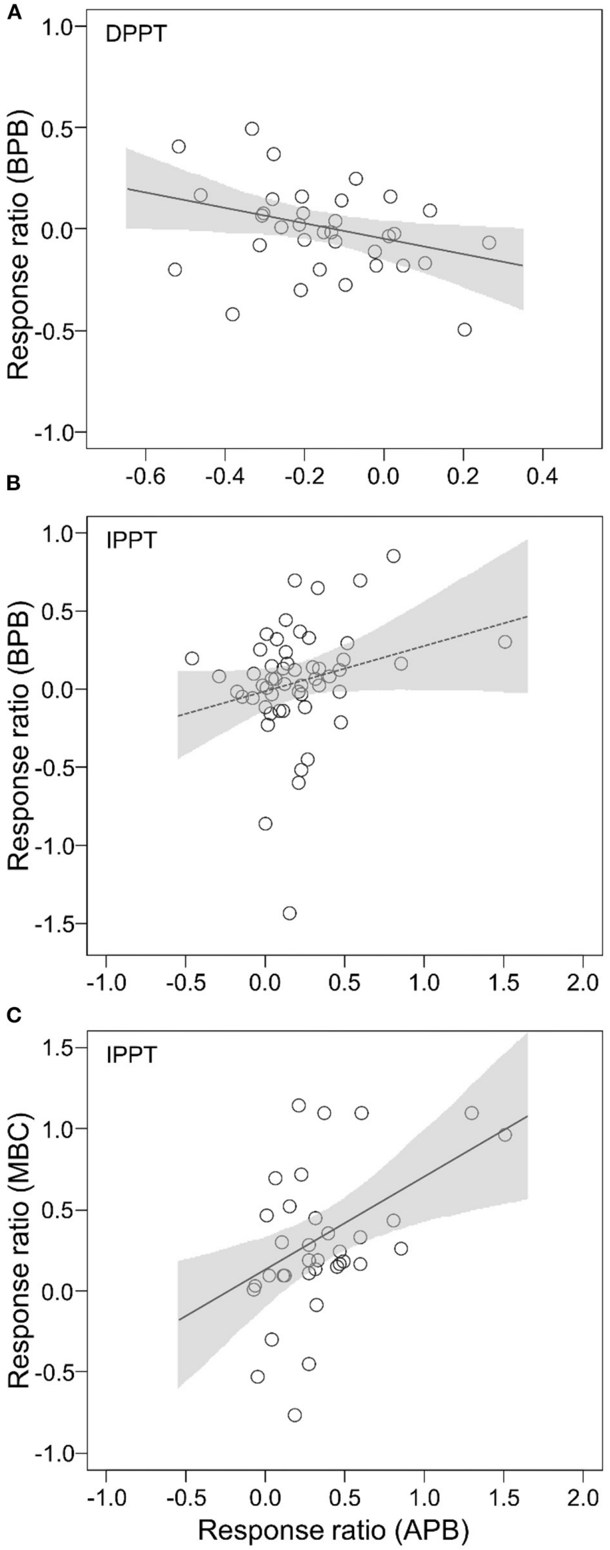

FIGURE 4 | Relationships between effect sizes of BPB, APB, and MBC to altered precipitation: **(A)** effect sizes of APB vs. BPB to DPPT; **(B)** effect sizes of APB vs. BPB to IPPT; **(C)** effect sizes of APB vs. MBC to IPPT. The shaded areas represent 95% confident intervals.

moisture (Schimel et al., 2007; Borken and Matzner, 2009). We did not detect a significant difference in response ratios of MBC vs. APB or BPB to IPPT (**Figure 2B**), and this finding may simply reflect the fact that increased soil moisture linearly mitigated water or substrate limitation for plants and soil microbes. Interestingly, there were positive correlations between responses of MBC and APB to IPPT (**Figure 4C**). We speculated that increased precipitation treatments probably increased litter inputs and decomposition rates because of the profuse leaf growth and speedy turnover so that soil microbes might be provided with recent photosynthates (Austin and Vitousek, 2000; Yahdjian et al., 2006). Of course, we cannot rule out the possibility that moderate increase in soil moisture may stimulate exudation of root metabolites that can, as enzymes, cause speedy degradation of organic matters and release of labile carbon (Dijkstra and Cheng, 2007; Canarini et al., 2019). Our results highlighted that the relationships between microbial biomass and plant production could not be simply linear when precipitation regimes change. The association between roots and soil microbes could be much stronger under increased precipitation conditions, while under decreased precipitation, stresses for microbial biomass were likely to be buffered because of drought-induced rhizodeposition.

CONCLUSIONS

This meta-analysis produced several key findings and filled knowledge gaps for combined responses of plant-soil systems to precipitation changes. Grassland responses to altered precipitation varied in the magnitude between different compartments, with greater APB responses than BPB or MBC responses. DPPT increased biomass allocation to roots for acquiring water, while IPPT increased biomass allocation to shoots for light capture. We detected a trade-off between response ratios of APB and BPB to DPPT, supporting the optimal allocation theory. Shifts in root biomass allocation probably neutralized the effects of precipitation changes on roots. Under DPPT, increased root allocation probably buffered drought stress for soil microbes and led to neutral responses of microbial biomass C. Our study provides evidence that plant biomass allocation mediates asynchrony between APB, BPB, and MBC, and emphasizes that forecasting the consequences of precipitation changes for grassland systems requires testing the effects on the plant-soil system as a whole.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

NX and CZ designed the study, CZ and NX performed data collection and conducted statistical analyses, and NX and CZ wrote the manuscript. Both authors contributed to the article and approved the submitted version.

FUNDING

This study was financially supported by the National Natural Science Foundation of China (31860668 and 32060385), the Project of Qinghai Science & Technology Department (2020-ZJ-733 and 2016-ZJ-Y01), and the Open Project of State Key Laboratory of Plateau Ecology and Agriculture, Qinghai University (2018-KF-01).

ACKNOWLEDGMENTS

We thank Dr. Juliette M.G. Bloor for her constructive advice.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2021.614968/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Plant Science

ORIGINAL RESEARCH
published: 13 April 2021
doi: 10.3389/fpls.2021.650802

Changes of Aboveground and Belowground Biomass Allocation in Four Dominant Grassland Species Across a Precipitation Gradient

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Climate change is predicted to affect plant growth, but also the allocation of biomass to aboveground and belowground plant parts. To date, studies have mostly focused on aboveground biomass, while belowground biomass and allocation patterns have received less attention. We investigated changes in biomass allocation along a controlled gradient of precipitation in an experiment with four plant species (*Leymus chinensis*, *Stipa grandis*, *Artemisia frigida*, and *Potentilla acaulis*) dominant in Inner Mongolia steppe. Results showed that aboveground biomass, belowground biomass and total biomass all increased with increasing growing season precipitation, as expected in this water-limited ecosystem. Biomass allocation patterns also changed along the precipitation gradient, but significant variation between species was apparent. Specifically, the belowground biomass: aboveground biomass ratio (i.e., B:A ratio) of *S. grandis* was not impacted by precipitation amount, while B:A ratios of the other three species changed in different ways along the gradient. Some of these differences in allocation strategies may be related to morphological differences, specifically, the presence of rhizomes or stolons, though no consistent patterns emerged. Isometric partitioning, i.e., constant allocation of biomass aboveground and belowground, seemed to occur for one species (*S. grandis*), but not for the three rhizome or stolon-forming ones. Indeed, for these species, the slope of the allometric regression between log-transformed belowground biomass and log-transformed aboveground biomass significantly differed from 1.0 and B:A ratios changed along the precipitation gradient. As changes in biomass allocation can affect ecosystem functioning and services, our results can be used as a basis for further studies into allocation patterns, especially in a context of environmental change.

Keywords: aboveground biomass, belowground biomass, climate change, grassland, grassland persistence, rangeland sustainability, precipitation amount

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Edited by:
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Reviewed by:
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Specialty section:
This article was submitted to Functional Plant Ecology, a section of the journal Frontiers in Plant Science

Received: *11 January 2021*
Accepted: *19 March 2021*
Published: *13 April 2021*

Citation:
Liu Y, Xu M, Li G, Wang M, Li Z and De Boeck HJ (2021) Changes of Aboveground and Belowground Biomass Allocation in Four Dominant Grassland Species Across a Precipitation Gradient. Front. Plant Sci. 12:650802. doi: 10.3389/fpls.2021.650802

INTRODUCTION

Climate change is affecting rainfall patterns in many regions around the world (Arnbjerg-Nielsen et al., 2013; Ohba and Sugimoto, 2019; Hyun and Yeh, 2020). Such changes can significantly alter plant growth and vegetation dynamics, both when precipitation amounts decrease or when they increase (Felton et al., 2019). Drought triggers mostly neutral or negative responses regarding growth and biomass (Zhang et al., 2012; Gherardi and Sala, 2019; Meng et al., 2019), while increased precipitation mostly leads to neutral or positive growth responses (Chu et al., 2016; Michaletz et al., 2018; Gherardi and Sala, 2019). While these are general patterns, where the biomass ends up under any response scenario (decreased, increased, or unchanged biomass) is also relevant as this can affect, for example, livestock feeding, soil stability, and carbon sequestration (Herrero et al., 2013; Maryol and Lin, 2015; Reinhart and Vermeire, 2017).

The optimal partitioning theory predicts that plants tend to allocate relatively more biomass to organs increasing the uptake of the most limiting resources (Bloom et al., 1985; Gedroc et al., 1996; Mao et al., 2012). Therefore, plants are expected to allocate more biomass belowground under dry conditions, and more aboveground when growing under wet conditions (Villar et al., 1998). The isometric partitioning theory suggests that aboveground biomass and belowground biomass follows an isometric pattern (Enquist and Niklas, 2002; Wang et al., 2014), implying that there is not necessarily a trade-off between aboveground and belowground. However, contrasting results have been found, with both studies in support (e.g., Enquist and Niklas, 2002; Wang et al., 2014) and studies that rejected isometric partitioning (e.g., Chen et al., 2016; Ma and Wang, 2021). Thus, further studies are needed to shed more light on this theory.

While it is clear that environmental changes can significantly affect biomass allocation (Fan et al., 2009; Zhang et al., 2017; Yang et al., 2018; Zhou et al., 2020), most studies that explored the effects of climate change on biomass allocation have focused on aboveground biomass (Bai and Xu, 1997; Mokany et al., 2006; Bai et al., 2008; Gonzalez-Dugo et al., 2010). Few studies include belowground biomass as this is more difficult to measure, especially in the field (Milchunas et al., 2005; Ma et al., 2008). Therefore, our knowledge of changes in plant allocation pattern triggered by changes in the environment is generally incomplete (Achten et al., 2010; Liu et al., 2015) and exact allocation strategies merit further investigation (Pan et al., 2005; Cai et al., 2005; Lv et al., 2016).

Grasslands, as one of the main terrestrial ecosystems, occupy more than 30% of the terrestrial area (Parton et al., 2012). They play an important role in biogeochemical cycles and energy transformation (Huang et al., 2010; Bai et al., 2012). Compared with forests, grasslands show more pronounced responses to climate change, at least in the short term (Eziz et al., 2017; Maurer et al., 2020), and are thus a relevant ecosystem to study in the context of environmental change. In grasslands, biomass allocation is a key mechanism for understanding the dynamics involved in plant growth, and changes therein can alter the structure and functioning of these systems (Poorter et al., 2012a,b).

To improve the knowledge on changes in biomass allocation patterns under varying environmental conditions in grasslands, we conducted an experiment to explore effects of growing season precipitation on biomass aboveground and belowground. We focused on four plant species (i.e., *Leymus chinensis*, *Stipa grandis*, *Artemisia frigida*, and *Potentilla acaulis*) dominant in Inner Mongolia steppe, and applied a gradient including eight levels of precipitation centered around the local annual mean precipitation. *L. chinensis* is a perennial forage grass with long strong rhizomes, *S. grandis* is a perennial tussock grass with closely clumped shoots, while *A. frigida* and *P. acaulis* are perennial herbs with stolons and developed adventitious roots (Li et al., 2005; Liu et al., 2006, 2007). The objective of this study was to test the optimal partitioning theory and the isometric partitioning theory at the species scale. Specially, we aimed to explore the relationships between precipitation amount and aboveground biomass, belowground biomass, total biomass and belowground biomass: aboveground biomass (B:A) ratio. Previous studies found that species with rhizomes or stolons tended to allocate more biomass to roots (i.e., belowground) (Schmid, 1987; Enquist and Niklas, 2002; Rhazi et al., 2009), leading to hypothesis (1), namely that the B:A ratio of *L. chinensis*, *A. frigida*, and *P. acaulis* is expected to be larger than that of *S. grandis*. Furthermore, if species with rhizomes or stolons indeed allocate more biomass belowground, they may respond differently along a gradient of changing precipitation compared to other species, according to the optimal partitioning theory. Under this hypothesis (2) the B:A ratios of *L. chinensis*, *A. frigida*, and *P. acaulis* would increase with precipitation amount, while a different pattern may be apparent in *S. grandis*. However, under the isometric partitioning hypothesis (3), the B:A ratios of these species are expected to be constant with precipitation amount (Enquist and Niklas, 2002; Yang and Luo, 2011; Wang et al., 2014). This same hypothesis also states that aboveground biomass should be scale with belowground biomass across our dataset.

MATERIALS AND METHODS

Field Site

This study was conducted on Inner Mongolia steppe in China (43°33′N, 116°40′E), where the mean elevation ranges from 1,200 to 1,250 m. Local climate is characterized by a mild humid summer and a dry cold winter, with the mean annual temperature (MAT) ranging from −1.1 to 0.2°C, and large seasonal differences (−21.4°C on average in the coldest month, January, and 18.5°C on average in the warmest month, July). Mean annual precipitation (MAP) is 350 mm (from 1980 to 2000), of which around 280 mm falls in the growing season.

Experimental Design

To explore biomass allocation to aboveground and belowground plant parts, a manipulation experiment was conducted from May 2000 to October 2001. Four plant species dominant in the Inner Mongolia steppe were subjected to eight levels of growing season precipitation (administered through watering), centered around the local MAP (i.e., 350 mm): 170, 250, 300, 350, 525, 595, 665, and 700 mm. Such a large gradient enabled us to explore the effects of precipitation (including both dry and wet conditions) on plant biomass and biomass allocation, and was not intended to mimic the variation of local rainfall expected under climate change (cf. Kayler et al., 2015). Our experiment was conducted in a plot with a rainout shelter in order to block natural rainfall. This shelter was covered by highly transparent plastic foil upward from 2 m above the ground in order to prevent warming and to allow wind circulation. The impact on temperature, air humidity and light with such a design is limited (Kreyling et al., 2017).

Plants were grown in pots of 50 cm height and 30 cm diameter, filled with soil collected from nearby grasslands (mainly dark chestnut soil with a thin humus layer, cf. Li and Li, 2002; Jia et al., 2005). We used soil from the top 50 cm, which was well mixed and from which roots were carefully removed. There were three replications of each treatment for each species. For *L. chinensis*, seeds were randomly sown in the pots in early May 2000, and four similar-sized individuals were retained after germination. For *S. grandis*, four ramets with similar size were transplanted into each pot in late May 2000 following unsuccessful seed germination in early May. For *A. frigida* and *P. acaulis*, plants were excavated and ramets were separated into similar size. Four of them were transplanted into each pot in early May 2001. All the plants were first grown in an open air area under natural conditions, and rainout shelters were deployed and treatments were applied from 10 June to 10 September 2001. During the experiment,

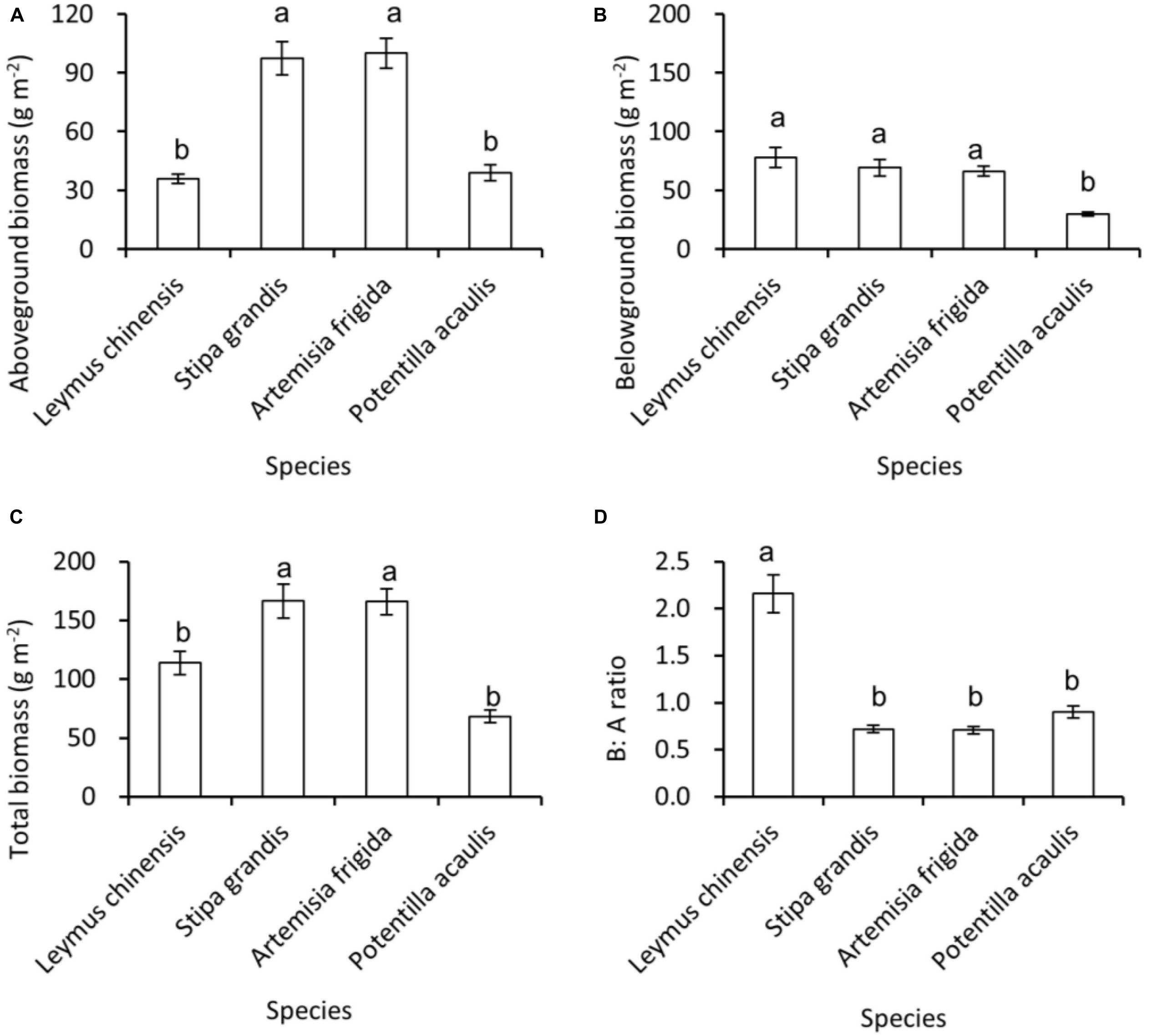

FIGURE 1 | At the pot scale, mean ± SE of **(A)** aboveground biomass, **(B)** belowground biomass, **(C)** total biomass, and **(D)** B:A ratio (i.e., ratio of belowground biomass and aboveground biomass), across the precipitation gradient, per species, i.e., *Leymus chinensis*, *Stipa grandis*, *Artemisia frigida*, and *Potentilla acaulis*. Significant ($P < 0.05$) differences between species have different letters (*post hoc* analyses with Bonferroni corrections).

water was added daily to each pot, with the water amount determined by dividing the total amount of precipitation amount in each treatment by the total growing days. To reduce water runoff, water was evenly added by hand at the soil surface. Note that around 80% of the annual rainfall occurs from June through August. The watering we provided thus covered most of the annual precipitation in line with previous studies (Hagiwara et al., 2010).

At the end of the experiment, all plants were washed free of soil with distilled water, and separated into aboveground and belowground parts. For *L. chinensis* and *S. grandis*, aboveground parts included leaves and stems, while belowground parts included roots and rhizomes. For *A. frigida*, aboveground parts included leaves, flowers, and stems, while belowground parts included roots. Finally, for *P. acaulis*, aboveground parts included leaves and stems, while belowground parts included roots. All of these were oven-dried at 65°C to constant weight and subsequently weighed.

Statistical Analysis

Aboveground and belowground biomass per square meter was calculated by dividing biomass of the four individuals in each pot by the surface area of each pot. Total biomass relates to the sum of aboveground and belowground biomass and the belowground biomass: aboveground biomass ratio (i.e., B:A ratio) was calculated by dividing belowground biomass by aboveground biomass.

Two-way analysis of variance (ANOVA) was conducted to explore the effects of species, precipitation amount and their interaction on the aboveground biomass, belowground biomass, total biomass and B:A ratio. *Post hoc* analysis (pairwise comparisons with Bonferroni corrections) was applied to test the differences among the target plant species. One data point of aboveground biomass of *S. grandis* at 700 mm precipitation was identified as an outlier and was removed. All statistics were carried out using SPSS 21.0.

Curve estimations were done to test the relationships between precipitation amount and aboveground biomass, belowground biomass, total biomass and B:A ratio, where linear, quadratic, power and exponential curves were tested. AIC (Akaike Information Criterion) and *P* value were used to identify better models, i.e., lower AIC and significant (and lower) *P* value (Cottingham et al., 2005).

The relationship between log-transformed belowground biomass and log-transformed aboveground biomass across the precipitation gradient was determined with ordinary least square regression and standardized major axis regression (Niklas, 2005; Cheng and Niklas, 2007). The slopes were tested against the 1:1 line, where non-significant difference indicates an isometric relationship between belowground and aboveground biomass. Slopes and intercepts were obtained with a software package developed by Falster et al. (2006).

RESULTS

Regarding species differences, *S. grandis* and *A. frigida* on average had more aboveground (**Figure 1A**) and total biomass (**Figure 1C**) than *L. chinensis* and *P. acaulis*. Meanwhile, *P. acaulis* had a lower belowground biomass than the other three plant species (**Figure 1B**). Interestingly, *L. chinensis* had a larger B:A ratio than the other species (**Figure 1D**). Precipitation amount significantly affected aboveground biomass, belowground biomass, total biomass and B:A ratio and these effects differed amount the target plant species (**Table 1**). Moreover, significant interactive effects of species and precipitation amount on the aboveground biomass, belowground biomass, total biomass and B:A ratio were found (**Figures 2–5** and **Table 2**). Specially, positive patterns were found in relationships between precipitation amount and (i) aboveground biomass (**Figure 2**), (ii) belowground biomass (**Figure 3**), and (iii) total biomass (**Figure 4**).

Along the precipitation gradient, we observed different B:A ratios in the four target plant species. Increasing precipitation did not significantly affect the B:A ratio of

TABLE 1 | Effects of species, precipitation amount and their interaction in two-way ANOVA on aboveground biomass, belowground biomass, total biomass, and B:A ratio (i.e., ratio of belowground biomass and aboveground biomass).

	Aboveground biomass			Belowground biomass		
	df	*F*	*P*	df	*F*	*P*
Species	3.64	104.595	**<0.001**	3.64	36.571	**<0.001**
Precipitation amount	7.64	23.252	**<0.001**	7.64	17.412	**<0.001**
Species × Precipitation amount	21.64	2.665	**0.001**	21.64	2.817	**0.001**
	Total biomass			**B:A ratio**		
	df	F	*P*	df	F	*P*
Species	3.64	89.819	**<0.001**	3.64	33.623	**<0.001**
Precipitation amount	7.64	33.479	**<0.001**	7.64	2.139	0.052
Species × Precipitation amount	21.64	3.606	**<0.001**	21.64	3.023	**<0.001**

Significant differences are indicated in bold.

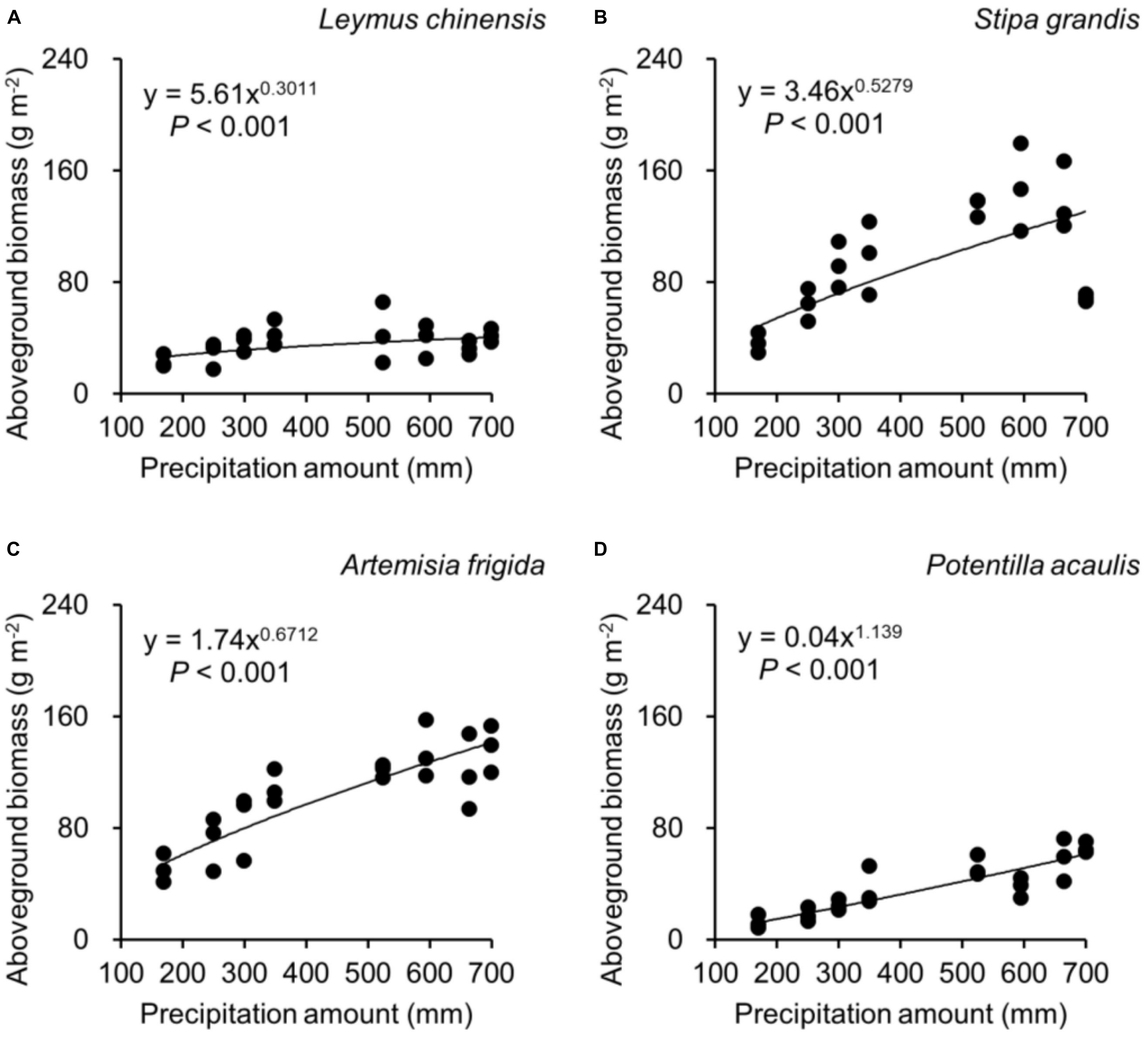

FIGURE 2 | At the pot scale, regressions between precipitation amount and aboveground biomass, separately for **(A)** *Leymus chinensis*, **(B)** *Stipa grandis*, **(C)** *Artemisia frigida,* and **(D)** *Potentilla acaulis.*

S. grandis (**Figure 5B**), while it increased the B:A ratio of *L. chinensis* (**Figure 5A**), decreased for *P. acaulis*, and seemingly first decreased and then increased for *A. frigida* (with a threshold around 475 mm). A greater B:A ratio suggests a greater biomass investment in the belowground organs.

Aboveground biomass was positively correlated with belowground biomass for all four target species, as expected (**Figure 6**). The slopes of the relationship between log-aboveground biomass and log-belowground biomass for *L. chinensis*, *S. grandis*, *A. frigida*, and *P. acaulis* were 1.25, 0.90, 0.49, and 0.53, respectively. These values differed significantly from 1.0 for three species (P = 0.001, <0.001, and <0.001 for *L. chinensis*, *A. frigida*, and *P. acaulis*, respectively), indicating non-isometric growth for these rhizome or stolon-forming species. The relationship did not differ significantly from the 1:1 line for *S. grandis* (P = 0.275).

DISCUSSION

In this study, we subjected four species common in grasslands of Inner Mongolia to a precipitation gradient. In general, we found that both aboveground biomass and belowground biomass production was stimulated as growing season precipitation was increased. This was unsurprising, given that these grasslands are known to be precipitation-limited (Kang et al., 2011; Guo et al., 2015). The focus in the current study was primarily on biomass allocation patterns, which we considered by testing three hypotheses. The first hypothesis stated that species with

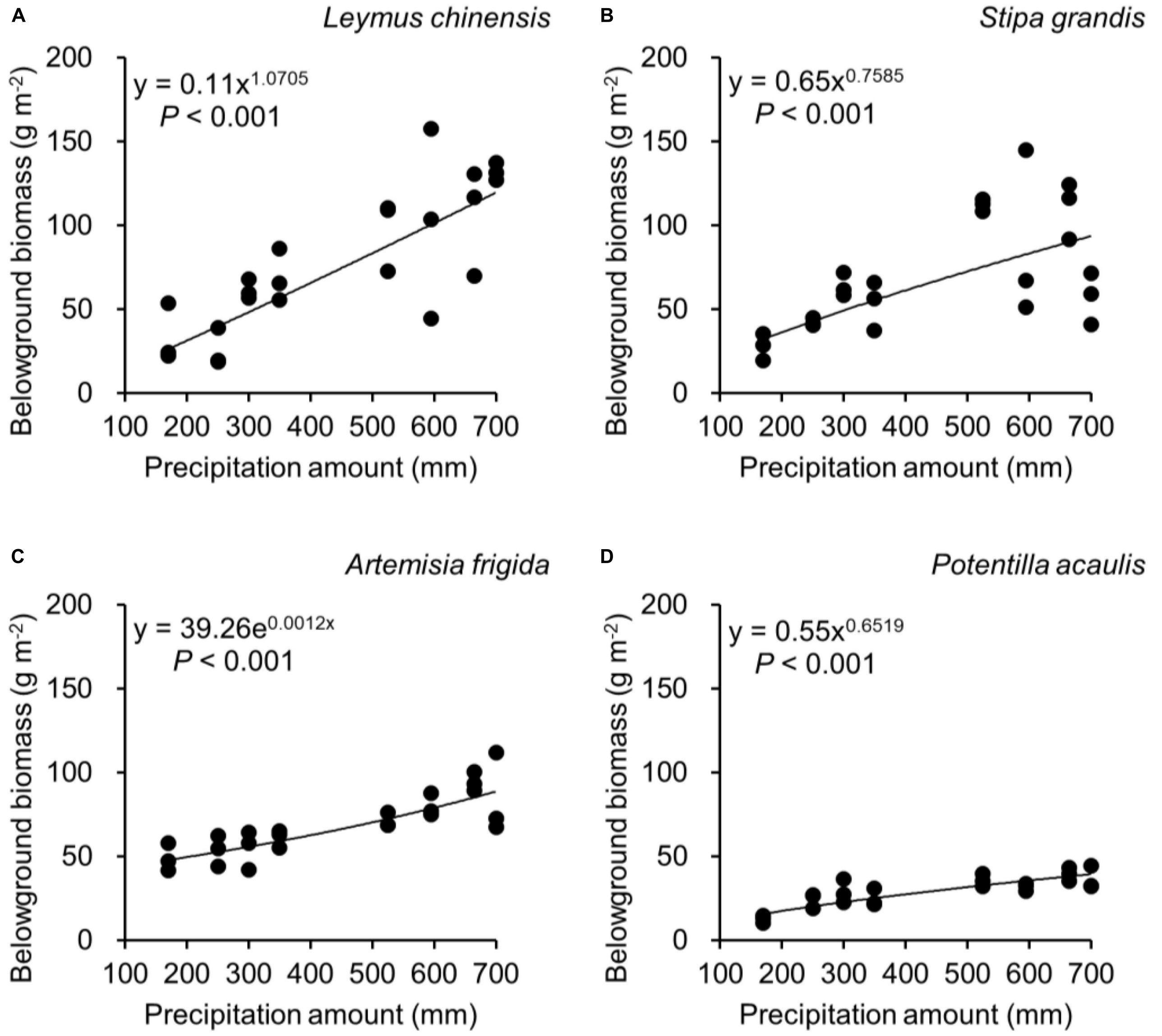

FIGURE 3 | At the pot scale, regressions between precipitation amount and belowground biomass, separately for **(A)** *Leymus chinensis*, **(B)** *Stipa grandis*, **(C)** *Artemisia frigida*, and **(D)** *Potentilla acaulis.*

rhizomes or stolons would allocate more biomass belowground. This pattern was only found for one rhizome and stolon forming species, namely *L. chinensis*. The other two such species, *A. frigida* and *P. acaulis*, displayed similar allocation patterns with the non-rhizome or stolon forming *S. grandis*. It should be noted that in contrast to studies calculating biomass allocation based on root biomass (e.g., Berendse and Möller, 2009), we considered the complete belowground biomass, including roots, rhizomes, and stolons.

The second hypothesis studied here, assumed that biomass allocation of species with rhizomes or stolons would increase along the precipitation gradient. This was not convincingly supported, with different patterns between precipitation amount and B:A ratios being observed for the four target plant species. Specifically, the B:A ratio of non-rhizome or stolon forming *S. grandis* remained constant along the precipitation gradient, suggesting that the biomass allocation of this species was not sensitive to precipitation amount. In line with our expectations, a positive pattern was found in *L. chinensis*, which could be explained by the fact that *L. chinensis* has a strong forage ability as a rhizomatous species (Wang et al., 2004), which enables it to allocate more biomass to roots when growing in wet conditions (Yang and Yang, 1998). Similar patterns were also found in species such as *Salix psammophila*, *Hedysarum leave*, *Artemisia ordosica*, and *Caragana korshinskii* (Dong et al., 1999; Xiao et al., 2001). Nevertheless, a contrasting (negative) pattern was apparent for *P. acaulis*, indicating more biomass was allocated aboveground with increasing precipitation amount. Interestingly, our data

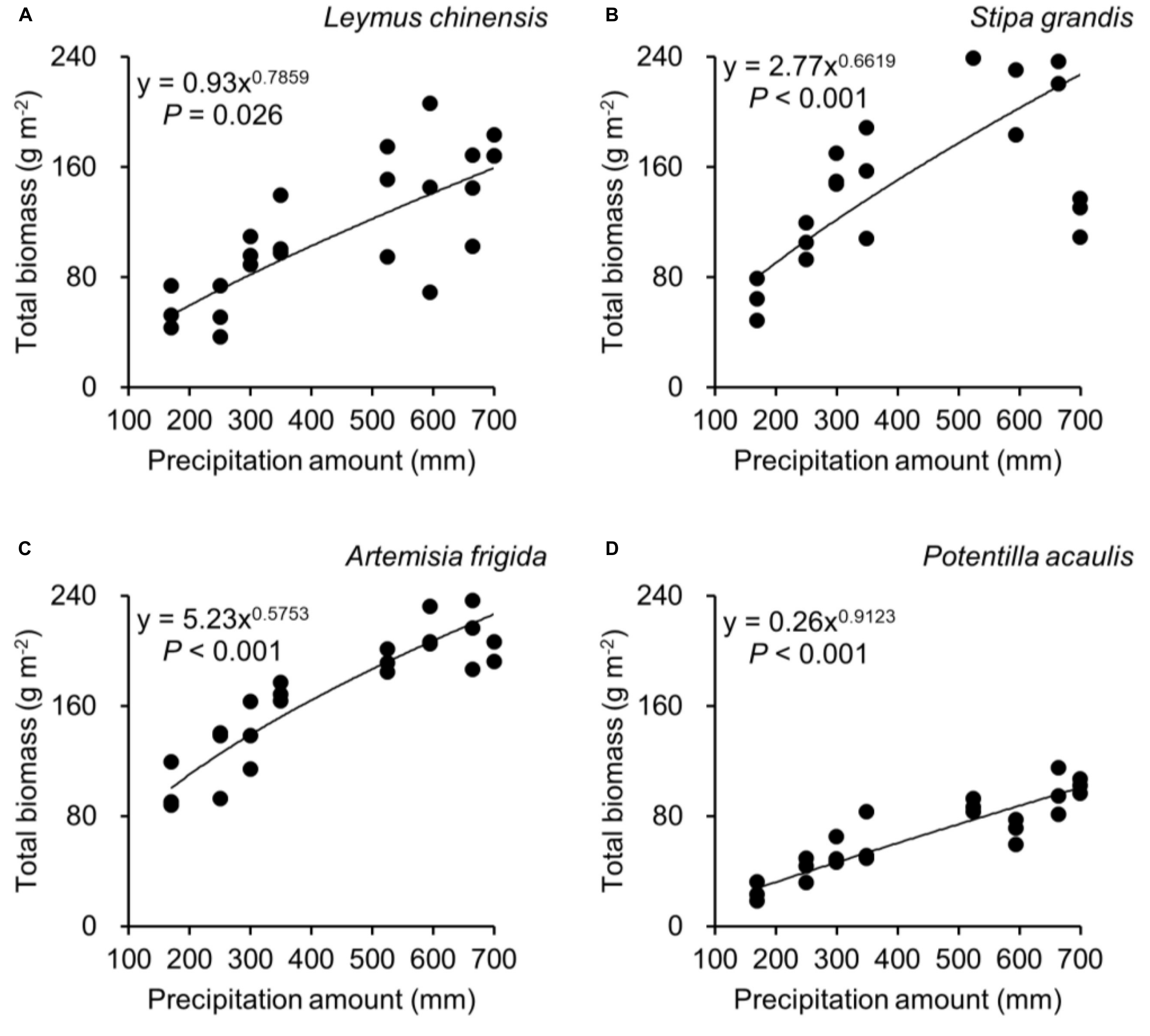

FIGURE 4 | At the pot scale, regressions between precipitation amount and total biomass, separately for **(A)** *Leymus chinensis*, **(B)** *Stipa grandis*, **(C)** *Artemisia frigida*, and **(D)** *Potentilla acaulis*.

suggested a unimodal pattern between precipitation amount and B:A ratio for *A. frigida*, with higher precipitation only increasing the biomass allocation belowground up to a certain point.

According to isometric partitioning, aboveground biomass and belowground biomass would be isometric at the species scale (hypothesis 3). This would suggest both no changes in B:A ratios along the precipitation gradient and no deviation from 1:1 lines in the aboveground biomass vs. belowground biomass relationship. Our results suggest that only *S. grandis* seemed to respond in line with isometric partitioning. The three rhizome or stolon-forming species did not adhere to isometric partitioning, with both asymmetrical variation between aboveground biomass and belowground biomass, in contrast with Enquist and Niklas (2002) and Yang et al. (2009), as well as differences in B:A ratios along the precipitation gradient. Regarding the allometric relationships between aboveground biomass and belowground biomass, the average slope of the four target plant species was 0.79, which is in line with the global grasslands' slope (i.e., 0.72, Wang et al., 2014), but smaller than China's grasslands' slope (i.e., 1.05, Wang et al., 2014). Such differences may be caused by the limited number of plant species used in this study, and because we explored allometric partitioning at the species scale, not at the individual or the community scale like in previous studies (Enquist and Niklas, 2002; Wang et al., 2010, 2014).

Biomass allocation between belowground biomass and aboveground biomass differed among species in our study,

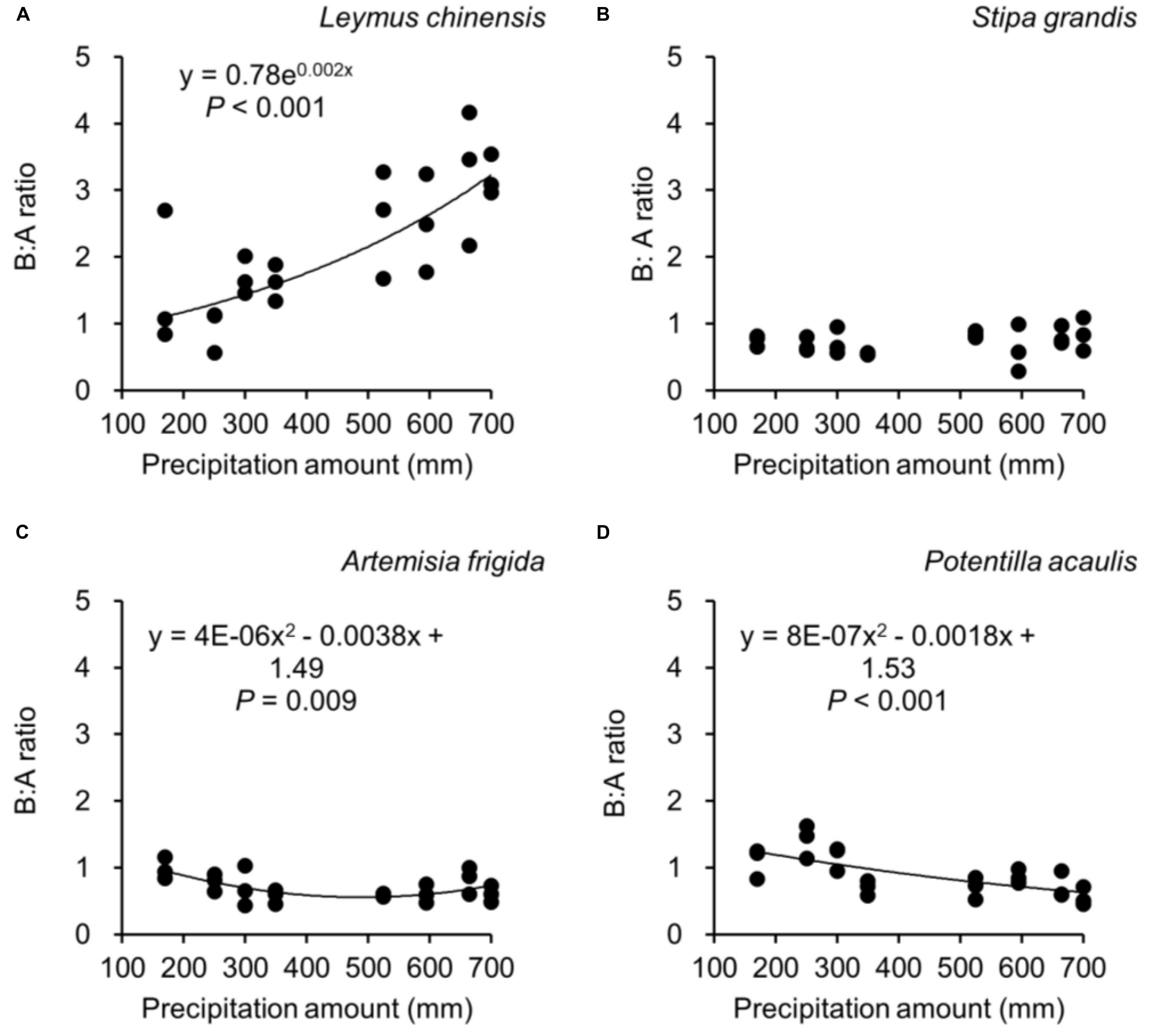

FIGURE 5 | At the pot scale, regressions between precipitation amount and B:A ratio (i.e., ratio of belowground biomass and aboveground biomass), separately for **(A)** *Leymus chinensis*, **(B)** *Stipa grandis*, **(C)** *Artemisia frigida*, and **(D)** *Potentilla acaulis*, where each dot refers to a B:A ratio from a pot.

in line with previous findings (Ma et al., 2008; Kang et al., 2013; Gong et al., 2015; Zhang et al., 2019). Mokany et al. (2006) suggested that the root/shoot (R/S) ratio in grasslands tends to decrease with increasing MAP. However, Yang et al. (2010) reported that the R/S ratio in China's grasslands did not show any significant pattern along increasing MAP. Several potential causes were proposed, relating to climatic factors (e.g., MAT and MAP). The plant species used in our experiment, which are dominant species in the Inner Mongolia steppe, displayed various relationships between B:A (similar to R/S) ratio and precipitation amount. Plant communities with species responding differently regarding biomass allocation, e.g., in an opposite direction, to precipitation may see little total effect at the community scale. Nevertheless, the species-specific changes in allocation patterns could lead to different competitive outcomes (Aerts et al., 1991), thus changing species composition in the longer term, and thus the B:A (or R: S) ratio of the community.

Results of this study should be interpreted and extrapolated with caution for a number of reasons. First, the experiment was short term, featuring a limited number of species. Studying longer term effects on more species would allow more extensive generalization. Furthermore, two species in this study were sown at the beginning of the experiment, while the other two were transplanted from local grasslands. It is possible that plant age affects allocation patterns, with for example Yu et al. (2019)

TABLE 2 | Results of the curve estimation of the relationships between precipitation amount and aboveground biomass, belowground biomass, total biomass, and B:A ratio (i.e., ratio of belowground biomass and aboveground biomass) of *Leymus chinensis*, *Stipa grandis*, *Artemisia frigida*, and *Potentilla acaulis* with linear, quadratic, power, and exponential equations, where AIC, F, df, and *P* value were showed.

	Aboveground biomass				Belowground biomass				Total biomass				B:A ratio			
	AIC	*F*	df	*P*	AIC	*F*	Df	*P*	AIC	*F*	df	*P*	AIC	*F*	df	*P*
***Leymus chinensis* Equation**																
Linear	116.2	3.1	1.22	0.094	155.1	45.5	1.22	**<0.001**	168.0	33.2	1.22	**<0.001**	−19.6	32.240	1.22	**<0.001**
Quadratic	111.5	4.0	2.21	**0.033**	155.0	21.8	2.21	**<0.001**	167.1	16.74	2.21	**<0.001**	−20.8	16.650	2.21	**<0.001**
Power	−56.2	5.7	1.22	**0.026**	−43.2	41.9	1.22	**<0.001**	−54.7	36.4	1.22	**<0.001**	−48.0	26.391	1.22	**<0.001**
Exponential	−54.6	4.0	1.22	**0.061**	−41.7	38.0	1.22	**<0.001**	−52.5	31.3	1.22	**<0.001**	−50.1	30.641	1.22	**<0.001**
***Stipa grandis* Equation**																
Linear	171.4	11.8	1.22	**0.002**	161.4	13.3	1.22	**0.001**	194.9	15.4	1.22	**0.001**	−79.5	1.2	1.22	0.285
Quadratic	154.9	21.6	2.21	**<0.001**	155.1	11.5	2.21	**<0.001**	180.4	22.1	2.21	**<0.001**	−81.0	1.3	2.21	0.284
Power	−49.1	23.0	1.22	**<0.001**	−46.4	24.0	1.22	**<0.001**	−52.1	28.6	1.22	**<0.001**	−57.1	0.2	1.22	0.655
Exponential	−43.4	13.5	1.22	0.001	−42.3	16.8	1.22	**<0.001**	−46.1	17.4	1.22	**<0.001**	−57.4	0.5	1.22	0.504
***Artemisia frigida* Equation**																
Linear	144.0	48.5	1.22	**<0.001**	114.2	49.4	1.22	**<0.001**	149.6	91.4	1.22	**<0.001**	−78.5	3.0	1.22	0.095
Quadratic	137.9	32.9	2.21	**<0.001**	113.9	24.0	2.21	**<0.001**	146.1	52.2	2.21	**<0.001**	−86.0	5.9	2.21	**0.009**
Power	−74.6	60.8	1.22	**<0.001**	−88.3	48.4	1.22	**<0.001**	−95.1	104.9	1.22	**<0.001**	−63. 8	4.3	1.22	0.051
Exponential	−68.2	41.4	1.22	**<0.001**	−90.1	53.9	1.22	**<0.001**	−88.5	74.6	1.22	**<0.001**	−62.1	2.5	1.22	0.127
***Potentilla acaulis* Equation**																
Linear	112.3	68.9	1.22	**<0.001**	83.8	41.3	1.22	**<0.001**	124.1	86.1	1.22	**<0.001**	−67.2	19.7	1.22	**<0.001**
Quadratic	112.2	33.1	2.21	**<0.001**	79.6	25.5	2.21	**<0.001**	122.8	43.8	2.21	**<0.001**	−67.4	9.5	2.21	**<0.001**
Power	−60.2	96.2	1.22	**<0.001**	−73.9	55.7	1.22	**<0.001**	−73.3	106.5	1.22	**<0.001**	−62.0	19. 1	1.22	**<0.001**
Exponential	−54.2	70.0	1.22	**<0.001**	−66.8	35.8	1.22	**<0.001**	−64.8	68.3	1.22	**<0.001**	−62.7	20.4	1.22	**<0.001**

A better estimation (marked in red) is determined by a smaller AIC (Akaike Information Criterion) and a significant P value (marked in bold).

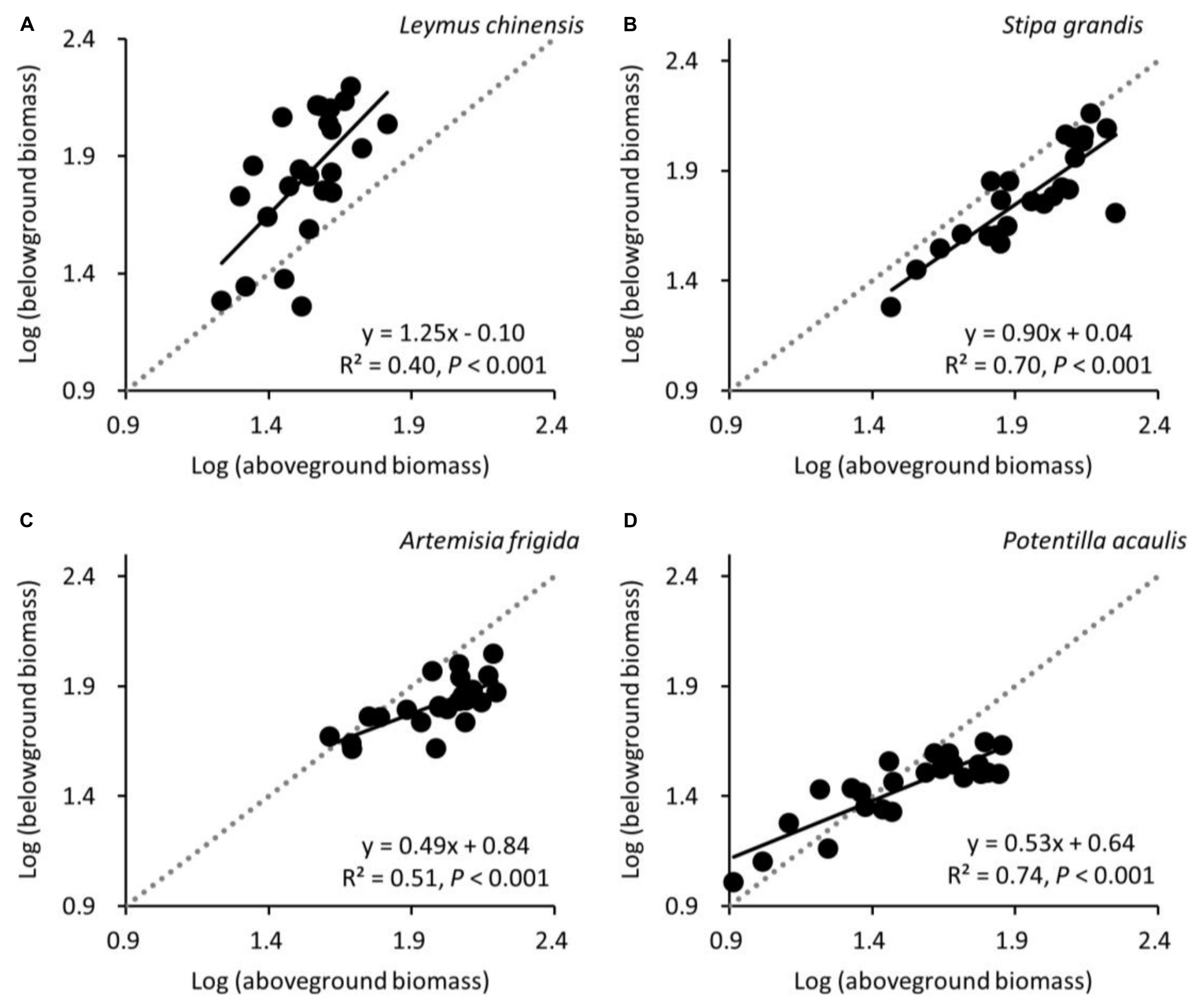

FIGURE 6 | At the pot scale, allometric relationships between log-transformed aboveground biomass and long-transformed belowground biomass for **(A)** *Leymus chinensis*, **(B)** *Stipa grandis*, **(C)** *Artemisia frigida*, and **(D)** *Potentilla acaulis*. The 1:1 line (dotted) is added for clarity.

reporting that resource limitation could be partially the reason of decreasing allocation with age, where resources such as nutrients and waters become limited with plant grow (age). Moreover, we allowed intraspecific competition in our study, which is realistic, but which would also alter allocation patterns (Yang et al., 2019). Comparisons with experiments considering individual plants (e.g., Lamb et al., 2007), are thus not straightforward. Another factor to consider in future studies is soil heterogeneity. Plants may allocate more biomass to roots when growing in higher levels of soil heterogeneity (James et al., 2003; Michael and Elizabeth, 2004; Hagiwara et al., 2010; Wu et al., 2014; Liu et al., 2017a), and plants growing on low-nutrient patches have been reported to grow more roots into their neighboring high-nutrient patches (Liu et al., 2017b, 2019).

In sum, in our experiment we found that changes in precipitation affected biomass allocation in general, but that significant species-specific differences were apparent. Increasing precipitation increased the biomass allocation to belowground organs for one species with rhizomes or stolons, while it did not impact the biomass allocation of the non-rhizomes or stolon-forming species in our study. Isometric partitioning, meaning constant allocation of biomass aboveground and belowground regardless of plant size or precipitation amounts, seemed to occur for one species, but not for the rhizome or stolon-forming ones. Increased knowledge of allocation patterns leads to improved understanding of the structure and functioning of grasslands under changes in the environment, such as altered precipitation. Moreover, changed allocation patterns matter as they can affect agricultural value, carbon sequestration, and climate resilience. The results of our study could be used as a basis for further research into allocation patterns in a changing environment, spanning a wider range of species, and explicitly considering consequences for ecosystem services.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

ZL designed and conducted the study. YL and ZL analyzed the data. All authors discussed the data and contributed crucially to the drafts.

FUNDING

YL holds a fund from the National Key Research and Development Program of China (2019YFC0507704) and a start-up fund from Lanzhou University (508000-561119213). This research was supported by the National Natural Science Foundation of China (41571505).

ACKNOWLEDGMENTS

We acknowledge Jinhua Li for the experimental assistance.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Plant Science

ORIGINAL RESEARCH
published: 03 September 2021
doi: 10.3389/fpls.2021.704138

Dominant Plant Functional Group Determine the Response of the Temporal Stability of Plant Community Biomass to 9-Year Warming on the Qinghai–Tibetan Plateau

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Specialty section:
This article was submitted to Functional Plant Ecology, a section of the journal Frontiers in Plant Science

Received: *01 May 2021*
Accepted: *09 August 2021*
Published: *03 September 2021*

Citation:
Li C, Lai C, Peng F, Xue X, You Q, Liu F, Guo P, Liao J and Wang T (2021) Dominant Plant Functional Group Determine the Response of the Temporal Stability of Plant Community Biomass to 9-Year Warming on the Qinghai–Tibetan Plateau. Front. Plant Sci. 12:704138. doi: 10.3389/fpls.2021.704138

Ecosystem stability characterizes ecosystem responses to natural and anthropogenic disturbance and affects the feedback between ecosystem and climate. A 9-year warming experiment (2010–2018) was conducted to examine how climatic warming and its interaction with the soil moisture condition impact the temporal stability of plant community aboveground biomass (AGB) of an alpine meadow in the central Qinghai-Tibetan Plateau (QTP). Under a warming environment, the AGB percentage of grasses and forbs significantly increased but that of sedges decreased regardless of the soil water availability in the experimental plots. The warming effects on plant AGB varied with annual precipitation. In the dry condition, the AGB showed no significant change under warming in the normal and relatively wet years, but it significantly decreased in relatively drought years (16% in 2013 and 12% in 2015). In the wet condition, the AGB showed no significant change under warming in the normal and relatively drought years, while it significantly increased in relatively wet years (12% in 2018). Warming significantly decreased the temporal stability of AGB of plant community and sedges. Species richness remained stable even under the warming treatment in both the dry and wet conditions. The temporal stability of AGB of sedges (dominant plant functional group) explained 66.69% variance of the temporal stability of plant community AGB. Our findings highlight that the temporal stability of plant community AGB is largely regulated by the dominant plant functional group of alpine meadow that has a relatively low species diversity.

Keywords: climate change, alpine meadow, aboveground biomass, Temporal stability of biomass, soil water availability

INTRODUCTION

The global surface temperature has remarkably increased by 0.85°C from 1880 to 2012. It is predicted that the temperature will continue to rise 0.3–4.8°C by the end of the 21st century (IPCC, 2013), especially in high altitudes and latitude regions (Chen et al., 2013). The Qinghai-Tibetan Plateau (QTP), with an average elevation >3,000 m, is the highest and largest plateau on the earth (Li et al., 2018). The annual mean temperature on the QTP will increase by 2.8–4.9°C at the end of the 21st century (IPCC, 2013). Besides, extreme drought/wet events are also increasing regardless of the no change in the total precipitation (Chen et al., 2015).

In general, climate warming can alleviate the temperature constraint on the plant growth, thus result in an increase of plant productivity and change the plant community composition in cold regions (Elmendorf et al., 2012). As the plant growth is regulated by the combination of temperature and available water, various even divergent responses of plant productivity to the climate warming were reported in the tundra, mountainous alpine ecosystems with different water availability (Walker et al., 2006; Wu et al., 2011; Elmendorf et al., 2012; Liu et al., 2018). The warming can induce a higher ecosystem evapotranspiration (Ganjurjav et al., 2016), therefore depletes soil moisture. In a cold and wet environment, the warming-induced change in soil moisture is not enough to limit the plant growth, thus sustain a consistent enhancement of plant productivity, while in a cold and dry environment plant growth may be suppressed by the reduction in soil moisture resulted from the warming (Li et al., 2018; Liu et al., 2018). For example, warming stimulates community biomass by increasing shrubs and graminoids biomass in tundra (Elmendorf et al., 2012) and plant height in an alpine meadow (Ganjurjav et al., 2016). By contrast, warming-induced water stress inhibits community biomass by reducing the cover of graminoids and forbs in an alpine steppe (Ganjurjav et al., 2016) and grasses biomass in a semi-arid grassland (Yang et al., 2011).

The response of different plants to warming determines the community level productivity in a warmer climate. Warming-induced change in soil moisture condition can mediate plant community composition, which may be partly attributable to the various root characteristics of different plant functional groups (Xu et al., 2020). Deep root species can use soil moisture in upper and deeper layers and have higher drought tolerance (Xu et al., 2018). A 4-year warming and drought experiment in a mesic alpine grassland on the northeastern QTP found that plant community composition gradually shifts from more sedges species to more graminoids and forbs species under warming and drought treatments (Liu et al., 2018). Graminoids and forbs species generally have deeper roots than sedges species (Li et al., 2018, 2021; Xu et al., 2018), making them better deal with the environment with limited soil water availability (Klein et al., 2007). These findings suggest that the response of different plant functional groups to warming may depend on soil water availability and functional traits. Therefore, the combined effect of temperature and water availability needs to be considered when exploring plant biomass and community composition responses to warming in different ecosystems. Meta-analyses studies suggest that the responses of plant biomass and community composition to warming vary with time and site (Elmendorf et al., 2012; Liu et al., 2018). For instance, the aboveground biomass (AGB) was increased in the first year of warming, while decreased after 5 years of warming in an alpine meadow on the QTP (Li et al., 2004), which suggest that warming may increase the interannual variability of AGB and decrease the temporal stability of plant community AGB (Quan et al., 2021). Without the consideration of the ecosystem functional stability, the accuracy of terrestrial ecosystem models in predicting future ecosystem service and terrestrial feedback to climate will be hampered (Oehri et al., 2017; Sasaki et al., 2019). The response of the productivity of alpine meadow, one of the major biomes on the QTP, to climate change, therefore, is crucial for understanding the natural processes and for the sustainability of pastoral agriculture on the QTP (Harrison et al., 2014; Zhou et al., 2019).

The stability of productivity may be affected by several mechanisms. Firstly, ecosystem functions and services are more stable with higher diversity due to both the "sampling effect" and "compensatory effect" in functionally similar groups (Tilman et al., 2014; Pennekamp et al., 2018), and the insurance theory in functionally dissimilar groups (Tilman, 1996; Zavaleta et al., 2010; Isbell et al., 2011). The "compensatory effect" or the "niche complementarity effect" increases the total resource use efficiency by spatial and temporal partitioning of resource use (Jiang and Pu, 2009). In the "sampling effect," the higher likelihood of the presence of productive species in the diverse community could enhance the resistance of community to environmental variations, therefore, maintain the high stability (Zhang and Zhang, 2006). Secondly, the mass-ratio hypothesis indicates that the temporal stability of plant community biomass is mainly controlled by dominant species (Grime, 1998; Ma et al., 2017). The dominant species usually have high canopy height and large specific leaf area (Mariotte, 2014), and are fewer in population, more expansive in morphology, and form a large proportion of the biomass (Yang et al., 2017). In contrast, subordinates and rare species are usually more numerous in population than the dominants, smaller in stature, and account for a lower proportion of the biomass (Yang et al., 2017). Therefore, changes in the temporal stability of dominant species may greatly affect the temporal stability of plant community AGB. Thirdly, the temporal stability of plant community AGB could vary with environmental context. For example, the strong environmental filtering selection for species that adapt to drought (e.g., C_4 species) may lead to the decrease of the variability of plant community, which increased the temporal stability of plant community AGB in the dry condition compared to wet condition (García-Palacios et al., 2018). In recent decades, the response of these stabilizing factors to climate change has been paid growing attention, and changes in these stabilizing factors consequently affect the temporal stability of plant community AGB (Shi et al., 2016).

Alpine meadow is dominated by shallow-rooted sedges on the QTP (Ganjurjav et al., 2016). Climate warming could decrease the sedges abundance because warming aggravates water stress in the top soil layer (Ganjurjav et al., 2016), which might reduce the temporal stability of plant community AGB (Quan et al., 2021). But previous studies have reported inconsistent effects of warming on the temporal stability of plant community AGB in alpine meadow on the QTP. For example, in a site with mean annual precipitation of 747 mm, Quan et al. (2021) reported that warming reduces the temporal stability of plant community AGB by decreasing dominant species' stability and co-existing species compensatory dynamics. However, in an area with annual precipitation ranges from 280 to 530 mm, Zhou et al. (2019) found that warming had little effect on the temporal stability of plant community AGB, primarily because the negative effect of daytime warming on plant community stability can be offset by the positive effect of night warming. Therefore, it is far from clear how the temporal stability of plant community biomass responds to warming and the underlying mechanisms and whether the warming effects on the temporal stability of plant community AGB vary with soil water availability. A better understanding of such knowledge is crucial for the sustainable development of alpine ecosystem.

In this study, we conducted a 9-year warming experiment with different soil moisture conditions in the permafrost region of the QTP. Specifically, the objectives of this study were (1) to explore warming effects on the plant AGB, community composition and the temporal stability of plant community AGB in the dry and wet conditions; and (2) to determine the mechanism that control the response of the temporal stability of plant community AGB to warming in the different water conditions.

MATERIALS AND METHODS

Study Site

A 9-year field warming manipulation experiment was carried out to investigate the temporal stability of vegetation productivity to climatic warming in both relatively dry and wet conditions. This study was conducted at the Beiluhe Permafrost Observation station, Chinese Academy of Science (92°56E', 34°49'N; **Figure 1A**). The station is in the Yangtze River's source region on the QTP, with a mean elevation of 4,635 m. The mean annual temperature and mean potential annual evaporation is −3.8°C and 1316.9 mm, respectively. The experimental site is a permafrost region with an active layer thickness of 2–3.2 m, and the permafrost period lasts from September to April (Wang et al., 2007). Plant roots in the 0–20 cm soil layers accounted for more than 80% of the total root biomass (0–50 cm layer; Li et al., 2018). The study site is dominated by alpine meadow species, such as *Kobresia pygmaea* (Sedge), *Kobresia capillifolia* (Sedge), and *Carex moorcroftii* (Sedge). Some forbs species like *Polygonum viviparum* are also widely distributed. The mean plant height at a community level is 5–10 cm. The experimental field was on a mountain slope with a mean inclination of 5°.

Experimental Design

The warming experiment began in 2010. In this study, we conducted a completely randomized split-plot experimental design (**Figure 1B**). In the design, soil moisture condition was used as the splitting factor and warming was the main treatment. More detailed information about soil properties (0–20 cm depth) and plant features for the sampling plots in the different soil moisture conditions were shown in **Supplementary Table S1**. The distance between the dry and wet condition varied from 20 to 50 m. The average elevation in the dry condition was 1 m higher than in the wet condition. The annual mean soil moisture at the lower slope location (wet condition; 12.09%, v/v%) was significantly higher than the upper slope location (dry condition; 6.76%, v/v%) at the top layer (0–10 cm) over 2010–2018.

There are four control plots and four warmed plots in the dry area, and six control plots and six warmed plots in the wet area. In total, 20 treatment plots were established. In the middle of each warming plot, one 165 cm × 15 cm infrared

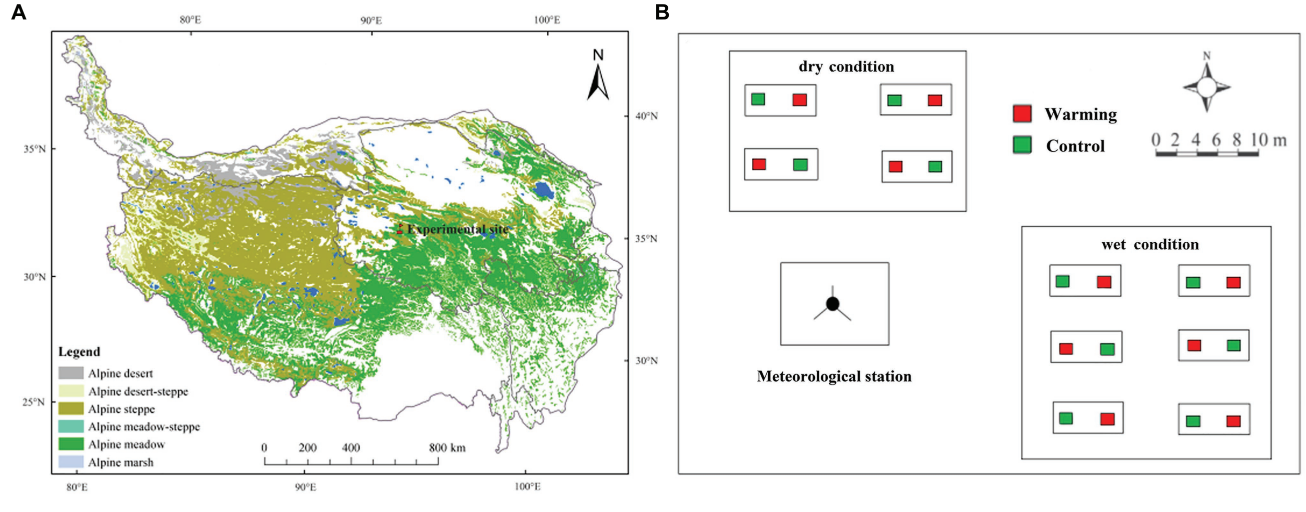

FIGURE 1 | The location of the experimental site **(A)**, and layout of experimental design **(B)**.

heater (MR-2420, Kalglo Electronics Inc., Utah, United States) with an output of 150 W m^{-2} was installed. A "dummy" radiator (no heating element) in each control plot was installed to eliminate any effects of shading by heaters in control plots (Li et al., 2018). Experimental warming increased daily mean soil temperature (at 10 cm depth) by 1.8°C compared to control plots (Xue et al., 2014). All the warming plots were heated yearly-round since July 1st, 2010. From July 2013, there was a malfunction of the substation and no power was available until May 2014. The precipitation and air temperature (2 m) from the ground were automatically recorded by a micro-meteorological observation station.

Soil Temperature and Moisture Measurements

Soil temperature was measured by a thermo-probe (Model 109, Campbell Scientific, Inc., Utah, United States), which was installed at the top layer (0–10 cm) and the deep layer (30–40 cm) in the center of each plot. A frequency domain reflectometry (FDR; EnviroSmart sensor, Sentek Pty Ltd., Stepney, Australia) was installed at depths of 10 and 40 cm to monitor the soil water content (v/v%). A CR-1000 data logger (Campbell Scientific, Inc., Utah, United States) was used to record the soil temperature and moisture every 10-min interval. The daily average soil temperature and moisture were averaged by the 10-min recorded data. The daily recorded data were then averaged into mean annual data and mean August data. Because no power was available from July 2013 until May 2014, soil temperature and moisture were recorded from July 2010 until June 2013 and June 2014 until December 2018.

Vegetation Characteristic Measurements

In late August of every year (from 2010 until 2018), we used the following methods to determine each plot's vegetation characteristics. Each plot (2 m × 2 m) was divided equally into four parts diagonally. The height of each functional group (grasses, sedges, and forbs) was randomly measured 10 times in each part, respectively. A frame with interior dimensions of 27 cm × 27 cm was used to measure the coverage of each functional group in each part. The height and coverage of each plot were obtained by averaging the heights and coverage from the four parts. Besides, in July and September of 2017, and June of 2018, 20 quadrats were investigated every month. In each plot, the aboveground part of each functional group was clipped (27 cm × 27 cm), and then dried in an oven to obtain the AGB. Then the dried AGB of each functional group was fitted against the average height and coverage using a multiple linear regression. The AGB of each functional group in each August (from 2010 until 2018) was estimated using the multiple regressions (Eqs. 1–3). The community AGB was obtained by the sum of AGB of sedges, forbs, and grasses.

$$\text{AGB of sedges} = 157.24c - 8.13h + 59.56 \quad \left(R^2 = 0.362;\,;\ p < 0.001;\,;\ n = 60\right) \tag{1}$$

$$\text{AGB of forbs} = 158.60c - 13.52h + 35.57 \quad \left(R^2 = 0.405;\,;\ p < 0.001;\,;\ n = 60\right) \tag{2}$$

$$\text{AGB of grasses} = 91.63c - 0.72h + 17.72 \quad \left(R^2 = 0.332;\,;\ p < 0.001;\,;\ n = 60\right) \tag{3}$$

Where, c is the coverage (%); h is the height (cm); and n is the number of plots used for establishing this multiple regression.

According to each species' ecological niches or functions, all species were classified into grasses, sedges, and forbs. The three functional groups differ in rooting depths. Grasses and forbs species generally have deeper roots that are more than 30 cm, while sedges have shallower roots that are less than 20 cm (Xu et al., 2018; Li et al., 2021).

Species Richness and Temporal Stability of AGB

We calculated the species richness (species richness; Sasaki and Lauenroth, 2011; Ma et al., 2017) from 2010 to 2018 to reflect the diversity. The species richness is the total number of plant species in each plot.

The temporal stability of the community and each functional group's AGB were calculated as the reciprocal coefficient of variation (ICV) of biomass (Tilman, 1996; Xu et al., 2015). Greater ICV means higher stability (Zhang and Zhang, 2006).

$$\text{Temporal stability} = \text{ICV} = \text{Mean} / \text{SD} \tag{4}$$

Where, ICV is the reciprocal coefficient of variation of community and each functional group's AGB; SD is SD of community and each functional group's AGB; Mean is mean biomass of community and each functional group's AGB.

Data Analysis

Repeated-measures ANOVA was used for testing the effects of warming, soil moisture condition, year, and their interaction on community AGB, the AGB of grasses, sedges, and forbs. The same analysis was used for testing the effects of warming, soil moisture condition, year, depth, and their interaction on soil temperature and soil moisture. The community AGB, AGB of grasses, sedges, and forbs were $\log_{10}$-transformed. The Tukey's honestly significant difference (HSD) test was conducted to examine the significant effect of warming on soil temperature, soil moisture, community AGB, the AGB of grasses, sedges, and forbs in different years under dry and wet conditions. Two-way ANOVA was used to explore the effects of warming, soil moisture condition and their interaction on the temporal stability of the community AGB, AGB of sedges, forbs, and grasses. The correlation between the temporal stability of plant community AGB and the temporal stability of AGB of grasses, sedges, forbs, and species richness were examined by simple linear regression analyses. The combined effects of species richness, the temporal stability of AGB of grasses, sedges, and forbs on the temporal stability of plant community AGB were evaluated by general linear models (GLMs).

RESULTS

Precipitation and Temperature During the Experiment Period

Based on meteorological station data, over 95% of the annual precipitation falls from May to October (**Figure 2A**). The annual precipitation ranges from 250 to 525 mm during the experimental period. The lowest annual precipitation was observed in 2013 (250 mm) and 2015 (267 mm; **Figure 2A**), which was 35 and 30% lower than the mean annual precipitation (382 mm, 2002–2019) in this area. The highest annual precipitation was observed in 2017 (483 mm) and 2018 (525 mm; **Figure 2A**), which was 27 and 37% higher than the mean annual precipitation. Therefore, 2013 and 2015 were considered as relatively drought years, and 2017 and 2018 were considered as relatively wet years. The mean annual temperature is −3.62°C and mean growing season temperature (May–September) is 4.12°C (2011–2019; **Figure 2B**). The mean annual temperature ranges from −4.28 to −3.00°C and mean growing season temperature ranges from 3.55 to 4.83°C during the experimental period (2011–2019; **Figure 2B**).

Soil Microclimate

The mean annual soil temperature was higher in the dry condition (0–10 cm, 0.57°C; 30–40 cm, 1.64°C) than wet condition (0–10 cm, 0.16°C; 30–40 cm, 0.40°C; **Supplementary Figure S1**; **Figure 3**) in the control plots over the study period. Warming has significant effects on soil temperature, which varied with soil depth and the soil moisture condition (**Table 1**). Warming treatments significantly increased the mean annual soil temperature. The largest increase was in 2015, which was 2.03 and 1.57°C in 0–10 cm layer in the dry and wet conditions (**Figure 3**), respectively. The lowest increase was in 2017, which was 1.77 and 1.28°C in 0–10 cm layer in the dry and wet conditions (**Figure 3**), respectively.

The mean annual soil moisture was higher in the wet condition (0–10 cm, 12%, v/v%; 30–40 cm, 14%, v/v%) than dry condition (0–10 cm, 6%, v/v%; 30–40 cm, 8%, v/v%; **Figure 4**). Warming decreased the mean daily, August, and annual soil moisture in 0–10 cm layer (**Supplementary Figure S2**; **Figure 4**), but increased it in 30–40 cm layer (**Figure 4**). Warming significantly decreased the mean annual soil moisture by 0.71–1.28 and 0.95–1.92% (v/v%) in 0–10 cm layer but increased it by 0.49–1.35 and 1.16–3.42% (v/v%) in 30–40 cm layer in the dry and wet conditions (**Figure 4**), respectively.

Aboveground Biomass

The AGB of grasses increased regardless of the soil water availability in the experimental plots, while the AGB of sedges decreased in the dry condition in the warmed plots during the experimental period (**Figure 5**). In general, the AGB percentage of grasses, sedges, and forbs were about 8, 55, and 37% in 2010 in the dry condition, and were 5, 63, and 32%

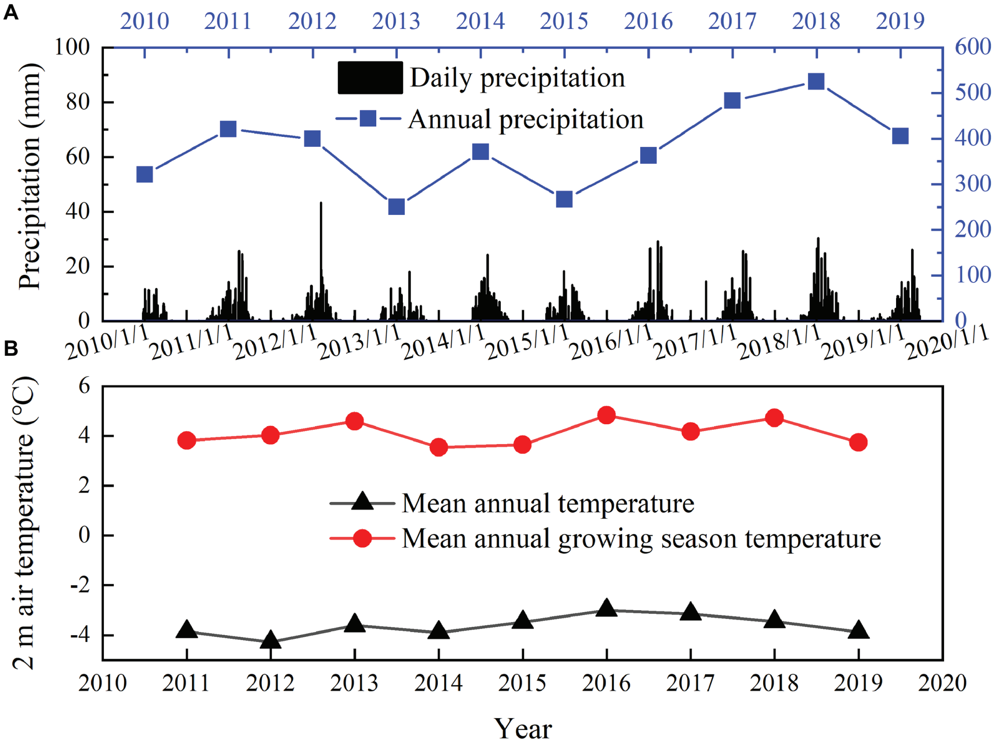

FIGURE 2 | Variations in mean daily precipitation and annual precipitation from 2010 to 2019 **(A)**, mean annual temperature and mean growing season temperature (May–September) from 2011 to 2019 **(B)**.

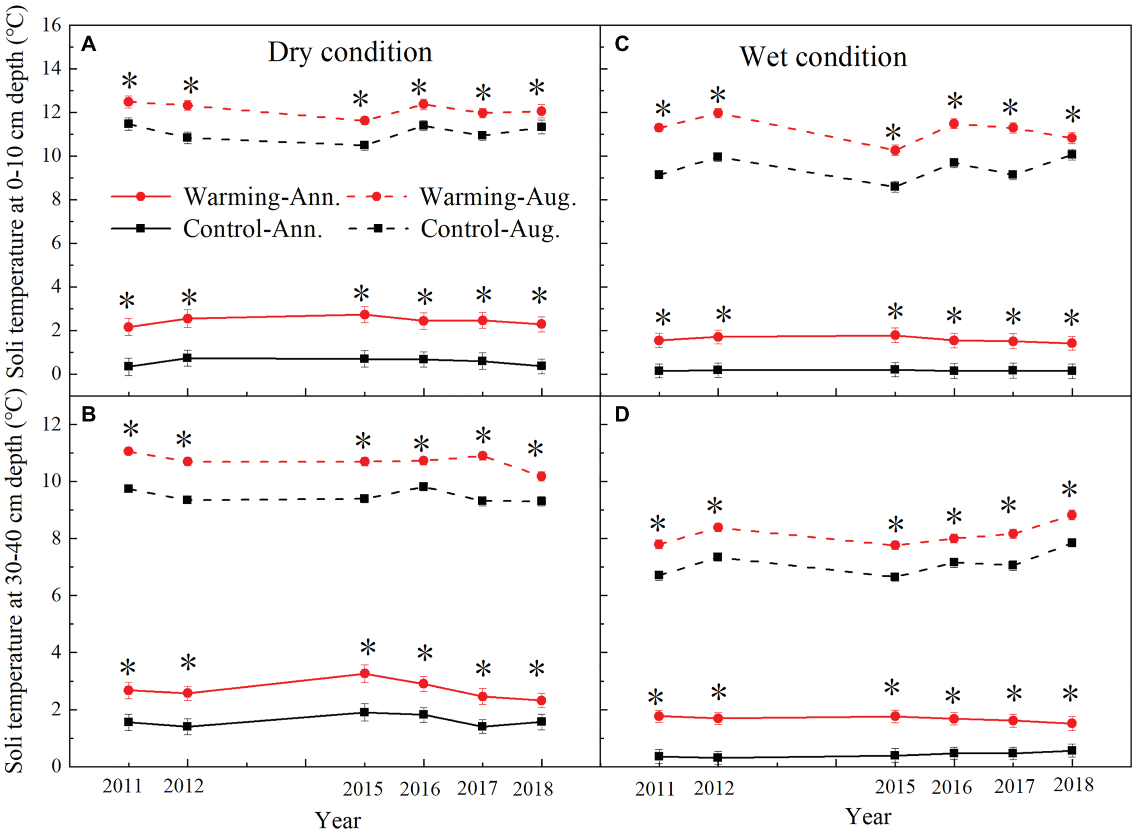

FIGURE 3 | Mean August and annual soil temperature at 0–10 cm and 30–40 cm depth in control and warmed plots in the dry **(A,B)** and wet **(C,D)** conditions from 2010 to 2018. Significance: $^{*}p < 0.05$.

TABLE 1 | Results (*F* values) of repeated-measures ANOVA of the effect of soil moisture condition (P), warming treatment (W), year, and their interactions on community aboveground biomass (AGB), AGB of grasses (Grasses), AGB of sedges (Sedges), and AGB of forbs (Forbs), and species richness (SR); the effect of soil moisture condition (P), warming treatment (W), year, depth, and their interactions on soil temperature (ST) and soil moisture (SM).

Variance source	ST	SM	AGB	Grasses	Sedges	Forbs	SR
P	57.43^{**}	381.23^{**}	38.38^{**}	1.67	71.99^{**}	9.06^{**}	1.21^{**}
W	146.49^{**}	4.35^{*}	2.41^{*}	21.22^{**}	3.37^{*}	10.79^{*}	1.21
Year	1.91	40.36^{**}	7.67^{**}	2.40^{**}	11.70^{**}	1.53^{**}	4.37^{*}
Depth	36.76^{**}	444.29^{**}	/	/	/	/	/
P*W	1.23	4.80^{*}	5.87^{*}	0.10	6.61^{**}	4.39^{*}	0.02
P*Year	0.86	10.19^{**}	1.45	1.71	1.91^{*}	0.61	0.33
P*Depth	11.94^{**}	53.31^{**}	/	/	/	/	/
W*Year	0.50	0.21	1.98^{*}	0.34	2.85^{*}	0.85	1.12
W*Depth	11.82^{**}	61.42^{**}	/	/	/	/	/
Year*Depth	0.64	1.69	/	/	/	/	/
P*W*Year	0.06	0.65	0.12	0.24	0.15	0.17	0.41
P*W*Depth	4.82^{*}	18.28^{**}	/	/	/	/	/
P*Year*Depth	0.47	0.71	/	/	/	/	/
W*Depth*Year	0.19	0.49	/	/	/	/	/
P*W*Year*Depth	0.05	1.70	/	/	/	/	/

$^{*}p < 0.05$; $^{**}p < 0.01$.

in 2010 in the wet condition, respectively. The AGB percentage of grasses and forbs increased, while the AGB percentage of sedges decreased in the warmed plots (**Figure 6**). The largest increase in the AGB percentage of grasses and forbs was observed in 2013 and 2015 in the dry condition. The largest decrease in the AGB percentage of sedges was also observed in 2013 and 2015 in the dry and wet conditions (**Figure 6**). Warming had no significant effect on species richness in both dry and wet conditions during the experimental period (**Table 1**; **Figure 7**).

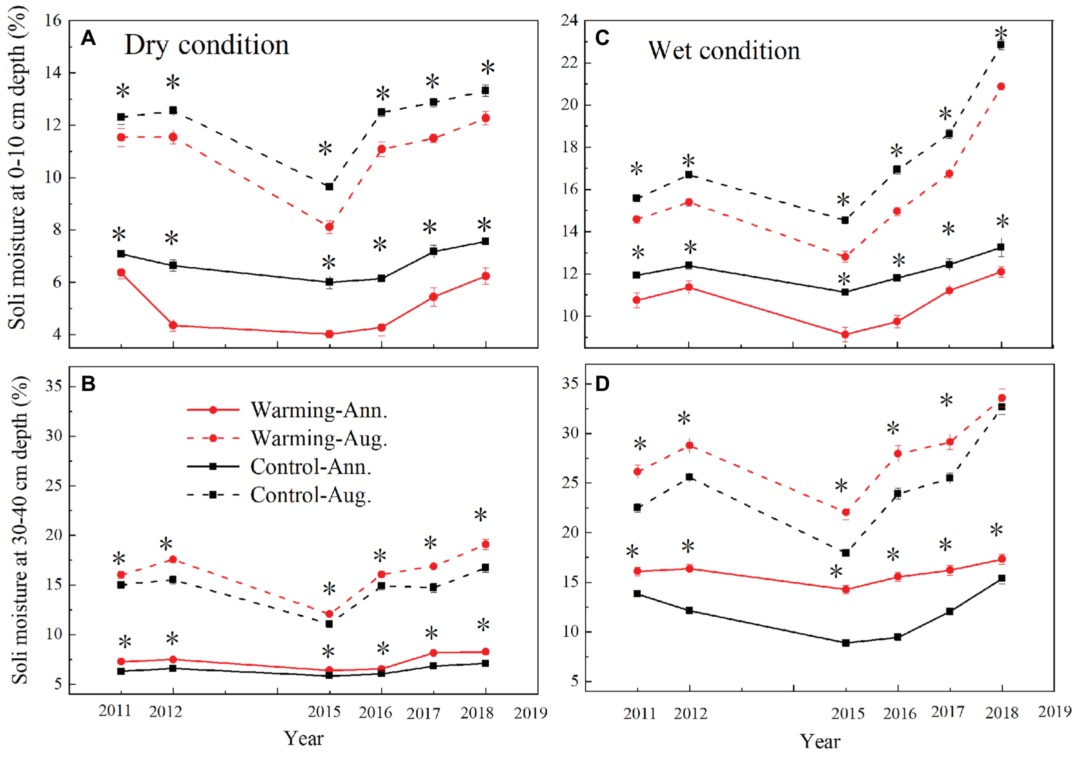

FIGURE 4 | Mean August and annual soil moisture at 0–10 cm and 30–40 cm depth in control and warmed plots in the dry **(A,B)** and wet **(C,D)** conditions from 2010 to 2018. Significance: $^{*}p < 0.05$.

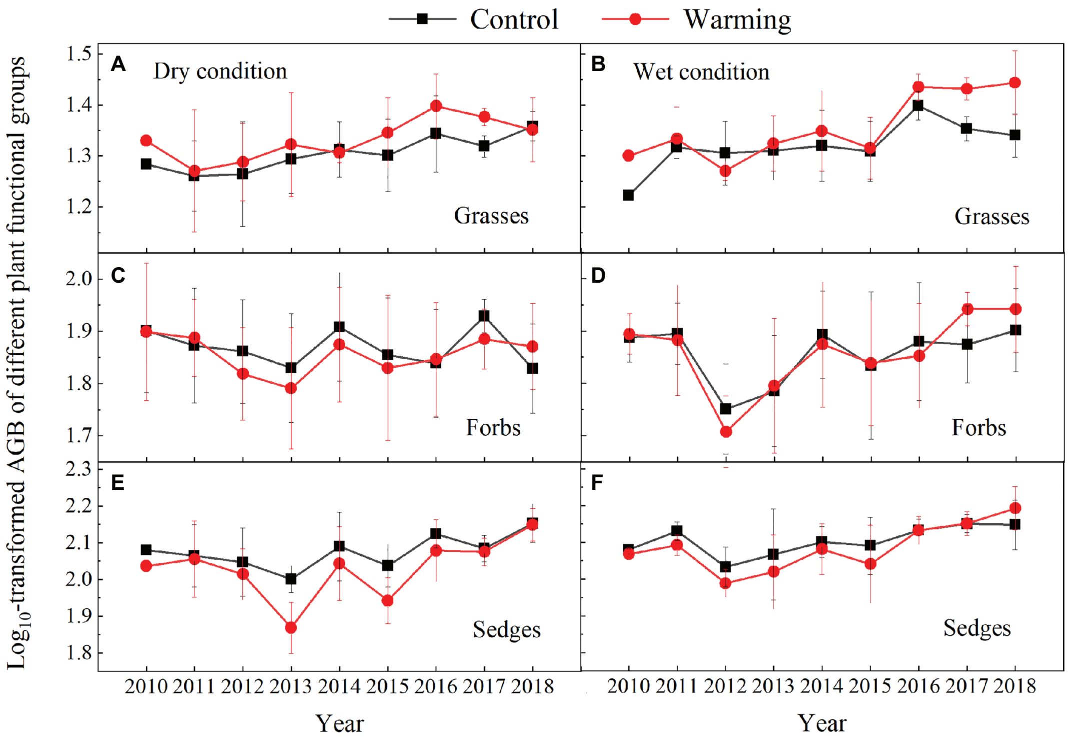

FIGURE 5 | Aboveground biomass of grasses **(A,B)**, forbs **(C,D)**, and sedges **(E,F)** in control and warmed plots in the dry **(A,C,E)** and wet **(B,D,F)** conditions from 2010 to 2018.

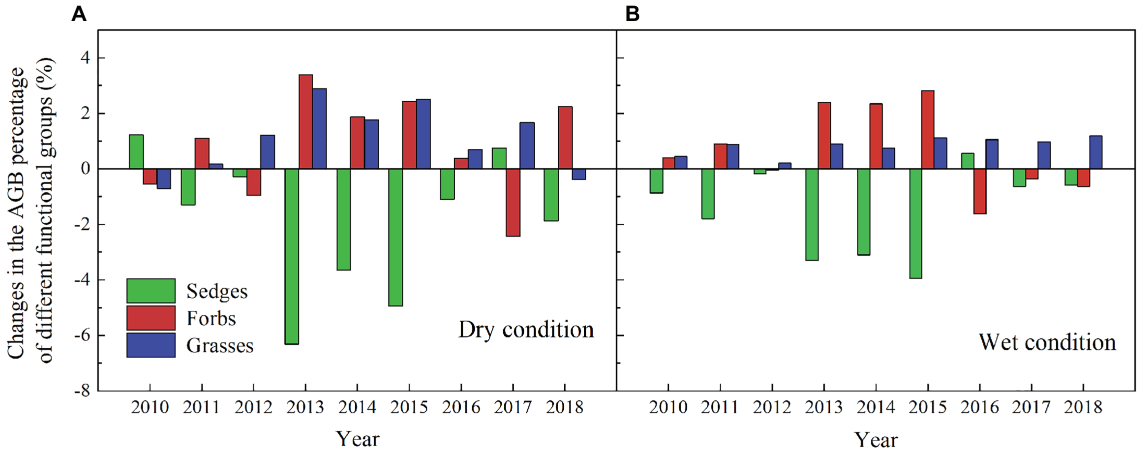

FIGURE 6 | Changes in AGB absolute percentage of grasses, forbs, and sedges (percentage of different functional groups in warmed plots – percentage of different functional groups in control plots) in the dry **(A)** and wet **(B)** conditions from 2010 to 2018.

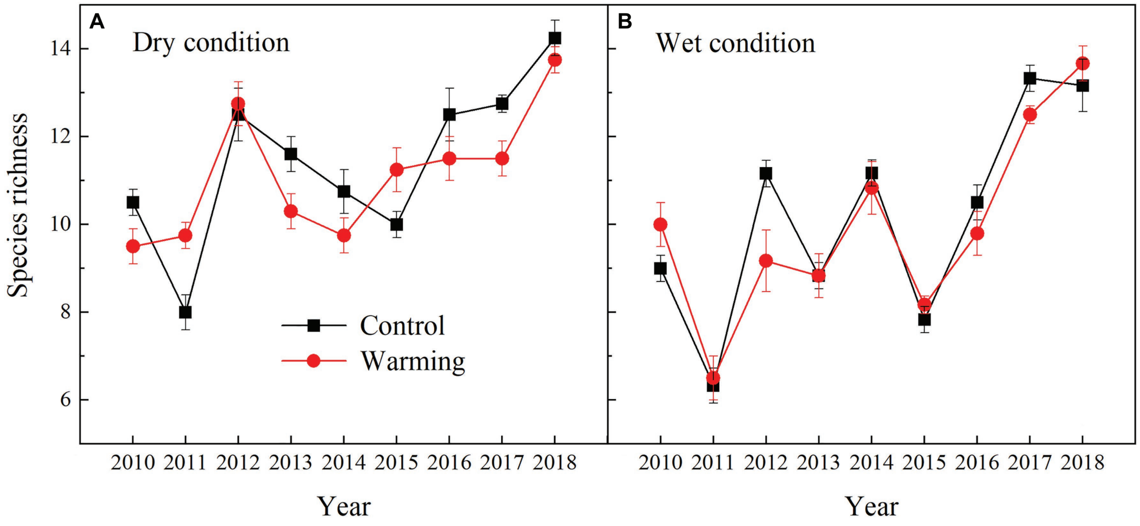

FIGURE 7 | Yearly species richness in control and warmed plots in the dry **(A)** and wet **(B)** conditions from 2010 to 2018.

Warming had a significant effect on the total AGB, which varied with the soil moisture condition and year (**Table 1**). The total AGB was higher in the wet condition than dry condition during the experimental period (**Figure 8**). It only significantly decreased by 16% in 2013 and 12% in 2015 in the dry condition (**Figure 8A**), but increased by 12% in 2018 in the wet condition, while showed no difference between warming and control plots in other years (**Figure 8B**).

The Temporal Stability of Plant Community and Different Functional Groups Biomass

Warming had a significant effect on the temporal stability of community AGB ($F = 28.51$, $p < 0.001$) and AGB of sedges ($F = 12.86$, $p = 0.002$). Warming had no significant effects on the temporal stability of AGB of forbs and grasses but significantly decreased the temporal stability of plant community AGB and AGB of sedges both in the dry and wet conditions (**Figure 9**).

Relationship Between the Temporal Stability of Plant Community AGB and Species Richness and the Temporal Stability of AGB of Three Functional Groups

The temporal stability of plant community AGB was positively correlated with species richness and the temporal stability of AGB of sedges and forbs (**Figures 10A,B,D**) but showed no relationship with the temporal stability of grasses AGB (**Figure 10C**). A GLM analysis showed that species richness and the temporal stability of AGB of three functional groups, together explained 79% of the variation in the temporal stability of plant community AGB (**Table 2**), with the largest proportion was contributed by the temporal stability of AGB of sedges (66.69%; **Table 2**).

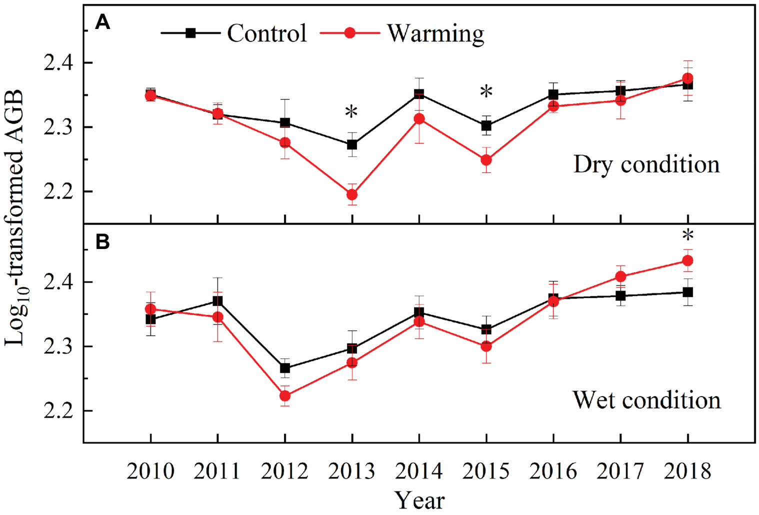

FIGURE 8 | Aboveground biomass in control and warmed plots in the dry **(A)** and wet **(B)** conditions from 2010 to 2018. Significance: $^{*}p < 0.05$.

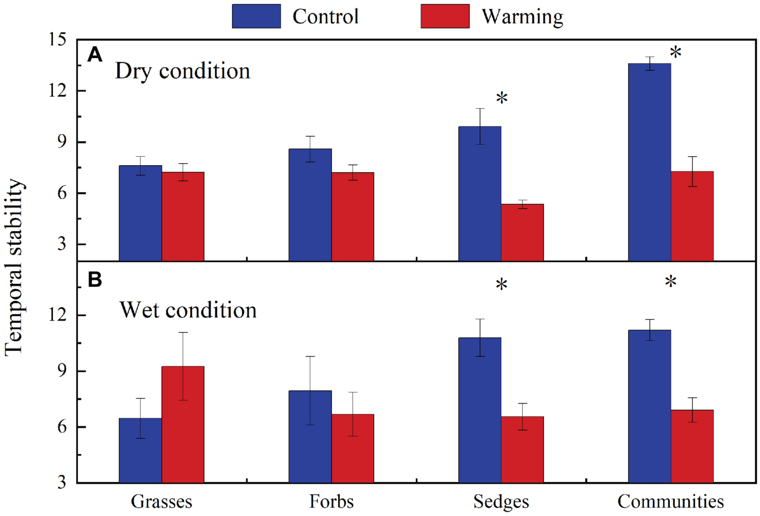

FIGURE 9 | The temporal stability of plant community AGB and each functional group's AGB in control and warmed plots in the dry **(A)** and wet **(B)** conditions. Significance: $^{*}p < 0.05$.

DISCUSSION

Plant Functional Groups Response to 9-Year Warming

Our 9-year warming experiment at an altitude of 4,630 m in the permafrost region of the QTP found that grasses, forbs, and sedges show different responses to experimental warming (**Figure 6**). Similar to the long-term observations (32 years) and a 4-year warming experiment on the eastern QTP (Liu et al., 2018), the AGB percentage of grasses and forbs significantly increased but that of sedges decreased regardless of the soil water availability in the experimental plots in our study (**Figure 6**). Different plant functional groups have different root traits, which may determine whether they have superior interspecific competition for limited resources in a warmer climate (Xu et al., 2018). Grasses and forbs species generally have roots deeper than 30 cm, while sedges species have roots shallower than 20 cm in our study site (Li et al., 2018, 2021). Warming induced a decrease in the soil moisture in the top layer (0–10 cm) and an increase in the soil moisture in the deep layer (30–40 cm; **Figure 4**). With the deep roots, grasses, and forbs species can access the soil moisture in the deep soil layer (Liu et al., 2018). By contrast, the deeper root systems and the increase in the soil moisture in the deep layer could make grasses and forbs species better able to cope with a warmer climate (Liu et al., 2018; Xu et al., 2020), thus leading to an increase in AGB of grasses and forbs in our study. However, sedges species growth would be inhibited because of the decrease in the soil moisture

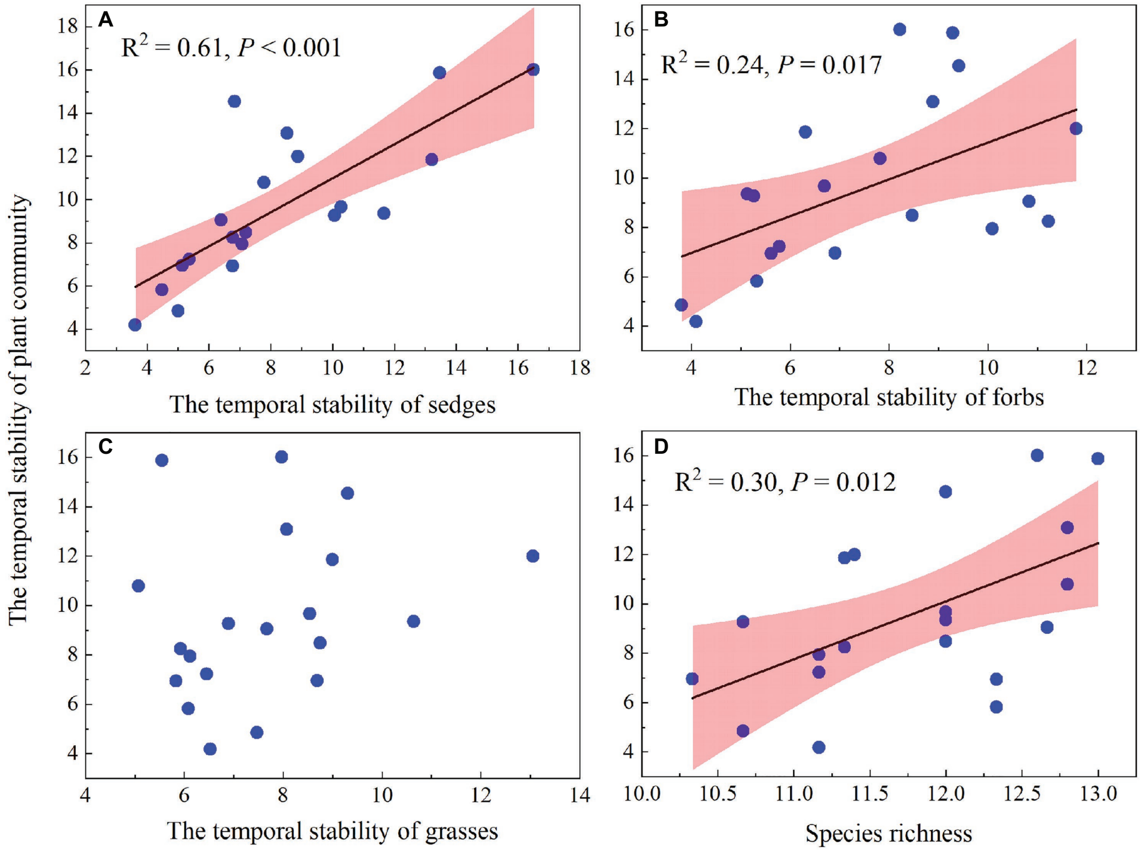

FIGURE 10 | Relationship of the temporal stability of plant community AGB and the temporal stability of sedges AGB **(A)**, the temporal stability of forbs AGB **(B)**, the temporal stability of grasses AGB **(C)**, and species richness **(D)**.

TABLE 2 | Integrative effects of species richness (RI), the temporal stability of AGB of sedges (Sedges), the temporal stability of AGB of forbs (forbs), the temporal stability of AGB of grasses (Grasses) on the temporal stability of plant community AGB in the dry and wet conditions based on the general linear models (GLMs).

Source	RI	Sedges	Forbs	Grasses
MS	7.23	134.13	15.73	1.20
SS%	3.60	66.69	7.82	0.60
p	0.183	**<0.001**	0.056	0.527

Bold values are statistically significant ($p < 0.05$). MS, mean squares; SS, proportion of the total variance explained by the variable. $R^2 = 0.79$.

in the top layer caused by warming (**Figures 4A,C**; Liu et al., 2018). The largest decrease in AGB of sedges (27 and 20%) induced by warming in relatively drought years (2013 and 2015) suggested that the AGB percentage of sedges is more sensitive to precipitation than warming (**Table 1**).

However, our findings were inconsistent with the decrease of grasses abundance in an alpine steppe under a warmer climate (Ganjurjav et al., 2016), in which warming decreased the soil moisture only in the top layer and had no significant change in the deep layer. In our study, the increase of soil moisture in the deep layer (**Figure 4**) could create a favorable environment for the growth of grasses.

The Community AGB Response to 9-Year Warming

The warming effects on community AGB varied with soil moisture condition (**Table 1**). Warming can affect plant growth directly and indirectly. The plant growth in alpine ecosystem is largely restricted by low temperature (Wang et al., 2012). The increase in temperature could directly alleviate the limitation of low temperature on plant growth (Li et al., 2018). An increase in temperature may indirectly stimulate plant growth by promoting soil nitrogen mineralization and increasing the growing season length (Sullivan and Welker, 2005; Peng et al., 2016). However, the associated soil moisture declining might suppress plant growth by aggravating water stress (Bai et al., 2004), which may offset the positive effect of increased temperature on plant biomass (Liu et al., 2018).

The decrease in the AGB of sedges species in the community can be partly compensated by the increase in the AGB of grasses and forbs species (**Figure 6B**). This might explain no significant change in community AGB during the normal and relatively wet years in the dry condition (**Figure 8A**). However, the largest decrease in soil moisture in the top layer constrained the growth of sedges (**Figure 4A**), leading to a dramatic decrease in AGB of sedges ($27\,g{\cdot}m^{-2}$) in relatively drought years (2013 and 2015) in the dry condition (**Figure 5E**). Simultaneously, the AGB of grasses only increased by 2 g·m^{-2} (**Figure 5A**) in relatively drought years (2013 and 2015). Therefore, the decrease in community AGB was attributed to a rapid decrease in AGB of sedges under warming in relatively drought years in the dry condition (**Figure 8A**). Our results were similar with the finding reported by an alpine steppe on the QTP (Ganjurjav et al., 2016), while inconsistent with the results that suggest no significant warming effects on aboveground net primary production even during the drought years (Liu et al., 2018). In study of Liu et al. (2018), the soil moisture was only decreased by 11% under warming treatment, the decrease in soil moisture in the mesic alpine grassland might not limit the plant growth. However, warming decreased the soil moisture by 49% in the dry condition in relatively drought years (2013 and 2015; **Figure 4A**), which could constrain the plant growth.

Although, warming reduced the soil moisture in the top layer in the wet condition the decreased soil moisture might not limit the plant growth (**Figures 5, 6B**; Liu et al., 2018), which explains no significant warming effect on the AGB of sedges (**Figure 8B**). Grasses and forbs have deeper root systems and the increase in the soil moisture in the deep layer leads to an increase in AGB of grasses and forbs under warming (**Figures 4D, 5**). Therefore, the significant increase in community AGB (**Figure 8B**) was the result of the stimulation of grasses and forbs by warming in the wet condition in relatively wet years (**Figures 6B,D**).

The Response of Temporal Stability of Plant Community AGB to Warming

Global climate change is expected to result in a high frequency of both drought and wet extremes, leading to changes in the temporal stability of plant community AGB (Zhang and Zhang, 2006; Xu et al., 2015). The decrease in the temporal stability of plant community AGB under warming in the dry condition in our study (**Figure 9A**) was consistent with previous findings from a 6-year warming experiment conducted in an alpine meadow on the eastern QTP (Quan et al., 2021), while inconsistent with the study reported by Zhou et al. (2019). Zhou et al. (2019) found there was no warming effect on the temporal stability of community AGB in an alpine meadow on the QTP. In study of Zhou et al. (2019), the decrease in the AGB of grasses species in the community can be compensated by the increase in the AGB of sedges and forbs species. The asynchrony among different plant functional groups makes the temporal stability of plant biomass remained stable under warming. However, the dramatic decrease in AGB of sedges (27 g·m^{-2}) in relatively drought years (2013 and 2015) in the dry condition (**Figure 5E**), while a minor increase in the AGB of grasses (2 g·m^{-2}; **Figure 5**), leads to a decrease of the community AGB (**Figure 8A**). Besides, warming had no effect on the community AGB in other years. Therefore, the temporal stability of plant community AGB decreased under warming in the dry condition in our study. The temporal stability of plant community AGB in the wet condition also decreased in the warmed plots (**Figure 9B**). Previous study suggests that warming increases the temporal stability of plant community AGB by increasing the biomass of dominant C_4 functional group in the moist condition (Shi et al., 2016), primarily because C_4 species have a higher tolerance to the water stress caused by warming (Way et al., 2014). However, in our study, the community is dominated by C_3 plants that are more sensitive to warming compared to C_4 species (Shi et al., 2016). Thus, the dominance by C_3 plants may result in the decrease of temporal stability of plant community AGB in the alpine meadow ecosystem. The positive relationship between soil moisture and AGB of sedges has been widely reported by previous studies in the alpine ecosystem (Dorji et al., 2014; Liu et al., 2018). The interannual variability of soil moisture in the top layer was increased under warming (**Figures 4A,C**). As sedges species have shallow root systems (Liu et al., 2018), the interannual variability of AGB of sedges (**Figure 8E**) was also increased, which might explain that warming decreases the temporal stability of AGB of sedges.

The mass-ratio hypothesis suggests that the temporal stability of plant community AGB is mainly controlled by dominant species (Grime, 1998; Ma et al., 2017). Warming leading to changes in the temporal stability of dominant species AGB may greatly affect the temporal stability of plant community AGB. In our study, the AGB of sedges accounted for 55 and 63% of the community AGB in the dry and wet conditions in the control plots, indicating that community AGB may be determined by the changes in AGB of sedges (dominant plant functional group). The temporal stability of AGB of sedges accounted for the largest proportion (66.69%) of the variance for the temporal stability of plant community AGB (**Table 2**), and the temporal stability of AGB of sedges was positively correlated with the temporal stability of plant community AGB (**Figure 10A**), suggesting that the decrease in the temporal stability of plant community AGB was mainly resulted from the decrease in the temporal stability of AGB of sedges under warming.

Many previous studies, such as field observations (Tilman and Downing, 1994; Tilman, 1996) and theoretical models (Mougi and Kondoh, 2012; Loreau and de Mazancourt, 2013), have suggested that the temporal stability of plant community AGB increased with species diversity. In this study, we also found the temporal stability of plant community AGB increased with increasing species richness (**Figure 10D**). However, species richness was not a significant pathway through which warming can impact the temporal stability of plant community AGB (**Table 2**; Xu et al., 2015; Wu et al., 2020). The possible explanation for no effect of species diversity on the temporal stability of plant community AGB in our study is that the positive relationships of species diversity-stability were mainly found in experiments that have relatively large species diversity gradients (Tilman et al., 2006, 2014). In our study with a relatively small species diversity, warming had no significant effect on species richness regardless of the soil water availability in the experimental plots (**Figure 7**). Therefore, the warming effects on the temporal stability of plant community AGB through species richness in our study may be small.

In this study, we attempted to explore the effects of warming on the temporal stability of plant community AGB in the dry and wet conditions. However, there were only one dry stand and one wet stand. Thus, the different warming impact of temporal stability of AGB in the dry and wet conditions should be interpreted with caution, which needs to be further studied.

CONCLUSION

Our results demonstrated that the community AGB had no significant change under warming in the normal years, it only decreased in the dry condition in relatively drought years and increased in the wet condition in relatively wet years. This suggests that the AGB response to warming depends on soil water availability. The temporal stability of plant community AGB is not driven by species diversity, but it is primarily regulated by the dominant plant functional group under warming. Our results suggest that the changes in the temporal stability of sedges species will directly affect the stability of natural grassland functions and services on the QTP under a warmer climate.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

CLi, CLa, and FP had the main responsibility for data curation and writing. XX and FP had the overall responsibility of experimental design. QY, FL, PG, JL, and TW contributed to data analysis and reviewed this manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

The study was financially supported by the National Natural Science Foundation of China (41771229 and 41907386) and Youth Innovation Promotion Association, Chinese Academy of Sciences.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2021.704138/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

ORIGINAL RESEARCH
published: 11 August 2021
doi: 10.3389/fpls.2021.674527

Precipitation Variability Affects Aboveground Biomass Directly and Indirectly *via* Plant Functional Traits in the Desert Steppe of Inner Mongolia, Northern China

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Clarifying the response of community and dominance species to climate change is crucial for disentangling the mechanism of the ecosystem evolution and predicting the prospective dynamics of communities under the global climate scenario. We examined how precipitation changes affect community structure and aboveground biomass (AGB) according to manipulated precipitation experiments in the desert steppe of Inner Mongolia, China. Bayesian model and structural equation models (SEM) were used to test variation and causal relationship among precipitation, plant diversity, functional attributes, and AGB. The results showed that the responses of species richness, evenness, and plant community weighted means traits to precipitation changes in amount and year were significant. The SEM demonstrated that precipitation change in amount and year has a direct effect on richness, evenness, and community-weighted mean (CWM) for height, leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen content (LNC), and leaf carbon content (LCC) and AGB; there into CWM for height and LDMC had a direct positive effect on AGB; LA had a direct negative effect on AGB. Three dominant species showed diverse adaptation and resource utilization strategies in response to precipitation changes. *A. polyrhizum* showed an increase in height under the precipitation treatments that promoted AGB, whereas the AGB of *P. harmala* and *S. glareosa* was boosted through alterations in height and LA. Our results highlight the asynchronism of variation in community composition and structure, leaf functional traits in precipitation-AGB relationship. We proposed that altered AGB resulted from the direct and indirect effects of plant functional traits (plant height, LA, LDMC) rather than species diversity, plant functional traits are likely candidate traits, given that they are mechanistically linked to precipitation changes and affected aboveground biomass in a desert steppe.

Keywords: precipitation, plant functional traits, aboveground biomass, ecosystem function, desert steppe

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Specialty section:
This article was submitted to
Functional Plant Ecology,
a section of the journal
Frontiers in Plant Science

Received: *01 March 2021*
Accepted: *07 June 2021*
Published: *11 August 2021*

Citation:
Cheng H, Gong Y and Zuo X (2021)
Precipitation Variability Affects
Aboveground Biomass Directly and
Indirectly via Plant Functional Traits in
the Desert Steppe of Inner Mongolia,
Northern China.
Front. Plant Sci. 12:674527.
doi: 10.3389/fpls.2021.674527

INTRODUCTION

For the past decades, studies on the relationship between climate change and ecosystem attributes, and potential feedback of plants have sprung up (Bai et al., 2004; Griffin Nolan et al., 2018; Zhang B. et al., 2020) because of growing unexpected climate changes and ecosystem responses. The climatic model predicted that precipitation was likely to be more uncertain (Power et al., 2013) and accompanying an increase in precipitation amount in the future in East Asia (Knapp et al., 2008; Chen and Sun, 2013). Beyond that, researchers also confirmed that precipitation has experienced intense changes in intensity and variability since the last century (Alexander et al., 2006; Trugman et al., 2018; Paschalis et al., 2020). Water availability fluctuations induced by changes in precipitation modulate plant community dynamic and ecosystem function (Yang et al., 2011; Wu et al., 2016; Peralta et al., 2019). For example, changes in the distribution of rainfall events influence the patterns of species richness and species composition (Zavaleta et al., 2003; Báez et al., 2013; Cleland et al., 2013; Libalah et al., 2020), ecosystem net primary productivity (Fay et al., 2003; Heisler-White et al., 2009), and C cycling (Harper et al., 2005). The response of a plant to variation in environment can differ among species, communities, and ecosystems, while a mechanistic comprehension of this modifiability remains open to question.

One helpful avenue to progress our understanding of plant responses to environmental change is the traits-based approach, which pays attention to environmental gradients, plant functional traits across numerous species, and physiologically and morphologically derived common performance (Nicotra et al., 2010; Wellstein et al., 2011). Studies on global patterns in plant height and seed mass are the representative practice (Moles et al., 2007, 2009). Additionally, this approach helps provide a better perspective of understanding on how environmental changes will affect the biosphere in a broad variety of circumstances, including regional climate patterns, biogeochemical cycles, ecosystem services, and functions. For example, plant height and leaf traits (specific leaf area, SLA; leaf nitrogen content, LNC; and leaf area index, LA) have been used to illustrate ecosystem function from tundra (Hudson et al., 2011; Bjorkman et al., 2018), grassland (Zirbel et al., 2017; Xu et al., 2018) to forest ecosystems (Báez and Homeier, 2018; Wang and Ali, 2021). Finegan et al. (2015) reported that biomass-weighted community mean value of max height [community-weighted mean (CWM) H max] was the most important predictor of initial standing biomass, and CWM SLA was the most important predictor of the biomass increment. Finally, they proposed CWM functional traits were strong drivers of ecosystem biomass and carbon-cycle processes in three rainforests. Therefore, the traits-based approach may support uncovering the underlying mechanism of ecosystem response to variation in water availability.

Numerous studies have indicated that the response of community and ecosystem to condition changes depends on the attributes of key species (Huston, 1997; Grime, 1998), relating mass-ratio hypothesis (Suding et al., 2008; Gross et al., 2017). However, the specific role of species in community dynamic remains elusive. Due to complementarity and the selection-effects hypothesis, plant responses to condition changes are not necessarily consistent with coexisting species (Schmid and Harper, 1985; Sinclair and Byrom, 2006). For instance, Zhang R. et al. (2020) found that different from *Stipa glareosa*, dominance of *Allium polyrhizum* and *Peganum harmala*, two of three dominant species, increased in drought treatments. Mahaut et al. (2020) also showed that positive biodiversity influenced both aboveground biomass and a positive complementarity effect resulting from the presence of *Plantago lanceolata* and the CWM trait; on the contrary, the presence of *Sanguisorba* negatively affected productivity in the grassland diversity–productivity relationship test. These results indicated that coexisting species contributed to the ecosystem functioning differently. Thus, disentangling the role of these key species in community functioning will help to develop a deeper comprehension of the adaptation strategies of plants and ecosystem processes.

Under global climate change scenarios, studies investigating on the response of community dynamics and the ecosystem process to climate change are increasing, few studies have investigated desert steppe ecosystems functioning along environmental gradient (Zuo et al., 2020). Desert steppe ecosystems, characterized by water limitations, are thought to be sensitive to climate change, especially precipitation fluctuation (Liu et al., 2016). Xerophytic species provide habitat for desert animals and adjust their attributes to adapt and resist environmental stress (Thomey et al., 2011; El-Keblawy et al., 2015), contributing to maintaining ecosystem productivity (John et al., 2018). However, with the intensification of global climate change and human activities over the last century, desert steppe ecosystem has been suffering degradation and desertification (Mu et al., 2013) because of species diversity loss, imbalance of the xerophytic community structure, and ecosystem function decline. For this reason, more researches on the response of desert steppe ecosystem to changes in precipitation are needed, which may be conducive to restoring fragile ecosystems and to predicting the tendency of the ecosystem dynamic more precisely.

In this study, we aimed to determine the effects of precipitation changes on patterns of ecosystem aboveground biomass by the controlled, manipulated precipitation experiments in a desert steppe. Specifically, we ask three main research questions: (1) Are community composition, species diversity, plant functional traits synchronously affected by precipitation changes in desert steppe? (2) How do the direct and indirect effects of species diversity and functional traits affect community biomass; and (3) what is the role of dominant species in the community responses, relating plant-adaptive and resource-use strategies? Accordingly, we hypothesize that the expected that plant diversity, and functional traits' response to precipitation change alters AGB, and varies with different species.

METHODS

Study Site

The study was conducted at the Urat Desert-grassland Research Station (Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, **Figure 1**), located in western

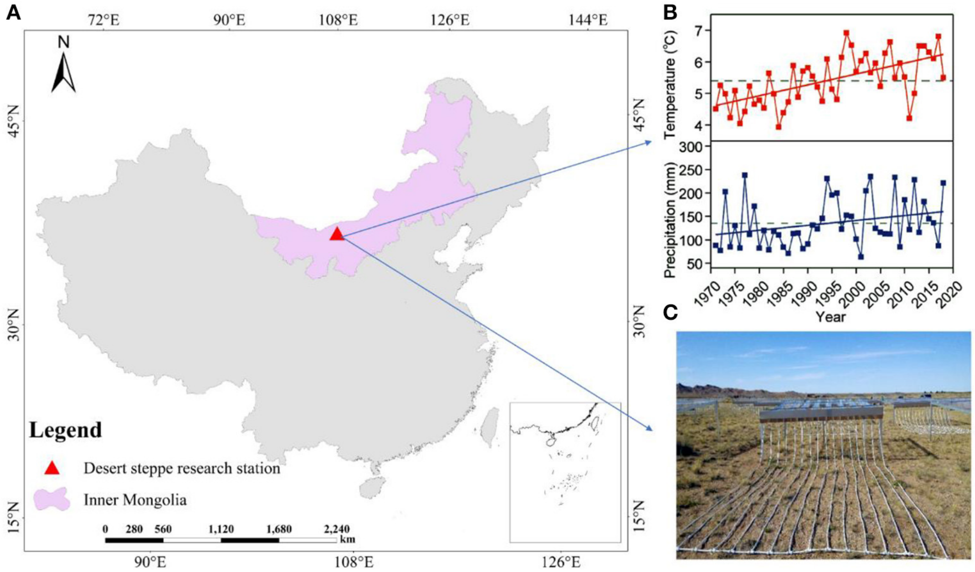

FIGURE 1 | Geographic and climatic characteristics of the study area. **(A)** The map of China depicting the locations of the Urat Desert Steppe Research Station in Inner Mongolia. **(B)** Annual temperature and precipitation from 1971 to 2018. Dotted line represents the mean temperature and precipitation of the last 48 years. The annual mean temperature was 5.4°C. The minimum and maximum temperature in this region were 3.9 and 6.1°C. For the total annual precipitation between these years, the minimum, maximum, and average ones were 63.2, 237.8, and 135.5 mm, respectively. **(C)** Precipitation change treatments were established in 2015 in a desert steppe in Inner Mongolia, China.

Inner Mongolia (Zhang R. et al., 2020; Zuo et al., 2020). The site is characterized by brown desert soil and gray-brown desert soil derived from proluvial gravel materials (China Soil Database, Institute of Soil Science, Chinese Academy of Sciences, 2019, http://vdb3.soil.csdb.cn/). Climatic conditions of this study area were measured continuously and recorded by the Hailisu National Meteorological weather station. The study area has a typical temperate continental monsoon climate, affected by the Mongolian continental high-pressure air mass and characterized by a mean annual temperature of 6.3°C (1971–2018) and a mean annual precipitation of 140 mm (1971–2018; **Figure 1B**). The vegetation is dominated by *Stipa glareosa* P. Smirn., *Peganum harmala* L., and *Allium polyrhizum* Turcz. ex Regel. And *Allium mongolicum*, *Artemisia frigida* Willd., *Convolvulus ammannii* Desr., and *Salsola collina* Pall were found in our study area, but their contribution to total biomass is limited.

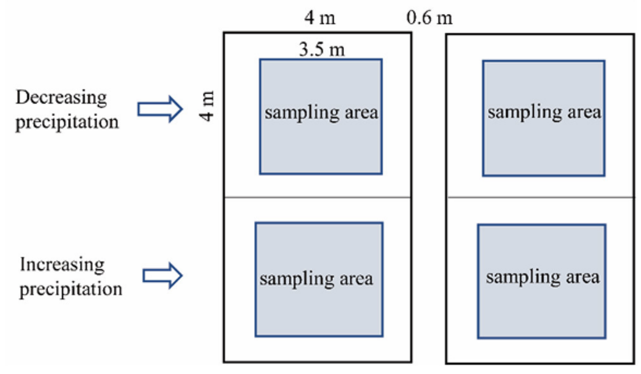

FIGURE 2 | Experimental design.

Experimental Design

The experimental design was implemented at the Urat Desert-Grassland Research Station (**Figure 1A**). In June, 2015, a manipulative, precipitation decrease and increase experiment was established using V-groove collector and drip irrigation distributor (**Figure 1C**). The rainout shelter (decreased precipitation systems) was 1.5 m high, and the V-groove collector was set on stainless-steel support with a 15° inclination. Polycarbonate plastic V-groove collector (nearly 90% penetration of UV radiation) were mounted in stainless-steel structure to collect water to induce precipitation by −60, −40, and −20%. A drip irrigation distributor consisting of stainless-steel containers in front of the V-grooves was connected to PVC pipes with holes to evenly distribute water that increased precipitation by +60, +40, and +20% (**Figure 1C**). The V-groove collector and drip irrigation distributor separately covered 16 m^2 (4 × 4 m) and were 0.6 m apart. The experiment was randomized complete block design, with six replications for each treatment (**Figure 2**). The control plots without shelters received natural precipitation. In this manner, we manipulated precipitation with 60% reduction to 60% increment, respectively, relative to the natural precipitation. All the treatments were applied from May 2015, 2 years before measurements. Totally, there were 42 sampling plots, including 6 for treatments and 1 for control. These precipitation levels cover the recorded long-term variability in local precipitation, and forming a precipitation gradient, ranging from extreme drought to high precipitation (**Figure 1B**).

Measurement of Precipitation Amount

Precipitation data were obtained from the weather station of Urat Desert-grassland Research Station (**Figure 1B**). The natural growing season precipitation (from May to September) were 28.8 and 21.4 mm in 2017 and 2018. In 2017, actual precipitations under −60, −40, −20, +20, +40, and +60% treatments during the growing season were 11.52, 17.82, 23.04, 28.8, 34.56, 40.32, 46.08 mm, respectively. In 2018, actual precipitations under −60, −40, −20, +20, +40, and +60% treatments during the growing season were 8.65, 12.84, 17.12, 21.4, 25.68, 29.96, 34.24 mm, respectively.

Community Composition and Plant Diversity

The manipulated experiment was constructed in 2013, and the sampling of this study was carried out in August 2017 and 2018. In 42 plots, plant coverage and height of each species were measured, and the number of individuals was counted.

Based on the collection data of plant coverage, height and numbers, the Shannon-Wiener diversity index and Pielou evenness index were calculated:

Shannon-Wiener diversity index (H):

$$H = -\sum_{i=1}^{S} (N_i \, ln \, N_i)$$

Pielou evenness index (J):

$$J = H/\ln S$$

where Ni is the relative abundance of species i and S is the total number of individuals.

Plant Functional Trait

Plant samples were collected at each site for functional trait measurements in mid-August 2017 and 2018. During the current growing season, several fully matured and healthy leaves were collected from 5 to 10 individuals of the dominant species within each plot to measure leaf functional traits according to standard methodologies (Wu et al., 2016). These traits including plant height, leaf area, specific leaf area (SLA), leaf dry matter content (LDMC), leaf thickness, leaf carbon content (LCC), and leaf nitrogen content (LNC) (Cornelissen et al., 2003), which were determined by an elemental analyzer (Costech ECS 4010, Italy). CWM summarized traits variation data as determined mainly by the dominant species (Valencia et al., 2015).

Response of Species Diversity and Aboveground Biomass to Precipitation Changes

To determine the effect of precipitation changes on community composition, a general linear model was performed with precipitation as an independent variable and community richness, Shannon's diversity index, and Pielou's evenness index as dependent variables. Goodness of fit for regressions was used by comparing their R^2values. The effects of precipitation changes were significant when $p < 0.05$, and analyses were conducted, using the function "lm."

Effect of Precipitation and Year on Functional Traits of Community-Weighted Means and Dominant Species

We calculated the CWM trait value for each plot:

$$\text{CWM trait} = \sum \mathrm{p_i x_i} \tag{1}$$

where CWM trait is the CWM for the x trait and p_i and x_i are the relative coverage and the trait value of species i in the community. CWM represents the community-level trait value and is controlled by the trait values of the dominant species weighted by their coverage for each plant functional trait on the 42 plots separately, using the "dbFD" function in the R package "FD."

We used ANOVA (with pairwise Tukey tests) to compare the CWMs trait distributions in the six precipitation treatments.

Response of CWM Traits

We built linear models of plant functional traits using a Bayesian approach, ranging in complexity from a single term to a two-way interaction with a focus on addressing the question of whether year, precipitation, or year-and-precipitation interactions influence plant functional traits. Thus, three models were run for each CWM trait. In all models, the CWM trait followed a normal distribution:

Plant functional $\text{trait}_\text{i} \sim$ dnorm $(\text{mu}_\text{i}, \text{sigma}_\text{i})$

where mu_i is the trait of each plot or species, sigma_i is the variance, and i is each plot or species. linear models were fitted where the plant functional trait was a function of precipitation, year, or precipitation and year interactions, where mu_i was the plant functional trait of each plot or species, α was the model intercept, b1 was the coefficient of precipitation, b2 was the coefficient of a year, and b3 was the coefficient of precipitation and year interactions.

$$mu_i = a + b1 * precipitation$$
$$mu_i = a + b1 * precipitation + b2 * year$$
$$mu_i = a + b1 * precipitation + b2 * year + b3 * precipitation * year$$

Response of the Dominant Species Traits

The role of species is rarely considered in models that assess the impact of functional traits. We built linear mixed-effects models of growth, using a Bayesian approach, ranging complexity from a single term to having a two-way interaction, with a focus on addressing whether species, year, precipitation, or year-and-precipitation interactions influenced leaf functional traits.

$$mu_j = a_j[spp] + b_j[spp] * precipitation$$
$$mu_j = a_j[spp] + b_j[spp] * precipitation + d_j[spp] * year$$
$$mu_j = a_j[spp] + b_j[spp] * precipitation + d_j\,[spp] * year + z_j[spp] * precipitation * year$$

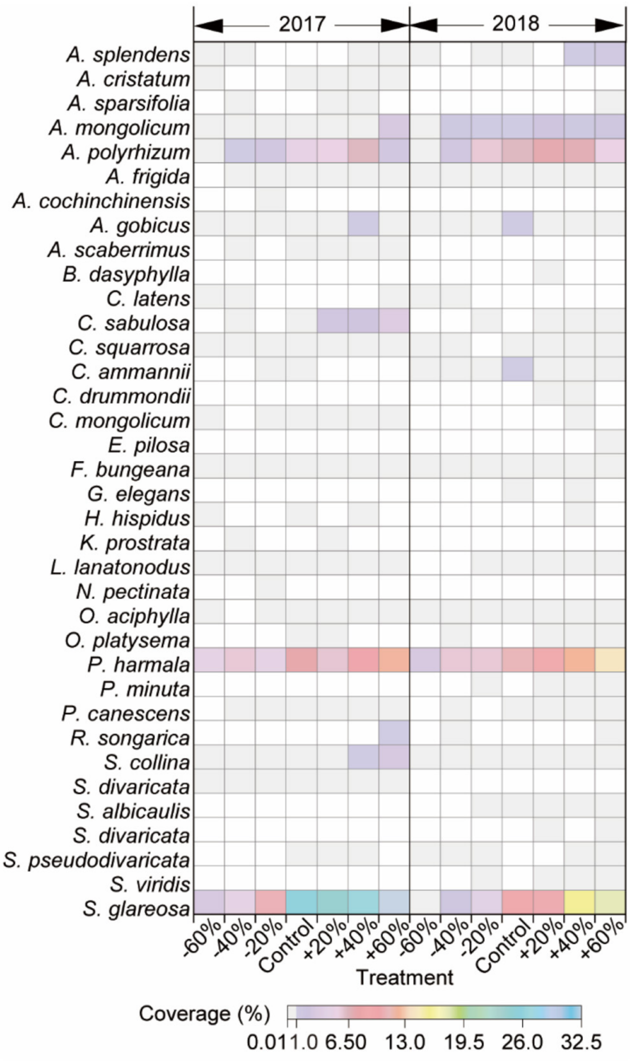

FIGURE 3 | Abundance of 36 species in this study under −60, −40, −20, +20, +40, +60% precipitation treatment, and control in 2017 and 2018. The color of each panel is proportional to the value of abundance.

where mu_j was the leaf functional trait of each species, α_j was the model intercept, [spp] was the random effects of species, b_j was the coefficient of precipitation, d_j was the coefficient of year, and z_j was the coefficient of the precipitation-and-year interaction.

In all models, the CWM trait (mui) and functional trait (muj) were modeled as normally distributed, and the variance hyperparameters were given diffuse gamma priors: N (mean = 0, precision = 0.01). We used the Wantanabe–Akaike information criterion (WAIC). The WAIC is a fully Bayesian information criterion valid for hierarchical models (Hooten and Hobbs, 2015). As with the other model selection criteria, smaller value of WAIC indicates a greater model predictive ability. All analyses were performed in R statistical software, version 3.6.1 (R Development Core Team, 2019).

Causal Relationship of Precipitation, Species Diversity, Plant Functional Traits, and AGB

Structural equation models were employed to analyze the causal relationship of precipitation variables, plant diversity variables, and functional trait, and AGB (a total of 12 variables). To develop the final SEMs, we started with our initial hypothesized relationships among the variables. A Pearson correlation analysis was conducted on plant diversity, precipitation, and functional traits (**Supplementary Tables 6**, **7**). The decision to remove a path was based on the performance of the overall model fit and the p-value for the path. To simplify the SEMs, we first deleted the functional traits with no significant relationship with precipitation and year according to the results of the previous correlation analysis. We did not establish the relationships between functional traits. In addition, we hypothesized that climatic variables would significantly affect plant functional traits in the optimal model. We deleted the correlation between precipitation, year, and plant functional traits when precipitation and year did not significantly affect plant functional traits or if their addition led to a decrease in the best model interpretation. Model evaluation was determined by the chi-square (χ^2) test ($p > 0.05$ for a satisfactory fit) and the standardized root mean square residual (SRMR < 0.05 for a satisfactory fit). The Akaike information criterion (AIC) was used to select the best model with a satisfactory fit. When a model met the criteria of the chi-square test and SRMR but contained non-significant paths in the relationship between precipitation, plant diversity indexes, and functional traits, we repeated the model fitting and evaluation by removing these paths. The total standardized effect that one variable had on another equaled the sum of its standardized direct and indirect effects. Non-significant paths of the relationship between precipitation, plant diversity indexes, and functional traits were not shown. Then we used the same criteria to structure the SEM model to show the causal relationship of precipitation, plant functional traits, and AGB of the dominant species level using the Amos graphics software.

RESULTS

Patterns of Species Composition and Coverage Under Manipulated Precipitation Treatments

About 14 families, 14 genera, and 36 species were collected in this study, and most were perennials. *A. polyrhizum*, *P. harmala*, and *S. glareosa*, with higher coverage relative to others, responded dramatically to precipitation variation and were defined as dominant species (**Figure 3**, **Supplementary Table 5**). Increasing and decreasing precipitation affected species composition. Concretely, *Neopallasia pectinata*, *Kochia prostrata*, *Astragalus scaberrimus*, *Agropyron cristatum*, and *Asparagus cochinchinensis* were present in 2017, and *A. cochinchinensis* and *N. pectinata* were only in plots receiving −20% precipitation alteration. While *Setaria viridis*, *Saposhnikovia divaricata*, *Scorzonera albicaulis*, *Plantago minuta*, *Gypsophila elegan.*, *Coreopsis drummondii*, and

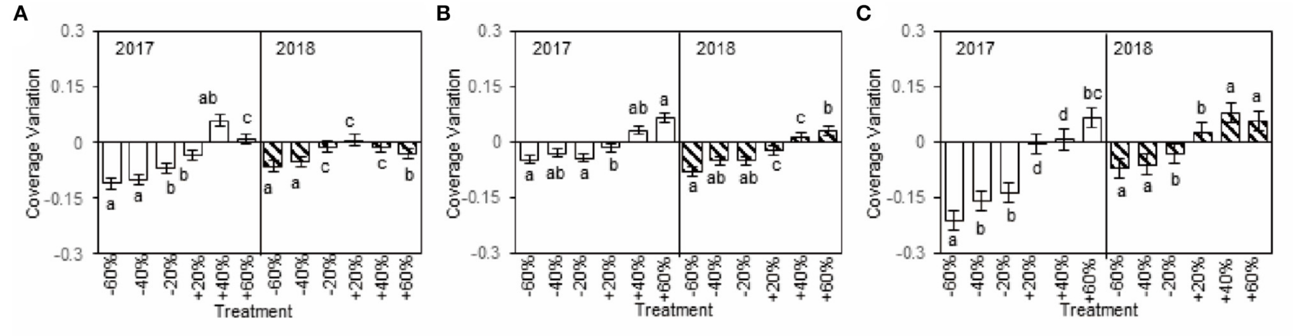

FIGURE 4 | Coverage variations of six precipitation treatments of *A. polyrhizum* **(A)**, *P. harmala* **(B)**, and *S. glareosa* **(C)**, compared to control in 2017 and 2018. The different capital letter indicates significant under difference treatments in 2017 and 2018 at $p < 0.05$ by Duncan test.

Bassia dasyphylla were present in 2018, and *Eragrostis pilosa*, *Bassia dasyphylla*, and *S. divaricata* were only in plots receiving +20, +40, or +60% precipitation alterations (**Figure 3**).

Sensitivity of Dominant Species to Precipitation Change

The sensitivity of dominant species to precipitation changes was reflected by coverage variation in our study. The coverage variations of *A. polyrhizum*, *P. harmala*, and *S. glareosa* were considerable and negative with decreased precipitation, while, under increased precipitation, the variations tended to be positive (+40 and +60% treatments), although this finding was not always the case (+20% treatment, **Figure 4**), and the coverage variation of the three dominant species varied between 2017 and 2018 (**Figures 3**, **4**). Additionally, the coverage variations of dominant species were related to alterations in precipitation intensity. Specifically, in the plots with decreased precipitation, the absolute coverage variation of *A. polyrhizum* reached a maximum under the −60 and −40% precipitation treatment in 2017, *P. harmala* reached a maximum under the −60% precipitation treatment in 2018, and *S. glareosa* reached a maximum under the −60% precipitation treatment in 2017 (**Figure 4**). In the increased precipitation treatments, the absolute coverage variation of *A. polyrhizum* reached a maximum under the +40% precipitation treatment in 2017, *P. harmala* reached a maximum under the +60% precipitation treatment in 2017, and *S. glareosa* reached a maximum under the +40% precipitation treatment in 2018 (**Figure 4**).

Response of Species Diversity Index and AGB to Precipitation Change

Relationship between species richness, Pielou evenness indexes, community AGB, and precipitation were significant (**Figure 5**). Species richness ($R^2 = 0.329$, $p < 0.001$) and community AGB ($R^2 = 0.463$, $p < 0.001$) were positively correlated with increasing precipitation, and Pielou evenness ($R^2 = 0.283$, $p < 0.001$) was negatively associated with increasing precipitation. However, there was no significant effect of precipitation change on Shannon's diversity (**Figure 5**).

Plant Functional Traits Under Precipitation Treatments

Based on linear models by Bayesian approach, we found precipitation amount changes had greater effects (with a greater coefficient) than year on CWM for height, LNC, and LCC, while the year had greater effects (with a greater coefficient) than precipitation amount changes on CWM for SLA and LA (**Figure 6A**). Under different precipitation treatments, significant decrease of the CWM LNC by increasing precipitation was mainly seen in plots receiving +40 and +60% precipitation treatments. And CWMs of height (especially in plots receiving +40 and +60% precipitation treatment), LA, LDMC (especially in plot receiving +60% precipitation treatment), and LCC (+60% treatment) increased with increasing precipitation. The CWMs of LA, SLA, and LNC were higher in 2018 than in 2017, involving all precipitation treatment (**Figures 6**, **7**, **Supplementary Tables 1**, **2**). For three dominant species, effects of precipitation and year on the leaf functional traits of species were species-specific. Response of height, leaf thickness (LT), LDMC, LNC of *A. polyrhizum*, height of *P. harmala*, and height, SLA, LDMC, LNC, and LCC of *S. glareosa* to precipitation were significant. Significant responses of functional traits of three dominant species to year and precipitation and year interaction were mainly shown in LT, LA, SLA, LDMC, LNC (lowest AIC, **Figures 6B–D**, **Supplementary Tables 3**, **4**, **8**).

Relationships Among Precipitation, Plant Functional Traits and AGB

In final SEM ($p = 0.102$, df = 17, $\chi^2 = 24.691$, GFI = 0.949, RMSEA = 0.071, AIC = 122.691, **Figures 8A1,A2**, **Supplementary Table 9**) for predicting the direct and indirect effects of precipitation and year changes on aboveground biomass of community. Precipitation ($\beta = 0.622$, a standardized coefficient) had an indirect effect on AGB of a community through CWM of height (0.318), LA (−0.279), LDMC (0.351). Precipitation had positive directive effects on height (0.58), LA (0.439), LDMC (0.281), whereas a year had a negative direct effect on LA (−0.689) and had a positive direct effect on LDMC (0.29). The total variance in AGB explained by these variables was close to 59.5%. These results implied that a variation in height,

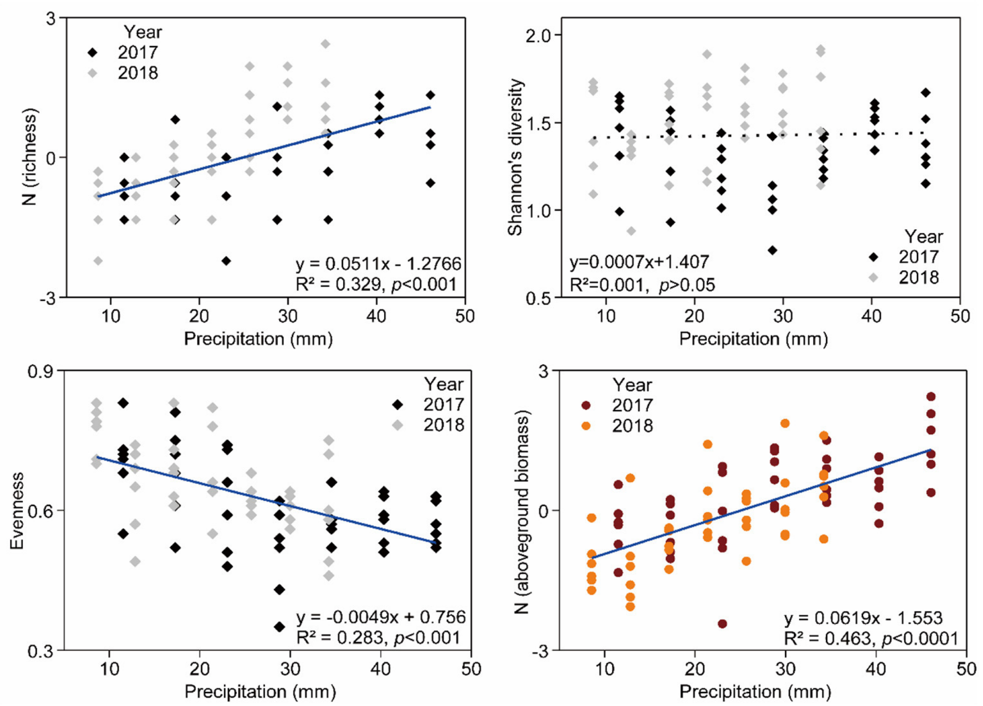

FIGURE 5 | General linear regression analysis for richness, Shannon's diversity, evenness, aboveground biomass, and precipitation amount. Details of the fitted models are given within each panel.

LA, LDMC due to precipitation and year changes resulted in an increase in AGB.

The AGB of *A. polyrhizum* was, however, driven by height owing to precipitation and year changes (p = 0.537, df = 11, χ^2 = 9.921, GFI = 0.952, RMSEA = 0.000, AIC = 59.921, **Figures 8B1,B2**, **Supplementary Table 10**). For *P. harmala* (p = 0.341, df = 13, χ^2 = 14.482, GFI = 0.953, RMSEA = 0.04, AIC = 60.482, **Figures 8C1,C2**, **Supplementary Table 11**) and *S. glareosa* (p = 0.481, df = 16, χ^2 = 15.607, GFI = 0.954, RMSEA = 0.000, AIC = 93.607, **Figures 8D1,D2**, **Supplementary Table 12**), precipitation and a year had significant effects on AGB through height and LA.

DISCUSSION

Precipitation Treatments Changed Community Composition and Species Diversity

We found a positive linear relationship between species richness and precipitation, implying that precipitation change influenced community composition. *E. pilosa* and *A. polyrhizum* were found to be more abundant in plots receiving increased precipitation in our study, which was characterized by rapid growth and low water-use efficiency (Blumenthal et al., 2020). Enhanced water availability contributed to the germination of dormant seeds or vegetation tissue of these species (Finch Savage and Leubner Metzger, 2006), plant photosynthesis and respiration (Huxman et al., 2004), further promoting growth and reproduction (Huang et al., 2018), consequently regulating community composition and species richness (Walck et al., 2011). *A. polyrhizum*, *P. harmala*, and *S. glareosa*, with higher coverage, responded to precipitation changes dramatically. A remarkable increase in dominant species abundance resulted in the increased dominance of these three species while the dominance of rare species decreased, explaining the negative linear relationship between evenness and precipitation. However, there is no significant effect of precipitation change on Shannon's diversity index, this may relate to condition-type specific (Thuiller et al., 2005; Irl et al., 2015). For example, a study in the Great Plains of USA (Byrne et al., 2017) reported that a positive linear relationship between precipitation and Shannon's diversity in shortgrass steppe and a negative relationship in a mixed grass prairie. In addition, in tropic forests and savannas, negative or unimodal patterns were found in species' or communities' responses to increasing precipitation and the relationship was amplified by biological and abiotic processes (Givnish, 1999). Hence, the effect of climatic factors on species diversity needs to be further explored in different ecosystem types.

Plant Functional Traits Were Altered by Precipitation Treatments and Year Variation

The present study indicated that CWMs of plant height, LA, LDMC, and LCC increased, and LNC decreased with increasing precipitation, which supported the leaf economics spectrum (Wright et al., 2004), indicating higher acquisition and turnover of resources in plants with increasing water availability

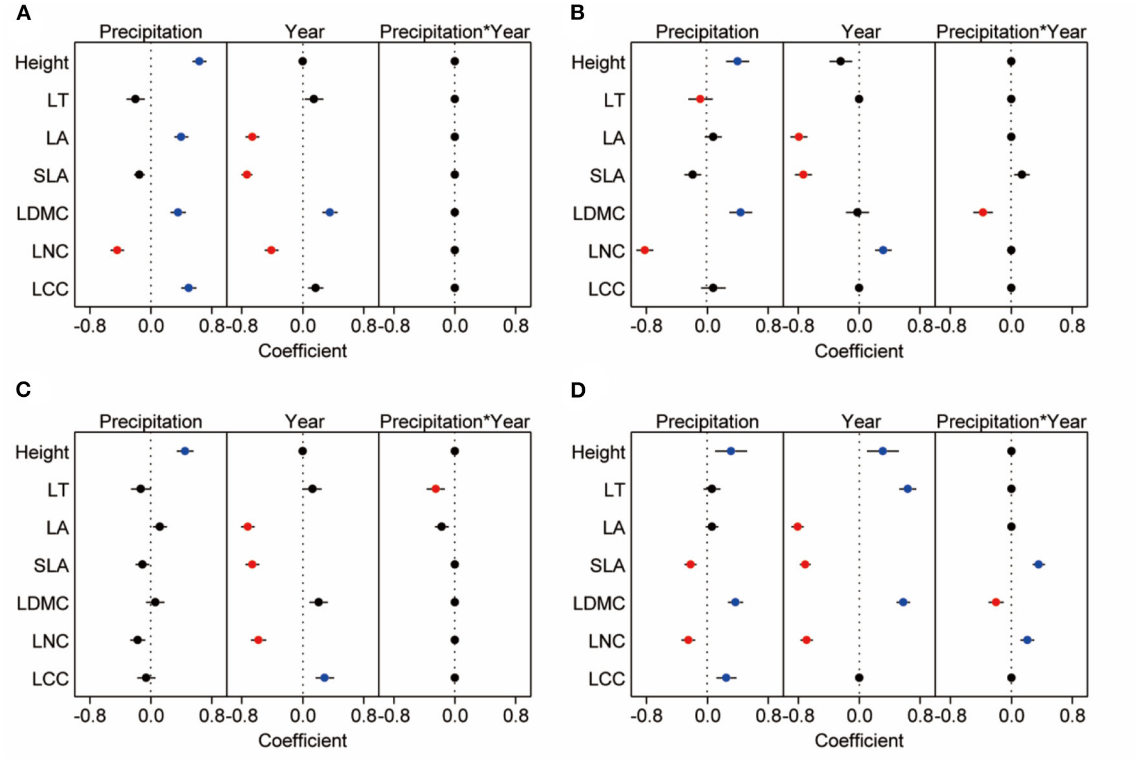

FIGURE 6 | The best model of community-weight means **(A)** and dominant species (*S. glareosa*, **B**; *P. harmala*, **C**; and *A. polyrhizum*, **D**) traits response to precipitation, year and precipitation*year. We extract the best from three possible Bayesian models, each row represents the model of traits, which are influenced by precipitation, year and precipitation*year. Blue dots indicate significant and positive response, red dots indicate significant and negative response, and black dots indicate non-significant or no response.

(Wright et al., 2004). Plant height is supposed to be a central part of the plant ecological strategy from our study and other previous studies (Westoby, 1998; Falster and Westoby, 2003; Moles et al., 2009; De Frenne et al., 2011). Moles et al. (2009) reported a remarkably tight relationship between latitude and height, pointing out that plant height was strongly correlated with a life span, seed mass, and time to maturity. With an increase in precipitation, the photosynthetic rate was promoted by increasing the leaf area, and more biomass accumulated in a short time (Wright et al., 2001; Barker et al., 2006; Wilcox et al., 2021). Increased precipitation should cause a pronounced shift toward communities with taller plants and with more resource acquisition and storage leaves (high LA, LDMC, and LCC). These relationships underline the potential importance of plant stature for growth, survival, and adaptation, and they may influence ecosystem dynamics and services during climate or condition changes (Lv et al., 2019). Furthermore, LA, SLA, LDMC, and LNC, "growth investment" traits changed greatly by year (Schellenberger Costa et al., 2018), as shown by greater CWMs for "fast" traits during wet years (Poorter and Bongers, 2006; Reich, 2014) and greater values for LDMC related to more tolerance during dry years (Markesteijn et al., 2011).

Additionally, we found that the extent of plant functional trait responses to precipitation changes varies with species type, implying the different adaptive and resource-use strategies of the three species (Reich et al., 2003; Fort et al., 2013). *A. polyrhizum* exhibited significant responses to precipitation changes in six of the seven traits (except for LCC), which was more sensitive to short-term precipitation changes (precipitation treatments) with greater height and LDMC, thinner thickness, and lower LNC to increased precipitation, which is related to a fast-growth strategy and fast resource acquisition (Reich, 2014). *P. harmala* was more tolerant to precipitation changes (Ahmed and Khan, 2010), with five significant traits (except for LT and LDMC). We believe that *S. glareosa* showed greater fitness by regulating more leaf traits (seven traits) when subjected to environmental stress or habitat change, which is related to its slow-growth strategy and slow resource acquisition.

Precipitation and Year Regulated AGB *via* Plant Functional Traits

Our study explains the pathway of precipitation effect on AGB in dryland. SEM analyses demonstrated that the patterns of CWMs for height, LA, and LDMC altered by the precipitation treatment and a year were strongly related to AGB. These results are in line with those of other studies that showed that CWMs have an important consequence for ecosystem

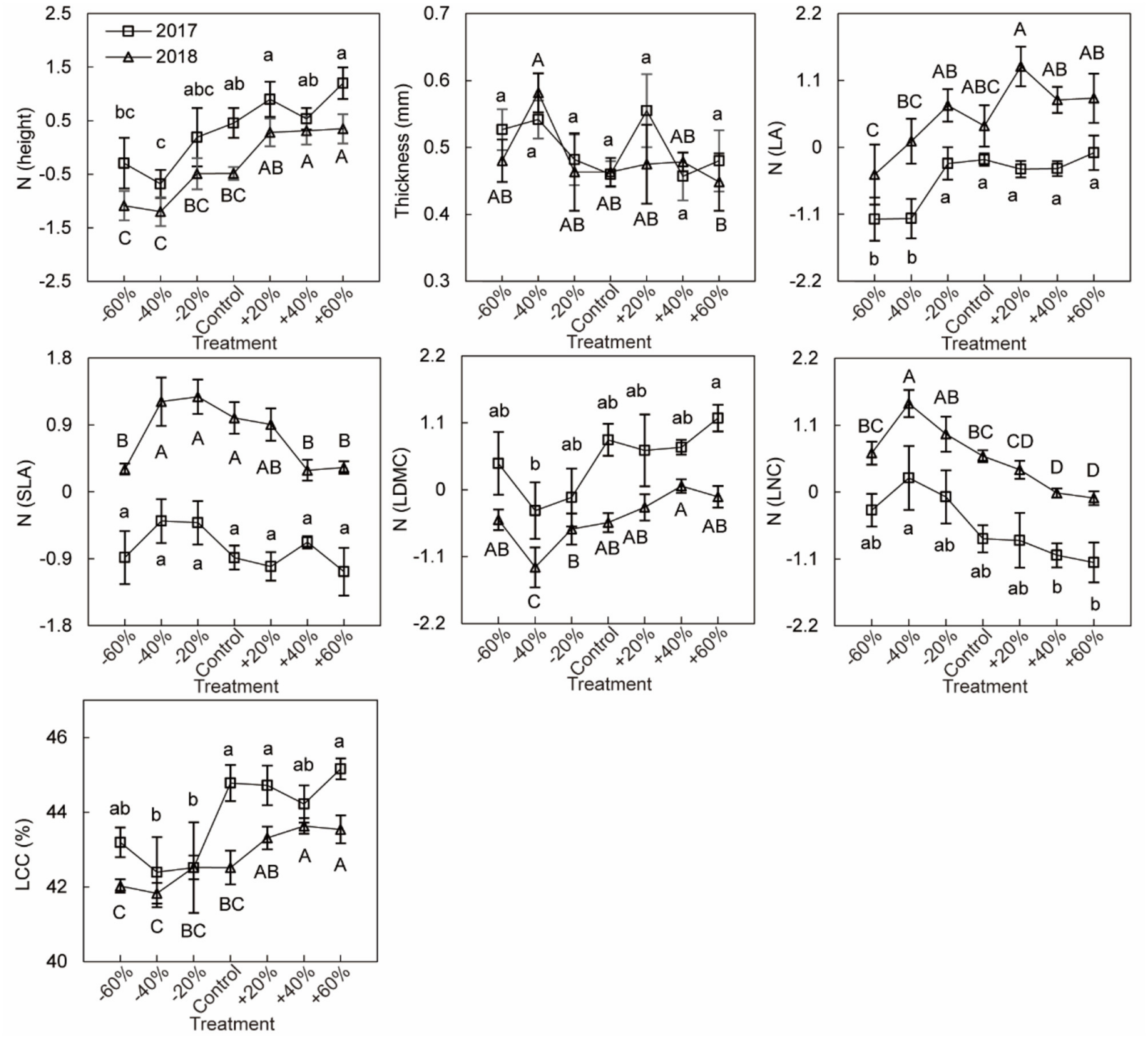

FIGURE 7 | Community-weight mean leaf traits under six precipitation treatments (−60, −40, −20, +20, +40, +60%) and control. Values represent means ± standard errors ($n = 6$). The different lowercase letters indicate significant difference in 2017 at $p < 0.05$ by Duncan test. The different capital letters indicate significant difference in 2018 at $p < 0.05$ by Duncan test.

functioning along environment gradient (Diaz et al., 2007; Roscher et al., 2012; Chiang et al., 2016; Cadotte, 2017). Van'T Veen et al. (2020) suggested that temperature and precipitation explained additional 22.1% of the variation in productivity, and that functional trait composition was an important predictor of grassland productivity in Switzerland grasslands. Combining previous studies, we believe that leaf functional traits (except for LT) are good response traits to precipitation change at the community level (Gross et al., 2008; Suding et al., 2008; Sterk et al., 2013). While the altered AGB results from direct effects of precipitation change on the part of response traits (plant height, LA, and LDMC).

An investigation of how traits of dominant species respond to precipitation changes and how they influence AGB can help understand the role of species in ecosystem dynamics and resource-use strategies (Lawton, 1994; Smith and Knapp, 2003; Sinclair and Byrom, 2006). In this study, the response of the plant height of *A. polyrhizum* to short-term precipitation changes affected AGB, supporting Hu et al. (2019). The shallow-root system, large mesophyll cells, and chloroplasts of *A. polyrhizum* promoted the utilization of surface soil water and provided the foundation for the high photosynthetic rate under conditions of sufficient water supply (Ivanov et al., 2004; Hu et al., 2019). Thus, *A. polyrhizum* was defined as an opportunist in our study and

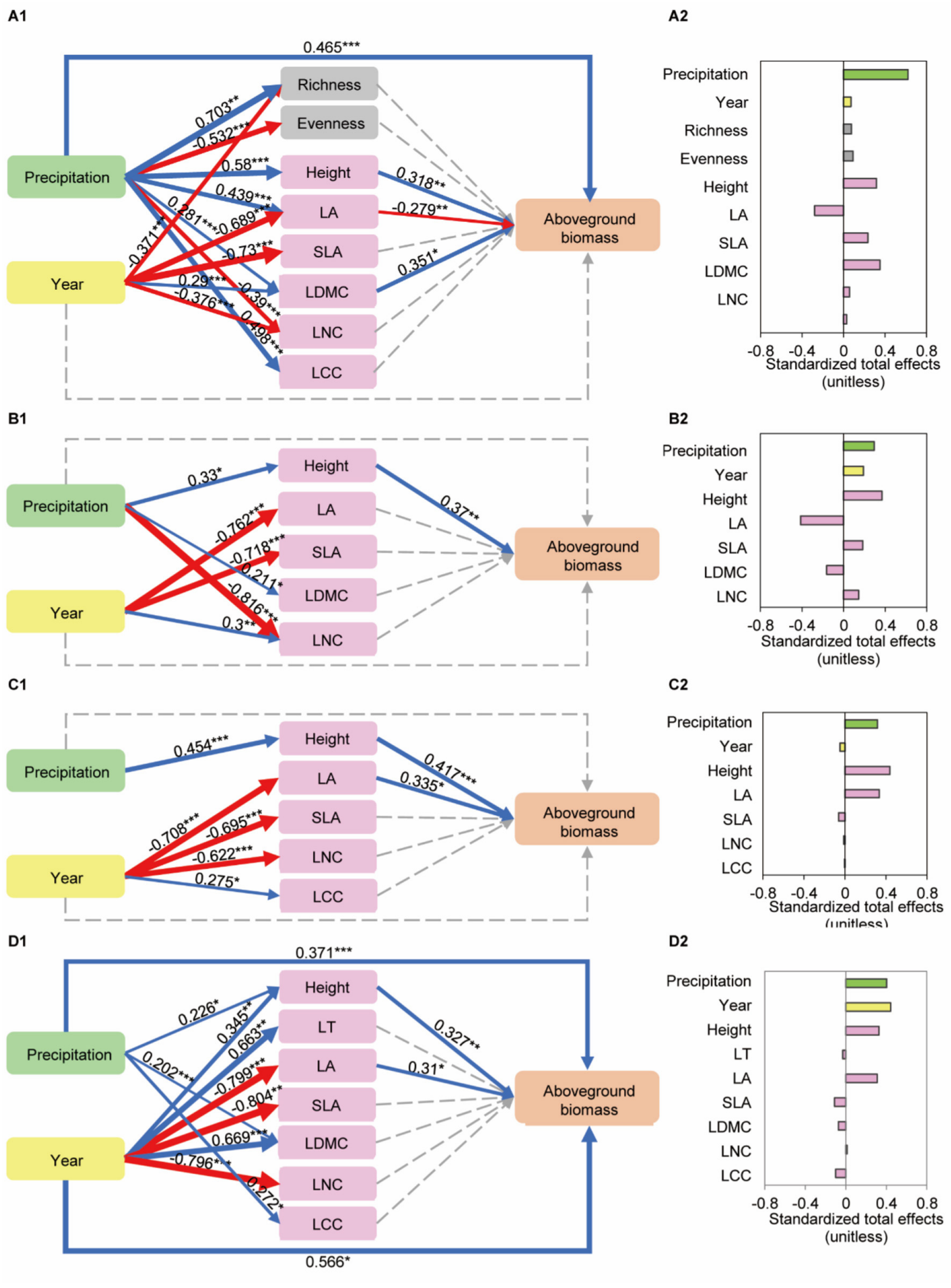

FIGURE 8 | Structural equation models (SEM) of the effects of precipitation and year on aboveground biomass of a community and three dominant species. **(A1)** CWM leaf traits: $p = 0.102$, df = 17, $\chi^2 = 24.691$, GFI = 0.949, RMSEA = 0.071, AIC = 122.691. **(A2)** Total standardized effects from the SEM of precipitation and year on community aboveground biomass. **(B1)** *A. polyrhizum*: $p = 0.537$, df = 11, $\chi^2 = 9.921$, GFI = 0.952, RMSEA = 0.000, AIC = 59.921. **(B2)** Total standardized effects from the SEM of precipitation and year on aboveground biomass of *A. polyrhizum*. **(C1)** *P. harmala*: $p = 0.341$, df = 13, $\chi^2 = 14.482$, GFI = 0.953,

(Continued)

FIGURE 8 | RMSEA = 0.04, AIC = 60.482. **(C2)** Total standardized effects from the SEM of precipitation and year on aboveground biomass of *P. harmala*. **(D1)** *S. glareosa*: $p = 0.481$, df = 16, $\chi^2 = 15.607$, GFI = 0.954, RMSEA = 0.000, AIC = 93.607. **(D2)** Total standardized effects from the SEM of precipitation and year on aboveground biomass of *S. glareosa*. The blue and red arrows represent significant positive and negative pathways, the gray dashed arrows represent no significant pathways, respectively. Numbers adjacent to the arrows are standardized path coefficients, analogous to relative regression weights and indicative of the effect size of the relation. The thickness of the arrows is proportional to the magnitude of the standardized path coefficient s. The arrow width is proportional to the strength of the relationship.

was characterized by fast growth in height within a short time, high water content in its leaves, and low water-use efficiency (Blumenthal et al., 2020). The response and adaptation strategies of *P. harmala* and *S. glareosa* were different from those of *A. polyrhizum*. Precipitation and annual changes affected AGB *via* height and LA in *P. harmala* and *S. glareosa*; they developed a great number of cells and chloroplasts in its leaves and a large leaf assimilation surface that provided greater photosynthetic rates and higher efficiency of water use (Ivanov et al., 2004; Baiakhmetov et al., 2020), resulting in a higher capacity for carbon storage and more fitness under water limitation. Overall, *P. harmala* and *S. glareosa* with more fitness and tolerance, are key species for maintaining ecosystem stability in this study (Richmond et al., 2005; Brotherton and Joyce, 2015), helping the ecosystem withstand disturbance, such as drought.

CONCLUSION

Our results suggested the significant responses of species diversity and plant functional traits were found when water deficiency was alleviated along a precipitation gradient. The structural equation models demonstrated that precipitation change in amount and year has a direct effect on richness, evenness, and CWM for height, LA, SLA, DLMC, LNC and LCC, and AGB; there into, CWM for height and LDMC had a direct positive effect on AGB; LA had a direct negative effect on AGB. For dominant species, *A. polyrhizum* showed an increase in height under the precipitation treatments that promoted AGB, whereas the AGB of *P. harmala* and *S. glareosa* was boosted through alterations in height and LA. In summary, changes in precipitation amount affected plant AGB through leaf functional traits (height, LA, LDMC) rather than species diversity. We supposed that plant height, LA, LDMC are likely candidate traits, given they are mechanistically linked to precipitation changes and affected aboveground biomass in desert-steppe. And the adaptation and resource utilization strategies in response to precipitation changes are species-specific.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

HC and YG conceived the idea and wrote most of the manuscript. XZ contributed to part of writing and overall improvement of the manuscript. All authors read and approved the manuscript.

FUNDING

This study was funded by the National Natural Science Foundation of China (42071140 and 41622103).

ACKNOWLEDGMENTS

We thank Dr. Nathan G. Swenson and Dr. Qianfeng Wang for advice on data analysis, and the members of the Urat Desert-grassland Research Station and Inner Mongolia Grassland Ecosystem Research Station (IMGERS) for their assistance in the experimental setup and data collection, as well as Sujun Liu for English language editing. We also thank the editors and peer reviewers for their insightful comments and suggestions.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2021.674527/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Plant Science

ORIGINAL RESEARCH
published: 21 February 2022
doi: 10.3389/fpls.2022.830856

Small Semi-Fossorial Herbivores Affect the Allocation of Above- and Below-Ground Plant Biomass in Alpine Meadows

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Specialty section:
This article was submitted to Functional Plant Ecology, a section of the journal Frontiers in Plant Science

Received: *07 December 2021*
Accepted: *18 January 2022*
Published: *21 February 2022*

Citation:
Wang Q, Pang XP and Guo ZG (2022) Small Semi-Fossorial Herbivores Affect the Allocation of Above- and Below-Ground Plant Biomass in Alpine Meadows. Front. Plant Sci. 13:830856. doi: 10.3389/fpls.2022.830856

Small semi-fossorial herbivores can affect plant aboveground biomass (AGB) in grasslands and possibly alter the allocation of AGB and belowground biomass (BGB). In this study, plateau pika (*Ochotona curzoniae*) was used to investigate such effects at three alpine meadow sites on the Eastern Tibetan Plateau, where pairs of disturbed vs. undisturbed plots were randomly selected and sampled. We also explored the relationships between soil properties and BGB/AGB across the plots in the presence and absence of plateau pikas, respectively. We found that BGB and BGB/AGB were 11.40 and 8.20% lower in the presence of plateau pikas than in their absence, respectively. We also found that the BGB/AGB was positively related to soil moisture and soil total nitrogen (STN) in the absence of plateau pikas. In contrast, BGB/AGB was positively related to STN, soil organic carbon (SOC), soil carbon/nitrogen (C/N), and soil total phosphorus in the presence of plateau pikas. These factors indicated plateau pika disturbance increased AGB allocation. The relationship between AGB and BGB of alpine meadow plants to soil variables was also different between sites with and without plateau pika disturbance. In conclusion, small semi-fossorial herbivore disturbance is likely to alter grassland carbon stock and should be well controlled for sustainable conservation and management of alpine meadows on the Tibetan Plateau.

Keywords: alpine meadow, biomass allocation, plateau pika, small semi-fossorial herbivore, soil properties

INTRODUCTION

The allocation of aboveground biomass (AGB) and belowground biomass (BGB) is widely used to characterize the carbon pool dynamics of grassland ecosystems (Pausch and Kuzyakov, 2018; Yang et al., 2018), which is closely related to temperature, precipitation, soil properties, and biotic factors (Patty et al., 2010; Gong et al., 2015). However, it is still unclear how herbivores affect plant biomass allocation, especially for alpine meadows of high elevations.

Herbivores are important biotic factors that can affect the allocation of AGB and BGB in grasslands (Frank et al., 2002; Zeng et al., 2015; Sun et al., 2018). Large grazing herbivores have been found to increase (Frank et al., 2002; Zeng et al., 2015; Sun et al., 2018) or decrease (Gao et al., 2008; Gong et al., 2015) the ratio of BGB to AGB. Furthermore, total soil bulk density (SBD) (Abaye et al., 1997) and soil nutrients (Sun et al., 2018) can regulate the allocation of AGB and BGB in the presence of large herbivores, which is mainly related to the fact that grazing grasslands and non-grazing grasslands experience the same temperature and precipitation levels in a given study area (Sun and Wang, 2016). In addition to the large grazing herbivores, numerous small semi-fossorial herbivores are underappreciated. These small semi-fossorial herbivores are key functional components in grassland ecosystems (Davidson et al., 2012; Davies et al., 2019; Smith et al., 2019; Cui et al., 2020) and often create extensive disturbances to vegetation and soil (Davidson et al., 2012; Wilson and Smith, 2015). Previous studies have shown that the presence of small semi-fossorial herbivores can decrease (Poe et al., 2019; Cui et al., 2020), increase (Root-Bernstein and Ebensperger, 2013; Galiano et al., 2014), or have no impact on plant AGB (Pang et al., 2020a). For example, higher population densities of small semi-fossorial herbivores decrease plant BGB (Sun et al., 2015; Liu et al., 2017). Therefore, small semi-fossorial herbivores might modify the allocation of AGB and BGB through their effect on aboveground and belowground interactions (Gao et al., 2008; Deyn, 2017).

Small semi-fossorial herbivores can affect soil properties by burrowing tunnels (Nicod et al., 2020; Andersen et al., 2021), excreting feces and urine (Clark et al., 2016; Cui et al., 2020; Zhang et al., 2020), and redistributing the soil (Davidson et al., 2012; Guo et al., 2012; Pang et al., 2020a). Previous studies have shown that small semi-fossorial herbivores can decrease SBD (Dobson et al., 1998; Wilson and Smith, 2015) and soil moisture (Pang and Guo, 2017) and increase the soil nitrogen concentration (Liu et al., 2013; Yu et al., 2017a; Mallen-Cooper et al., 2019; Cui et al., 2020) and soil organic carbon (SOC) (Clark et al., 2016; Pang et al., 2019) in grasslands. The changes in soil carbon and nitrogen concentrations caused by small semi-fossorial herbivores can affect plant biomass (Yang et al., 2021), which is ultimately determined by the plant community and soil (Patty et al., 2010; Gong et al., 2015; Prommer et al., 2020). Thus, small semi-fossorial herbivores may indirectly affect the allocation of AGB and BGB. However, the effects of disturbance by small semi-fossorial herbivores on the allocation of AGB and BGB in grasslands are not well documented.

Plateau pika (*Ochotona curzoniae*) is a small semi-fossorial herbivore that is philopatric (Dobson et al., 1998), prefers open-vegetation habitats, and lives in family groups (Smith et al., 2019; Wang et al., 2020). Plateau pika families of various sizes often live together within their home range (Fan et al., 1999; Smith et al., 2019) and are distributed patchily in grasslands (Pang et al., 2020b). Open-vegetation habitats free of plateau pikas are considered potentially suitable areas (Li et al., 2021), and the diffusion of plateau pikas through the landscape is a gradual process (Pang et al., 2020b). Disturbance by plateau pikas decreases (Liu et al., 2013) or has no impact on the plant AGB (Pang et al., 2020a) in their home range compared with areas lacking plateau pikas. Disturbance by plateau pikas also decreases SBD (Yu et al., 2017b) and soil moisture (Pang and Guo, 2017; Wang et al., 2018) and increases the soil nitrogen concentration (Qin et al., 2019) and phosphorus concentration (Yu et al., 2017b; Pang et al., 2021). Plateau pikas inhabit alpine meadows varying in dominant plants, topography, soil type, and climate on the Qinghai-Tibetan Plateau (Guo et al., 2012; Smith et al., 2019; Wang et al., 2020). Therefore, data from a single site are insufficient for inferring how disturbance by plateau pikas, coupled with environmental factors, affects the ratio of BGB to AGB (Li et al., 2021). Data from multiple sites with similar environmental conditions with and without pikas are needed to evaluate the general effect of pika disturbance on the allocation of AGB and BGB. In this study, the effect of plateau pikas on the allocation of AGB and BGB in three sites was examined. Specifically, a hypothesis-based structural equation model was used to determine whether and how disturbance by plateau pikas affects the ratio of BGB to AGB. The results of this study enhance our understanding of the effect of small semi-fossorial herbivore disturbance on grassland ecosystem carbon cycling.

MATERIALS AND METHODS

Study Sites

Plots for plant biomass and soil sampling were established at three different sites on the Qinghai-Tibetan Plateau in Gonghe County (35.5°–37.2°N, 99°–101.5°E), Gangcha County (36.9°–38°N, 99.3°–100.6°E), and Luqu County (34°–34.8°N, 101.6°–103°E). The elevations of the three sites were 3,750, 3,265, and 3,505 m; the average annual precipitation was 400, 572.3, and 644 mm; and the average annual temperature was 4.1, 0.89, and 3.16°C, respectively. According to the Chinese Soil Classification System (Gong et al., 2007), the soils of these sites are alpine meadow soils. The alpine meadow at the three sites is divided into warm and cold grazing areas; the cold grazing areas were fenced from mid-April to early October, and these fences were opened for grazing by Tibetan sheep and yak from late October to early April. The dominant plants in the alpine meadows were *Kobresia humilis, K. pygmaea,* and *K. humilis* at the Luqu, Gonghe, and Gangcha sites, respectively. Although there were many small herbivores at the three sites, plateau pikas were the only small semi-fossorial herbivores in the survey areas at each site.

Experimental Design

Field surveys at each site were conducted in the cold grazing areas of the alpine meadows. A random stratified and paired design was used to establish plots at each site. The plot size was 35 m × 35 m, which was close to the size of the average home range of plateau pikas (1,262.5 m^2; Fan et al., 1999). First, 10 disturbed plots in which plateau pikas or active burrow entrances were present were selected along the driving route at each site, and the distance between these disturbed plots ranged from 5 to 10 km. Second, a paired undisturbed plot in which plateau pikas and active burrowing entrances were absent was selected for each disturbed plot, and the distance between each disturbed plot and its paired undisturbed plot ranged from 500 to 1,000 m. Thus, the undisturbed plot experienced the same environmental conditions, including temperature, precipitation, and topography, as its paired disturbed plot. The movement of plateau pikas might affect the undisturbed plot if the distance between the paired plots was close; however, the vegetation and topography might differ between paired plots when the

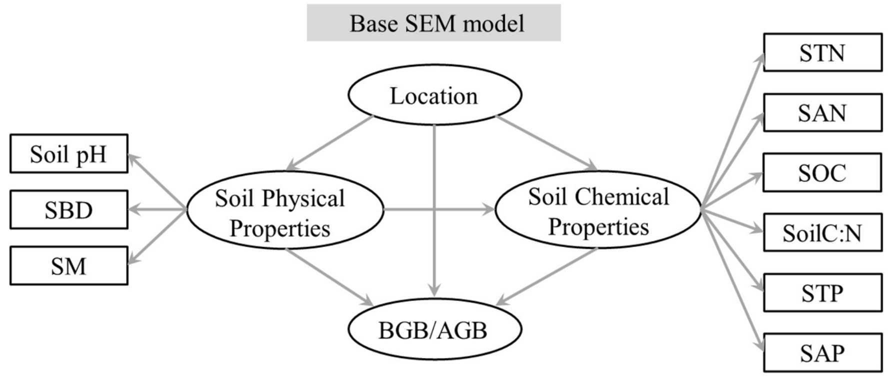

FIGURE 1 | Graphical representation of the hypothesis-based structural equation model of site and soil properties on BGB/AGB. Significant variables were included to predict BGB/AGB. AGB, aboveground biomass; BGB, belowground biomass.

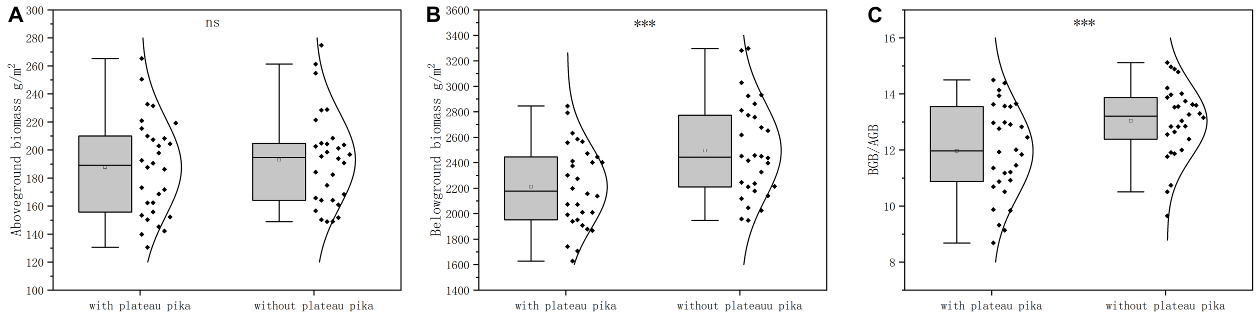

FIGURE 2 | The **(A)** plant AGB, **(B)** BGB, and **(C)** ratio of BGB and AGB in the presence and absence of plateau pikas across three sites. The statistics were from the linear mixed model, in which the three sites (site) and disturbance by plateau pikas (Dist.) were fixed effects, and paired plots nested within the site were a random effect. The quadrilateral points in the box represent the average of variables in the presence and absence of plateau pikas. *Significant differences at $p < 0.05$, **$p < 0.01$, ***$p < 0.001$, ns $p > 0.05$.

distance is large. There was a total of 10 paired plots at each site and 60 plots across the three sites, including 30 disturbed plots and 30 undisturbed plots. Grazing management, including the stocking rate of yaks, was the same for each paired plot in the cold season. In this experimental design, the stocking rate of yaks varied among the 30 paired plots, which permitted the general pattern relating to the effect of plateau pika disturbance on the allocation of AGB and BGB to be determined. In addition, the disturbance intensity by plateau pikas varied among the 30 disturbed plots (which was similar to variation in the degree of degradation of alpine meadows), which permitted the general pattern relating to the effects of plateau pika disturbance on the allocation of AGB and BGB to be determined.

Field Survey

The field survey was conducted during early August 2017, as this coincides with the peak in the plateau pika population (Davidson et al., 2012; Pang et al., 2019) and thus the level of disturbance. There were five subplots (1 m × 1 m) in each plot that was arranged in a "W" distribution pattern. Although there were many kinds of bare soil patches in alpine meadows, the bare soil patches caused by plateau pikas were easily visible and differed from signs of disturbance caused by other factors (Yu et al., 2017a). Thus, the placement of subplots in the disturbed plots was altered slightly to prevent bare soil patches created by plateau pikas from falling within them. The distance between each subplot was greater than 8 m. In each subplot, plant shoots were harvested by hand at ground level, and soil moisture (SM) was measured using a time-domain reflectometer with five replicates. The plant root system was mainly distributed in the 0–20 cm layer in the alpine meadow, which accounted for approximately 85% of the total BGB (Li et al., 2011b; Xu et al., 2016). Therefore, an auger with a 10 cm diameter was used to collect soil cores in the 0–20 cm layer in the center of each subplot, and this soil core was used to measure the BGB. The soil profile was used to sample 500 g of fresh soil to measure soil pH, SOC, soil available nitrogen (SAN), soil total nitrogen (STN), soil available phosphorus (SAP), and soil total phosphorus (STP). A cutting ring (100 cm^3, 50.46 mm diameter × 52 mm height) was used to collect soil samples for the measurement of SBD. The plant shoots, soil cores, and soil samples were stored at 4°C.

In the laboratory, plant shoots were dried at 80°C in an oven to a constant weight and weighed to calculate the AGB. Soil cores were placed into 0.45-mm mesh filter gauze

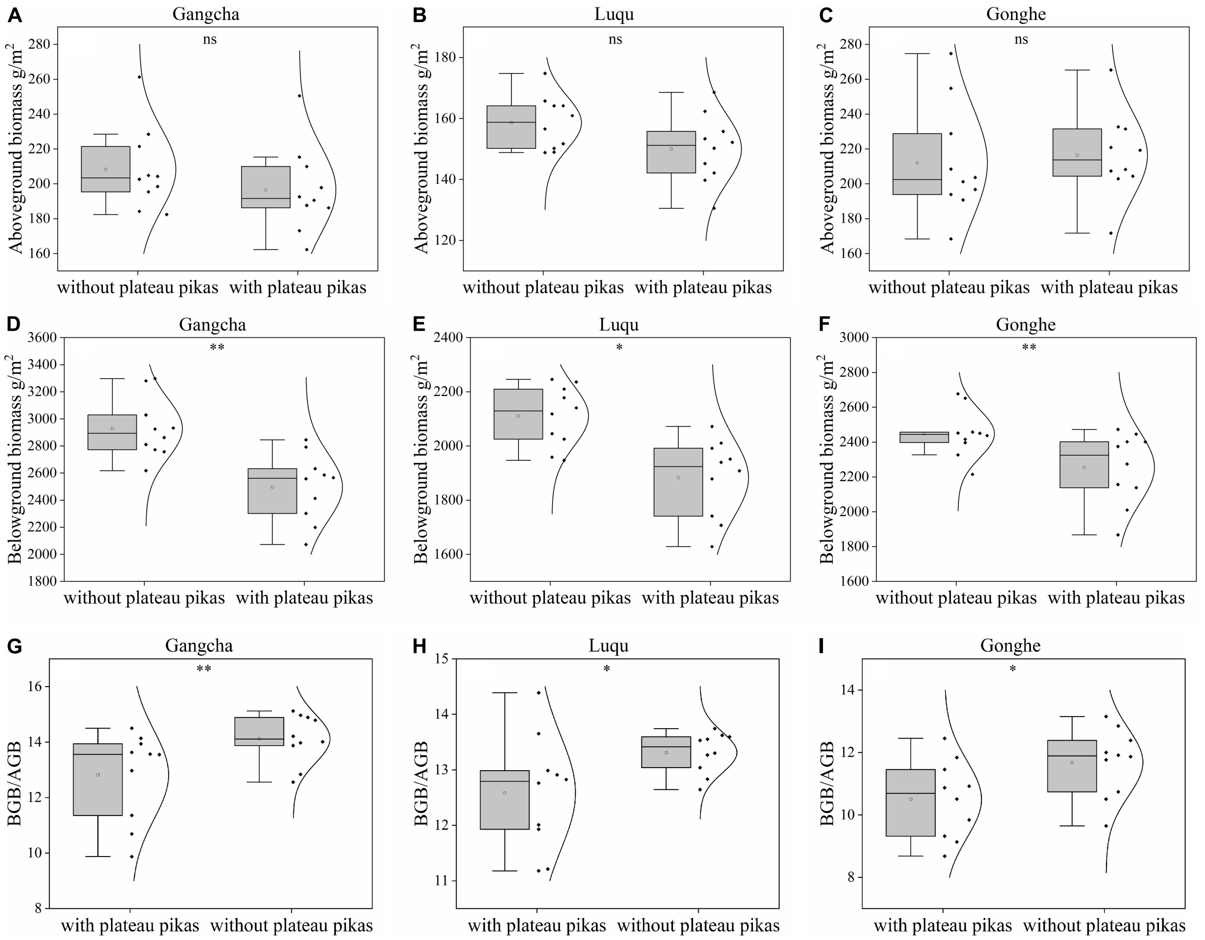

FIGURE 3 | AGB, BGB, and ratio of BGB and AGB in the presence and absence of disturbance by plateau pikas at Gangcha (**A**: AGB, **D**: BGB, **G**: BGB/AGB), Gonghe (**B**: AGB, **E**: BGB, **H**: BGB/AGB), and Luqu (**C**: AGB, **F**: BGB, **I**: BGB/AGB). *Significant differences at $p < 0.05$, **$p < 0.01$, ***$p < 0.001$, ns $p > 0.05$.

bags to collect the BGB by washing. For each soil core, fresh roots were divided into live roots and dead roots by color, consistency, and presence of attached fine roots (Yang et al., 2009; Xu et al., 2016), and the live roots were dried at 80°C to a constant weight to estimate BGB. Soil samples for measuring the SBD were dried at 80°C to a constant weight. The soil samples were air-dried and passed through a 2-mm sieve to remove gravel and roots for measurements of soil pH, SOC, SAN, and SAP and passed through a 0.15-mm sieve to remove gravel and roots for measurements of STN and STP. The soil pH was measured with an acidimeter (PHSJ-6 L, REX, China). SOC was measured using the Walkley (1947) method. Soil nitrate nitrogen (NH_4^+-N) and ammonium nitrogen (NO_3^--N) were extracted with potassium chloride (KCl, 2 mol L^{-1}), and their concentrations were measured using the flow injection method (FIA star 5000 Analyzer, FOSS, Denmark). STN was measured using the Kjeldahl method (Foss Kjeltec 8400, FOSS, Denmark). STP and SAP were analyzed using inductively coupled plasma spectrometers (UV-2102 PCS, China). SAN was the sum of the NH_4^+-N and NO_3^--N concentrations.

The AGB, BGB, BGB/AGB, SM, soil pH, SBD, SOC, STN, SAN, STP, and SAP data for each plot were generated by pooling the values of these variables for each of the five subplots. Soil carbon/nitrogen (C:N) for each plot was the average SOC/STN of the five subplots.

Statistical Analyses

We first checked the data for normality using the Shapiro-Wilk test. A linear mixed model (LMM) from "lmer" in the lme4 package of R version 4.1.1 (R, Vienna, Austria) was then used to analyze the effects of plateau pika disturbance on the AGB, BGB, and BGB/AGB at each site. In the LMM, AGB, BGB, and BGB/AGB were response variables, the presence/absence of plateau pika disturbance (Dist.) and the three sites (site) were fixed effects, and paired plots within site was a random effect. When site effects were significant, a non-parametric paired *t*-test was used to evaluate the effects of plateau pika disturbance on the AGB, BGB, and BGB/AGB at each site.

Pearson's rank correlations were used to select the explanatory variables and subordinate explanatory variables by testing for the significance of relationships of BGB/AGB with soil

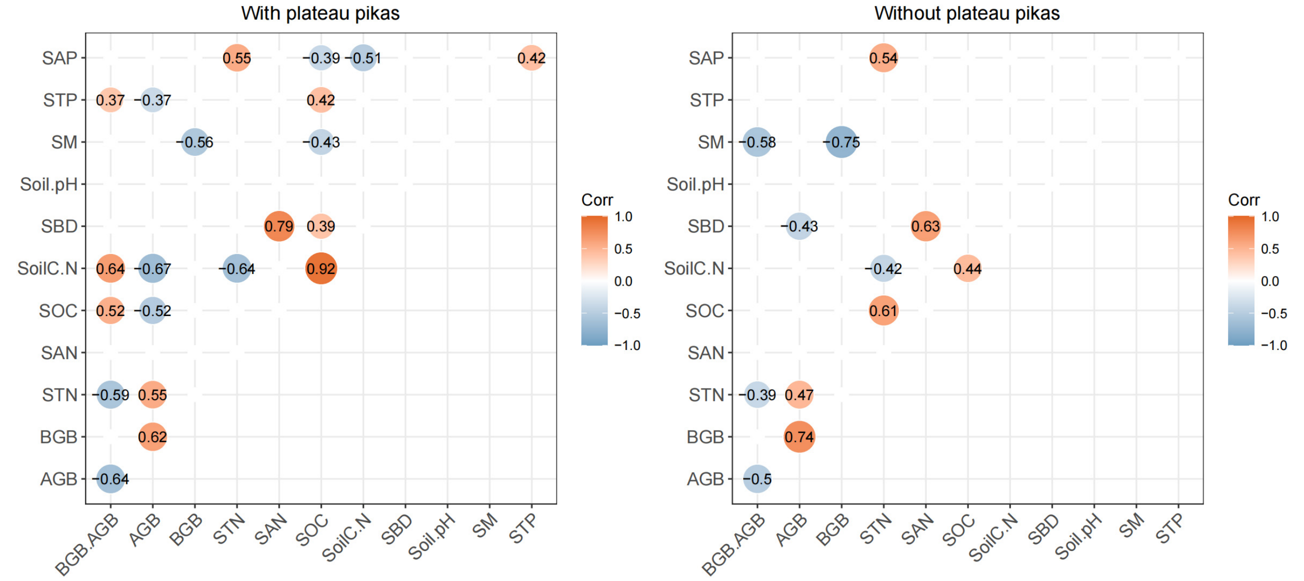

FIGURE 4 | The relationships of BGB/AGB with environmental factors in areas with and without plateau pikas. Orange indicates a positive correlation at $p < 0.01$, and blue indicates a negative correlation at $p < 0.01$. STN, soil total nitrogen; SAN, soil available nitrogen; SOC, soil organic carbon; soil C:N, soil carbon/soil nitrogen; STP, soil total phosphorus; SAP, soil available phosphorus; SM, soil moisture; SBD, soil bulk density.

physical properties (SM, SBD, and soil pH) and soil chemical properties (SOC, SAN, STN, STP, SAP, and soil C:N). The main explanatory variables were soil variables that were significantly related to BGB/AGB ($p < 0.05$); soil variables not showing significant relationships to BGB/AGB were common explanatory variables. Subordinate explanatory variables were common explanatory variables that were significantly related to each of the main explanatory variables ($p < 0.05$).

Generalized additive models (GAMs) in the "mgcv" package in R were used to analyze the effect of each main explanatory variable on the BGB/AGB in the presence and absence of plateau pika (Wood et al., 2017). Sites differing in elevation and precipitation were included as covariates because these variables were suspected *a priori* to affect the ratio of BGB to AGB. Each main explanatory variable was included in the model as smoothers. GAMs were selected based on the *p*-value ($p < 0.05$) and Akaike information criterion (AIC) (δ AICc < 2).

To quantify the integrated effect of the main explanatory variables and subordinate explanatory variables on BGB/AGB, a structural equation model (SEM) in the "lavaan" package in R was used to identify the pathway and direct or indirect effect of each main and subordinate explanatory variable. As soil properties are mutual interaction between AGB and BGB, BGB/AGB was used to construct an SEM. A hypothesis-oriented pathway was used to construct a base SEM (**Figure 1**). The three sites represented a single variable group; the main and subordinate explanatory variables from the Pearson's rank correlations were then classified into soil physical and chemical property variable groups; and the SEM analysis and a path model were used to examine the direct and indirect effects of the three variable groups on BGB/AGB. The chi-square (χ^2) statistic, whole model *p*-value, goodness-of-fit index (GFI), and root-mean-square error of approximation (RMSEA) were used to optimize the base SEM and improve model fit. This improved model had low χ^2-values, low RMSEA values (< 0.08), high GFI values (> 0.96), and low *p*-values (> 0.05), and the differences between this model and observed values were the lowest.

RESULTS

Aboveground Biomass, Belowground Biomass, and Belowground Biomass/Aboveground Biomass

When the data from the three sites were analyzed together, the plant BGB and BGB/AGB were 11.40 and 8.20% lower in the presence of plateau pikas than in their absence, respectively; plant AGB did not significantly differ among plots with and without plateau pikas (**Figure 2**). When data from individual sites were analyzed separately, the responses of AGB, BGB, and BGB/AGB to disturbance by plateau pikas were consistent at each site (**Figure 3**).

Pearson's Rank Correlations Between Soil Properties and Belowground Biomass/Aboveground Biomass and Generalized Additive Model Analysis

Pearson's rank correlations indicated that BGB/AGB was significantly correlated with STN ($R^2 = 0.63$, $p < 0.05$), SOC

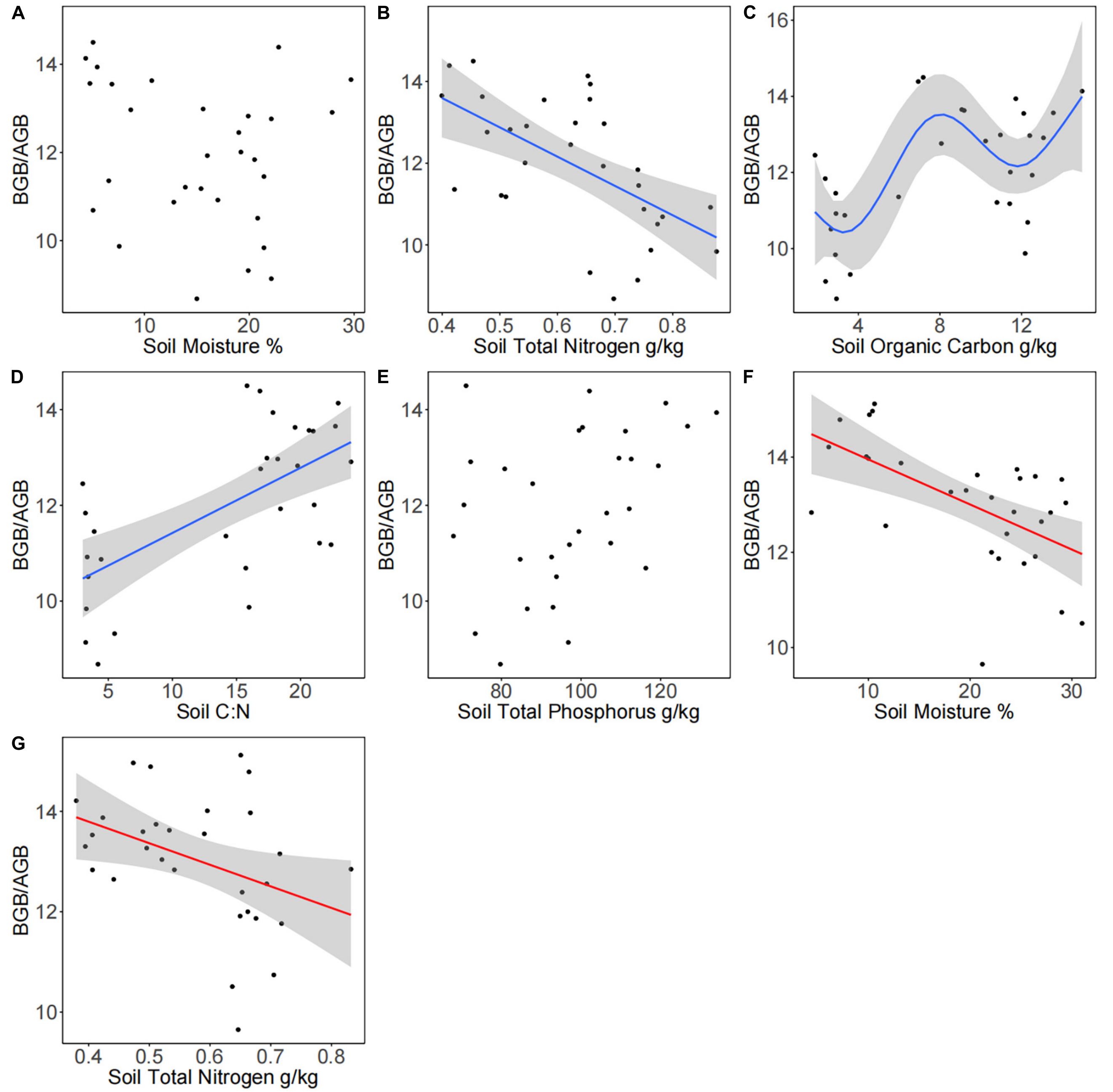

FIGURE 5 | Relationships between environmental factors and the ratio of BGB to AGB in the presence and absence of plateau pikas in alpine meadows. The effects of **(A)** soil moisture, **(B)** STN, **(C)** SOC, **(D)** soil C:N, and **(E)** STP on the BGB/AGB in the presence of plateau pikas. The effects of **(F)** SM and **(G)** STN on BGB/AGB in the absence of plateau pikas. Ten replicates within each of the three sites in the presence (*n* = 30) and absence (*n* = 30) of plateau pikas are presented. The best-fit GAM had a significant *p*-value ($p < 0.5$), the lowest Akaike information criterion (AIC), the lowest generalized cross-validation (GCV), and the highest *r*-squared values, and site was included as a random factor.

($R^2 = 0.44$, $p < 0.05$), soil C:N ($R^2 = 0.55$, $p < 0.05$), and STP ($R^2 = 0.40$, $p < 0.05$) in the presence of plateau pikas and with SM ($R^2 = 0.59$, $p < 0.05$) and STN ($R^2 = 0.40$, $p < 0.05$) in the absence of plateau pikas (**Figure 4**), indicating that the disturbance caused by plateau pikas altered the relationships of BGB/AGB with SM and STN. Thus, SM, STN, SOC, soil C:N, and STP were the main explanatory variables.

Soil organic carbon was the only main explanatory variable significantly correlated with SBD in the presence of plateau pikas ($R^2 = 0.39$, $p < 0.05$); no other soil property variables were significantly related to each of the main explanatory variables in the absence of plateau pikas. These results indicated that SBD was a subordinate explanatory variable.

According to the GAM analysis, there was no significant linear or non-linear relationship of BGB/AGB with SM and STP; however, there was a negative linear relationship of BGB/AGB with SM, soil C:N, and STN in the presence of plateau pikas. BGB/AGB increased in a fluctuating manner as SOC increased from approximately 8 to 12 g/kg in the presence of plateau pikas. There was a negative linear relationship of BGB/AGB with SM and STN in the absence of plateau pikas (**Figure 5** and **Table 1**).

Relationships Between Belowground Biomass/Aboveground Biomass and Explanatory Variables According to the Structural Equation Model

The results of the SEM analysis explained 53 and 58% ($R^2 = 0.53$ and 0.58) of the variance in BGB/AGB in the presence and absence of plateau pikas, respectively. The SEM analysis showed that BGB/AGB at each site was affected through different pathways in the presence and absence of plateau pikas (**Figure 6**).

TABLE 1 | Generalized additive models of the relationships of BGB/AGB with plant community biomass and soil properties in the presence and absence of plateau pika.

	df	GCV	F	*p*	R^2
Plateau pikas present					
Soil moisture	1.848	2.774	2.311	0.109	0.151
Soil total nitrogen	1	1.980	14.570	0.000	0.319
Soil organic carbon	5.487	1.622	5.953	0.000	0.515
Soil C:N	1	1.888	19.330	0.000	0.387
Soil total phosphorus	2.555	2.483	2.994	0.070	0.178
Plateau pikas absent					
Soil moisture	4.587	1.278	4.194	0.000	0.375
Soil total nitrogen	1	1.613	4.979	0.001	0.121

Df = 1 denotes the linear relationship between two variables. AGB, aboveground biomass; BGB, belowground biomass.

DISCUSSION

Large grazing herbivores have been found to affect the allocation of AGB and BGB in shrub-steppes (Bagchi and Ritchie, 2010), semiarid grasslands (Patty et al., 2010), and alpine grasslands (Sun and Wang, 2016) and contribute to carbon cycling in grassland ecosystems (Hermans et al., 2006; Bardgett and Wardle, 2010; Pausch and Kuzyakov, 2018; Yang et al., 2018). In this study, multiple sites were used to examine the effect of plateau pikas on the allocation of AGB and BGB in alpine meadow ecosystems.

The results of our study revealed that disturbance by plateau pikas had no impact on AGB, but it decreased BGB and BGB/AGB, which indicates that plateau pikas can affect the allocation of AGB and BGB. This is consistent with the result of some previous studies (Pang and Guo, 2017; Pang et al., 2020a) but inconsistent with the results of others (Liu et al., 2013). This variation in the effect of plateau pikas on AGB among studies likely stems from differences in the placement of sampling plots. Paired plots were used in this study, and each set of paired plots (disturbed plot and undisturbed plot) was placed in the same alpine meadow type, similar to studies carried out by Pang and Guo (2017) and Pang et al. (2020a). In contrast, Liu et al. (2013) placed plots with or without plateau pikas in areas that differed in dominant plants; thus, low plant AGB in plots with plateau pikas compared with plots without plateau pikas could stem from differences in plateau pika presence of vegetation.

Although the consumption of plants by plateau pikas can decrease AGB (Smith et al., 2019; Pang et al., 2020a), there are three ways that plateau pika disturbance can increase AGB. First, herbivory by plateau pikas can lead to compensatory plant growth (McNaughton, 1983). Second, plateau pikas clip older and taller plant tissues (Liu et al., 2009) to increase light availability for shorter plants (Pang et al., 2020a; Zhang et al., 2020). Third, higher concentrations of SAN in the presence of plateau pikas (Yu et al., 2017a) are beneficial for the accumulation of nitrogen in leaves and can enhance the allocation of photosynthate to the aboveground parts of plants. The results of the statistical analyses indicate that plateau pika disturbances appear to have a zero-net effect on plant AGB; however, this stems from the fact that the increases in AGB *via* the aforementioned three consequences of plateau pika disturbance are offset by the decrease in AGB associated with plant consumption.

Plateau pika disturbance contributes to a decrease in BGB in three ways. First, plateau pika disturbance increases the heterogeneity of the soil (Pang et al., 2019; Zhang et al., 2020), and this enhancement of the habitat promotes the conversion of live fine roots to dead fine roots (Bardgett and Wardle, 2010). Second, plants require fewer roots to acquire nutrients because nutrient concentrations are higher in the presence of plateau pikas (Bagchi and Ritchie, 2010; Kiaer et al., 2013; Yu et al., 2017a; Maskova and Herben, 2018; Cleland et al., 2019; Qi et al., 2019). Third, the higher soil nitrogen concentration in the presence of plateau pikas (Yu et al., 2017a) can increase the mortality of roots (Bai et al., 2008; Li et al., 2011a). The response of BGB/AGB to plateau pika disturbance depends on changes in both AGB and BGB. Low BGB/AGB in the presence of plateau pikas indicates that plateau pika disturbance permits plants to allocate more biomass to the aboveground parts.

The main soil factors affecting BGB/AGB differed in the presence and absence of plateau pikas. The presence of plateau pikas increased the net effect of soil chemical properties on BGB/AGB but decreased the net effect of soil physical properties on BGB/AGB. BGB/AGB is closely related to SM and STN in the absence of plateau pikas; however, in the presence of plateau pikas, BGB/AGB is closely related to STN, SOC, soil C:N, and STP, suggesting that disturbance by plateau pikas can alter the main soil physical and chemical factors that control BGB/AGB. There are three likely causes for the differences in the soil properties most closely related to BGB/AGB in the presence and absence of plateau pikas.

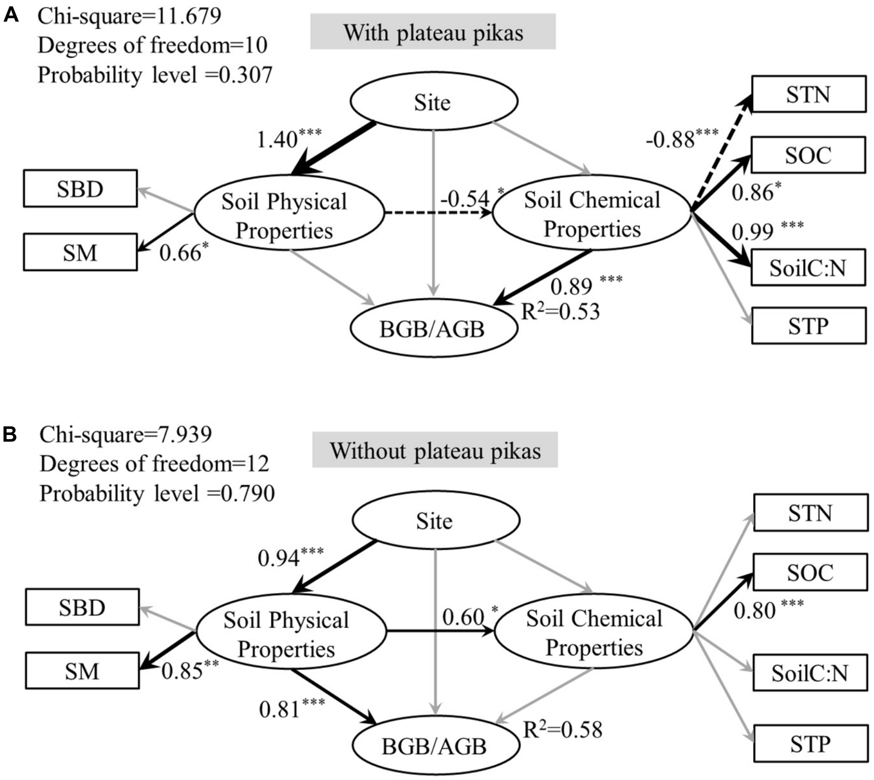

FIGURE 6 | Structural equation model (SEM) exploring the direct and indirect effects and standardized total effects of site, soil physical properties (SBD, SM), and soil chemical properties (STN, SOC, soil C:N, STP) on BGB/AGB in areas with **(A)** or without **(B)** plateau pikas. The black arrows indicate that the effect is significant, and gray arrows indicate insignificant effects. Asterisks next to path coefficients indicate *p*-values. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. Solid lines and dotted line arrows indicate positive and negative significant relationships, respectively, and arrow thickness indicates the strength of the relationships. STN, soil total nitrogen; SOC, soil organic carbon; Soil C:N, soil carbon/soil nitrogen; SM, soil moisture; SBD, soil bulk density; AGB, above-ground biomass; BGB, below-ground biomass; BGB/AGB, below-ground biomass/above-ground biomass.

First, compared with alpine meadow microhabitats with small semi-fossorial herbivores, alpine meadow microhabitats without small semi-fossorial herbivores are relatively stable (Bagchi and Ritchie, 2010), and the soil nutrients and light sources at these sites are relatively homogeneous (Pang et al., 2020a). In a stable, homogeneous microhabitat, SM changes more readily than soil nutrients in the short term; consequently, SM is one of the main factors affecting the allocation of AGB and BGB in the absence of plateau pikas. Second, plateau pika disturbance increases heterogeneity in the amount of fertilizer in alpine meadows (Yu et al., 2017b), and the uneven distribution of soil nutrients in the presence of plateau pikas enables plants to compete for soil nutrients to maintain their growth. In addition, the higher SOC in the presence of plateau pikas is closely related to soil nitrogen. Thus, STN, SOC, soil C:N, and STP were the main factors affecting the allocation of AGB and BGB in the presence of plateau pikas. Third, selective consumption and clipping by plateau pikas (Smith et al., 2019; Pang et al., 2020a; Wang et al., 2020) can stimulate the compensatory growth of the aboveground parts of plants (Wang et al., 2018; Pang et al., 2020a), which enables plant roots to absorb more soil nutrients to maintain the growth of the entire plant. This increases the importance of soil nutrients and carbon in the presence of plateau pikas and explains why SOC, soil C:N, and STP were the variables most closely related to the allocation of AGB and BGB in the presence of plateau pikas.

CONCLUSION

The effects of plateau pikas on the allocation of AGB and BGB were examined across three sites ranging in elevation from 3,265 to 3,750 m and ranging in average annual precipitation from 250 to 633 mm. BGB and BGB/AGB were lower in the presence of plateau pikas than in their absence, and AGB did not vary in the presence and absence of plateau pikas. The main factors affecting the allocation of AGB and BGB might shift from SM and STN in the absence of plateau pikas to SOC, STN, soil C:N, and STP in the presence of plateau pikas. These results reveal the general effects of small semi-fossorial herbivores on the allocation of AGB and BGB and provide new insight into the relationships between small semi-fossorial herbivores and the carbon stock in grassland ecosystems.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

QW and ZG designed the experiments, analyzed the data, and wrote the manuscript. QW and XP performed the experiments. All authors read and approved the manuscript.

FUNDING

This work was supported by the National Natural Science Foundation of China (32171675), the 111 Project (B12002), and the Fundamental Research Funds for the Central Universities of Lanzhou University, China (lzujbky-2021-it02).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2022.830856/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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ORIGINAL RESEARCH
published: 10 June 2022
doi: 10.3389/fpls.2022.869418

Competitive Relationship Between *Cleistocalyx operculatus* and *Syzygium jambos* Under Well-Watered Conditions Transforms Into a Mutualistic Relationship Under Waterlogging Stress

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Specialty section:
This article was submitted to
Functional Plant Ecology,
a section of the journal
Frontiers in Plant Science

Received: *08 February 2022*
Accepted: *19 May 2022*
Published: *10 June 2022*

Citation:
Yang F, Zhang J, Cisse E-HM, Li D-D, Guo L-Y, Xiang L-S and Miao L-F (2022) Competitive Relationship Between Cleistocalyx operculatus and Syzygium jambos Under Well-Watered Conditions Transforms Into a Mutualistic Relationship Under Waterlogging Stress. Front. Plant Sci. 13:869418. doi: 10.3389/fpls.2022.869418

Competition and abiotic stress such as waterlogging (WL) represent main factors limiting plant growth and determining plant resistance and distribution patterns in wetland ecosystems. One of the basic steps for wetland restoration is to plant trees to ensure a quicker recovery and prevent erosion. Plant survival and adaptation are considered criteria of principal priority for the screening of plant species for wetland ecosystem restoration. WL influences plant species in wetlands *via* the deterioration of the plant root environment which leads to oxygen deficiency that affects plant growth, photosynthesis, respiration, and other metabolic processes. A suitable plant species was determined according to tolerance to WL during wetland vegetation recovery activities. Thus, two tree species (*Cleistocalyx operculatus* and *Syzygium jambos*) that showed a certain waterlogging tolerance were chosen to study their behaviors in different planting model and environmental conditions. Given that interspecific relationship should be considered during plant community construction, the eco-physiological adaptable mechanisms between these woody plants under well-watered condition and waterlogging stress were explored. Results showed that both species were waterlogging-tolerant species due to their ability to adapt to submergence conditions for 120 days. Moreover, *C. operculatus* possessed stronger tolerance to waterlogging stress because of a significant adventitious roots biomass accumulation. A competitive relationship was found between *C. operculatus* and *S. jambos* under well-watered condition, and *C. operculatus* showed better growth performance benefited from morphological responses (plant height, number of blade and leaf area) and endogenous hormone variations. In comparison, *S. jambos* suffered some negative effects when the well-watered mixed planting was used. However, the competitive relationship under well-watered condition was transformed into mutualistic relationship under waterlogging stress. The mixed planting under waterlogging condition significantly improved the tolerance of *C. operculatus* and *S. jambos* to waterlogging stress, compared with the monoculture., Especially, *S. jambos* showed improvements in root length, root surface area, and redox equilibration between lower levels of relative conductivity, malondialdehyde, and $O_2^{\cdot-}$ and had increased levels of non-enzymatic antioxidant components, such as reduced glutathione and soluble proteins. The interspecific relationship between *C. operculatus* and *S. jambos* was altered by waterlogging stress, and both showed improved tolerance to waterlogging stress. This study can provide a glimmer of light on suitable plant species selection and plant community construction during the revegetation activities in wetland zones. *C. operculatus* and *S. jambos* represent potential candidates in wetland restoration in a mixed planting model.

Keywords: adventitious roots, endogenous hormone balance, interspecific relationship, mixed planting pattern, pure planting pattern, redox equilibration

HIGHLIGHTS

- *Cleistocalyx operculatus* with better growth performance benefits from water-watered mixed planting pattern.
- *C. operculatus* possessed stronger tolerance to waterlogging stress than *Syzygium jambos*.
- Plant competitive interactions under well-watered conditions become mutualistic under waterlogged conditions; *S. jambos* which has a low tolerance to waterlogging stress seems to gain more benefits.
- The results of this study showed a promising perspective to use *C. operculatus* and *S. jambos* in the restoration of areas that are subject constantly to submergence conditions.

INTRODUCTION

In riparian and wetland zones, waterlogging is the most important environmental stress, which greatly limits the growth, distribution, and survival of terrestrial plants (Miao et al., 2017). This is because the root systems of terrestrial plants in wetland zones suffer from oxygen deficiency in water-saturated soil (Kreuzwieser and Rennenberg, 2014; Li et al., 2022). Thus, many metabolic processes for satisfying the oxygen demand are seriously inhibited, aerobic respiration is transformed into anaerobic respiration, and many enzymes involved in the glycolysis pathway are activated (Yin et al., 2009; Yang et al., 2015). These effects not only affect the absorption and availability of nutrients and water but also limit energy production and stimulate reactive oxygen species (ROS) formation. Indeed ROS are crucial toxic and regulatory molecules in plant which play a main role in plant stress tolerance responses. They are responsible for the oxidative stress caused by their over-accumulation in plant under stress such as waterlogging. Furthermore, ROS are able to catalyze cations signaling events involved in plant stress tolerance (Demidchik, 2015). Metabolic processes are considerably altered by changes in membrane lipid peroxidation, pigments, proteins, nucleic acids, osmoregulation substance, enzyme activity, and hormone levels, which will finally damage the whole growth performance, even to death. However, waterlogging-tolerant species generally have specific adaptable strategies to avoid or tolerate the negative effects of waterlogging, such as the formation and development of aerenchyma tissues and adventitious roots and other physiological adjustments, including the antioxidant machinery that are responsible to scavenge the excessive ROS production during the stress (Seago et al., 2005; Li et al., 2022). Indeed, the antioxidant system plays a crucial role in the detoxification of ROSs in wetland plants and includes both non-enzymatic components and enzymatic components. The non-enzymatic component is composed by molecules such as ascorbic acid (ASA), reduced glutathione (GSH), and proline. Meanwhile the antioxidant enzymatic system is constitute by enzymes such as peroxidase (POD), catalase (CAT), and superoxide dismutase (SOD; Yang et al., 2015). Antioxidant enzymes, such as POD, CAT and SOD, are activated by plants to control ROS production under waterlogging stress (Yang et al., 2015; Seymen, 2021). The over-production of ROS in plant under stress regulated by antioxidants involves also the plant hormone. In fact, ROS represent important second messengers in hormone signaling that play a massive part in the regulation of plant development and stress tolerance (Xia et al., 2015). Furthermore, the hormonal hierarchy of abscisic acid (ABA), indole-acetic acid (IAA), and gibberellin A3 (GA_3) is involved in the regulation of waterlogging tolerance (Li et al., 2022), and methyl jasmonate (JA-Me) is associated with plant leaf senescence and plant caducity and promotes ethylene production (Voesenek and Bailey-Serres, 2015). The physiological adjustments including the regulation of ROS and the involvement of plant hormones are crucial for the adaptations of plants to environmental stress like WL. Indeed, the tolerance of plant species to WL depends on their capacity to change their morphological and physiological traits (Bertolde et al., 2010). But, also it has been proven that positive plant–plant interactions such as facilitation are very helpful for some species under stressful conditions and such positive interactions usually co-occur with competition (Zhang and Tielbörger, 2019). Thus, it is clear that the adaptation of plant to submergence conditions depends on intern (i.e., physiological processes) and extern factors (i.e., interspecific relation with others species).

Interspecific relationship (competition or facilitation) is an important biotic factor affecting plant species distribution, population dynamics, community construction, and ecosystem services (Lin et al., 2012). It has been reported that the evaluation (experimentally) of the impact of environmental stress on interaction strengths can significantly participate to understand the crucial importance of these two processes (competition or facilitation) in structuring plant communities (Callaway and Walker, 1997; Paquette and Hargreaves, 2021). Competitive relationship indicates the ability of adjacent plants to obtain and use natural resources, such as nutrients, light, and water. For instance, a competitive interaction between adjacent plants occurs when they are competing for limited resources such as soil nutrients that can affect particularly their growth and structure (Xiao et al., 2009). In another hand, facilitation is known as positive interactions among organisms in communities and it has been considered as the primary driving biotic mechanism of plant community succession. It can increase species richness in a large range of environmental conditions (Brooker et al., 2008; Xiao et al., 2009; Michalet and Pugnaire, 2016). Competition and facilitation usually occur simultaneously under environmental stress, and the final neighboring relationship is the net effect of these relationships (Gersani et al., 2001; Mommer et al., 2010). Therefore, the neighboring relationship between plants is variable, and they still mainly use resources for root growth when growth environment resources are insufficient. A previous study showed that morphological and physiological responses to waterlogging stress depend on the comprehensive influences of different abiotic stress stresses, such as the severity, duration, and level (depth) of waterlogging stress, and biotic factors, including life history strategies that enable survival in a highly disturbed environment and neighboring relationship (Vreugdenhil et al., 2006). Moreover, it has been demonstrated that interspecific neighbors relationship depends on abiotic stress (waterlogging) gradient (Grime, 1973; Brose and Tielbörger, 2005). Brose and Tielbörger (2005) reported that abiotic and biotic factors interact in determining plant abundance and distribution in wetlands under submergence conditions. These finding is consistent with the stress gradient hypothesis proposed by Bertness and Callaway (1994).

Although there are many studies that focused on the physiological and morphological adaptations of plant species commonly used in restoration practices for individuals grown in monoculture, there is still a poor understanding of how species interactions may induce competitive or facultative interactions that ultimately modify the environmental conditions that individual plants are growing in despite the anaerobic conditions associated with waterlogging in wetlands. This is of particular importance in different regions threatened by submergence conditions, where two species such *Cleistocalyx operculatus* and *Syzygium jambos* are often used in restoration and reconstruction of riparian and wetland areas. Indeed, *Cleistocalyx operculatus* and *S. jambos* belong to the Myrtaceae family. They are evergreen medicinal woody plants with waterlogging tolerance and often used in the restoration and reconstruction of riparian zones of tropical and subtropical regions (Jing et al., 2001; Sharma et al., 2013; Nguyen et al., 2017; Ma et al., 2019). In the present study, the pure and mixed planting patterns of *C. operculatus* and *S. jambos* under well-watered condition and waterlogging stress were designed and used in answering the following questions: (1) Can these two species benefit from the mixed planting pattern under well-watered conditions? (2) Whether the woody plant with strong waterlogging tolerance gain more benefits than a plant species which possesses a less waterlogging tolerance when they are subjected to waterlogging in a mixed planting? (3) Whether waterlogging environments alter neighboring relationships between two species and whether competition or facilitation is preferred? Thus, changes in interspecific relationships between *C. operculatus* and *S. jambos* under well-watered and waterlogging conditions were explored through physiological analysis based on phenotypic traits, photosynthetic performance, lipid peroxidation, non-enzymatic antioxidant components, antioxidant enzymatic activities, and endogenous hormones.

MATERIALS AND METHODS

Experimental Designs

Two 6-month-old tree species seedlings of *C. operculatus* and *S. jambos* from Zengcheng, Guangdong Province were planted in pairs in a 43 cm × 19 cm × 14 cm (L × W × H) plastic bar-shaped basin, which was filled with red soil, sand, and coconut coir in 4:2:1 (v:v:v) ratio. The chemical and physical properties of the red soil were: pH = 6.23, 33.65 $g.kg^{-1}$ of organic carbon, 58.01 $g.kg^{-1}$ of organic matter, 1.77 $g.kg^{-1}$ of total nitrogen, 0.64 $g.kg^{-1}$ of total phosphorus. Before treatment, fertilizer solution was applied two times at 300 ml in each pot (day 1 and after 2 weeks from March 28, 2019). The experiment was carried out in a greenhouse at Hainan University (20° 03′ 33.2″ N, 110° 20′ 16.9″ E). Healthy plants were selected for a randomized design with treatments consisting of combinations of two irrigation levels (well-watered and waterlogging conditions), and three different planting systems (monoculture of *C. operculatus* or *S. jambos*, and mixed planting between *C. operculatus* and *S. jambos*, two seedlings in each pot) were arranged. Each treatment had at least 24 replicates, which implied at least 144 pots for the whole experiment. The waterlogging depth was 10 cm above the soil surface. For each species, the well-watered and waterlogging treatments were marked as CK and W, respectively, in the monoculture, and marked as CK-M and W-M, respectively, in the mixed planting. For the well-watered treatment, pots were watered daily (100% field capacity). All the experiments were arranged in a complete randomized design. The morphological and physiological assays were determined after 120 days.

Morphological Parameters

To determine the increments in plant height (IPH) and blade number (IBN), the plant height and number of blades were measured at the beginning (day 1) and the end (day 120) of treatments. The IPH was calculated as $Height_{120}$-$Height_{1}$, and IBN was calculated as N_{120}-N_{1}. The leaf area (LA) was determined before the end of the experiment with a portable area meter (LI-3000C; Li-COR, Lincoln, United States; Pu et al., 2021) in 3 leaves for each pot and 8 pots for each treatment. The fresh weights (direct index of plant growth) of adventitious roots, original roots, underground biomass, and aboveground biomass were measured immediately after harvesting. The roots were scanned with a scanner (Epson v750, China), and root length and root surface area were determined with a WinRHIZO analysis system (Li et al., 2022).

Photosynthesis-Related Parameters

The young fresh leaves were collected at the end of the treatment. Chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll, and carotenoids (Caro) were quantified after extraction in 95% (v/v) ethanol with a spectrophotometer (6,800 PC, Shanghai Metrum Instrument Co., Ltd) at 470, 640, and 665 nm. The net photosynthetic rate (Pn), intercellular carbon dioxide (Ci), stomatal conductance (Gs), and transpiration rate (Tr) were determined once at the end of the treatment from 08:30 to 11:30 h using a 3051D photosynthetic device (Zhejiang Top Instruments Co., Ltd.) according to the methods of Li et al. (2022). Fv/Fm (maximum photochemical quantum yield of PSII) was measured with a Junior-PAM chlorophyll fluorometer (Walz, Effeltrich, Germany) according the method of Liu et al. (2020).

Relative Conductivity, Malondialdehyde, and Superoxide Anion (O_2^-) Contents

Relative conductivity was measured according to the method described by Fan et al. (2015) with some modifications. Fresh leaves were cleaned with deionized water, and 10 discs from the fresh leaves were incubated with 15 ml of deionized water. Initial conductivity (C1) was recorded after 2 h, and then the samples were boiled for 45 min, and then the final conductivity C2 was measured. RC was calculated with the following formula: relative conductivity (%) = C1/C2 × 100.

Malondialdehyde (MDA) was determined according to the method of Yang and Miao (2010). Fresh samples were homogenized with 0.1% trichloroacetic acid (TCA) and then centrifuged at 11000 × g for 8 min. The supernatant (1 ml) was mixed with 4 ml of 20% TCA solution containing 0.5% thiobarbituric acid and incubated at 100°C for 30 min. The reaction mixture was cooled on an ice bath and then centrifuged at 11,000 × g for 8 min. Absorbance was measured first at 530 nm and corrected at 600 nm.

The production rate of O_2^- was quantified using the modified method described by Yang et al. (2011). Fresh samples (0.15 g) were homogenized in 2 ml of phosphate buffer (pH 7.8) and then centrifuged at 10000 × g for 15 min. The supernatant was decanted and mixed with phosphate buffer. The reaction mixture included 1 ml of supernatant, 0.75 ml of 65 mM phosphate buffer, and 0.25 ml of 10 mM hydroxylamine hydrochloride. The mixture was incubated at 25°C for 20 min and then added to 1 ml of 17 mM sulfanilamide and 1 ml of 7 mM α-naphthylamine. The mixture was kept at 30°C for 30 min and then mixed with 4 ml of trichloromethane before centrifugation at 10,000 × g at 4°C for 3 min. Absorbance was measured at 530 nm, and $NaNO_2$ was used as the standard curve for the calculation of the O_2^- content.

Non-enzymatic Antioxidant Matter Determination

The concentration of proline was measured with the method of Bates et al. (1973) and Yang and Miao (2010) with some modifications. Approximately 200 mg of fresh leaf samples was mixed with 5 ml of 3% sulfosalicylic acid. An acid–acetic ninhydrin solution was used as the reagent. Then, 1 ml of an acid–acetic ninhydrin reagent and 1 ml of glacial acetic acid were successively added to 1 ml of the homogenate. The mixture was then incubated at 100°C for 1 h. The reaction was stopped by cooling the samples on ice water. Toluene was used in extracting the chromophore-containing phase, and absorbance was recorded at 520 nm.

Soluble proteins were determined according to the method described by Bradford (1976). Coomassie Brilliant Blue G-250 was used. Approximately 2 ml of phosphate buffer (pH 7.8) was used as the extraction solution, and 100 mg of fresh samples was mixed with phosphate buffer. Absorbance was read at 595 nm, and protein concentration was determined with a standard curve.

Reduced GSH (reduced glutathione) and ASA (ascorbic acid) levels were measured according to the manufacturer's instructions with the method of Yang et al. (2015) and Anee et al. (2019). Approximately 100 mg of fresh leaves was ground in liquid nitrogen and homogenized with PBS (5 mg of fresh leaves in 50 μl of PBS). The mixture was centrifuged at 10,000 rpm for 30 min at 4°C. The assay was performed with kits provided by Nanjing Jiancheng Bioengineering Institute (China).

Antioxidant Enzymatic Activity Determination

Fresh leaf samples (0.2 g) were ground and homogenized with tissue grinder instrument scientific laboratory homogenizer equipment (JXFSTPRP-24, Shanghai Jingxin Industrial Development Co., Ltd., China). The mixture contained liquid nitrogen, 5 ml of 50 mM sodium phosphate buffer (pH 7.8), and 1% polyvinylpolypyrrolidone. The mixture was centrifuged at 10,000 rpm, 4°C for 15 min, and the supernatant was used to perform for the antioxidant enzymatic activities determination.

Expressed as unit· g^{-1}·FW·min^{-1}, POD (peroxidase) activity was determined with the method described Yang and Miao (2010) according to absorption change caused by guaiacol oxidation at 470 nm. SOD (superoxide dismutase) activity was measured using the method described by Yang and Miao (2010) according to the inhibition of nitroblue tetrazolium chloride reduction. Absorbance was recorded at 560 nm with a spectrophotometer (UV-1800PC, Shanghai Mapada Instruments Co., Ltd., China). CAT (catalase) was determined in accordance with the manufacturer's instructions with the method described by Yang et al. (2015). Phosphate buffer was provided with the assay kit from Nanjing Jiancheng Bioengineering Institute, China.

Endogenous Hormone Parameters

Endogenous IAA, ABA, GA_3, and JA-Me were extracted and purified with the methods described by Bollmark et al. (1988). Hormones were quantified through ELISA with the methods described as Yang et al. (2001). The mouse monoclonal antigens and antibodies against IAA, ABA, GA_3, and JA-Me horseradish peroxidase used in ELISA were produced at the Phytohormones Research Institute, and fresh samples were sent for determination in China Agricultural University.

Statistical Analyses

Experimental data processing statistics, analysis, and mapping were performed using SPSS 23.0, Canoco 5.0 and GraphPad Prism 9. All data were tested for normal distribution and homogeneity of variance before analysis. One-way analysis of variance followed by Tukey's multiple comparison tests was used in establishing significant differences between pure planting and mixed planting under waterlogging stress at 1 and 5% levels of significance. Correlation analysis was performed with R software (R Development Core Team, 2019, version 3.6.1). PCA was used in assessing and comparing the important parameters of monoculture and mixed planting on *C. operculatus* and *S. jambos* under waterlogging conditions.

RESULTS

Effects on Morphological Characteristics

Cleistocalyx operculatus had better growth rates and performance (IPH, LA, IBN and fresh biomass accumulation) under well-watered conditions compared to *S. jambos*. All waterlogging-treated seedlings from *C. operculatus* and *S. jambos* survived after 120 days of waterlogging treatment, but their growth rates significantly varied from each other. In *C. operculatus*, compared with CK treatment, CK-M treatment significantly increased the IPH and LA ($p < 0.05$), whereas non-significant differences in the IBN were found between the CK and CK-M treatments (**Table 1**). However, in *S. jambos* CK-M had only increased significantly the IBN compared to the control. Waterlogging significantly increased plant height and leaf area in the monoculture group of *C. operculatus* compared to the CK group, whereas non-significant differences in IPH, IBN, and LA were found between W and W-M treatments ($p < 0.05$). In *S. jambos*, compared with CK treatment, W treatment significantly decreased the IPH, IBN, and LA in the group subjected to the monoculture. W treatment also significantly decreased IBN and LA in the mixed planting, but the W-M treatment significantly increased the IPH relative to the CK-M treatment ($p < 0.05$; **Table 1**).

Effects on Biomass Characteristics

Cleistocalyx operculatus showed a massive accumulation of the fresh weight from adventitious and original roots, aboveground and belowground biomass compared to *S. Jambos* under well-watered conditions. Moreover, results showed that no significant differences in the fresh weights of original roots, aboveground and underground biomass were found between the CK and CK-M treatments in both species (**Figure 1**). As shown in **Figure 1A**, W-M treatment significantly increased the fresh weights of the adventitious roots of both species, compared with the W treatment, and the fresh weights of the adventitious roots of *C. operculatus* were significantly higher than those of *S. jambos* ($p < 0.05$) under the W-M treatment. Interestingly, the W treatment significantly increased the aboveground biomass and underground biomass of *C. operculatus* in the monoculture group, whereas *S. jambos* showed the opposite trends ($p < 0.05$). Compared with the monoculture group, the mixed planting under waterlogging conditions increased significantly the aboveground and underground biomass of *S. jambos* but only increased the underground biomass of *C. operculatus* ($p < 0.05$; **Figures 1C,D**).

TABLE 1 | The variations of IPH (increment in plant height), IBN (increment in number of blades), and LA (leaf area) in *Cylindrocopturus operculatus* and *Syzygium jambos* among different treatments.

Species	Treatments	IPH (cm)	IBN (piece)	LA (cm^2)
C. operculatus	CK	13.8 ± 0.87 b**	20.4 ± 1.60 a**	333.63 ± 14.12 c**
	CK-M	22.3 ± 0.26 a**	22.8 ± 0.80 a**	619.93 ± 37.68 a**
	W	23.9 ± 0.24 a**	21.8 ± 0.20 a**	425.41 ± 39.08 b**
	W-M	22.6 ± 0.40 a**	21.4 ± 0.25 a**	509.34 ± 17.79 b**
S. jambos	CK	8.2 ± 0.46 B	5.2 ± 0.58 C	214.0 ± 14.32 AB
	CK-M	8 ± 0.27 B	16.2 ± 0.20 A	234.8 ± 59.35 A
	W	4.5 ± 0.22 C	4.0 ± 0.0 D	119.5 ± 7.91 C
	W-M	10.8 ± 0.30 A	11.8 ± 0.37 B	174.2 ± 3.30 B

*Values are means ± SE (n = 6). Different little and capital letters indicate significant differences among different treatments within the same species according to ANOVA's test ($p < 0.05$). CK, pure planting pattern under well-watered condition; CK-M, mixed planting pattern under well-watered condition; W, pure planting pattern under waterlogging condition, W-M; mixed planting pattern under waterlogging condition. The signs such as ** represent the significant difference between the two species under the same treatment at $p < 0.05$ and $p < 0.01$; ns, means non-significant.*

Under well-watered conditions *C. operculatus* displayed a greater root length increment compared to *S. jambos* (**Figure 2A**). Moreover, the root length and root surface area of *C. operculatus* within the same treatment were significantly higher than those of *S. jambos* ($p < 0.01$). Further, *S. jambos* showed a significant increase of its surface areas of roots compared to *C. operculatus*. The results showed no significant differences in the root lengths and root surface areas of *C. operculatus* and *S. jambos* between the CK and CK-M treatments (**Figure 2**). The W treatment significantly inhibited increases in the root length and root surface area of *S. jambos*, whereas the W-M treatment alleviated this inhibition, significantly improving these parameters. However, waterlogging stress significantly increased the root surface area in *C. operculatus* in the W and W-M treatments, and the root surface areas in the waterlogging treatments were significantly larger than those in the well-watered treatments. The W treatment significantly inhibited increase in root length in *C. operculatus*, whereas W-M could alleviate this inhibition.

Effects on Photosynthesis-Related Characteristics

As shown in **Table 2**, the levels of Chl a, Chl b, and total chlorophyll in the CK-M treatment were significantly higher than those in the CK treatment in *C. operculatus* ($p < 0.05$)

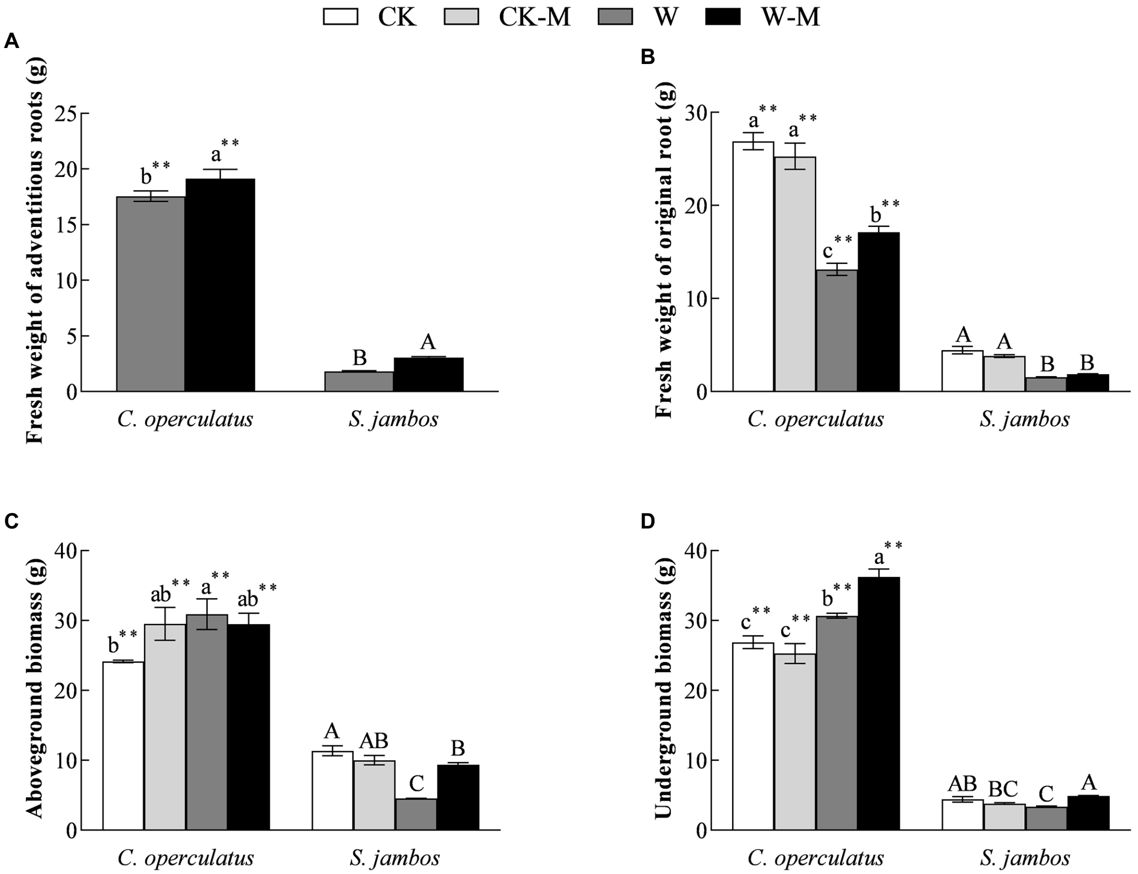

FIGURE 1 | The variations of fresh weight of adventitious roots **(A)**, fresh weight of original root **(B)**, aboveground biomass **(C)** and underground biomass **(D)** in *Cylindrocopturus operculatus* and *Syzygium jambos* among different treatments. Values are means ± SE ($n = 6$). Different little and capital letters indicate significant differences among different treatments within the same species according to ANOVA's test ($p < 0.05$). CK, pure planting pattern under well-watered condition; CK-M, mixed planting pattern under well-watered condition; W, pure planting pattern under waterlogging condition, W-M; mixed planting pattern under waterlogging condition. The sign ** concerns the significance difference between the two species under the same treatment. $^{**}p < 0.01$.

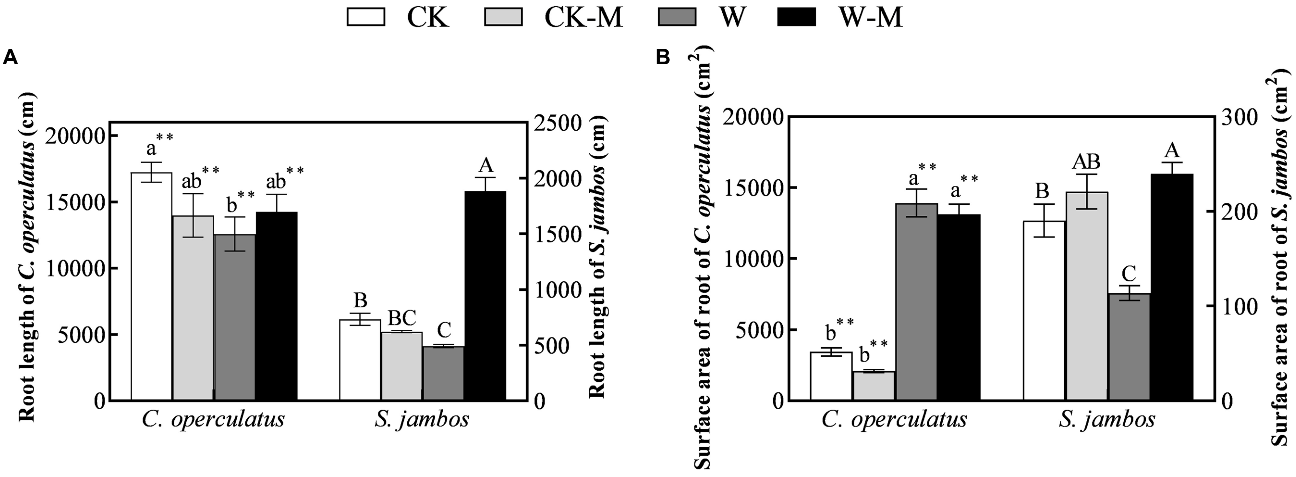

FIGURE 2 | The variations of root length **(A)** and root surface area **(B)** in *C. operculatus* and *S. jambos* among different treatments. Values are means ± SE ($n = 6$). Different little and capital letters indicate significant differences among different treatments within the same species according to ANOVA's test ($p < 0.05$). CK, pure planting pattern under well-watered condition; CK-M, mixed planting pattern under well-watered condition; W, pure planting pattern under waterlogging condition, W-M; mixed planting pattern under waterlogging condition. The sign ** concerns the significance difference between the two species under the same treatment. $^{**}p < 0.01$.

but obviously decreased after the W treatment. The W-M treatment did not offset the decreases. In *S. jambos*, the Chl a, Chl b, total chlorophyll, and Caro levels were significantly lower in the CK-M and W treatments than in the CK treatment. The W-M treatment significantly improved these parameters, compared with the W treatment.

The W treatment significantly decreased the levels of Pn, Gs, and Ci in both species in the monoculture group, and the mixed planting under waterlogging conditions (W-M) increased Pn and Ci in both species ($p < 0.05$; **Table 3**). The Pn values of *C. operculatus* were significantly higher than those of *S. jambos* in the same treatment ($p < 0.01$), and the values of Gs and Tr in *C. operculatus* were significantly higher than those of *S. jambos* ($p < 0.01$) under mixed planting patterns (CK-M and W-M).

As shown in **Figure 3A**, compared with the monoculture group (CK), the mixed planting (CK-M) had no significant effects on Fv/Fm in both species under well water conditions. The W treatment significantly decreased Fv/Fm in *S. jambos* but had no significant effects on *C. operculatus*. Compared with the monoculture group (W), the mixed planting (W-M) significantly improved Fv/Fm in *C. operculatus* and decreased Fv/Fm in *S. jambos* under waterlogging conditions ($p < 0.01$). In addition, significant difference in Fv/Fm was found between *C. operculatus* and *S. jambos* in the CK and W-M treatments ($p < 0.01$).

Effects on Relative Conductivity, MDA, and O_2^{-} Contents

Compared with the CK treatment, the W treatment significantly increased relative conductivity (**Figure 3B**), MDA content (**Figure 3C**), and $O_2^{\cdot -}$ content (**Figure 4D**) in both species. The mixed planting under well water conditions (CK-M) significantly decreased the $O_2^{\cdot -}$ level of *C. operculatus* and significantly increased relative conductivity and $O_2^{\cdot -}$ level in *S. jambos*, compared with the monoculture (CK). Compared with the monoculture (W), the mixed planting under waterlogging conditions (W-M) significantly inhibited the accumulation of $O_2^{\cdot -}$ in both species. In addition, compared with the W treatment, the W-M treatment significantly reduced the relative conductivity in *S. jambos* ($p < 0.05$) and had insignificant effects on relative conductivity and MDA in *C. operculatus* ($p \geq 0.05$).

Effects on Proline, Soluble Protein, GSH, and ASA Contents

Compared with the CK treatment, the W treatment significantly increased proline, soluble protein, GSH, and ASA content in *S. jambos* (**Figures 4A–D**) and significantly increased the content of proline and GSH in *C. operculatus*. The mixed planting under well water conditions (CK-M) significantly decreased

TABLE 2 | The variations of chlorophyll a, chlorophyll b, total chlorophyll and carotenoids in *C. operculatus* and *S. jambos* among different treatments.

Species	Treatments	Chlorophyll a (μg/g·Fw)	Chlorophyll b (μg/g·Fw)	Total Chl (μg/g·Fw)	Carotenoids (μg/g·Fw)
C. operculatus	CK	277.1 ± 5.56 b**	42.76 ± 1.79 b**	319.85 ± 6.95 b**	202.66 ± 6.69 a**
	CK-M	304.97 ± 10.94 a*	55.05 ± 1.78 a**	360.02 ± 12.49 a^{ns}	191.24 ± 9.37 ab**
	W	206.98 ± 7.92 c^{ns}	36.70 ± 3.66 bc**	243.68 ± 10.92 c*	209.09 ± 5.71 a**
	W-M	212.23 ± 5.37 c**	30.59 ± 1.68 c**	242.82 ± 5.93 c**	171.39 ± 7.38 b**
S. jambos	CK	598.8 ± 13.82 A	124.98 ± 8.64 A	723.78 ± 19.47 A	141.69 ± 7.15 A
	CK-M	269.1 ± 4.9 B	72.04 ± 3.68 B	341.18 ± 5.93 B	84.59 ± 3.54 B
	W	209.50 ± 4.25 C	50.69 ± 3.55 C	260.18 ± 2.00 C	66.67 ± 4.25 C
	W-M	273.53 ± 5.84 B	67.73 ± 4.71 B	341.26 ± 6.84 B	87.23 ± 4.12 B

*Values are means ± SE (n = 6). Different little and capital letters indicate significant differences among different treatments within the same species according to ANOVA's test (p < 0.05). CK, pure planting pattern under well-watered condition; CK-M, mixed planting pattern under well-watered condition; W, pure planting pattern under waterlogging condition, W-M; mixed planting pattern under waterlogging condition. The signs such as *, ** represent the significant difference between the two species under the same treatment at p < 0.05 and p < 0.01; ns, means non-significant.*

TABLE 3 | The variations of Pn, Gs, Tr, and Ci in *C. operculatus* and *S. jambos* among different treatments.

Species	Treatments	Pn (μmol·m^{-2}·s^{-1})	Gs (mol·m^{-2}·s^{-1})	Tr (mmol·m^{-2}·s^{-1})	Ci (μmol·mol^{-1})
C. operculatus	CK	6.53 ± 0.05 b*	0.13 ± 0.01 b^{ns}	3.48 ± 0.34 a*	455.78 ± 14.14 a^{ns}
	CK-M	7.7 ± 0.05 a**	0.14 ± 0.01 ab**	3.41 ± 0.13 a**	477.2 ± 11.95 a^{ns}
	W	4.52 ± 0.05 d**	0.07 ± 0.01 c^{ns}	2.9 ± 0.04 a**	415.54 ± 1.57 b**
	W-M	4.91 ± 0.07 c**	0.17 ± 0.01 a**	3.29 ± 0.19 a**	479.28 ± 7.95 a^{ns}
S. jambos	CK	6.03 ± 0.15 A	0.14 ± 0.01 A	2.41 ± 0.1 A	438.38 ± 14.6 A
	CK-M	5.39 ± 0.07 B	0.06 ± 0.01 B	2.40 ± 0.13 A	467.58 ± 10.51 A
	W	3.03 ± 0.12 D	0.06 ± 0.01 B	1.41 ± 0.25 B	363.02 ± 11.23 B
	W-M	3.4 ± 0.05\u00B0C	0.06 ± 0.01 B	1.54 ± 0.06 B	467.12 ± 10.3 A

*Values are means ± SE (n = 6). Different little and capital letters indicate significant differences among different treatments within the same species according to ANOVA's test (p < 0.05). CK, pure planting pattern under well-watered condition; CK-M, mixed planting pattern under well-watered condition; W, pure planting pattern under waterlogging condition, W-M; mixed planting pattern under waterlogging condition. The signs such as *, ** represent the significant difference between the two species under the same treatment at p < 0.05 and p < 0.01; ns, means non-significant.*

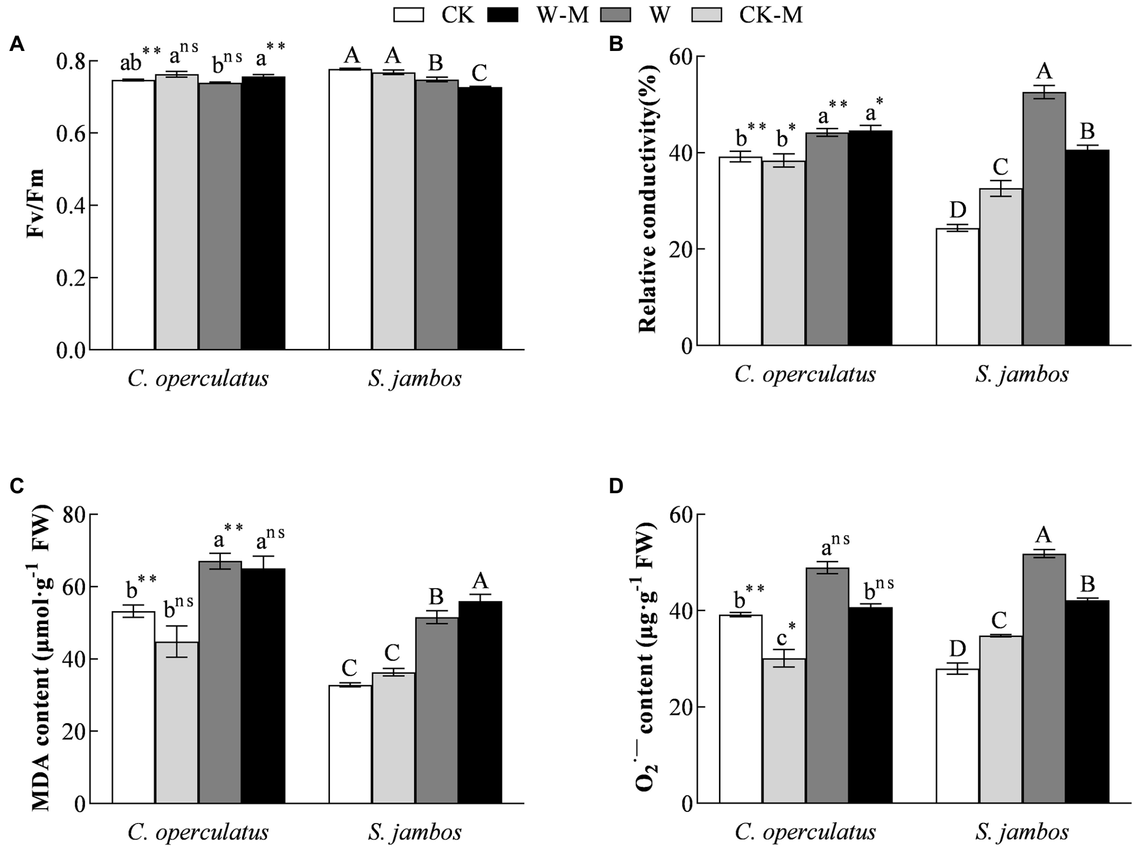

FIGURE 3 | The variations of Fv/Fm (maximum photochemical quantum yield of PSII) **(A)**, relative conductivity **(B)**, MDA content **(C)** and $O_2^{\cdot-}$ content **(D)** in *C. operculatus* and *S. jambos* among different treatments. Values are means ± SE ($n = 6$). Different little and capital letters indicate significant differences among different treatments within the same species according to ANOVA's test ($p < 0.05$). CK, pure planting pattern under well-watered condition; CK-M, mixed planting pattern under well-watered condition; W, pure planting pattern under waterlogging condition, W-M; mixed planting pattern under waterlogging condition. The signs such as *, **, and ns concern the significance difference between the two species under the same treatment. $^{*}p < 0.05$; $^{**}p < 0.01$; ns, non-significant.

proline content in both species and GSH content in *C. operculatus* and significantly increased the content of soluble protein and GSH in *S. jambos*, compared with the monoculture (CK). Compared with the monoculture (W), the mixed planting under waterlogging conditions (W-M) significantly decreased proline content in both species, GSH content in *C. operculatus*, and ASA in *S. jambos*. The W-M treatment significantly increased the content of soluble protein and GSH in *S. jambos*. In addition, compared with the W treatment, the W-M treatment significantly reduced relative conductivity in *S. jambos* ($p < 0.05$).

Effects on Antioxidant Enzymatic Activities

The mixed planting under well water conditions (CK-M) significantly increased POD activities in both species, significantly decreased SOD activities in *S. jambos*, and had effects on CAT activities in both species, compared with the monoculture (CK; **Figure 5**). Compared with the CK treatment, the W treatment significantly increased POD activities (**Figure 5A**) in both species and SOD activities (**Figure 5B**) in *S. jambos* but significantly decreased CAT activities (**Figure 5C**) in both species. Compared with the monoculture (W), the mixed planting under waterlogging conditions (W-M) significantly increased POD activities in both species, decreased SOD activities in *S. jambos*, and had effects on CAT activities in both species. In addition, POD activity in *C. operculatus* was significantly higher than that in *S. jambos* within the same treatment ($p < 0.05$). The mixed planting resulted in a slightly higher increase in SOD activity in *C. operculatus* than the monoculture under well-watered or waterlogging conditions and significantly decreased SOD activity in *S. jambos* (**Figure 5**; $p < 0.05$).

Effects on Endogenous Hormones Contents

Compared with the monoculture (CK), the mixed planting under well water conditions (CK-M) significantly increased the levels of IAA (**Figure 6A**), ABA (**Figure 6B**), GA_3 (**Figure 6C**), and JA-Me (**Figure 6D**) in the leaves of *C. operculatus*, and significantly increased JA-Me content but significantly decreased IAA content in leaves of *S. jambos*, and had no effects on ABA content in the leaves of *S. jambos*. Compared with the CK treatment, the W treatment significantly decreased ABA and GA_3 content in both species; meanwhile

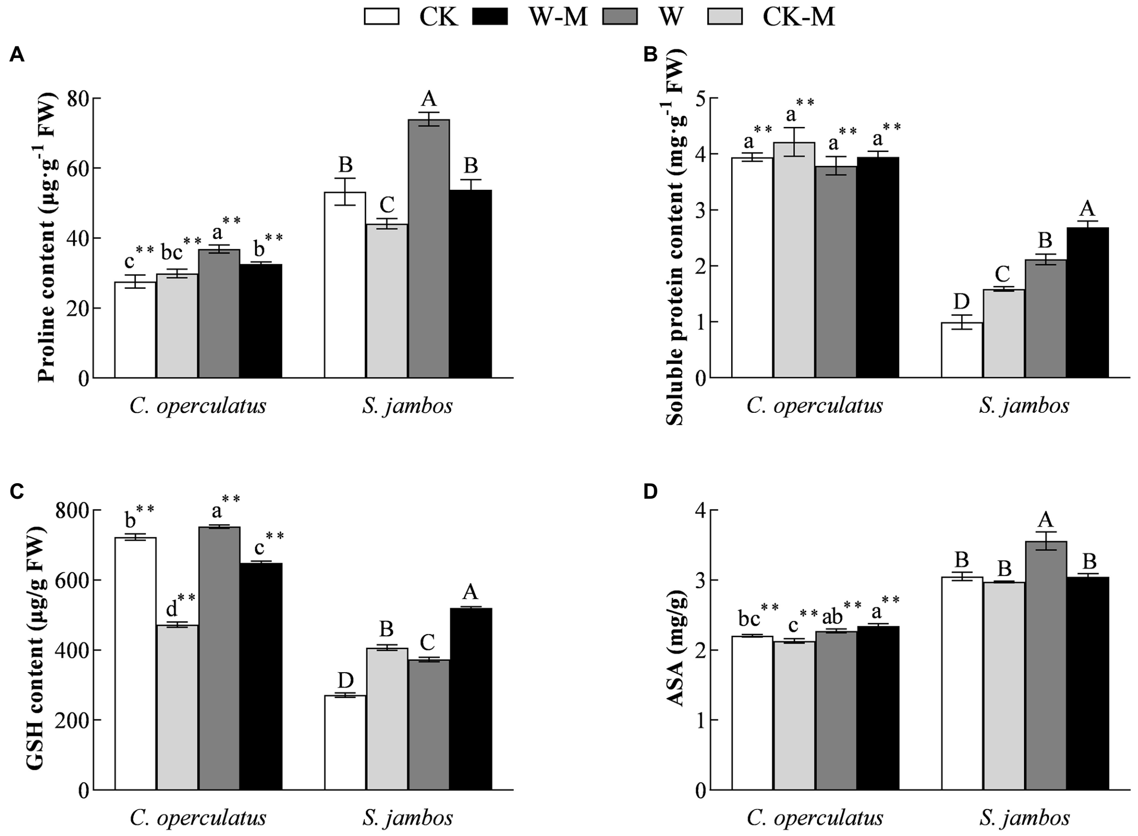

FIGURE 4 | The variations of proline **(A)**, soluble protein content **(B)**, GSH content **(C)** and ASA **(D)** in *C. operculatus* and *S. jambos* among different treatments. Values are means ± SE ($n = 6$). Different little and capital letters indicate significant differences among different treatments within the same species according to ANOVA's test ($p < 0.05$). CK, pure planting pattern under well-watered condition; CK-M, mixed planting pattern under well-watered condition; W, pure planting pattern under waterlogging condition, W-M; mixed planting pattern under waterlogging condition. The sign ** concerns the significance difference between the two species under the same treatment. $^{**}p < 0.01$.

it decreased significantly IAA content in *S. jambos*, significantly decreased JA-Me content in *C. operculatus*, and significantly increased JA-Me content in *S. jambos*. Compared with the monoculture (W), the mixed planting under waterlogging conditions (W-M) significantly increased the content of GA_3 and JA-Me in *C. operculatus*, significantly decreased their content in *S. jambos*, significantly decreased IAA content in *C. operculatus*, had no effect on *S. jambos*, and had no effects on ABA content in both species (**Figure 6**).

Correlation Analysis, PCA, and Subordinate Function Analysis

The results of PCA showed that the total contribution rates of PC1 and PC2 reached 92.81% in *C. operculatus*. The driving factors included photosynthetic pigment indexes (Chl a, Chl b, and total Chl), Pn, fresh weight of original root biomass, root length, root surface area, MDA, GSH, ASA, O_2^{-} content, relative conductivity, CAT activity, and leaf hormones (ABA, GA_3, IAA, and JA-Me). The differences among treatment groups were significant and can be easily differentiated and identified (**Supplementary Figure 1**). The total contribution rates of PC1 and PC2 were 80.89% for *S. jambos* (**Supplementary Figure 2**). The driving factors included root surface area, adventitious root biomass, original root biomass, photosynthetic pigment indexes (Chl a, Chl b and total Chl), Pn, Tr, Fv/Fm, MDA, GSH, ASA, O_2^{-} content, relative conductivity, and ABA, GA_3, and JA-Me content.

DISCUSSION

The results of the present research work showed that *C. operculatus* displayed more improvement in plant growth in the pure planting and monoculture. The mixed planting showed better advantages in plant growth and development for *S. jambos* seedlings under waterlogging stress. Indeed, the increase in morphological traits (IPH, IBN, LA, root length, and root surface area) and the enhancement of biomass accumulation in *C. operculatus* in the CK-M treatment (**Table 1** and **Figures 1, 2**) suggested that *C. operculatus* had good growth performance and received greater benefits than *S. jambos*, which showed poor growth performance and suffered from negative effects when both were species were cultured under well-watered

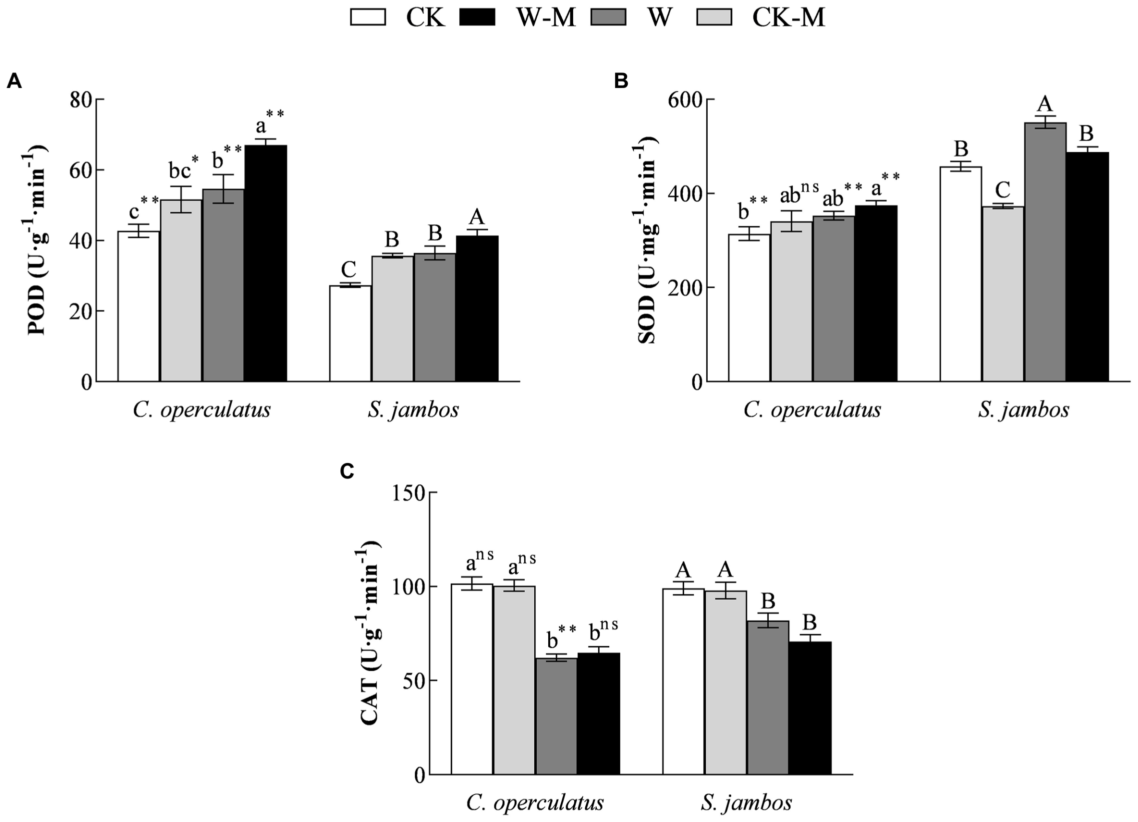

FIGURE 5 | The variations of POD (peroxidase, **A**), SOD (superoxide dismutase, **B**), and CAT (catalase, **C**) in *C. operculatus* and *S. jambos* among different treatments. Values are means ± SE (n = 6). Different little and capital letters indicate significant differences among different treatments within the same species according to ANOVA's test ($p < 0.05$). CK, pure planting pattern under well-watered condition; CK-M, mixed planting pattern under well-watered condition; W, pure planting pattern under waterlogging condition, W-M; mixed planting pattern under waterlogging condition. The signs such as *, **, and ns concern the significance difference between the two species under the same treatment. $^{*}p < 0.05$; $^{**}p < 0.01$; ns, no-significant.

condition. In another words, a competitive relationship existed between *C. operculatus* and *S. jambos* under this condition. Moreover, mixed planting system under stress conditions was significantly benefit for *S. jambos* in term of root length and root surface area, whereas it has no obvious effects in *C. operculatus* seedlings. Also compared to *C. operculatus*, the mixed planting has significantly alleviated damages in photosystem apparatus in *S. jambos* under waterlogging stress. Waterlogging has induced MDA, relative conductivity and superoxide anions production in both species. The soluble protein and GSH content in *C. operculatus* within the same treatment was significantly higher than that of *S. jambos*, whereas proline and ASA content showed an opposite trend. The antioxidant machinery played a major role in both species under stress. Furthermore, the phytohormonal profile was affected significantly by the type of specie, planting system and stress.

The survival of all the tested plants after 120 days of waterlogging suggested that *C. operculatus* and *S. jambos* are waterlogging-tolerant woody tree species, but the morphological and physiological responses to waterlogging of *C. operculatus* were better than those of *S. jambos*. Hence, *C. operculatus* possessed stronger waterlogging tolerance. Long-term waterlogging stress inhibited the growth of original root systems and even caused partial death of the original root system by causing root anoxia (Kaur et al., 2020). Thus, waterlogging stress caused a significant reduction in original root biomass, Pn, and pigment content in both species. Moreover, waterlogging induces the growth and development of adventitious roots at the bases of plant stems in waterlogging-tolerant species; this feature is an important survival and regulation mechanism (Bellini et al., 2014; Li et al., 2022). Adventitious roots can replace the normal functions of original roots that died from severe waterlogging stress and oxygen deficiency.

The competitive or facilitative effects among adjacent plants can be modified by environmental factors or biotic factors. For instance, the relationship between *Phragmites australis* and *Spartina alterniflora* decreased with tidal zone, and the mixed planting promoted the tillering production of the two species (Yuan et al., 2013). Waterlogging can decrease the growth, primary root fresh weight, total plant fresh weight, and total leaf area of *C. operculatus* when it is planted alone in one pot (Li et al., 2022). However, the W treatment increased the IBH levels, root surface area, aboveground biomass, and

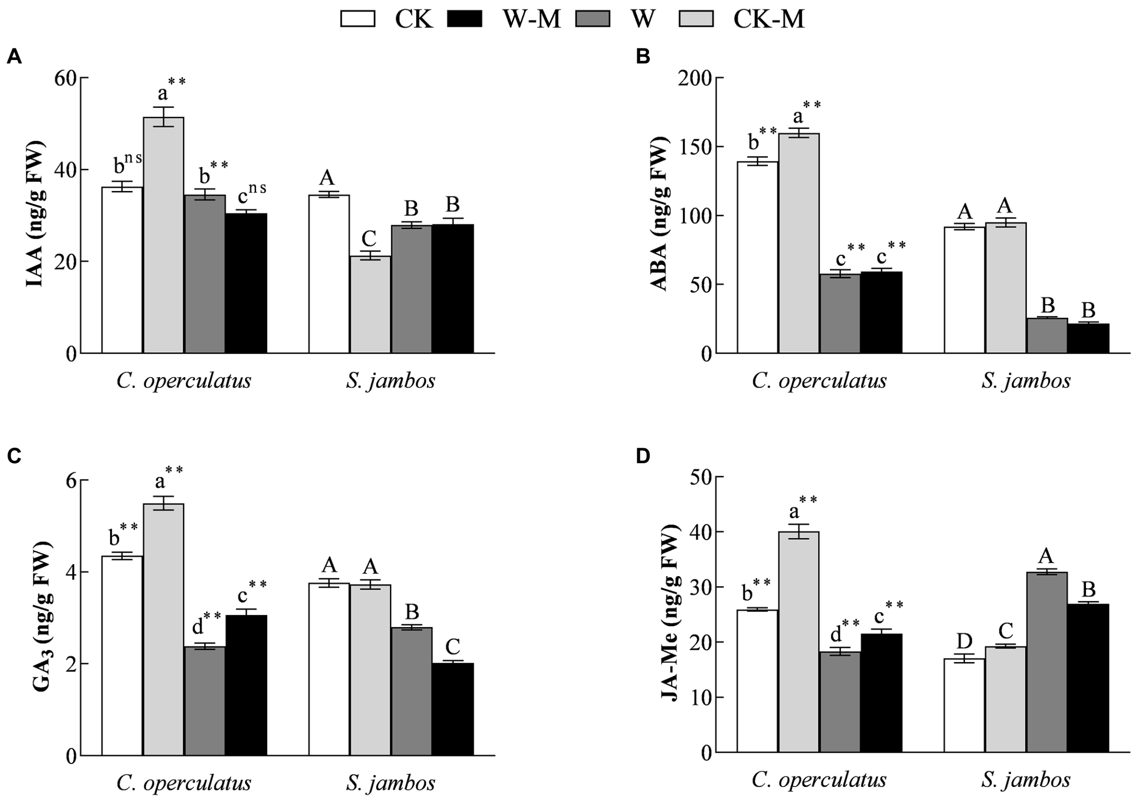

FIGURE 6 | The variations of IAA **(A)**, ABA **(B)**, GA_3 **(C)**, and JA-Me **(D)** in *Cylindrocopturus operculatus* and *Syzygium jambos* among different treatments. Values are means ± SE ($n = 6$). Different little and capital letters indicate significant differences among different treatments within the same species according to ANOVA's test ($p < 0.05$). CK, pure planting pattern under well-watered condition; CK-M, mixed planting pattern under well-watered condition; W, pure planting pattern under waterlogging condition, W-M; mixed planting pattern under waterlogging condition. The signs such as ** and ns concern the significance difference between the two species under the same treatment. $^{**}p < 0.01$; ns, no-significant.

underground biomass (**Table 1**; **Figures 1, 2**) in *C. operculatus* relative to those in the CK treatment when the plants were placed in one pot. This result suggested that the intra-specific relationship of *C. operculatus* further improved waterlogging tolerance. This effect was further enhanced by the abundant adventitious roots. These mechanisms may be the adaptable strategies that *C. operculatus* uses to survive under waterlogging stress. The adventitious roots facilitated O_2, water, and nutrient uptake (Ayi et al., 2016; Li et al., 2022). *C. operculatus* possesses efficient and positive adaptable strategies for alleviating waterlogging damage and can reform up-vertical adventitious roots from primary roots to adapt to waterlogging stress after the artificial removal of normal adventitious roots (Li et al., 2022).

Syzygium jambos suffered from negative effects under the well-watered mixed planting (CK-M), and its growth and development were negatively affected by in contrast to *C. operculatus* in the pure planting (CK). Nevertheless, the mixed planting under waterlogging conditions significantly improved IPH, IBN, LA, pigment content, fresh weight of adventitious roots, accumulations of aboveground biomass and underground biomass, root length, and root surface area in *S. jambos* (**Figures 1, 2**), in contrast to the pure planting (W). This result suggested that the mixed planting significantly improved the waterlogging adaptability of *S. jambos*. The increases in root length and root surface area expanded the contact area with soil, thereby facilitating the absorption of oxygen and nutrients (Ayi et al., 2016; Li et al., 2022). Moreover, *C. operculatus* has received few benefits from the mixed planting under waterlogging. The transformation of interspecific relationship under waterlogging condition may be attributed to the abundant adventitious roots of *C. operculatus*, which promoted the uptake and release of oxygen to water. This relationship improved the development and function of the adventitious root systems of *S. jambos* through aerobic rhizosphere. Therefore, the mixed planting pattern alleviated the negative responses of *S. jambos* to waterlogging. Bertness and Callaway (1994) and Lin et al. (2012) showed that the highest plant biomass accumulation and survival rates can be obtained under adverse external environmental stress, indicating the mutualistic relationship among adjacent plants under severe stressed conditions. Waterlogging-tolerant species can maintain high and stable photosynthetic capacity under submerged conditions. The chlorophyll is an essential component for the absorption and transmission of light energy and can adjust the ratio of light energy absorption and consumption in plants under stress and maximize the use of light energy (Klimov, 2003). Fv/Fm reflects the potential maximum photosynthetic capacity of plants and is an important indicator for studying photosynthesis. Although prolonged waterlogging reduced chlorophyll content, Pn, and Fv/Fm in both species as in previous studies (Bhusal et al., 2020), the mixed planting significantly increased pigment content, Pn, Gs, and Fv/Fm in *C. operculatus* and *S. jambos* under waterlogging stress (**Tables 2** and **3; Figure 3**). This finding suggested that mixed planting protected photosynthetic characteristics and was beneficial.

Waterlogging can trigger oxidative stress on plants at the sub-cellular level by overproducing ROSs and promoting their accumulation, such as hydrogen peroxide (H_2O_2) and O_2^-. The levels of relative conductivity and MDA reflected cell membrane stability, which is an indicator of stress tolerance (Yang et al., 2011, 2015). As the final product of membrane lipid peroxidation, MDA content not only directly expresses the degree of damage in plants under waterlogging stress but also indirectly reflects the tolerance of plants to stress (Yang et al., 2011, 2015). Some stress-tolerant plants can develop complete antioxidant systems that protect cell structures and sub-cellular organelles from oxidative damage, including non-enzymatic antioxidant components, such as proline, soluble proteins, GSH, and ASA, and antioxidant enzymatic systems, including POD, SOD, and CAT. Both types of components can act as ROS scavengers and lipid peroxidation inhibitors (Yang et al., 2015; Miao et al., 2017). The high relative conductivity and MDA and O_2^- levels (**Figure 3**) in *C. operculatus* and *S. jambos* under waterlogging stress suggested that waterlogging caused some oxidative stress and damaged the integrity of the cell membrane. However, their levels in the leaves of both plants decreased when the mixed planting was used, suggesting that the patter efficiently alleviated the damage due to waterlogging stress, especially in *S. jambos*. In addition, the mixed planting under waterlogging condition induced significant increases in the levels of GSH and soluble proteins in *S. jambos* and slightly increased SOD and CAT activities in *C. operculatus*, suggesting that *C. operculatus* and *S. jambos* employed different antioxidant systems to maintain the redox equilibrium and improve their waterlogging tolerance under waterlogging stress in the mixed planting.

The interactions of some hormones can activate defense responses and regulate plant growth and development under stress. IAA and GA_3 play important roles in the regulation of plant growth and fruit development, and ABA and JA-Me can inhibit the growth-promoting effects of IAA and GA_3 (Horbowicz et al., 2021). In the present study, the mixed planting under well-watered condition significantly increased the levels of IAA, ABA, GA_3, and JA-Me in *C. operculatus* but induced significant decrease in IAA content and increase in JA-Me content in *S. jambos* (**Figure 6**), suggesting that mixed planting exerted a positive effect on *C. operculatus* but caused some negative effects on *S. jambos* under well-watered condition. Khan et al. (2018) suggested that waterlogging stress improves flooding tolerance of *Glycine max* by suppressing endogenous ABA production and increasing JA-Me content and the dynamics of these hormones play an important role in the regulation of photosynthesis. The mixed planting under waterlogging condition significantly increased the levels of GA_3 and JA-Me in *C. operculatus* but induced significant decrease in their levels in *S. jambos* (**Figure 6**), indicating that *C. operculatus* benefited more in terms of growth advantages and waterlogging tolerance than *S. jambos* given that *S. jambos* gained more facilitation from the waterlogging mixed planting.

CONCLUSION

In general, *C. operculatus* and *S. jambos* are waterlogging-tolerant species, but *C. operculatus* has a higher waterlogging tolerance than *S. jambos*. A competitive relationship was found between *C. operculatus* and *S. jambos* under water-watered condition, and *C. operculatus* showed better growth performance and gained more benefits. *S. jambos* suffered from some negative effects under the well-watered mixed planting. However, the competitive relationship under well-watered condition transformed into a mutualistic one under waterlogging condition, and the mixed planting significantly improved the waterlogging tolerance of *C. operculatus* and *S. jambos* in comparison with the monoculture under waterlogging condition, especially *S. jambos*. The results showed that the interspecific relationship between *C. operculatus* and *S. jambos* can be transformed by waterlogging stress and improve their waterlogging tolerance. This study shed light on the relegation activities in the riparian areas and ecological watershed, especially for suitable plant species selection and plant community construction.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding authors.

AUTHOR CONTRIBUTIONS

FY designed the experiment and rewrote the manuscript. JZ performed the experiments, analyzed the data, and wrote the draft manuscript. E-HC performed the revisions. D-DL, L-YG, and L-SX assisted to carry the partial experiments. L-FM provided funding and managed the experiment. All authors contributed to the article and approved the submitted version.

FUNDING

This work was supported by Hainan Province Science and Technology Special Fund (ZDYF2022SHFZ054),Hainan Provincial Natural Science Foundation of China (Grant Nos. 421RC1033, 320RC507, and 421QN192), and National Science Foundation of China (Grant Nos. 32060240 and 31660165).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2022.869418/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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TYPE Original Research
PUBLISHED 13 October 2022
DOI 10.3389/fpls.2022.999793

OPEN ACCESS

EDITED BY
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SPECIALTY SECTION
This article was submitted to
Functional Plant Ecology,
a section of the journal
Frontiers in Plant Science

RECEIVED 21 July 2022
ACCEPTED 26 September 2022
PUBLISHED 13 October 2022

CITATION
Yang B-Y, Ali A, Xu M-S, Guan M-S,
Li Y, Zhang X-N, He X-M and
Yang X-D (2022) Large plants enhance
aboveground biomass in arid natural
forest and plantation along differential
abiotic and biotic conditions.
Front. Plant Sci. 13:999793.
doi: 10.3389/fpls.2022.999793

Large plants enhance aboveground biomass in arid natural forest and plantation along differential abiotic and biotic conditions

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Big-sized trees, species diversity, and stand density affect aboveground biomass in natural tropical and temperate forests. However, these relationships are unclear in arid natural forests and plantations. Here, we hypothesized that large plants (a latent variable of tall-stature and big-crown, which indicated the effect of big-sized trees on ecosystem function and structure) enhance aboveground biomass in both arid natural forests and plantations along the gradients of climate water availability and soil fertility. To prove it, we used structural equation modeling (SEM) to test the influences of large plants located in 20% of the sequence formed by individual size (a synthetical value calculated from tree height and crown) on aboveground biomass in natural forests and plantations while considering the direct and indirect influences of species diversity as well as climatic and soil conditions, using data from 73 natural forest and 30 plantation plots in the northwest arid region of China. The results showed that large plants, species diversity, and stand density all increased aboveground biomass. Soil fertility declined aboveground biomass in natural forest, whereas it increased biomass in plantation. Although climatic water availability had no direct impact on aboveground biomass in both forests, it indirectly controlled the change of aboveground biomass *via* species diversity, stand density, and large plants. Stand density negatively affects large plants in both natural forests and plantations. Species diversity positively affects large plants on plantations but not in natural forests. Large plants increased slightly with increasing climatic water availability in the natural forest but decreased in plantation, whereas soil fertility inhibited large plants in plantation only. This study highlights the extended generality of the big-sized trees hypothesis, scaling theory, and the global importance of big-sized tree in arid natural forests and plantations.

KEYWORDS

big-sized trees effect, climate water availability, niche complementarity effect, scaling theory, soil fertility

Introduction

How species diversity loss affects ecosystem functioning has sparked numerous concerns over the past three decades (Hector et al., 1999; Hooper et al., 2005; Huang et al., 2018). Evidence is mounting that a decline in species richness or diversity has a negative effect on plant productivity in grasslands (Tilman et al., 1996; Liang et al., 2016; van der Plas, 2019). Through this understanding, the niche complementarity hypothesis suggests that plant productivity or aboveground biomass increases with increasing plant species diversity because the coexistence of species can use the available resources more efficiently (Tilman et al., 1997; Loreau and Hector, 2001; Hooper et al., 2005). The selection effect hypothesis proposes that community productivity is often shifting with increasing species diversity due to the higher probability of productive species. In forest ecosystems, a considerable number of studies have demonstrated that large-diameter trees (big-sized trees) contribute disproportionally to aboveground biomass at either the individual or stand level (Clark and Clark, 1996; Lutz et al., 2012; Bastin et al., 2015). In addition to the influence of big-sized trees on carbon enhancement, species diversity and stand structure have been tested to promote forest productivity or aboveground biomass through the niche complementarity mechanism (Yachi and Loreau, 2007; Mensah et al., 2018). Although aboveground biomass shifting with big-sized trees and species diversity has been well documented in natural tropical and temperate forest ecosystems with high diversity and strong resistance (Ali et al., 2019b; Yuan et al., 2021), these responses and mechanisms in species-poor arid temperate forests (particularly in arid natural forest and plantation) remain largely understudied (Figure 1).

In global forests and woodlands, big-sized trees dominate above- and belowground carbon storage and reallocation processes, as well as provide abundant habitats for vertebrates, invertebrates, and microorganisms through their individual specific traits, such as large diameter, tall height, and big crown (Luyssaert et al., 2008; Lindenmayer et al., 2012; Lutz et al., 2012). More specifically, the scaling theory suggests that a few big-sized trees contribute a great quantity of the aboveground biomass (Clark and Clark, 1996; Slik et al., 2013). A study from moist tropical forests found that 1.5% large-diameter trees explain more than 50% of aboveground biomass variation at a regional scale (Bastin et al., 2015). Moreover, a global study of 48 primary and secondary forests indicated that the largest 1% of trees comprised 50% of aboveground live biomass, and the diameter threshold of big-sized trees has a positive effect on aboveground biomass (Lutz et al., 2018). However, what kind of role the big-sized trees play in species diversity-aboveground biomass is still unclear. A recent study of tropic forests revealed that big-sized trees have a strong positive effect on forest carbon storage in the natural forest but a negligible effect in plantations, which proved that the regulation of big-sized trees in species diversity-aboveground biomass might be dependent on vegetation types (Mensah et al., 2020). Compared to natural forests, plantations characterized by lower species diversity consisted of fast-growing woods (Erskine et al., 2006; Kelty, 2006; Subedi et al., 2012). There are unpredictable feedback differences in carbon sequestration to species diversity and large plants (a latent variable of tall-stature and big-crown of big-sized trees, which indicate the effect of big-sized trees on ecosystem function and structure) between natural forest and plantation. Nevertheless, we know little about the joint effects of species diversity and large plants on aboveground biomass in plantations.

Aboveground biomass responds differently to species diversity with various stand structures in natural forests, such as stand density (Forrester et al., 2013; Yoshida et al., 2017; Ouyang et al., 2019). Most studies assume that stand density promotes carbon sequestration *via* the complementarity of crown light resources (Vitamin, 2015; Forrester et al., 2018). Nevertheless, there is a great difference between the stand density of plantations and natural forests. Previous studies demonstrated that higher stand density has a negligible effect on aboveground biomass in plantations due to asymmetric resource competition (Poorter et al., 2012; Condés et al., 2013; Ma et al., 2021). Furthermore, competition has been confirmed to cause a negative density dependence, which would promote species diversity (LaManna et al., 2017), and thus, a shifting species diversity-aboveground biomass relationship would occur in plantations among various stand densities. Some studies have shown that stand structure and large plants regulate aboveground biomass jointly in natural forests (Ali et al., 2019a; Ouyang et al., 2019). Yet, we do not know whether the joint effects of stand density, species diversity, and large plants on aboveground biomass exist in plantations.

In natural forests and plantations, the effects of large plants and species diversity on aboveground biomass could be mediated by the variability of climate and soil conditions (Zhang and Chen, 2015; Ali et al., 2019b; Li et al., 2020). Studies have often shown that climatic water availability rather than soil fertility plays a major role in determining aboveground biomass directly and indirectly *via* large plants and species diversity in natural forests (Ali et al., 2019b), but these mechanisms are yet to be understood in plantations. Furthermore, a study focusing on natural shrub forests in arid regions demonstrated that increasing climatic water availability weakens the response of biomass to species diversity and density because of strong interspecific competition between drought-sensitive species (Guo et al., 2019). However, several studies in tropical and subtropical natural forests found that soil fertility increased aboveground biomass *via* large plants (Ali et al., 2019a; Ouyang et al., 2019). These studies suggest that the responses of aboveground biomass to biotic factors are shifting with climate and soil conditions among different ecosystems. Therefore, to

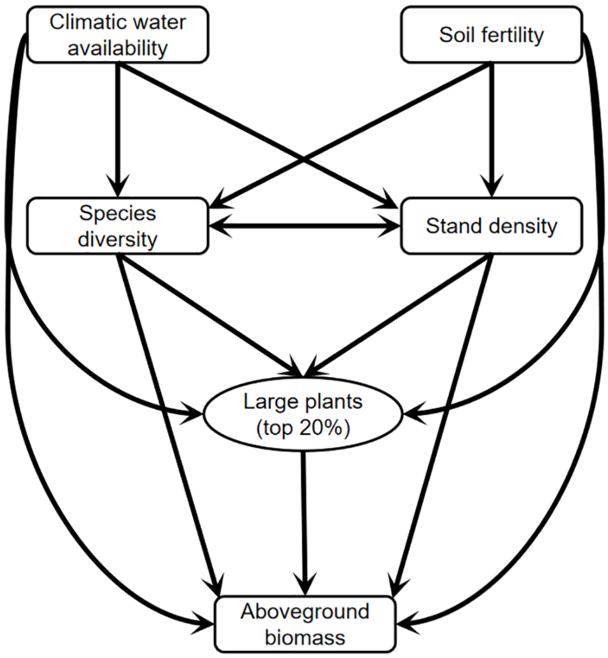

FIGURE 1
A conceptual model for testing the linkages among climatic water availability, soil fertility, large plants, species diversity, stand density, and aboveground biomass in natural forest and plantation of the arid temperate region in China.

better understand and predict carbon sequestration, we need to consider species diversity, large plants, and stand density under various climate and soil conditions in natural forest and plantation ecosystems.

Arid ecosystems cover more than 41% of the global land surface and are one of the most frangible biosystems to climate change and human activities due to lower biodiversity (Reynolds et al., 2007). A double warming tendency over arid regions than humid areas has been confirmed because of the reduced carbon sequestration (Huang et al., 2016). Numerous public efforts have been made to slow down the expansion rates of environmental degradation (i.e., desertification and desert expansion), such as afforesting plantations (Raich and Tufekcioglu, 2000; Paul et al., 2002; Piao et al., 2009). However, as mentioned above, there are many unknowns about the response of carbon storage to species diversity, large plants, and stand density in arid regions. Consequently, we aim to evaluate the relative effects of large plants, species diversity, and stand density on aboveground biomass in arid natural forests and plantations under climate and soil conditions in this study (Figure 1). We expect that (1) large plants play a central role in driving aboveground biomass in natural forest and plantation, whereas species diversity and stand density are of additional importance; (2) large plants and species diversity do not maintain each other in both natural forest and plantation, and hence, both of them play an independent role in driving aboveground biomass; (3) climatic water availability and soil fertility regulate species diversity, large plants, stand density, and aboveground biomass in natural forest and plantation through several underlying ecological mechanisms.

Materials and methods

Study area and forest inventory

The study area is located in the northwest arid region of China (31° 42′–53° 23′ N, 73° 40′–126° 04′ E), and it includes five provinces (Xinjiang, Gansu, Inner Mongolia, Shaanxi, and Ningxia). The total area is about 3.55 million square kilometers, accounting for about 78% of the arid area of China. The study area belongs to a typical arid temperate continental climate, with an annual average rainfall ranging from 75 to 557 mm, an annual average evaporation ranges 700 to 2,300 mm, and an average temperature ranging from −1.5°C to 9.6°C (Chen et al., 2016; Chen et al., 2017).

In this study, 103 plots (73 natural forest and 30 plantation plots, Figure 2) with sample areas equaling 25 and 400 m^2 were investigated haphazardly in the northwest arid region of China from June to September 2019. According to previous studies, 25 and 100 m^2 were the minimum sampling areas of shrub and forest communities, respectively, which covered the main changes in species and plant community composition in the

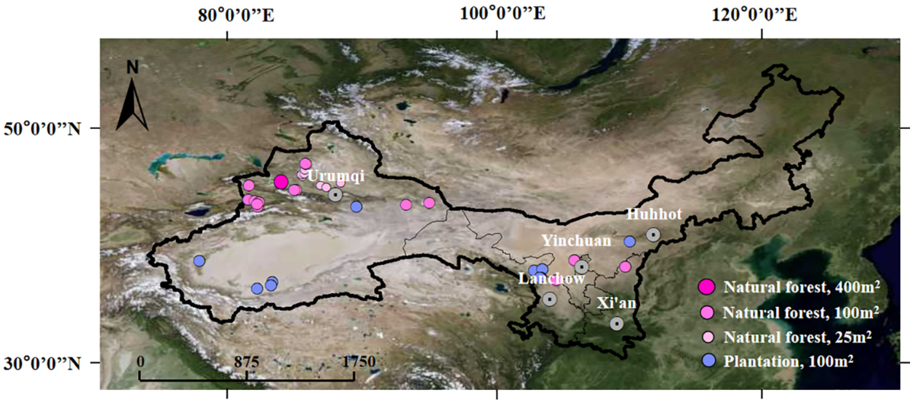

FIGURE 2
Sampling plot locations in the northwest arid region of China.

arid ecosystem (Chen et al., 2017; Guo et al., 2019). The influence of the total study area on the sampling intensity was not considered in this study, because most arid areas in northwest China are deserts, while plant community types and species in other areas are few and have an uneven distribution (Guo et al., 2019). In the sampling process, we first considered plant communities and included all community types as much as possible. Meanwhile, we haphazardly set up sample points. However, the distance between sampling points was expanded largely to ensure that information contained by different points overlapped less.

In each plot, tree height, diameter at breast height (DBH, 1.3 m from the ground), basal diameter (0.2 m from the ground), and crown width of all woody plants were determined by using a Vertex meter (Vertex-IV, Haglöf Haglof, Dalarna, Sweden) and a tape, and a meter stick, respectively. Crown width was calculated as the average diameter of the east-west and north-south cross sections of the crown using a meter stick. Crown area was estimated using the equation $(\pi \times D_{\text{east-west}} \times D_{\text{north–south}})/4$. Chinese Flora Database (http://foceflora.cn/) was used to identify species at the taxonomic level.

Natural forest plots included 2,915 individuals belonging to 21 species, 20 genera, and 11 families. *Haloxylon ammodendron*, *Populus euphratica*, *Tamarix chinensisare*, and *Caragana Korshinskii* are the common species in arid natural forests. Plantation plots included 780 individuals belonging to 14 species, 12 genera, and nine families. The frequent species are *Haloxylon ammodendron*, *Ulmus glaucescens*, and *Elaeagnus angustifolia*.

Aboveground biomass

We estimated the aboveground biomass of individual plants based on the species-specific allometric equations, which were based on the combinations of plant height, diameter, and crown dimensions (Supplementary Table S1). Total aboveground biomass is the sum of the aboveground biomass of all individual plants within each plot, which is then converted to a mega gram per hectare (Mg ha^{-1}).

Stand density, species diversity, and big-sized trees

Based on the forest inventory data, stand density was quantified as the total number of individuals per plot, which was then converted to stems per hectare. The Shannon–Wiener index was calculated to represent species diversity for each plot. In the forest community, a few big-sized trees could occupy the vast majority of the aboveground biomass (Slik et al., 2013; Bastin et al., 2015; Lutz et al., 2018). However, there is no universal definition for big-sized trees, but the general understanding is that big-sized trees vary among ecosystems (Lutz et al., 2018). For example, trees with a DBH of ≥20 cm in a cold coniferous forest, a DBH of ≥60 cm in temperate deciduous forests, and a DBH of ≥100 cm in tropical forests are generally defined as big-sized trees (Lutz et al., 2012). Still, different abiotic and biotic conditions may limit the threshold size for big-sized trees in different forest types and statuses. However, many woody plants have no DBH due to their short stature in arid regions (Guo et al., 2019). Precious studies have indicated that big-sized trees could be defined based on big-sized stature, for instance, plant height and crown (Lutz et al., 2018; Ali et al., 2019a). In order to characterize the big-sized trees, we used the entropy weight method (EWM) to calculate the weight of plant height and crown, then got the integrative values (58.62% stdheight + 41.38% stdcrown), which were then used to define the top 20% large trees within each plot. The proportion of the aboveground biomass of individuals in the top 1%, 5%, 10%, and

20% in the ranking position to the aboveground biomass was analyzed, respectively. In arid regions, especially in arid desert regions, severe environment makes the vast majority of individuals in sampling plots to be shrub species. Also, the effect of severe environment on plant growth results in small abundance in sampling plots. All big-sized trees might not be involved in the top 1%~10% of the ranking position. Therefore, the top 20% of individuals in the rank of DBH or base diameter were selected as the big-sized trees in this study. Our results indicated that there were 17 and 10 large plant species in natural forests and plantations, respectively (for more details, see Supplementary Table S2).

As suggested by Ali et al. (2019a), the influence of the top 20% of individuals in the rank of DBH or base diameter on forest structure and function was defined as the effect of the big-sized tree. It was a latent variable, represented by the "large plants," and composed of tree height and crown area in this study. The internal reason for this design was that the tree height and crown area of big-sized trees have a greater impact on ecosystem processes, such as light acquisition, interspecific competition, and shading, in the forest compared with DBH and basal diameter. After that, the ratio of the sum of the top 20% of individual biomass to the total biomass was calculated to verify the existence of large plants in arid regions.

Climatic water availability and soil fertility

To explore the influence of climatic water availability and soil fertility on the relationships among species diversity, stand density, large plants, and aboveground biomass, the annual climatic aridity index (CAI; mean annual precipitation/mean annual potential evapotranspiration) of each plot was downloaded from CGIAR-CSI (Trabucco and Zomer, 2009) to represent climatic water availability. Higher values of the aridity index represent the higher water content available for plant growth. The soil cation exchange capacity (CEC) of topsoil (0–30 cm) and subsoil (30–100 cm) were then obtained from Harmonized World Soil Database (FAO et al., 2012). Here, we used the mean soil CEC of topsoil and subsoil to define the soil fertility (Ali et al., 2019a).

Statistical analyses

The structural equation model (SEM) was used to test the conceptual model for linking climatic water availability, soil fertility, species diversity, stand density, large plants (a latent variable of tall-height and big-crown, indicating the influences of big-sized trees on forest structure and function) and aboveground biomass in arid natural forest and plantation (Figure 1). The degree of model fit was evaluated by using the following three indicators: standardized root means square residual (SRMR <0.08), comparative fit index (CFI >0.90), and goodness-of-fit index (GFI >0.90). We also employed the Wald statistic test to assess the significance of each hypothesized pathway in SEM ($p < 0.05$). We used a maximum estimator with standard errors and scaled statistics to estimate standardized coefficients. Direct, indirect, and total effects were estimated by using standardized coefficients. After testing the SEM, we calculated the relative contribution of each predictor variable (i.e., climatic water availability, soil fertility, species diversity, stand density, large plants) to explain variance in aboveground biomass (Ali et al., 2019a). As suggested by Grace et al. (2016) and Yuan et al. (2021), the relative contribution of each predictor referred to its proportion in explaining the variation of AGB (total variance) among all sampling plots. To be specific, in the SEM models, the total AGB variance was evaluated from two stratifications: (1) the direct contribution of each predictor to the total AGB variance. According to the variance partition of the multiple regression, the total AGB variance was reduced to the part that could be explained by each predictor (regression sum of the square) and the other part that could not be explained by them (residual sum of variance). In the first part, the proportion of each predictor in explaining the total AGB variance was considered its contribution and (2) the indirect contribution of each predictor to the total AGB variance *via* mediator variables. For each pathway (e.g., Figure 3), the variance partition of the binary regression was used to calculate the contributions of the predictor to the total variance of the mediator variable, and the latter to the total AGB variance. The product of these two contributions was taken as the indirect contribution of the predictor to the total AGB variance. The sum of the direct and indirect contributions at two stratifications was the total contribution of each predictor to the change in AGB among all samples. The SEM was implemented using the *lavaan* package (Rosseel, 2012) in R 3.6.0 (R Core Team, 2020).

Before the analysis, we performed a natural logarithmic transformation of the data to meet the requirements of normality and linearity. In order to validate the results from SEM, we also performed simple linear regression for each pathway in SEM. A summary of the variables used in the analyses is presented in Table 1.

Results

Differences in the drivers of aboveground biomass between natural forest and plantation

Based on the statistical results of 73 natural forest and 30 plantation plots, our study found that climatic water availability, species diversity, stand density, and aboveground biomass of 20% of the big-sized trees in the natural forest were significantly

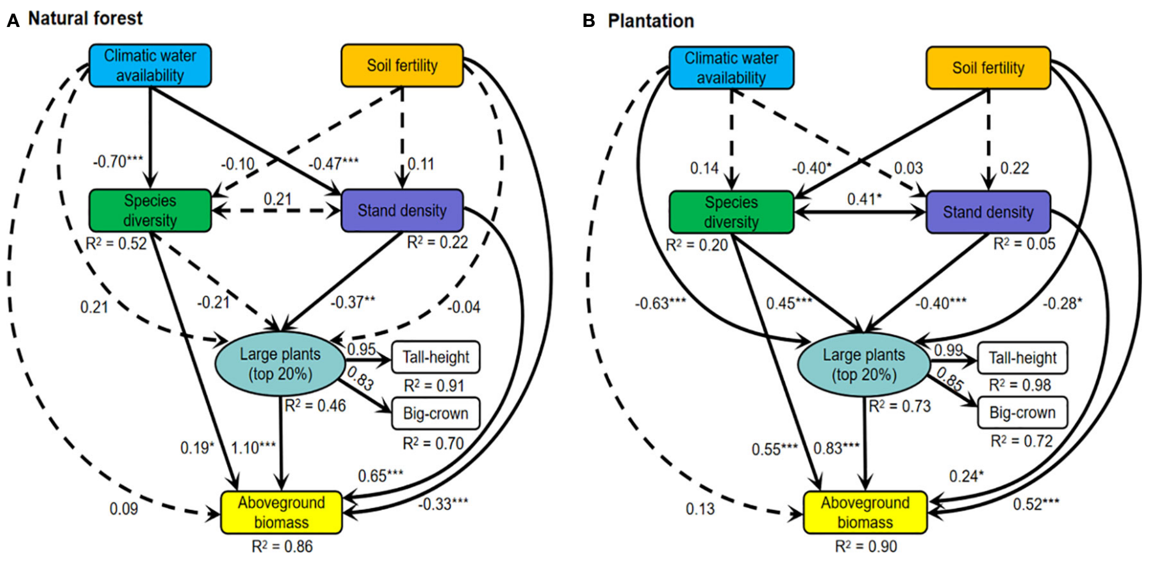

FIGURE 3
Structural equation models for linking climatic water availability, soil fertility, large plants (a latent variable of tall stature and big crown; indicated the influences of big-sized trees on ecosystem function and structure), species diversity, stand density, and aboveground biomass in **(A)** natural forest and **(B)** plantation of the arid temperate region in China. Solid lines represent significant paths ($p < 0.05$), while dashed lines indicate nonsignificant paths ($p > 0.05$). The confidence degree of the relationship between two paired variables at less than *0.05, **0.01, and ***0.001, respectively. For each path, the standardized regression coefficient is shown (Supplementary Tables S3, and S4). Model-fit statistics for **(A)**: comparative fit index (CFI) = 0.953, goodness-of-fit index (GFI) = 0.941, and the standardized root mean square residual (SRMR) = 0.052; **(B)**: CFI = 0.911, GFI = 0.941, SRMR = 0.055.

higher than in plantations. There were no significant differences in soil fertility between natural forest and plantation. Specifically, the mean of aboveground biomass in natural forest (27.02 ± 7.00 Mg ha^{-1}/mean ± SE) was higher than that of plantation (16.62 ± 2.98 Mg ha^{-1}/mean ± SE). The top 20% of individuals, based on the rank of integrative values, hold 59.25% of total aboveground biomass in natural forest, whereas they account for 39.66% of total aboveground biomass in plantations (Table 1). The

TABLE 1 Summary of the variables, from 73 natural forest plots and 30 plantation plots, was used in this study.

Forest type	Variable	Unit	Mean	SE	Minimum	Maximum
Natural forest	Top 20% tall height	m	5.58 a	1.01	0.73	41.00
	Top 20% big crown	m^2	8.00 a	1.25	0.19	59.96
	Hs	#	0.84 a	0.06	0.00	1.66
	SD	N ha^{-1}	3,859.93 a	324.15	800.00	18,400.00
	CAI	%	19.32 a	1.74	11.01	86.37
	Soil fertility	cmol kg^{-1}	12.19 a	0.58	5.00	28.00
	AGB	Mg ha^{-1}	27.02 a	7.00	0.03	353.28
	AGB proportion of 20% big-sized trees	Percentile	59.25 a	3.91	3.56	99.59
Plantation	Top 20% tall height	m	2.89 a	0.24	0.53	5.37
	Top 20% big crown	m^2	4.34 a	0.48	0.61	12.17
	Hs	#	0.44 b	0.07	0.00	1.06
	SD	N ha^{-1}	2,583.33 b	162.40	800.00	7,500.00
	CAI	%	11.64 b	1.94	1.23	33.43
	Soil fertility	cmol kg^{-1}	12.00 a	0.70	6.00	26.00
	AGB	Mg ha^{-1}	16.62 a	2.98	0.20	88.92
	AGB proportion of 20% big-sized trees	Percentile	39.66 b	4.10	7.82	97.53

Hs, species diversity; SD, stand density; CAI, climatic aridity index; AGB, aboveground biomass. All variables presented here are nontransformed "#" means that the index (Hs) has no unit (i.e., original data). Natural logarithm transformed values were used in the statistical analyses. Lowercase letters indicate significant differences between natural forest and plantation.

standard deviation in the proportion of the top 20% of individuals to total aboveground biomass in natural forest (0.33) was obviously higher than plantation (0.22) (Table 1).

SEMs: What determines aboveground biomass directly and indirectly in natural forest and plantation

The SEMs for natural forest and plantation showed that large plants, species diversity, and stand density had significant positive direct effects on aboveground biomass (Figure 3). Stand density declined for large plants directly in both natural forest and plantation ($r_{\mathrm{NA}} = -0.37$; $r_{\mathrm{PL}} = -0.40$). Species diversity had a negligible direct effect on large plants in the natural forest but a significant positive direct effect on the plantation ($r_{\mathrm{NA}} = -0.21$; $r_{\mathrm{PL}} = 0.45$). Climatic water availability had a negligible direct effect on aboveground biomass in natural forest and plantation ($r_{\mathrm{NA}} = 0.09$; $r_{\mathrm{PL}} = 0.13$), while soil fertility directly decreased aboveground biomass in natural forest but increased in plantation ($r_{\mathrm{NA}} = -0.33$; $r_{\mathrm{PL}} = 0.52$). Climatic water availability had a negative effect on species diversity and stand density directly in natural forest ($r_{\mathrm{NA}} = -0.70$; $r_{\mathrm{PL}} = -0.47$) but negligible direct effects in plantation ($r_{\mathrm{NA}} = 0.14$; $r_{\mathrm{PL}} = 0.03$). Soil fertility exerted a negligible influence on species diversity in the natural forest but decreased species diversity directly in plantation ($r_{\mathrm{NA}} = -0.10$; $r_{PL} = -0.40$). Large plants increased slightly with an increase in climatic water availability in natural forest but decreased in plantation ($r_{\mathrm{NA}} = 0.21$; $r_{\mathrm{PL}} = -0.63$), whereas soil fertility inhibited large plants in plantation only ($r_{\mathrm{NA}} = -0.04$; $r_{\mathrm{PL}} = 0.28$; Figure 3).

The comparative analysis of direct and indirect effects showed that large plants possessed a strong positive direct effect on aboveground biomass than species diversity and stand density in natural forest, while species diversity possessed stronger positive direct and indirect effects on aboveground biomass than large plants and stand density in plantation (Figures 3, 4A). Stand density possessed indirect negative effects on aboveground biomass *via* large plants in both natural forests and plantations. Species diversity possessed an indirect positive effect on aboveground biomass *via* large plants in the plantation but a negligible indirect effect in natural forests (Figures 3, 4A). Soil fertility possessed a strong indirect negative effect on aboveground biomass *via* species diversity and large plants in the plantation but a negligible indirect effect in natural forests. Climatic water availability possessed a strong

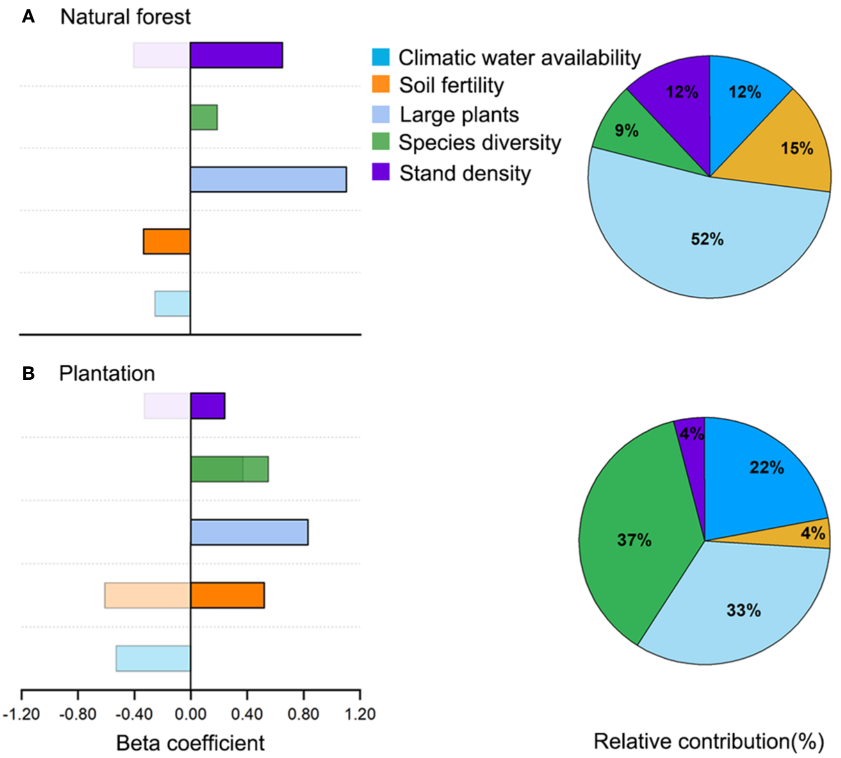

FIGURE 4
Total relative contribution (**A**; pie charts) of predictors to aboveground biomass and comparison of direct and indirect effects (**B**; bar charts) of predictors on aboveground biomass in natural forest and plantation. Solid-filled color represents direct effect, whereas pattern-filled color represents indirect effect.

indirect effect on aboveground biomass *via* stand density, species diversity, and large plants in natural forests and to a little extent in plantations (Figures 3, 4A).

The comparative analysis of the relative contribution (based on total effect or direct effect if there was no indirect effect) of drivers of aboveground biomass showed that, in natural forests, large plants explained higher variation in aboveground biomass followed by soil fertility, species diversity, climatic water availability, and stand density (Figure 4B). With respect to the plantation, species diversity explained higher variation in aboveground biomass, followed by large plants, climatic water availability, soil fertility, and stand density (Figure 4B). Bivariate relationships for each hypothesized path in natural forest and plantation are shown in Supplementary Figures S3, S4, respectively.

Discussion

In this study, we explored the relative effects of large plants, species diversity, and stand density on aboveground biomass along climate and soil gradients in natural forests and plantations in an arid region. We found that large plants and species diversity increased aboveground biomass directly in natural forests and plantations, hence providing theoretical support to niche complementarity and big-sized trees effects (Morin et al., 2011; Ali et al., 2019a). However, these positive effects were different in plantations and natural forests, which might be due to the differential mechanisms and direct effects of climatic water availability and soil fertility on aboveground biomass, as well as indirect effects *via* large plants, species diversity, and stand density (Zhang and Chen, 2015; Ali et al., 2019b; Ouyang et al., 2019; Li et al., 2020). In sum, our results suggest that the small portion of biotic drivers (i.e., large plants, species diversity, and stand density) enhance aboveground biomass through similar mechanisms whereas the small portion of abiotic drivers regulates aboveground biomass through opposing mechanisms in natural forest versus plantation (van der Sande et al., 2017; Mensah et al., 2020; Wu et al., 2020).

Large plants increased aboveground biomass in both natural forests and plantations, providing the first evidence of the generality of the big-sized trees hypothesis as well as to scaling theory and the global importance of big-sized trees (Clark and Clark, 1996; Slik et al., 2013; Bastin et al., 2015; Lutz et al., 2018; Ali et al., 2019a). The strong positive effect of large plants on carbon sequestration in natural forests and plantations is because big-sized trees modulate the above- and belowground resource allocation *via* luxuriant branches and fine roots which has positive feedback on carbon storage (Luyssaert et al., 2008; Lutz et al., 2012). More specifically, we found that the taller and bigger crown plants dominate (i.e., top 20%) 59.25% and 39.66% of the biomass in a plot, respectively. The natural forests have a higher increase in aboveground biomass than plantation. These result is consistent with a recent local-scale study that showed that large plants have a stronger positive influence on aboveground biomass in natural forests than mixed plantations (Mensah et al., 2020). The change in the effect of large plants between natural forest and plantation largely results from the similar stand age in the plantation, which, against the generation of big-sized trees, further leads to a weaker big-sized tree effect (Ruiz-Jaen and Potvin, 2011; Subedi et al., 2012; Ouyang et al., 2019). Interestingly, we found no relationship between species diversity and large plants in natural forests but found a positive relationship in plantations. In natural forests, there is no relationship between species diversity and large plants, which might be further attributable to the environmental filtering effect (Morin et al., 2018). Drought-sensitive species and near-drought–resistant neighbors tend to aggregate in arid regions after environmental filtering (Guo et al., 2019; Wright et al., 2021), indicating that diverse community compositions may buffer multiple biotic interactions, such as the influence of species diversity on large plants. The positive relationship in the plantation is the result of niche complementarity, but we found a negative relationship between large plants and stand density in both natural forest and plantation. These results point to a competitive exclusion mechanism in the natural forest, whereas niche complementarity among species of dominant functional group in plantations (Yachi and Loreau, 2007; Subedi et al., 2012; Forrester et al., 2013; Liu et al., 2020), and thus lead to species competition due to big-sized trees in different ways, resulting in a reduction in stand density directly and aboveground biomass indirectly (van der Sande et al., 2017; Ouyang et al., 2019).

Aboveground biomass in the natural forest and plantation was mainly explained by large plants and species diversity, even though the relative contribution of the drivers varied due to the indirect effects in some cases. This pattern indicates species diversity and large plants may govern carbon sequestration in various ecosystems (Ruiz-Jaen and Potvin, 2011; Mensah et al., 2020). In plantations, species diversity promotes aboveground biomass through facilitating abiotic and biotic conditions simultaneously, for instance, light interception and seed dispersion (Binkley et al., 2010; Nagaike et al., 2012). In a natural forest, the positive relationship between species diversity and aboveground biomass was expected due to the complementarity effect, particularly in water availability complementarity (Guo et al., 2019; Wright et al., 2021; Yang et al., 2022). Previous studies showed that the positive facilitation between different plant species was common in arid regions, for instance, the hydraulic redistribution of soil water (Yu et al., 2013; Guo et al., 2019). Thus, deep-rooting species (such as *Populus euphratica* and *Tamarix chinensis*) would lift groundwater or deep soil water to the soil surface for the survival of other species (e.g., *Kali collinum* and *Alhagi sparsifolia*). However, the resource-use complementarity mechanism might have influenced aboveground biomass differentially in natural forests and plantations, probably due to the contrasting influences of resource supply patterns on species diversity.

Stand density has a strong positive effect on aboveground biomass in both natural forests and plantations. This similarity may be due to the resource complementarity effect, which means higher stand density intensifies the positive interspecies interactions that drive plants to make effective utilization of light, water, and soil nutrients (Morin et al., 2011; Forrester et al., 2018). However, stand density also had an indirect negative effect on the aboveground biomass of natural forest and plantation *via* large plants, indicating stand density may regulate the aboveground biomass in both natural forest and plantation by suppressing the dominant species, such as big-sized trees (Boyden et al., 2005; Subedi et al., 2012; Ouyang et al., 2019). Previous studies suggested that the direct and indirect effects of stand density on aboveground biomass are related to stand age, stand structure, functional diversity, and ecosystem types (Paquette and Messier, 2011; Guo and Ren, 2014; Yuan et al., 2018; Ouyang et al., 2019). For example, in subtropical forests, the positive regulation of stand density on aboveground biomass would be stronger with the increase of stand age. These results indicate the importance of stand density on aboveground biomass *via* different pathways in natural forests and plantations. However, our results differed from those of previous studies, which high densities result in lower biomass due to increased mortality from competition (Fernandez Tschieder et al., 2012; Sun et al., 2018). The potential reason for our results may be the complementarity effect of the resource. Two reasons may be explained for it: (1) the influences of stand closure or stand age (Guo and Ren, 2014; Ouyang et al., 2019): aboveground biomass decreased as stand density increased due to intensive sapling competition before stand closure. After stand closure, aboveground biomass shows an upward tendency with the increase of stand density because of resource complementarity; and (2) the influences of functional diversity (like RaoQ or CWM trait) (Yuan et al., 2018; Yuan et al., 2021): higher density may lead to lower productivity when the community consists of the same functional species, such as acquisitive species. On the contrary, it would increase productivity if the community had a higher functional diversity.

Climatic water availability had a negligible positive effect on aboveground biomass in both natural forest and plantation, whereas soil fertility directly increased aboveground biomass in plantation only, indicating that plant physiological and metabolic processes are directly influenced by the length of the growing season and nutrient availability, but the directions of these influences are context-dependent (Poorter et al., 2017; Ali et al., 2019a). However, it is also expected that species diversity, large plants, and stand density might be spatially structured and might be driven in part by abiotic factors differentially in natural forests and plantations (Van et al., 2017; van der Sande et al., 2017; Wang et al., 2017; Wu et al., 2020). As such, we found that climatic water availability and soil fertility influenced species diversity, large plants, and stand density through opposing mechanisms in natural forest and plantation, and hence differentially determined aboveground biomass indirectly *via* biotic factors (Morin et al., 2018; Ali et al., 2019b). Previous studies have shown that climatic water availability and soil nutrients regulate forest productivity *via* shifting inter-intraspecific relationships, but their direction and intensity are closely related to species functional composition, succession stage, and stand age (Page-Dumroese et al., 2010; Coomes et al., 2014; Guo and Ren, 2014; Ouyang et al., 2019). For instance, it has been confirmed that the positive responses between productivity to mean annual precipitation and soil fertility are stronger in the mature forest than in young forest (Michaletz et al., 2014; Ouyang et al., 2019). More specifically, soil fertility decreased aboveground biomass in plantations indirectly *via* species diversity, large plants, and stand density, whereas the indirect effects were negligible in natural forests, indicating that the influences of abiotic factors are largely dependent on underlying biotic factors and thus context-dependent (Poorter et al., 2015; Ali et al., 2019b; Li et al., 2020). In plantations, abiotic factors regulated aboveground biomass *via* biotic factors. The strong indirect effect might be that the influence of initial anthropogenic inference on carbon sequestration decreases with stand age, and then the environmental resource availability intensifies the biotic process, which may decrease aboveground biomass (Subedi et al., 2012; Forrester, 2014; Wu et al., 2020). Previous studies have confirmed that with increasing stand age, there are stronger biotic interactions in plantation, such as self-thinning (Subedi et al., 2012; Guo and Ren, 2014). In an arid natural forest, the negligible indirect effect between soil fertility and aboveground biomass *via* biotic factors might be related to resource limitation (Guo et al., 2019; Li et al., 2020). Poor soil conditions limit plants' growth process and hence weaken the indirect effect.

Conclusions

A vast literature has explored the relationship between species diversity, stand structure, and forest function, but less so about the relationships among species diversity, large trees, and forest functions. Our study presents the first empirical results on the relationship among large plants, species diversity, stand density, and aboveground biomass in arid natural forests and plantations. This study highlights the importance of large plants to aboveground biomass in both natural forests and plantations along abiotic and biotic gradients, hence supporting the generality of the big-sized tree hypothesis and scaling theory. Although our results show that large plants, species diversity, and stand density increase aboveground biomass in both natural forests and plantations, the roles of climatic water availability and soil fertility seem to be differential in natural forests and plantations. We need to point out that the regulation of plant species diversity and large plants to aboveground biomass is dependent on spatial scale, indicating that numerous samplings across a large spatial scale for further exploration are necessary, particularly in sensitive and species-poor arid regions. Moreover, we argue that further work is still needed to explore the underlying role of plant species' functional strategies, in terms of functional diversity and composition, in order to fully explore the underlying ecological mechanisms in natural forests and plantations.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

Author contributions

X-DY and AA developed the idea and designed the study. B-YY, YL, X-DY collected the data. B-YY analyzed the data and wrote the paper with full support from AA, YL, X-NZ, X-MH, and X-DY. All authors contributed to the article and approved the submitted version.

Funding

This work was supported by the National Natural Science Foundation of China (Grant Nos. 41871031 and 31860111), Natural Science Foundation of Xinjiang (Grant No. 2017D01C080), and the Science and Technology Innovation 2025 Major Project of Ningbo City (Grant No. 20212ZDYF020049). Arshad Ali was supported by Hebei University (Grant No. 521100221033).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2022.999793/full#supplementary-material

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frontiers | Frontiers in Plant Science

TYPE Original Research
PUBLISHED 13 January 2023
DOI 10.3389/fpls.2022.1088955

OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to Functional Plant Ecology, a section of the journal Frontiers in Plant Science

RECEIVED 03 November 2022
ACCEPTED 22 December 2022
PUBLISHED 13 January 2023

CITATION
Liang Z, Liu T, Chen X, Xu W, Dong T, Liu Q and Xu X (2023) Twigs of dove tree in high-latitude region tend to increase biomass accumulation in vegetative organs but decrease it in reproductive organs. *Front. Plant Sci.* 13:1088955. doi: 10.3389/fpls.2022.1088955

Twigs of dove tree in high-latitude region tend to increase biomass accumulation in vegetative organs but decrease it in reproductive organs

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Adaptive traits are an important dimension for studying the interactions between rare plants and environment. Although the endangered mechanism of rare plants has been reported in many studies, how their twigs adapt to heterogeneous environments associated with latitude is still poorly known. Dove tree (*Davidia involucrata* Baill.), a monotypic rare species in China, was employed as a model species in our study, and the differences in functional traits, growth relationships and resource allocation among components of annual twig were investigated in three latitudinal regions (32°19′ N, 30°08′ and 27°55′) in the Sichuan, Southwest China. Compared with low- and middle-latitude regions, the twig diameter in high-latitude region decreased by 36% and 26%, and dry mass decreased by 32% and 35%, respectively. Moreover, there existed an allometric growth between flower mass and stem mass or leaf mass in high-latitude region but an isometric growth in low- and middle-latitude regions. At the flower level, an isometric growth between bract area and flower stalk mass was detected among in three latitudinal regions, and the flower stalk mass in the low-latitude region was higher than in the middle- and high-latitude regions for a given bract area and flower mass. At the leaf level, the growth rate of petiole mass was significantly higher than those of leaf area, lamina mass and leaf mass among three latitudinal regions, and the petiole mass in the low-latitude region was higher than in the other two regions for a given leaf mass. Our research demonstrated that the twigs of dove tree in high-latitude region tend to become smaller, and resource input increase in stems and leaves but decrease in flowers, which reflects that dove tree can adapt to the environmental changes across different latitudes by adjusting phenotypic traits growth and biomass allocation of twigs.

KEYWORDS

biomass, *Davidia involucrata*, functional adaptation, latitude, twig components

1 Introduction

The mutual relationship between plants and the environment is one of the research focuses in ecology. In many environmental factors, changes in latitude can significantly influence plants' growth and reproduction. Due to changes in latitudes, the ambient temperature, rainfall, soil conditions, solar radiation and abundance of pollinators also change accordingly (Li et al., 1998; Silva and Eguiarte, 2003; Shi et al., 2019; Shi et al., 2020a), resulting in significant differences in individual size, resource allocation, flower morphology, as well as reproduction strategy of plants (Mcintosh, 2002; Herrera et al., 2006; Cosacov et al., 2014). These phenomena reflect the response of plants to environmental heterogeneity by phenotypic plasticity. Moreover, some studies reported that the interaction between plants and environmental factors could change the biomass allocation and the investment-benefit-cost relationship of plants, which may be a trade-off between various traits of plant organs (Liu M. D. et al., 2020; Shi et al., 2020b; Li et al., 2021; Shi et al., 2022). The trade-off mean that an organism gains benefits from one trait, another trait pays appropriate costs. This evolutionary problem faced by all plants living in a given environment is how to allocate their limited resources to maximize their survival and reproduction possibilities (Stearns, 1989). Plants can change the investment cost between different organs or within the level of organ through trade-off relationship to allocate the limited resources reasonably and achieve the optimal return to adapt the needs of different growth and development stages. Such a trade-off relationship in turn may influence morphological construction, nutrient adsorption and transportation of plants, which reflect the ecological strategy of plants in the evolution of life histories (Sun et al., 2006; Dai et al., 2020).

In addition, as the most active part of the plant branch system, annual twigs are an important channel for water and organic transportation in plants. They support the growth and development of leaves, flowers and fruits, and their biomass allocation among organs will directly affects the growth and reproduction of the plant. Therefore, it is important to study the biomass allocation and configuration characteristics in twigs for plant life history strategy (Osada, 2006). As far as the component of a twig is concerned, leaf is the important organ for plants to acquire resources. Their morphological characteristics and biomass allocation influence the capacity of carbon acquisition (Givnish and Vermeij, 1976). Stem serve as an important structural unit of plants, transporting nutrients and providing mechanical support, they also can adjust branch and leave distribution patterns in the canopy to improve photosynthetic efficiency by changing their lengths, diameters and arrangement modes (Day et al., 2002; Thomas and Winner, 2002). As a vital functional organ for the reproduction of angiosperms, flower plays an important role in attracting pollinators and in the accurate coupling of pollinators (Alexandersson and Johnson, 2002; Herrera, 2005). Since functional traits of plants are often in harmony with each other, plants have to properly allocate biomass and nutrients among different structures and functions for survival and reproduction, such as the balance among stems, leaves, flowers, and other organs, which is an important biological characteristic for plants to coordinate growth (Normand et al., 2008; Campbell et al., 2011). For example, stem and leaf present isometric growth relationship and the same proportional biomass allocation pattern holds across extant seed plant species (Niklas and Enquist, 2002). The size of branches and leaves of woody plants exhibit an isometric growth relationship in temperate forest community (Sun et al., 2006). Stem mass and leaf mass of twigs present an isometric scaling relationship in plant *Populus cathayana* (Yang et al., 2015). The size and weight of bract of *D. involucrata* population in low-altitude areas are significantly higher than those in high-altitude areas, but the latter prefers to allocate more resources in supporting structures (Liu T. T. et al., 2020). Nevertheless, the above studies mainly focused on the stem-leaf relationship or reproduction strategies, but the growth relationships between functional traits and resource allocation patterns among reproductive organ (flower), support organ (stem) and vegetative organ (leaf) at the level of twig in different latitudinal regions were rarely involved.

Davidia involucrata Baill. belongs to *Davidiaceae*. It is a Tertiary relict deciduous trees in China and has been listed in China Red Data Book as a Class I species for protection (Fu and Jin, 1992). As climatic changes intensify in recent decades, the habitat conditions of *D. involucrata* have changed accordingly, which resulting in a sharp decrease in natural population size (Tang et al., 2017). Therefore, it is very important to pay attention to the variations in functional traits and the relationships between resource allocation and heterogeneous environments in *D. involucrata* plants. However, previous studies on *D. involucrata* mainly focus on reproductive capability, population dynamics, community characteristics, molecular biology and physiological ecology (Li et al., 2016; Liu et al., 2019; He et al., 2020; Yang et al., 2020; Liu et al., 2021). Since changes in latitude may lead to corresponding changes in the temperature, water and light intensity in plant habitats (Osada et al., 2015), we speculated that such changes might influence functional traits and biomass allocation pattern at the twig level, especially in rare endangered plant groups with poor habitat adaptability. To test this hypothesis, three natural *D. involucrata* populations with similar altitude which located at Pingwu (PW; 104°32′ E, 32°19′ N), Tianquan (TQ; 102°26′ E, 30°08′ N) and Gongxian county (GX; 104°52′ E, 27°55′ N) in Sichuan, Southwest China, were chosen as representative groups in high, middle and low-latitude region, respectively. The functional traits (leaf, flower and stem) of annual *D. involucrata* twig were measured. Based on these findings, the growth relationships between traits were analysed with the standardized major axes (SMA) to determine whether latitude may influence the functional traits and resource allocation strategies in *D. involucrata* populations.

2 Materials and methods

2.1 Study sites

Natural *D. involucrata* populations located at three latitude regions in Sichuan Province were chosen as the research objects (Figure 1). The geological distribution is PW, TQ and GX from north to south. All three regions are located at the intersection zone between the southeast edges of the Qinghai-Tibet Plateau and the Sichuan Basin. The soil of three sampling sites is yellow-brown forest soil, with pH value and organic matter of 6.6 and 2.66%, respectively (Chen et al., 1992). They all belong to subtropical monsoon climates with a latitude gap of about 2°, which reflects an excellent zonal characteristic of latitude. General information about the basic environment is shown in Table 1.

2.2 Plant sampling

In the flowering stage of *D. involucrata* populations from mid-April to early May, 6 – 8 healthy plants with similar DBH (diameter at breast height) and no insect pests were randomly selected from the three natural populations in PW, TQ and GX. Selected trees were (a) healthy with similar habitats (soil type, slope and aspect, in Table 1); (b) full grown with similar canopy size; (c) not to be located near the edge of the forest, or next to previously sampled trees. Then, to avoid growth differences derived from light intensity, 3 – 5 annual twigs (including stem and all leaves and flowers above the stem) were randomly collected from the sunny side of the lower crown of each plant. The range of mean DBH and mean crown was from 32.01 to 37.50 cm and from 8.55 to 10.93 m, respectively, and no significant differences were detected among three sampling sites ($P = 0.275$ and $= 0.207$, respectively). The plant samples were collected in sealed bags and numbered before being placed in an incubator with ice bags. They were brought back to the laboratory and stored in a 4°C refrigerator.

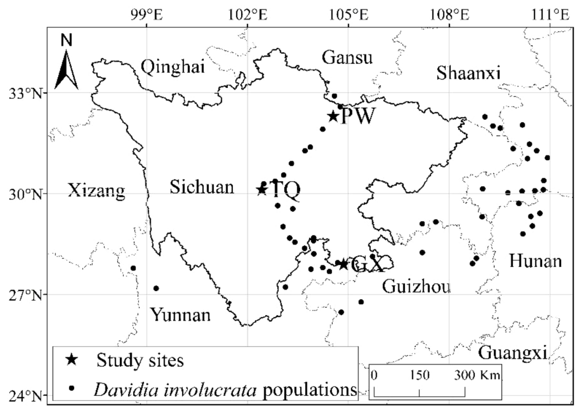

FIGURE 1
Location of study site in Sichuan, China.

2.3 Measurement of twig traits

The morphological and biomass traits of leaf, stem and flower from each twig were measured. Lamina, petiole, bract and flower stalk were scanned using CanoScan LiDE210, and then the length, width and area of lamina and bract, as well as the petiole length and flower stalk length were measured by the software Image J version 1.47v (National Institutes of Health, USA). The diameter of stem and flower stalk were measured with an electronic vernier calliper (0.01 mm), respectively. Biomass samples were oven-dried to constant mass (70°C, 72 h), then the lamina mass, petiole mass, bract mass, receptacle mass, capitulum mass, flower stalk mass and stem mass for each twig were separately measured. The leaf area or leaf mass was the sum of lamina area and petiole area, or lamina mass and petiole mass. The flower mass was the sum of mass of bract, receptacle, capitulum and flower stalk. The twig mass was the sum of the mass of stem, leaves and flowers. The mean of leaf area, lamina length and lamina width was calculated as the total area, length or width divided by leaf number for each twig, respectively.

2.4 Data analysis

Statistical analyses were performed using SPSS version 25.0 (SPSS, Inc., Chicago, IL, USA). Data were checked for normality and the homogeneity of variances, and log-transformed to correct deviations from these assumptions when needed. The Shapiro-Wilk normality test was used to evaluate normal distribution. One-way ANOVAs were used to determine differences among three latitudinal regions, and the Least Significant Difference (LSD) test was employed to detect possible differences among means. Differences were considered significant if the $P < 0.05$. The growth relationships between traits were analysed with a type II regression model, and the standardized major axes (SMA) were performed using the SMATR Version 2.0 (Falster et al., 2006). Confidence intervals for individual regression slopes were calculated according to Pitman (1939), and tests for heterogeneity of regression slopes between the sexes and calculation of common slopes where homogeneity of slopes were demonstrated followed Warton and Weber (2002).

3 Results

3.1 Comparisons of the traits of twig components in three latitude regions

The morphological traits of the reproductive organ, support organ and nutritive organ of *D. involucrata* twig were significantly different among different latitude regions. Stem diameter and flower stalk diameter decreased significantly with increasing latitude ($P <$

TABLE 1 The general information of *D. involucrata* populations in three latitude regions.

Population	PW	TQ	GX
Site	Pingwu	Tianquan	Gongxian
Longitude	104°32′ E	102°26′ E	104°52′ E
Latitude	32°19′ N	30°08′ N	27°55′ N
Altitude	1600 m	1803 m	1600 m
Mean annual temperature	10.1°C	15.1°C	18.2°C
Mean annual precipitation	866.5 mm	1735.6 mm	1126.0 mm
Soil type	Yellow-brown forest soil	Yellow-brown forest soil	Yellow-brown forest soil
Slop	40°	40°	45°
Aspect	Northeast	West	North
Forest type	Deciduous broad-leaved and Evergreen broad-leaved mixed forest	Deciduous broad-leaved forest	Deciduous broad-leaved and Evergreen broad-leaved mixed forest
Main woody species	Macrophanerophytes: *Davidia involucrata*, *Carya cathayensis*, *Quercus aliena*, *Cornus controversa*, *Machilus nanmu* Frutex: *Viburnum dilatatum*, *Litsea pungens*, *Cornus officinalis*	Macrophanerophytes: *Davidia involucrata*	Macrophanerophytes: *Davidia involucrata*, *Fagus longipetiolata*, *Sassafras tzumu*, *Acer pictum*, *Rehderodendron macrocarpum* Frutex : *Ternstroemia gymnanthera*, *Eurya loquaiana*, *Litsea pungens*,
Dominant species	*Davidia involucrata*	*Davidia involucrata*	*Davidia involucrata*
Population size	40 – 50 ha	1000 – 1100 ha	50 – 65 ha

PW, Pingwu; TQ, Tianquan; GX, Gongxian.

0.001 and < 0.001, respectively). The bract area and flower stalk length were the highest in low-latitude region, and the bract area showing significant differences from that in the middle- and high-latitude regions, and the flower stalk length was significantly different from that in the middle-latitude region (P = 0.014 and = 0.005, respectively). Moreover, the mean leaf area, mean lamina length and mean lamina width in high-latitude region were significantly higher than those in the other two regions (P < 0.001 and < 0.001 and < 0.001, respectively). Moreover, there was no significant difference in leaf area among different latitude areas (P = 0.614) (Table 2).

The biomass traits of reproductive, support and nutritive organ of *D. involucrata* twigs were significantly different in different latitude regions. Compared with the low- and middle-latitude regions, there were significantly lower twig mass, stem mass, flower mass and flower stalk mass in high-latitude region (P = 0.004 and < 0.001 and = 0.001 and < 0.001, respectively). The leaf mass and lamina mass was the minimum in the high-latitude region, which was significantly different from that in the middle-latitude region (P = 0.025 and = 0.019, respectively). Furthermore, the petiole mass and bract mass did not differ among different latitude regions (P = 0.16 and = 0.23, respectively) (Table 3).

3.2 Growth relationships among twig component organs in three latitude regions

The flower mass was positively related to stem mass and leaf mass. The slopes between flower mass and stem mass, flower mass and leaf mass were significantly different in the three latitude regions (P = 0.019 and = 0.014, respectively), but there was no common slope for a regression between these traits. The slopes between flower mass and stem mass in low- and middle-latitude regions were 0.973 (95% CI = 0.598~1.585) and 1.075 (95% CI = 0.794~1.455), respectively. Moreover, the slopes between flower mass and leaf mass in low- and middle-latitude regions were 1.419 (95% CI = 0.881~2.285) and 1.009 (95% CI = 0.771~1.320), respectively, which indicated an isometric growth relationship. On the other hand, the slopes between flower mass and stem mass, flower mass and leaf mass in high-latitude region were 0.586 (95% CI = 0.431~0.797) and 0.650 (95% CI = 0.463~0.911), respectively, which suggested an allometric growth relationship, and the growth rate of flower mass was significantly lower than that of stem mass or leaf mass (Table 4; Figures 2A, B).

TABLE 2 The morphological traits of annul *D. involucrata* twig in three latitude regions (mean ± *SE*).

Traits	Population			df	F	*P*
	PW	TQ	GX			
Stem diameter (mm)	3.79 ± 0.10c	5.09 ± 0.12b	5.90 ± 0.28a	2	43.637	< 0.001***
Leaf area (cm²)	490.23 ± 40.75a	502.86 ± 42.65a	436.07 ± 46.68a	2	0.491	0.614 ns
Mean leaf area (cm²)	60.62 ± 3.58a	42.60 ± 2.21b	39.67 ± 3.79b	2	13.182	< 0.001***
Mean lamina length (cm)	10.33 ± 0.31a	8.33 ± 0.23b	7.56 ± 0.32b	2	23.538	< 0.001***
Mean lamina width (cm)	7.82 ± 0.26a	6.54 ± 0.18b	6.46 ± 0.35b	2	9.677	< 0.001***
Bract area (cm²)	153.31 ± 11.95b	130.32 ± 13.14b	205.96 ± 29.61a	2	4.569	0.014*
Flower stalk length (cm)	5.00 ± 0.18ab	4.47 ± 0.18b	5.68 ± .043a	2	5.786	0.005**
Flower stalk diameter (cm)	0.21 ± 0.01c	0.23 ± 0.01b	0.26 ± 0.01a	2	23.680	< 0.001***

Different lines letters in the same column meant significant difference ($P<0.05$). PW, Pingwu, n = 24; TQ, Tianquan, n = 30; GX, Gongxian, n = 14. The significance values of analyses are denoted as: ns, not significant; * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

In addition, stem mass was positively related to leaf mass in different latitude regions, with a common slope of 1.130 (95% CI = 0.943~1.324), indicating an isometric growth relationship (Table 4; Figure 2C). Furthermore, a significant shift was found between different latitude regions both in the y-intercept and along the common slope ($P < 0.001$ and < 0.001, respectively), suggesting high-latitude region had smaller stem mass for a given leaf mass than the low- and middle- latitude regions did (Table 5; Figure 2C).

3.3 Growth relationships among reproductive organ traits in three latitude regions

Bract area was significantly related with flower stalk mass and flower mass, and the common slopes for these relationships were 1.065 (95% CI = 0.895~1.269), and 1.090 (95% CI = 0.947~1.243), respectively (Table 4; Figures 3A, B), which results indicated an isometric growth relationship. Moreover, a significant shift was also found between different latitude regions in the y-intercept and along the common slope ($P < 0.001$ and $= 0.026$; $P = 0.001$ and $= 0.017$, respectively), suggesting low-latitude region had smaller bract area for a given flower stalk mass or flower mass than the middle- and high-latitude regions did (Table 5; Figures 3A, B).

In addition, the flower stalk mass was also closely related to the flower mass in different latitude regions, with a common slope of 1.054 (95% CI = 0.921~1.195), which indicated an isometric growth relationship (Table 4; Figure 3C). Moreover, a significant difference in elevation was found between different latitude regions in the y-intercept and along the common slope ($P < 0.001$ and < 0.001, respectively), suggesting that the low-latitude region had higher flower stalk mass for a given flower mass than the middle- and high-latitude regions did (Table 5; Figure 3C).

TABLE 3 The biomass traits of annul *D. involucrata* twig in three latitude regions (mean ± *SE*).

Traits	Population			df	F	*P*
	PW	TQ	GX			
Twig mass (g)	3.52 ± 0.29b	5.45 ± 0.45a	5.17 ± 0.57a	2	6.176	0.004**
Stem mass (g)	0.90 ± 0.10b	1.94 ± 1.07a	2.04 ± 0.27a	2	12.962	< 0.001***
Leaf mass (g)	2.25 ± 0.19b	3.17 ± 0.28a	2.53 ± 0.25ab	2	3.901	0.025*
Lamina mass (g)	2.11 ± 0.18b	2.99 ± 0.26a	2.34 ± 0.23ab	2	4.204	0.019*
Petiole mass (g)	0.14 ± 0.01a	0.18 ± 0.02a	0.20 ± 0.02a	2	1.887	0.160 ns
Flower mass (g)	0.37 ± 0.03b	0.34 ± 0.04b	0.60 ± 0.09a	2	7.256	0.001**
Bract mass (g)	0.19 ± 0.01a	0.21 ± 0.02a	0.16 ± 0.02a	2	1.502	0.230 ns
Flower stalk mass (g)	0.03 ± 0.01b	0.03 ± 0.01b	0.07 ± 0.01a	2	25.053	< 0.001***

Different lines letters in the same column meant significant difference ($P<0.05$). PW, Pingwu, n = 24; TQ, Tianquan, n = 30; GX, Gongxian, n = 14. The significance values of analyses are denoted as: ns, not significant; * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

TABLE 4 Common slopes and SMA regression parameters for the relationships among the functional traits of *D. involucrata* twig in three latitude regions.

Y-X	SMA regression parameters						Common slopes		
	Site	R^2	P(r)	Slope	Y-intercept	P(h)	Slope-c	CIs	$P_{(slop)}$
Flower mass – Stem mass	PW	0.500	< 0.001***	0.586	0.847	0.019 ns	—	—	—
	TQ	0.368	< 0.001***	1.075	-1.015				
	GX	0.350	0.026*	0.973	-0.449				
Flower mass – Leaf mass	PW	0.390	< 0.001***	0.650	0.394	0.014 ns	—	—	—
	TQ	0.507	< 0.001***	1.009	-1.012				
	GX	0.381	< 0.001***	1.419	-2.070				
Stem mass – Leaf mass	PW	0.611	< 0.001***	1.109	-0.772	0.06 ns	1.130	0.943~1.324	0.196 ns
	TQ	0.574	< 0.001***	0.939	-0.003				
	GX	0.791	< 0.001***	1.458	-1.666				
Bract area – Flower stalk mass	PW	0.371	0.002**	1.046	0.669	0.988 ns	1.065	0.895~1.269	0.472 ns
	TQ	0.520	< 0.001***	1.084	0.577				
	GX	0.694	< 0.001***	1.055	0.365				
Bract area – Flower mass	PW	0.655	< 0.001***	1.227	-0.963	0.268 ns	1.090	0.947~1.243	0.232 ns
	TQ	0.707	< 0.001***	0.955	-0.295				
	GX	0.855	< 0.001***	1.147	-0.873				
Flower stalk mass – Flower mass	PW	0.813	< 0.001***	1.173	-1.560	0.129 ns	1.054	0.921~1.195	0.447 ns
	TQ	0.680	< 0.001***	0.881	-0.805				
	GX	0.831	< 0.001***	1.088	-1.173				
Petiole mass – Leaf area	PW	0.934	< 0.001***	1.192	-1.066	0.697 ns	1.151	1.073~1.235	<0.001***
	TQ	0.893	< 0.001***	1.122	-0.781				
	GX	0.953	< 0.001***	1.130	-0.698				
Petiole mass – Lamina mass	PW	0.918	< 0.001***	1.142	-1.651	0.350 ns	1.131	1.053~1.207	0.001**
	TQ	0.903	< 0.001***	1.056	-1.419				
	GX	0.971	< 0.001***	1.175	-1.675				
Petiole mass – Leaf mass	PW	0.928	< 0.001***	1.135	-1.661	0.387 ns	1.124	1.052~1.194	0.001**
	TQ	0.913	< 0.001***	1.055	-1.443				
	GX	0.976	< 0.001***	1.160	-1.666				

R^2 represents the correlation coefficients between traits, P(r) represents the level of significance testing for relationship between traits, Slope represents the allometric growth slope between traits, y-intercept represents the intercept of y axial, P(h) represents the heterogeneity of slope, Slope-c represents the common slope, CIs represents the 95% confidence intervals, $P_{(slop)}$ represents the level of significance testing for common slope. PW, Pingwu, n = 24; TQ, Tianquan, n = 30; GX, Gongxian, n = 14. The significance values of analyses are denoted as: ns, not significant; * P < 0.05, ** P < 0.01, and *** P < 0.001. Y-X represents the Y-axis and the X-axis, respectively.

3.4 Growth relationships among vegetative organ traits in three latitude regions

Petiole mass was significantly related to leaf area, lamina mass and leaf mass, and the common slopes for these relationships were 1.151 (95%CI = 1.073~1.235), 1.131 (95%CI = 1.053~1.207) and 1.124 (95%CI = 0.990~1.000), respectively. These results indicated an allometric growth relationship and the growth rate of petiole mass was significantly higher than those of leaf area, lamina mass and leaf mass in different latitude regions (Table 4; Figures 4A–C). Furthermore, between different latitude regions, a significant shift was found along the common slope of the relationship of petiole mass and leaf area ($P < 0.001$).

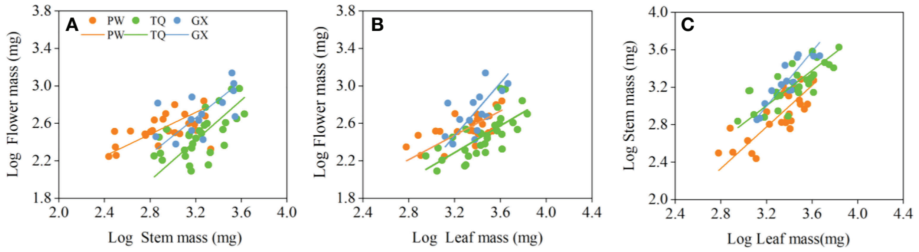

FIGURE 2
Growth relationships between flower mass and stem mass **(A)**, flower mass and leaf mass **(B)**, stem mass and leaf mass **(C)** in three latitude regions. PW, Pingwu; TQ, Tianquan; GX, Gongxian.

Meanwhile, a significant difference in elevation was found in the y-intercept of the growth relationship of petiole mass and lamina mass, petiole mass and leaf mass ($P < 0.001$ and < 0.001, respectively). There was significantly higher petiole mass per unit lamina mass or per unit leaf mass in low- latitude region than in middle- and high-latitude regions (Table 5; Figures 4A–C).

4 Discussion

Plants have the ability of plastic growth, and their morphological and physiological characteristics will change with environmental changes. In different habitats, plants may adopt the corresponding adaptive mechanism. For example, in high latitudes, *Pinus hwangshanensis* adjust the size of branches and leaves to adapt to the reduction of xylem vessel diameter caused by temperature reduction (Li et al., 2017), and *Lavandula latifolia* extend the length of labellum to cope with the low temperature environment (Herrera et al., 2006). Frenne et al. (2013) studied 98 species of plants worldwide and found that mean annual temperature and mean annual precipitation on the latitudinal gradient were the main factors affecting plant leaf traits. These studies demonstrated that environmental factors such as temperature and water content decrease as latitude increases, plants show some phenotypic adaptability to survive environmental changes. On this basis, we speculated that the functional traits and distribution strategies of *D. involucrata* twigs vary with latitudinal gradient. In this study, the individual size and biomass of *D. involucrata* twigs were the smallest in high-latitude region, with a trend of becoming smaller and shorter, which is consistent with previous studies (Kollmann and Bañuelos, 2004; Méndez-Alonzo et al., 2008; Moles et al., 2009). This phenomenon be explained that low-temperature in high-latitude region may constrain the photosynthesis of leaves, and reduce the absorption of carbon dioxide and the flow of important mineral elements in plants, thus restricting twig growth (Costa et al., 2017). Meanwhile, low temperature also

TABLE 5 Tests for heterogeneity of slope, and shift in intercept for the relationships among functional traits of annual *D. involucrata* twig in three latitude regions.

Y-X	Shift along the common slope				Shift in elevation			
	PW	TQ	GX	P	PW	TQ	GX	P
Flower mass – Stem mass	—	—	—	—	—	—	—	—
Flower mass – Leaf mass	—	—	—	—	—	—	—	—
Stem mass – Leaf mass	6.621	7.135	7.067	<0.001***	-0.842	-0.656	-0.559	<0.001***
Bract area – Flower stalk mass	3.663	3.515	4.145	0.001**	0.642	0.603	0.347	<0.001***
Bract area – Flower mass	4.919	4.746	5.207	0.017*	-0.614	-0.627	-0.715	0.026*
Flower stalk mass – Flower mass	4.095	3.966	4.647	<0.001***	-1.258	-1.232	-1.081	<0.001***
Petiole mass – Leaf area	5.135	5.251	5.254	<0.001***	-0.957	-0.858	-0.753	0.643 ns
Petiole mass – Lamina mass	5.795	6.069	6.031	0.121 ns	-1.617	-1.676	-1.530	<0.001***
Petiole mass – Leaf mass	5.803	6.073	6.046	0.122 ns	-1.625	-1.681	-1.544	<0.001***

PW, Pingwu, n = 24; TQ, Tianquan, n = 30; GX, Gongxian, n = 14. The significance values of analyses are denoted as: ns, not significant; * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. Y-X represents the Y-axis and the X-axis, respectively.

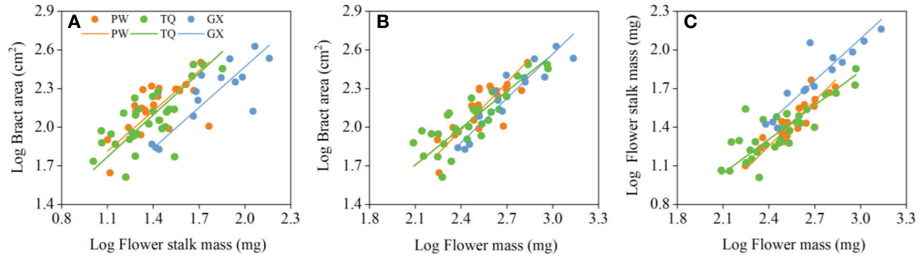

FIGURE 3
Growth relationships between bract area and flower stalk mass **(A)**, bract area and flower mass **(B)**, flower stalk mass and flower mass **(C)** in three latitude regions. PW, Pingwu; TQ, Tianquan; GX, Gongxian.

inhibit the activities of metabolic enzymes, resulting in suppression of the related biochemical reactions and hence decrease in the growth rate (Reich and Oleksya, 2004). Furthermore, low temperature and water constraints may shorten the growing season of plants and prolong the dormancy period in winter. Long time of low temperature inhibits the enzymes rich in N and P in plants, the biochemical reaction rate of plants decreases and the growth rate slows down (Reich and Oleksya, 2004). As a result, the biomass of annual twigs in high-latitude region is lower than in low- and middle-latitude regions. On the other hand, as the supporting structure of the plant, stem has to bear the weights of branches and accessories like leaves, flowers and fruits to assure mechanical safety (Yang et al., 2010). Accordingly, the biomass of *D. involucrata* stem decreases due to the reduced biomass of leaves, flowers and other organs in high-latitude region. Therefore, the total resource acquisition of plants decreases with the increase in latitude, and the total resources allocated to different organs will decrease accordingly. However, we found some functional traits of *D. involucrata* twig did not change with latitudinal gradient. For example, with the increase of latitude, the mass of twig, leaf, lamina and bract first increased and then decreased, especially for leaf traits. This phenomenon may be caused by differences in temperature and water conditions among different latitude regions. Rainfall in the middle-latitude region is the most abundant among three *D. involucrata* population distribution regions, and water conditions are obviously better than the other two regions when the temperature is suitable. Hence, biomass will be more allocated to the leaves under good hydrothermal conditions, so as to improve the resource utilization efficiency by increasing the effective photosynthetic leaf area.

At the twig level, we found that investment in leaf and stem increased continuously although the total biomass of *D. involucrata* twig decreased with the increase of latitude. Flower mass, stem mass and leaf mass present isometric growth relationships in low- and middle-latitude regions, while the growth rate of flower mass in high-latitude region is significantly lower than that of stem mass and leaf mass. This demonstrates that *D. involucrata* twig increases nutrition and supports allocations in high-latitude region but decreases reproduction allocation. In high latitudes, low temperature causes damage to the photosynthetic carboxylation process of leaves (Frenne et al., 2013). Plants increase resource allocation to leaves, which is beneficial for light interception and carbon fixation. In this study, the mean leaf area of *D. involucrata* twig increased with increasing latitude, which also proved the increasing resource allocations to leaves. Moreover, the heat exchange capacity of large leaf edges is relatively weak, which is conducive to adapting to a low-temperature environment (Ackerly et al., 2002; Yang et al., 2008). In addition, the low-temperature environment in high-latitude region is easy to cause

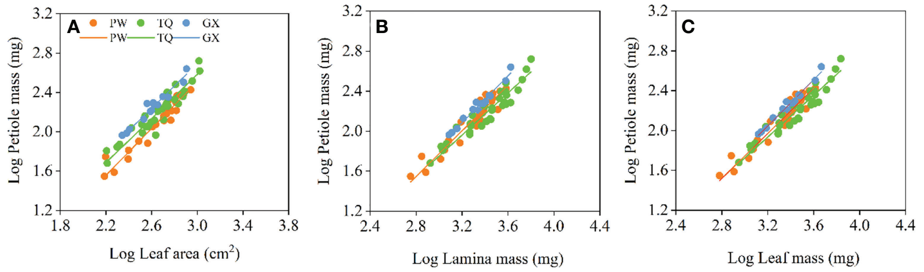

FIGURE 4
Growth relationships between petiole mass and leaf area **(A)**, petiole mass and lamina mass **(B)**, petiole mass and leaf mass **(C)** in three latitude regions. PW, Pingwu; TQ, Tianquan; GX, Gongxian.

embolism of stem, resulting in low transmission efficiency and metabolic decomposition (Li et al., 2017). Thus, enhanced resource allocations to stem help plants to improve transportation efficiency and relieve metabolic stress. This is consistent with previous research conclusions that the risk of plant nutrient and water transport will increase with the increase in habitat stress, whereas such risks can be reduced by increasing resource allocation to stem (Sun et al., 2006; Xiang et al., 2009). Sun et al. (2006) studied 59 woody plants in temperate zones and found that the biomass allocated to stems was usually more at the level of twigs under a low temperature environment. Wright et al. (2002) studied the leaf traits of 2500 vascular plant species from 175 sites around the world, and found that leaves had a higher average leaf area under a low temperature environment. These results are consistent with our findings that a isometric growth relationship between flower mass and stem mass or between flower mass and leaf mass in low- and middle- latitude regions, but a allometric growth relationship (slope < 1) in high-latitude region to cope with lower temperature environmental. Therefore, increased nutrition and support allocations suggest that *D. involucrata* twig adapts to a high-latitude, cold environment by allocating the limited resources to leaf and stem and decreasing allocation to flower. This also reflects a trade-off of *D. involucrata* twigs in the investment of various organs to resist cold environment.

At the flowering level, there is an isometric relationship between the bract area and flower stalk mass. However, the variations in the common slope shows that the bract area and flower stalk mass of the population in low-latitude region are larger and higher than those in high-latitude region. Due to a more appropriate environment and many insect species in low-latitude region, a larger bract area can attract more pollinators, thereby increasing the probability of pollination (Harder and Johnson, 2009). Compared to the plants in low-latitude region, plants in high-latitude region have smaller and thicker bract, which can better protect the capitulum from low-temperature disturbances (Liu T. T. et al., 2020). In addition, as a support organ, the flower stalk has to bear the weights of two prominent bracts and the capitulum at the end. Plants *D. involucrata* in low-latitude region have a larger flower than other two regions, thus increasing the possibility of being attacked by strong wind and rain, means that the mechanical force on the flower stalk increases correspondingly. According to Niklas (1999), large plants usually have high reproduce cost, which requires them to invest more resources to strengthen mechanical support and protect flower organs from bad climates. In this study, we found that flower stalk mass in low-latitude region was more than in high-latitude region for a given flower mass. This also proved the increased resource allocation to flower stalks in low-latitude region. Therefore, *D. involucrata* tend to develop larger bract and stronger flower stalk in low-latitude region but a smaller bract to cope with low-temperature environmental stress.

At the leaf level, there was an allometric growth relationship between lamina and petiole in different latitude regions, with petiole having higher biomass growth rate than that of lamina. This result is consistent with previous studies (Niinemets et al., 2006; Niinemets et al., 2007; Li et al., 2008). Li et al. (2008) also found that in all species, there was an allometric relationship with a slope < 1.0 between leaf mass or area and petiole mass. This indicates that the increase of blade investment cannot keep up with the increase of blade support structure investment, which is a mode of diminishing returns (Shi et al., 2020b; Guo et al., 2021; Li et al., 2022). Petiole has to not only transport water and nutrients to leaves but also support the static weight of leaves and resist dynamic tensile forces, such as winds and rains (Li et al., 2008). These require extra biomass resource allocation to the petiole. Hence, there is an allometric relationship between leaves and petiole rather than an isometric one. In this study, the petiole mass in low- and middle-latitude regions is higher than that in high-latitude region for a given lamina mass, indicating a higher resource allocation to supports. The reason is that the petiole has to bear more weight in low- and middle-latitude regions than in high-latitude region, which is attributed to the higher lamina mass. On the other hand, it has been mentioned in the above study that the growing season of plants shortens, and the dormancy period prolongs in the high-latitude region due to the decreased temperature. Compared with high-latitude region, *D. involucrata* leaves in low- and middle-latitude regions germinate earlier but fall later. Increasing resource allocation to petiole is to prepare for early germination of new leaves, and delivery of water and nutrients to leaves that fall later. This is consistent with the finding of Li et al. (2008) that temperate evergreen broad-leaved tree species have higher investment in petioles than deciduous species. In order to keep consistent with leaves, petioles have to increase their resistance to freezing blockage by increasing more investment (Cavender-Bares et al., 2005). Therefore, we concluded that increasing resource allocation to petiole in low- or middle-latitude region represents an adaptive response of *D. involucrata* twig to a relative temperate environment.

Furthermore, according to the future prediction of climate models, the change of global climate may lead to the reduction of species distribution and the serious loss of biodiversity (Pearson and Dawson, 2003; Thomas et al., 2004; Rı´o and Penas, 2006). *D. involucrata* is highly sensitive to environmental factors such as temperature seasonality, precipitation in the hottest seasons and mean annual temperature. Meanwhile, the habitat of *D. involucrata* is affected by human activities and increased land use, which result in the narrowing of its distribution range. According to the findings of Tang et al. (2017), the projected decline in potential habitat area by 2070 under global climate change, which indicate that the habitat of *D. involucrata* will become very vulnerable. In view of the influence of climate change on the geographic distribution of *D. involucrata*, we suggest that undisturbed wild *D. involucrata* communities should be protected firstly, and build nature reserves, breeding bases and monitoring sites in the existing habitats of *D. involucrata*.

In conclusion, this study confirmed that *D. involucrata* adjusted the resource allocation and reproduction strategy with the change of latitude. The morphology and biomass of *D. involucrata* twig are negatively related to latitude, and resource is invested more to leaf and stem but less to flower in high-latitude region. Our results suggest that *D. involucrata* adapts to heterogeneous environments by changing the phenotypic plasticity and the relationship of trade-off of the investment-benefit-cost among traits to achieve population reproduction. These results can provide valuable information for the protection of the rare plant *D. involucrata*. Furthermore, there exist some disadvantages in our study that only three populations along latitude were selected, and the response of branchlet mechanical strength, leaf element content to latitude were ignored, which may have potential limitations to our results. More research work needs to be carried out from these perspectives in the future.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding authors.

Author contributions

XX conceived and designed the study. ZL, TL, XC, WX, TD and QL performed the experimental work. ZL analyzed the data and wrote the paper. All authors contributed to the article and approved the submitted version.

Funding

This research was supported by the National Natural Science Foundation of China (31900277).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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frontiers | Frontiers in Plant Science

TYPE Original Research
PUBLISHED 01 December 2022
DOI 10.3389/fpls.2022.999636

OPEN ACCESS

EDITED BY
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SPECIALTY SECTION
This article was submitted to Functional Plant Ecology, a section of the journal Frontiers in Plant Science

RECEIVED 21 July 2022
ACCEPTED 04 November 2022
PUBLISHED 01 December 2022

CITATION
Yao Z, Xin Y, Yang L, Zhao L and Ali A (2022) Precipitation and temperature regulate species diversity, plant coverage and aboveground biomass through opposing mechanisms in large-scale grasslands. *Front. Plant Sci.* 13:999636.
doi: 10.3389/fpls.2022.999636

Precipitation and temperature regulate species diversity, plant coverage and aboveground biomass through opposing mechanisms in large-scale grasslands

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Introduction: Although the relationships between species diversity and aboveground biomass (AGB) are highly debated in grassland ecosystems, it is not well understood how climatic factors influence AGB directly and indirectly *via* plant coverage and species diversity in large-scale grasslands along a topographic gradient. In doing so, we hypothesized that climatic factors would regulate plant coverage, species diversity and AGB due to maintaining plant metabolic and ecological processes, but the relationship of plant coverage with AGB would be stronger than species diversity due to covering physical niche space.

Methods: To test the proposed hypothesis, we collected data for calculations of species richness, evenness, plant coverage and AGB across 123 grassland sites (i.e., the mean of 3 plots in each site) dominated by *Leymus chinensis* in northern China. We used a structural equation model for linking the direct and indirect effects of topographic slope, mean annual precipitation and temperature on AGB *via* plant coverage, species richness, and evenness through multiple complex pathways.

Results: We found that plant coverage increased AGB, but species evenness declined AGB better than species richness. Topographic slope influenced AGB directly but not indirectly *via* plant coverage and species diversity, whereas temperature and precipitation increased with increasing topographic slope. Regarding opposing mechanisms, on the one hand, precipitation increased AGB directly and indirectly *via* plant coverage as compared to species richness and evenness. On the other hand, temperature declined AGB indirectly *via* plant coverage but increased *via* species evenness as compared to species richness, whereas the direct effect was negligible.

Discussion: Our results show that niche complementarity and selection effects are jointly regulating AGB, but these processes are dependent on climatic factors. Plant coverage promoted the coexistence of species but depended greatly on precipitation and temperature. Our results highlight that precipitation and temperature are two key climatic drivers of species richness, evenness, plant coverage and AGB through complex direct and indirect pathways. Our study suggests that grasslands are sensitive to climate change, i.e., a decline in water availability and an increase in atmospheric heat. We argue that temperature and precipitation should be considered in grassland management for higher productivity in the context of both plant coverage and species diversity which underpin animals and human well-being.

KEYWORDS

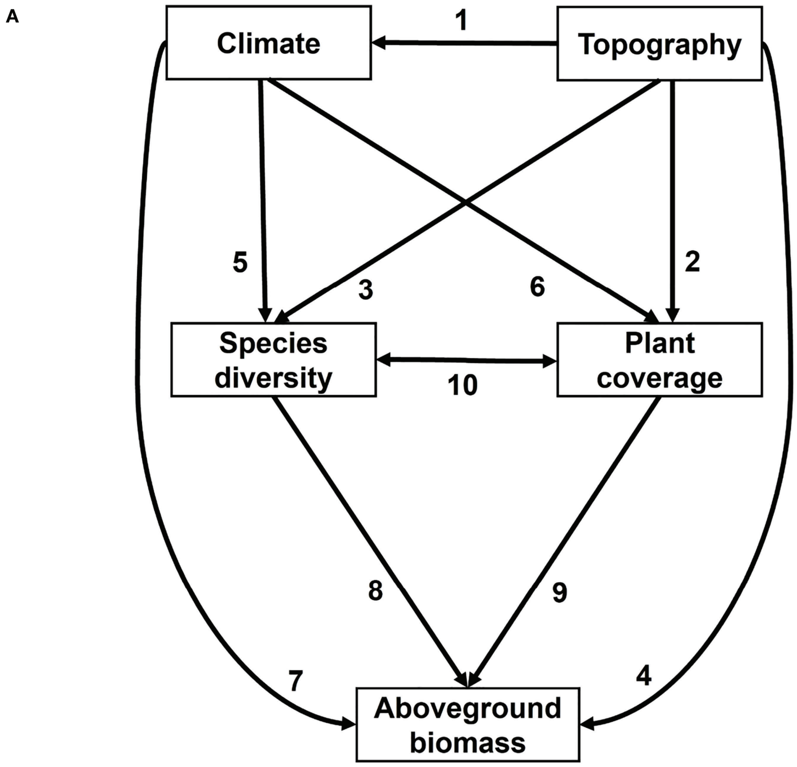
climate, ecological mechanisms, *Leymus chinensis* community, topography, biotic factors

Introduction

Understanding the divergent relationships (i.e., positive, negative and negligible) between biodiversity and aboveground biomass (AGB) has received much attention during the last few decades (Díaz et al., 2007; Grace et al., 2016). These divergent relationships are highly debated in grassland ecosystems and remain elusive (Gross, 2016; van der Plas, 2019). Nevertheless, climatic factors, such as precipitation and temperature, can greatly regulate biodiversity and AGB directly through plant metabolic, physiological and ecological processes, and such, as well as indirectly *via* species diversity and plant coverage through maintaining plant community assembly processes and species interactions in natural plant communities (Chu et al., 2016; Michaletz et al., 2018). However, few studies have focused on the role of plant coverage *versus* species diversity in regulating AGB in large-scale grasslands which are dominated by a specific plant species (Grace et al., 2016; Sanaei et al., 2018). Thus, our understanding is relatively unclear of how temperature and precipitation regulate AGB directly and indirectly *via* plant coverage and species diversity along a large-scale topographic gradient in natural grasslands (see a conceptual model in Figure 1A).

It is generally predicted that species diversity (either species richness, evenness or Shannon's diversity) promotes AGB in grassland ecosystems due to the niche differentiation processes by component coexisting species (Tilman et al., 1996; Grace et al., 2016). There are two general ecological mechanisms, i.e., 1) the niche complementarity effect, and 2) the mass ratio or selection effect, which are usually put forward to explain variation in AGB which are underpinned by species (including functional trait and phylogenetic) diversity in grasslands (Diaz et al., 2007; van der Plas, 2019). The niche complementarity mechanism suggests that species with different niches are often able for more efficient use of available resources, thereby increasing AGB or productivity (Tilman et al., 1996; Loreau et al., 2001; Flombaum and Sala, 2008). For example, the presence of nitrogen-fixing legumes could promote other plant species and thus increase AGB (Hector et al., 2007; Marquard et al., 2009). The selection effect predicts that AGB is primarily determined by the characteristics of dominant or highly functioning species (Grime, 1998; Hector et al., 1999). For example, dominant species are considered to be more stable in the community and thus play an important role in regulating AGB whereas rare species play a negligible role (Sanaei and Ali, 2019). In most cases, studies have shown that the niche complementarity and selection effects may not act independently but jointly in explaining AGB in different plant communities (Diaz et al., 2007; Sanaei et al., 2018; van der Plas, 2019). Moreover, this situation is complex due to the strength, magnitude and direction of the relationship between species diversity and AGB as well as multiple indices of species diversity (Wilsey and Potvin, 2000; Polley et al., 2010). For example, it is always not true that species diversity increases AGB, and thus, negative and negligible relationships have also been reported in grasslands (van der Plas, 2019, and references therein). These divergent relationships between species diversity and AGB suggest that several internal (e.g., plant coverage) and external (e.g., topography and climate) factors are shaping species diversity and AGB in grasslands which needs further investigation across biomes for better understanding (Figure 1).

As compared to species diversity, plant coverage could be the best predictor of AGB due to physical coverage of the niche



B

Paths	Ecological mechanisms	Expectations
1	Topographic effect	Temperature and precipitation are influenced by topographic slope at a large scale.
2, 3 and 4	Topographic effect	Species richness, evenness, plant coverage and aboveground biomass increase with increasing topographic slope if the patten is coupled with favourable climatic conditions at a large scale.
5, 6 and 7	Climate effect	Species richness, evenness, plant coverage and aboveground biomass increase with increasing climatic water availability but declined with increasing unfavouralble temperatures causing heat at a large scale.
8, 9 and 10	Niche complementarity and selection effects	Aboveground biomass increases with increasing species richness, evenness and plant coverage due to the niche complementarity effect, but dominant species may restrict this relationship due to the selection effect or competitive exclusion effect. Plant coverage would be the best driver of aboveground biomass due to covering physical niche space, but it may lead to increased species competition, and thus species diversity may be a poor driver of aboveground biomass.
Indirect pathways	Multiple abiotic and biotic effects	Topographic slope, temperature and precipitation affect aboveground biomass indirectly via species richness, evenness and plant coverage. The indirect positive effects of climatic water availability on aboveground biomass via plant coverage would be stronger than via species diversity due to coverage of dominant species and increased species competition during growing seasons. As such, the negative indirect effect of temperature on aboveground biomass via plant coverage would be stronger due to adaptation of species to heat, and thus, species evenness would mediate positive response due to the role of dominant species.

FIGURE 1
The brief conceptual model **(A)** and explanation of mechanisms and expectations **(B)** for elaborating the research questions and hypothesis in this study. Composite paths are labelled with numbering **(A)** for brief explanation **(B)**. Topography is represented by terrain slope, climate is represented by mean annual temperature (MAT) and mean annual precipitation (MAP), and species diversity is represented by species richness (S) and species evenness (J).

space which is in turn related to multiple ecological processes such as nutrient cycling, secondary productivity, and livestock feed (Marquard et al., 2009; Ji et al., 2009; Sanaei et al., 2018b, Grace et al., 2016). Although plant coverage is not the direct measure of biodiversity, it can greatly predict species richness, plant density and AGB due to the proportional physical use of a certain space by plants which can be directly and indirectly related to the niche space (Marquard et al., 2009). For example, plant communities with high plant coverage may use more environmental resources than communities with low plant coverage (Ji et al., 2009), and thus, plant coverage can increase species diversity and AGB (Sanaei et al., 2018). Moreover, high plant coverage may increase AGB directly and indirectly *via* species diversity through the coexisting of a diverse array of species having different plant coverage which could be able to use the available resources more efficiently, i.e., the mixture of shade-tolerant and shade-intolerant species (Yachi and Loreau, 2010; Schmid and Niklaus, 2017; Sanaei and Ali, 2019). However, the overruling effect of a few dominant species having high plant coverage may modulate the relationship between species diversity and AGB through the selection or competitive exclusion effect (Grime, 1998; Hector et al., 1999; Sanaei and Ali, 2019).

Beyond species diversity and plant coverage, climatic factors (e.g., mean annual temperature and mean annual precipitation), soil properties (e.g., soil nutrients and textures), and topographic factors (e.g., altitude and slope) are also known to be important direct and indirect drivers of AGB *via* its biotic factors such as species diversity and plant coverage (Chu et al., 2016; Grace et al., 2016; Sanaei et al., 2019; Cheng et al., 2021). For example, the amount of optimal precipitation can increase the length of the growing season through climatic water availability, and hence, plants can grow well under favorable climatic conditions, and this process promotes AGB directly and indirectly *via* species diversity and plant coverage (Chu et al., 2016; Poorter et al., 2017; Ali et al., 2019). However, the effects of mean annual temperature on plant diversity, coverage and AGB depend on climatic zones. For example, in cold regions, low temperature is the primary limiting factor for plant growth, and thus, an optimal increase in temperature could promote AGB (Heskel et al., 2016). However, in warmer regions, high temperatures may decline AGB due to changes in the plant metabolic processes (Kerkhoff et al., 2005). Likewise, topographic factors can influence AGB by regulating water availability and temperature (De Frenne et al., 2021). In middle and high latitudes, the topographic slope is an important factor in determining ecological conditions through the amount of solar radiation received by the ground, which can produce unique microclimates (Bennie et al., 2008). As such, environmental factors such as climatic water and temperature differ markedly at different altitudes (Sun et al., 2013) which in turn affect the availability of soil moisture and nutrients (Sanaei et al., 2019). Yet, we do not fully understand how temperature and precipitation influence AGB directly and indirectly *via* species diversity and plant coverage in large-scale grasslands (Figure 1A).

In this study, we examined the direct and indirect effects of topographic and climatic factors on AGB directly and indirectly *via* species richness, evenness and plant coverage in the natural grassland communities dominated by *Leymus chinensis* in northern China (Figure 1A). As the studied plant communities were dominated by *L. chinensis*, we, therefore, used species richness and species evenness as two independent drivers of AGB to represent the two aspects of species diversity while considering plant coverage as the physical coverage of vegetation. As such, we used topographic slope, mean annual precipitation and mean annual temperature as the main regulators of species diversity, plant coverage and AGB because the studied sites show substantial temperature and precipitation seasonality along topographic gradients. In doing so, we address the following research questions: 1) How do topographic slope, mean annual precipitation and mean annual temperature affect species richness, evenness, plant coverage and AGB in the grasslands dominated by *L. chinensis*; 2) what is the main mediating factor – species richness, evenness and/or plant coverage – for linking the response of AGB to mean annual precipitation and mean annual temperature along topographic gradient; and 3) what is the main ecological mechanism – the niche complementarity and/or selection effect – for explaining the relationships between species richness, evenness and AGB while considering plant coverage as a potential endogenous factor? We hypothesize that climatic factors regulate plant coverage, species diversity and AGB due to maintaining plant metabolic and ecological processes, but the relationship of plant coverage with AGB is stronger than species diversity due to covering physical niche space (see Figure 1A for a brief model, and Figure 1B for a brief explanation).

Materials and methods

Study area and grassland communities

The study was conducted in grassland communities, dominated by *L. chinensis* at a large scale, and the study sites are located between 109°37′—125°16′ E and 38°56′—50°31′ N, spanning the Loess Plateau, the Inner Mongolia Plateau and the northeast Plain in northern China (Figure 2). The altitude is high in the west and low in the east, dropping from 2023 m to 129 m. The region has a temperate climate with a mean annual temperature between -2.9 and 7.9°C. Mean annual precipitation varies greatly, with precipitation being mainly concentrated in the growing season. There is also a notable rainfall gradient spanning from 209 mm in the west to 498 mm in the east on average. The main soil types are chestnut, chernozem, and salinized meadow and loess soil.

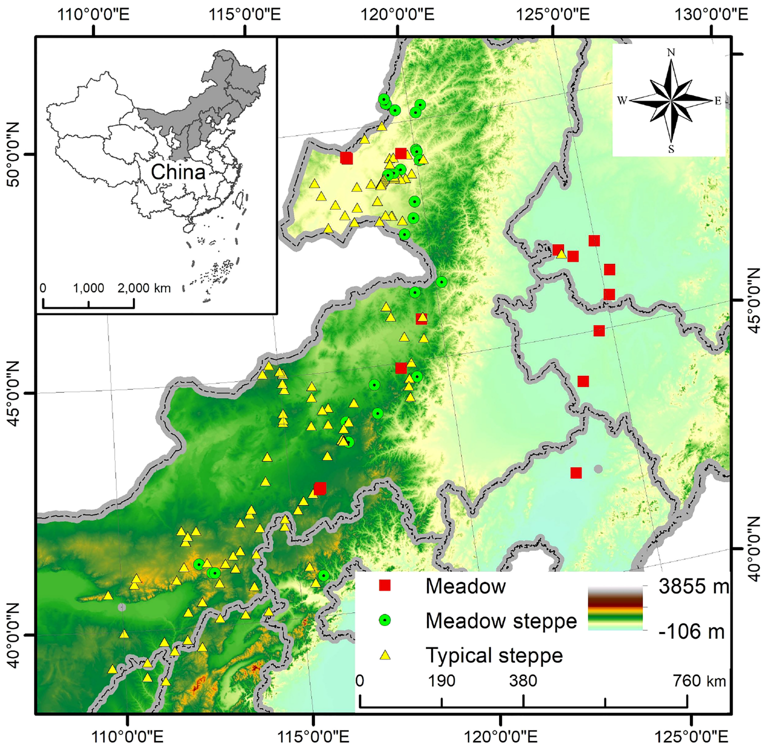


FIGURE 2
Map of the sampling sites of the grasslands dominated by *Leymus chinensis*. Different shapes and colors show three different community types dominated by *L. chinensis* in the study area.

Vegetation types from the west to east are desert steppe, typical steppe and meadow steppe where the meadow. *L. chinensis* communities are continuously distributed in southern Eastern Siberia, northern Mongolia, the middle and lower parts of the hilly area of the eastern and western foothills of China's Great Khingan Mountains, and the Songnen Plain. In the central and western Mongolian Plateau and northern Loess Plateau, *L. chinensis* communities are largely distributed in relatively humid areas. Due to the wide distribution, there are several types of grassland communities across the region. Specifically, *L. chinensis* meadows are formed on the non-zonal soils (saline-alkali soil and meadow soil) in the northeast plain and within the eastern Greater Khingan Mountains. Meadow steppe is formed on zonal soils (chestnut soil or chernozem soil) in the west, whereas the Mongolian Plateau and the loess plateau to the west form a typical steppe (Zhu, 2004). These areas span semi-humid, semi-arid, and arid climatic zones. The plant growing seasons in the study area start in May and end in October.

Data collection and quantification of variables used in the analyses

Field surveys were conducted during peak grass plant productivity from mid-July to late August during 2016-2020. We randomly selected those sites where *L. chinensis* was dominant. Then, three 1×1 m plots were established within each site, and thus, we sampled 369 plots in total across 123 sites. Within each plot, we recorded species composition, total coverage, density and height. We harvested and weighed the aboveground parts of the plants. For measuring AGB, samples were oven-dried to a constant mass at 65°C for 48 hours before weighing.

The total plant coverage of each species was recorded as the ratio of the vertical projection area of each species to the total area of the plot (Ji et al., 2009). Species richness was calculated by the observed number of species in each plot, whereas species evenness was calculated as the distribution of relative AGB across the species in a plot. These biotic calculations were conducted in the *vegan* package in R statistical software (Oksanen et al., 2015; R Development Core Team, 2019). We used mean data within each site, and thus, we used 123 sites in total.

A handheld Global Positioning System (GPS) was used to measure the geographical position and elevation of each sample site. The slope of each sample site was extracted using ArcGIS (10.5). To test the direct and indirect influences of climatic factors on plant coverage, species diversity and AGB, we extracted mean annual precipitation and mean annual temperature from the WorldClim database (https://www.worldclim.org/) at a resolution of 30 seconds (~1 km) (Fick and Hijmans, 2017).

Note that we used mean data for each biotic variable per site (Table S1), and thus, 123 sites were used in the statistical analyses for better representation of meta-sites to cover the gradient in abiotic and biotic factors. The list of observed species in the study region and their basic summary are provided in Table S2.

Statistical analyses

The Kruskal-Wallis H test (also known as the "one-way ANOVA on ranks") was used to determine if there were statistically significant differences in species richness, evenness, plant coverage and AGB as well as topographic and climatic variables among three types of grassland communities dominated by *L. chinensis*. To test the proposed research questions and hypothesis, we used a brief conceptual model (Figure 1A) with the following specific paths in structural equation modelling (SEM): 1) topographic slope affected mean annual precipitation, mean annual temperature, species richness, evenness, plant coverage and AGB directly; 2) mean annual precipitation and mean annual temperature affected species richness, evenness, plant coverage and AGB directly; 3) species richness, evenness and plant coverage affected AGB directly; and 4) species richness, evenness and plant coverage provided feedback to each other. We used cut-off criteria to evaluate the SEM fit to the meta-site data, which included the maximum likelihood chi-square (χ^2) test and standardized root means square residual (SRMR) (Grace et al., 2016). The SEM was considered accepted if the χ^2 test statistic had $P > 0.05$ and SRMR < 0.08. We also considered the comparative fit index (CFI), which shows that results could be less affected by sample size if the value is greater than 0.95 and validated this calculation using the goodness-of-fit index (GFI), which suggests a good SEM fit if the value is greater than 0.95 (Hoyle, 2012). We preferred to use the SEM for testing the research questions and hypothesis as it allows us to integrate multiple factors in a single model structure, which is the best tool to test the multiple research questions and hypotheses in a single framework (Grace et al., 2016). We dropped the correlation path between mean annual precipitation and temperature to avoid the saturated or overfitted SEM, following the χ^2 test statistic with an associated *P*-value. The SEM was conducted using the *lavaan* package in R (Rosseel, 2012).

To complement the results from SEM, we also tested the linear regression models between tested variables by using a bivariate plot and Pearson's correlation matrix. All data were standardized before analysis (standard deviation = 1, mean value = 0) to improve the linearity and normality as well as to compare the standardized effects of multiple predictors on response variables (Zuur et al., 2009; Grace et al., 2016; Ali et al., 2019).

Results

The site maximum, minimum and mean (± SD) observed AGB values across all *L. chinensis* communities were 490.8g m^{-2}, 28.5g m^{-2} and 160.9 (± 71.2) g m^{-2}, respectively. The maximum, minimum and mean (± SD) observed species richness values were 49, 6 and 24 (± 9) species per site. Among biotic factors, AGB, species richness and plant coverage of the typical steppe community were the lowest and were significantly different from the other two communities. Species evenness was significantly different across three community types. As such, we found significant differences in topographic and climatic factors across three *L. chinensis* community types (Figure 3; Table S1).

The tested SEM explained 52%, 42%, 34% and 30% of the variations in AGB, species richness, plant coverage and species evenness, respectively (Figure 4A). Mean annual temperature and precipitation increased significantly with increasing topographic slope, and they were somehow positively correlated with each other (Figure 5, S1). However, topographic slope did not significantly alter species richness, plant coverage and species evenness, but imposed non-significant positive effects on them (Figure 4A). However, species richness and plant coverage increased significantly with increasing mean annual precipitation but declined with mean annual temperature. In partial contrast, species evenness declined significantly with mean annual temperature but declined non-significantly with mean annual precipitation (Figure 4A). As such, AGB increased significantly with increasing mean annual precipitation and topographic slope as compared to mean annual temperature. Importantly, AGB increased significantly with increasing plant coverage but declined with species evenness, whereas species richness possessed a non-significant negative effect on AGB. Species richness, evenness and plant coverage were positively correlated in SEM but this positive correlation was stronger between species richness and evenness (Figure 4A).

The comparison of direct and indirect effects (bar charts) showed that plant coverage was the top direct driver of AGB followed by mean annual precipitation, topographic slope, species evenness, species richness, and mean annual temperature (Figure 4B). Topographic slope increased AGB indirectly *via* mean annual precipitation, temperature and plant coverage but somehow declined *via* species richness and evenness, and thus, the indirect effect size was higher *via* precipitation (Figure 4B; Table S3). As such, precipitation increased AGB indirectly *via* plant coverage, species richness and evenness, and the indirect effect size was higher *via* plant coverage. In contrast, temperature declined AGB *via* plant

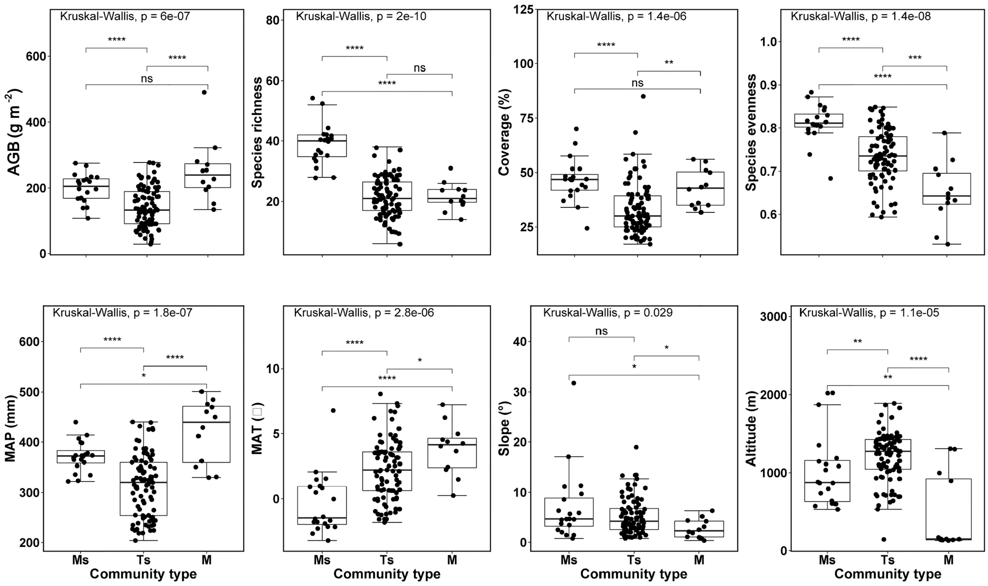


FIGURE 3
Differences for variables, used in the structural equation modelling, among three grassland community types dominated by *Leymus chinensis* in northern China. See Tables S1, S2 for the summary. MAP, mean annual precipitation; MAT, mean annual temperature; and AGB, aboveground biomass; Ms, meadow steppe; Ts, typical steppe; M, meadow. p:****and ***<0.001, **<0.01, *<0.05, and ns >0.05.

coverage and species richness but increased *via* species evenness, and thus, the total indirect effect was negative (Figure 4B; Table S3).

The bivariate relationships (Figure 5) and Pearson's correlation matrix (Figure S1) showed almost similar trends as shown by the paths of SEM (Figure 4).

Discussion

Although the relationships between species diversity and AGB are highly debated in grassland ecology (Gross, 2016; van der Plas, 2019), we show how temperature and precipitation regulate plant coverage, species diversity and AGB in grasslands dominated by *L. chinensis* along topographic gradient in northern China. We found that mean annual precipitation and temperature controlled AGB directly and indirectly *via* plant coverage and species diversity through opposing mechanisms along increasing topographic slope. On the one hand, precipitation increased AGB directly and indirectly *via* plant coverage better than species richness and evenness, indicating the role of a longer length of growing season due to the water availability which is an important factor for plant physiological, metabolic and ecological processes (Gillman and Wright, 2014; Poorter et al., 2017; Ali et al., 2019; Cheng et al., 2021). On the other hand, mean annual temperature decreased AGB directly and indirectly *via* plant coverage better than species richness but increased *via* species evenness, indicating that plant coverage and species richness are sensitive to an increase in temperature (i.e., heat) but species evenness can maintain this adverse effect through the compensatory role (Isbell et al., 2015; Chu et al., 2016; Michaletz et al., 2018; Sullivan et al., 2020). By considering the divergent effects of precipitation and temperature, we found that plant coverage increased AGB better than species richness and evenness, indicating the role of occupancy of physical niche space (Marquard et al., 2009; Ji et al., 2009; Sanaei et al., 2018b).

We found that AGB, but somehow species richness, plant coverage and species evenness, were positively controlled by the topographic slope. However, it is noteworthy that the slope of the studied region is gentle, i.e., low slope (see Table S1), which is usually conducive to the growth of plants due to the higher availability of light and soil nutrients (Sanaei et al., 2018; Jucker et al., 2018). Moreover, the topographic slope can greatly control soil moisture and solar radiation, and thus, an increasing gentle slope can result in greater water availability which could promote biodiversity and AGB with high plant coverage (Sanaei et al., 2019; De Frenne et al., 2021). As such, we found that temperature and precipitation increased equally with increasing topographic slope, and they were somehow positive correlated with each other, which in turn influenced species diversity, plant coverage and AGB through opposing mechanisms.

On the one hand, we found that mean annual precipitation promoted AGB directly and indirectly *via* plant coverage, but not *via* species richness and evenness, in the studied grasslands. This is possibly due to the reason that rain events provide enough soil moisture and maintain high climatic water

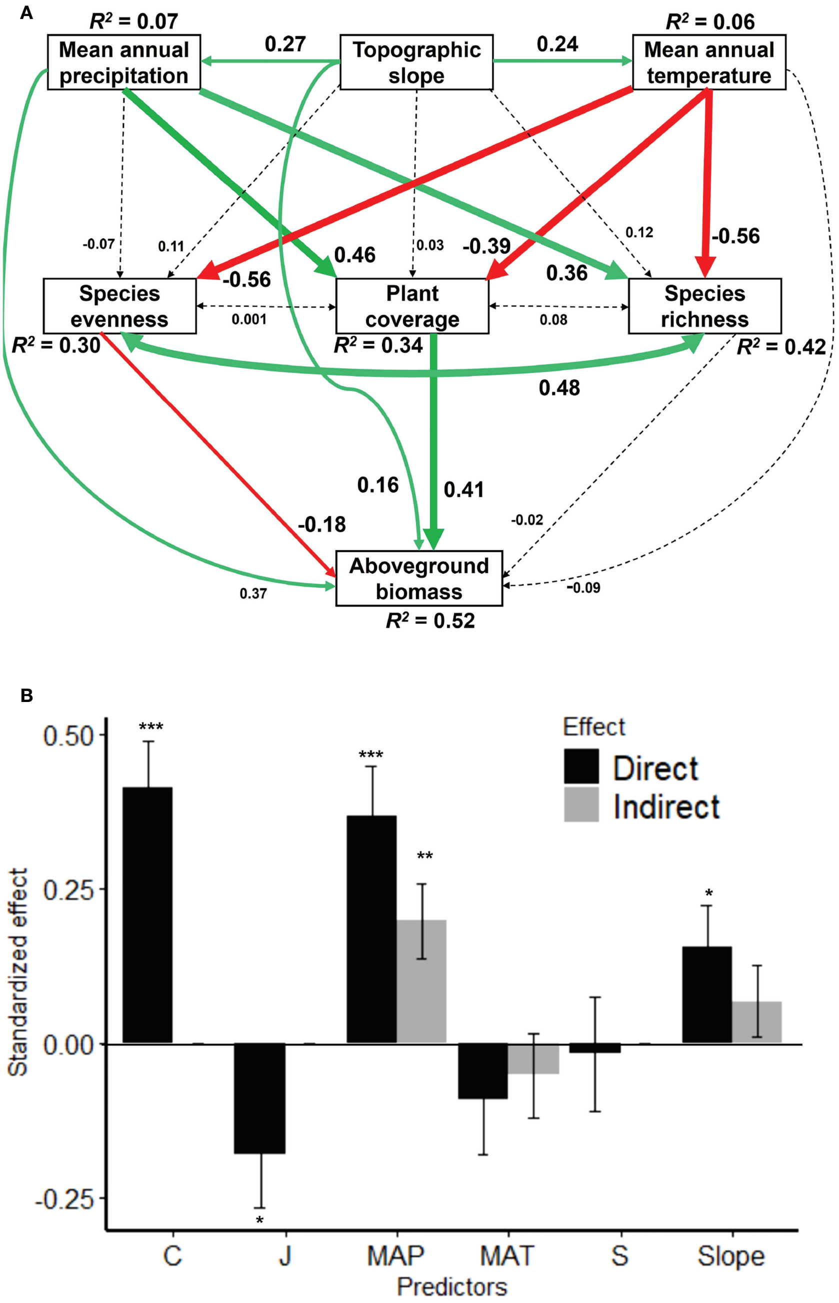


FIGURE 4

Structural equation model **(A)** for linking the direct and indirect effects of topographic slope and climatic factors (MAT and MAP) on aboveground biomass (AGB) *via* plant coverage, species richness, evenness in large-scale scale grasslands dominated by *Leymus chinensis* in northern China. Solid arrows represent significant ($P < 0.05$) effects and dashed arrows represent non-significant effects ($P > 0.05$). Red arrows represent negative effects while green arrows represent positive effects with a standardized value near each arrow. R^2 value associated with the response variable indicates the proportion of variation explained by predictors. Bar chart comparison of the direct and indirect effects of predictors on AGB **(B)**. See Table S3 for the summary. Model-fit statistic: CFI = 0.999; GFI = 0.996; SRMR = 0.034; Chi-square test statistic = 1.344 with P-value = 0.248 and degrees of freedom = 1. Significance levels **(B)**: ***P < 0.001; **P < 0.01; *P < 0.05. MAP, mean annual precipitation; MAT, mean annual temperature; C, plant coverage; J, species evenness; S, species richness; and AGB, aboveground biomass.

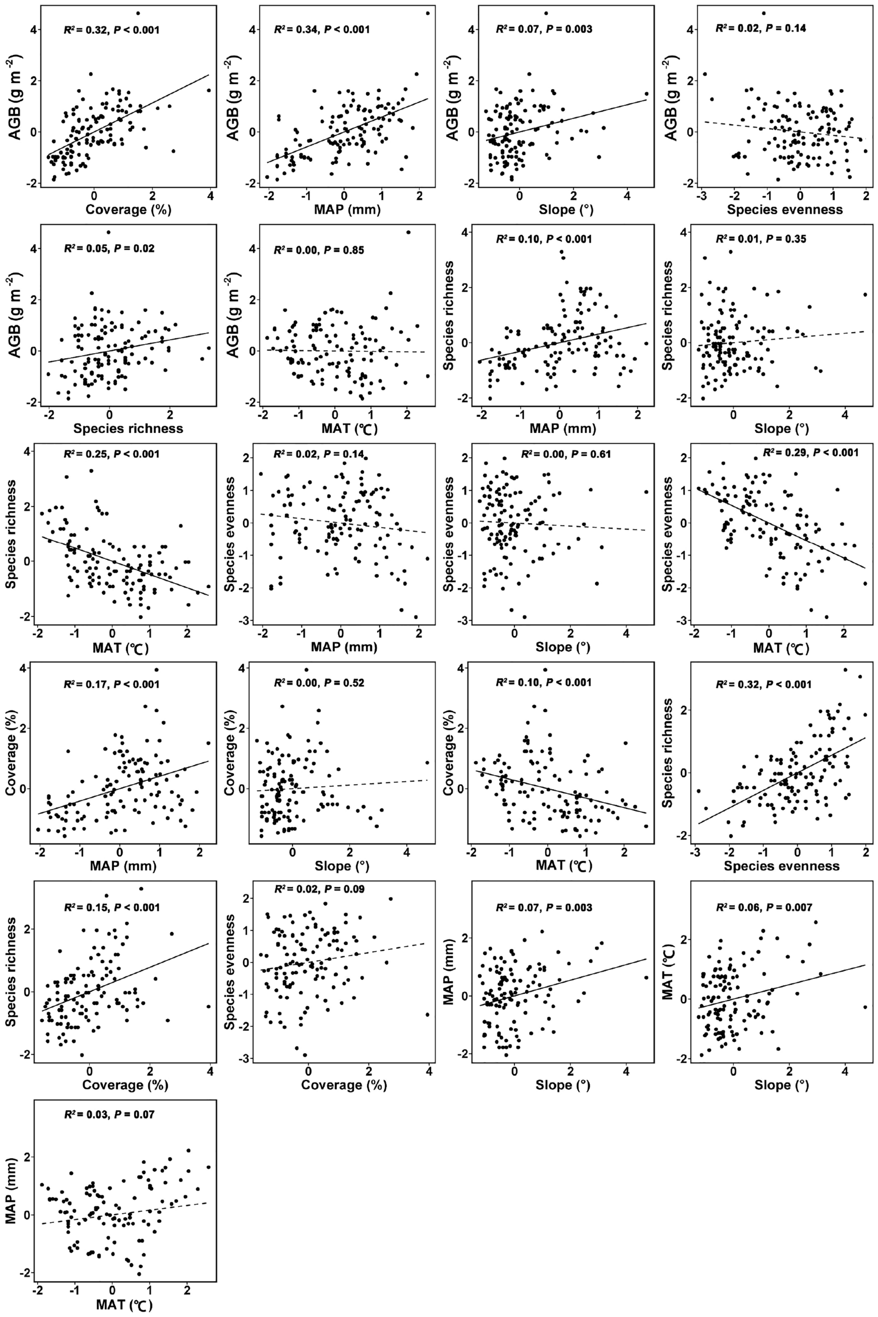


FIGURE 5
The bivariate relationships between tested variables used in the SEM for linking topographic slope, climatic factors (MAP and MAT), plant coverage, species richness, evenness and AGB of *Leymus chinensis* communities in northern China. Solid line represents a significant relationship whereas a dashed line represents a non-significant relationship. Abbreviations are explained in the caption of Figure 4.

availability (Gillman and Wright, 2014; Poorter et al., 2017; Ali et al., 2019; Cheng et al., 2021). In arid and semiarid regions, climatic and soil water availability is typically a limiting factor for plant growth, and thus, available moisture generally promotes plant coverage and AGB as compared to species diversity due to the species' competition for available resources (Butterfield, 2015; Berdugo et al., 2019). The plant coverage and AGB stock of perennial plant species is the result of photosynthesis which depends on water availability, and thus, high water availability can promote carbon sequestration *via* high plant coverage, thereby increasing AGB in plants (Kerkhoff et al., 2005; Yang et al., 2019; Cabon et al., 2022). In addition, the water use efficiency of plant species is generally influenced by the depth of the root system, and thus, grasses have higher water use efficiency because their root systems are shallow and have many fibrous roots (Nippert and Knapp, 2007). Through this understanding, grasses can efficiently use surface water for growth and to maintain plant coverage and AGB. As such, our studied grasslands were dominated by *L. chinensis* which is a perennial tall and erect grass, as most of the grasses occupy the top layers of the studied grassland communities. In sum, our results warn that drought (i.e., a decline in water availability) can greatly decline AGB directly and indirectly *via* plant coverage in the studied grasslands (Trenberth et al., 2014).

On the other hand, we found that mean annual temperature did not regulate AGB directly but did regulate indirectly *via* species evenness and plant coverage through opposing effects. Through declined species evenness, temperature increased AGB indirectly *via* adjusting plant metabolic and physiological processes of dominant resistive species to temperature sensitivity. The increase in temperature can promote the metabolism of certain adaptive plants to high temperatures which could prolong the growth cycle of plants, thereby increasing the AGB of a community (Gillman and Wright, 2014; Sullivan et al., 2020). However, we found that temperature declined plant coverage and species richness as well and that the indirect effect of temperature on AGB *via* plant coverage than species richness was negative. This result indicates that certain adaptive plant species can occupy the physical niche space, which could lead to less AGB due to the selection effect as compared to the niche complementarity effect (Loreau et al., 2001; Heskel et al., 2016). In sum, our result shows that temperature regulates the metabolic, physiological and ecological processes of certain species with uneven distribution of plant coverage, which in turn leads to less AGB indirectly. The overall negative indirect effect of temperature on AGB *via* plant coverage, species richness and evenness is consistent with ecophysiological theories, i.e., the acclimation potential of respiration might be higher than that of photosynthesis (Brown et al., 2004; Sullivan et al., 2020; Cabon et al., 2022). Also, thermal resistance and resilience are probably due to a combination of individual acclimation and plasticity as well as differences in species-specific responses to climate which could lead to shifts in community composition due to variations in demographic rates or plant coverage through species shift at high temperatures (Ulrich et al., 2014; Butterfield, 2015; Berdugo et al., 2019).

Importantly, we also found that plant coverage was the top regulator of AGB, and even the direct effect was stronger than temperature and precipitation, confirming again that plant coverage is the best indicator of AGB in grasslands worldwide (Ji et al., 2009; Sanaei et al., 2018a). It is not surprising that the observed direct effect of species richness was weak positive as it has been reported by many studies across the globe, indicating that species richness alone is not the best predictor of AGB which is even contrary to the predictions of the niche complementarity effect (van der Plas, 2019). As such, we found that species evenness declined AGB better than species richness, indicating again that certain species could adapt to thermal resistance. However, the positive associations among plant coverage, species richness and evenness, and their positive responses to precipitation indicate that niche complementarity plays a role in enhancing AGB in grassland communities under favourable climatic conditions. However, the negative effect of species evenness suggests that the selection effect cannot be teased apart from the niche complementarity effect in regulating AGB when temperature sensitivity is modulating the response of grassland communities. The negative effect of species evenness on AGB is likely because community AGB is determined primarily by dominant species (Smith and Knapp, 2003), i.e., *L. chinensis* is a dominant species, accounting for as much as 90% of total AGB in some sites. Moreover, *L. chinensis* is a clonal plant, likely giving it an advantage in terms of resource capture because individuals of *L. chinensis* are also usually higher than other species in the community, which further reduces evenness and increases AGB. However, if this is the situation, then *L. chinensis* is sensitive to higher temperatures but needs higher water availability for high plant coverage and AGB, which requires further experimental investigations. In addition, although we found that temperature and precipitation regulated AGB directly and indirectly *via* plant coverage and species diversity, they were positively correlated. Thus, further studies should also focus on the long-term observations of grassland communities in response to climate change factors such as temperature and precipitation seasonality as well as soil nutrients availability and heterogeneity.

Conclusions

We show that plant coverage, as compared to species richness and evenness, plays a key role in maintaining the AGB of grasslands in northern China. As such, plant coverage promotes the coexistence of species but depends greatly on precipitation and temperature. Thus, we show that the niche complementarity and selection effects are playing a joint role in determining the AGB of grasslands. In sum, our results highlight that precipitation and temperature are two key climatic drivers of species richness, evenness, plant coverage and AGB through complex direct and indirect pathways. Our study suggests that grasslands are sensitive to climate change, i.e., a decline in water availability and an increase in atmospheric heat. We argue that plant coverage and climate change drivers related to precipitation and temperature should be included in ecological models for predicting the performance and stability of grassland communities.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

ZY:Conceptualization, methodology, software, validation, formal analysis, investigation, data curation, writing - original draft. YX: Data curation, investigation. LY: Investigation. LZ: Investigation, supervision, resources, project administration, writing - review & editing. AA: Writing - review & editing. All authors contributed to the article and approved the submitted version.

Funding

This work was supported by Research on the Second Comprehensive Scientific Expedition to the Qinghai-Tibet Plateau (Grant No. 2019QZKK0301), the Science and Technology Planning Project of Inner Mongolia Autonomous Region (Grant No. 2021GG0405), the National Science and Technology Fundamental Work Special Key Special Project Editing and Researching of “Chinese Vegetation” (Grant No. 2015FY210200-24), the National Natural Science Foundation of China (Grant No. 31670532), the National Natural Science Foundation of China (Grant No. 42177347), and the National Natural Science Foundation of Inner Mongolia (Grant No. 2019MS03026). AA is supported by the special project of Hebei University (Grant No. 521100221033).

Acknowledgments

The authors would like to thank Dr. Ma Wenhong and Dr. Feng Gang for their insightful comments on the earlier version of this manuscript. We are highly grateful to the Associate Editor (Dr. Paolo Giordani), Dr. Chang Bae-Lee and three reviewers for their insightful comments which greatly improved an earlier version of this manuscript.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher’s note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2022.999636/full#supplementary-material

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Frontiers in Plant Science

TYPE Original Research
PUBLISHED 09 January 2023
DOI 10.3389/fpls.2022.1088202

OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to
Functional Plant Ecology,
a section of the journal
Frontiers in Plant Science

RECEIVED 03 November 2022
ACCEPTED 19 December 2022
PUBLISHED 09 January 2023

CITATION
Xie M, Li L, Liu B, Liu Y and Wan Q
(2023) Responses of terrestrial
ecosystem productivity and
community structure to intra-annual
precipitation patterns: A meta-analysis.
Front. Plant Sci. 13:1088202.
doi: 10.3389/fpls.2022.1088202

Responses of terrestrial ecosystem productivity and community structure to intra-annual precipitation patterns: A meta-analysis

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Introduction: The productivity and community structures of terrestrial ecosystems are regulated by total precipitation amount and intra-annual precipitation patterns, which have been altered by climate change. The timing and sizes of precipitation events are the two key factors of intra-annual precipitation patterns and potentially drive ecosystem function by influencing soil moisture. However, the generalizable patterns of how intra-annual precipitation patterns affect the productivity and community structures of ecosystems remain unclear.

Methods: We synthesized 633 observations from 17 studies and conducted a global meta-analysis to investigate the influences of intra-annual precipitation patterns on the productivity and community structures of terrestrial ecosystems. By classifying intra-annual precipitation patterns, we also assess the importance of the magnitude and timing of precipitation events on plant productivity.

Results: Our results showed that the intra-annual precipitation patterns decreased diversity by 6.3% but increased belowground net primary productivity, richness, and relative abundance by 16.8%, 10.5%, and 45.0%, respectively. Notably, we found that the timing uniformity of precipitation events was more important for plant productivity, while the plant community structure benefited from the increased precipitation variability. In addition, the relationship between plant productivity and community structure and soil moisture dynamic response was more consistent with the nonlinear model.

Comclusions: The patterns of the responses of plant productivity and community structure to altered intra-annual precipitation patterns were revealed, and the importance of the timing uniformity of precipitation events to the functioning of production systems was highlighted, which is essential to enhancing understanding of the structures and functions of ecosystems subjected to altered precipitation patterns and predicting their changes.

KEYWORDS

community structure, plant productivity, precipitation pattern, soil moisture, synthesis

Introduction

Precipitation is a key factor driving the structures and functions of terrestrial ecosystems by affecting plant growth (Jongen et al., 2013; Zhang et al., 2018), plant productivity (Hu et al., 2010; Reichstein et al., 2013; Hu et al., 2018), plant community structure (Koerner et al., 2013; Jones et al., 2016), litter decomposition (Cui et al., 2021), and microbial community structure (Ochoa-Hueso et al., 2020). Global warming caused by human activities not only has altered total precipitation amount (Baker & Fritz, 2015) but also has increased the inter-annual and intra-seasonal variability in precipitation, resulting in frequent precipitation events and extreme events on the global, regional, and local scales (Trenberth et al., 2003; Sala et al., 2015; IPCC, 2022). Continuous extreme precipitation events undoubtedly alter the distribution of precipitation patterns and exert considerable impact on ecosystems by regulating plant productivity and community structure, eventually affecting global carbon cycles, even though precipitation amounts remain consistent (Sala et al., 2000; Knapp et al., 2002; Knapp et al., 2008). Hence, increasingly frequent changes in precipitation patterns are expected to regulate ecosystem processes to a greater extent than the other driving factors of global change (Fang et al., 2001).

Terrestrial ecosystems are highly sensitive to altered intra-annual precipitation patterns (Fay et al., 2003; Heisler-White et al., 2008; Didiano et al., 2016; Smith et al., 2016). Precipitation patterns influence ecosystem structure and function by affecting ecosystem water availability (Huang et al., 2010; Schwinning et al., 2003; Scott & Biederman, 2017). For example, the alterations to precipitation patterns can affect rainfall use efficiency by changing the stem leaf ratio and ultimately impact plant productivity (Yang et al., 2020). Altered precipitation patterns lead to the dominance of resource-conservative species with large root-shoot ratio and small specific leaf area (Fay et al., 2011). In general, intra-annual precipitation patterns are normally caused by alterations to the timing and sizes of precipitation events. In a semiarid steppe, increase in the size of precipitation events increases the amount of runoff and decreases evaporation losses (Robertson et al., 2009), and increase in interval between precipitation events increases soil moisture variability (Knapp et al., 2002) and reduces plant productivity (Fay et al., 2003), leaf carbon assimilation (Nippert et al., 2009), and soil CO_2 outflow (Harper et al., 2005). At present, the direction and extent of terrestrial ecosystems worldwide response to altered precipitation patterns are still unclear due to the highly uncertainty of precipitation patterns.

Soil water availability directly affects plant growth and is commonly related to precipitation timing and size (Wang et al., 2016). First, large precipitation events alter the distribution ratio of soil moisture among different layers (Goldstein & Suding, 2014), thereby affecting the growth of plants using shallow or deep soil moisture. Second, increase in interval between precipitation events reduces ecosystem water use efficiency by extending the drying time of soil while decreasing the plant leaf area index (Liu et al., 2017) and stimulating respiratory pulses (Huxman et al., 2004). In addition, soil moisture changes caused by different distribution of precipitation events can also lead to significant differences in soil nutrients and nutrient use availability (Nitschke et al., 2017; Wang et al., 2017). For example, small precipitation events with short intervals can contribute to enhanced plant productivity by improving soil nutrient availability (Harpole et al., 2007; Nielsen & Ball, 2015). However, excessive precipitation will cause nutrient loss through leaching or surface flow, which is not conducive to plant growth (Yahdjian & Sala, 2010).Given that soil moisture is a link between precipitation and vegetation response (Wang et al., 2018), its variability limits plant transpiration and photosynthesis and affects ecosystem stability (Schneider et al., 2011). Therefore, assessing how the size and timing of precipitation events affect global terrestrial ecosystem productivity through soil moisture and their relative importance for plant productivity is necessary.

Ecosystems respond to altered intra-annual precipitation patterns, and the response depend on ecosystems type (Knapp et al., 2002; Zhang et al., 2013). For example, in three grassland ecosystems, tallgrass prairie showed 18% reduction in aboveground net primary productivity, whereas semiarid steppe and mixed prairie showed 30% and 70% increases when precipitation timing was altered (Heisler-White et al., 2009). In addition, precipitation variability plays a substantial role in ecosystems during the growing season (Bai et al., 2004; Swemmer et al., 2007; Robinson et al., 2013). For instance, a 24 year study in the Inner Mongolia grassland showed that the cumulative precipitation from January to July had a greater impact on plant productivity than precipitation in other periods (Bai et al., 2004). However, another study indicated that increased summer rainfall in combination with winter drought significantly increased diversity, and increased winter precipitation led to the emergence of new grass species conducted in semiarid steppe (Prevéy et al., 2014). Given the multitudinous distribution of intra-annual precipitation patterns and ecosystem types, the effects of precipitation patterns on terrestrial ecosystems on the global scale are inadequately studied, and thus further assessment of how terrestrial ecosystems respond to climate change is currently limited. Therefore, the responses of ecosystems and experimental periods to altered intra-annual precipitation patterns should be investigated on the global scale.

In response to the current research gap, we conducted a meta-analysis using 633 observations from global precipitation manipulation experiments to synthesize the effect of altered precipitation patterns on terrestrial ecosystem productivity and community structure. Using a comprehensive dataset, we analyzed the response of plant productivity and community structure to intra-annual precipitation patterns and how the size and timing of precipitation events affect plant productivity by altering soil moisture. We asked two questions: How will plant productivity and community structure respond to intra-annual precipitation patterns? How important are the size and timing of precipitation events to ecosystems and how do they affect plant productivity through soil moisture? Based on the above two research questions, we proposed the following hypothesis: (1) Altered intra-annual precipitation patterns will increase plant belowground productivity and reduce diversity. (2) The timing uniformity of precipitation events will reduce soil moisture variability, increase soil moisture content and contribute to plant productivity. Precipitation pattern affects plant productivity and community structure by changing soil moisture availability, and the relationship between them is more consistent with the nonlinear model.

Materials and methods

Data collection and extraction

We used the Web of Science database to search peer-reviewed publications (2000-2021.10) on primary production and community structure with the following keywords: (rainfall distribution OR precipitation distribution OR rainfall event* OR precipitation event* OR rainfall regime* OR precipitation regime* OR rainfall pattern* OR precipitation pattern* OR rainfall frequency OR precipitation frequency) AND (net primary product* OR community structure OR divers* OR species divers* OR species rich* OR composition shifts OR primary product* OR ANPP OR BNPP OR NPP) AND (experiment* OR treatment*). Studies were incorporated when they met the following criteria: (1) precipitation manipulated must be carried out in natural terrestrial ecosystems, excluding studies conducted in laboratories; (2) plant communities were not artificial cultivated; (3) ambient and treatment were performed under the same biotic and abiotic conditions; (4) the study included at least one productivity variables or community structure indicators, and the duration of the experiment was clearly reported; (5) for years of experimental observation results, only results reported separately by year were collected; (6) for the treatment group controlled by precipitation patterns, temperature, N addition, added root-feeding scarabs, grazed and other factors, the multi-factor treatment group, such as temperature and N addition, was used as the ambient group for meta-analysis. If experiments at multiple sites were reported in an article, they were treated as independent studies.

Using these criteria, we obtained 633 observations results from 17 published studies (Figure 1B; Table S1; Supplementary File 1). Base on precipitation frequency of experimental and ambient conditions, we divided them into two groups. In the different precipitation frequency group (the precipitation frequency of experimental and ambient were inconsistent), 207 observations reported even event timing (e_{timing}, defined as the uniform precipitation event timing), 26 reported even event size and timing (even, defined as uniform precipitation event size and timing), and 229 reported non-even event size and timing (non-even, defined as non-uniform precipitation event size and timing). In same precipitation frequency group (the precipitation frequency of experimental and ambient were consistent), 11 had even event size (E_{size}, defined as uniform precipitation event size), 12 had even event timing (E_{timing}, defined as the uniform precipitation event timing), 11 had even event size and timing (EVEN, defined as uniform precipitation event size and timing), and 137 had non-even event size and timing (NON-EVEN, defined as non-uniform precipitation event size and timing). Soil nutrient data were only obtained from 3 studies, which mainly included NO_3^- concentrations, NH_4^+ concentrations, total N, carbon pools, nitrogen pools and C:N. We failed to analyze the impact of altered precipitation pattern on plant productivity due to insufficient data.

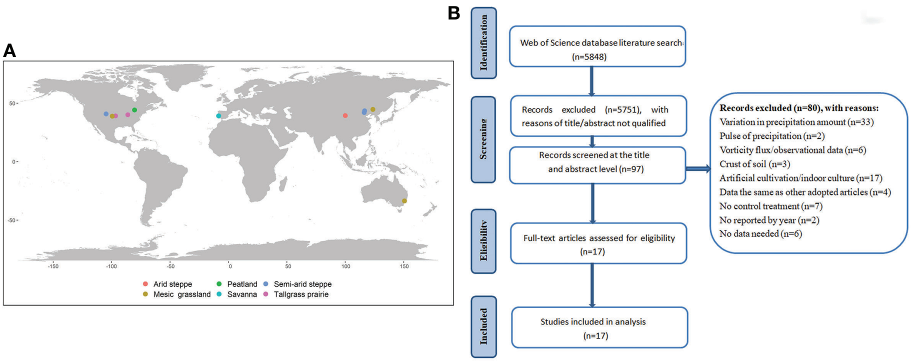

FIGURE 1
Map of the global distribution of study sites **(A)** and a flow chart of criteria for study selection **(B)** used in this meta-analysis. The distribution of 17 studies in 19 different biomes.

We used GetData Graph Digitizer 2.26 to extract the means, sample sizes (if reported), and standard errors for each study. Data were derived from tables, figures, and appendices of the original publications. For each study, we collected information about latitude, longitude, mean annual temperature (MAT), and precipitation (MAP), altitude, ecosystem type, and experiment duration (i.e., the start and end dates of the experiment). For articles missing MAT and MAP, we used the names of countries, states, or experimental study sites to search for other publications. In addition, we also collected soil background data (including soil texture, pH, soil organic matter content, total N and total P) at the study sites, but most of the studies lacked relevant data (Table S1). Given that most of the ecosystem types we collected were grassland ecosystems, we classified grassland ecosystems by the precipitation and vegetation types of the research sites. The collected articles were grouped into different biomes: arid steppe, semi-arid steppe, mesic grassland, tallgrass prairie, peatland, and savanna (Figure 1A). Due to the few global precipitation pattern manipulation experiments, there is a lack of precipitation pattern manipulation experiments conducted in South America and Africa in the publications we collected.

Variable selection

We selected plant productivity and community structure from published studies and divided them into four categories of response variables (Table S2): (1) biomass, usually refers to the total amount of live organic matter in per unit area at a certain time, including aboveground biomass (AGB) and belowground biomass (BGB); (2) net primary productivity, aboveground net primary productivity (ANPP) was calculated from the peak biomass per unit area aboveground with no carry of live biomass from previous years. Belowground net primary productivity (BNPP) was estimated according to the dry mass of root growth per unit area per unit time, which was measured by root growth into cores and soil drilling; (3) community structure indicators, species richness is simply the number of species per unit of area, and the usual measures are typically separated into measures of α, β, and γ diversity (Brown et al., 2007). Cover can be used in measuring the luxuriance and growth situation of vegetation. Shannon-Wiener (H) index reflects the diversity of plant community according to the number of species. Pielou's evenness index (E) can reflect the evenness of plant community. Relative abundance refers to the abundance of one species as a percentage of the total abundance of all species in a community; (4) root-shoot ratio, refers to the ratio of fresh or dry weight between the belowground and aboveground parts of a plant and is used in assessing changes in carbon allocation in biomass or carbon allocation in response to climate change (Song et al., 2019).

Data analysis

Effect size can be compared, and the treatment effects of all studies can be expressed on a common scale and used in highlighting general responses over a broad range of ecosystems (Wu et al., 2011). We used log response ratio (lnRR) to test the responses of plant productivity and community structure to intra-annual precipitation patterns following Hedges et al. (1999):

$$\ln RR = \ln\left(\frac{Xt}{Xc}\right) = \ln(Xt) - \ln(Xc)$$

where Xt and Xc are the mean values of productivity and community structure, respectively, in the treatment and ambient groups. Variance in each lnRR was calculated as follows:

$$v = \frac{SD_t^2}{N_t X_t^2} + \frac{SD_c^2}{N_c X_c^2}$$

where SD_t and SD_c represent standard deviations; N_t and N_c represent sample sizes of the treatment and ambient groups, respectively.

We used MetaWin (Version 2.1, Rosenberg et al., 1997) to calculate the weighted response ratio (lnRR++) and 95% confidence interval (95% CI) of the mixed-effects. The effects of precipitation patterns were considered significant ($p < 0.05$) when 95% CI of response variables does not overlap with zero. To determine whether the responses were different among groups, we grouped the response variables according to the information collected (ecosystem type, precipitation distribution, and experiment period) and conducted a between-group heterogeneity test (Q_B tests). If Q_B values were significant ($p < 0.05$), the responses were considered significantly different among groups (Liu et al., 2016). We converted weighted response ratios (lnRR++) and there 95% CIs for each explanation back to the percentage change as follows: ($e^{\ln RR++} - 1$) x 100%.

We examined differences in plant productivity and community structure among different treatments according to the research method of Griffin-Nolan et al. (2021). We divided the treatment groups according to precipitation pattern in the growing season: (1) non-even event size and timing (non-even/ NON-EVEN), (2) even event size (E_{size}), (3) even event timing (e_{timing}/E_{timing}), and (4) even event size and timing (even/ EVEN). We used different soil moisture indicators to evaluate difference in soil moisture among the treatment groups. Soil moisture indicators included coefficient of variation (CV) of soil moisture, change in soil moisture (CSWC), median soil moisture, the consecutive disparity index (D) of soil moisture, soil moisture skewness, and soil moisture kurtosis. The CV is one of the most commonly used indicators for evaluating time variability (Fernández-Martínez et al., 2018), but they have mean dependence on or high sensitivity to rare events. By using the consecutive disparity index, we can evaluate the rates of changes in time for consecutive values. The calculation formula of consecutive disparity index is as follows:

$$D = \frac{1}{n-1}\sum_{i=1}^{n-1}\left|\ln\frac{p_{i+1}}{p_i}\right|$$

where *pi* is the series value at time *i* and *n* is the series length (Fernández-Martínez et al., 2018).

The TSA package in R V.4.0.2 (R Core Team, 2020) was used in calculating the skewness and kurtosis of soil moisture (Chan et al., 2020). We used SPSS 25.0 to analyze the soil moisture among treatments. Differences in plant productivity and community structure were analyzed by independent sample t-test and one-way analysis of variance (Duncan). Linear and polynomial regression models were used in determining the relationship between soil moisture and relative changes in predictor variable.

Results

The observations we collected in compliance with the criteria were mainly distributed in North America and Asia (Figure 1A). The study areas were located from 33.61 S to 44.67 N, and the MAT of experimental sites ranged from -0.48°C to 17.0°C and MAP ranged from 117 mm to 835 mm. The treatment periods of these studies fall into the growing season (May-October) and non-growing season (November-May; Table S1).

Overall of plant productivity and community structure response to intra-annual precipitation patterns

In general, altered intra-annual precipitation significantly affected plant community structure but had little effect on plant productivity (Figure 2). Compared with ambient treatment, altered intra-annual precipitation significantly enhanced BNPP, richness, and relative abundance by 16.8%, 10.5%, and 45.0%, respectively but decreased diversity by 6.3% in the total precipitation pattern group. In the different precipitation frequency group, ANPP and diversity were significantly reduced by 5.1% and 6.3%, whereas richness and relative abundance remained consistent with the total precipitation pattern, increasing by 11.2% and 39.7%, respectively. By contrast, all variables have no significant changed in the same precipitation frequency group.

Plant productivity exhibited different responses under the group of ecosystem type, precipitation distribution and experimental periods (Figure 3; Table S3). Significant difference in ANPP was observed among the ecosystem types with the changing of intra-precipitation patterns ($p < 0.001$).The responses of ANPP in semi-arid steppe (19.16%) and other ecosystem (110.85%) increased significantly, whereas the response in tallgrass prairie (-11.42%) decreased significantly (Figure 3). The responses of ANPP to altered intra-annual precipitation patterns showed significant difference among different precipitation frequency ($p < 0.001$). The ANPP values

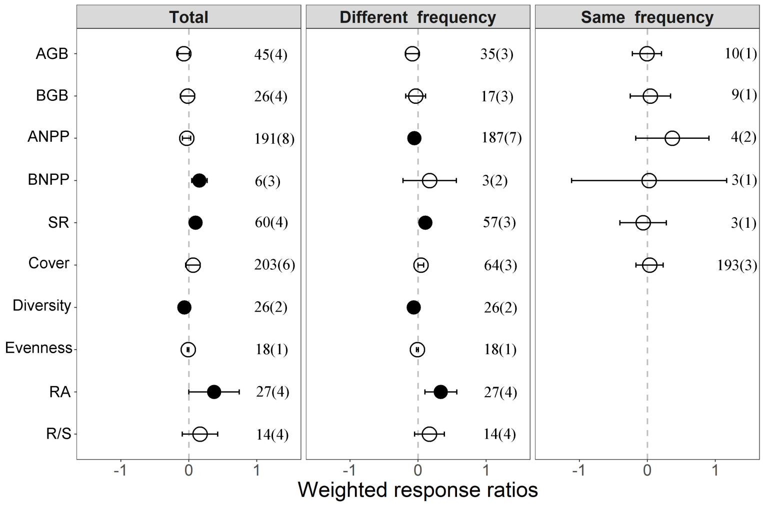

FIGURE 2

Responses of plant productivity and community structure to intra-annual precipitation patterns (including total precipitation pattern group, different precipitation frequency group and same precipitation frequency group). Values are weighted response ratios and their 95% confidence intervals (95% CI). Values indicate the intensity of the impact of altered intra-annual precipitation distribution on plant productivity and community structure relative to the values in the ambient treatment. The vertical dashed line represents weighted response ratios = 0. If 95% CI did not overlap with zero, the effects of precipitation pattern on variables were considered significant (denoted by black circles). Numbers corresponding to each variable represent the number of data observations, and the number in parentheses represents the number of studies. AGB, aboveground biomass; BGB, belowground biomass; ANPP, aboveground net primary productivity; BNPP, belowground net primary productivity; SR, species richness; RA, relative abundance; R/S, root−shoot ratio.

of the e_{timing} and even treatments increased by 12.54% and 110.90%, whereas the ANPP of the non-even treatment decreased by 11.15% (Figure 3). Alterations to precipitation patterns in the growing season reduced ANPP by 6.23%, whereas the ANPP in the non-growing season increased by 110.96% (Figure 3).

The effects of intra-annual precipitation patterns on plant community structure differed by ecosystem type, precipitation distribution, and experimental period (Figure 3; Figure S1; Table S3). Across ecosystems, the responses of root–shoot ratio increased by 34.38% only in the mesic grassland. Similarly, only e_{timing} treatment significantly enhanced root-shoot ratio by 34.38% at different precipitation frequency. In the growing season, significantly increase in root–shoot ratio by 38.20%, while no change was found in the non-growing season (Figure 3). In all groups, only difference precipitation frequency cover reached a statistically significant level ($p < 0.001$; Figure S1). Among them, e_{timing} treatment significantly reduced cover by 12.36%, while non-even treatment significantly increased cover by 7.42%. Across ecosystems, tallgrass prairie significantly increased richness by 11.43%, whereas semi-arid steppe and mesic grassland did not affect richness (Figure S1).

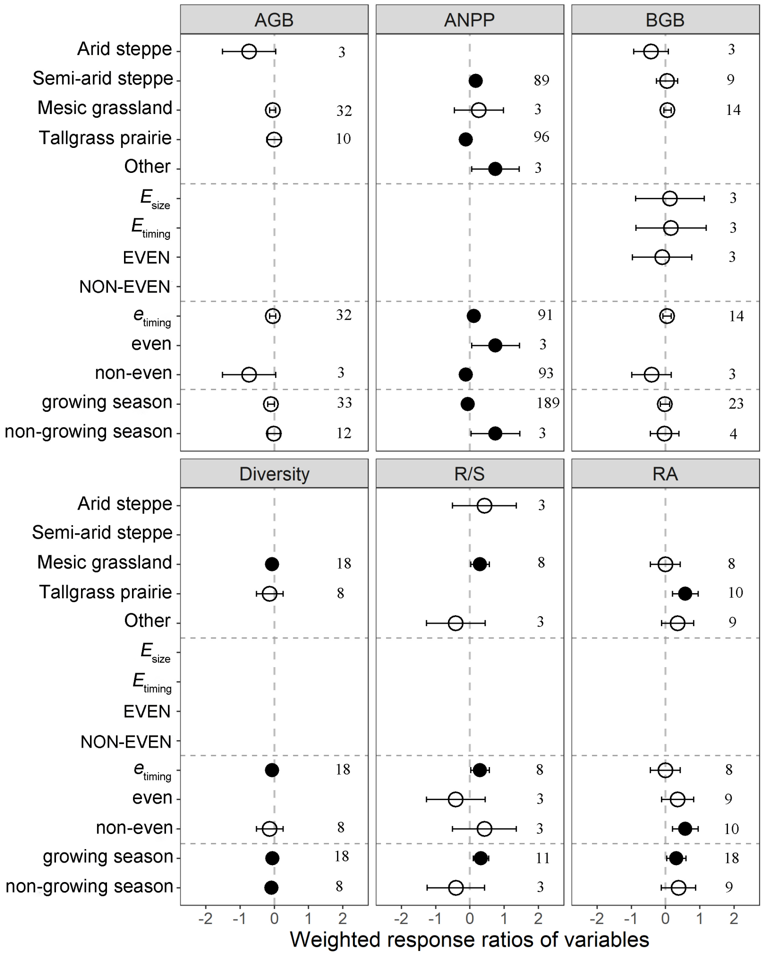

FIGURE 3
Subgroup analysis of plant productivity and community structure on altered intra-annual precipitation patterns. Between-group heterogeneity (Q_B) was tested according to ecosystem type, precipitation distribution and experimental period. If 95% CI did not overlap with zero, the effects of precipitation pattern on variables were considered significant (denoted by black circles). Error bars represent 95% confidence intervals (CI). The vertical dashed line represents weighted response ratios = 0. Numbers indicate the number of data observations. The Q_B statistical test was used to compare the differences in weighted response ratios among groups divided by ecosystem type, precipitation distribution and experimental period. A significant Q_B value ($p < 0.05$) suggested that the weighted response ratios of a given variable differed among groups. E_{szie}, even event size treatment; E_{timing}, even event timing treatment; EVEN, even event size and timing treatment; NON-EVEN, non-even event size and timing treatment; e_{timing}, even event timing treatment; even, even event size and timing treatment; non-even, non-even event size and timing treatment. See Figure 2 for abbreviations.

Effects of intra-annual precipitation patterns on soil moisture

In the different precipitation frequency groups, CV in soil moisture was lower in the even treatment, while was higher in the e_{timing} treatment and non-even treatment compare with the ambient treatment, and the non-even treatment was significantly higher than other two treatments ($p < 0.001$; Figure 4A). As for change in soil moisture, three treatments were lower than ambient treatment, and no significant difference was found among all treatments ($p = 0.516$; Figure 4B). The median soil moisture in the e_{timing} treatment was significantly higher than that in the even treatment ($p < 0.01$), and no significant difference was found among other treatments (Figure 4C). The consecutive disparity index (D) in the e_{timing} treatment was higher than that in the ambient treatment, with and significant differences were observed among all treatments ($p < 0.001$; Figure 4D). The even treatment had the highest skewness and kurtosis in soil moisture, but the even treatment had significantly higher soil moisture skewness than the other treatments ($p < 0.001$; Figure 4E). No significant difference in soil moisture kurtosis was found among all treatments ($p = 0.435$; Figure 4F).

In the same precipitation frequency group, the CV, change in soil moisture and median of soil moisture in the E_{size} and EVEN treatments were significantly higher than those in the E_{timing} and NON-EVEN treatments (Figures 4G-I). Moreover, the median soil moisture in the E_{timing} treatment was significantly higher than that in the NON-EVEN treatment ($p < 0.001$; Figure 4I). The EVEN treatment had significantly higher D than the E_{timing} treatment and NON-EVEN treatment ($p < 0.05$), and no significant difference was found among other treatments (Figure 4J). The soil moisture skewness in the E_{timing} treatment was significantly higher than that in the other treatments ($p < 0.001$; Figure 4K). Significant difference in soil moisture kurtosis was observed among all treatments ($p < 0.001$; Figure 4L).

Plant productivity and community structure response to precipitation event size and timing

In general, plant productivity and community structure were changed in different precipitation frequency (Figure 5). AGB and BGB in the non-even treatment were significantly lower than those in the e_{timing} treatment ($p < 0.05$; Figures 5A, B). In the difference precipitation frequency group, decrease in the time variation of precipitation resulted in an increase in ANPP in all treatments, and the order of the treatments by time variation was as follows: non-even < e_{timing} < even. In addition, ANPP was significantly lower in the non-even treatment than in the e_{timing} treatment ($p < 0.001$; Figure 5C). By contrast, the cover of non-even treatment was significantly higher than that in the e_{timing} treatment ($p < 0.05$; Figure 5H). The root-shoot ratios of the e_{timing} and non-even treatments were significantly higher than the root-shoot ratio of the even treatment ($p < 0.05$; Figure 5G).

The same precipitation frequency treatment had little effect on plant productivity and community structure (Figure 5). BGB in E_{size} and E_{timing} treatments were higher than that in ambient treatment and the EVEN treatment (Figure 5L). The cover only in NON-EVEN treatment was higher than that in the ambient treatment (Figure 5M). However, no significant differences in BGB and cover were found among all treatments ($p = 0.081$; $p = 0.847$; Figures 5L, M).

Factors influencing the responses of plant productivity and community

In the total precipitation pattern group, BGB had significant relationship with the multiple indices of soil moisture, which had negatively correlated relationships among the BGB, consecutive disparity index, and kurtosis of soil moisture and was positively correlated with soil moisture skewness, promoting the fitness of BGB with the CV of soil moisture, median soil moisture, and soil moisture change after quadratic and quartic polynomial fitting (Table 1; Figure S2). ANPP increased as soil moisture changed, and had quartic polynomial relationship with the consecutive disparity index of soil water (Table 1; Figure S2). Moreover, the correlation among the diversity and evenness and median soil moisture was quadratic fitting (Table 1; Figure S3). The richness and soil moisture change were matched cubic fitting, and the root-shoot ratio was negatively correlated with soil moisture change (Table 1; Figure S4).

In the different precipitation frequency group, soil moisture change, AGB, and ANPP were significantly positively correlated, whereas BGB showed a quadratic and cubic fitting relationship with the CVs of soil moisture and soil moisture change (Table 1; Figure S5). Increase in soil moisture change and median soil moisture increased cover, whereas increase in the soil moisture consecutive disparity index reduced cover (Table 1; Figure S6). In addition, median soil moisture had a quadratic fitting relationship with diversity and evenness (Table 1; Figure S6). We also found that the richness and root-shoot ratio were negatively correlated with soil moisture change (Table 1; Figure S7).

Discussion

In this meta-analysis, we first investigated the responses of plant productivity and community structure to intra-annual precipitation patterns, and further compared differences in these factors among varied treatments at the same precipitation frequency and different precipitation frequency on the global scale. Our results suggested that different precipitation frequency reduced ANPP, while total precipitation frequency significantly

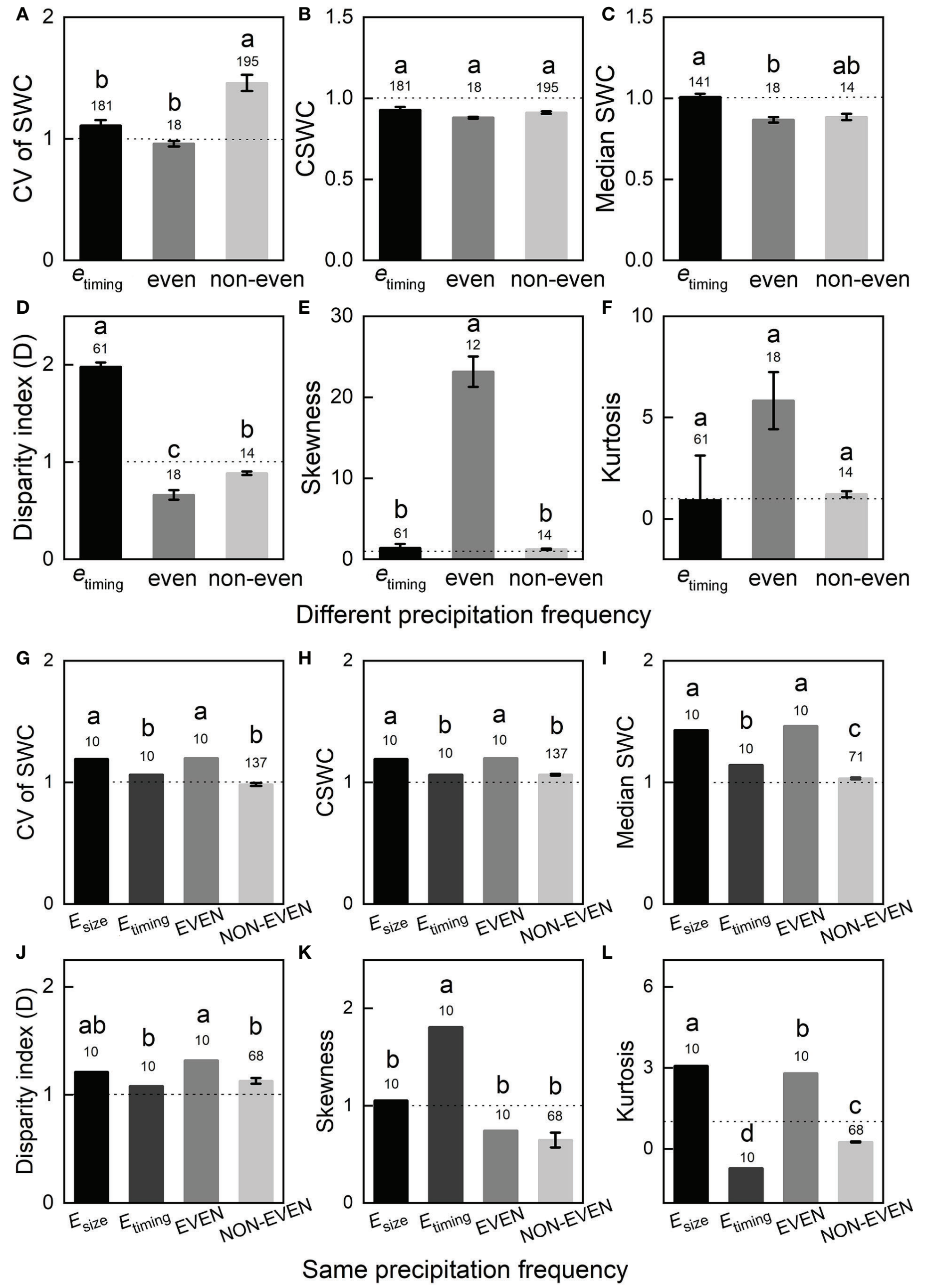

FIGURE 4
The bar chart indicate the treatment effects on multiple indices of soil moisture including **(A, G)** the coefficient of variation (CV) of soil moisture, **(B, H)** change in soil moisture (CSWC), **(C, I)** median soil moisture, **(D, J)** the consecutive disparity index (D) of soil moisture, **(E, K)** soil moisture skewness, **(F, L)** soil moisture kurtosis in different precipitation frequency and same precipitation frequency. Data are reported as mean ± SE, and numbers indicate the number of data observations. The dotted lines indicate the reference line for treatment intensity. Significant differences among treatments ($p < 0.05$) are indicated by different letters. See Figure 3 for abbreviations.

enhanced BNPP. Both precipitation frequencies had positive effects on richness and relative abundance, and have a negative effect on diversity. Plant productivity and community structure showed higher levels of responses to ecosystem types and difference precipitation frequency. Moreover, ecosystem functioning was more influenced by the timing uniformity of precipitation events, whereas the combination of increased precipitation event size and timing variability had greater effects on plant community structure. More importantly, the relationship among soil moisture and plant productivity and community caused by altered precipitation pattern were more aligned with the nonlinear model.

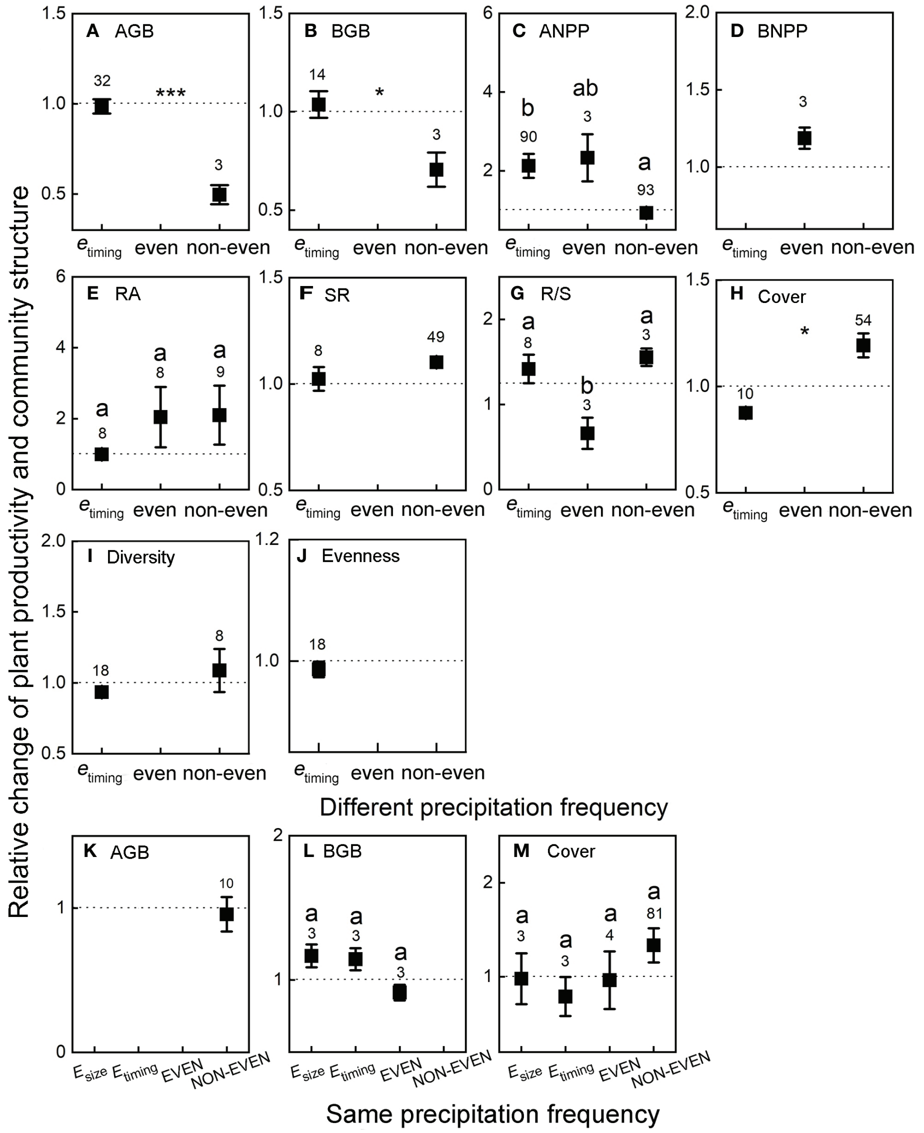

FIGURE 5
Treatment effects on plant productivity and community structure relative to the ambient in different precipitation frequency **(A–J)** and same precipitation frequency **(K–M)**. Data are reported as mean ± SE and numbers indicate the number of data observations. The dotted lines indicate the reference line for treatment intensity. Significant differences among treatments are indicated by different lettering ($p < 0.05$) and * (*$p < 0.05$, ***$p < 0.001$). See Figure 2 and Figure 3 for abbreviations.

Plant productivity

The responses of ANPP and BNPP to the intra-annual precipitation patterns were different. In the total precipitation pattern group, the response of ANPP decreased slightly, but the difference was nonsignificant. Meanwhile, BNPP increased significantly (Figure 2). The response of ANPP decreased significantly, while BNPP did not change significantly in the difference precipitation frequency group (Figure 2). In addition, the response of productivity had no significant changes in the same precipitation frequency group. These results can be attributed to three reasons. First, the responses of ANPP and BNPP to soil moisture, which was regulated by precipitation frequency, may have been different. In the different precipitation frequency group, all of the collected articles showed increased precipitation event size and decreased frequency. Thus, low precipitation frequency and extended precipitation interval would reduce temporally soil moisture availability and increased duration of soil desiccation (Liu et al., 2017), thereby exacerbating drought stress during two precipitation events and was adverse to plant growth (Knapp et al., 2002). Second, altered precipitation patterns

TABLE 1 Effects (R^2 and p-values) of soil moisture indices on plant productivity and community structure.

Variable	Total precipitation pattern											
	CV of SWC		CSWC		Median SWC		Disparity index (D)		Skewness		Kurtosis	
	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p
AGB	0.015	0.470	0.146	0.142	0.051	0.289	0.035	0.378	0.112	0.099	0.041	0.345
BGB	0.355	0.019*	0.555	0.008**	0.591	0.011*	0.602	0.002**	0.609	0.002**	0.417	0.017*
ANPP	0.016	0.099	0.039	0.009**	0.002	0.650	0.599	0.041*	0.072	0.332	0.070	0.339
Cover	0.000	0.964	0.003	0.508	0.001	0.790	0.008	0.504	0.002	0.723	0.002	0.717
Diversity	0.018	0.565	0.185	0.052	0.588	0.005**	0.007	0.772	0.021	0.608	0.102	0.246
Evenness	0.065	0.380	0.015	0.677	0.591	0.007**	0.500	0.022*	0.007	0.770	0.002	0.873
RA	0.014	0.550	0.045	0.290	0.157	0.292	0.193	0.236	0.125	0.350	0.016	0.747
SR	0.049	0.112	0.206	0.010**	NA	NA	NA	NA	NA	NA	NA	NA
R/S	0.259	0.110	0.831	0.000***	NA	NA	NA	NA	NA	NA	NA	NA
Different precipitation frequency												
AGB	0.045	0.296	0.280	0.005**	0.057	0.338	0.139	0.128	0.134	0.136	0.106	0.188
BGB	0.541	0.030*	0.787	0.005**	NA	NA	NA	NA	NA	NA	NA	NA
ANPP	0.016	0.102	0.040	0.009**	0.003	0.584	0.070	0.407	0.072	0.332	0.067	0.416
Cover	0.018	0.324	0.169	0.002**	0.537	0.004**	0.643	0.000***	0.017	0.669	0.049	0.470
Diversity	0.018	0.565	0.185	0.052	0.588	0.005**	0.007	0.772	0.021	0.608	0.102	0.246
Evenness	0.065	0.380	0.015	0.677	0.591	0.007**	0.500	0.022*	0.007	0.770	0.002	0.873
RA	0.014	0.550	0.045	0.290	0.157	0.292	0.193	0.236	0.125	0.350	0.016	0.747
SR	0.041	0.159	0.204	0.001**	NA	NA	NA	NA	NA	NA	NA	NA
R/S	0.259	0.110	0.831	0.000***	NA	NA	NA	NA	NA	NA	NA	NA
Same precipitation frequency												
AGB	0.029	0.639	0.000	0.961	0.092	0.559	0.092	0.559	0.092	0.559	0.092	0.559
BGB	0.128	0.344	0.128	0.344	0.153	0.298	0.348	0.095	0.253	0.167	0.079	0.465
Cover	0.005	0.521	0.000	0.898	0.005	0.619	0.003	0.703	0.017	0.385	0.004	0.679

The implications of soil moisture indices are defined in the legend to Figure 4.
p-values < 0.05 are considered significant.
*p < 0.05 **p < 0.001 ***p < 0.001.

generally stimulated plant root growth resistance to soil water deficit to prevent even large reductions in aboveground productivity (Fay et al., 2003). These results were consistent with our results that the response of root-shoot ratio increased to intra-annual precipitation pattern, although no significant change was observed (Figure 2). Finally, altered intra-annual precipitation pattern affect ecosystem productivity, mediate the availability of soil nutrients, such as excessive precipitation, and would lead to nutrient loss because of leaching, thereby limiting plant growth and productivity (Yahdjian & Sala, 2010). Notably, the synthetic effects of soil nutrients on ecosystem productivity were deficient because of insufficient data.

Across ecosystems, altered intra-annual precipitation pattern significantly increased the ANPP in semiarid steppe and other ecosystems, but decreased the ANPP in tallgrass prairie (Figure 3). Although small rainfall events can intermittently alleviate water stress and improve plant water status (Yahdjian & Sala, 2010), high atmospheric evaporation demand rapidly depletes soil water after these small rainfall inputs (Scott and Biederman, 2017) due to soil moisture stress and inferior availability in semi-arid steppe (Peng et al., 2013). Therefore, large precipitation size enables water to access deep soil and increases the duration of high soil moisture pulse (Moore et al., 2020), and the amount of water consumed through transpiration increases; thus, plant productivity improves. As for tallgrass prairie, increased interval between precipitation events can reduce plant biomass because C_4 grasses are strongly limited; while C_3 grasses and forbs are resistant to altered precipitation variability (Fay et al., 2003). In the different precipitation frequency group, e_{timing} and even treatments significantly increased ANPP, whereas non-even treatment significantly decreased ANPP (Figure 3). Each treatment with progressively reduced precipitation variability allocated this precipitation evenly and thus increased and maintained soil moisture pulse in the growing season, eliminating the challenge imposed by seasonal precipitation environment on plants (Moore et al., 2020; Griffin-Nolan et al., 2021).

Plant community structure

Our results showed that the responses of richness and relative abundance to precipitation pattern significantly increased and diversity decreased significantly on a global scale (Figure 2). Similarly, given that most of the collected literature has shown reduction in the frequencies of precipitation events. This reduction changed the resource allocation of water between shallow and deep soil may contribute to the growth of plants using deep soil water, while exacerbating the stress of plants using shallow soil water (Jones et al., 2016). Therefore, altered precipitation pattern decreased the abundance of one species and then would be compensated by increases in the abundance of other species, resulting in strong species asynchrony (Hallett et al., 2014). In addition, dominant plants usually can resist variable precipitation patterns (Fay et al., 2011). Hence, altered precipitation patterns reduced plant species evenness by affecting plant abundance, consistent with our results (Figure 2). Given that species diversity is a comprehensive reflection of species richness and evenness (Strong, 2016) which was significantly reduced by an altered precipitation pattern (Figure 2).

Responses of different ecosystems were distinct. Our results showed that the response of diversity in mesic grassland was reduced, and responses of relative abundance and richness in tallgrass prairie increased (Figure 3; Figure S1). These discrepancies can be explained by increased time interval between precipitation events, which reduces soil moisture in mesic grasslands (Heisler-White et al., 2009). Reduction in soil moisture in turn reduces the number of plant species because plants have low resistance to high precipitation variability. By contrast, tallgrass prairie can resist long-term precipitation variability and is relatively resilient to short-term extreme precipitation, and plants can utilize deep soil moisture (Jones et al., 2016).

As individual ecosystems typically provide few observations with little statistical power (Button et al., 2013), we tested their overall effect. It was found that the precipitation distribution pattern with decreasing precipitation frequency and increasing precipitation interval may significantly affect plant productivity and community diversity by changing the soil water available to plants and its availability, and this precipitation distribution pattern has a significant effect on plant growth in semi-arid steppe.

Relationships among precipitation variability, plant productivity, and community

Integrating observations of global terrestrial ecosystem, we divided the collected results into different treatments (Griffin-Nolan et al., 2021), and their precipitation variability gradually decreased. By comparing the variable quantity across these treatments, the impacts of precipitation size and timing variability on global terrestrial ecosystems can be understood in general. In brief, in difference precipitation frequency, the timing uniformity of precipitation events had greater effects on plant productivity (Figures 5A-C), whereas the combination of increased precipitation event size and timing variability had greater effects on plant community structure (Figures 5E-I). In addition, in the same precipitation frequency group, all treatments slightly affected plant productivity and community structure (Figures 5K-M). Furthermore, we estimated the relationship among plant productivity and community and soil moisture in an altered precipitation pattern and found that BGB, diversity, and evenness were the most significantly affected by soil moisture change but were limited by linear description (Table 1; Figures S2-S8).

Our results showed that the timing uniformity of precipitation events had a greater effect on ANPP (Figure 5C), inconsistent with previously results, which indicated that variability in precipitation event size was reduced, timing increased ANPP, and increase in ANPP was correlated with increase in soil moisture and consecutive disparity in soil moisture, lower soil moisture variability (Griffin-Nolan et al., 2021). One reason for this difference may be difference in response between an ecosystem type and global terrestrial ecosystem. We then studied the relationship between terrestrial ecosystem and soil moisture affected by precipitation pattern, and found that ANPP was associated with high soil moisture variation, and had a quartic polynomial fitting relationship with the consecutive disparity index of soil moisture (Table 1; Figure S2). Studies have shown that the correlation between ANPP and precipitation presents an asymmetric response under the influence of spatial models, and the relationship between them is suitable for a nonlinear concave-down relationship when precipitation years are extreme (Knapp et al., 2017). Our results showed that the correlation between ANPP and soil moisture variability decreased gradually and exponentially in each group, although we failed to find an appropriate fitting function (Table 1; Figures S2 and S5). This finding indicated that the relationship between soil moisture change and ANPP is complicated in an altered precipitation pattern.

We found that the linear relationship was inadequate to describe variation in BGB with soil moisture (Table 1; Figures S2 and S5), and other studies have shown that underground production has greater stability in response to intra-annual precipitation variability (Griffin-Nolan et al., 2021), partially consistent with our results. Our results indicated that BGB had stronger resistance when soil water variability was small and the resistance of BGB decreased gradually with increasing soil moisture variability. This result suggested that subsurface processes play a major role responding to precipitation variability and thereby enable ecosystems to buffer this effect. In addition, we found that diversity and evenness first increased and then decreased with increasing soil moisture, and a study showed that the increase of precipitation variability promoted diversity, but we did not find this phenomenon (Table 1; Figures S3 and S6). Our results show that complex variations in precipitation pattern cause soil moisture variability alter, and the above and below ground productivity of plant is resistant when the variability is slight, but with the increase of soil moisture variability, the resistance effect of plant will gradually weaken, ultimately affecting the community composition of the ecosystem.

Implications and future research

By conducting a meta-analysis, we quantitatively evaluated the patterns of the responses of terrestrial ecosystem structure and function to intra-annual precipitation pattern on a global scale. Our results indicated that terrestrial ecosystems are affected by altered intra-annual precipitation pattern (Figure 2), the timing uniformity of precipitation events is a critical factor for ecosystem functioning, and increase in precipitation variability is conducive to ecosystem community structure (Figure 5). Our results highlighted the importance of precipitation pattern to terrestrial ecosystems and implied the importance of considering the influence of variation in precipitation pattern on global carbon cycle apart from changes in precipitation amount.

Altered intra-annual precipitation pattern decreased ANPP and diversity but enhanced BNPP, richness, and relative abundance (Figure 2). However, few field experiments have been conducted on the effects of precipitation redistribution on terrestrial ecosystems when annual precipitation is constant. These limited data may cause inaccuracy in our conclusions. In addition, owing to the complexity of precipitation patterns, we failed to convert precipitation pattern into precipitation magnitude (Wang et al., 2021a) or divide it into increased or decreased precipitation (Wang et al., 2021b) to separately consider its impact on terrestrial ecosystem in the same manner as it was in other meta-analyses. Our current understanding of the impact of intra-annual precipitation pattern on ecosystem productivity across temporal and spatial scales is still limited. We considered the effects of ecosystem types on plant productivity and community structure (Figure 3; Figure S1). Most existing studies have been conducted in grassland ecosystems, and few experiments were conducted in peatland, savannas, and other ecosystems. However, owing to the complex processes and factors involved, different ecosystems may have different responses to precipitation patterns (Holmgren et al., 2013), and thus future studies need to consider the responses of other ecosystem types to precipitation pattern.

We assessed the impact of the size and timing variability of precipitation events on ecosystems (Figure 5). Given the precipitation times of the ambient and the treatment is a controlling factor, in the studies we collected, most of the precipitation times of ambient and treatment were distinct. Although eligible articles were few, a large proportion of data collected from the same literature. Therefore, such a small amount of data severely limited the assessment of precipitation event size and timing variability impact on global ecosystem structure and function. This limitation should be considered in future field rainfall experiments. An altered precipitation pattern may exert an impact on plant productivity by affecting soil moisture and nutrients (Yahdjian and Sala, 2010; Jones et al., 2016). Owing to the different monitoring methods and reported data of soil moisture dynamics in the articles we collected, uncertainty in our soil moisture data for assessing its impact on productivity may be present. In addition, the lack of soil nutrient data limited assessment of the impact of altered precipitation pattern. Therefore, the effects of altered precipitation patterns on soil nutrients should be considered in future works. Finally, the timing and size of a precipitation event are the two most important aspects that affect ecosystem structure and function. However, most current experiments have only used a single indicator of ecosystem function to evaluate the impact of precipitation pattern and rarely have paid attention to the response of community dynamics to intra-annual precipitation patterns. Thus, the importance of variability in precipitation timing and size in ecosystems cannot be fully assessed. Future studies should focus on the effects of variability in precipitation timing and size on community stability in ecosystems.

Conclusions

Our study presents a general pattern of plant productivity and community structure, the dynamic response of soil moisture to altered precipitation patterns, and its relationship to plant productivity and community structure. BNPP increased in the total precipitation pattern, while ANPP decreased in different precipitation group, and species richness and relative abundance increased and diversity decreased under both groups. We also found that the timing uniformity of precipitation promoted the increase of ANPP, while the increase of precipitation variability was beneficial to plant community structure and the relationship between plant productivity and community structure and soil moisture was limited by a linear model. The results further elucidate the intrinsic link between plant productivity, community structure and precipitation pattern relationships, and plant productivity and soil moisture. The differences in plant productivity, community structure, and soil moisture indicate the importance of precipitation pattern as a driver of ecosystem processes for biome-specific.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

MX analyzed data and wrote the manuscript. LL conceived the work and supervised this research. BL, YL and QW contributed to analyze of the manuscript. All authors contributed to the article and approved the submitted version.

Funding

Xinjiang Outstanding Young Scholars Foundation (2022D01E98), Shandong Province College Youth Innovation Technology Support Program (2020KJE009), Shandong Provincial Natural Science Foundation (ZR2020MC040), Youth Innovation Promotion Association of the Chinese Academy of Sciences (2020434).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2022.1088202/full#supplementary-material

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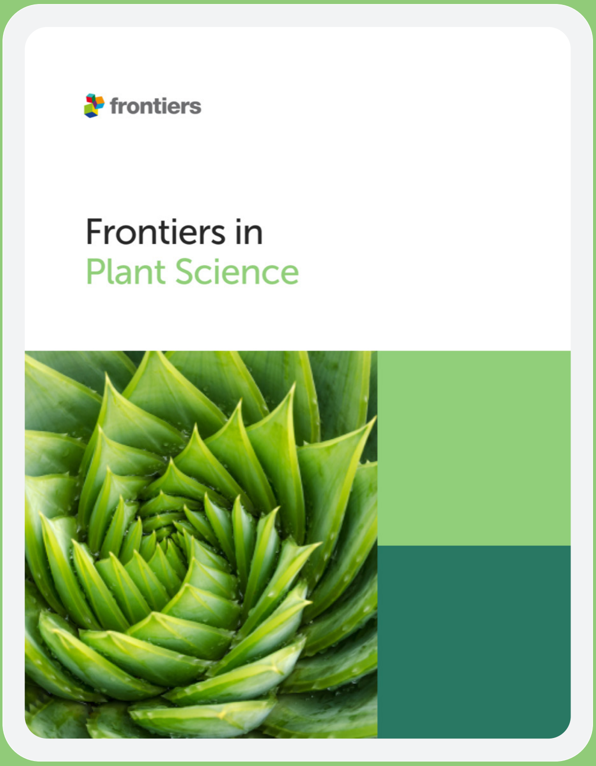

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