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**Non-additive effect of  
day and night  
warming**

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# Non-additive effect of day and night warming on soil respiration in a temperate steppe

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## Abstract

This study was conducted to examine potentially differential effects of day and night warming on soil respiration in a temperate steppe in northern China. A full factorial design with day and night warming was used in this study, including control (C), day (6 a.m.–6 p.m., local time; D) warming, night (6 p.m.–6 a.m.; N) warming, and diurnal warming (W). Day warming showed neutral effect on soil respiration, whereas night warming significantly increased soil respiration by 7.1% over the first 3 growing seasons. The insignificant effect of day warming on soil respiration could be attributable to the offset of the direct positive effects by the indirect negative effects via aggravating water limitation and suppressing ecosystem C assimilation. The positive effects of night warming on soil respiration were largely due to the stimulation of ecosystem C uptake and substrate supply via over-compensation of plant photosynthesis. In addition, day and night warming showed antagonistic effects on soil respiration, which could be ascribed to their contrasting effects on ecosystem C assimilation. The results suggest differential and non-additive effects of day and night warming on soil respiration, which was driven by the treatment-induced changes in substrate supply.

## 1 Introduction

With the unprecedented magnitude of global temperature rising associated with anthropogenic activities since industrial revolution, it is of great concern how terrestrial biosphere responds and feeds back to climate change, especially through carbon (C) cycling (Luo et al., 2009). In the past decades, findings from temperature manipulation experiments have greatly improved our understanding of the impacts of climate warming on terrestrial C cycling. Nevertheless, there are still many uncertainties remaining to be addressed. For example, historical meteorological records and model projections reveal a warming trend that is more pronounced at night than day (Karl et al., 1991; Easterling et al., 1997; IPCC 2001; Zhou et al., 2007). Although such an asymmetric

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diurnal warming is still under debate (Vose et al., 2005; IPCC 2007), it has been widely observed over the land since 1950 (Easterling et al., 1997; Zhou et al., 2007). From the perspective of plant ecophysiology, since most plant photosynthetic processes occur during daytime whereas there is only plant respiration at night, it is theoretically reasonable to expect that day and night warming can have different impacts on plant and ecosystem C uptake and release processes, with consequent impacts on the balance of these two aspects for both plants and ecosystems. In fact, differential responses of plant growth and crop yield to increasing daily minimum vs. maximum temperature have been demonstrated by manipulative experiments (Ziska and Manalo, 1997; Volder et al., 2007), long-term observations (Stooksbury and Michaels, 1994; Nicholls, 1997; Alward et al., 1999; Peng et al., 2004; Schlenker and Roberts, 2006; Lobell and Ortiz-Monasterio, 2007; Lobell, 2007), and model simulations (Rosenzweig and Tubiello, 1996; Dhakhwa and Campbell, 1998). At the ecosystem scale, Wan et al. (2009) have recently found differential impacts of day (negative) and night warming (positive) on gross ecosystem productivity (GEP) and net ecosystem productivity (NEP) in a semi-arid temperate steppe in northern China.

All the previous observations suggest that day and night warming could differentially affect ecosystem C processes. However, most of the manipulative experiments were conducted with diurnal or constant warming (Rustad, 2008). To our knowledge only a few experiments (Volder et al., 2004; Beier et al., 2008) have designed to examine the effect of night-time warming on ecosystem C processes and in these studies no daytime warming was included. In order to better understand the mechanisms controlling ecosystem C processes and to convincingly project climate change-carbon feedback under the diurnally asymmetric climate warming, it is essential to examine the effects of day and night warming separately and compare their respective effects with those when they are in combination (e.g., diurnal warming). If the effects day and night warming are non-additive and their summed effects do not equal to those of diurnal warming, we can not predict the responses of terrestrial C cycling to diurnally asymmetric climate warming based on diurnal or constant warming treatment.

As the second largest C flux between terrestrial ecosystems and the atmosphere, soil respiration plays an important role in regulating ecosystem C cycling and climate-carbon feedbacks. Temporal and spatial variability of soil respiration are generally associated with changes in temperature and water availability (Lloyd and Taylor, 1994; Davidson and Janssens, 2006; Luo and Zhou, 2006; Luo, 2007). Moreover, as a substrate-regulated process, it has been widely reported that soil respiration is tightly coupled with ecosystem C uptake which determines the availability of C supply to respiratory activities (Högberg et al., 2001; Wan and Luo, 2003; Tang et al., 2005; Bahn et al., 2008). Thus, responses of soil respiration to climate warming can not be fully assessed if it is taken as an isolated belowground soil process without considering aboveground C assimilation.

Here, we present the results from a field study to investigate effects of day and night warming on soil respiration with four treatments, including control (C), day (6 a.m.–6 p.m., local time; D) warming, night (6 p.m.–6 a.m.; N) warming, and diurnal warming (W) in a semiarid temperate steppe in northern China since 2006. Historical meteorological record in this region has shown greater increases in daily minimum than that maximum temperature in the past 55 years (Wan et al., 2009). Given that day and night warming has been found to have contradictory effects on GEP in this ecosystem (Wan et al., 2009), we expect that soil respiration differently responds to day and night warming. We specifically addressed three questions in this study: (1) whether will soil respiration differentially respond to day and night warming? (2) will day and night warming additively or non-additively affect soil respiration? and (3) what drives soil respiration in response to day and night warming?

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## 2 Materials and methods

### 2.1 Study site

The research was conducted in a semiarid temperate steppe in Duolun County (42°02' N, 116°17' E, 1324 m a.s.l) in Inner Mongolia, China. The grassland was dominated by C<sub>3</sub> grasses – *Stipa krylovii* Roshev., *Agropyron cristatum* (L.) Gaertn.; C<sub>4</sub> grass – *Cleistogenes squarrosa* (Trin.) Keng.; and C<sub>3</sub> forbs – *Artemisia frigida* Willd., *Potentilla acaulis* L., *Allium bidentatum* Fisch. ex Prokh. Long-term (1953–2007) mean annual precipitation is approximately 383 mm with 90% distributing from May to October. Mean annual temperature is 2.1°C with monthly mean temperature ranging from 18.9°C in July to –17.5°C in January. The sandy soil of the study site is classified as chestnut according to the Chinese classification, or Haplic Calcisols according to the FAO classification. Mean bulk density is 1.31 g cm<sup>-3</sup> and pH is 7.7.

### 2.2 Experimental design

We used a complete random block design with 6 treatments, including control, day warming (6 a.m.–6 p.m.), night warming (6 p.m.–6 a.m.), diurnal (24 h) warming, nitrogen addition, and diurnal warming plus nitrogen addition, and replicated 6 times (Wan et al., 2009). Thirty-six 3×4 m<sup>2</sup> plots were arranged in 6×6 matrix, with a 3 m distance between any two adjacent plots. The effects of nitrogen addition and warming plus nitrogen addition on ecosystem C processes were reported in a previous study (Xia et al., 2009) and not included in this study. In late August 2005, we compared ecosystem C fluxes, aboveground biomass, and root biomass in the plots which would be assigned to different treatments in 2006 and did not find any statistically significant difference (all  $P > 0.05$ ). All the warmed plots were heated continuously by MSR-2420 infrared radiators (Kalglo Electronics Inc, Bethlehem, PA, USA) suspended 2.25 m above the ground. In each control plot, one “dummy” heater with the same shape and size as the infrared heater was suspended 2.25 m high to simulate the shading effects of the

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infrared radiator. All the heaters under the warming treatments were set at a radiation output of approximately 1600 W. The warming treatment started from 23 April 2006.

## 2.3 Measurements

To measure soil respiration, two PVC collars (11 cm in internal diameter and 5 cm in height) were inserted 2–3 cm into the soil at two opposite corners in each plot. A LI-8100 portable soil CO<sub>2</sub> fluxes system (Li-Cor, Inc., Lincoln, NE, USA) was used to measure diurnal cycles (twice a month at 3-h intervals) of soil respiration. Soil CO<sub>2</sub> Flux Chamber attached to LI-8100 was put 1–2 min on the collars to measure soil respiration and then move to the next collar. Living plants (if there are) inside the soil collars were removed by hand at least 1 day before the measurements to exclude plant respiration from the aboveground parts, and the clipped plant materials were left in the collars for inclusion of CO<sub>2</sub> released from decomposition of aboveground litter.

Diurnal cycle of soil temperature (°C) at the depth of 10 cm was measured adjacent to each PVC collar using a thermocouple probe (LI-8100-201) connected to the LI-8100 at the same time of soil respiration measurement. Soil moisture (0–10 cm) was measured using a portable soil moisture device (Diviner 2000, Sentek Pty Ltd., Balmain, Australia) adjacent to the PVC collars between 9:00–12:00 on the same day of soil respiration measurement.

Gross ecosystem exchange (GEE) was measured twice a month at 3-h intervals (from 6:00 to 18:00) on the same day of soil respiration measurement. We first measured net ecosystem C exchange (NEE) with a transparent chamber (0.5×0.5×0.5 m<sup>3</sup>) attached to an infrared gas analyzer (IRGA; LI-6400, LiCor, Lincoln, NE, USA). The chamber was placed and sealed on an aluminum frame (0.5×0.5 m<sup>2</sup>) inserted 2–3 cm into the soil at two corners of each plot. The PVC collars for soil respiration measurement were inside the frames in order to relate soil respiration with ecosystem C fluxes. This static-chamber method has been successfully used to evaluate plot-level fluxes of CO<sub>2</sub> in this ecosystem (Niu et al., 2008; Xia et al., 2009), and validated in some previous studies (Steduto et al., 2002; Huxman et al., 2004; Potts et al., 2006; Bubier

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et al., 2007; Risch and Frank, 2007). The polyethelene sheeting used for chamber construction allows >90% of photosynthetic active radiation to pass into the chamber. Two small fans ran continuously to mix the air inside the chamber during measurement. Consecutive recordings of CO<sub>2</sub> concentrations were taken during a 90-s period after steady-state conditions were achieved within the chamber for 20 s. Increases in air temperature within the chamber during the measuring time period were less than 0.2°C. CO<sub>2</sub> concentrations were build up or draw down insufficiently (upper limit of range above and below ambient of about 10 μmol mol<sup>-1</sup>) to significantly alter stomatal conductance, canopy photosynthesis or soil respiration (Huxman et al., 2004). Following the NEE measurement, the chamber was vented, replaced on each frame and covered with an opaque cloth. Because of elimination of light (and hence photosynthesis), the values of CO<sub>2</sub> exchange represented ecosystem respiration (ER). GEE was calculated as the difference between NEE and ER. GEE was integrated to calculate gross ecosystem productivity (see Wan et al., 2009 for detail). In order to examine impacts of treatments on ecosystem water use efficiency (WUE), we first calculated evapotraspiration (ET) from the time-courses of the H<sub>2</sub>O concentration, then WUE was calculated as GEE divided by ET (WUE=GEE/ET).

Leaf-level gas exchange of *S. Krylovii* was monitored at 3-h intervals (6:00, 9:00, 12:00, 15:00, 18:00, 21:00, 0:00, and 3:00 local time), using LI-6400 Portable Photosynthesis System. One individual for *S. Krylovii* was selected to measure leaf photosynthesis in each plot.

## 2.4 Data analysis

Three-way ANOVAs were used to examine effects of year, day warming, night warming, and their possible interactions on soil respiration, soil temperature, soil moisture, and GEE. Change in soil respiration was presented as the absolute differences between the warmed plots and the control plots. Since the total heating time and energy inputs in the day and night warming plots were the same with those in the diurnal warming plots, we took the sum of day and night warming effects as the predicted effects of whole day

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warming and the measured effects of diurnal warming as the observed ones. Then we plotted the predicted effects against the observed effects (Fig. 5). The slopes of the linear regression were investigated whether they were significantly different from the 1:1 line, which infers additive effects of day and night warming (i.e., diurnal warming effects equal the added effects of day and night warming, Zalaveta et al., 2003). Simple and multiple linear regression analyses were used to examine relationships between soil respiration and soil temperature, soil moisture, and GEE, and leaf photosynthesis. All statistical analyses were conducted with SAS software (SAS Institute Inc., Cary, NC, USA).

### 3 Results

#### 3.1 Soil microclimate and substrate supply

Soil temperature at the depth of 10 cm varied among the 3 growing seasons ( $P < 0.0001$ ; Table 1), ranging from 15.2°C (2008) to 18.2°C (2007) with an average of 17.0°C in the control plots. Both day ( $P < 0.0001$ ) and night ( $P < 0.0001$ ) warming significantly increased daily mean soil temperature across the 3 growing seasons (Table 1, Fig. 1a). As expected, night warming caused greater increase in nighttime mean soil temperature (0.38°C) than day warming did (0.17°C). However, no difference was found between the changes in daytime mean temperature induced by day (0.47°C) and night warming (0.46°C). As a result, daily mean soil temperature increased greater under night (0.42°C) than day (0.32°C) warming. There was no interaction between day and night warming ( $P = 0.462$ ) to affect soil temperature. In addition, no interaction was found between year and day warming ( $P = 0.498$ ), night warming ( $P = 0.290$ ), or their combination ( $P = 0.956$ ; Fig. 1a).

Similar to soil temperature, volumetric soil moisture at 0–10 cm depth fluctuated greatly among the growing seasons ( $P < 0.0001$ ; Table 1). Both day ( $P = 0.006$ ) and night ( $P = 0.027$ ) warming significantly reduced volumetric soil moisture, but no inter-

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actions ( $P=0.854$ ) were observed (Table 1, Fig. 1a). Night warming caused a slight lower reduction (0.31 v/v%, absolute difference) in soil moisture than day warming did (0.39 v/v %). No interactions between year and day warming ( $P=0.759$ ), night warming ( $P=0.927$ ), and their combination ( $P=0.813$ ) were detected to influence soil moisture (Table 1).

In contrast to their similar impacts on soil temperature and moisture, day and night warming showed opposite influences on GEP. Day warming significantly reduced GEP by 4.68% ( $P=0.025$ ) whereas night warming marginally increased GEP by 4.24% ( $P=0.051$ ) over the 3 growing seasons (Fig. 1b)(Wan et al., 2009). No interaction between day and night warming ( $P=0.137$ ) was detected to impact GEP over the 3 growing seasons. In addition, there was no interaction between year and day warming ( $P=0.837$ ), night warming ( $P=0.933$ ), or their combination ( $P=0.759$ ) to affect GEP (Table 1).

### 3.2 Soil respiration

Seasonal mean soil respiration ranged from  $0.78 \mu\text{mol m}^{-2} \text{s}^{-1}$  (2007) to  $2.56 \mu\text{mol m}^{-2} \text{s}^{-1}$  (2008) with an average of  $1.69 \mu\text{mol m}^{-2} \text{s}^{-1}$  in the control plots. No main effect of day warming ( $P=0.978$ ) or its interaction with night warming ( $P=0.124$ ) was observed to affect soil respiration (Table 1, Fig. 2). However, night warming significantly stimulated soil respiration by 7.1% over the 3 growing seasons (Table 1, Fig. 2). There was no interaction between year and day warming ( $P=0.807$ ), night warming ( $P=0.216$ ), or their combination ( $P=0.799$ ) to influence soil respiration.

### 3.3 Effects of soil microclimate and substrate supply on soil respiration

When pooling together data of all the measured dates across the 3 growing seasons, we found soil respiration ( $SR$ ) in the control plots increased exponentially with soil temperature ( $r^2=0.16$ ,  $P=0.018$ ) and linearly with soil moisture ( $r^2=0.49$ ,  $P<0.0001$ ) and GEE ( $r^2=0.78$ ,  $P<0.0001$ ). A combination ( $SR=ae^{bT} * M * GEE+c$ ) of soil tempera-

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ture ( $T$ ), soil moisture ( $M$ ), and GEE explained 87.5% of the temporal variation in soil respiration.

Across the 48 collars, soil respiration (mean values over the 3 growing seasons) showed positively linear dependence upon soil moisture ( $r^2=0.10$ ,  $P=0.034$ ; Fig. 3b) and GEE ( $r^2=0.21$ ,  $P=0.001$ ; Fig. 3c). Stepwise multiple regression analyses demonstrated that 21.1% ( $P=0.001$ ) of the spatial variation in soil respiration can be explained by GEE only. Simple regression showed that changes in soil respiration under day warming decreased linearly with the treatment-induced soil temperature differences ( $r^2=0.17$ ,  $P=0.014$ ; Fig. 3d), but increased linearly with changes in GEE ( $r^2=0.17$ ,  $P=0.013$ ; Fig. 3f). However, changes in soil respiration under night warming showed positive linear dependence upon changes in both soil moisture ( $r^2=0.12$ ,  $P=0.036$ ; Fig. 3e) and GEE ( $r^2=0.16$ ,  $P=0.018$ ; Fig. 3f). Stepwise multiple regression analyses showed that the treatment-induced changes in GEE can explain 16.7% and 15.8% of the changes in soil respiration under day and night warming, respectively.

During the period of peak growth in 2007 (from late July to late August), we analyzed the relationship between daily mean soil respiration and daytime mean leaf photosynthesis of *S. krylovii*, which was the predominant grass in this ecosystem. Daily mean soil respiration showed positively linear ( $r^2=0.25$ ,  $P=0.013$ ; Fig. 4a) dependence upon daytime mean leaf photosynthesis of *S. krylovii* across the 24 experimental plots. Changes in daily mean soil respiration under both day ( $r^2=0.44$ ,  $P=0.018$ ; Fig. 4b) and night ( $r^2=0.35$ ,  $P=0.045$ ; Fig. 4b) warming increased linearly with treatment-induced changes in daytime mean leaf photosynthesis of *S. krylovii*.

### 3.4 Relative effects of day and night warming on soil respiration and its controlling factors

We plotted the summed changes in soil respiration (Fig. 5a), soil temperature (Fig. 5b), soil moisture (Fig. 5c), and GEE (Fig. 5d) under day and night warming (predicted values in the  $Y$ -axis) against the observed changes under diurnal warming (observed values in the  $X$ -axis). Slopes of day and night warming for soil respiration ( $P=0.049$ )

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and GEE ( $P < 0.0001$ ) were greater than the 1:1 line, whereas slopes for soil temperature ( $P = 0.711$ ) and soil moisture ( $P = 0.080$ ) did not differ from the 1:1 line.

## 4 Discussion

### 4.1 Different effects of day and night warming on soil respiration

5 Our study provides direct experimental evidence that day and night warming can differently affect soil respiration. Warming-induced changes in soil respiration likely result from changes in multiple processes (Shaver et al., 2000; Wan et al., 2007). For example, increased soil temperature can directly stimulate root and microbial activities and respiration (Wan et al., 2007), and indirectly influence soil respiration via changes in ecosystem C uptake (Högberg et al., 2001; Wan and Luo, 2003; Larsen et al., 2007) and decreases in soil water availability (Harte et al., 1995; Wan et al., 2002; Liu et al., 2009). In this system, it has been demonstrated that warming-induced higher daytime temperature and vapour pressure deficit (VPD) could reduce leaf stomatal conductance, leading to lower canopy photosynthesis (Niu et al., 2008). In this study, day  
10 warming not only decreased soil water availability, but also showed a negative impact on ecosystem WUE ( $P = 0.002$ , three-way ANOVA; Fig. 6). This could aggravate the negative impact of day warming on ecosystem C assimilation, which supplies C substrate for soil respiration. Thus, the neutral response of soil respiration to day warming could result from the counteraction between direct positive impacts of temperature and negative influence of the treatment-induced decreases in soil moisture and GEP. Although night warming also reduced soil water availability in this study, night warming significantly enhanced ecosystem WUE ( $P = 0.047$ , three-way ANOVA; Fig. 6), suggesting that changes in plant production processes under night warming could counteract the negative impacts of treatment-induced water depletion. The contrasting responses  
15 of ecosystem C assimilation to day and night warming and their impacts on soil respiration responses (Fig. 3f) suggest that C substrate supply drives the differential re-

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sponses of soil respiration to day and night warming.

The differential effects of day and night warming on ecosystem C assimilation could be explained by the hypothesis of sink regulation on plant photosynthesis, which suggests that activities of source photosynthetic production and sink growth appear to be closely coordinated (Paul and Foyer, 2001; Paul et al., 2001; McCormick et al., 2006). Wan et al. (2009) has found that day warming reduced GEP, resulting from day warming-induced decreases in sugar (21.4%) and starch (35.4%) depletion. In contrast, night warming increased leaf respiration of 3 dominant plant species, enhanced consumption of carbohydrates in the leaves, and subsequently simulated photosynthesis and GEP in the following day.

In consistent with our finding, it has been reported by both historical data analyses and modeling simulations that day and night warming could have differential impacts on terrestrial ecosystem processes (Ryan, 1991; Coughenour and Chen, 1997; Alward et al., 1999; Griffin et al., 2002; Turnbull et al., 2002, 2004). For example, long-term observations in a shortgrass steppe in Northern America showed significant responses of aboveground net primary production of different plant species to increasing daily minimum, but not mean or maximum temperatures (Alward et al., 1999). Similar results were reported that increasing daily minimum, but not maximum, temperatures significantly influence rice yield in Philippines (Peng et al., 2004). In Southeastern US, reductions in corn yield were associated with increases in daytime temperatures whereas increased yield was related to night warming over 40 years (Rosenzweig and Tubiello, 1996). All these results support the differential effects of day and night warming on plant photosynthesis and GEP in this experiment, suggesting day and night warming can differently affect substrate supply to soil respiration.

In the recent decades, a growing body of evidence from case studies of tree girdling (Högberg et al., 2001) and shading or clipping (Craine et al., 1999; Wan and Luo, 2003; Bahn et al., 2006), and large-scale synthesized research (Bahn et al., 2008) has demonstrated regulation of ecosystem C assimilation on soil respiration. In this study, at both leaf and ecosystem levels, not only soil respiration was positively correlated

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with photosynthesis, but also treatment-induced changes in soil respiration increased linearly with the photosynthesis increases. The observations in previous studies and this study indicate that simulation and prediction of soil respiration in response to climate change should take into consideration of changes in biotic factors (plant growth and substrate supply) in addition to those of abiotic factors (temperature and moisture; Wan et al., 2007).

## 4.2 Non-additive effect of day and night warming on soil respiration

Greater total effect of day and night warming on soil respiration than diurnal warming ( $P=0.001$ ; Fig. 5a) demonstrates that day and night warming could non-additively affect soil respiration in this system. Most experimental studies were conducted with diurnal or constant warming and some models used daily, monthly, and annual mean temperatures as the climate drivers in simulating and predicting the responses and feedbacks of terrestrial ecosystem C cycling to global warming. Our results suggest that future experimental and model studies could incorporate the differential and non-additively effects of day and night warming into the projection of the climate-carbon feedback.

It has long been identified that soil temperature, soil moisture, and C substrate supply were the main controlling factors over soil respiration in terrestrial ecosystems (Raich and Tufekcioglu, 2000; Rustad et al., 2001; Högberg et al., 2001; Wan et al., 2007) and the fundamental parameters in predicting soil respiration responses to global change (Cox et al., 2000; Reichstein et al., 2005; Trumbore, 2006). In this study, day and night warming additively affected soil temperature ( $P=0.711$ ) and soil moisture ( $P=0.080$ ), but non-additively influenced GEE ( $P<0.0001$ ). The antagonistic effects (greater slope than one; Fig. 5d) of day and night warming on GEE in this study suggest that C substrate supply could be more important than soil temperature and moisture in regulating the non-additive effects of day and night warming on soil respiration in this ecosystem. In this study, averaged across the 3 growing seasons and the 3 dominant species (*A. cristatum*, *S. krylovii*, and *A. frigida*), diurnal warming showed no effect on nighttime sugar ( $P=0.351$ ) and starch ( $P=0.896$ ) depletion. Therefore, the over-compensation

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of plant photosynthesis observed under night warming will not occur in the following day under diurnal warming. In fact, diurnal warming did not change GEE ( $P=0.874$ ; Repeat-measured ANOVA) across the 3 growing seasons in this study. Thus, the antagonistic effect of day and night warming on GEE could be due to the disappearance of plant photosynthetic over-compensation when ecosystem exposed to diurnal warming.

### 4.3 How much do the changes in soil respiration affect ecosystem carbon balance?

Because temperature influences all terrestrial C processes, climate warming likely enhances ecosystem C fluxes which potentially feeds back to climate change (Luo, 2007). It has been expected that if C stored in soil is transferred to the atmosphere by elevated temperature, a positive feedback to climate change would occur. Conversely, if increases in plant-derived C inputs to soils exceed increases in soil respiration, the feedback would be negative (Davidson and Janssens, 2006). In this study, soil respiration was significantly increased by night warming (Table 1, Fig. 2). However, it does not necessarily mean a positive feedback to climate change in this ecosystem. In fact, we have found that photosynthetic over-compensation under night warming enhances C sequestration in this system (Wan et al., 2009). In addition, over the past 53 years (1953–2005), local climate in our study area (Duolun County, Inner Mongolia, China) experienced asymmetrical diurnal warming (0.57, 0.45, and 0.30°C increases in daily minimum, mean, and maximum temperature per decade; Wan et al., 2009, Appendix E). Therefore, though night warming enhances soil respiration, a negative feedback to climate change will occur because of the greater stimulation of ecosystem C assimilation (Table 1, Fig. 1b) under night warming in the temperate steppe in northern China (Wan et al., 2009). The findings in this and a previous study (Wan et al., 2009) indicate that effects of climate warming on ecosystem C cycling can not be fully evaluated without taking into consideration of all ecosystem C processes.

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## 5 Conclusions

This experiment is one of the first field experiments that have tested the differential effects of day and night warming on soil respiration. The neutral effect of day warming on soil respiration could have been contributable to the offset of the direct positive temperature effects by the indirect negative effects of water depletion and reduction in C assimilation, whereas the increases in soil respiration under night warming could be explained by its strong positive effect on C substrate supply. The non-additive effects of day and night warming on soil respiration in this ecosystem could result from their non-additive effects on ecosystem C assimilation and substrate supply. Often warming is applied as a constant increase above ambient temperature both in field and modeling studies, in spite of the observed greater nighttime warming trend (Karl et al., 1991; Easterling et al., 1997; IPCC 2001; Zhou et al., 2007). Our observations indicate that influences of day and night warming on ecosystem C flux are not equivalent in our system. This finding highlights the need for future research to incorporate differential impacts of day and night warming on terrestrial ecosystem C processes.

*Acknowledgements.* This study was financially supported by the National Natural Science Foundation of China (90511006, 30590382, and 30821062), Chinese Academy of Sciences (Hundred Talents Program), and State Key Laboratory of Vegetation and Environmental Changes. Authors thank S. Niu, Z. Li, W. Cheng, Y. Zhang, H. Yang, D. Lin, T. Li, Y. Li, and C. Bai for their helps in the field measurement.

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**Table 1.** Results (P-values) of three-way ANOVA on the effects of day (D) and night (N) warming and their interactions on soil respiration (soil R), soil temperature (soil T), soil moisture (soil M), and gross ecosystem productivity (GEP).

Source of variance	Soil R	Soil T	Soil M	GEP
Year	<.0001	<.0001	<.0001	<.0001
D	0.978	<.0001	0.006	0.025
N	0.001	<.0001	0.027	0.051
D*N	0.124	0.462	0.854	0.137
D*Year	0.807	0.498	0.759	0.837
N*Year	0.216	0.290	0.927	0.933
D*N*Year	0.799	0.956	0.813	0.759

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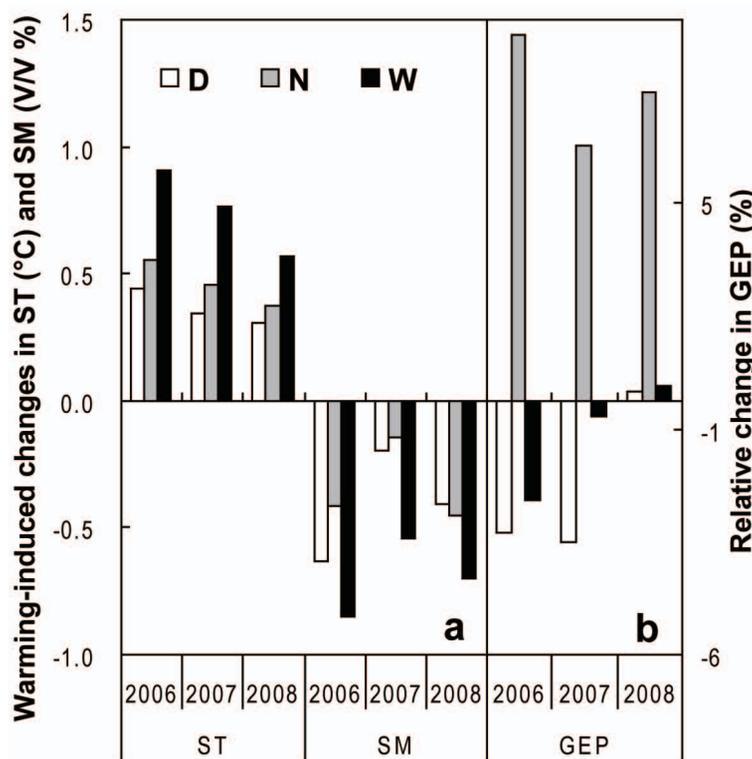


Fig. 1. Warming-induced (a) absolute changes in soil temperature (ST), soil moisture (SM), and (b) relative changes in gross ecosystem productivity (GEP). D, day warming; N, night warming; W, diurnal warming.

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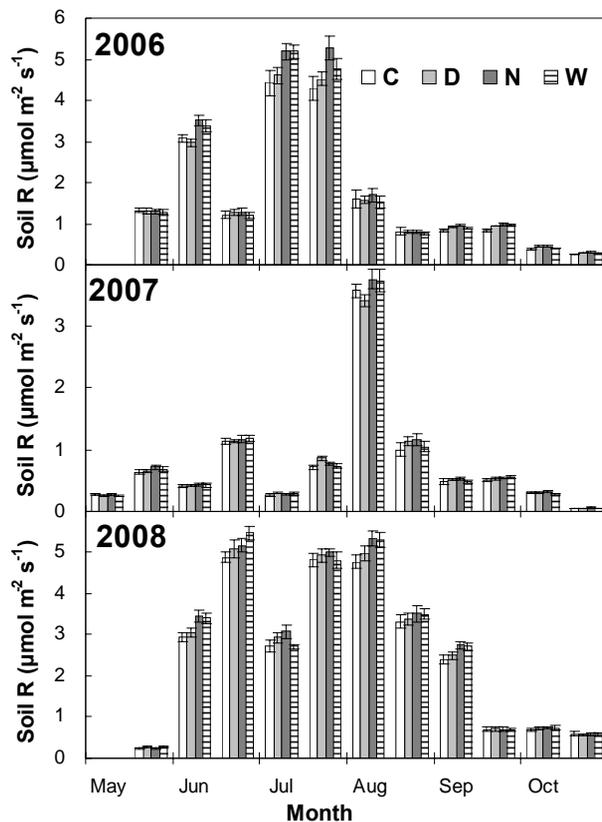
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**Fig. 2.** Diurnal mean soil respiration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) under control (C), day warming (D), night warming (N), and diurnal warming (W).

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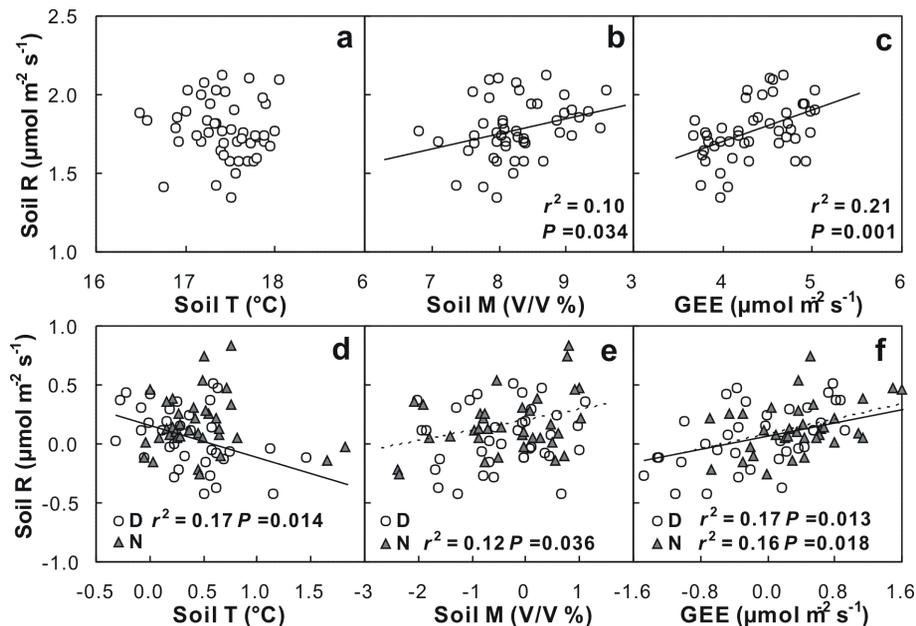
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**Fig. 3.** Spatial dependence of mean soil respiration (soil R) over the 3 growing seasons on soil temperature (soil T; **a**), soil moisture (soil M; **b**), and gross ecosystem exchange (GEE; **c**) across the 48 collars, and correlations between effects on soil respiration of day (**d**, **e**, and **f**; open circles and solid lines) and night (**d**, **e**, and **f**; gray triangles and dashed lines) warming and the treatment-induced changes in soil moisture, temperature, and GEE over the 3 growing seasons ( $n=36$ ).

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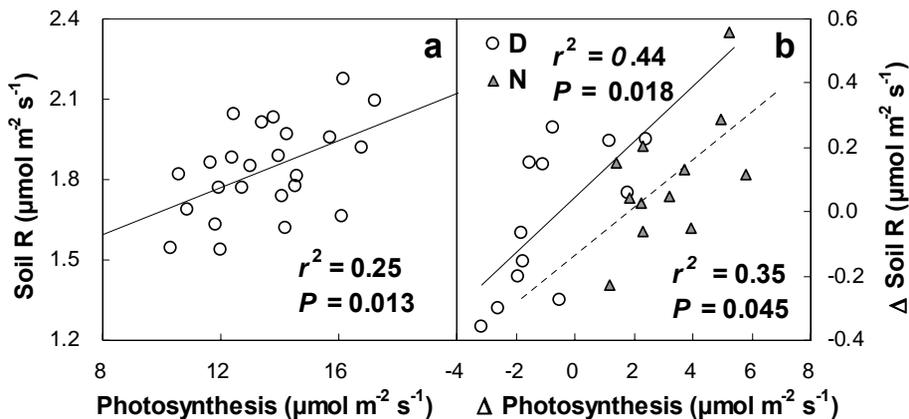
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**Fig. 4.** Spatial dependence of mean soil respiration (soil R) on daytime mean leaf photosynthesis of *S. Krylovii* (a); and correlations between effects on mean soil respiration of day (b, open circles and solid lines) and night (b, gray triangles and dashed lines) warming and the treatment-induced changes in daytime mean leaf photosynthesis of *S. Krylovii* during the peak growth period in 2007.

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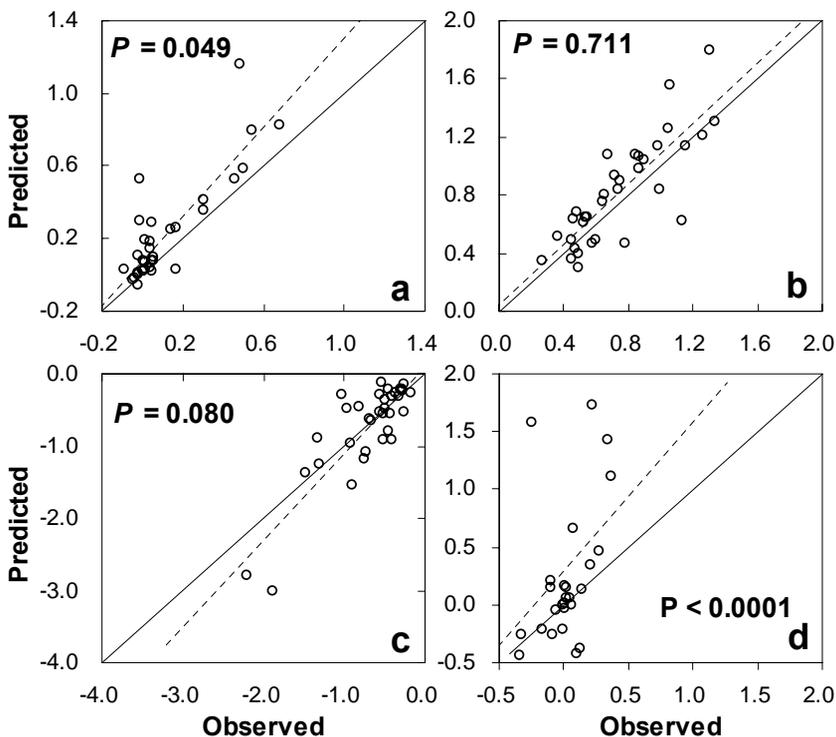
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**Fig. 5.** Predicted and observed effects of day and night warming on **(a)** daily mean soil respiration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), **(b)** daily mean soil temperature ( $^{\circ}\text{C}$ ), **(c)** soil moisture (V/V%), and **(d)** mean gross ecosystem productivity (GEE,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Predicted values are the summed changes under day and night warming, and the observed values are the changes under diurnal warming. If  $P > 0.05$ , the slope for the linear function (dashed lines) did not differ from the 1:1 line (solid lines), suggesting additive effects of day and night warming. If  $P < 0.05$ , the slope for the linear function was significantly different from the 1:1 line, suggesting non-additive effects of day and night warming. Each data point represents daily mean of each measuring dates.

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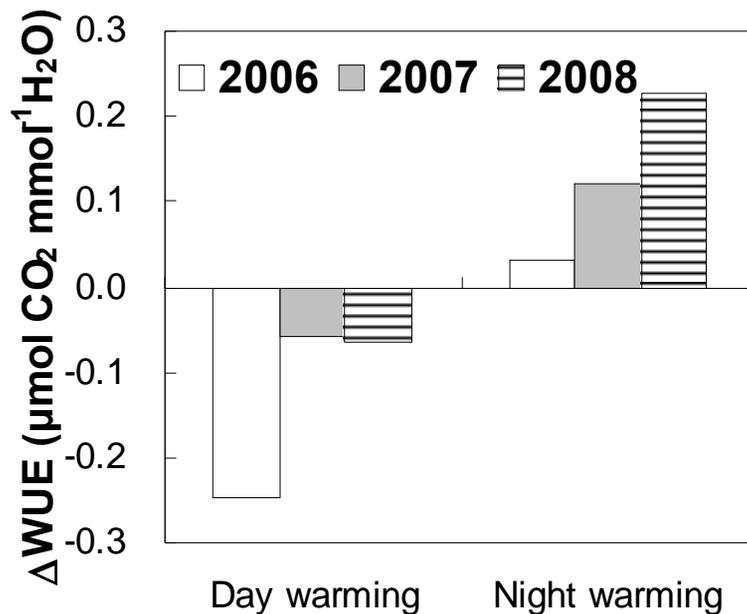
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**Fig. 6.** Changes in ecosystem water use efficiency (WUE) induced by day and night warming over the three experimental years (2006–2008).

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