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# Long-term N addition, not warming, increases net ecosystem CO<sub>2</sub> exchange in a desert steppe in northern China

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**Key words:** C<sub>3</sub> and C<sub>4</sub> plants; desert steppe; ecosystem CO<sub>2</sub> flux; global warming; nitrogen deposition

## Abstract

Grasslands cover a major part of the global terrestrial area and provide important ecosystem functions such as sequestration of carbon (C). Desert steppes are unique ecosystems with properties in between desert and grasslands. They are considered to be vulnerable ecosystems that are at risk of desertification due to global change. To provide a robust prediction of the effect of climate warming and increased nitrogen (N) deposition on desert steppe, long-term studies that capture the annual variation in precipitation are needed. We conducted a 12-year field experiment in a desert steppe which showed that warming did not change ecosystem C exchange whereas N addition increased ecosystem C storage. Moreover, warming did not change total aboveground biomass, mainly due to the contrasting responses of C<sub>4</sub> and C<sub>3</sub> plants, especially in the presence of additional N. Therefore, our study predicts that warming do not necessarily lead to degradation of the desert steppe and N addition may have a positive effect on CO<sub>2</sub> sequestration, providing a negative feedback on climate change. However, these global change drivers do alter vegetation composition in the desert steppe, which can have consequences on a diversity of ecosystem functions.

## Introduction

Grasslands cover 41% of the earth's land surface and contain about 34% of terrestrial carbon (C) stocks (White et al. 2000). Global warming and elevated levels of nitrogen (N) deposition are two of the most important factors affecting ecosystems (Boutin et al. 2017; Lin et al. 2010). Both increased temperature and N deposition can significantly affect plant growth and the carbon (C) cycle with potential feedback effects on climate change (Liu et al. 2018; Peng et al. 2017).

Net ecosystem CO<sub>2</sub> exchange (NEE), the difference between gross ecosystem productivity (GEP) and ecosystem respiration (ER), indicates whether the grassland ecosystem is a carbon sink or source (Oberbauer et al. 2007; Xia et al. 2009). Warming or N addition may increase (Niu et al. 2009), decrease (Jiang et al. 2012) or not affect NEE (Xia et al. 2009), and thus might have a positive, a negative or no effect, respectively, on climate change. These and several other studies show that the effects of warming and N addition on NEE depend on ecosystem type (Shi et al. 2015; Xia et al. 2009), and there has been no study on desert ecosystem so far. Furthermore, relatively few long-term warming and N deposition studies have been conducted, and the interactive effects of N deposition and warming on ecosystem CO<sub>2</sub> fluxes in the desert steppe are not well understood.

Warming and N addition can also affect NEE by changing the relative abundance of species within grassland plant communities (Chen et al. 2016; Xu et al. 2015; Zhang et al. 2015). This might involve changes in the relative abundance of C<sub>3</sub> versus C<sub>4</sub> species (Song et al. 2012; Xu et al. 2014), and such changes in their composition have been shown to be correlated with ecosystem CO<sub>2</sub> fluxes (Niu et al. 2013; Xu et al. 2015). The growth of C<sub>3</sub> species is in general more constrained by low N conditions and it seems probable that additional N application would stimulate their growth more than that of C<sub>4</sub> species (Gowik and Westhoff 2011). However, C<sub>4</sub> species could have a better adaptation on warmer conditions than C<sub>3</sub> species (Gowik and Westhoff 2011). As warming and N application might have opposite effects on the growth of C<sub>3</sub> and C<sub>4</sub> species, it is of special interest to determine their combined effect.

The desert steppe is an important and unique part of the steppe in Mongolia and northern China (Inner Mongolia), and is considered to be a fragile ecosystem and probably at risk to desertification due to global change (Angerer et al. 2008). It plays an important role in C sequestration, biodiversity, animal husbandry and regional economic development. Therefore, it is important to study the effects of warming and elevated levels of N deposition on the desert steppe. In this current study, we conducted a long-term (12 years) field experiment in a desert steppe in northern China to examine the effects of warming and N addition on ecosystem

CO<sub>2</sub> flux and the aboveground biomass of two photosynthetic types (C<sub>3</sub> vs. C<sub>4</sub> plants), to explore if there was a long-term individual effects as well as interactive effects of warming and N addition on ecosystem CO<sub>2</sub> fluxes and how this relates to an effect on the aboveground biomass of C<sub>3</sub> versus C<sub>4</sub> species.

## Methods and Study Site

The study was conducted at Siziwang Banner (41°46'43.6" N, 111°53'41.7" E, at 1456 m above sea level); an arid region in Inner Mongolia in northern China. We used a split-plot design with warming as the main plot and N addition as the subplot. One plot in each pair was assigned to warming (W1) and the other was maintained at ambient temperature (W0, or no-warming). Each main plot was divided into two 2 m × 3 m subplots, one of which was randomly assigned to receive supplemental N (N1) and the other received no additional N (N0). Thus, 24 subplots were established with the following treatment combinations: no-warming without N addition (W0N0), no-warming with N addition (W0N1), warming without N addition (W1N0) and warming with N addition (W1N1), with each treatment combination replicated six times. Each year, N was applied prior to a rainfall event in about the third week of June using granular NH<sub>4</sub>NO<sub>3</sub> (10 g N m<sup>-2</sup> yr<sup>-1</sup>). Each warmed plot was heated continuously starting from May 2006 using a 165 cm × 15 cm MSR-2420 infrared radiator (Kalgo Electronics, Bethlehem, PA, USA). The infrared radiator was hung 2.25 m above the ground in the warming plot and was set at an electrical power output of 2000 W. In the non-warming plots, a dummy radiator of the same size was hung at 2.25 m height to simulate the shading effect of the heater.

Ecosystem CO<sub>2</sub> fluxes were measured with a transparent chamber (0.5 m × 0.5 m × 0.5 m) attached to an infrared gas analyzer (IRGA; LI-6400, LiCor Biosciences, Lincoln, NE, USA). Ecosystem CO<sub>2</sub> fluxes were measured on sunny days between 9:00 am and 12:00 pm once or twice a month across the growing seasons from 2007 to 2018. A permanent 1 × 1 m quadrat was established in each of the 24 subplots. In each quadrat, visual estimates of plant canopy cover of each species were made with the aid of a 10 cm × 10 cm grid in late August (at peak plant biomass, 2007 to 2018). We employed a nondestructive method to estimate the biomass of each species to minimize the disturbance to the plots. Forty locations outside the study plots were randomly selected and a quadrat was placed at each location to measure the cover of each species. We then we clipped all the aboveground plant materials of each species in the quadrat, and the samples were oven-dried at 65 °C for 48 h and weighed. We developed regression equations for each year between biomass and cover for each species with data from the forty quadrats. Finally, we estimated aboveground biomass of each species in the quadrat of the experimental plots using the equations established for each year. Total aboveground biomass was the sum of aboveground biomass of each species in August.

## Results

### Warming and N addition effects on aboveground biomass of C<sub>3</sub> and C<sub>4</sub> species

Across the 12 years, total aboveground biomass was increased by N addition ( $F_{1,10} = 12.62$ ;  $P = 0.005$ ), but was not affected by warming ( $F_{1,10} < 0.01$ ;  $P = 0.951$ ) or the interaction of warming and N addition ( $F_{1,10} < 0.01$ ;  $P = 0.940$ ). Warming had significant but opposite effects on the aboveground biomass of both C<sub>3</sub> and C<sub>4</sub> plants, especially when N was added (Fig. 1). The biomass of C<sub>3</sub> species was reduced whereas that of C<sub>4</sub> species was increased (W0N1 vs W1N1) ( $P < 0.05$ ; Fig. 1). However, there were no interactive effects of warming and N addition on C<sub>3</sub> and C<sub>4</sub> species across the 12 years (Fig. 1).

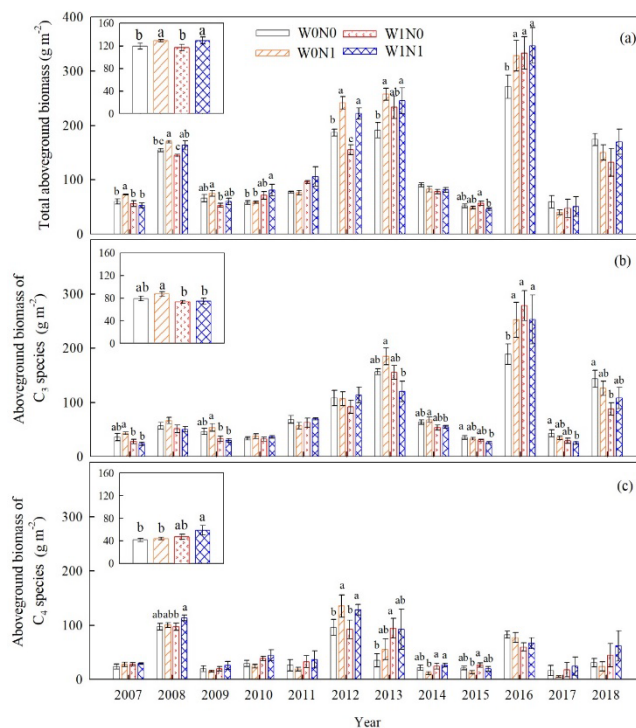


Fig. 1 Mean values ( $\pm$  SE) of (a) total aboveground biomass and the aboveground biomass of (b) C<sub>3</sub> species and (c) C<sub>4</sub> species from 2007 to 2018 in a desert steppe in northern China. The inserts represent the means ( $\pm$  SE) across 12 years. Treatment codes are: W0N0: control, W0N1: N addition without warming, W1N0: warming without N addition and W1N1: warming plus N addition. Different lowercase letters indicate significant differences among treatments ( $P < 0.05$ )

### Warming and N addition effects on ecosystem CO<sub>2</sub> exchange

Ecosystem CO<sub>2</sub> fluxes, including NEE, ER and GEP, had strong inter-annual variations (Fig. 2). N addition increased NEE ( $F_{1,10} = 13.00$ ;  $P = 0.005$ ; Fig. 2) and GEP ( $F_{1,10} = 6.48$ ;  $P = 0.029$ ; Fig. 2), but warming and the interaction of warming and N addition had no effects on them. However, the average ER was not significantly altered by warming, N addition or their interaction (Fig. 2).

### Discussion

During the 12 years of this study, we observed that long-term warming did not change net ecosystem C exchange, but N addition did significantly increase the capacity of the desert steppe to sequester CO<sub>2</sub> (Fig. 2). Thus, the ecosystem C flux in the desert steppe was resistant to climate warming, but was sensitive to N addition. However, warming affected the composition of the vegetation as it increased aboveground biomass of C<sub>4</sub> species, but decreased that of C<sub>3</sub> species (Fig. 1). The unchanged ecosystem carbon flux under warming could be caused by the unchanged total aboveground biomass due to the opposite responses of C<sub>3</sub> and C<sub>4</sub> species. The increased net ecosystem CO<sub>2</sub> exchange induced by N addition correlates with increased total aboveground biomass regardless of warming.

N addition is one of the most limiting nutrients in grassland, so the effect of warming may have less impact on ecosystem functioning when available N is limiting. Addition of N caused a significant increase of total aboveground biomass under both ambient and warming conditions. The increase under ambient conditions was especially contributed by C<sub>3</sub> species, whereas at elevated temperature it was especially contributed by C<sub>4</sub> species (Fig. 1). The increase in aboveground biomass of C<sub>3</sub> plants under ambient conditions is well in line with general theoretical predictions, as C<sub>3</sub> plants have a lower N use efficiency than C<sub>4</sub> species (Gowik and Westhoff 2011). Therefore, the low level of available N seems to be limiting for the growth of C<sub>3</sub> plants but not for C<sub>4</sub> plants. Under warming conditions, available N increased in most years. However, it did not lead to an increased biomass of C<sub>3</sub> plants, probably because they are less adapted to increased temperature than C<sub>4</sub> species (Gowik and Westhoff, 2011). The biomass of C<sub>4</sub> plants increased by the addition of N under warming conditions, indicating that under these conditions N availability has become limiting for these species.

It has been reported that the warming effects on CO<sub>2</sub> fluxes are likely caused by changes in plant community structure (Chen et al. 2016; Xia et al. 2009; Xu et al. 2015). However, average CO<sub>2</sub> fluxes in our desert steppe were not affected by warming alone, which is consistent with the only slight changes observed in plant community composition under warming conditions. Therefore, compared with other grassland ecosystem, the desert steppe seems to be less sensitive to warming. This is counter intuitive as desert steppe is relatively species-poor compared to the temperate grasslands, and according to the portfolio theory higher species richness is predicted to cause less fluctuation in parameters like biomass (Lehman and Tilman, 2000). The desert steppe is located in a region with high temperature during the growing season and plants in this ecosystem might have a better tolerance to the “slight” increases in temperature due to climate change than species from temperate areas. We hypothesise that this might also be true for other desert grasslands.

NEE and GEP were significantly increased by N addition in our study and similar results were obtained by studies in a temperate steppe (Xia et al. 2009) and a meadow steppe in northern China (Jiang et al. 2012). The increase in average GEP (and NEE) by N addition correlates well with total aboveground biomass. The addition of N under both warming and ambient conditions led to a net increase, or was equal to the control treatment in all years (Fig. 2). In contrast, warming alone led to positive and negative changes in NEE which resulted in average values across the 12 years that were equal to that of the control. These positive and negative changes of NEE could be due to the water availability in each year.

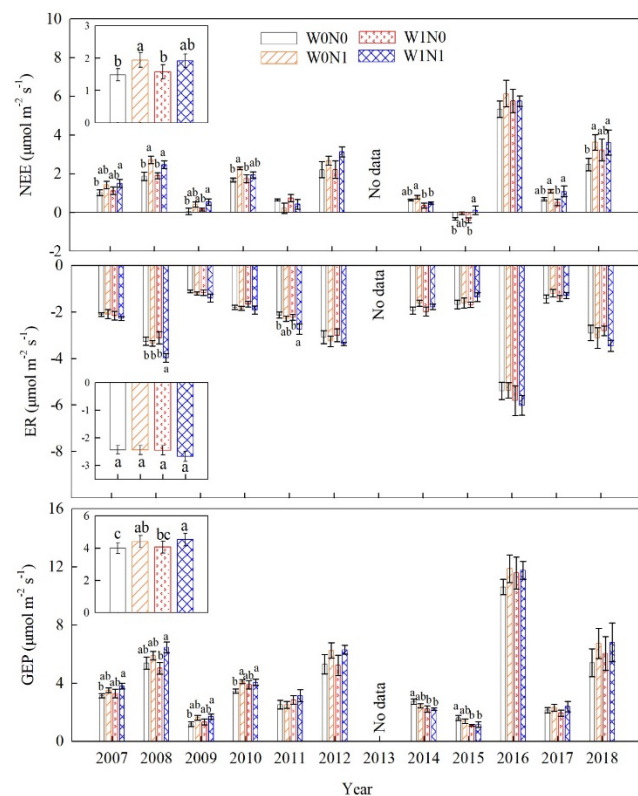


Fig. 2 Mean values ( $\pm$  SE) of net ecosystem CO<sub>2</sub> exchange (NEE), ecosystem respiration (ER) and gross ecosystem productivity (GEP) during 2007-2018 in a desert steppe in northern China. The inserts represent the means ( $\pm$  SE) across 12 years. Treatment codes are the same as in Fig. 1.

Our study indicates that long-term warming does not change net ecosystem carbon flux but N addition does promote carbon sequestration in the desert steppe by which it could provide a negative feedback on climate change. Surprisingly the desert steppe, as one of the most arid grasslands in the Eurasian temperate steppe, appeared to be less vulnerable with respect to warming and N addition, and it is probable that these global changes will not cause degradation of the desert steppe. The observed shift towards C<sub>4</sub> species probably has no effect on the suitability of the desert steppe for animal husbandry because most of the C<sub>4</sub> species in the desert steppe. In combination with the increased plant productivity, change in species composition might improve the conditions for sustainable animal husbandry and continued economic development in this pastoral region.

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