



Effects of water and nitrogen addition on ecosystem respiration across three types of steppe: The role of plant and microbial biomass



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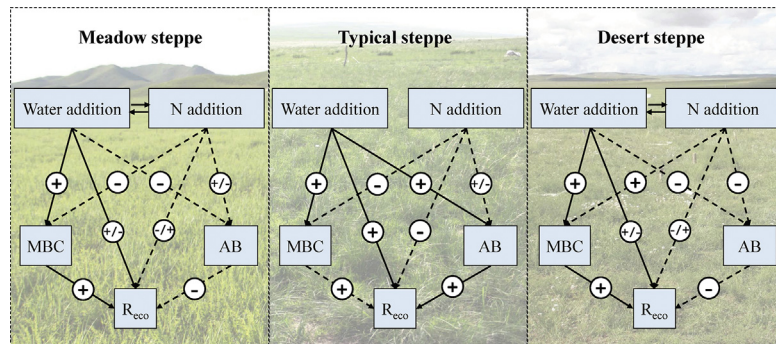
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HIGHLIGHTS

- Response of ecosystem respiration (R_{eco}) to water and N addition was studied.
- R_{eco} showed higher sensitivity to water addition than to N addition in three steppes.
- R_{eco} in typical steppe was more sensitive to water and N addition than other steppes.
- Plant aboveground biomass correlated with variations in R_{eco} in typical steppe.
- Microbial biomass carbon correlated with variations in R_{eco} in meadow/desert steppe.

GRAPHICAL ABSTRACT

Water and N addition differentially affected microbial biomass carbon (MBC), plant aboveground biomass (AB), and thus ecosystem respiration (R_{eco}) in meadow steppe, typical steppe, and desert steppe, northern China. Solid arrows indicate significantly positive (+) and negative (–) effects ($P < 0.05$), respectively; the pathways without significant effects are indicated by broken lines ($P > 0.05$).



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ABSTRACT

Evaluating the regional variation of ecosystem respiration (R_{eco}) in its response to the changes of soil water and nitrogen (N) availability is crucial for fully understanding ecosystem carbon (C) exchange and its feedbacks to global changes. Here, we examined the responses of R_{eco} , plant community aboveground biomass (AB), microbial biomass carbon (MBC) and soil moisture (SM) to water and N addition, using intact soil monoliths from three different temperate steppes along a precipitation gradient, including meadow steppe, typical steppe, and desert steppe in northern China. We found that the meadow steppe held the highest value of R_{eco} . Water addition significantly enhanced R_{eco} while N addition had no effect on R_{eco} in all three ecosystems. The response of R_{eco} in the typical steppe was more sensitive than the other two ecosystems. The changes of plant community AB exhibited a much stronger explanatory power than that of MBC for R_{eco} in the typical steppe. In contrast, MBC was the dominant factor explaining the variation of R_{eco} in the desert steppe and the meadow steppe. These findings contribute to our understanding of regional patterns of ecosystem C exchange under scenarios of global changes and highlight the importance of water availability in regulating ecosystem processes in temperate steppe grasslands.

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1. Introduction

On a global basis, Nitrogen (N) deposition has been increased substantially since the Industrial Revolution, and N deposition in 11% of the world's natural vegetation have exceeded the "critical load" threshold (Dentener et al., 2006; Galloway et al., 2008). From 1980 to 2010, average bulk N deposition in China increased by 60% and reached to 21.1 kg N ha⁻¹ yr⁻¹ (Liu et al., 2013), and the total N deposition reached 39.9 kg N ha⁻¹ yr⁻¹ in 2014 (Xu et al., 2015). Given the limited supply of N in the terrestrial biosphere, N deposition has important influences on ecosystem respiration (R_{eco}) across all biomes (Zhou et al., 2014). N deposition generally reduces heterotrophic respiration (R_{h}) through inhibition of soil microbial activity but increases autotrophic respiration (R_{a}) through stimulation of plant growth in grasslands (Zhou et al., 2014). As the largest source of C flux from terrestrial ecosystems to the atmosphere, R_{eco} plays a vital role in regulating the concentration of atmospheric CO₂ (Luo et al., 2006; Fierer et al., 2009).

Climate change is expected to change the intensity and the pattern of precipitation (IPCC, 2013). The relationship between R_{eco} and precipitation has been widely studied during the past decades (Cable et al., 2008; Thomey et al., 2011; Zhang et al., 2015b). Increased availability of water can stimulate R_{eco} by promoting the activity of extracellular enzymes and enhancing substrate availability (Xiang et al., 2008; Suseela et al., 2012). When the availability of water rises beyond its optimal level, however, R_{eco} may decrease or have no change as a result of suppressed microbial and root activity due to the lower concentration of oxygen (Risch and Frank, 2007; Zhao et al., 2016). Previous studies have demonstrated that the responses of R_{eco} to water addition depend on natural precipitation amount (Chimner and Welker, 2005; Yan et al., 2011; Xu et al., 2016). Positive changes of R_{eco} in response to increasing precipitation were found in normal or dry years (Yepez et al., 2007; Niu et al., 2009), but not in wet years (Talmon et al., 2010; Zhang et al., 2016).

Soil water and N availability are two of the primary drivers of the plants and microbes' activities in grasslands, both are key drivers for soil carbon (C) cycling (Knapp et al., 2008; Janssens et al., 2010). Furthermore, variation in precipitation may also regulate the N cycle, and have the potential to cause complex interactions among different ecosystem functions (Hooper and Johnson, 1999). One study in grassland spanning two hydrologically contrasting years demonstrated that N addition positively affected soil microbial community composition only when sufficient moisture was available (Zhang et al., 2015a). Additionally, antecedent soil moisture also plays an important role in modulating the responses of R_{eco} to N addition, mainly because greater availability of water can stimulate net N mineralization and increases the availability of soil N (Potts et al., 2006; St Clair et al., 2009). Positive (Yan et al., 2010; Zhang et al., 2015b; Tian et al., 2016), negative (Yan et al., 2010), and neutral changes of R_{eco} (Xia et al., 2009; Jiang et al., 2013; Zhang et al., 2015b) in response to N addition have all been reported in different precipitation years in the same site.

While many studies have focused on the effects of water and N addition on R_{eco} in a single ecosystem, less attention has been paid to investigate ecosystem-specific sensitivity of C fluxes to water and N manipulations across different ecosystems (Pardo et al., 1999; McCulley et al., 2005; Bahn et al., 2008). Affected by precipitation patterns and nutrient availability, plant and microbial community composition varies among different grassland types (Bai et al., 2008; Chen et al., 2015b). Previous work in the Great Plains showed that the sensitivity of aboveground net primary production to interannual variability in precipitation is greatest in the mixed-grass prairie community (Pardo et al., 1999). The shortgrass steppe exhibited the most sensitive C-cycling responses to interannual precipitation change (McCulley et al., 2005). Even in microsite scale, shrub and intershrub sites showed different responses of R_{eco} to rainfall or fire (Talmon et al., 2010; Muñoz-Rojas et al., 2016). R_{eco} tends to be more sensitive to increased precipitation in the more arid regions and years (Liu et al., 2016).

Constrained by variations in natural climatic factors, it is hard to compare the effect of water and N addition on R_{eco} across different ecosystems. As important vegetation types in the Eurasian continent, the temperate steppes hold 31.6% of the total grassland C in China, which is sensitive to climate change (Ni, 2002; Niu et al., 2008).

Previous studies examining the responses of R_{eco} to global change drivers typically use natural climatic gradients or experimental manipulations. We combined both methods in an effort to better understand the responses of R_{eco} to precipitation change and N deposition along a precipitation gradient in the temperate steppes in northern China. We measured R_{eco} of soil monoliths from three steppes (i.e. desert steppe, typical steppe, and meadow steppe) subjected to two levels of water and N addition and hypothesized that: (1) Water and N addition may increase R_{eco} across the three steppes, (2) the response of R_{eco} in desert steppe would be more sensitive to water and N addition than in typical or meadow steppe (McCulley et al., 2005).

2. Materials and methods

2.1. Site description

We collected intact soil monoliths (including plants growing on the soil) from three temperate steppes in northern China (Fig. 1). The three sites – a meadow steppe, a typical steppe, and a desert steppe – lay along a clear gradient in terms of precipitation and N deposition from east to west, which have been fenced off in May 2012. The mean annual air temperature and precipitation (1990–2011) are 3.6 °C and 380 mm in the meadow steppe, 0.1 °C and 339 mm in the typical steppe, and 4.3 °C and 316 mm in the desert steppe. The inorganic N deposition rates ranged from 4.53 to 12.21 kg N ha⁻¹ during the entire growing season from desert steppe to meadow steppe (Li et al., 2015a).

The meadow steppe site was in Zhalute Banner, in eastern Inner Mongolia, China (45°06' N, 120°20' E; elevation 656 m a.s.l.). The dominant species include *Lespedeza daurica* and *Leymus chinensis*, which represent the plant functional types (PFTs) of semi-shrubs (SS) and perennial rhizomatous grasses (PR), respectively. The typical steppe site was in Baiyinxile, in central Inner Mongolia, China (43°33' N, 116°40' E; elevation 1100 m a.s.l.). The dominant species is *Stipa grandis*, which belonged to perennial bunchgrass (PB). The desert steppe site was in Siziwang Banner, in western Inner Mongolia, China (41°47' N, 111°53' E; elevation 1443 m a.s.l.). The dominant species include *Salsola collina* and *Allium polyrhizum*, which are annual and biennials (Fig. 1).

2.2. Experimental design and treatments

The soil monoliths were extracted in late July 2012. From each site, 12 intact soil monoliths (each 30 cm long and 15.2 cm in diameter) were obtained by driving a 40 cm long polyvinyl chloride (PVC) tube (outer diameter 16 cm) into the soil and withdrawing the tube carefully without disturbing the monolith. Thus the PVC tubes still had a head-space of 10 cm on the top of the intact soil monoliths, which was adequate for gas sampling. The bottom of each soil monolith was covered with a PVC cap and sealed with silica gel prior to transport. The soil monoliths were brought to a climatron at the Institute of Botany, Chinese Academy of Sciences, within two days of removing them. The temperatures of the climatron were set to be 25 °C during daytime and 20 °C at night. A fluorescent lamp was used to provide illumination from 6 am to 8 pm, thereby simulating the natural conditions at that time of the year.

The experiment was laid out as a randomized block design with two levels of N addition (no N vs. 10 g m⁻² of N) and two levels of water addition (30 mm vs. 102 mm) with three replications, thus accounting for 12 soil monoliths collected from each site. Previous study showed that changes in aboveground biomass, species richness, and plant functional group composition saturate at N addition rates of 10.5 g N m⁻² yr⁻¹ in inner Mongolia Grassland (Bai et al., 2010). Hence, we added

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