Divergent responses of plant biomass and its allocation to the altered precipitation regimes among different degraded grasslands in China

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Abstract
Purpose Climate models predict shifts in precipitation patterns characterized by increased precipitation amount and decreased frequency for semi-arid grasslands in northeast China. However, under these novel climatic conditions, potential differences in plant biomass and its allocation among different degraded grasslands remain unclear.

Methods We conducted a mesocosm experiment to test the effects of higher precipitation amount (increased by 50% from the long-term mean) and lower frequency (decreased by 50%) on plant biomass and allocation in the lightly, moderately, and severely degraded grasslands.

Results Lower precipitation frequency promoted belowground biomass but reduced aboveground biomass through enhancing soil water variability. Higher precipitation amount enhanced aboveground biomass in the lightly and moderately degraded grasslands, but not in the severely degraded grassland due to lower soil nitrogen availability. Lower precipitation frequency weakened or ended the positive effects of higher precipitation amount on aboveground and belowground biomass, and higher precipitation amount suppressed the enhancement of lower precipitation frequency on belowground biomass, which could be attributed to temporary waterlogging. Plants in the moderately degraded grassland preferred to adjust root vertical distribution, which was impacted by the changes in plant community composition. However, adjustment of aboveground biomass vs. belowground biomass was the primary biomass allocation strategy in the other two grasslands.

Conclusions Our findings emphasized the importance of considering the degradation level of grasslands when predicting responses of ecosystem functions to the projected changes in precipitation.
regimes. These findings are critical for making feasible decisions for the sustainable management of degraded grasslands.

**Keywords**  Precipitation frequency · Precipitation amount · Degraded grassland · Biomass allocation · Community composition · Mesocosm

**Abbreviations**

| Abbreviation | Description |
|--------------|-------------|
| LDG          | Lightly degraded grassland |
| MDG          | Moderately degraded grassland |
| SDG          | Severely degraded grassland |
| CPF          | Control precipitation frequency |
| CPA          | Control precipitation amount |
| DPF          | The decreased precipitation frequency treatment |
| IPA          | The increased precipitation amount treatment |
| AGB          | Aboveground biomass (g pot$^{-1}$) |
| BGB$_{0-10}$ | Belowground biomass in the 0–10 cm soil layer (g pot$^{-1}$) |
| BGB$_{10-30}$ | Belowground biomass in the 10–30 cm soil layer (g pot$^{-1}$) |
| BGB$_{0-30}$ | Belowground biomass in the 0–30 cm soil layer (g pot$^{-1}$) |
| TB           | Total biomass (g pot$^{-1}$) |
| BGB$_{0-10}$ (%) | BGB proportion in the 0–10 cm soil layer (%), $\frac{\text{BGB}_{0-10}}{\text{BGB}_{0-30}} \times 100$ |
| $f_{\text{AGB}}$ | AGB / TB (%) |
| SWC          | Mean of soil water content (%) |
| CV$_{\text{SWC}}$ | Variation of soil water content (%) |
| SINC         | Soil inorganic content (mg kg$^{-1}$) |

**Introduction**

General circulation models predict an intensification in the global hydrological cycle, which may be manifest in many ways, such as an increase in annual precipitation amount and/or a decrease in precipitation frequency (IPCC 2013). Such changes have already been observed in many areas including northeast China over the last decades (Heisler-White et al. 2009; Shang et al. 2019). Ongoing and future variation in precipitation regimes will strongly alter soil water availability, which is the primary constraint to plant growth in many drought-prone biomes (Gao et al. 2019; Knapp et al. 2001). Most of the studies about the impact of changes in precipitation on plant biomass accumulation focus on aboveground biomass (AGB), with much less attention given to the hidden belowground portion of biomass (BGB) (Zhang et al. 2019a). Shoots and roots have distinct responsibilities for resource acquisition in the response of plants to resource stress (Freschet et al. 2018). Under increased precipitation amount, plants prefer to develop shoots instead of roots, with aim of improving competition for light (Zhang et al. 2020b). Considering contrasting aboveground and belowground sensitivity to altered precipitation, this oversight questions the validity of our current understanding of how plants adjust biomass allocation to mitigate abiotic stress. Furthermore, investigating the changes in BGB under altered precipitation is critically important for understanding the responses of belowground processes, such as soil nutrient cycling and plant-soil feedbacks to changing precipitation regimes (Freschet et al. 2018; Wilcox et al. 2015).

As the most widespread vegetation type, grasslands are mainly located in arid and semiarid areas, with higher sensitivity to altered precipitation (Knapp et al. 2016). Moreover, grassland plants allocate a large fraction of biomass (33–86%) into belowground (Xu et al. 2013). Previous studies focus on non-degraded grasslands to explore responses of plant biomass and its allocation to altered precipitation (Knapp et al. 2018; Wilcox et al. 2016; Zhang et al. 2020a). However, some 20% of the world’s grasslands are at a severely degraded state; some others are under lightly and moderately degraded levels suffering shifts to less-desirable species (Michalk et al. 2018). Because of overgrazing and global climate change, more than 61% of grasslands in China have experienced salinization and/or desertification to various extents (Zhou et al. 2014). Due to differences in plant community compositions and soil properties, the responses of plant biomass and its allocation to altered precipitation are likely divergent among grasslands with different degrees of degradation (Dong et al. 2020).

In general, increased precipitation amount promotes AGB through enhancing photosynthetic rate (Ren et al. 2017). Besides, higher precipitation amount is likely to increase soil nitrogen (N) mineralization, N availability (Schaeffer et al. 2013), and plant N acquirement (Ren et al. 2015), which will eventually benefit AGB accumulation. Along increasing degradation levels of grasslands, the enhancement degree of increased precipitation amount on biomass
may be different. One possibility is that the positive relationship between increased precipitation amount and biomass may be strengthened with the intensification of grassland degradation. The reason is that grasslands with higher degradation levels are characterized by more annual plants, which have the ability to grow quickly and actively when water stress is relieved (Fry et al. 2013). Another converse possibility is that severe nitrogen limitation in the grasslands with higher degradation levels may weaken or even end the positive relationship between increased precipitation amount and AGB (Ren et al. 2017). Furthermore, the nitrogen demand of plants would increase when the water stress is alleviated, leading to more severe nitrogen limitation (Zhang et al. 2019a). Moreover, based on the meristem limitation hypothesis, severely degraded grasslands have limited positive responses to higher precipitation amount, due to meristem limitation, such as lower plant density, fewer seed and bud banks (Knapp and Smith 2001). In addition, relevant studies paid more attention to altered precipitation amount, rather than precipitation frequency and their interactions. Larger rainfall events resulted from lower precipitation frequency contribute to deeper penetration of soil water and greater soil water retention (Heisler-White et al. 2009). The improved soil water environment promotes AGB and further decreases the root/shoot ratio (Heisler-White et al. 2008). On the contrary, larger but fewer rainfall events may increase soil water fluctuation, which is likely to enhance biomass allocation into BGB to alleviate water stress (Post and Knapp 2020; Wilcox et al. 2015). In addition, lower precipitation frequency may enhance the aforementioned positive effects of higher precipitation amount on biomass accumulation.

Besides AGB vs. BGB allocation, plants can adjust root vertical distribution along the soil profile to optimize their water and nutrient acquisition (Zhang et al. 2019a). Developing roots in the surface soil is a cost-effective strategy for plants when drought stress is relieved as a result of increments in precipitation amount (Wijk 2011), leading to consistent responses of different degraded grasslands to altered precipitation. However, under the conditions of lower precipitation frequency, surface soil experienced larger amplitude drying-wetting cycles, causing plants to allocate more biomass to the deeper soil layers where the soil water environment is more stable (Knapp et al. 2008). Grasslands with higher degradation levels, which have more shallow-rooted species, would substantially develop more roots to deeper soil layers to acquire water (Zhang et al. 2019a). While, lightly degraded grasslands are characterized by more deep-rooted species, ensuring water acquisition without altering root vertical distribution (Liu et al. 2018). Besides, the greater variation in soil moisture in the surface soil may suppress shallow-rooted species and further alter community composition, resulting in a decline of BGB proportion in the surface soil (Gibson-Forty et al. 2016). Hence, degraded grasslands with a large proportion of shallow-rooted species would considerably alter root vertical distribution under lower precipitation frequency. In short, responses of root vertical distribution to altered precipitation in different degraded grasslands are likely divergent (Zhang et al. 2019b). Exploring biomass allocation under altered precipitation in different degraded grasslands, and identifying primary allocation strategy are necessary to understand how plants satisfy their resource requirement, which have seldom been reported.

In this study, we conducted a precipitation manipulation experiment on temperate steppes with varying degradation status (light, moderate and severe degradation) in northern China. We simulated changes in precipitation amount and precipitation frequency, and measured plant species composition, AGB, BGB in different soil layers, soil water content, and soil inorganic nitrogen content. We hypothesized that: 1) lower precipitation frequency results in higher soil water variation, causing plants to allocate more biomass to roots so as to alleviate water stress; 2) the promotion of AGB by higher precipitation amount is likely to be weakened by N limitation in the severely degraded grassland; 3) due to differences in plant community compositions, the primary biomass allocation strategies are divergent among different degraded grasslands.

Materials and methods

Study site

The studied area (43°47’ N, 123°41’ E, 345 m a.s.l.), which has a temperate continental semiarid monsoon
climate, is located on the eastern edge of Horqin sandy land, Jilin province, China. Relatively low precipitation defines the region, with annual mean precipitation of about 395.5 mm and an annual mean temperature of around 6.5 °C (1968–2018). The annual frost-free period is 130–150 days. The annual mean wind speed is 3.4 m s⁻¹ (Zhou et al. 2008). The original soil type is a Chernozem, with silt and sand dominating its surface layer (Zeng et al. 2018). The original vegetation was a meadow steppe dominated by *Leymus chinensis*. As a result of continuous overgrazing, the dominant species has been gradually replaced by degradation indicator species such as *Puccinellia tenuiflora*. Many of the fine particles in the soil surface layer have been blown off due to the decline of vegetation cover, resulting in a coarse soil texture. The lower vegetation cover, less precipitation, and higher concentration of alkaline ions in the soil further lead to salinization. Since the 1970s, many ecological restoration projects have been conducted in China, contributing to effective grassland restoration (Liu et al. 2008; Lu et al. 2014). As a result, the studied grasslands now vary in terms of degradation status. Three sites with different degradation levels were chosen, and the distances between sites were less than 2 km ensuring the same original soil and vegetation type before degradation.

Grassland degradation evaluation

Grassland degradation index (GDI) was used to evaluate grassland degradation status (Dong et al. 2020; Zeng et al. 2018). Thresholds of GDI values for different levels of degradation were evaluated on the basis of the GDI value of non-degraded grassland, which was close to studied degraded grasslands (Liu et al. 2018; Xu et al. 2020). Compared with the GDI value of non-degraded grassland, the decrease amplitude of GDI value of degraded grassland was used to classify grassland degradation status (Gao et al. 2010). According to the characteristics of the studied grassland, we have modified GDI and further assessed grassland degradation level through calculating the modified GDI (MGDI) for each site using the following equation:

\[
\text{MGDI} = \frac{1}{3} \left( \frac{1}{3} P_1 + \frac{2}{3} P_2 + P_3 \right) + \frac{1}{3} \left( \frac{1}{2} \text{STC} + \frac{1}{2} \text{STN} \right) + \frac{1}{3} \left( \frac{1}{3} \text{SBD} + \frac{1}{3} \text{pH} + \frac{1}{3} \text{EC} \right)
\]

where \(P_1\), \(P_2\) and \(P_3\) are the relative abundances of annual pioneer species, degradation indicator species and climax species, respectively; \(\text{STC}\) and \(\text{STN}\) represent soil total C and N concentration, respectively; \(\text{SBD}\) is soil bulk density; and \(\text{EC}\) is soil electrical conductivity. The details of the properties involved in Eq. 1 were listed in Table S1.

A natural reserve (43°79' N, 123°58' E), adjacent to our studied area was selected as non-degraded grassland, which was fenced to prevent grazing for nearly 20 years and characterized by relatively higher plant species richness and soil fertility. We have calculated MGDI of non-degraded grassland (NMGDI), which was 3.76. Based on the national standard (GB19377-2003), MGDI in the range of 80–90%, 60–80% and <60% of NMGDI represent light, moderate and severe degradation levels, respectively. So, three studied grasslands were classified into lightly degraded (MGDI: 3.09 = 82% of NMGDI), moderately degraded (MGDI: 2.74 = 73% of NMGDI) and severely degraded grasslands (MGDI: 1.60 = 43% of NMGDI).

Experimental protocol

Experimental grassland mesocosms were established at the beginning of the growing season of 2019 (11 April). The undisturbed soil cores (diameter: 40 cm; height: 50 cm) with their standing vegetation were collected in the grasslands with different degradation levels and were put into cylindrical PVC tubes (diameter: 40 cm; height: 50 cm) with a sealed bottom. These tubes (mesocosms) were transported to the Jilin Songnen Grassland Ecosystem National Observation and Research Station of Northeast Normal University, Jilin Province, China. The ecological research station and the studied grasslands are similar in climatic conditions because the distance between the two sites is less than 100 km (Table S2).

This experiment was established using a full factorial design with different degradation levels of grasslands, precipitation amounts and precipitation frequencies (Table S3). The simulated precipitation
amount and frequency were designed based on historical precipitation records and model predictions for future trends. Using daily precipitation data from China Meteorological Data Network (http://data.cma.cn) for the time period of 1968–2018, we characterized the growing season (May–August) long-term average precipitation amount (305 mm) and frequency (14 events) for the studied area (Fig. S1), which were regarded as control precipitation amount (CPA) and control precipitation frequency (CPF), respectively. The precipitation event and frequency were defined based on Heisler-White’s study (2008). Precipitation ≥ 2 mm was considered biologically effective and included in our analyses. An individual day of recorded precipitation constituted a precipitation event; consecutive days of measured precipitation were identified as one precipitation event; > 3 days of consecutive measured precipitation was divided into two events. Finally, the total number of precipitation events during a growing season was regarded as precipitation frequency. The precipitation treatment settings were selected to simulate projected precipitation patterns characterized as an increase in growing season precipitation amount and a decline in rainfall frequency. Manipulated precipitation treatments were well within the range of documented rainfall regimes of the past 50 years in this region (Fig. S1). Hence, 457.5 mm (increased by 50% of long-term average) and 7 events (decreased by 50% of long-term average) were defined as the increased precipitation amount treatment (IPA) and decreased precipitation frequency treatment (DPF), respectively. There were four precipitation patterns in this study: CPF + CPA, DPF + CPA, CPF + IPA, and DPF + IPA. In summary, the precipitation quantity of 305 mm or 457.5 mm was added to mesocosms and distributed as 14-events or 7-events along the growing season (Fig. S2a). Under one precipitation pattern, the rainfall intervals were consistent. Moreover, precipitation events were applied based on the historical month course of rainfall inputs (Fig. S2a), and the replicate was 7 times per regime for each grassland type. The simulated precipitation experiment was conducted from 1 May 2019 to 28 August 2019 (Fig. S2a). Groundwater was added to each mesocosm with hand sprayers to simulate rainfall events. The reason for using belowground water rather than collected rainwater was that its sufficient quantity can meet the water need of each rainfall event (Heisler-White et al. 2008).

Plant community composition and biomass

On 28 August 2019, plant samples were collected, and all the aboveground plant samples in each mesocosm were harvested and sorted by species. Roots were collected from two soil layers (0–10 and 10–30 cm) and were separated from the soil by washing. Only roots in the 0–30 cm soil layer were considered, because more than 85% of roots grow in this soil layer (Zhu 2004). All plant samples were dried at 105 °C for 15 min, and dried at 65 °C for 48 h, then weighed to calculate the individual AGB and BGB in the 0–10 (BGB0–10) and 10–30 cm soil layers (BGB10–30) (Fig. 1).

To elucidate the effects of the altered precipitation patterns on plant community composition, all the plant species in the experimental plots were divided into three functional groups: gramineous species, legume species and forbs (Table S4). However, low soil water content caused by the lower soil water-holding capacity in our sandy grassland cannot meet the water needs of legume species, leading to its absence (Table S4). Besides, we analyzed the dominance of the dominant species in the three degraded grasslands. The species with the highest important value and relative AGB is identified as the dominant species (Du et al. 2021). Leymus chinensis (perennial grass species), Puccinellia tenuiflora (perennial grass species) and Chloris virgata (annual grass species) were the dominant species in the lightly degraded, moderately degraded and severely degraded grasslands, respectively. Further, the relative aboveground biomass (RAGB) of the two functional groups (Fig. 2a), and RAGB of the dominant and non-dominant species were calculated based on individual biomass (Fig. 2b).

Soil sample collection

For the measurements of soil properties, we collected 15 soil samples (0–10 cm) in each degraded grassland using a 2.54 cm diameter soil core on 25 April 2019. After visible roots were excluded, the moist soil was passed through a 2 mm mesh sieve and separated into two parts. One part was maintained fresh (4 °C) for the determination of soil water content. The other half...
was air-dried for the determination of soil pH, electric conductivity, total nitrogen, total carbon, and total organic carbon. Besides, soil cores with 10 cm height and 5 cm diameter were sampled for the measurements of soil bulk density (Table S5).

Because the precipitation amount and event size of June are at an average level among May–August (Fig. S2a), we selected one representative rainfall cycle in June for measuring soil water content in order to characterize soil water content of the whole growing season (Fig. S2b). Under CPF + CPA and CPF + IPA, 4 cm diameter soil cores were collected in the 0–10 and 10–30 cm soil layers in each mesocosm on 18 (beginning of one rainfall cycle), 21 (middle) and 24 June (end), respectively (Fig. S2b). Under DPF + CPA and DPF + IPA, soil cores were sampled on 12 (beginning of one rainfall cycle), 20 (middle) and 27 June (end), respectively (Fig. S2b). The soil samples were used for investigating the changes in soil water content during one rainfall cycle (Fig. S3).

The soil samples were used for investigating the changes in soil water content during one rainfall cycle (Fig. S3).

On 28 August 2019, soil samples of two soil layers (0–10 and 10–30 cm) in each mesocosm were collected and stored in a fridge at 4 °C after removing the roots, litter and small stones by hand, and sieving with a 2 mm mesh sieve. The sampled soils were used for the determination of soil NH$_4^+$ and NO$_3^-$ concentration (Table S6).

**Soil properties**

Soil water content (%) was measured after drying 10 g of fresh soil at 105 °C until a constant weight was achieved. 10 g fresh soil sample was extracted with 2 mol L$^{-1}$ KCl solution. The filtered solutions were used to analyze soil NH$_4^+$ (mg-N kg$^{-1}$ dry soil) and...
NO$_3^-$ (mg-N kg$^{-1}$ dry soil) content with a continuous flow analyzer (Alliance Flow Analyzer, Futura, Frépillon, France). Soil pH was determined using a 1:5 ratio of air-dried soil to deionized water with a pH meter (PhS-3E, Lei Magnetic, Shanghai, China). Total nitrogen (g kg$^{-1}$ dry soil) and total carbon (g kg$^{-1}$ dry soil) were analyzed with an elemental analyzer (vario EL cube, Elementar, Langenselbold, Germany). Total organic carbon was analyzed with an elemental analyzer (Vario TOC, Elementar, Hanau, Germany) after acidizing the air-dried soil samples with 1 mol L$^{-1}$ HCl.

Data analysis

In order to demonstrate the main effects of precipitation frequency (PF) and precipitation amount (PA) on soil properties, plant biomass and its allocation, and plant community composition, $X_{CPF}$ (Eq. 2), $X_{DPF}$ (Eq. 3), $X_{CPA}$ (Eq. 4) and $X_{IPA}$ (Eq. 5) were calculated.

\[
X_{CPF} = \frac{(X_{CPF} + CPA + X_{CPF} + IPA)}{2}, \quad (2)
\]

\[
X_{DPF} = \frac{(X_{DPF} + CPA + X_{DPF} + IPA)}{2}, \quad (3)
\]

\[
X_{CPA} = \frac{(X_{CPF} + CPA + X_{DPF} + CPA)}{2}, \quad (4)
\]

\[
X_{IPA} = \frac{(X_{CPF} + IPA + X_{DPF} + IPA)}{2}. \quad (5)
\]

where $X$-mean and variation of soil water content, soil inorganic nitrogen content, total biomass ($TB=AGB+BGB_{0-30}$), AGB and BGB in different soil layers, the fraction of AGB to TB ($f_{AGB}$) and BGB proportion in the 0–10 cm soil layer ($BGB_{0-10}$), RAGB of plant functional groups (RAGB of gramineous species $= AGB_{gramineous species}$ / AGB$_{total} \times 100$; RAGB of non-dominant species = AGB$_{non-dominant species}$ / AGB$_{total} \times 100$). Different lowercase letters indicate significant differences among the precipitation treatments in all grasslands ($P<0.05$). Three-way ANOVAs results of the effects of degradation level of grassland (DL), precipitation frequency treatment (PF) and precipitation amount treatment (PA), and their interactive effects on biomass are presented. *$P<0.05$, **$P<0.01$, ***$P<0.001$, NS: $P>0.05$.

Fig. 2 Relative aboveground biomass (RAGB) of (a) plant functional groups and (b) dominant and non-dominant species under control (CPF) and decreased precipitation frequency treatment (DPF), and control (CPA) and increased precipitation amount treatment (IPA) in the lightly degraded (LDG), moderately degraded (MDG) and severely degraded grasslands (SDG). X$_{CPF}$=(X$_{CPF}+CPA$+X$_{CPF}+IPA$) / 2, where X represents RAGB. X$_{DPF}$=(X$_{DPF}+CPA$+X$_{DPF}+IPA$) / 2. X$_{CPA}$=(X$_{CPF}+CPA$+X$_{DPF}+CPA$) / 2. X$_{IPA}$=(X$_{CPF}+IPA$+X$_{DPF}+IPA$) / 2. RAGB of gramineous species = $AGB_{gramineous species}$ / $AGB_{total} \times 100$. RAGB of forbs = $AGB_{forbs}$ / $AGB_{total} \times 100$. RAGB of dominant species = $AGB_{dominant species}$ / $AGB_{total} \times 100$. RAGB of non-dominant species = $AGB_{non-dominant species}$ / $AGB_{total} \times 100$. Different lowercase letters indicate significant differences among the precipitation treatments in all grasslands ($P<0.05$). Three-way ANOVAs results of the effects of degradation level of grassland (DL), precipitation frequency treatment (PF) and precipitation amount treatment (PA), and their interactive effects on biomass are presented. *$P<0.05$, **$P<0.01$, ***$P<0.001$, NS: $P>0.05$. 

![Fig. 2](image_url)
Three-way ANOVAs were used to assess the influence of precipitation frequency, precipitation amount and grassland degradation level on soil environmental factors, plant community composition, biomass and its allocation. The effects of different precipitation treatments and grassland degradation levels on these variables were examined by one-way ANOVA with LSD test. The treatment differences in the impact values of biomass and its allocation, and the sensitivity of biomass fraction were analyzed using the Independent Samples T-test. The potential influences of precipitation treatments on biomass and its allocation were analyzed using Pearson correlations. We tested for normality using the Shapiro-Wilk test and natural log-transformed some datasets to satisfy the assumptions of parametric analyses. All statistical analyses were conducted with SPSS 20.0 software program (SPSS Inc., Chicago, IL, USA).

Results

Soil properties

With the intensification of degradation, we detected an increase in soil pH and bulk density, but a decrease in contents of soil total nitrogen, total carbon, and organic carbon (Table S5).

SWC of 0–10 cm soil layer increased, whereas it decreased at 10–30 cm soil layer along increasing degradation level gradient, which was evaluated through calculating the average of four rainfall
treatments (Table 1). SWC was significantly promoted by IPA in two soil layers (Table 1). DPF notably increased soil water variation in the surface soil, whereas the soil water environment in the deep soil layer was relatively stable (Table 1).

Under the four precipitation treatments, compared with lightly degraded and moderately degraded grasslands, the severely degraded grassland had the lowest soil inorganic nitrogen content (Table S6).

Changes in biomass and plant community composition

Total biomass (Fig. 1a), BGB$_{0-30}$ (Fig. 1c) and BGB$_{0-10}$ (Fig. 1d) decreased along increasing degradation gradient. Precipitation frequency treatment had no significant effects on total biomass, whereas it was promoted by higher precipitation amount (Fig. 1a). Lower precipitation frequency significantly reduced AGB (Fig. 1b). Higher precipitation amount considerably promoted AGB in the lightly and moderately degraded grasslands, but not for AGB in the severely degraded grassland (Fig. 1b). DPF notably promoted BGB$_{0-30}$ (Fig. 1d) and BGB$_{0-10}$ in the three degraded grasslands (Fig. 1e). Nevertheless, precipitation amount treatment had only limited effects on BGB in different soil layers, and only BGB$_{10-30}$ in the moderately degraded grassland significantly increased (Fig. 1e). There were significant interactive effects of precipitation frequency treatment and precipitation amount treatment on total biomass (Fig. 1a), AGB (Fig. 1b), BGB$_{0-30}$ (Fig. 1c) and BGB$_{0-10}$ (Fig. 1d). The decreased precipitation

| Variables | Soil layer (cm) | Degraded grasslands | Precipitation treatments | ANOVA results |
|-----------|-----------------|----------------------|--------------------------|--------------|
|           |                 |                      | CPF                      |              |
| SWC (%)   | 0–10            | LDG                  | 10.19 ± 0.30 fg          |              |
|           |                  | MDG                  | 11.76 ± 0.29 de          |              |
|           |                  | SDG                  | 12.05 ± 0.51 cd          |              |
| CV$_{SWC}$| 0–10            | LDG                  | 0.35 ± 0.02 fg           |              |
|           |                  | MDG                  | 0.29 ± 0.02 g            |              |
|           |                  | SDG                  | 0.37 ± 0.03 ef           |              |
|           | 10–30            | LDG                  | 0.28 ± 0.04 abc          |              |
|           |                  | MDG                  | 0.20 ± 0.02 de           |              |

Table 1 Variables of mean (SWC) and variation (CV$_{SWC}$) of soil water content under control (CPF) and decreased precipitation frequency treatment (DPF), and control (CPA) and increased precipitation amount treatment (IPA) in the lightly degraded (LDG), moderately degraded (MDG) and severely degraded grasslands (SDG). $X_{CPF}=(X_{CPF+CPA}+X_{CPF+IPA})/2$, where $X$ represents SWC and CV$_{SWC}$. $X_{DPF}=(X_{DPF+CPA}+X_{DPF+IPA})/2$. Different lowercase letters indicate significant differences at $P < 0.05$ level among the precipitation treatments in an identical soil layer in all grasslands. Three-way ANOVAs results of the effects of degradation level of grassland (DL), precipitation frequency treatment (PF) and precipitation amount treatment (PA), and their interactive effects on two variables are presented. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, NS: $P > 0.05$.
frequency treatment weakened or ended the positive effects of higher precipitation amount on AGB and BGB (Fig. 3f–i). The increased precipitation amount treatment suppressed the promotion of lower precipitation frequency to BGB (Fig. 3c–d). In addition, altered precipitation frequency had greater effects on different biomass components than altered precipitation amount among the three grasslands (Fig. 4). Plants in the moderately degraded grassland preferred to develop BGB10–30 under the altered precipitation patterns (Fig. 4).

In order to explore the effects of the altered precipitation on plant community composition, the changes in two plant functional groups (Table S4) and the dominance of the dominant species were investigated (Fig. 2). Altered precipitation had little impact on the plant functional groups in the three grasslands (Fig. 2a). However, the dominance of the dominant species of the moderately degraded grassland (*Puccinellia tenuiflora*) was significantly suppressed by the two precipitation treatments (Fig. 2b).

Shifts in biomass allocation

Lower precipitation frequency considerably reduced the fraction of AGB to total biomass in all grasslands (Fig. 5a). We detected a considerable increase in the fraction of AGB to total biomass in the lightly degraded and moderately degraded grasslands under IPA. However, the opposite trend was observed in the severely degraded grassland (Fig. 5a). The precipitation treatments had a limited effect on the root vertical distribution in the lightly degraded and severely degraded grasslands (Fig. 5b). Nevertheless, in the moderately degraded grassland, the two precipitation treatments significantly decreased BGB proportion in the 0–10 cm soil layer (Fig. 5b).

In the lightly degraded (Fig. 6a) and severely degraded grasslands (Fig. 6c), the sensitivities of fraction of AGB to total biomass to the altered precipitation patterns were higher than the sensitivities of BGB proportion in the 0–10 cm soil layer. However, plants in the moderately degraded grassland preferred to adjust root vertical distribution, rather than alter biomass allocation in AGB vs. BGB under the changing precipitation regimes (Fig. 6b).

Influencing factors controlling biomass and its allocation

Higher SWC significantly promoted AGB in the lightly degraded grassland (Fig. 7a) and moderately degraded grassland (Fig. 7b). However, this significantly positive relationship was not detected in the severely degraded grassland (Fig. 7c). BGB0–30 was positively correlated with soil water variation in all grasslands (Fig. 7). The fraction of AGB to total biomass was directly controlled by soil water in the three degraded grasslands (Fig. 7). In the moderately degraded grassland, BGB proportion in the 0–10 cm soil layer was mainly impacted by relative AGB of the dominant species (Fig. 7b). Moreover, relative AGB of the dominant species was negatively impacted by soil water variation at a significant level (Fig. 7b). These results indicated root vertical redistribution was notably impacted by the changes in the plant community composition, which was affected by soil water variation.

Discussion

Divergent responses of plant biomass to the altered precipitation among grasslands with varying degradation status

The decreased precipitation frequency treatment resulted in greater soil water variation in the 0–10 cm soil layer (Table 1), which significantly promoted root growth, whereas suppressed AGB accumulation (Fig. 7). Under the decreased precipitation frequency treatment, SWC decreased from 74.84% to 18.33% of field capacity under control precipitation amount, and
Summary of the baskets of biomass associated to the different precipitation treatments, presenting the impact values of the decreased precipitation frequency treatment (DPF) and the increased precipitation amount treatment (IPA) on biomass. AGB-aboveground biomass, $BGB_{0-30}$, $BGB_{0-10}$, $BGB_{10-30}$-belowground biomass in the 0–30, 0–10 and 10–30 cm soil layers, respectively. (a) Impact-DPF = \[ \frac{(X_{\text{DPF} + \text{CPA}} + X_{\text{DPF} + \text{IPA}})}{2} - \frac{(X_{\text{CPF} + \text{CPA}} + X_{\text{CPF} + \text{IPA}})}{2} \] / \[ \frac{(X_{\text{CPF} + \text{CPA}} + X_{\text{CPF} + \text{IPA}})}{2} \]. (b) Impact-IPA = \[ \frac{(X_{\text{CPF} + \text{IPA}} + X_{\text{DPF} + \text{IPA}})}{2} - \frac{(X_{\text{CPF} + \text{CPA}} + X_{\text{DPF} + \text{CPA}})}{2} \] / \[ \frac{(X_{\text{CPF} + \text{CPA}} + X_{\text{DPF} + \text{CPA}})}{2} \].

The fraction of aboveground biomass to total biomass ($f_{\text{AGB}}$) and the belowground biomass proportion in the 0–10 cm soil layer ($BGB_{0-10}$) = $BGB_{0-10}$ / $BGB_{0-30}$ × 100 under control (CPF) and decreased precipitation frequency treatment (DPF), and control (CPA) and increased precipitation amount treatment (IPA) in the lightly degraded (LDG), moderately degraded (MDG) and severely degraded grasslands (SDG). $X_{\text{CPF}}$ = (X$_{\text{CPF} + \text{CPA}} + X_{\text{CPF} + \text{IPA}}$) / 2, where X represents biomass fraction. $X_{\text{DPF}}$ = (X$_{\text{DPF} + \text{CPA}} + X_{\text{DPF} + \text{IPA}}$) / 2.

Different lowercase letters indicate significant differences among the precipitation treatments in all grasslands and different uppercase letters indicate significant differences among the degraded grasslands ($P < 0.05$). Three-way ANOVAs results of the effects of degradation level of grassland (DL), precipitation frequency treatment (PF) and precipitation amount treatment (PA), and their interactive effects on biomass are presented. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, NS: $P > 0.05$.
declined from 106.57% to 34.79% of field capacity under increased precipitation amount treatment in one rainfall cycle (calculated based on Fig. S3 and water field capacity of each grassland). The greatly unstable soil water environments which were caused by large rainfall events and longer rainfall intervals, posed plants to waterlogging and severe drought (Wang et al. 2019; Zhang et al. 2017). Under such a severe water environment, plants tended to allocate more biomass to roots in order to maintain sufficient uptake of soil water (Didiano et al. 2016). However, lower precipitation frequency has been reported to promote AGB through alleviating water stress in other studies (Gong et al. 2020; Heisler-White et al. 2009). Lower precipitation frequency associated with large rainfall events resulted in deeper penetration of rainfall water along the soil profile and less proportional loss to evaporation, which eventually increased the amount of water in the soil for plant uptake (Nielsen and Ball 2015). Whereas, in the present study, DPF

![Fig. 6](image-url) Sensitivity of the fraction of aboveground biomass to total biomass ($f_{AGB}$) and belowground biomass proportion in the 0–10 cm soil layer ($\text{BGB}_{0-10} (%) = \text{BGB}_{0-10} / \text{BGB}_{0-30} \times 100$) to the altered precipitation patterns in (a) the lightly degraded, (b) moderately degraded, and (c) severely degraded grasslands. Sensitivity of biomass fraction to the decreased precipitation frequency treatment (DPF) under control precipitation amount (CPA) = $|X_{\text{DPF+CPA}} - X_{\text{CPF+CPA}}|$, where $X$ represents biomass fraction. Sensitivity of biomass fraction to DPF under the increased precipitation amount treatment (IPA) = $|X_{\text{DPF+IPA}} - X_{\text{CPF+IPA}}|$. Sensitivity of biomass fraction to IPA under control precipitation frequency (CPF) = $|X_{\text{CPF+IPA}} - X_{\text{CPF+CPA}}|$. Sensitivity of biomass fraction to IPA under DPF = $|X_{\text{DPF+IPA}} - X_{\text{DPF+CPA}}|$. * denotes Independence Samples T-test results between sensitivity of $f_{AGB}$ and sensitivity of $\text{BGB}_{0-10} (%)$ in an identical condition ($P<0.05$

![Fig. 7](image-url) Pearson correlations between biomass and its allocation, and characteristics of soil water and plant community composition in (a) the lightly degraded, (b) moderately degraded and (c) severely degraded grasslands. SWC and CV$_{\text{SWC}}$-mean and variation of soil water content in the surface soil layer, AGB-aboveground biomass, $\text{BGB}_{0-30}$-belowground biomass in the 0–30 cm soil layer, $f_{\text{AGB}}$-the fraction of AGB to total biomass, RAGB-relative AGB, $\text{BGB}_{0-10} (%)$-$\text{BGB}_{0-10} / \text{BGB}_{0-30} \times 100$. *, **, and *** indicate significance at the levels of $P<0.05$, $P<0.01$ and $P<0.001$, respectively.

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did not induce notable enhancement of SWC in the deeper soil layer (Table 1), which could be partially explained by the lower water retention capacity of the studied sandy grasslands. Moreover, longer rainfall intervals (17 days) under DPF (Fig. S2), might counteract the aforementioned positive effects of decreased precipitation frequency on soil water and AGB. Furthermore, the enhancement of higher soil water variation on roots in the severely degraded grassland was less than it in the other two grasslands, because the lower soil inorganic nitrogen availability limited BGB accumulation (Fig. 7, Table S6).

Higher precipitation amount enhanced AGB through increasing SWC in the lightly degraded and moderately degraded grasslands (Table 1, Fig. 7a, b). This observation was consistent with the prior study, in which photosynthetic characteristics such as stomatal conductance and estimated leaf chlorophyll concentration were improved by the increment in precipitation amount, which contributed to higher photosynthetic rate and AGB (Ren et al. 2011). However, the positive effect of SWC on AGB vanished in the severely degraded grassland (Fig. 7c). This result was particularly surprising because plants in the severely degraded grassland were all annuals, which were expected to use water quickly under relieved soil water environments (Zhang et al. 2020b). There are two potential causes for the insensitivity of plants in the severely degraded grassland to increased SWC. First, compared with the lightly degraded and moderately degraded grasslands, the severely degraded grassland suffered from a much poorer soil nutrient status (Table S6), leading to severe nitrogen co-limitation. Moreover, the improved soil water environment further strengthened plant nutrient limitation in the nitrogen co-limitation ecosystem. This could be verified through the unchanged soil inorganic nitrogen content in the surface soil layer under the increased precipitation amount treatment (Fig. S5). The nutrient limitation would weaken or end the positive relationship between SWC and AGB. This was also observed in other studies (Ren et al. 2017; Zhang et al. 2019a). This result supported our second hypothesis that N limitation in the severely degraded grassland weakened the promotion of AGB by higher precipitation amount. Second, this result could be explained by the meristem limitation hypothesis, which predicts that lower productivity ecosystems have limited capacities to respond to pulses of higher resource availability, due to existing traits of resident species, like fewer seed and bud banks (Knapp and Smith 2001). In our study, plant densities in the lightly degraded and moderately degraded grasslands were approximately 2.7 and 4.6 times higher than the plant density in the severely degraded grassland. Hence, the lower plant density (meristem limitation) suppressed the positive response of plants to the higher precipitation amount in the severely degraded grassland. In summary, lower soil nitrogen availability and meristem limitation in the severely degraded grassland inhibited the enhancement of higher precipitation amount on plant biomass. Our results suggest that the improvement of the projected higher precipitation amount to plant growth in the grasslands under severely degraded status is very limited.

There were interactions between precipitation frequency and amount on biomass (Figs. 1 and 3). DPF weakened or ended the enhancement of IPA on AGB and BGB (Fig. 3f-i), and IPA suppressed the promotion of DPF to BGB (Fig. 3c-d). These phenomena might be partially explained by temporary waterlogging resulted from larger precipitation events under the combined DPF and IPA. It could be further confirmed by higher SWC (104, 91.75 and 123.95% of field capacity in the lightly degraded, moderately degraded and severely degraded grasslands, respectively) at the beginning of one rainfall cycle (Fig. S3). On the one hand, anoxic conditions induced by waterlogging impaired photosynthetic efficiency and antioxidant system of plants, suppressing plant growth (Jiménez et al. 2015). On the other hand, the nutrient demand was supposed to be high under soil anoxia for maintaining plant biomass (Rubio and Lavado 1999). However, lower inorganic nitrogen content in the studied degraded grasslands cannot meet the nutritional needs of plants, resulting in a decrease in plant biomass.

Different patterns of biomass allocation in response to the altered precipitation in the degraded grasslands

The decreased precipitation frequency treatment associated with unstable soil environment resulted in lower fraction of AGB to total biomass (Table 1, Fig. 7). This result supported our first hypothesis that
plants preferred to allocate more biomass to roots under lower precipitation frequency due to higher soil water variation. This biomass allocation pattern could be partially explained by the optimal partitioning theory, which suggests plants preferentially allocate biomass to the organ that is more efficient in obtaining limited resources (Zhang et al. 2019a). Furthermore, under unstable water environments, the suppression of the growth of aboveground reproductive organs limited the water needs of plants so as to alleviate water stress, resulting in lower fraction of AGB to total biomass (Freschet et al. 2018). Higher precipitation amount enhanced AGB, which subsequently caused a higher fraction of AGB to total biomass in the lightly degraded and moderately degraded grasslands (Figs. 1b and 5a, b), which was consistent with the previous study (Wang et al. 2018). However, a decline of fraction of AGB to total biomass in the severely degraded grassland under IPA was observed (Fig. 5a). Especially under the decreased precipitation frequency treatment, higher precipitation amount considerably decreased the fraction of AGB to total biomass (Fig. S4b), which could be attributed to the decrease in AGB (Fig. 3f) and the increase in BGB\(_{0-30}\) (Fig. 3g). Under DPF, IPA suppressed AGB might be the result of aforementioned temporary waterlogging. The increase in BGB\(_{0-30}\) may be associated with lower soil inorganic content. In the water and nitrogen co-limited system, the nitrogen demand of plants would intensify when the water stress was alleviated (Zhang et al. 2019a). Therefore, plants would allocate more biomass to roots which were most critical to relieve nitrogen limitation and improve nitrogen acquisition for plant maintenance (Freschet et al. 2018).

Among the three degraded grasslands, only the moderately degraded grassland preferred to devote more root tissue to the deeper soil layer (Figs. 1e and 4), and to adjust root vertical distribution under the altered precipitation patterns (Fig. 5b), which could be attributed to changes in the dominance of the dominant species (Fig. 7b). The increased precipitation amount treatment mitigated water limitation in the moderately degraded grassland (SWC increased to 60–70% of field capacity, Table 1), and turned plants’ competition for water into competition for other resources, such as light (Zhang et al. 2020b). Because of lower height (compared with climax species), the dominant species (Puccinellia tenuiflora) in the lower layer had weak light competitiveness, and was further limited by light resource (Hautier et al. 2009), resulting in the decrease in its dominance accordingly. In addition, P. tenuiflora, which was a shallow-rooted species, tended to be inhibited by greater soil water variation in the surface soil resulted from DPF. Having all this in mind, all precipitation treatments decreased relative AGB of P. tenuiflora in the moderately degraded grassland (Fig. 2b). Since the predominant shallow-rooted species had greater shallow root proportion compared with the deep-rooted species, the decline of P. tenuiflora in all precipitation treatments caused a lower shallow root proportion (Fig. 5b). In total, root vertical redistribution in the moderately degraded grassland was a result of plant competition for resources, and it was also a biomass allocation strategy for improving resource utilization efficiency of the plant community. From Table 1, in the moderately degraded grassland, compared with the surface soil layer, the deeper soil layer had a relatively stable water environment and provided a harbor for roots under all precipitation treatments. Hence, plants allocated more roots to the deeper layer so as to satisfy plant water needs. Furthermore, a general conclusion could be deduced that root vertical redistribution is the primary biomass allocation strategy for the degraded grasslands dominated by the species characterized by lower height than climax species and shallow roots. In addition, decreased dominance of the dominant species increased Shannon-Wiener indexes by 8.70–63.04% in the moderately degraded grassland, which potentially improved plant community stability and functional diversity (Zhou et al. 2020). Contrastingly, changing precipitation had little effect on plant community composition in the lightly and severely degraded grasslands (Fig. 2), attributed to higher dominant species stability (Kang et al. 2019; Song and Yu 2015). Rhizomatous grass Leymus chinensis, as the dominant species in the lightly degraded grassland, has well-developed roots, and higher stability under resource-limited environments (Bai et al. 2010). Similarly, in the severely degraded grassland, Chloris virgata (the dominant species) composed more than 80% of total AGB. The higher height and greater fine roots of C. virgata contributed to higher dominant species stability in the severely degraded grassland, and further improved community stability.

Overall, plants in the moderately degraded grassland preferred to adjust root vertical distribution...
due to unstable community composition attributed to lower dominant species stability. However, biomass allocation in AGB vs. BGB was the primary biomass allocation strategy in the lightly degraded and severely degraded grasslands. The observation was consistent with the result from another study, which showed the altered precipitation had only a limited effect on root vertical distribution (Wilcox et al. 2015). Plants could acquire water and nutrients through mycorrhizal fungi (Li et al. 2019), hence adjusting root vertical distribution was not a preferred biomass allocation strategy. These results supported our third hypothesis that the primary biomass allocation strategies are divergent among different degraded grassland due to different plant community compositions.

Conclusions

To cope with the decreased precipitation frequency associated with an increase in soil water content variation, plants in all studied grasslands tended to allocate more biomass into belowground to secure water acquisition ability. The positive effects of higher precipitation amount on aboveground biomass were significant in the lightly degraded and moderately degraded grasslands, but not in the severely degraded grassland due to lower soil nitrogen availability. The decreased precipitation frequency treatment weakened or ended the enhancement of higher precipitation amount on AGB and BGB, and the increased precipitation amount treatment suppressed the promotion of lower precipitation frequency to BGB. Biomass allocation in AGB vs. BGB was the primary biomass allocation strategy in the lightly degraded and severely degraded grasslands. However, plants in the moderately degraded grassland primarily adjusted root vertical distribution, which was impacted by the changes in plant community composition. Our study has theoretical and practical significance for predicting the direction and magnitude of changes in grasslands under future climates, for instance, the expected positive effects of the projected increased precipitation amount pattern on the restoration of degraded grasslands highly depend on changes in precipitation frequency. The scientific strategies to restore degraded grasslands could be established based on the divergent responses of plant biomass and allocation in different degraded grasslands.

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Data availability Not applicable.

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Declarations

Conflicts of interest/Competing interests The authors declare that they have no conflict of interest.

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