



Effects of warming and increased precipitation on net ecosystem productivity: A long-term manipulative experiment in a semiarid grassland

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ABSTRACT

The balance between ecosystem carbon dioxide (CO₂) uptake and release determines the level of carbon (C) sequestration in terrestrial ecosystems and its potential impact on CO₂ concentration in the atmosphere. However, how changes in temperature and precipitation will affect the relationships of net ecosystem productivity (NEP) with gross primary productivity (GPP) and ecosystem respiration (ER) remains unclear. In this study, a nine-year field manipulative experiment was conducted with elevated temperature and increased precipitation in a semiarid steppe of Inner Mongolia, China. Experimental warming reduced GPP and ER by almost the same amount, leading to a slight change in NEP ($-0.16 \mu\text{mol m}^{-2} \text{s}^{-1}$), whereas increased precipitation stimulated GPP more than ER during the growing seasons, resulting in an enhanced NEP ($+0.63 \mu\text{mol m}^{-2} \text{s}^{-1}$). In addition, seasonal patterns of ecosystem C fluxes and the NEP–GPP or NEP–ER relationships were not altered by experimental warming. However, increased precipitation delayed the peak of GPP during the growing seasons and enhanced the correlation between NEP and GPP in the steppe ecosystem. The enhanced control of GPP over NEP under the increased precipitation suggests that ecosystem C sequestration is attributed more to C uptake than C release when water availability is improved in the semiarid grassland. Our findings provide an insight into the response mechanism of ecosystem C flux to warming and precipitation change in semiarid grasslands, and facilitate the projection of terrestrial ecosystem C dynamics and climate feedbacks in the future.

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1. Introduction

Terrestrial ecosystems absorb carbon (C) from the atmosphere through photosynthesis (i.e. gross primary productivity, GPP) and release C into the atmosphere via ecosystem respiration (ER) (Chen et al., 2015; Lasslop et al., 2010; Law et al., 2002; Valentini et al., 2000; van Dijk and Dolman, 2004; Yu et al., 2013). As the net balance of these two processes, net ecosystem productivity (NEP) is an indicator of the C sink or source in terrestrial ecosystems. Therefore, quantifying the NEP–GPP and NEP–ER relationships and their responses to climate warming and changing precipitation regime

is critical for projections of net C balance and global C cycling in the future.

The NEP–GPP and NEP–ER relationships generally vary with climate zones and biomes. Global assessments in forest, grassland, cropland, and wetland ecosystems have demonstrated that NEP change is more closely related to variation in GPP than in ER (Law et al., 2002; Niu et al., 2012; van Dijk and Dolman, 2004; Wohlfahrt et al., 2008). Inter-annual fluctuation in NEP is more similar to that in GPP than that in ER, implying that NEP is more strongly controlled by GPP (Beringer et al., 2007; Saigusa et al., 2005; Urbanski et al., 2007). By contrast, a study across 15 European forests revealed that spatial variability of NEP is influenced more by ER change because ER increases with latitudes, but GPP remains relatively constant (Valentini et al., 2000). The closer relationship between NEP and ER is also supported by several previous studies in tropical forests

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(Saleska et al., 2003; Yan et al., 2013; Zhang et al., 2010). The conflicting results on the NEP-GPP and NEP-ER relationships may be attributable to the differences in vegetation types, soil nutrients, precipitation, temperature, and solar radiation at different sites (Goulden et al., 1996; van Dijk et al., 2005; Wilson and Baldocchi, 2001). Understanding of the NEP-GPP and NEP-ER relationships in different ecosystems is necessary to resolve the disputes.

Moreover, the current knowledge on the NEP-GPP and NEP-ER relationships is primarily obtained by using the eddy covariance technique under natural climate conditions, with the potential impacts of changes in temperature and precipitation on the relationships largely being neglected. Concurrent climate warming and changes in global and regional precipitation regimes (IPCC, 2013) will have profound impacts on temperature- and water-associated biological processes, with subsequent influences on terrestrial C balance (Hui et al., 2003; Liu et al., 2009; Niu et al., 2008; Scanlon and Albertson, 2004; Wan et al., 2009; Wu et al., 2011; Xia et al., 2014). It has been well illustrated that GPP and ER have differential responses and sensitivities to changes in temperature and water availabilities (Luo, 2007; Ma et al., 2007; Niu et al., 2012; Urbanski et al., 2007; Yan et al., 2013), suggesting shifts in contributions of GPP and ER to NEP in response to climate warming and changing precipitation regimes.

Grassland in arid and semiarid regions is one of the major terrestrial biomes and plays an important role in driving dynamic of global land C sink (Poulter et al., 2014). A field manipulative experiment was established in April 2005 in a semiarid temperate steppe in the Mongolian Plateau to examine the potential impact of warming and increased precipitation on ecosystem C cycling. Ecosystem C fluxes were measured using the chamber-based technique during the growing seasons from 2005 to 2013. The specific objectives of this study were: (1) to examine long-term effect of warming and increased precipitation on ecosystem C fluxes, and (2) to investigate the possible impacts of warming and increased precipitation on the NEP-GPP and NEP-ER relationships in the semiarid grassland.

2. Materials and methods

2.1. Experimental site

The experimental field site was located in a temperate steppe in Duolun County (42°02'N, 116°17'E, 1324 m a.s.l), Inner Mongolia, China. Mean annual temperature (1960–2013) was 2.4 °C with a monthly mean temperature ranging from −17.6 °C in January to 19.2 °C in July. Mean annual precipitation (1960–2013) was 374.5 mm, fluctuating greatly between years, and approximately 90% of precipitation occurred during the growing season (from May to October). The plant community was dominated by grasses (*Stipa krylovii*, *Cleistogenes squarrosa*, *Agropyron cristatum*) and forbs (*Artemisia frigida*, *Potentilla acaulis*, *Allium bidentatum*). Plant community cover was estimated using a canopy interception technique based on a 1 × 1 m² frame with 100 equally distributed grids (10 × 10 cm²) at the middle of the growing season for each year from 2005 to 2013. Plant community cover was calculated as the percentage of grids occupied by plant canopy, which ranged from 20 to 70%. The aboveground primary productivity of grassland at the study site was approximately 100–200 g m⁻² yr⁻¹ (Niu et al., 2008). The soil at the site was classified as chestnut according to the Chinese soil classification system and pH value was 6.84 ± 0.07.

2.2. Experimental design

A split-plot design was employed in the current study with precipitation as the primary factor and temperature as the secondary factor. In April 2005, three pairs of 10 × 15 m² plots were

selected in the fenced study area and the distance between the two plots of each pair was 1 m. One plot in each pair was assigned to the increased precipitation treatment and another to the ambient precipitation treatment. In each of the increased or ambient precipitation plots, four 3 × 4 m² subplots were chosen and randomly treated as warmed or unwarmed subplots. Therefore, there were 4 treatments including control, warming, increased precipitation, and warming plus increased precipitation. For each treatment, there were 6 replicates.

The increased precipitation treatments were performed using 6 sprinklers during the growing seasons from 2005 to 2013. In July and August of each year, a total amount of 120 mm water was evenly added (15 mm wk⁻¹ × 8 wk) to the increased precipitation plots. The warming treatments were conducted with 165-cm (Length) × 15-cm (Width) MSR-2420 infrared radiators (Kalglo Eletronics, Bethlehem, PA, USA) fixed 2.5 m above the ground. The warmed subplots were heated continuously from March 15 to November 15 each year. To simulate the shading effects of the infrared radiator on the warmed subplot, a “dummy” heater with the same shape and size as the heat equipment was suspended 2.5 m high in the unwarmed subplots. More details of the experimental design were described in Niu et al. (2008), Liu et al. (2009), and Yang et al. (2011).

2.3. Measurements of environmental variables

Soil temperature at 5 cm depth was measured with thermocouples and recorded in a CR1000 datalogger (Campbell Scientific, Logan, UT, USA) every hour from June 2005 to October 2013. Volumetric soil water content (0–10 cm) was measured with a portable device (Diviner 2000, Sentek Pty Ltd, Balmain, Australia) 2–6 times per month throughout the 9 growing seasons from 2005 to 2013.

2.4. Measurements of ecosystem C fluxes

Ecosystem C fluxes were measured using a transparent sampling chamber (50 cm length × 50 cm width × 50 cm height) attached to the LI-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE, USA) for all the subplots. In each subplot, two aluminum (stainless steel later) frames (50 × 50 cm² for each) were installed into soil to a depth of 2–3 cm at two opposite corners in April 2005. The fixed frames acted as a linkage between the sampling chamber and the soil surface.

The measured C fluxes included the fluxes of net ecosystem CO₂ exchange (NEE, NEP = −NEE) between ecosystem and atmosphere and ER. During each measurement of NEE, the sampling chamber was placed on the frame surface and two small fans fixed at two opposite top corners of chamber ran continuously to mix the air inside the sampling chamber. The concentration of CO₂ in the chamber was analyzed by the infrared gas analyzer every 10 s and recorded in the flash card of LI-6400 Portable Photosynthesis System during a 90-s period. NEP was calculated from changes in CO₂ concentration during the measuring period. Following the measurements of NEE, the chamber was opened for over 30 s, replaced on the frame again, and then covered with an opaque cloth for ER measurement. NEE and ER were measured between 9:00 a.m. and 12:00 p.m. (local time) on the measuring days during each month. Ecosystem CO₂ fluxes were usually measured twice per month in the first six years (2005–2010) and three times per month in the last three years (2011–2013).

2.5. Statistical analyses

Positive and negative NEP values represented CO₂ uptake by and release from the ecosystem, respectively. Ecosystem respiration and NEP were averaged for the 2 frames in each subplot repre-

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