



Day and night warming have different effect on root lifespan

W. M. Bai, J. Y. Xia, S. Q. Wan, W. H. Zhang, and L. H. Li

State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, the Chinese Academy of Sciences, Beijing 100093, China

Correspondence to: L. H. Li (llinghao@ibcas.ac.cn)

Received: 28 September 2011 – Published in Biogeosciences Discuss.: 26 October 2011

Revised: 29 December 2011 – Accepted: 9 January 2012 – Published: 18 January 2012

Abstract. Roots are key components of C cycling in terrestrial ecosystems and play an important role in the regulation of response of terrestrial ecosystems to global climate warming, which is predicted to occur with greater warming magnitudes at night than during daytime across different regions on the Earth. However, there has been no detailed study to investigate the effect of asymmetrical warming on root dynamics at the level of terrestrial ecosystems. To understand the effects of day and night warming on root lifespan in the semiarid temperate steppe in northern China, a field study with a full factorial design including control, day warming, night warming and continuous warming was conducted using modified rhizotron technique during three growing seasons in 2007–2009. Our results show that day, night and continuous warming had different effects on longevity of roots born in spring, summer and autumn, and that day warming significantly prolonged overall lifespan for the roots born in the three growing seasons, while night warming had no effect on overall lifespan. Day and night warming had different effects on root non-structural carbohydrate content, suggesting that allocation of photoassimilate may account for the differential responses of root lifespan to day and night warming. These results differ from other processes associated with ecosystems C cycle such as total ecosystem productivity, net ecosystem productivity and soil respiration. Our findings highlight that it is essential to incorporate the differential effects of day and night warming on root dynamics into simulating and predicting the responses and feedbacks of terrestrial ecosystems C cycling to global warming.

1 Introduction

Model projection and field experimental observations have demonstrated that global warming can have significant impact on the structure and function of terrestrial ecosystems in general, and carbon (C) cycle of terrestrial ecosystems in particular (Ciais et al., 2005; Luo, 2007; Piao et al., 2008; Wan et al., 2009; Bai et al., 2010). Climate warming is expected to result in unequal changes in daily minimum and maximum temperatures, with the greater trends of night warming than day warming (Eastering et al., 1997; Alward et al., 1999; Zhou et al., 2007). It has been reported that increased daily minimum and maximum temperatures have different effects on biomass and yield (Dhakhwa et al., 1998; Alward et al., 1999; Peng et al., 2004; Lobell, 2007; Lobell and Ortiz-Monasterio, 2007) as well as C cycling (Wan et al., 2009; Xia et al., 2009) in terrestrial ecosystems. However, it remains unclear whether asymmetrical warming may have different effects on root growth, mortality and turnover, which plays critical roles in regulating nutrient and C cycling between above- and belowground.

Photosynthesis takes place predominantly during day time, while respiration becomes dominant at night time. Day warming would stimulate photosynthesis, while night warming would stimulate respiration. Therefore, day and night warming may have different effects on C absorption and release. Recent studies revealed that day and night warming have different effects on total ecosystem productivity, net ecosystem productivity and soil respiration in semi-arid temperate steppe of northern China (Xia et al., 2009; Wan et al., 2009). The differential response of semi-arid steppe to day and night warming may result from stimulation of plant respiration by night warming, thus altering C allocation due to compensatory response of leaf photosynthesis (Wan et

al., 2009). Numerous studies have reported that terrestrial ecosystems are highly sensitive to night warming (Alward et al., 1999; Peng et al., 2004; Volder et al., 2004; Lobell, 2007; Beier et al., 2008). Root growth is closely dependent on soil temperature (Pregitzer et al., 2000). Our previous studies showed that root dynamics were also sensitive to continuous warming in the temperate steppe (Bai et al., 2010). Given that root growth, mortality and turnover are closely associated with plant photosynthesis, respiration and belowground C allocation, and that asymmetrically continuous warming has differential impacts on plant photosynthesis and respiration, we hypothesize that root dynamics exhibit differential response to day and night warming.

Roots are an important source of soil organic C and plays a key role in the regulation of ecosystem C cycle (Loya et al., 2004; Sullivan et al., 2007). In addition, roots, as key component of ecosystems C cycling, are also closely related to processes associated with ecosystem C cycling (Farrar and Jones, 2000; Norby and Jackson, 2000). Our recent studies demonstrated that increases in root production and reduced mortality in response to increased temperature and precipitation were significantly correlated with total ecosystem productivity, net ecosystem productivity and soil respiration in the typical grassland in Inner Mongolia (Bai et al., 2010). These findings indicate that root dynamics can have important impacts on ecosystems C cycle under climate change. The responses of root dynamics to warming and precipitation differ from other ecosystem processes such as total ecosystem productivity, net ecosystem productivity and soil respiration. For instance, an increase in temperature and precipitation has an additive effect on gross ecosystem productivity, net ecosystem productivity, ecosystem respiration and soil respiration in Inner Mongolia typical grassland (Niu et al., 2008; Liu et al., 2009). In contrast, there were significant interactive effects of increased temperature and precipitation on cumulative root production and mortality (Bai et al., 2010). These findings indicate that different C processes in ecosystems may vary in response to climate change. Therefore, understanding whether response of root dynamics to asymmetric warming differs from other ecosystem C cycling processes would shed important light on C cycle-climate change feedback.

Root lifespan is an important parameter that determines acquisition of water and nutrients, and affects soil organic C pool. However, to the best of our knowledge, there has been no report to evaluate the response of root lifespan to day and night warming. In the present study, we investigated the effects of day and night warming on root lifespan in semiarid temperate steppe in northern China. More specifically, we addressed the following two questions: (1) Does root lifespan have a different response to day and night warming? (2) Is the response of root lifespan to day and night warming comparable to other C cycle process in ecosystems such as gross ecosystem productivity, net ecosystem productivity, ecosystem respiration and soil respiration?

2 Materials and methods

2.1 Study site

The study was conducted in a semiarid temperate steppe in Duolun County (42°02' N, 116 °17' E, 1324 m above sea level) in Inner Mongolia, China. Long-term (1953–2007) mean annual rainfall is approximately 383 mm with 90 % of the precipitation falling from May to October. Mean annual temperature is 2.18 °C, with the minimum and maximum temperatures ranging from –17.58 °C in January to 18.98 °C in July. 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 soil bulk density is 1.31 g cm⁻³ and pH is 7.7. Soil organic C and total N contents are 16.1 g kg⁻¹ and 1.48 g kg⁻¹, respectively. The plant community at our experimental site is dominated by *Stipa krylovii* and *Artemisia frigida*.

2.2 Experimental design

We used a complete random block design with 4 treatments, including control (C), day warming (06:00 a.m.–06:00 p.m.; D), night warming (06:00 p.m.–06:00 a.m.; N), continuous (24 h; W) warming and replicated each treatment 6 times (Wan et al., 2009). Each plot was 3 × 4 m in size with a 3-m distance between any two adjacent plots. The warming in the warmed plots was achieved by continuously heating with MSR-2420 infrared radiators (Kalglo Electronics Inc, Bethlehem, PA, USA) suspended 2.25 m above the ground. To simulate the shading effects of the infrared radiator, one “dummy” heater with the same shape and size as the infrared heater was suspended 2.25 m above ground in each control plot. All the heaters under the warming treatments were set at a radiation output of about 1600 watts. The warming treatment commenced on 23 April 2006. The detailed description of warming treatment can be found in previous publications (Wan et al., 2009; Xia et al., 2009).

2.3 Measurement of root dynamics

Root production and mortality were measured by protocols described previously (Bai et al., 2008, 2010). Briefly, on 30 August 2006, one glass root-window was installed in each plot. The glass window (0.4-cm thick) of 35 cm in height and 20 cm in length was installed vertically into the soil. On each glass window, a 35 × 20 cm panel (with 5-cm distance to the bottom and 5 cm to the right and left sides) was separated into three 10 × 10 cm squares by carving the glass. In order to minimize the impacts of light on root growth, the upper edge of the glass window was installed under the soil surface and a piece of dark iron (20 cm in length, 1.5 cm in breadth and 0.5 mm in thickness) was covered on the top of the glass. A hole was dug in each plot with a vertical profile for the glass window to be installed. The glass window was put tightly to the trench and fixed with one iron stick at each

side. After the root-windows were inserted, soil was back-filled as tightly as originally. The soil was closely attached to the glass throughout the whole study period.

A digital camera was used to monitor root growth. Observations began on 30 June 2007, which was about 10 months after the installation of glass windows, and lasted until 19 October 2009 with sampling intervals of 15 d. On each sampling date, the soil on one side of the glass window was removed and the screen was cleaned with tissue paper. One digital picture was taken for each of the three 10×10 cm numbered squares. Removed soil was carefully backfilled again after pictures were taken as described previously (Bai et al., 2008, 2010).

Appearance and disappearance of roots were analyzed by the software of Mapinfo Professional (5.0; Pitney Bowes Mapinfo Corporation, New York, US) as described by Bai et al. (2008, 2010). For the initially collected images, each root was assigned with an identification number and distinguished it as living or dead based on its colors as described in our previous paper (Bai et al., 2008). For the following image sets, the tracings from the previous date were compared with the new images, thus allowing previously existing roots to be identified. Newly emerged roots were also identified and numbered. Roots that had disappeared at subsequent images were assumed to be dead and decomposed. Complete records were kept for all roots, even for those that were classified as dead.

2.4 Measurements of soil temperature and soil moisture

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 average of the six measurements within 1 h was stored as the hourly means. Soil moisture (0–10 cm) was measured weekly using a Diviner-2000 Portable Soil Moisture Probe (Sentek, Balmain, Australia).

2.5 Measurements of soluble sugars, starch and ecosystem parameters

Root samples that were obtained from the root in-growth measurement in 0–30 cm soils by the end of growing seasons in late October were used to determine soluble sugars and starch following protocols described by Wan et al. (2009). Soluble sugar and starch concentrations in roots were determined as described by Ranwala and Miller (2008). Root non-structural carbohydrate was taken as the sum of root soluble sugars and starch (Pregitzer et al., 2000).

Aboveground net primary productivity (ANPP) was determined during the peak at the end of August in each year. Belowground primary productivity (BNPP) in 0–30 cm soils was measured by the end of growing seasons in late October in each year. Gross ecosystem productivity (GEP), net

ecosystem productivity (NEP), ecosystem respiration (ER), soil respiration (SR), and soil inorganic N were measured as described previously (Wan et al., 2009; Xia et al., 2009).

2.6 Data analysis and statistics

Root lifespan was calculated as the date on which roots were observed as black or disappeared minus the date on which roots were initially observed on the window. The date of root appearance or disappearance was estimated as the date midway between the sampling periods because they might have occurred on any day during the approx. 15-d sampling interval between two consecutive observations (Hooker et al., 2000; López et al., 2001; Anderson et al., 2003).

We selected total of 10 887 new roots germinated in spring (1–15 and 15–30 May), summer (1–16 and 16–31 July) and autumn (31 August–15 September, 15 September–1 October) of 2008 and 3207 new roots germinated in spring (18 April–2 May, 2–17 May), summer (19 June–3 July, 3–19 July) and autumn (19 August–4 September, 4 September–19 October) of 2009 to analyze the effects of different treatments on their survival rates and longevity. To analyze the effects of day warming and night warming on their survival rates and longevity, we selected a total of 20 007 new roots germinated in control, day warming, night warming, and continuous warming plots during the growing seasons of 2007–2009. We calculated their mean longevity through a survival curve using the Kaplan-Meier method with SPSS (12.0) software, and compared the root survival rates by Log-rank test.

A stratified Cox proportional hazards regression was used to estimate the effects of treatment on root lifespan as described by Gill et al. (2002). In the Cox model, the hazard for an individual root at time t is computed based upon the combination of a non-parametric baseline (h_0) function and an exponential function of k covariates:

$$h_i(t) = h_0(t) \exp(\beta_1 \chi_{i1} + \dots + \beta_k \chi_{ik})$$

The Cox model was used to determine β coefficient for each model covariate and test the null hypothesis of $\beta = 0$ with a chi-square statistic. A negative β coefficient indicates a decreased risk of mortality with an increase in the covariate values. A risk ratio ($\exp\beta$) was used to calculate the percent change in the risk of mortality with a one unit change in the covariate was calculated as well (Wells and Eissenstat, 2001; Gill et al., 2002).

A full factorial design with day and night warming was used in this study. The three-way ANOVAs were used to examine effects of year, day warming, night warming, and their possible interactions on soil temperature and soil moisture. Two-way ANOVAs were used to examine effects of day and night warming on root longevity, root nonstructural carbohydrate content (RNC), ANPP, and BNPP. Regression with correction for autocorrelation and stepwise multiple linear regression analyses were used to examine the relationships between root longevity and soil temperature, soil moisture,

Table 1. Results (P -values) of three-way ANOVAs on the effects of day (D) and night (N) warming and their interactions on soil temperature and soil moisture over the four experimental years (2006–2009).

Source of variance	Soil temperature	Soil moisture
Year	< 0.0001	< 0.0001
D	< 0.0001	0.0324
N	< 0.0001	0.0247
D×N	0.4672	0.6245
D×Year	0.1625	0.9956
N×Year	0.9548	0.8848
D×N×Year	0.7482	0.9639

ANPP, BNPP, BNPP/ANPP, GEP, ER, NEP, SR, RNC, and soil inorganic N. All statistical analyses were conducted with SAS software (SAS Institute Inc., Cary, NC, USA).

3 Results

3.1 Soil temperature and moisture

Soil temperature at 10-cm depth varied among the four growing seasons (2006–2009). The experimental design was a 2-factorial one with day and night warming as main factors. Both day ($P < 0.0001$) and night ($P < 0.0001$) warming significantly elevated daily mean soil temperature across the four growing seasons (Table 1; Fig. 1a). Day and night warming increased daily mean soil temperature by 0.38 and 0.50 °C, respectively. No interactive effect between day and night warming ($P = 0.467$) on soil temperature was observed. In addition, no interaction was found between year and day warming ($P = 0.163$), night warming ($P = 0.955$), or their combination ($P = 0.748$; Table 1; Fig. 1a).

Similar to soil temperature, there were great fluctuations in volumetric soil moisture at 0–10 cm depth among the growing seasons (Table 1; Fig. 1b). Both day ($P = 0.003$) and night ($P = 0.025$) warming significantly reduced volumetric soil moisture, while no interactions ($P = 0.625$) between them were observed (Table 1; Fig. 1b). In contrast to soil temperature, day and night warming significantly reduced daily mean soil moisture by 3.85 % and 4.04 % V/V, respectively (Fig. 1b). No interactive effects between year and day warming ($P = 0.996$), night warming ($P = 0.885$), or their combination ($P = 0.964$) on soil moisture were detected (Table 1; Fig. 1b).

3.2 Effect of day warming and night warming on root longevity

Roots initiated in the three growing seasons (spring, summer and autumn) of 2008 and 2009 in the control and warming plots exhibited different survival rates and longevity,

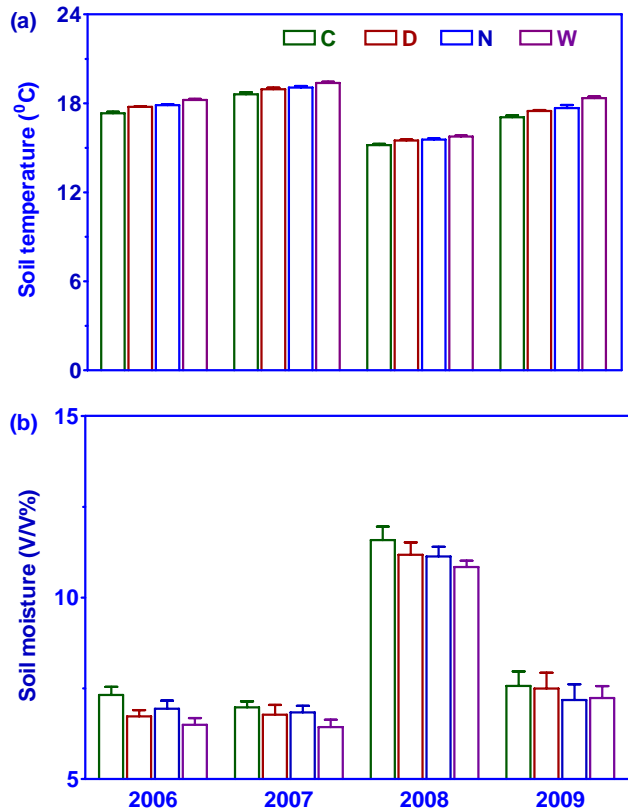


Fig. 1. Effects of control (C) and day warming (D), night warming (N) and continuous warming (W) on temperature (a) and moisture (b) in the soil layer of 0–10 cm over the experimental period from 2006 to 2009. Data are mean \pm SE of six plots.

and responded to day, night and continuous warming differently (Fig. 2; Table 2). Log-rank test revealed that day warming significantly increased survival rate (Fig. 2a, d) and longevity for the roots initiated in spring ($P < 0.05$; Table 2); while both night and continuous warming had no effect on survival rate (Fig. 2a, d) and longevity for the roots initiated in spring of 2008 and 2009 ($P > 0.05$; Table 2). In contrast, survival rate (Fig. 2b) and longevity ($P < 0.001$; Table 2) of the roots initiated in summer of 2008 were significantly enhanced by continuous warming, while survival rate (Fig. 2e) and longevity ($P = 0.001$; Table 2) of the roots initiated in summer of 2009 were significantly enhanced by day warming. Moreover night warming had no impacts on survival rate and longevity of the roots initiated in summer of 2008 and 2009 ($P > 0.05$; Fig. 2b, e; Table 2). Day warming significantly reduced survival rate (Fig. 2c) and longevity of the roots born in autumn of 2008 ($P = 0.006$; Table 2), while night warming increased survival rate (Fig. 2c) and longevity of the roots initiated in autumn of 2008 ($P = 0.0101$; Table 2). Both survival rate and longevity for the roots initiated in autumn of 2008 were not affected by continuous warming ($P > 0.05$; Table 2). Unlike the roots born in autumn of 2008,

Table 2. Longevity of roots born in spring, summer and autumn in different treatments during the growing seasons of 2008 and 2009 (mean \pm standard error). The Kaplan–Meier method was used to estimate mean lifespan. Longevity differences between different treatments were compared using Log-rank test. In each vertical row, the values with same superscript letters are not significantly different from each other at $P = 0.05$.

Treatment	2008			2009		
	Spring	Summer	Autumn	Spring	Summer	Autumn
Control	51 \pm 3a	95 \pm 4a	152 \pm 5a	34 \pm 1a	24 \pm 1a	22 \pm 1a
Day warming	62 \pm 2b	103 \pm 4a	133 \pm 5b	39 \pm b	35 \pm 2b	25 \pm 1b
Night warming	50 \pm 2a	80 \pm 4a	175 \pm 4c	35 \pm 1a	26 \pm 2a	21 \pm 1a
Continuous warming	52 \pm 2a	135 \pm 6b	159 \pm 4a	33 \pm 1a	21 \pm 2a	21 \pm 1a

Table 3. Analyses of different warming treatments (day warming, night warming and continuous warming) on the root hazard ratio by the Cox proportional hazards regression. Hazard ratios for categorical covariates are the risk of death relative to a reference level, given for each covariate in the left-hand column. A negative parameter indicates that increases in the covariate would result in decreases in the risk of mortality, and the opposite trend reflects positive parameter values. The values for 95 % confidence intervals are upper and lower limits and are not symmetrical about the hazard ratio. $P < 0.05$ is considered to be significant.

Covariate	Parameter estimate	SE	Hazard Ratio	95 % CI		P -value
				Lower	Upper	
Control (Ref.)						
Day warming	−0.053	0.020	0.965	0.928	1.004	0.080
Night warming	−0.005	0.022	0.995	0.954	1.038	0.811
Continuous warming	−0.188	0.022	0.828	0.793	0.865	<0.001

day warming prolonged root longevity in 2009 ($P = 0.001$), while night and continuous warming had no effect on root longevity in 2009 ($P > 0.05$; Fig. 2f; Table 2). Note that values for longevity of roots born in the three seasons in 2009 were significantly shorter than those in 2008 ($P < 0.001$; Fig. 2).

To obtain the overall response of root survival rate and longevity to day, night and continuous warming, we pooled the survival data for roots initiated in the three growing seasons of 2007–2009 and calculated the overall root longevity. In comparison with the overall root longevity in the control plots (118 d), the overall root longevity in the plots of day and continuous warming was significantly different. For instance, the mean overall root longevity in day and continuous warming plots was 7 and 34 d longer than in control plots, respectively (Fig. 3). The results of the Cox proportional hazards regression (Table 3), the mortal risk for roots in day warming and continuous warming plots were marginally ($P = 0.08$) and significantly reduced ($P < 0.001$), respectively. Furthermore, day warming had significant impact on the overall root longevity ($P = 0.032$), but no effect ($P = 0.187$) of night warming on the overall root longevity was observed as analyzed by two-way ANOVAs. There was no interactive effect ($P = 0.139$) between day and night warming on the overall root longevity (Fig. 3). Further analyses revealed that the overall root longevity in the day warmed subplots was 19.8 % higher ($P < 0.05$) than in the

un-warmed, control subplots, whereas no significant change in the overall root longevity ($P > 0.05$) was observed in the night warmed subplots. These results indicate that day warming has a significant effect on the overall root longevity.

3.3 Effect of day warming and night warming on root nonstructural carbohydrate content (RNC)

Day warming had significant effect on root nonstructural carbohydrate content ($P < 0.001$), but no effect ($P = 0.4889$) of night warming on root nonstructural carbohydrate content was observed as analyzed by two-way ANOVAs. Day warming increased root nonstructural carbohydrate content by 42.0 %. There were no interactive effects ($P = 0.2195$) of day and night warming on root nonstructural carbohydrate content (Fig. 4).

3.4 Warming-induced changes in root longevity varied with root nonstructural carbohydrate content (RNC) and BNPP/ANPP

Our results demonstrated that the overall root longevity was affected by day warming, but not night warming (Fig. 3). We therefore examined the correlation between root longevity and nonstructural carbohydrate in roots treated with day warming. Across the 24 plots, the day warming-induced changes in root longevity showed positive linear dependence on the day warming-induced changes in RNC ($r^2 = 0.69$;

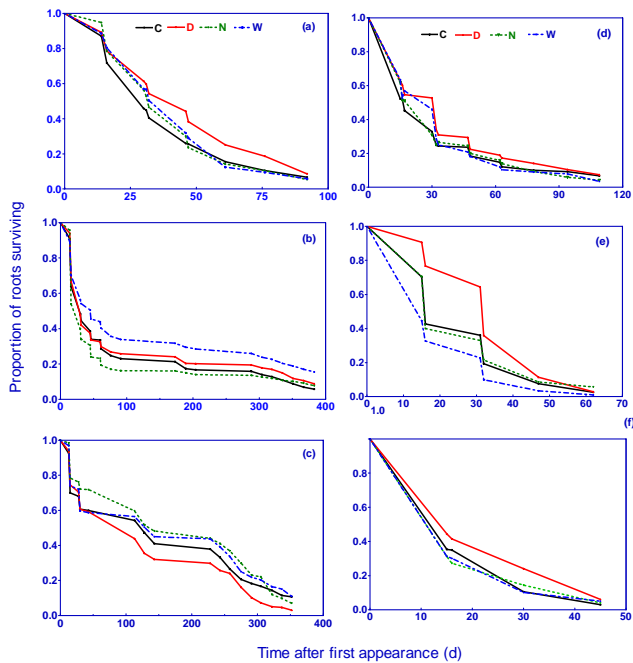


Fig. 2. Survival curves of roots born in spring (a, d), summer (b, e) and autumn (c, f) in 2008 and 2009 under the control (C) and day warming (D), night warming (N) and continuous warming (W) at soil depth of 0–30 cm. Data were based on the total numbers of 3450, 4100 and 3337 individual roots born in spring, summer and autumn in 2008, and 1780, 334 and 1093 individual roots born in spring, summer and autumn in 2009. The Kaplan–Meier method was used to generate curves. Survival differences between different treatments were compared using Log-rank test.

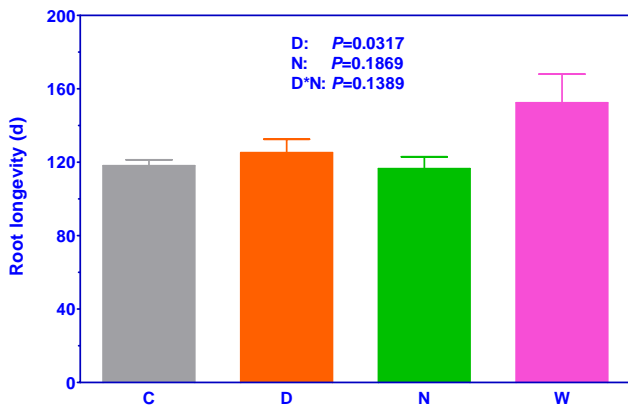


Fig. 3. Root longevity under conditions of control (C), day warming (D), night warming (N), and continuous warming (W) at soil depths of 0–30 cm during the growing seasons of 2007–2009. Data shown in the figure were based on a total number of 4442 and 6435 and 4655 and 4475 individual roots for control, day warming, night warming and continuous warming, respectively. Mean lifespan were generated using the Kaplan–Meier method. Data are mean \pm SE of six plots.

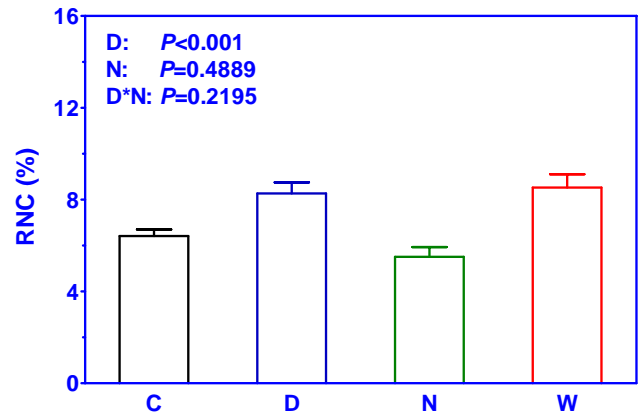


Fig. 4. Effect of different warming regimes (control C, day warming D, night warming N, and continuous warming W) on root nonstructural carbohydrate content (RNC). Data are mean \pm SE of six plots.

$P = 0.0407$; Fig. 6a). Neither day nor night warming affected ANPP and BNPP (Fig. 5). In addition, no interactive effects ($P = 0.6074$; $P = 0.8030$) of day and night warming on ANPP and BNPP were observed (Fig. 5a, b). In contrast, there was an increasing trend of the ratio of BNPP/ANPP under conditions of day and continuous warming (Fig. 5c). Across the 24 plots, the day warming-induced changes in root longevity was positively dependent on changes in the ratio of BNPP/ANPP induced by day warming ($r^2 = 0.85$, $P = 0.0095$; Fig. 6b). Stepwise multiple regression analyses revealed that 41.06 % of the spatial variation in root longevity can be explained by root nonstructural carbohydrate content (partial $r^2 = 0.2181$, $P = 0.0214$) and soil temperature (partial $r^2 = 0.1925$, $P = 0.0319$). In contrast, soil moisture, ANPP, BNPP, BNPP/ANPP, GEP, ER, NEP, SR and soil inorganic N were not significantly correlated with root longevity ($P > 0.05$).

4 Discussion

Several studies have demonstrated that root dynamics in the ecosystems are sensitive to continuous warming (Majdi and Ohrvik, 2004; Wan et al., 2004; Bai et al., 2010). However, there has been no study to evaluate whether day, night and continuous warming have different effects on root dynamics. In the present study, we provide direct experimental evidence demonstrating that day and night warming had different effect on root lifespan in the semi-arid grassland in northern China. More specifically, we found that roots initiated in different seasons differed in their response to day, night and continuous warming as evidenced by the three warming regimes had different effect on their root survival rate and longevity (Fig. 2, Table 2). In addition to seasonal variations of root longevity in response to the warming treatments, we found that the response of root lifespan to the warming

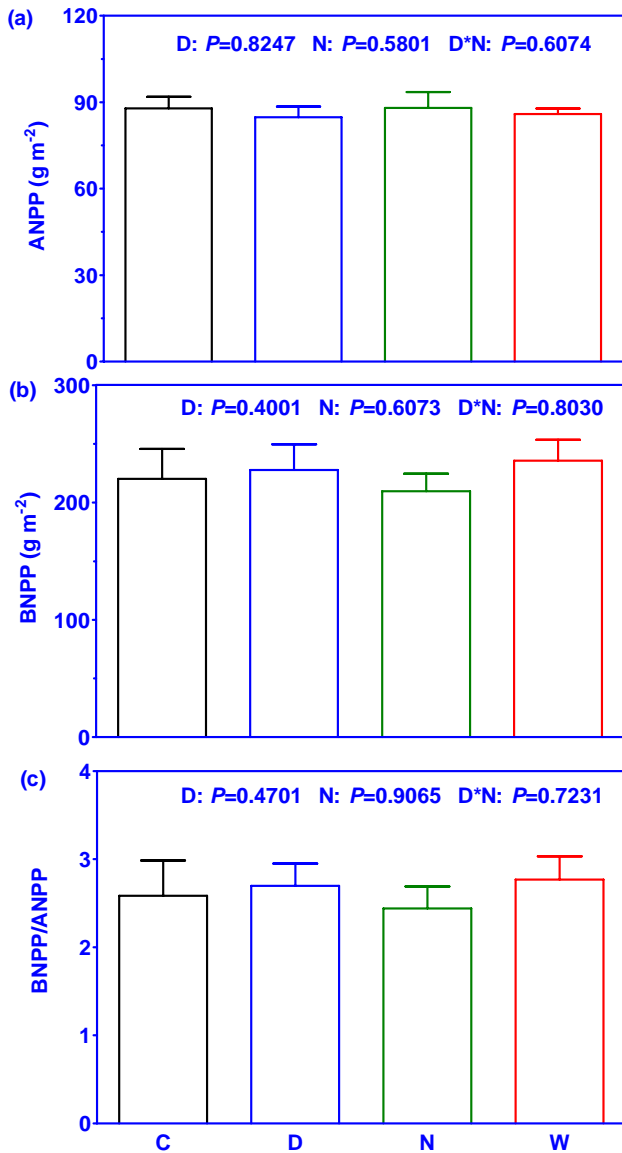


Fig. 5. Effect of different warming regimes (control C, day warming D, night warming N, and continuous warming W) on aboveground net primary productivity (ANPP) (a), belowground net primary productivity (BNPP) (b) and the ratio of BNPP and ANPP (c) during the growing seasons of 2007–2009. The values of ANPP, BNPP and BNPP/ANPP were mean values of 2007–2009 from six plots with bars as standard errors.

treatments differed between 2008 and 2009 (Table 2). To the best knowledge of authors, there has been no report to compare longevity of roots born in different years in the literature. Our results revealed that longevity of roots born in 2008 was longer than those born in 2009. In our experiments, since the majority of roots born in 2009 were still alive by the end of experiment in October of 2009, the calculated longevity value for roots born in 2009 was underestimated because only those roots with short lifespan were

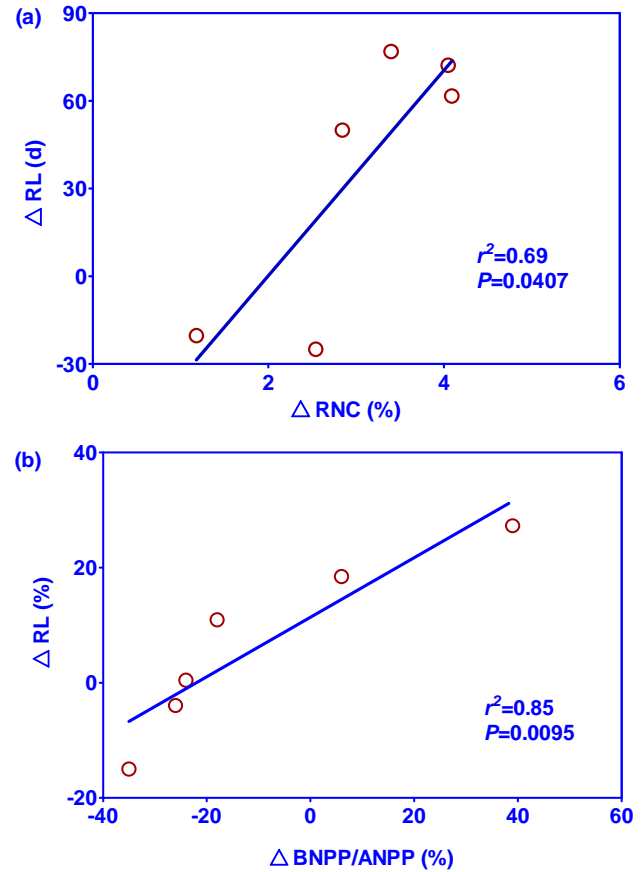


Fig. 6. Spatial dependence of day warming-induced changes in root longevity (RL) on day warming-induced changes in root nonstructural carbohydrate content (RNC) (a) and BNPP/ANPP (b) across the 24 plots. Each data point represents the relative or absolute difference between the adjacent plots (ambient vs. elevated temperature).

included. Therefore, root longevity data obtained by monitoring root growth for longer periods and larger numbers of roots using rhizotron would be more accurate and reliable. In this context, a general trend that day warming, but not night warming, significantly increased the overall root lifespan was found when data for root survival rate in the three growing seasons of 2007–2009 were pooled as a whole. Our results showed that both day and continuous warming significantly increased the overall root lifespan, while night warming had no effect on the overall root lifespan (Fig. 3). No consistent results have been reported on the effect of continuous warming on root production and mortality in the literature. For instance, it has been reported that root mortality is increased by continuous warming (Majdi and Ohrvik, 2004; Wan et al., 2004), while Johnson et al. (2006) demonstrated that continuous warming has no effect on root production and mortality in Douglas-fir. Gill and Jackson (2000) investigated the effect of mean annual temperatures on root turnover using a

global dataset and found that the higher mean annual temperatures stimulate root turnover in grasslands. In contrast, our previous study showed that continuous warming had negative effects on root production and mortality in the same steppe in northern China (Bai et al., 2010). The different responses of root production to temperature among different ecosystems may largely be explained by the relative contributions between the direct and indirect (via changing soil moisture) effects of warming on ecosystem processes (Shaver et al., 2000; Wan et al., 2005; Bai et al., 2010). In the ecosystems where water availability is relatively abundant, the stimulatory effects of warming are likely to be stronger than the inhibitory effects, thus leading to an enhanced root production and mortality (Gill and Jackson, 2000; Majdi and Ohrvik, 2004; Wan et al., 2004). However, in the arid and semiarid ecosystems as in our study, water availability is a major limiting factor. Therefore, the inhibitory effects are likely to be stronger than the stimulatory effects of warming such that root productivity and mortality would be suppressed (Bai et al., 2010). Our findings that day warming especially continuous warming, significantly increased soil temperature and concurrently decreased soil moisture (Table 1, Fig. 1; Xia et al., 2010) are in line with this proposition. As a consequence, this would reduce root death hazard (Table 3) and prolong root lifespan.

There have been several studies examining the effect of day and night warming on ecosystem productivity, species composition and soil respiration in different ecosystems in general and in semiarid grassland in particular (Alward et al., 1999; Peng et al., 2004; Xia et al., 2009; Wan et al., 2009). However, there has been no detailed study to compare the effect of day warming on root dynamics with that of night warming in the literature so far. In the present study, we studied the response of root dynamics to day and night warming in a semiarid steppe. One important finding is that day and night warming had different effect on root lifespan such that day warming prolonged the overall root lifespan by 19.8%, while night warming had no impact on the overall root lifespan (Fig. 3). The differential response of root lifespan to day and night warming could be explained by the allocation of ecosystem C. It has been documented that root lifespan is closely related to C supply from shoot to root (Farrar and Jones, 2000; Norby and Jackson, 2000). A decrease in C allocation to root has been suggested to shorten root lifespan (Eissenstat and Yanai, 1997; Hogberg et al., 2001). Our previous studies showed that root lifespan was negatively correlated with aboveground biomass such that an increase in C allocation to aboveground shortened root lifespan (Bai et al., 2008). In the semiarid temperate steppe ecosystem, day warming, but not night warming, has been shown to decrease soil moisture (Xia et al., 2010), thus exacerbating water stress. Our previous studies on the same experimental sites revealed that the direct effect of warming on root production and mortality was less than its indirect effect (drought effect) (Bai et al., 2010). Therefore, plants

have to allocate more proportional C to roots for more efficiently acquiring water resources under warming conditions. In this context, Wan et al. (2009) reported that leaf sugar and starch depletion is reduced by day warming. This would facilitate allocation of more carbohydrates to roots. Our results that day warming increased RNC in roots (Fig. 4) are in line with their explanation. Moreover, the observations that a positive dependence of root lifespan on the day warming-induced changes in root nonstructural carbohydrate content and BNPP/ANPP (Fig. 6) provide strong evidence in support of regulation of root lifespan by C allocation in response to asymmetric warming. Our result that root nonstructural carbohydrate content accounted for 21.8% of the spatial variation in root longevity is also consistent with this argument.

In the present study, we found that day warming, but not night warming, significantly affected the overall root lifespan in the semi arid steppe in northern China. This finding is in contrast to those results that night-warming mainly influences the processes associated with ecosystem C exchange such as GEP, NEP, ER and SR in the same experimental platform (Wan et al., 2009; Xia et al., 2009). For example, Xia et al. (2010) found that night warming significantly increases soil respiration, while day warming has no effect on soil respiration. Wan et al. (2009) reported that day and night warming significantly decrease and increase gross ecosystem productivity and net ecosystem productivity, whereas day and night warming have no any impact on ecosystem respiration. Our previous studies also demonstrated that there were interactive effects of continuous warming and precipitation on root production and mortality, and that these effects were significantly related to gross ecosystem productivity, ecosystem respiration and soil respiration (Bai et al., 2010). However, in the present study, we did not observe any correlation between the day and night warming induced-changes in root longevity and GEP, NEP, ER and SR. These results may imply that water is a key factor in the mediation of ecological processes associated with C cycle in the semi-arid steppe. Research findings in this study and two previous studies (Wan et al., 2009; Xia et al., 2009) in the same experimental platform suggest independence of above- and belowground plant and ecosystem C processes in response to climate warming, highlighting the importance of taking into account the differential response of root lifespan to day and night warming for projection and model simulation of climate-C feedback.

5 Conclusions

We provide the first direct experimental evidence demonstrating that the overall root lifespan in the semiarid temperate steppe in northern China was sensitive to asymmetrical warming such that day warming, but not night warming, significantly prolonged the overall root lifespan. The findings that day and night warming had differential effects on root lifespan in the semiarid temperate steppe could be largely

explained by changes in allocation of photoassimilate. Our results revealed that the response of root dynamics to day and night warming differed from other ecosystem processes associated with C cycling. Therefore, these novel findings highlight the necessity of incorporation of the differential effects of day and night warming into the simulating and predicting the responses and feedbacks of terrestrial ecosystem C cycling to global warming.

Acknowledgements. We would like to thank Guangquan Wang and Yunfeng Dong for their help in field and laboratory work. This research was supported by the State Key Basic Research Development Program of China (No. 2011CB403200-04), the National Natural Science Foundation of China (31070432, 90511006 and 30925009), and Beijing Institutes of Life Science, Chinese Academy of Sciences (2010-Biols-CAS-0101).

Edited by: R. Conant

References

- Alward, R. D., Detling, J. K., and Milchunas, D. G.: Grassland vegetation changes and nocturnal global warming, *Science*, 316, 229–231, 1999.
- Anderson, L. J., Comas, L. H., Lakso, A. N., and Eissenstat, D. M.: Multiple risk factors in root survivorship: a 4-year study in Concord grape, *New Phytol.*, 158, 489–501, 2003.
- Bai, W. M., Wan, S. Q., Niu, S. L., Liu, W. X., Chen, Q. S., Wang, Q. B., Zhang, W. H., Han, X. G., and Li, L. H.: Increased temperature and precipitation interact to affect root production, mortality, and turnover in a temperate steppe: Implications for ecosystem C cycling, *Global Change Biol.*, 16, 1306–1316, 2010.
- Bai, W. M., Wang, Z. W., Chen, Q. S., Zhang, W. H., and Li, L. H.: Spatial and temporal effects of nitrogen addition on root life span of *Leymus chinensis* in a typical steppe of Inner Mongolia, *Funct. Ecol.*, 22, 583–591, 2008.
- Beier, C., Emmett, B. A., Penuelas, J., Schmidt, I. K., Tietema, A., Estiarte, M., Gundersen, P., Llorens, L., Riis-Nielsen, T., Sowerby, A., and Gorissen, A.: Carbon and nitrogen cycles in European ecosystems respond differently to global warming, *Sci. Total. Environ.*, 407, 692–697, 2008.
- Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A. D., Friedlingstein, P., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J. M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Sousana, J. F., Sanz, M. J., Schulze, E. D., Vesala, T., and Valentini, R.: Europe-wide reduction in primary productivity caused by the heat and drought in 2003, *Nature*, 437, 529–533, 2005.
- Dhakhwa, G. B. and Campbell, C. L.: Potential effects of differential day-night warming in global climate change on crop production, *Clim. Change*, 40, 647–667, 1998.
- Easterling, D. R., Horton, B., Jones, P. D., Peterson, T. C., Karl, T. R., Parker, D. E., Salinger, M. J., Razuvayev, V., Plummer, N., Jamason, P., and Folland, C. K. Maximum and minimum temperature trends for the globe, *Science*, 277, 364–367, 1997.
- Eissenstat, D. M., Yanai, R. D.: The ecology of root life span, *Adv. Ecol. Res.*, 27, 1–60, 1997.
- Farrar, J. F. and Jones, D. L.: The control of carbon acquisition by roots, *New Phytol.*, 147, 43–53, 2000.
- Gill, R. A., Burke, I. C., Lauenroth, W. K., and Milchunas, D. G.: Longevity and turnover of roots in the shortgrass steppe: influence of diameter and depth, *Plant Ecol.*, 159, 241–251, 2002.
- Gill, R. A. and Jackson, R. B.: Global patterns of root turnover for terrestrial ecosystems, *New Phytol.*, 147, 13–31, 2000.
- Hogberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Hogberg, M. N., Nyberg, G., Ottosson-Löfvenius, M., and Read, D. J.: Largescale forest girdling shows that current photosynthesis drives soil respiration, *Nature*, 411, 789–792, 2001.
- Hooker, J. E., Hendrick, R., Atkinson, D. A.: The measurement and analysis of fine root longevity, in: *Root methods: A handbook*, edited by: Smit, A. L., Bengough, A. G., Engels, C., van Noordwijk Pellerin, S., van de Geijn, S. C., Springer-Verlag, Berlin, Germany, 273–304, 2000.
- Johnson, M. G., Rygielwicz, P. T., Tingey, D. T., and Phillips, D. L.: Elevated CO₂ and elevated temperature have no effect on Douglas-fir fine-root dynamics in nitrogen-poor soil, *New Phytol.*, 170, 345–356, 2006.
- Liu, W. X., Zhang, Z., and Wan, S. Q.: Predominant role of water in regulating soil and microbial respiration and their responses to climate change in a semiarid grassland, *Global Change Biol.*, 15, 184–195, 2009.
- Lobell, D. B.: Changes in diurnal temperature range and national cereal yields, *Agr. Forest Meteorol.*, 145, 229–238, 2007.
- Lobell, D. B. and Ortiz-Monasterio, J. I.: Impacts of day versus night temperatures on spring wheat yields: A comparison of empirical and CERES model predictions in three locations, *Agron. J.*, 99, 469–477, 2007.
- López, B., Sabate, S., and Gracia, C. A.: Fine-root longevity of *Quercus ilex*, *New Phytol.*, 151, 437–441, 2001.
- Loya, W. M., Johnson, L. C., and Nadelhoffer, K. J.: Seasonal dynamics of leaf- and root-derived C in arctic tundra mesocosms, *Soil Biol. Biochem.*, 36, 655–666, 2004.
- Luo, Y. Q.: Terrestrial carbon-cycle feedback to climate warming, *Ann. Rev. Ecol. Syst.*, 38, 683–712, 2007.
- Majdi, H. and Ohrvik, J.: Interactive effects of soil warming and fertilization on root production, mortality, and longevity in a Norway spruce stand in Northern Sweden, *Glob. Change Biol.*, 10, 182–188, 2004.
- Niu, S. L., Wu, M. Y., Han, Y., Xia, J. Y., Li, L. H., and Wan, S. Q.: Water-mediated responses of ecosystem carbon fluxes to climatic change in a temperate steppe, *New Phytol.*, 177, 209–219, 2008.
- Norby, R. J. and Jackson, R. B.: Root dynamics and global change: seeking an ecosystem perspective, *New Phytol.*, 147, 3–12, 2000.
- Peng, S. B., Huang, J. L., Sheehy, J. E., Lanza, R. C., Visperas, R. M., Zhong, X., Centeno, G. S., Khush, G. S., and Cassman, K. G.: Rice yields decline with higher night temperature from global warming, *Prog. Natl. Acad. Sci.*, 101, 9971–9975, 2004.
- Piao, S. L., Ciais, P., Friedlingstein, P., Peylin, P., Reichstein, M., Luysaert, S., Margolis, H., Fang, J. Y., Barr, A., Chen, A. P., Grelle, A., Hollinger, D. Y., Laurila, T., Lindroth, A., Richardson, A. D., and Vesala, T.: Net carbon dioxide losses of northern ecosystems in response to autumn warming, *Nature*, 451, 49–52, 2008.
- Pregitzer, K., King, J. S., Burton, A. J., and Brown, S. E.: Re-

- sponses of tree fine roots to temperature, *New Phytol.*, 147, 105–115, 2000.
- Ranwala, A. P. and Miller, W. B.: Blackwell Publishing Ltd Analysis of nonstructural carbohydrates in storage organs of 30 ornamental geophytes by high-performance anion-exchange chromatography with pulsed amperometric detection, *New Phytol.*, 180, 421–433, 2008.
- Shaver, G. R., Canadell, J., Chapin, F. S., Gurevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L., and Rustad, L.: Global warming and terrestrial ecosystems: a conceptual framework for analysis, *BioScience*, 50, 871–882, 2000.
- Sullivan, P. F., Sommerkorn, M., Rueth, H. M., Nadelhoffer, K. J., Shaver, G. R., and Welker, J. M.: Climate and species affect fine root production with long-term fertilization in acidic tussock tundra near Toolik Lake, Alaska, *Oecologia*, 153, 643–652, 2007.
- Volder, A., Edwards, E. J., Evans, J. R., Robertson, B. C., Schortemeyer, M., and Gifford, R. M.: Does greater night-time, rather than constant, warming alter growth of managed pasture under ambient and elevated atmospheric CO₂, *New Phytol.*, 162, 397–411, 2004.
- Wan, S. Q., Hui, D. F., Wallace, L., and Luo, Y. Q.: Direct and indirect warming effects on ecosystem carbon processes in a tallgrass prairie, *Global Biogeochem. Cy.*, 19, GB2014, doi:10.1029/2004GB002315, 2005.
- Wan, S. Q., Norby, R. J., Pregitzer, K. S., Ledford, J., and O'Neill, E. G.: CO₂ enrichment and warming of the atmosphere enhance both productivity and mortality of maple tree fine roots, *New Phytol.*, 162, 437–446, 2004.
- Wan, S. Q., Xia, J. Y., Liu, W. X., and Niu, S. L.: Photosynthetic over-compensation under nocturnal warming enhances grassland carbon sequestration, *Ecology*, 90, 2700–2710, 2009.
- Wells, C. E. and Eissenstat, D. M.: Marked differences in survivorship among apple roots of different diameters, *Ecology*, 82, 882–892, 2001.
- Xia, J., Han, Y., Zhang, Z., Zhang, Z., and Wan, S.: Effects of diurnal warming on soil respiration are not equal to the summed effects of day and night warming in a temperate steppe, *Biogeochemistry*, 6, 1361–1370, doi:10.5194/bg-6-1361-2009, 2009.
- Xia, J. Y., Chen, S. P., and Wan, S. Q.: Impacts of day versus night warming on soil microclimate: Results from a semiarid temperate steppe, *Sci. Total Environ.*, 408, 2807–2816, 2010.
- Zhou, L., Dickinson, R. E., Tian, Y., Vose, R. S., and Dai, Y. Impact of vegetation removal and soil aridation on diurnal temperature range in a semiarid region: application to the Sahel, *Prog. Natl. Acad. Sci.*, 104, 17937–17942, 2007.