Photosynthetic overcompensation under nocturnal warming enhances grassland carbon sequestration

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Abstract. A mechanistic understanding of the carbon (C) cycle–climate change feedback is essential for projecting future states of climate and ecosystems. Here we report a novel field mechanism and evidence supporting the hypothesis that nocturnal warming in a temperate steppe ecosystem in northern China can result in a minor C sink instead of a C source as models have predicted. Nocturnal warming increased leaf respiration of two dominant grass species by 36.3%, enhanced consumption of carbohydrates in the leaves (72.2% and 60.5% for sugar and starch, respectively), and consequently stimulated plant photosynthesis by 19.8% in the subsequent days. Our experimental findings confirm previous observations of nocturnal warming stimulating plant photosynthesis through increased draw-down of leaf carbohydrates at night. The enhancement of plant photosynthesis overcompensated the increased C loss via plant respiration under nocturnal warming and shifted the steppe ecosystem from a minor C source (1.87 g C·m^{-2}·yr^{-1}) to a C sink (21.72 g C·m^{-2}·yr^{-1}) across the three growing seasons from 2006 to 2008. Given greater increases in daily minimum than maximum temperature in many regions, plant photosynthetic overcompensation may partially serve as a negative feedback mechanism for terrestrial biosphere to climate warming.

Key words: carbohydrate; carbon; China; climate warming; ecosystem; photosynthesis; respiration; temperate steppe; temperature.

Introduction

Global mean temperature has increased by ~0.76°C since 1850 and is predicted to rise an additional 1.8°–4.0°C by the end of this century (IPCC 2007). There is substantial spatial and temporal variability in the magnitudes of temperature increases, which can profoundly impact ecosystem carbon (C) cycling with consequent feedbacks to climate change. For example, it has been recently revealed that both extreme warming events (Ciais et al. 2005), which are predicted to increase in frequency, and autumn warming (Piao et al. 2008) have the potential to reverse terrestrial ecosystems from net C sinks to net C sources. In addition to the seasonal and interannual variability in the warming trend, historical meteorological records and climate model projections have shown greater increases in daily minimum than maximum temperature and subsequent declining diurnal temperature ranges (Karl et al. 1991, Eastering et al. 1997, Stone and Weaver 2002, Vose et al. 2005, Lobell et al. 2007, Zhou et al. 2007). A growing body of evidence from long-term observations (Stooksbury and Michaels 1994, Nicholls 1997, Alward et al. 1999, Peng et al. 2004, Lobell et al. 2005, Schlenker and Roberts 2006, Lobell 2007), manipulative experiments

(Ziska and Manalo 1996, Volder et al. 2007), and model simulations (Rosenzweig and Tubiello 1996, Dhakhwa and Campbell 1998) has demonstrated differential impacts of increasing daily minimum vs. maximum temperatures on biomass production and yield of grassland plant and crop species. However, underlying mechanisms for the differential responses of terrestrial plants to asymmetrical vs. symmetrical diurnal warming and their consequent influence on terrestrial ecosystem C cycling remain elusive.

To examine possible differences in the role of day vs. night warming on C cycling in terrestrial biomes, we have conducted a field warming experiment using infrared radiators in a temperate steppe in northern China since 23 April 2006 (see Plate 1). The temperate steppe is an expansive arid and semiarid biome that stretches across the Eurasian continent and is sensitive to climate change (Christensen et al. 2004, Niu et al. 2008). Twenty-four 3 × 4 m plots were randomly assigned to one of the four treatments: (1) control, (2) day (06:00–18:00, local time) warming, (3) night (18:00–06:00) warming, and (4) diurnal (24-h) warming. Because most plant photosynthetic processes occur during daytime and there is only plant respiration at night, we specifically tested (1) whether the asymmetrical diurnal warming regimes differentially influence plant photosynthesis and nighttime respiration, thus leaf C balance and (2) whether leaf-level physiological responses of plants are manifested at an ecosystem scale.

Materials and Methods

Site description and experimental design

The research site (42°02′ N, 116°17′ E, 1324 m above sea level) is located in Duolun County, Inner Mongolia, China. Mean annual precipitation is 385.5 mm, with ~86% occurring from May to September. Mean annual temperature is 2.1°C, with the minimum and maximum temperatures ranging from −17.5°C in January to 18.9°C in July. The sandy soil in the study site is classified as chestnut according to the Chinese classification or Haplic Calcisols according to the Food and Agricultural Organization of the United Nations (FAO) classification, with 62.75% ± 0.04% sand (mean ± SE), 20.30% ± 0.01% silt, and 16.95% ± 0.01% clay. Soil bulk density and pH are 1.31 g/cm^3 and 6.84 ± 0.07, respectively. Soil organic C and total N contents are 16.10 ± 0.89 g/kg and 1.48 ± 0.10 g/kg, respectively. The plant community at our experimental site is dominated by *Stipa krylovii*, *Artemisia frigida*, *Potentilla acaulis*, *Cleistogenes squarrosa*, *Allium bidentatum*, and *Agropyron cristatum*. This research site was overgrazed by cattle from the early 1980s to 2001, resulting in severe degradation. In 2001, it was fenced to exclude grazing for ecological restoration.

We used a complete random block design with six treatments replicated six times. Thirty-six 3 × 4 m^2 plots were arranged in a 6 × 6 matrix. The distance between any two adjacent plots was 3 m. One of the six plots in each row (i.e., a replication) was randomly assigned to one of the six treatments, including (1) control, (2) day (06:00–18:00, local time) warming, (3) night (18:00–06:00) warming, (4) diurnal (24-h) warming, (5) nitrogen (N) fertilization, and (6) diurnal warming plus N fertilization. The effects of N fertilization and its interaction with diurnal warming were not included in this study. Day, night, and diurnal warming plots were heated by MSR-2420 infrared radiators (Kalglo Electronics, Bethlehem, Pennsylvania, USA) suspended 2.25 m above the ground (see Plate 1). In each control plot, one "dummy" heater with the same shape and size as the infrared heater was used to replace the heater to simulate the shading effect. All the heaters under the three warming treatments were set at a radiation output of ~1600 W. The experimental plots were set up in September 2005 and the warming treatments began on 23 April 2006. The heaters were turned off in the second winter from 15 November 2007 to 14 March 2008.

Measurements

Soil temperatures at the depth of 10 cm were recorded automatically with a Datalogger (STM-01 Soil Temperature Measurement System, Henan Electronic Institute, Zhengzhou, China). Temperature measurements were taken every 10 min and the averages of the six measurements within 1 h were stored as the hourly means. Daily maximum and minimum temperatures were also recorded. Soil moisture (0–10 cm) was measured weekly using a Diviner-2000 Portable Soil Moisture Probe (Sentek, Balmain, Australia).

Diurnal cycles of net ecosystem gas exchanges (NEE) and daytime ecosystem respiration (ER) were measured twice per month over the growing seasons (May–October) of 2006, 2007, and 2008. The measurements were taken at 3-h intervals (06:00, 09:00, 12:00, 15:00, 18:00, 21:00, 0:00, and 03:00 local time) on each measuring date. Ecosystem gas exchange was measured with an infrared gas analyzer (IRGA, LI-6400, LI-COR, Lincoln, Nebraska, USA) attached to a transparent chamber (0.5 × 0.5 × 0.5 m^3) to measure CO_2 and water fluxes. Two aluminum frames (0.5 × 0.5 m^2) were inserted in each plot at the depth of 3 cm in October 2005. The frame provided a flat surface between the soil surface and the sampling chamber. During the measurement, the chamber was sealed to the surface of an aluminum frame. Two small fans were running continuously to mix the air inside the chamber during the measurement. Nine consecutive recordings of CO_2 and water vapor concentrations were taken on each base at 10-s intervals during a 90-s period after steady-state conditions were achieved within the chamber. These nine CO_2 concentrations were plotted against the measuring time to calculate NEE. Following the measurements of NEE, the chamber was lifted and vented, placed back on the frame, and covered with an opaque cloth. The CO_2 exchange measurements were repeated. Because this second set of measurements eliminated light (and hence photosynthesis), the values obtained represented ER during daytime. As light and dark measurements were made within a few minutes of one another, the difference between NEE and ER was considered to represent the gross ecosystem exchange (GEE) at that light level for the vegetation within the chamber.

Diurnal cycles of soil respiration were measured at 3-h intervals twice per month on the same day as ecosystem gas exchange using a soil CO_2 flux system LI-8100 (LI-COR). Two PVC collars (11 cm in diameter and 5 cm in height) were permanently installed 2–3 cm into the soil at two diagonal corners in each plot. All above parts of living plants inside the collar were removed by hand at least one day before the measurement to avoid inclusion of plant leaf respiration. A soil CO_2 flux chamber attached to the LI-8100 was placed for 1–2 min on each collar to measure soil respiration and then moved to the next collar.

Two soil cores (15 cm in depth and 8 cm in diameter) were collected from each plot on 5 August 2006, 3 August 2007, and 3 August 2008. After removing roots or stones by sieving with 2-mm mesh, the samples were stored on ice and subsequently transferred to the laboratory for microbial analysis. Microbial respiration (MR) was measured by alkali absorption of CO_2 evolved at 25°C for 4 d followed by titrating the residual OH^- with a standardized acid (Hu and Bruggen 1997). Briefly, one fresh soil sample (equivalent to 20 g oven-dried soil at 105°C, 24 h) was placed evenly in a 500-mL

Table 1. Changes in mean soil temperature (T, mean $\pm$ SE) under day and night warming during the time periods of 1 August 2006 to 31 October 2007 and 1 May 2008 to 29 October 2008.

Treatments	Day warming (°C)	Night warming (°C)
Diurnal mean soil T	0.82 ± 0.16	0.95 ± 0.14
Daytime mean soil T	1.04 ± 0.24	1.03 ± 0.19
Nighttime mean soil T	0.61 ± 0.12	0.87 ± 0.11
Maximum soil T	1.18 ± 0.25	1.23 ± 0.22
Minimum soil T	0.49 ± 0.14	0.90 ± 0.10

Note: All $P < 0.01$ (two-way ANOVAs).

glass flask. The glass flask was connected with a glass tube (6 cm in diameter) in which 5 mL of 0.05 mol/L NaOH solution was injected to capture CO_2 evolved by soil in flask. Then the soil in the glass flask tube was incubated at 25°C in the dark for 4 d.

Diurnal cycles of leaf-level gas exchange of two dominant grass species (*Agropyron cristatum* and *Stipa krylovii*) were monitored at 3-h intervals (06:00, 09:00, 12:00, 15:00, 18:00, 21:00, 0:00, and 03:00 local time) on 23 July, 15 August, and 25 August 2007 and 3 August 2008 using an LI-6400 portable photosynthesis system (LI-COR). One individual of each species was selected to measure leaf photosynthesis in each plot. Leaf-level daytime C uptake, nighttime C release, and daily net C balance (the difference between C uptake and release) were calculated using the gas exchange parameters. Leaves (0.2 g dry mass) of the above two dominant grass species and one dominant forb species (*Artemisia frigida*) were sampled from each plot after sunset on 2 September 2006, 5 September 2007, and 5 September 2008 and before sunrise on 3 September 2006, 6 September 2007, and 6 September 2008 to measure sugar and starch concentrations using the anthrone method (Hassid and Neufeld 1964, Yemm and Willis 1964) and a UV-VIS7500 spectrophotometer (Techcomp, Shanghai, China).

We used a nondestructive method to estimate aboveground net primary productivity (ANPP) in this study. In May 2006, two permanent 1×1 m^2 quadrats were established in each plot. Percent cover of each plant species was measured in each quadrat during the peak biomass at the end of August in each year. During the measurement, a 1×1 m^2 frame with 100 equally distributed grids (10×10 cm^2) was put above the canopy in each quadrat. The percent cover of each species was visually estimated in all the grids and summed as the species cover in each quadrat.

Forty calibration plots (2×2 m^2) were set up in the south and north sides (20 in each side) of the experimental area in 2006. Each calibration plot was divided into four quadrats. Cover of each species in one of the four quadrats was measured in late August of each year. Then we clipped all aboveground plant materials (including living aboveground biomass, standing litter, and ground litter) in the quadrat. Plant

aboveground tissues (including living aboveground biomass and standing litter in the current year) were separated from standing litter in the previous years and ground litter and into different species, oven dried at 70°C for 48 h, and weighed. We developed regression equations between biomass and cover for each species in the 40 calibration quadrats each year. The majority of the species showed good correlations between biomass and cover. Finally, we estimated aboveground biomass of each species in the experimental plots using the equations in the calibration quadrats. Aboveground net primary productivity was calculated as the sum of aboveground biomass for all plant species.

Belowground net primary productivity (BNPP) was measured using the root in-growth method. In early May of each year, we excavated two 50 cm deep cylindrical holes using a soil auger (8 cm in diameter) in each experimental plot. The soils were refilled to the same hole after removing roots via 2-mm sieves. We collected the root in-growth samples in late October by using a smaller soil auger (6 cm in diameter) at the center of the original root in-growth holes. The dry mass of root was determined by oven drying at 70°C to constant mass.

A standard of canopy greenness, the normalized difference vegetation index (NDVI), which was frequently used for satellite studies (e.g., Myneni et al. 1997), was monitored over the growing seasons of 2007 and 2008. To monitor NDVI, we measured spectral reflectance under cloud-free conditions by using an ASD FieldSpec Handheld spectrometer (Analytical Spectral Devices, Boulder, Colorado, USA). Reflectance measurements were made throughout the growing season at approximately 15-d intervals between 11:00 and 13:00. Each sample was the mean of four spectra obtained with a fiber optic collector (25° field of view) at a height of 50 cm. The NDVI was calculated as (reflectance at 775 nm − reflectance at 675 nm)/(reflectance at 775 nm + reflectance at 675 nm).

Statistical analyses

A full factorial design with day and night warming was used in this study. The measured NEE, daytime ER, and GEE rates were averaged for each measuring date and integrated on the daily basis (as grams of C per square meter per day). Annual growing-season net ecosystem productivity (NEP), daytime ER, and gross ecosystem productivity (GEP) were calculated by multiplying daily integrated values of NEE, ER, and GEE, respectively, by the number of days since the last measuring date. Three-way ANOVAs were used to examine the effects of year, day warming, night warming, and their interactions on NEP, ER, GEP, soil respiration, and soil microbial respiration. Four-way ANOVAs were used to examine the effects of date (year), species, day warming, night warming, and their interactions on leaf temperature, daytime photosynthesis, nighttime respiration, daily net C accumulation, sugar and starch concentrations after sunset and before
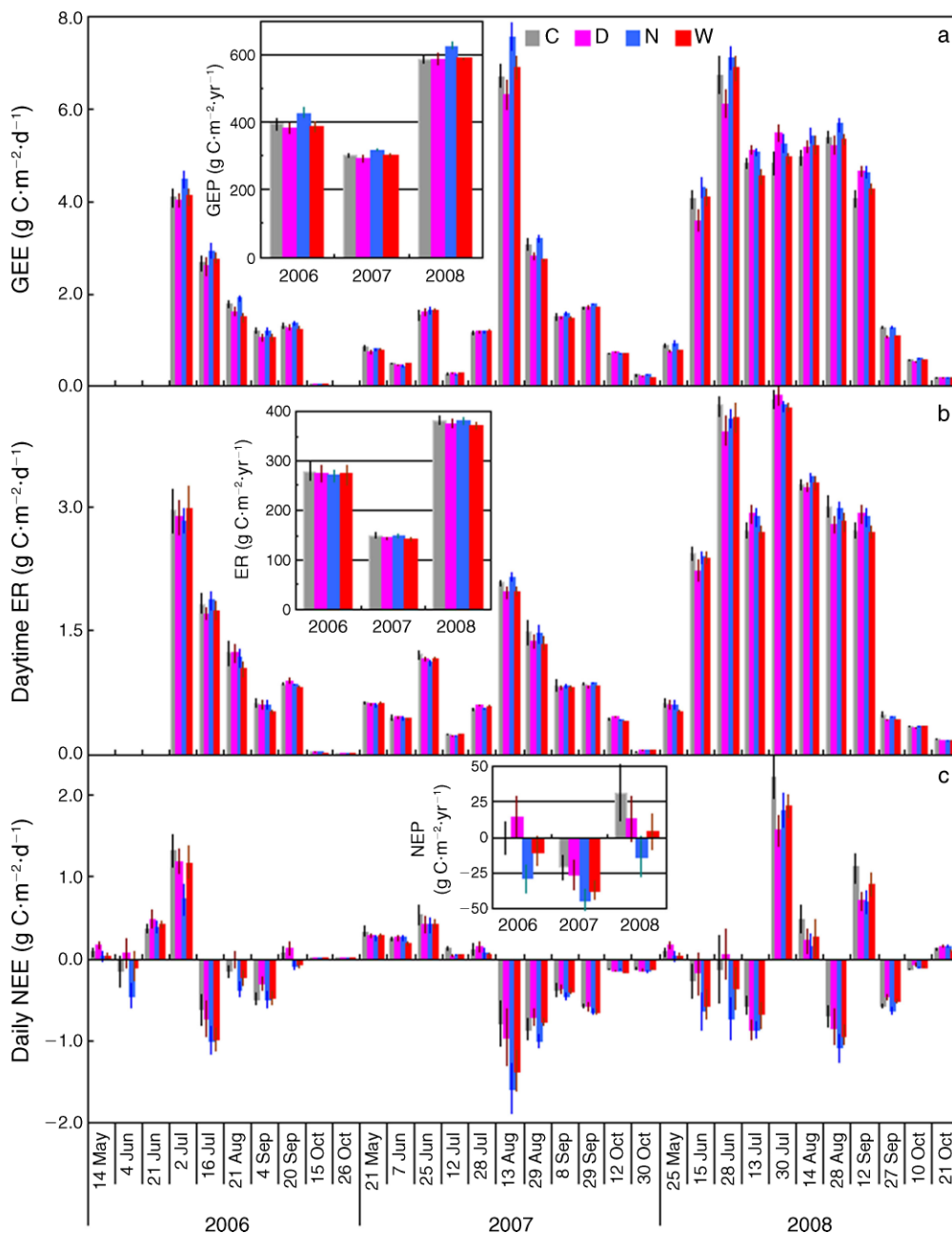
Fig. 1. Daily integrated values of (a) gross ecosystem exchange (GEE), (b) daytime ecosystem respiration (ER), and (c) net ecosystem gas exchange (NEE) under the control (C), day warming (D), night warming (N), and diurnal warming (W) treatments (mean ± SE, $n = 12$). Annual growing-season (1 May to 31 October) gross ecosystem productivity (GEP), ecosystem respiration (ER), and net ecosystem productivity (NEP) in the three experimental years (2006–2008) were calculated by multiplying daily integrated values of GEE, ER, and NEE by the number of days since the last measuring date and are shown as insets. Positive and negative NEE or NEP values refer to net C source and sink, respectively.

sunrise, and depletions of sugar and starch over night. All statistical analyses were conducted with SAS software (SAS Institute, Cary, North Carolina, USA).

RESULTS AND DISCUSSION

Day and night warming elevated daily mean soil temperature at the depth of 10 cm by 0.82° and 0.95°C,

respectively, for the automated temperature record (1 August 2006 to 31 October 2007 and 1 May to 29 October 2008; Table 1). As expected, night warming caused greater increases in nighttime mean and daily minimum soil temperatures (0.87° and 0.90°C) than day warming did (0.61° and 0.49°C). However, there were no differences in daytime mean and daily maximum
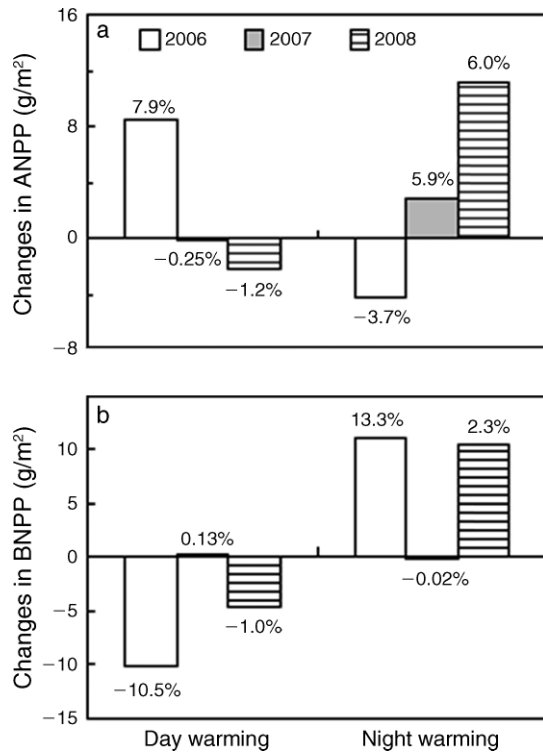
FIG. 2. (a) Changes in aboveground net primary productivity (ANPP) and (b) belowground net primary productivity (BNPP) induced by day and night warming, respectively, over the three experimental years (2006–2008). Values associated with the bars indicate relative changes.

temperatures induced by either day warming (1.04° and 1.18°C) or night warming (1.03° and 1.23°C).

Day warming significantly reduced GEP by 4.7% ($P = 0.025$), whereas night warming marginally increased GEP by 4.2% ($P = 0.051$; Fig. 1a) over the three growing seasons of 2006, 2007, and 2008. However, neither day ($P = 0.505$) nor night ($P = 0.681$) warming affected daytime ER (Fig. 1b). As consequences of the differential responses of GEP and lack of change in ER, NEP showed an insignificant decrease of 46.2% ($P = 0.436$) under day warming. In contrast, night warming changed the steppe ecosystem from a minor C source (1.87 g C·m^{-2}·yr^{-1}) to a C sink (21.72 g C·m^{-2}·yr^{-1}, $P = 0.002$) when averaged over the three growing seasons of 2006, 2007, and 2008 (Fig. 1c). There were no interactive effects of day and night warming on GEP, daytime ER, and NEP. In addition, the main effects of day and night warming on the three parameters did not vary with year (all $P > 0.10$), irrespective of the strong interannual variability in GEP, daytime ER, and NEP (all $P < 0.0001$).

Neither day nor night warming caused significant changes in ANPP or BNPP (all $P > 0.10$) over the three years (Appendix A). However, there was a decreasing and an increasing trend of ANPP changes in response to day and night warming, respectively (Fig. 2a). In addition, BNPP showed negative responses to day

warming but positive responses to night warming in both 2006 and 2008 (Fig. 2b). Moreover, day warming tended to decrease the NDVI, whereas night warming tended to increase NDVI over the growing seasons in 2007 and 2008 (Appendix B). Given the trajectory, it is expected that stimulation of GEP would ultimately lead to a statistically significant difference in NPP under night warming compared to the control in the future.

To reveal mechanisms underlying the enhanced net C sink under night warming, we measured diurnal cycles of leaf temperature and gas exchange of two dominant grass species (*Agropyron cristatum* and *Stipa krylovii*) on 23 July, 15 August, and 25 August 2007 and 3 August 2008 (Fig. 3). Day warming marginally increased daily mean leaf temperature by 0.11 ($P = 0.091$), but did not affect daytime or nighttime mean leaf temperature ($P > 0.10$). By contrast, night warming significantly raised nighttime mean leaf temperature by 0.13°C ($P = 0.007$) but had no effects on daily and daytime mean leaf temperature ($P > 0.10$; Appendix C).

Elevated nighttime temperature under nocturnal warming may stimulate plant respiration (Ryan 1991, Atkin et al. 2000, Griffin et al. 2002). Averaged across all four measuring dates and the two species, night warming increased nighttime leaf C release via respiration by 36.3% ($P < 0.0001$), but day warming decreased it by 14.0% ($P < 0.0001$; Figs. 3 and 4). There were also interactive effects ($P = 0.044$) of day and night warming on nighttime C release. In comparison with that in the control plots, nighttime leaf respiration of *A. cristatum* and *S. krylovii* was 41.0% and 43.2% higher under night warming, 17.1% and 18.3% higher under diurnal warming, but 9.2% and 9.6% lower under day warming, respectively. Nocturnal warming increased not only leaf respiration, but also root respiration. Soil respiration was significantly increased by 7.1% ($P < 0.001$) under night warming, but not affected by day warming ($P = 0.977$) across the three growing seasons (Appendix D). Night and day warming caused insignificant ($P > 0.10$) reductions of 6.7% and 7.2% in soil microbial respiration, respectively (Appendix D), indicating stimulated plant root respiration under night warming.

Enhanced nighttime leaf and root respiration could cause greater depletion of carbohydrates, including sugar and starch, in plants (Ryan 1991, Alward et al. 1999). Averaged across the three years and the three species (*A. cristatum*, *S. krylovii*, and *A. frigida*), night warming significantly increased both sugar (72.2%, $P = 0.017$) and starch depletion (60.5%, $P = 0.003$). By contrast, day warming decreased sugar and starch depletion by 21.4% ($P = 0.279$) and 35.4% ($P = 0.006$), respectively (Fig. 5). No interactive effects of day and night warming on either sugar or starch depletion were observed ($P > 0.10$).

The sink–source hypothesis of plant photosynthesis (Paul and Foyer 2001, Paul et al. 2001, McCormick et al. 2006) proposes that greater carbohydrate consumptions by plant respiration during the previous night can
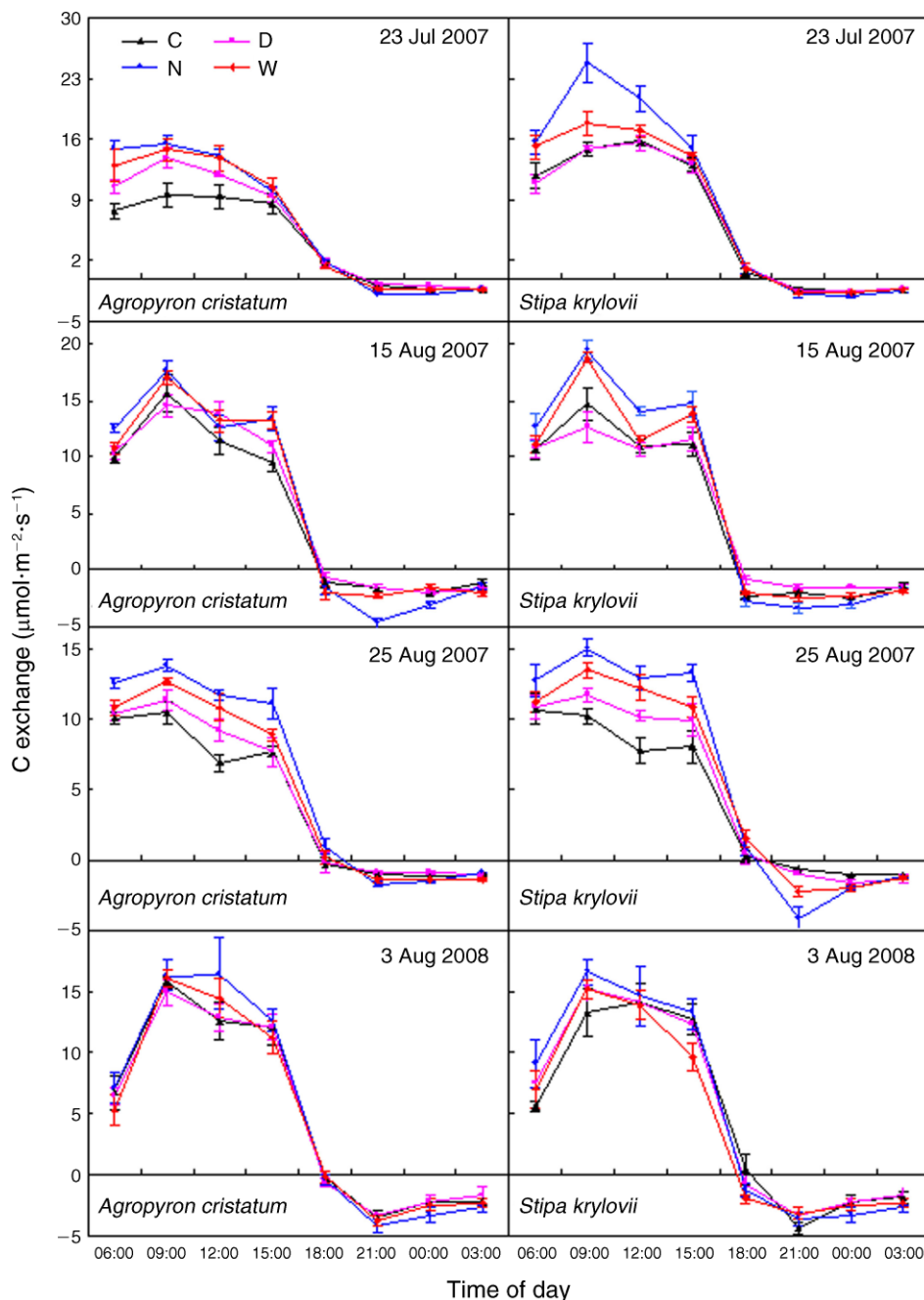
FIG. 3. Diurnal patterns of leaf gas exchange (mean ± SE, $n = 6$) for two dominant grass species, *Agropyron cristatum* and *Stipa krylovii*, under the control (C), day warming (D), night warming (N), and diurnal warming (W) treatments measured on four dates. Negative and positive values indicate net C release through leaf respiration at night and net C uptake via leaf photosynthesis during the day, respectively.

stimulate plant photosynthesis in the following day in return (Ryan 1991, Atkin et al. 2000, Will 2000, Xiong et al. 2000, Griffin et al. 2002, Turnbull et al. 2002, 2004). In our study, night-warming-induced increases in nighttime leaf respiration (Figs. 3 and 4) and sugar and starch depletion (Fig. 5) resulted in enhanced daytime C uptake via leaf photosynthesis (Figs. 3 and 6a). Averaged across all the measuring dates and the

species, night warming significantly stimulated daytime C uptake via leaf photosynthesis by 19.8% ($P < 0.001$), whereas day warming marginally decreased it by 3.0% ($P = 0.092$). Day and night warming interacted to affect daytime C uptake ($P < 0.0001$). Taken together, these results provide field confirmation of a mechanism previously hypothesized that night warming stimulated plant respiration and carbohydrate consumption and

PLATE 1. Infrared heaters to conduct day (6:00 a.m.–6:00 p.m.), night (6:00 p.m.–6:00 a.m.), and diurnal (24 hours) warming in a temperate steppe in northern China. Photo credit: J. Xia.

subsequently induced a compensatory enhancement of photosynthesis (Griffin et al. 2002, Turnbull et al. 2002, 2004).

Greater enhancement of daytime leaf photosynthesis could have resulted in accumulations of carbohydrates during daytime. In our study, the main effects of night warming were statistically significant on both sugar (+23.1%, $P = 0.001$) and starch concentrations (+6.8%, $P = 0.006$) after sunset (Appendix E). By contrast, day warming caused significant reductions of starch (−6.1%,
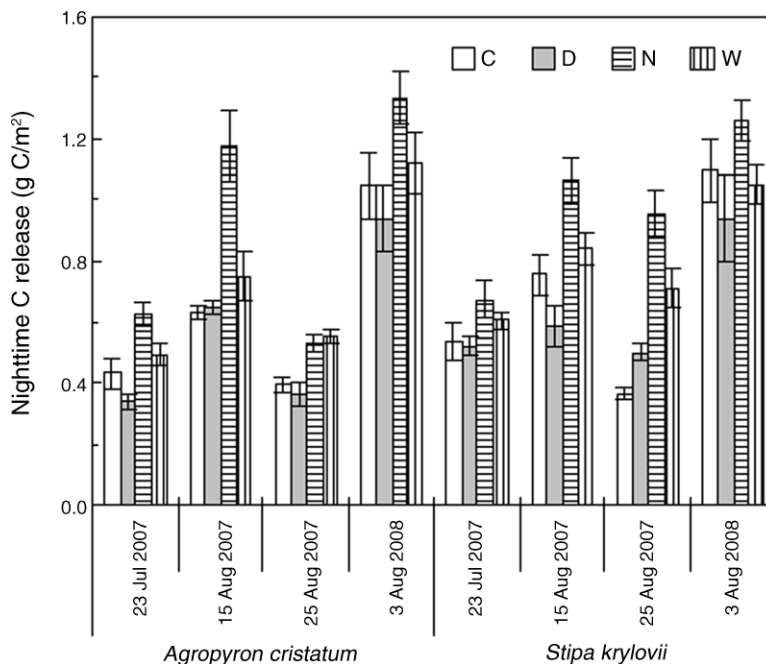

FIG. 4. Nighttime C release via leaf respiration of *Agropyron cristatum* and *Stipa krylovii* under the control (C), day warming (D), night warming (N), and diurnal warming (W) treatments (mean ± SE, $n = 6$).
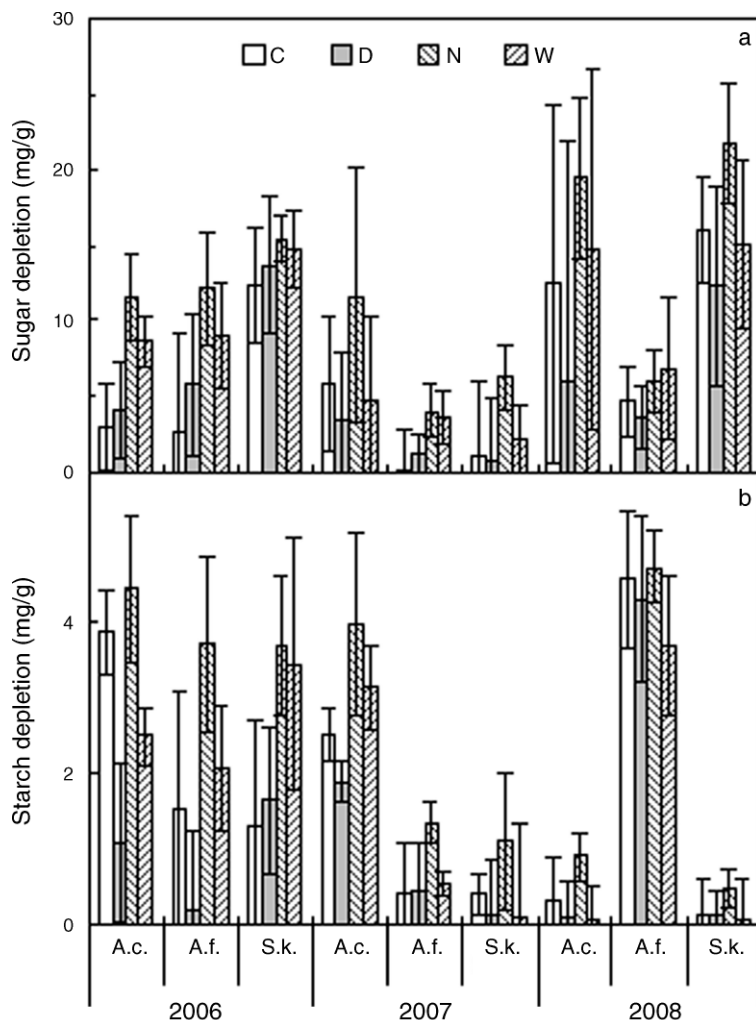
Fig. 5. Nighttime (a) sugar and (b) starch depletion in leaves of three dominant species under the control (C), day warming (D), night warming (N), and diurnal warming (W) treatments (mean ± SE, $n = 6$). Species abbreviations are: A.c., *Agropyron cristatum*; A.f., *Artemisia frigida*; S.k., *Stipa krylovii*.

$P = 0.009$), but not sugar (-1.5%, $P = 0.449$) concentrations after sunset. However, neither day warming nor night warming or their interactions affected sugar or starch concentrations before sunrise in the second day (all $P > 0.10$). Greater carbohydrate contents after sunset under night warming provide more substrate for plant respiratory activities, further enhance nighttime respiration, and stimulate carbohydrate depletion. These processes in combination with stimulation of photosynthesis in the following day form a positive feedback loop under nocturnal warming (Griffin et al. 2002, Turnbull et al. 2002, 2004).

Differences in daytime leaf photosynthesis and nighttime leaf respiration represent daily C balance or accumulation at the leaf level. Averaged across the four measuring dates over the growing seasons of 2007 and 2008, daytime C uptake via photosynthesis (Fig. 6a) was 4.8–18.2 and 4.6–14.1 times greater than nighttime C

release via leaf respiration (Fig. 4) for *A. cristatum* and *S. krylovii*, respectively, resulting in daily net C accumulation (Fig. 6b) at the leaf level under all the four treatments. Comparing to the enhancement of nighttime leaf respiration induced by night warming, the subsequent stimulation of leaf photosynthesis in the following day was much higher and thus overcompensated for the increased leaf respiration during the previous night. As consequences, night warming caused a 17.5% ($P < 0.0001$) increase in daily net C accumulation at the leaf level but no main effect of day warming was detected ($P = 0.556$; Fig. 6b). There were significant interactive effects ($P < 0.0001$) of day and night warming on daily net C accumulation. Comparing to the control plots, night warming caused the greatest increases in daily net C accumulation in both *A. cristatum* (27.6%) and *S. krylovii* (29.5%) among the three warming treatments. The enhanced leaf-level
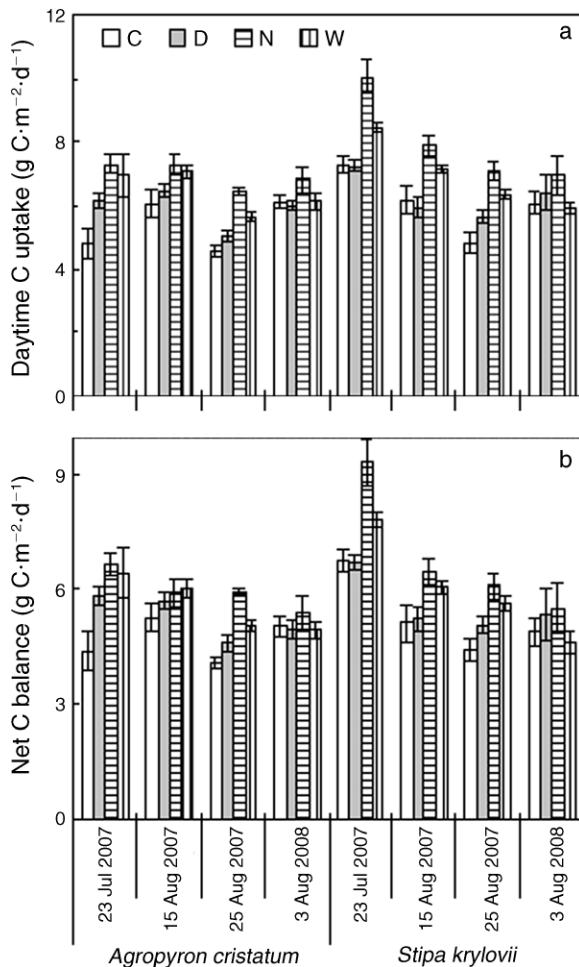
FIG. 6. (a) Daytime C uptake via photosynthesis and (b) daily net C balance (difference between daytime C uptake and nighttime C release) in leaves of *Agropyron cristatum* and *Stipa krylovii* under the control (C), day warming (D), night warming (N), and diurnal warming (W) treatments (mean ± SE, $n = 6$).

net C accumulation induced by night warming (Fig. 6b) has resulted in a net C sink at the ecosystem level (Fig. 1c).

Our experimental evidence of differential responses of C balance to asymmetrical diurnal warming at both leaf and ecosystem levels are supported by historical data analyses, manipulative experiments (Ziska and Manalo 1996, Volder et al. 2007), and model simulations. For example, biomass production and density of plant species in a shortgrass steppe in North America have responded significantly to long-term increases in daily minimum, but not mean or maximum temperatures (Alward et al. 1999). In the Philippines, rice yield is negatively correlated with increasing daily minimum but not maximum temperatures (Peng et al. 2004). Other analyses on historical data have also widely demonstrated differential impacts of asymmetrical vs. symmetrical diurnal warming on the crop yield in the United States (Stooksbury and Michaels 1994, Schlenker and

Roberts 2006, Lobell 2007, Lobell and Ortiz-Monasterio 2007), Mexico (Lobell et al. 2005, Lobell and Ortiz-Monasterio 2007), and Australia (Nicholls 1997). In addition, modeling simulations have revealed that the negative responses of biomass and yield of maize, soybean, and wheat can be alleviated under asymmetrical comparing to symmetrical diurnal warming (Rosenzweig and Tubiello 1996, Dhakhwa and Campbell 1998).

It was surprising that we have observed a larger stimulation of plant leaf respiration (36.3%; Fig. 3) given the minor increase in nighttime leaf temperature (0.13°C; Appendix C) whereas a much higher increase in nighttime soil temperature (0.87°C; Table 1) has enhanced soil respiration only by 7.1% under night warming. The leaf respiration measurements have been made for two grass species among the ~50 species in our experimental plots. In a previous pot experiment in the same area, responses of leaf respiration to increased temperature have been observed to be species-specific (S. Niu, *unpublished data*). Therefore, other species in the plant community might not show similar magnitudes of leaf respiration stimulation in response to night warming. On the other hand, soil respiration consists of plant root respiration and microbial respiration. Given a 6.7% reduction in soil microbial respiration (Appendix D), the actual increase in plant root respiration should be larger than the observed simulation of total soil respiration (7.1%) under night warming.

In the temperate steppe in northern China, night warming has stimulated plant respiration and carbohydrate consumption and subsequently induced a compensatory enhancement of photosynthesis. Our observations support the hypothesis of sink regulation on plant photosynthesis (Paul and Foyer 2001, Paul et al. 2001, McCormick et al. 2006). Numerous previous studies (Ryan 1991, Atkin et al. 2000, Will 2000, Xiong et al. 2000, Griffin et al. 2002, Turnbull et al. 2002, 2004) have also clearly demonstrated compensatory responses of leaf photosynthesis under higher night temperature through increased drawdown of leaf carbohydrates at night (Turnbull et al. 2002, 2004). Greater increases in photosynthesis than in respiration have resulted in consequent net C accumulation at both leaf and ecosystem levels, implying that the leaf-level physiological responses of plants can be up-scaled to the C cycle at the ecosystem level. Therefore, our study, for the first time, to the best of our knowledge, provides direct ecosystem-level evidence that photosynthetic overcompensation induced by nocturnal warming is a mechanism by which terrestrial ecosystems can act as a net C sink in a warmer world in the future. Not only has the local climate in our study area experienced asymmetrical diurnal warming (0.57°, 0.45°, and 0.30°C increases in daily minimum, mean, and maximum temperatures per decade, respectively) over the past half century (1953–2005; Appendix F), but similar diurnal scenarios of climate warming have been widely reported at the

regional and global scales (Karl et al. 1991, Eastering et al. 1997, Stone and Weaver 2002, Vose et al. 2005, Lobell et al. 2007, Zhou et al. 2007). The photosynthetic overcompensation induced by nocturnal warming can be another critical mechanism, in addition to changes in phenology, nutrient availability, and species composition (Luo 2007), to regulate terrestrial C sequestration and negatively feed back to climate change.

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APPENDIX A

Aboveground net primary productivity and belowground net primary productivity over the three growing seasons in 2006, 2007, and 2008 (*Ecological Archives* E090-191-A1).

APPENDIX B

Changes in the normalized difference vegetation index (NDVI) under day warming and night warming, respectively, over the growing seasons in 2007 and 2008 (*Ecological Archives* E090-191-A2).

APPENDIX C

Daytime, daily, and nighttime mean leaf temperature measured at the same time as leaf photosynthesis under the control and three heating regimes (*Ecological Archives* E090-191-A3).

APPENDIX D

Mean soil respiration and microbial respiration across the three experimental years under the control and three heating regimes (*Ecological Archives* E090-191-A4).

APPENDIX E

Sugar and starch concentrations in leaves of the three dominant species sampled after sunset in the first day and before sunrise on the second day under the control and three heating regimes (*Ecological Archives* E090-191-A5).

APPENDIX F

Changes in annual averages of daily mean, maximum, and minimum air temperatures over the past half-century (1953–2005) in Duolun County, Inner Mongolia, China (*Ecological Archives* E090-191-A6).