**Biogeosciences
Discussions**

As different as day and night: evidence from root lifespan

W. Bai, J. Xia, S. Wan, W. Zhang, and L. Li

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

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

Title Page

Abstract	Introduction
Conclusions	References
Tables	Figures

◄ | ►

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Abstract

Roots are key components of terrestrial ecosystem C cycling and play an important role in regulation of the response of terrestrial ecosystem to global climate warming, which occurs with greater warming magnitudes at night than during daytime across different regions on the Earth. However, there has been no detailed study to examine the effect of asymmetrical warming on root dynamics at the level of terrestrial ecosystem. 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 diurnal warming was conducted. The responses of root survivorship to day and night warming with modified rhizotron technique were monitored during the growing seasons of 2007–2009. We demonstrate, for the first time, that longevity of roots born in spring, summer and autumn showed different response to day, night and diurnal warming, and that day warming significantly prolonged the overall lifespan for the roots born in the growing seasons of 2007–2009 pooled as a whole, while night warning had no effect on the overall lifespan in the semiarid grassland in Northern China. The differential response of root lifespan to day and night warming may be accounted for by the photoassimilate allocation as evidenced by that day and night warming had different effect on root non-structural carbohydrate content. This finding differed from other processes associated with ecosystem C cycle such as total ecosystem productivity, net ecosystem productivity and soil respiration. Thus our findings highlight that it is essential to incorporate 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.

1 Introduction

Model projection and field experimental observations have demonstrated that global warming can have significant impact on the structure and function of terrestrial ecosystem in general, and carbon (C) cycle of terrestrial ecosystem in particular (Ciais

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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). There are reports demonstrat-
5 ing that increased daily minimum and maximum temperatures have different effects on the biomass and yield of plants (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 ecosystem. However, it remains unclear whether symmetrical and asymmetric warming may have different effect on root growth, mortal-
10 ity, and turnover of plants, which plays critical role in regulating nutrient and C cycling between above- and belowground.

Photosynthesis takes place predominantly during the day time, while respiration becomes dominant at the night time. Day and night warming would stimulate photosynthesis and respiration, respectively. Therefore, day and night warming may have
15 different effect on C absorption and release. Recent studies have 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 warning may result from stimulation of plant respiration by night warm-
20 ing, thus leading to alteration of C allocation due to compensatory response of leaf photosynthesis (Wan et al., 2009). Numerous studies have reported that the terrestrial ecosystem is 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). It has been shown that root dynamics were
25 also sensitive to diurnal 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 diurnal warming has differential impacts on plant photosynthesis and respiration, we hypothesize that root dynamics exhibit differential response to day and night warming.

Root lifespan and asymmetric warming

W. Bai et al.

Title Page

Abstract	Introduction
Conclusions	References
Tables	Figures

| ◄◄ | ►► |
| ◄ | ► |

| Back | Close |

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Root lifespan and asymmetric warming

W. Bai et al.

Roots are an important source of soil organic C and play a key role in the regulation of ecosystem C cycle (Loya et al., 2004; Sullivan et al., 2007). In addition, roots, as key components of ecosystem C cycling, are also closely related to other 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 in 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 ecosystem 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 process of ecosystem is complex in response to climate change. Therefore, understanding of 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 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 of ecosystem 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 a.s.l.) in Inner Mongolia, China. Long-term (1953–2007) mean annual precipitation (without the precipitation fall as snow) 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 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), diurnal (24 h; W) warming, diurnal warming (uniform 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 were 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 (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 root windows were inserted, soil was backfilled as tightly as originally. The soil was closely attached to the glass throughout the whole study period.

A digital camera was used to monitor the growth of roots. Observations began on 30 June 2007, which was about 10 months after the installation of glass windows, and lasted untill 19 August 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 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) and a computer mouse as described by Bai et al. (2008, 2010). For the initially collected images, each root was assigned with an identification number and distinguished as living or dead based on color 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, 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 Data-logger (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. 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 obtained from the root in-growth measurement in soils of 0–30 cm were used to measure soluble sugars and starch as described by Wan et al. (2009). Root soluble sugar and starch concentration was 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), belowground net primary productivity (BNPP), 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 the roots were initially observed on the window. The date of root appearance or disappearance was estimated as the date midway between the sampling period 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 10887 new roots germinated in spring (1–15 May, 15–30 May), summer (1–16 July, 16–31 July) and autumn (31 August–15 September, 15 September–1 October) of 2008 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 20007 new roots germinated in control, day warming, night warming, and diurnal 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:

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

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 non-structural carbohydrate content (RNC), ANPP, and BNPP. Simple and multiple linear regression analyses were used to examine the relationships between root longevity

Root lifespan and asymmetric warming

W. Bai et al.

and soil temperature, soil moisture, 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 experiment was a 2-factorial one with day and nigh 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, volumetric soil moisture at 0–10 cm depth fluctuated greatly 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 (Table1; 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 effect between year and day warming ($P = 0.996$), night warming ($P = 0.885$), or their combination ($P = 0.964$) on soil moisture was detected (Table 1; Fig. 1b).

3.2   Effect of day warming and night warming on root longevity

The roots initiated in the three seasons (spring, summer and autumn) in the control and warming plots exhibited different survival rate and longevity and responded to day,

Discussion Paper | Discussion Paper | Discussion Paper | Discussion Paper

BGD

8, 10459–10486, 2011

Root lifespan and asymmetric warming

W. Bai et al.

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◀ | ▶|

◀ | ▶

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

night and diurnal warming differently (Fig. 2, Table 2). Log-rank test revealed that day warming significantly increased survival rate (Fig. 2a) and longevity for the roots initiated in spring ($P < 0.001$, Table 2); while both night and diurnal warming had no effect on survival rate (Fig. 2a) and longevity for the roots initiated in spring ($P > 0.05$, Table 2). In contrast, survival rate (Fig. 2b) and longevity ($P < 0.001$, Table 2) of the roots initiated in summer were significantly enhanced by diurnal warming. But survival rate and longevity of the roots initiated in summer were not affected by either day or night warming. Day warming significantly reduced survival rate (Fig. 2c) and longevity of the roots born in autumn ($P = 0.006$, Table 2), while night warming increased survival rate (Fig. 2c) and longevity of the roots initiated in autumn ($P = 0.0101$, Table 2). However, both survival rate and longevity for the roots initiated in autumn were not affected by diurnal warming (Table 2).

To obtain the overall response of root survival rate and longevity to day, night and diurnal warming, we pooled the survival data for roots initiated in during the 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 diurnal warming was significantly different. For instance, the mean overall root longevity in the day and diurnal warming plots was 7 and 34 d longer than in the control plots, respectively (Fig. 3). The results of the Cox proportional hazards regression (Table 3), the mortal risk for roots in day warming and diurnal warming plots was marginally ($P = 0.08$) and significantly reduced ($P < 0.001$), respectively. Furthermore, day warming had significantly affected 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 were no interactive effects ($P = 0.139$) of day and night warming on the overall root longevity (Fig. 3). Further analysis 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 changes in the overall root longevity ($P > 0.05$) were observed in the night warmed subplots. These results indicate that the effect of day warming on the overall root longevity is significant.

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 carbo-hydrate content was observed as analyzed by two-way ANOVAs. Day warming in-creased root nonstructural carbohydrate content by 42.0 %. There were no interactive effects ($P = 0.2195$) of day and night warming on root nonstructural carbohydrate con-tent (Fig. 4).

3.4 Treatment-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 further examined correlation between root longevity and nonstructural carbohydrate in the roots under conditions of day warm-ing. Across the 24 plots, the day warming-induced changes in root longevity showed positive linear dependence on the day warming-induced changes in RNC ($r^2 = 0.69$, $P = 0.0407$; 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 increas-ing trend of the ratio of BNPP/ANPP under conditions of day and diurnal 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 $r^2 = 0.1925$, $P = 0.0319$).

4 Discussion

Several studies have demonstrated that root dynamics in the ecosystems are sensitive to diurnal 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 diurnal 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 diurnal warming as evidenced by the three warming treatments had different effect on their root survival rate and longevity (Fig. 2, Table 2). A general trend that day warming, but not night warming, significantly increased the overall root lifespan was found if the data for root survival rate were pooled as a whole. In the semiarid temperate steppe in Northern China, our results showed that both day and diurnal 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 diurnal warming on root production and mortality in the literature. For instance, it has been reported that root mortality is increased by diurnal warming (Majdi and Ohrvik, 2004; Wan et al., 2004), while Johnson et al. (2006) demonstrated that diurnal warming has no effect on root production and mortality in Douglas-fir. Gill and Jackson (2000) analyzed 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 diurnal warming had negative effects on root production and mortality in the semiarid temperate 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 enhanced root production and mortality (Gill and Jackson, 2000; Majdi and Ohrvik, 2004; Wan et al., 2004). However, in the arid and semiarid ecosystems such 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). In the present study, we found that day warming, especially diurnal warming, significantly increased soil temperature and concurrently decreased soil moisture (Table 1, Fig. 1; Xia et al., 2010). 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 we found 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 did not affect the overall root lifespan (Fig. 3). The differential effects of day and night warming on root lifespan could be explained by the ecosystem C allocation. 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 reduce root lifespan (Eissenstat and Yanai, 1997; Hogberg et al., 2001). Our previous studies found that root lifespan was negatively correlated with aboveground biomass such that more 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). The decrease in soil moisture by day warming would exacerbate 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 day warming induced a decrease in leaf sugar and starch depletion. This may facili-
5 tate allocation of more carbohydrate to root. 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 day warming-induced changes in root non-structural carbohydrate content and BNPP/ANPP (Fig. 6) provide strong evidence in support of regulation of root lifespan by C allocation in response to asymmetric warm-
10 ing. 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 find-ing is in contrast to those results that night-warming mainly influenced the processes
15 associated with ecosystem C exchange such as GEP, NEP, ER and SR in the same ex-perimental 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
20 productivity, whereas day and night warming have no any impact on ecosystem res-piration. Our previous studies also demonstrated that there were interactive effects of diurnal warming and precipitation on root production and mortality, and that these ef-fects 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
25 any correlation between 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 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 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.

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.

Printer-friendly Version

Interactive Discussion

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.

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, Glob. Change Biol., 16, 1306–1316, 2010.

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., Ogée, 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., Soussana, 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, Climatic 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. and 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. and Jackson, R. B.: Global patterns of root turnover for terrestrial ecosystems, New Phytol., 147, 13–31, 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.

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

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◀ | ▶

◀ | ▶

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

current photosynthesis drives soil respiration, Nature, 411, 789–792, 2001.

Hooker, J. E., Hendrick, R., and 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., and van de Geijn, S. C., Springer-Verlag, Berlin, 273–304, 2000.

Johnson, M. G., Rygiewicz, P. T., Tingey, D. T., and Phillips, D. L.: Elevated CO_2 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, Glob. Change Biol., 15, 184–195, 2009.

Lobell, D. B.: Changes in diurnal temperature rand 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, Annu. 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., Lazza, 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, P. Natl. Acad. Sci. USA, 101, 9971–9975, 2004.

Root lifespan and asymmetric warming

W. Bai et al.

Title Page

Abstract	Introduction
Conclusions	References
Tables	Figures

|◄ | ►|

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Piao, S. L., Ciais, P., Friedlingstein, P., Peylin, P., Reichstein, M., Luyssaert, 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.: Responses 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 CO_2, New Phytol., 162, 397–411, 2004.

Wan, S. Q., Norby, R. J., Pregitzer, K. S., Ledford, J., and O'Neill, E. G.: CO_2 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., 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., 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, Biogeosciences, 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, P. Natl. Acad. Sci. USA, 104, 17937–17942, 2007.

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

Table 2. Longevity of roots born in spring, summer and autumn in different treatments during the growing seasons of 2008 (mean ± 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	Spring	Summer	Autumn
Control	51 ± 3 a	95 ± 4 a	152 ± 5 a
Day warming	62 ± 2 b	103 ± 4 a	133 ± 5 b
Night warming	50 ± 2 a	80 ± 4 a	175 ± 4 c
Diurnal warming	52 ± 2 a	135 ± 6 b	159 ± 4 a

Table 3. Analyses of different warming treatments (day warming, night warming and diurnal 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 Lower	95 % CI Upper	P-value
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
Diurnal warming	−0.188	0.022	0.828	0.793	0.865	< 0.001
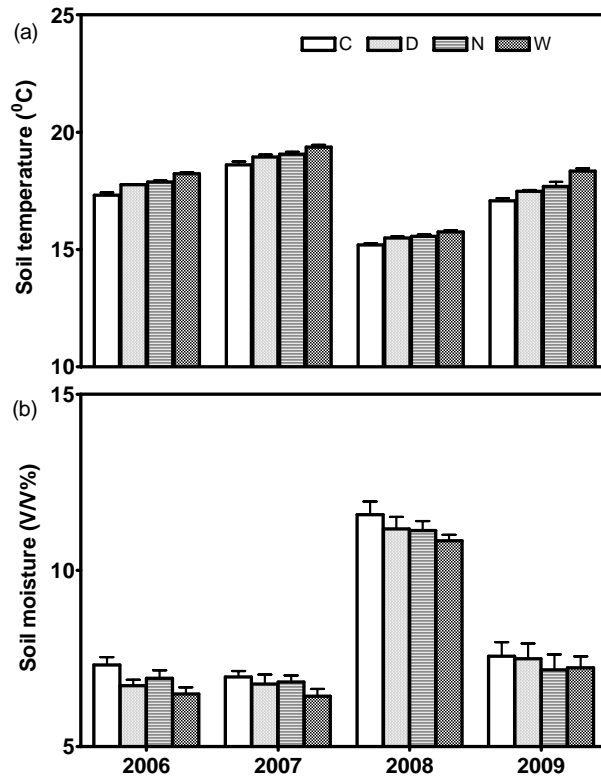
Fig. 1. Effects of control (C) and day warming (D), night warming (N) and diurnal warming (W) on temperature **(a)** and moisture **(b)** in the soil layer of 0–10 cm over the experimental period from 2006 to 2009. Data are mean ± SE of six plots.
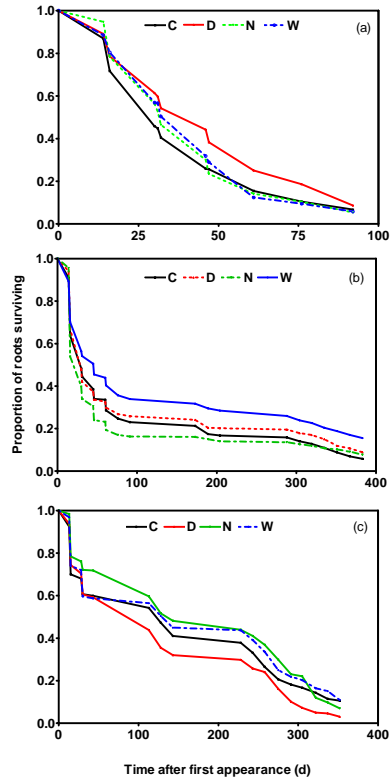
Printer-friendly Version

Interactive Discussion

**Fig. 2.** Survival curves of roots born in spring **(a)**, summer **(b)** and autumn **(c)** in under the control (C) and day warming (D), night warming (N) and diurnal warming (W) at soil depths of 0–30 cm during the growing seasons of 2008. Data were based on the total numbers of 3450, 4100 and 3337 individual roots born in spring, summer and autumn, respectively. The Kaplan–Meier method was used to generate curves. Survival differences between different treatments were compared using Log-rank test.
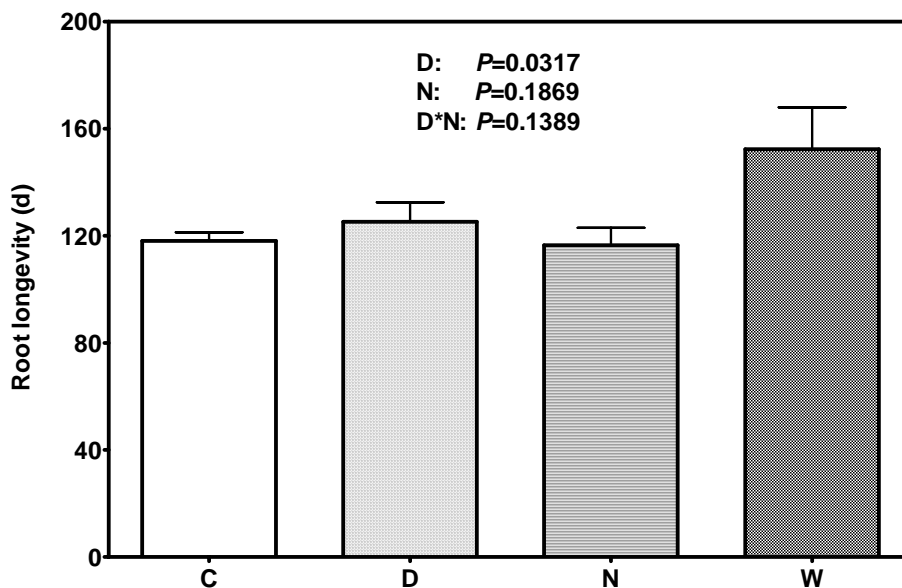
Fig. 3. Root longevity under conditions of control (C), day warming (D), night warming (N), and diurnal warming (W) at soil depths of 0–30 cm during the growing seasons of 2007–2009. Data shown in the figure were based on a total number of 4442 and 6435 and 4655 and 4475 individual roots for control, day warming, night warming and diurnal warming, respectively. Mean lifespan were generated using the Kaplan–Meier method. Data are mean ± SE of six plots.
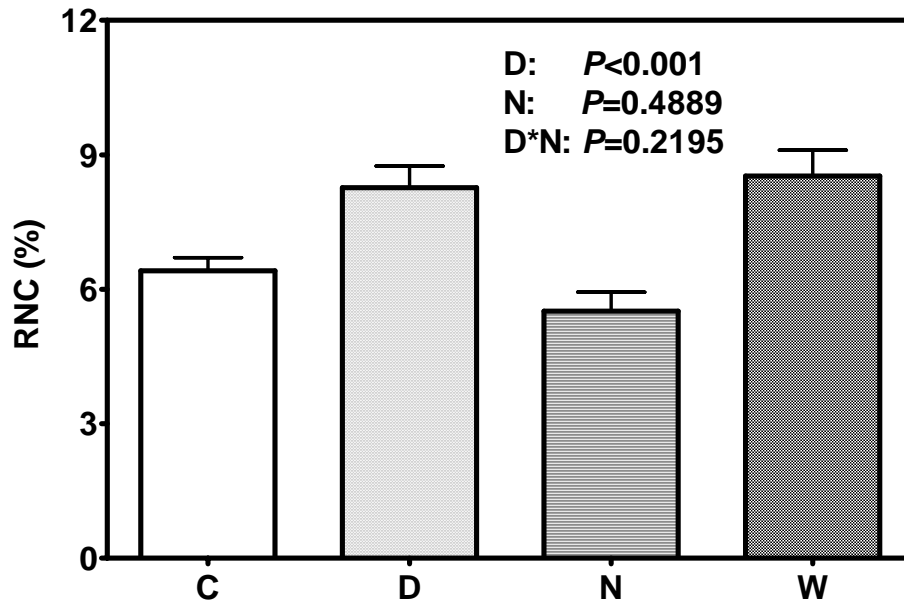
Fig. 4. Effect of different warming regimes (control C, day warming D, night warming N, and diurnal warming W) on root nonstructural carbohydrate content (RNC). Data are mean ± SE of six plots.

Full Screen / Esc

Printer-friendly Version
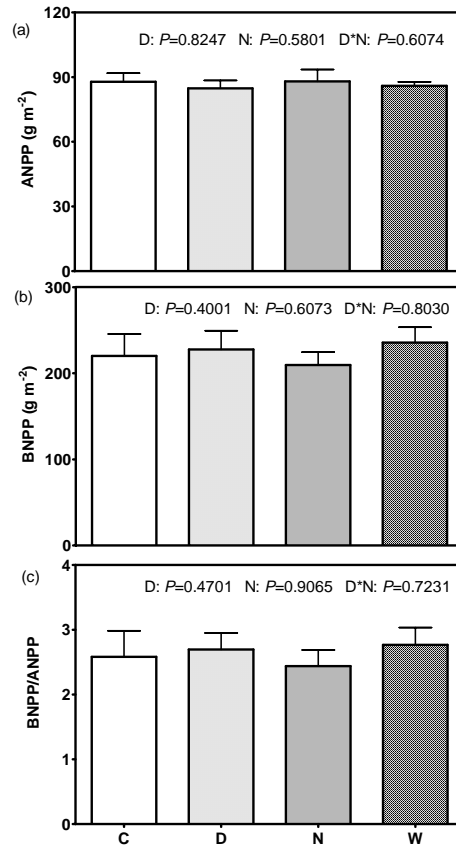
Interactive Discussion

Fig. 5. Effect of different warming regimes (control C, day warming D, night warming N, and diurnal 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.
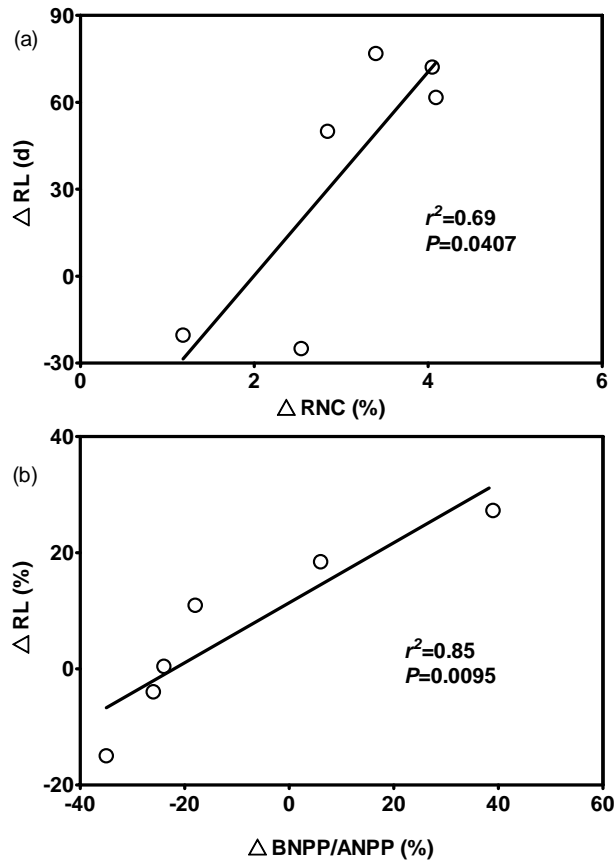
Fig. 6. Spatial dependence of day warming-induced changes in root longevity (RL) on day warming-induced changes in root nonstructural carbohydrate content (RNC) **(a)** and BNPP/ANPP **(b)** across the 24 plots. Each data point represents the relative or absolute difference between the adjacent plots (ambient vs. elevated temperature).

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

⏮ | ⏭

◀ | ▶

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion