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Grassland species respond differently to altered precipitation amount and pattern

Bin Zhang[a,b,1], Jianjun Zhu[a,1], Qingmin Pan[a,*], Yanshu Liu[c], Shiping Chen[a], Dima Chen[a], Yue Yan[a], Shande Dou[a], Xingguo Han[a]

[a] State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, The Chinese Academy of Sciences, Beijing 100093, China
[b] College of Ecology and Environmental Science, Inner Mongolia Agricultural University, Huhhot 010018, China
[c] Institute of Desertification Studies, Chinese Academy of Forestry, Beijing 100091, China

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ABSTRACT

An increase in precipitation amount with prolonged inter-rainfall intervals is predicted to occur in the Inner Mongolia grassland in the future. However, how the native species respond to such alterations remains poorly understood. We collected the seeds of eight species from a natural community and raised their seedlings by pot culture. The responses of these species to manipulated precipitation amount and inter-rainfall intervals were examined by rainout shelters. The biomass production in seven out of eight species was enhanced by increased precipitation amount. However, the impacts of prolonged inter-rainfall interval differed substantially among species, with one being promoted, two suppressed and five not affected. For most species, biomass allocations among vegetative organs were neither affect by precipitation amount nor by inter-rainfall intervals. In contrast, the impacts on species' reproductive allocation were highly species-dependent. Soil moisture, soil temperature and soil inorganic nitrogen played important roles in affecting species' biomass production but the pathways, directions (positive or negative) and magnitudes were species-dependent. Given that these eight species jointly represent about 80% of community biomass production, the impact of altered precipitation pattern on grassland ecosystems may be more difficult to predict than that of altered amount.

1. Introduction

Human-induced global warming has greatly changed the global hydrological cycles, resulting in alterations in both the amounts and patterns of precipitation (Easterling et al., 2000; Groisman et al., 2005). In the Inner Mongolia grassland for example, the annual precipitation amount is predicted to increase in the future as global warming causes a northwestward migration of the eastern Asia monsoon rain belt (Yang et al., 2015). At the same time, the frequency of heavy precipitation events with longer inter-rainfall intervals (prolonged drought period) is predicted to increase in this area (IPCC, 2013). These changes may have profound impacts on the growth, biomass allocation and reproduction of these grassland species, as water is a primary limiting factor for biomass production in arid and semiarid ecosystems (Easterling et al., 2000; Weltzin et al., 2003; Reynolds et al., 2004; Schwinning et al., 2004).

Previous studies have shown that alterations in precipitation amount and pattern may greatly affect the structure and functioning of natural ecosystems (Fang et al., 2005; Heisler-White et al., 2008; Knapp et al., 2002; Yang et al., 2011; Robertson et al., 2009; Wilcox et al., 2015). However, the direction (positive or negative) and magnitude of these impacts were highly context-dependent and the underlying mechanisms remain poorly understood. In fact, the community level change is an integrative outcome of all changes at the species level, therefore examining species-level responses to altered precipitation regimes can help us better understand and predict the community-level changes (Gutschick and BassiriRad, 2003; Nippert et al., 2009; Robertson et al., 2009). For example, Robertson et al. (2009) have found that three Chihuahuan species respond to precipitation timing and magnitude in different ways, resulting in different community-level changes between wet years and dry years. By contrast, the

* Corresponding author.
E-mail addresses: zhangbin_158@163.com (B. Zhang), zhujianjun@ibcas.ac.cn (J. Zhu), pqm@ibcas.ac.cn (Q. Pan), liuyanshu@caf.ac.cn (Y. Liu), spchen@ibcas.ac.cn (S. Chen), chendima@ibcas.ac.cn (D. Chen), yanyue@ibcas.ac.cn (Y. Yan), doushande@ibcas.ac.cn (S. Dou), xghan@ibcas.ac.cn (X. Han).
[1] These authors contributed equally to this work.

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Inner Mongolian grassland ecosystem can maintain strong stability of community primary productivity for 24 years mainly due to the compensatory responses of species to precipitation variations (Bai et al., 2004), implying that the co-occurring species respond differently to precipitation variations. However, our knowledge about how species from the same community differ in their responses to changes in precipitation amount and pattern remains poorly understood.

Biomass allocation in plants plays a central role in response to unpredictable environmental changes (Bazzaz and Grace, 1997). According to optimal partitioning theory, plants allocate biomass to the organs that acquire the most limiting resource (Mccarthy and Enquist, 2007). In consistence with this theory, it has been demonstrated that under water deficient scenarios plants can increase biomass allocation to roots to maximize acquisition of water and nutrients from soils (Mokany et al., 2006) or reduce biomass allocation to shoots to minimize water loss (Wang and Gao, 2003). Moreover, species adapted to desert and Mediterranean environments may display different plasticity in reproductive allocations under conditions of water stress (Aronson et al., 1993). These results highlight the role of allocation strategy in plant performance under conditions of varying water supply. However, to what extent plant species in the Inner Mongolian grassland may adjust their allocation patterns to adapt the alterations in amount and inter-rainfall interval of precipitation remains largely unknown.

Alterations in precipitation amount and pattern not only alter the availability of soil moisture but also modify other edaphic factors such as soil temperature and soil nitrogen availability. Different species may differ in their response to these feedbacks. For example, in the Chihuahuan desert ecosystem, the above-ground net primary productivity (ANPP) of *Dasylirion leiophyllum* was primarily affected by N availability in wet years and by water availability in dry years (Robertson et al., 2009). This is explained by the fact that *Dasylirion* is a shrub with both deep and shallow roots making its ANPP more dependent on overall levels of resource availability (Fay 2009). In contrast, the ANPP for *Opuntia phaeacantha* was primarily regulated by precipitation seasonality and pattern rather than by soil variables (Robertson et al., 2009), because *Opuntia* is a succulent with shallow root system. Thus its growth was sensitive to precipitation seasonality and pattern (Fay, 2009).

To examine the responses of grassland species to altered precipitation amount and pattern, we collected the seeds of eight species from a mature natural community and raised their seedlings by pot culture. These species covered a spectrum of dominant, subdominant and minor species and represent the major plant life forms in this community. After two years, the seedlings of each species were subjected to manipulated precipitation amount and inter-rainfall interval during growing season in rainout shelters. We address the following three specific questions: 1) how do changes in precipitation amount and inter-rainfall interval affect the biomass production of these species? 2) How do changes of precipitation amount and inter-rainfall interval affect species' biomass allocation patterns between above- and belowground parts, between leaves and stems, and between vegetative and reproductive organs? 3) What are the relative roles of soil moisture, soil temperature and soil inorganic nitrogen in affecting the biomass production of eight species?

We hypothesize that these co-occurring species may differ substantially in biomass production in monoculture under altered precipitation amounts and patterns but such a change may not affect their biomass allocation patterns as species' allocation strategy is shaped by long-term evolutionary processes and relatively stable. The effects of altered precipitation amounts and patterns on soil moisture, soil temperature and soil inorganic nitrogen may be highly species-specific as plants have strong feedback regulations on these environmental factors.

2. Materials and methods

2.1. Study site and species selection

This experiment was conducted at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS), the Chinese Academy of Sciences from 2007 to 2009. This station is located in the central part of the Inner Mongolia Autonomous Region of China (116°40′40″ E, 43°32′45″ N, 1250–1280 m a.s.l.). Climatically, this area belongs to middle temperate and semiarid zone, characterized by the alteration of dry and cold winters and relatively wet and warm summers. The mean annual precipitation and mean annual temperature (1982–2008) is 337 mm and 0.92 °C, respectively, with about 75% of precipitation events occurring during the period from June to September.

Communities in this area usually consist of about 20 vascular plant species. Eight species were selected based on their abundance and life form in a natural community. These species were *L. chinensis*, *S. grandis*, *Achnatherum sibiricum*, *Agropyron michnoi*, *Cleistogenes squarrosa*, *Setaria viridis*, *Artemisia frigida* and *Kochia prostrate*. *L. chinensis* (a rhizomatous grass) and *S. grandis* (a bunchgrass) were two dominant species. Three bunchgrasses, *A. sibiricum*, *A. michnoi*, and *C. squarrosa* were subdominant species while two semi-shrubs, *A. frigida* and *K. prostrata*, and an annual, *S. viridis*, were minor species. Thus our selection included species from dominants to subdominants and minors and represented major plant life forms in this community. Based on the monitoring data of Inner Mongolia Grassland Ecosystem Research Station (2008–2012), these species together constituted 71.7–95.1% of the aboveground biomass and 72.6–92.7% of vegetation cover of this plant community.

2.2. Seedlings preparation

For each species, we collected their seeds from a natural community in 2007. These seeds were sown in a seedbed on May 2 of 2008 and covered with a plastic film. Seedlings were carefully nursed for 40 d and then acclimatized for 10 d by removing the plastic film. Uniform seedlings were selected and transplanted to pots (28 cm diameter by 26 cm depth) with a density of 3 plants per pot at middle June of 2008. For each species, 100 pots were transplanted and buried into the soil (24 cm in depth) in a field. Then these seedlings received natural rainfalls in 2008. The seeds of *S. viridis* (an annual species) were collected on August 28 of 2008 and were sown again on May 2 of 2009.

2.3. Rainout shelter

We constructed four rainout shelters with steel frames, each covering an area of 90 m^2 (6 m × 15 m) (Fig. S1). Each shelter had a slanting roof made of waterproof cloth that can be removed by a steel roller fixed on the top of each shelter. The height of the south and north sides of the frame were 50 cm and 90 cm, respectively. On fine days, the waterproof cloth was wound to the roller and placed on the top of north side, thus leading to the removal of the roof from the shelter. The cloth was wound off the roller to form the roof for the shelter prior to the onset of rainfall. After rain, the cloth was wound back on the roller again. As the roof was only formed during rain events, there is no significant difference within and outside the shelter in air temperature, air moisture and light, which are important factors for rainout shelter design (Beier et al., 2012).

2.4. Experiment design and field manipulation

We used a two-way factorial design to manipulate the amount and pattern (interval between rainfall events) of precipitation from June 1 to September 30 in 2009. Two levels of precipitation