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Response of primary production and biomass allocation to nitrogen and water supplementation along a grazing intensity gradient in semiarid grassland

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ABSTRACT

Herbivory and resource availability interactively regulate plant growth, biomass allocation, and production. However, the compensatory growth of plants under grazing intensities and manipulated environmental conditions is not well understood. A 2-year experiment with water (unirrigated and irrigated) and nitrogen fertilizer (0 and 75 kg N ha^{-1} $year^{-1}$) addition was conducted at sites with 4 grazing intensities (0–7 sheep ha^{-1}) in an annually rotational grazing system in Inner Mongolia. In this study, grazing had no significant effect on aboveground net primary production (ANPP) and net primary production (NPP). However, high grazing intensity strongly reduced the fraction of belowground net primary production to NPP. Water and nitrogen additions significantly increased ANPP by 39% and by 23%, respectively, but had no effect on belowground net primary production. ANPP showed lower response to nitrogen addition at high grazing intensity sites than at low grazing intensity sites. We found no evidence for grazing optimization on primary production of semiarid steppe, regardless of resource supplementations. Grazed plants minimized the reduction of ANPP by altering allocation priority and morphological traits. Our study highlights the "whole-plant" perspective when studying plant–herbivore interactions.

1. Introduction

The responses of primary production of natural grassland to herbivory have been investigated in numerous studies concerning plant–animal interactions. Compensatory growth, which is termed as a positive response to injury, leads to three consequences (Belsky, 1986): overcompensation (increase of primary production by grazing), exact compensation (no change of production by grazing), and under compensation (decrease of production by grazing). Overcompensation has been demonstrated in some studies (McNaughton, 1979; Oesterheld and McNaughton, 1988; Turner et al., 1993), and the mechanisms underlying was phrased as grazing optimization hypothesis (Hilbert et al., 1981; McNaughton, 1979). However, many studies have found no evidence for overcompensation (Biondini et al., 1998; Ferraro and Oesterheld, 2002; Georgiadis et al., 1989; Milchunas and Lauenroth, 1993), and the validity and biological justification on grazing optimization theory has been questioned (Belsky, 1986; Belsky et al., 1993). Although the debate exists, grazing optimization theory has been used to justify heavy livestock grazing in western North American rangelands, and some authors recommended caution in application of this theory, especially in ecosystem with high risk of overgrazing (Briske, 1993; Painter and Belsky, 1993).

Other plant–herbivore theories, including compensatory continuum model (Maschinski and Whitham, 1989) and limiting resource model (Wise and Abrahamson, 2005), claim that compensatory growth was regulated by resource availability. This claim, has been supported by many experimental studies, shows that plant regrowth after defoliation was regulated by water and nitrogen availability (Ferraro and Oesterheld, 2002; Georgiadis et al., 1989; McNaughton et al., 1983; Schiborra et al., 2009). Therefore,

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it is suggested that the grazing optimization occurs occasionally in some species and systems, given the appropriate combination of environmental factors (Briske, 1993).

Compensatory growth is an intensively studied topic; however, most studies on grazing optimization have only focused on aboveground net production (ANPP), and the "whole-plant" level response is less known. Belowground net production (BNPP) is an important component of net primary production (NPP), which is about 40–90% of NPP in grassland (Hui and Jackson, 2006). Plants are able to reprioritize carbon allocation in response to imbalance of sources and sinks (Briske et al., 1996). Thus, an enhancement in ANPP, in many cases, should be attributed to the shift in C allocation rather than the overcompensation of the whole plant. ^{13}C labeling experiments indicate that C allocation to shoot growth is promoted by defoliation (Briske et al., 1996) or by N fertilizer addition (Gong et al., 2014). Therefore, to test grazing optimization theory, both ANPP and BNPP need to be studied under well controlled conditions of resource availability. Moreover, plants have considerable morphological plasticity in response to biotic and abiotic influences as reviewed by Poorter et al. (2012). Thus, evaluation of plant traits brings more insight to the underlying mechanism of plant–herbivore interactions.

This study aims at a clear understanding of plant compensatory growth under sheep grazing with manipulated resources availability in the semiarid steppe. As a typical semiarid steppe of North China, Xinlingole grassland has been subjected to advanced degradation (Tong et al., 2004), attributed to the rapid rise in numbers of livestock and overgrazing (Wang and Ripley, 1997). In this grassland, water limitation on herbage production is well known (Bai et al., 2004, 2008), and nitrogen and water interactively constrain primary production (Burke et al., 1997; Chen et al., 2011; Gong et al., 2011a,b; Hooper and Johnson, 1999; Vitousek et al., 1992). We have performed a grazing experiment with four grazing intensities as main plots and water and nitrogen fertilizer additions in the subplots in this semiarid steppe. We hypothesized that (1) grazing has a negative or neutral effect on NPP; (2) overcompensation of ANPP (grazed ANPP > ungrazed ANPP) happens at the expense of BNPP; (3) N effect on ANPP is more significant at sites with lower grazing intensity.

2. Materials and methods

2.1. Study area

The Xilin River Basin (latitude 43°26′–44°29′N, longitude 115°32′–117°12′E, and mean elevation 1200 m ASL) is located in the center of the Inner Mongolia grassland. The region has a semiarid continental climate with a short growing period from May to September (Chen, 1988). In the Xilin River Basin, during 1982–2008, average annual air temperature was 0.7 °C and average annual rainfall was 335 mm of which more than 80% occurred from May to September. The precipitation and air temperature during experimental period are shown in Fig. 1. The dominant soil types are Calcic Chernozems derived from aeolian sediments above volcanic rock (Steffens et al., 2008), which is the only soil type found in our experimental sites. Total carbon and nitrogen contents of the top soil (0–30 cm) prior to the start of the study were 1.2% and 0.1%, respectively. Plant available nutrients of the top soil prior to the start of the study were plant available N content ($CaCl_2$ extraction), 6.4 mg kg^{-1}; plant available P content ($NaHCO_3$ extraction), 2 mg kg^{-1}; and plant available K content (NH_4OAc extraction), 152 mg kg^{-1}. Soil pH at 0–30 cm depth was 6.6. Detailed soil physical and chemical characteristics of this grassland were sampled at a adjacent site and were published elsewhere (moderate grazing site, Gong et al., 2011a). Dominant species were *Leymus chinensis* (Trin.) Tzvel., a perennial C_3 rhizomatous grass; and *Stipa grandis* (P.) Smirn., *Agropyron cristatum* (L.) Gaertn., perennial C_3 bunchgrasses; *Cleistogenes squarrosa*, a perennial C_4 bunchgrass. According to the data collected before the onset of the fertilizer experiment (beginning of June 2007), these four species totally accounted for 74–85% of aboveground biomass across grazing intensities (data not shown).

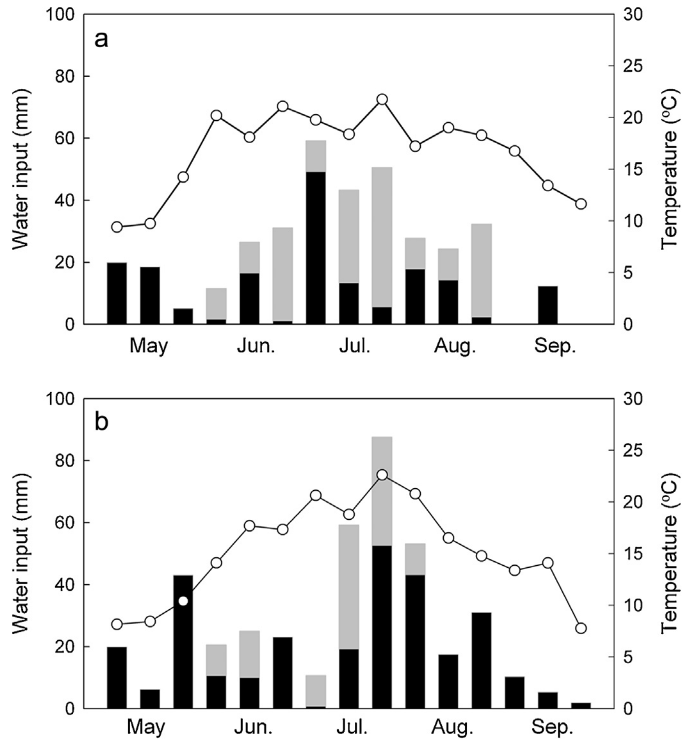

Fig. 1. Accumulated precipitation (black bars) and irrigation (grey bars) of each 10 days, and air temperature in growing season 2007 (a) and 2008 (b). The total precipitation from May to September was 178 mm in 2007 and 277 mm in 2008. The total amount of irrigation water was 185 mm in 2007 and 120 mm in 2008.

2.2. Experimental design

This experiment was designed as a randomized complete block with a split–split plot arrangement with two replications. Four grazing intensities represented the main plots each including subplots with two water supply levels (W0, unirrigated; W1, irrigated simulating precipitation in a wet year) and two N fertilizer treatments (N0, unfertilized control; N1, 75 kg urea–N ha^{-1} year^{-1}). There was an annual shift between grazing and hay making on the main plots.

2.2.1. Grazing treatment

We chose four grazing intensities in a rotational grazing system as the main plots of grazing intensities (Fig. 2). Four grazing intensities, ungrazed (*G*0), low (*G*1), moderate (*G*2), and high (*G*3) grazing intensities, were defined according to the mean stocking rates of two years (0, 2, 4, and 7 sheep ha^{-1}, respectively, see Appendices Table A1). In this rotational grazing system, annual shifts between grazing and hay-making plots were carried out. Experimental period covered the main grazing season from beginning of June to end of August, which was coincident with the grazing period of the local management regime. The main plots of grazing treatment were replicated in two fixed blocks. Plot size of each grazing plot was 2 ha, except for the low grazing intensity (*G*1) which had 4 ha, in order to have at least 6 sheep in each plot.