Direct and indirect effects of experimental warming on ecosystem carbon processes in a tallgrass prairie

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[1]   This study was conducted to examine direct and indirect impacts of global warming on carbon processes in a tallgrass prairie in the U.S. Great Plains. Infrared radiators were used to simulate global warming, and clipping was used to mimic hay mowing. Experimental warming caused significant increases in green biomass in spring and autumn and total biomass in summer on most of the measuring dates. Green aboveground biomass showed positive linear correlations with soil temperature in spring and autumn whereas total aboveground biomass in summer was negatively correlated with soil temperature. Experimental warming also affected aboveground biomass indirectly by extending the length of growing season and changing soil nitrogen process. Elevated temperature tended to increase net nitrogen mineralization in the first year but decrease it in the second year, which could be attributable to stimulated plant growth and belowground carbon allocation and consequently enhanced microbial nitrogen immobilization. Warming-induced changes in soil respiration were proportional to those of total aboveground biomass. Clipping significantly reduced aboveground biomass and increased root biomass, but had no effect on net nitrogen mineralization and annual mean soil respiration. The proportional changes in soil respiration to those of aboveground biomass indicate warming-stimulated ecosystem carbon uptake could be weakened by increased carbon release through soil respiration.

1. Introduction

[2]   Rising atmospheric CO_2 concentration due to land-use change and fossil fuel combustion has resulted in a $0.6°C$ increase in the Earth's surface temperature in the twentieth century and is predicted to increase global mean temperature by about $1.4°–5.8°C$ in the twenty-first century [*Houghton et al.*, 2001]. Elevated global mean temperature can substantially impact global carbon (C) budget, leading to positive or negative feedbacks to global climate change [*Keeling et al.*, 1995, 1996; *Schimel et al.*, 1996; *Braswell et al.*, 1997; *Cox et al.*, 2000; *Luo et al.*, 2001; *Rustad et al.*, 2001; *Melillo et al.*, 2002]. Global warming influences ecosystem and global C cycling primarily through affecting the two major C fluxes, i.e., net primary production (NPP) and heterotrophic respiration (HR), between terrestrial ecosystems and the atmosphere. The balance of these two major C fluxes determines whether terrestrial ecosystems will act as a net C sink or source under changing climate. It is not clear whether, how, and to what extent the warming responses of NPP and HR are related to each other.

[3]   With the temperature impacts on almost all physical, chemical, and biological processes, global warming can directly influence C processes in terrestrial ecosystems by changing plant photosynthesis and growth and soil respiration [*Shaver et al.*, 2000]. Global warming can also indirectly affect plant growth and production by extending the length of growing season and changing plant phenology [*Price and Waser*, 1998; *Chmielewski and Rötzer*, 2001; *Dunne et al.*, 2003; *Fang et al.*, 2003; *Norby et al.*, 2003], increasing soil nitrogen (N) mineralization and availability [*Rustad et al.*, 2001; *Shaw and Harte*, 2001; *Melillo et al.*, 2002], reducing soil water content [*Harte et al.*, 1995; *Wan et al.*, 2002b], and shifting species composition and community structure [*Harte and Shaw*, 1995; *Shaver et al.*, 2000; *Saleska et al.*, 2002; *Weltzin et al.*, 2003]. Our current knowledge about whether these direct and indirect factors concomitantly influence ecosystem C cycling under global warming is extremely limited.

[4]   It has long been recognized that N is the most limiting nutrient for plant growth and net primary productivity

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[*Vitousek and Howarth*, 1991] and plays a critical role in regulating terrestrial C sequestration under global environmental change. As a consequence of ecological stoichiometry [*Sterner and Elser*, 2002], C and N cycling are usually coupled in terrestrial ecosystems [*Shaver et al.*, 1992; *Asner et al.*, 1997; *McGuire et al.*, 1997]. However, will the coupling of C and N cycling in terrestrial ecosystems under the past and current environments hold for the future climate scenarios? For example, it has been recently proposed that terrestrial N availability and supply may not meet the demands for the projected plant growth under global change, and thus will progressively limit C sequestration in terrestrial ecosystems [*Hungate et al.*, 2003; *Luo et al.*, 2004].

[5] As part of a comprehensive warming experiment in a tallgrass prairie in the U.S. Great Plains [*Luo et al.*, 2001; *Wan et al.*, 2002a, 2002b; *Zhang et al.*, 2005], this study was conducted to examine the potential influences of global warming, land-use change, and their interactions on the C and N processes in a tallgrass prairie in the U.S. Great Plains. Great Plains grasslands occupy 1.5 million km^2 of land area and are primary resources for livestock production in North America [*Knapp et al.*, 1998]. The responses of NPP and soil respiration to global warming and land use in the tallgrass prairie could substantially influence regional and global C budgets. We used infrared radiators to simulate global warming and clipping to mimic hay mowing, a common land-use practice in the U.S. Great Plains. The specific questions we would like to answer are as follows: (1) How does global warming affect NPP directly and indirectly in the tallgrass prairie? (2) Does warming differentially affect C and N processes? (3) Are the warming responses of ecosystem C uptake and release related to each other?

2. Methods and Materials

2.1. Site Description

[6] The experimental site is located at the Great Plain Apiaries (34°58′54″N, 97°31′14″W), 40 km from the Norman campus of the University of Oklahoma. This site has not been grazed for the past 20 years. The grassland is dominated by C_4 grasses (*Schizachyrium scoparium* and *Sorghastrum nutans*) and C_3 forbs (*Ambrosia psilostachyia*, *Gutierrezia dracunculoides*, *Aster ontarionis*, and *Xanthocephalum texanum*). Mean annual temperature is 16.0°C with monthly mean temperature of 3.1°C in January and 28.0°C in July. The annual precipitation is 967.2 mm (average values from 1948 to 1999, data from Oklahoma Climatological Survey). The soil is part of the Nash-Lucien complex (sand: 32%; silt: 60%; clay: 8%), which is characterized as having a low permeability rate, high available water capacity, and deep and moderate penetrable root zone [*National Cooperative Soil Survey*, 1963].

2.2. Warming Experiment

[7] The experiment used a split-plot design with warming as the main factor and clipping nested within temperature manipulations. There were six pairs of 2 × 2 m plots. In each pair, one plot has been warmed continuously using infrared heaters since 21 November 1999 and the other was the control. One 165 × 15 cm infrared heater (Kalglo Electronics Inc, Bethlehem, Pennsylvania) had a radiation output of approximately 100 watts/m^2 and was suspended 1.5 m above the ground in each warmed plot. In a previous study, it was found that the effects of infrared heaters on soil temperature were spatially uniform in the warmed plots [*Wan et al.*, 2002b]. In the control plot, one "dummy" heater with the same shape and size as the infrared heater was suspended 1.5 m high to simulate the shading effects of the heater. For each paired plot, the distance between the control and the warmed plot was approximately 5 m to avoid heating the control plot by the infrared heater. The distances between the individual sets of paired plots varied from 20 to 60 m.

[8] Each 2 × 2 m plot was divided into four 1 × 1 m subplots. Two diagonal subplots in each plot were clipped 10 cm above the ground on 15 November 1999, 28 July 2000, 24 July 2001, and 24 July 2002; the other two were the unclipped controls. Clipping in the manner effectively mimicked mowing hay, a common land-use practice in the southern Great Plains. As with the hay mowing, all clipped material was removed from the subplots. After clipping, plants were allowed to grow until the next clipping. The four treatments in the experiment were unclipped control (UC), unclipped warmed (UW), clipped control (CC), and clipped warmed (CW).

2.3. Soil Temperature and Moisture

[9] At the centers of one clipped and one unclipped subplot in each plot, thermocouples were installed at the depth of 2.5 cm to measure soil temperature. All the thermocouples were connected to a CR10 data-logger (Campbell Scientific Inc., Utah). Soil temperature was measured every 10 min, and then the average within 1 hour was stored in an SM196 Storage Module. In addition, soil temperature at the depth of 5 cm was measured adjacent to each PVC collar at the time of the soil respiration measurement using a thermocouple connected to LI-6400.

[10] Soil moisture content was measured gravimetrically twice a month from September 1999 to December 2000. Soil samples at the top 5 cm were taken from one clipped and one unclipped subplot in each plot and oven dried at 105°C for 24 hours and weighed. Soil moisture was expressed as a percent of dry soil on a mass basis. Beginning from January 2001, soil moisture (% volumetric) at the depth of 0–15 cm was measured twice a month using Time Domain Reflectometry (Soilmoisture Equipment Corp., Santa Barbara, California).

2.4. Aboveground Biomass and Root Biomass

[11] Plants were clipped annually from two diagonal subplots in July to mimic hay mowing and were also used to determine total aboveground biomass (AGB) above 10 cm height. The point frame method was used to record the contact numbers of the pins with plants in both the unclipped and clipped subplots. In each subplot, the point frame was placed 4 times in each of the four cardinal directions. Linear correlation functions were developed between the total contact number and total AGB in the clipped subplots

Table 1. Annual Mean Soil Temperature (°C) and Soil Moisture (%) From January 2000 to December 2002[a]

	Soil Temperature			Soil Moisture		
	2000	2001	2002	2000	2001	2002
Unclipped control	17.0	17.3	16.4	23.1	34.5	40.8
Unclipped warmed	19.0	19.1	17.7	21.7	33.4	39.1
Clipped control	17.5	17.8	16.7	19.2	33.3	40.4
Clipped warmed	20.2	20.4	19.0	17.1	32.9	39.0
Warming effect	d	d	c	a	a	b
Clipping effect	c	d	d	d	c	a
Warming × clipping	a	b	c	a	a	a

[a]Soil moisture was measured using gravimetric method at the depth of 0–5 cm in 2000 and using time domain reflectometry (Soilmoisture Equipment Corp., Santa Barbara, California) at the depth of 0–15 cm in 2001 and 2002. The last three rows represent the statistical significance of the warming and/or clipping effects on soil temperature and moisture; a, b, c, and d: statistically significant at p > 0.05, <0.05, <0.01, and <0.001, respectively.

each year. These linear functions were used to estimate total AGB in the unclipped subplots. In April and November of each year, point frame was used to record the contact numbers of the pins with green part of plants in the experimental plots and in eighteen 1×1 m calibration plots. The calibration plots were 5 m away from the experimental plots and clipped. Green plant materials from the calibration plots were separated from the dead plant materials and oven-dried to measure green AGB. Linear correlation functions were developed between the total contact number and green AGB in the calibration plots in April and November of each year. The linear functions were used to calculate green AGB in both the unclipped and clipped subplots of the experimental plots. In January 2002, soil cores (5.2 cm in diameter and 0–5 cm, 5–15 cm, and 15–30 cm in depth) were taken from one unclipped and one clipped subplots in each plot to measure root biomass. The clipped plant material and roots were oven-dried at 65°C for 48 hours.

2.5. Net N Mineralization

[12] In situ net N mineralization was measured using the incubation method for 2 years (from November 1999 to December 2001). The incubations were performed on "undisturbed" soil using perforated PVC tubes (15 cm in length and 4 cm in diameter). Two PVC tubes were pushed into the soil within 15 cm of one another. One tube was removed immediately and taken back for chemical analysis as the control treatment. The second tube was left in the field for approximately 2 months. Parafilm covered the top of each tube to avoid leaching of NO_3^-. Soil samples were sent to Soil, Water, and Forage Analytical Laboratory in Oklahoma State University for chemical analysis. Soil samples were extracted with 2 M KCl solution and ammonium and nitrate concentrations were analyzed using Lachat-800 Flow Injection Analyzer (Loveland, Colorado). From November 1999 to May 2000, soil cores were taken from all the subplots. Then the soil cores were only put in half of the subplots in order to reduce the disturbance to the experimental sites. Net N mineralization was calculated as the difference in inorganic N ($NH_4^+ + NO_3^-$) between the control and incubated samples. Available N presented in

Figure 4 in section 3.4 was the sum of ammonium and nitrate in the unincubated soil samples.

2.6. Soil Respiration

[13] A PVC collar (80 cm^2 in area and 5 cm in height) was installed 2–3 cm into the soil permanently at the center of each subplot to measure total soil respiration. Living plants inside the soil collars were clipped at the soil surface to avoid leaf respiration; the clipped plant material was left inside the collars. In order to detect the response of heterotrophic soil respiration to warming, the original soil collars (see above) in one clipped and one unclipped subplot in each plot were replaced with PVC tubes (80 cm^2 in area and 70 cm in depth) in October 2001. The 70-cm-long PVC tubes cut off old plant roots and prevented new roots from growing inside the tubes. The measurements of CO_2 efflux above these PVC tubes began in January 2002, leaving enough time for the plant roots inside the tubes to die. Thus CO_2 efflux measured above these PVC tubes derived solely from heterotrophic respiration. Soil respiration was measured once or twice a month using LiCor 6400 Portable Photosynthesis System with an attachment of LiCor 6400-9 soil chamber.

2.7. Statistical Analysis

[14] Analysis of variance (ANOVA) of split-plot design was used to examine the statistical significance of warming, clipping, and their interactive effects on AGB, soil respiration, and net N mineralization. In order to examine the relationship between AGB and soil temperature and soil moisture and the relationship between soil respiration and AGB, soil temperature, and soil moisture across different subplots, stepwise multiple regression analyses were conducted. All statistical analyses were conducted using SAS software (SAS Institute Inc., Cary, North Carolina).

3. Results

3.1. Microclimate and Growing Season Length

[15] The main effects of experimental warming and clipping on annual mean soil temperature were statistically significant ($p < 0.01$) across all the three years. Warming and clipping had significantly interactive effects on annual mean soil temperature in 2001 and 2002 ($p < 0.05$), but not in 2000 ($p > 0.05$). Annual mean soil temperature was 2.3, 2.2, and 1.9°C higher in the warmed plots than in the control plots in 2000, 2001, and 2002, respectively (Table 1). Clipping significantly increased annual mean soil temperature by 0.9, 0.9, and 0.8°C in 2000, 2001, and 2002, respectively. The warming effect on annual mean soil moisture was statistically significant only in 2002 (−3.7%, $p < 0.05$) whereas clipping significantly reduced annual mean soil moisture by 9.0% ($p < 0.001$) in 2000 and 2.3% ($p < 0.01$) in 2001, respectively. There were no interactive effects of warming and clipping on annual mean soil moisture in any of the 3 years.

[16] Because plant phenology is closely related to temperature regime [*Fitter et al.*, 1995; *Fitter and Fitter*, 2002; *Chmielewski and Rötzer*, 2001], we used soil temperature as a proxy estimate for the length of growing season. The

Table 2. Experimental Warming Extended the Length of Growing Season[a]

Year	Unclipped Control	Unclipped Warmed	Clipped Control	Clipped Warmed
		Spring		
2000	Feb. 21	Feb. 15 (7)	Feb. 21	Feb. 13 (8)
2001	March 10	March 4 (6)	March 10	March 2 (8)
2002	March 12	Feb. 19 (21)	March 12	Feb. 18 (22)
		Autumn		
2000	Nov. 6	Nov. 7 (1)	Nov. 6	Nov. 7 (1)
2001	Nov. 26	Dec. 7 (11)	Nov. 26	Dec. 7 (11)
2002	Nov. 15	Nov. 24 (9)	Nov. 15	Nov. 24 (9)

[a]The first day in spring and the last day in autumn when soil temperature was continually above $10°C$ for 5 days were taken as the beginning and end of growing season shown as calendar dates. Values in parentheses are the number of days the growing season was advanced in spring and delayed in autumn in warmed plots compared with control plots for the two land-use scenarios.

length of growing season was defined as the time period between the first day in spring and the last day in autumn when soil temperature was continually above $10°C$ for 5 days. Experimental warming, on average, extended the length of growing season by approximately 19 days with an advance of 12 days in spring and a delay of 7 days in autumn whereas clipping had no effect on the length of growing season (Table 2).

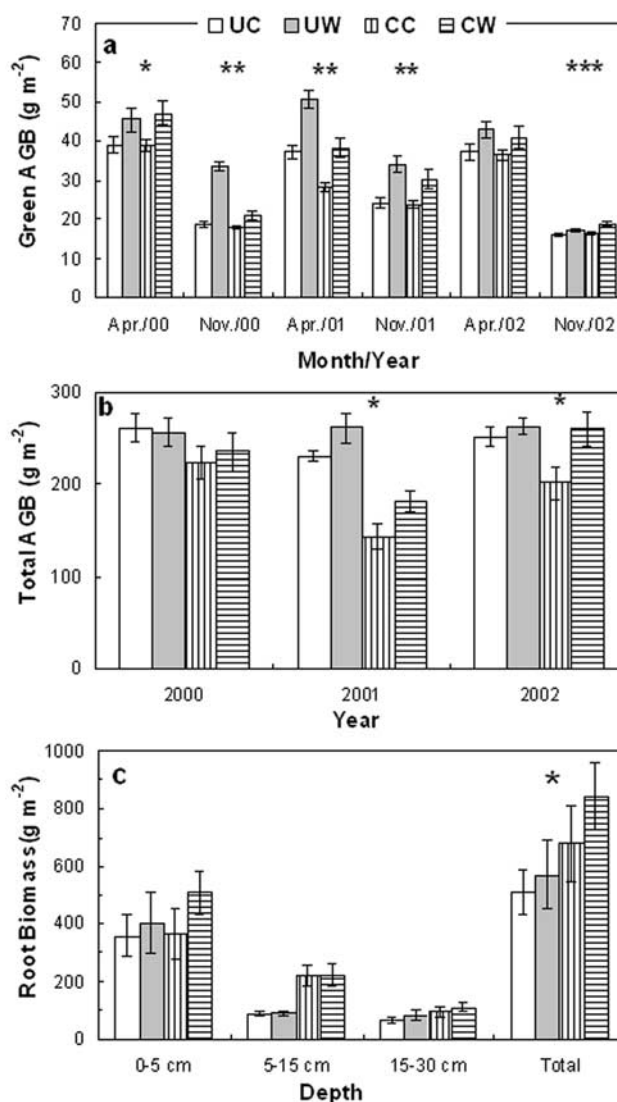### 3.2. Aboveground Biomass and Root Biomass

[17] Experimental warming significantly ($p < 0.05$) increased green aboveground biomass (AGB) in five out of the six measuring dates in spring (April) and autumn (November) except for April 2002 when warming caused a marginally significant increase ($p < 0.10$) in green AGB (Figure 1a). Green AGB was 19.0, 36.4, and 14.0% in spring and 49.3, 34.2, and 9.6% in autumn greater in the warmed than control plots in 2000, 2001, and 2002, respectively.

[18] The clipping effects on green biomass were not consistent across the six measuring dates (Figure 1a). Green AGB in the clipped subplots was significantly lower in November 2000 (25.4%, $p < 0.001$) and April 2001 (24.4%, $p < 0.001$) but significantly higher in November 2002 (5.9%, $p < 0.05$) than that in the unclipped subplots. There were no clipping effects on green AGB in other three measuring dates ($p > 0.05$). The interactive effects of warming and clipping on green AGB were only significant in November 2000.

[19] There was an interannual variability in the responses of total AGB to experimental warming (Figure 1b). Warming with infrared heaters did not affect total AGB in 2000 ($p > 0.05$) but significantly increased total AGB by 18.8% ($p < 0.05$) in 2001 and 15.7% ($p < 0.05$) in 2002. Clipping caused significant reductions in total AGB by 11.4 ($p < 0.01$), 34.2 ($p < 0.001$), and 10.1% ($p < 0.05$) in 2000, 2001, and 2002, respectively. The interactions of warming and clipping did not affect total AGB in 2000 and 2001 ($p > 0.05$) but had significant effects on total AGB in 2002 ($p < 0.05$, Figure 1b). In order to examine whether the interannual variation in the warming response of total AGB was related to weather condition, mean air temperature and total

precipitation before total AGB measurement each year were calculated using data from a meteorological station operated by Oklahoma Climatological Survey. The meteorological station is 500 m away from our experimental site. Mean air temperature was $16.1°$, $15.2°$, and $14.7°C$ and total precipitation was 549, 396, and 447 mm before total AGB measurement in 2000, 2001, and 2002, respectively. It seems that the significant increases in total AGB occurred in years (2001 and 2002) with lower mean air temperature irrespective of the lower total precipitation in 2001 and 2002.

[20] The main effects of both warming and clipping on total root biomass (0−30 cm, measured in January 2002)

Figure 1. Warming and clipping effects on (a) green aboveground biomass, (b) total aboveground biomass, and (c) root biomass (mean ± 1 SE). UC: Unclipped control, UW: Unclipped warmed, CC: Clipped control, CW: Clipped warmed. Stars represent the statistical significance of warming effect. One, two, and three asterisks: statistically significant at $p < 0.05$, 0.01, and 0.001, respectively.
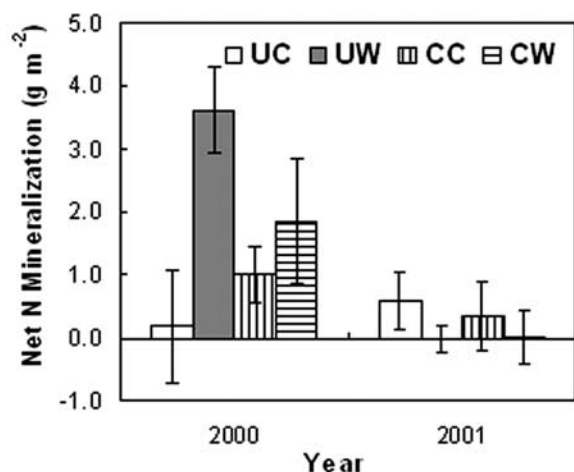
Figure 2. Warming and clipping effects on annual total net N mineralization (mean ± 1 SE). See Figure 1 for abbreviations.

were statistically significant (Figure 1c). Total root biomass in the warmed plots (706.7 g m^{-2}) was 18.8% (p < 0.05) greater than that in the control plots (595.1 g m^{-2}). Clipping also stimulated total root biomass by 40.7% (p < 0.05) in the clipped subplots (761.1 g m^{-2}) in comparison with the unclipped subplots (540.7 g m^{-2}) irrespective of the negative clipping effects on AGB. However, when analyzed by different depths, there were no differences in root biomass (p > 0.05) between the warmed and control plots at any of the three depths (0−5, 5−15, and 15−30 cm). Clipping significantly increased root biomass by 155.4% (p < 0.001) and 28.6% (p < 0.05) at the depths of 5−15 cm and 15−30 cm, respectively, but did not affect root biomass at the depth of 0−5 cm (p > 0.05). The percentage of root biomass at the depth of 0−5 cm in the total root biomass was significantly greater (p < 0.05) under warming (64.5%) than under control (59.8%). The percentages of root biomass in total root biomass in the clipped subplots were significantly lower at the depth of 0−5 cm (56.2%; p < 0.01) and higher at the depth of 5−15 cm (30.1%; p < 0.01) than those in the unclipped subplots (0−5 cm: 68.1%; 5−15 cm: 17.9%). The above results suggest that warming tended to increase the root density at the soil surface (0−5 cm) whereas clipping stimulated the root biomass and density at the subsurface in soils. There were no interactive effects of warming and clipping on either the amounts or the percentages of root biomass in any of the three depths (p > 0.05).

3.3. Net N Mineralization

[21] Neither the main effect of warming nor the main effect of clipping on net N mineralization was statistically significant (p > 0.05) in the first 2 years of the experiment (Figure 2). However, warming and clipping significantly interacted with each other to increase net N mineralization (p < 0.05) in 2000, but not in 2001. Net N mineralization in the warmed plots in 2000 was 1885% and 87% higher than that in the control plots without and with clipping, respectively. By contrast, warming decreased net N mineralization

by 104% and 99% in the unclipped and clipped subplots, respectively, in 2001. Clipping stimulated net N mineralization by 449% under control but reduced it by 48% under warming in 2000. In 2001, net N mineralization in the clipped subplots was 41 and 124% lower than in the unclipped subplots under control and warming, respectively. Our results that experimental warming tended to decrease soil N mineralization in 2001 were consistent with those of a laboratory microbial study in the same experiment [*Zhang et al.*, 2005].

3.4. Relationships of AGB With Temperature and Soil Available N Across Different Subplots

[22] To examine the direct effect of elevated temperature on AGB in different seasons, AGB was plotted against mean soil temperature 30 days before each biomass measurement across different subplots. The results showed
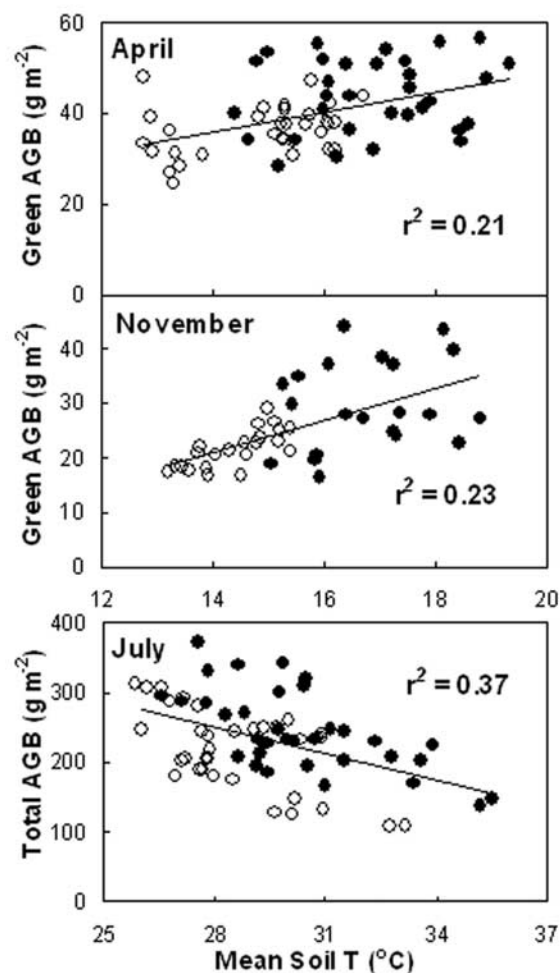
Figure 3. Linear correlations between green AGB in (top) spring and (middle) autumn and (bottom) total AGB in summer with monthly mean soil temperatures. Each data point stands for the average AGB of the two unclipped or clipped subplots in the control (open circle) or warmed (solid circle) plot from 2000 to 2002.
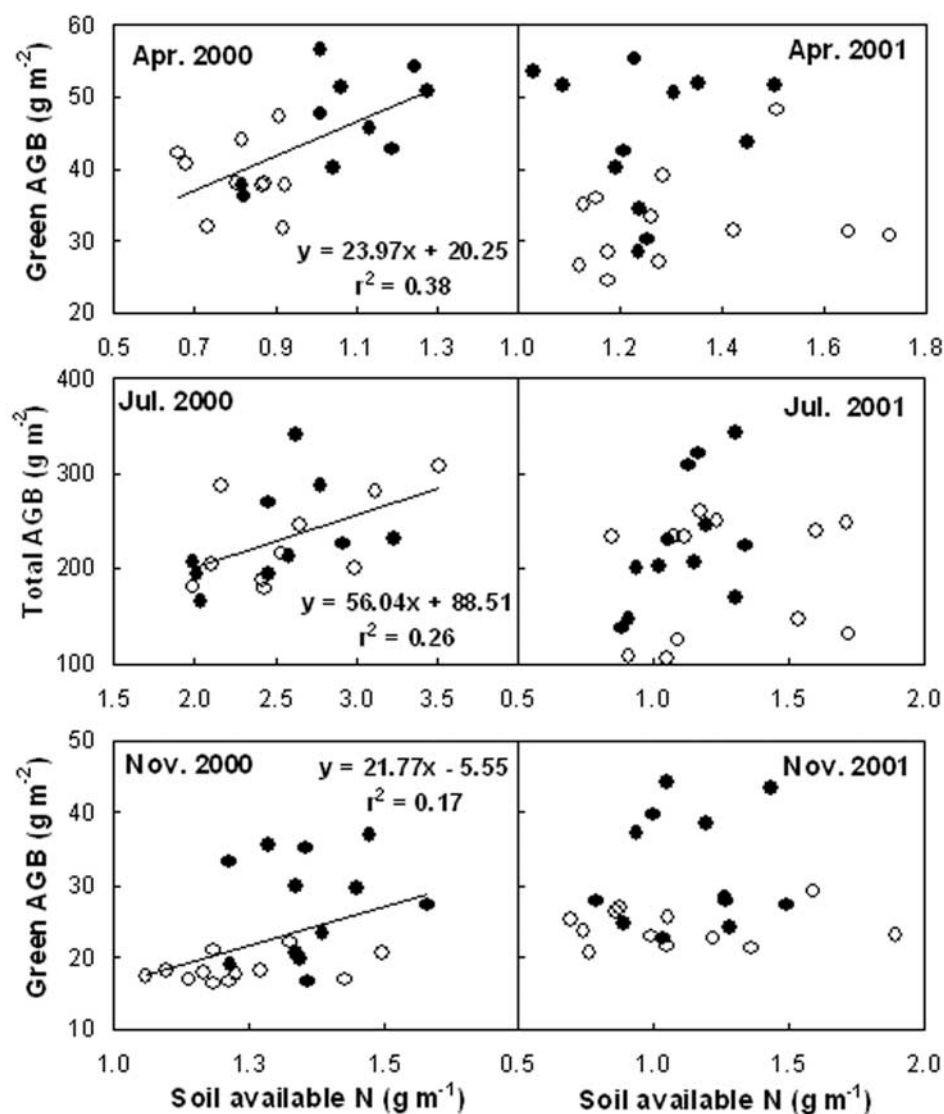
Figure 4. Relationships between green AGB in spring and autumn and total AGB in summer and soil available N 6 months before each biomass measurement. The positive correlation between AGB and available N was statistically significant only in the first year ($p < 0.01$). Each data point was the average AGB in the two unclipped or clipped subplots in each control (open circle) and warmed (solid circle) plot.

that green AGB was positively correlated with mean soil temperature in spring (April, $p < 0.001$) and autumn (November, $p < 0.001$). On the contrary, total AGB was negatively correlated with mean soil temperature in summer (July, $p < 0.001$, Figure 3).

[23] The relationship between the AGB increment and the magnitude of soil temperature increase in each paired (control versus warmed) plot showed similar patterns, i.e., positive in spring and negative in summer (data not shown). However, we found no such relationship in autumn, likely because of the large difference in green AGB between the clipped and unclipped subplots in autumn. The above results suggest differential effects of elevated temperature in affect-

ing aboveground biomass in different seasons. Soil water availability might act as a potential confounding factor, but our data showed no significant correlation ($p > 0.05$) between AGB and soil moisture across different subplots.

[24] It is well documented that elevated soil temperature could stimulate net N mineralization and availability and thus enhance plant growth [*Rustad et al.*, 2001; *Shaw and Harte*, 2001; *Melillo et al.*, 2002]. In order to examine the indirect warming effect via changing soil N availability, AGB in the first 2 years was plotted against the average soil N availability 6 months before each biomass measurement across the different subplots. AGB showed positive linear correlations with soil N availability in 2000 (Figure 4, left).

Available soil N accounted for 38% (p < 0.01), 26% (p < 0.05), and 17% (p < 0.05) of the variability in AGB in spring, summer, and autumn, respectively. However, the linear correlations disappeared in 2001 (p > 0.05, Figure 4, right).

3.5. Soil Respiration

[25] The temporal dynamics of soil respiration generally followed the seasonal patterns of soil temperature and were opposite to those of soil moisture during the time period from January 2000 to December 2002 (Figures 5a and 5b). However, frequent droughts (August–September 2000, July 2001, August 2001, July 2002) caused lower soil respiration rates in summer irrespective of the higher soil temperature. During the 3-year experimental period, soil respiration showed an exponential relationship with soil temperature with $r^2 = 0.65$ (p < 0.001) in the unclipped control subplots. A polynomial function described the relationship between soil respiration and soil moisture with a correlation coefficient of $r^2 = 0.34$ (p < 0.001). We combined the two functions to examine the interactive effects of soil temperature (T) and soil moisture (M) in regulating the seasonal dynamics of soil respiration (R),

$$R = \alpha e^{\beta T} \frac{\chi M^2 + \delta M + \varepsilon}{\chi M_0^2 + \delta M_0 + \varepsilon}, \quad (1)$$

where M_0 is the soil moisture content at which soil respiration is greatest; α, β, χ, δ, and ε are constants. The inclusion of soil temperature and moisture explained 82% (p < 0.001) of the seasonal changes in soil respiration. The above results suggest that temperature is the dominant environmental factor in regulating seasonal dynamics of soil respiration across years and water availability is less important.

[26] Soil respiration was greater in the warmed than control plots in most of the measuring dates (Figure 5c). Clipping in July caused immediate and substantial reductions in soil respiration in 2000 and 2002, but not 2001. Lower soil respiration rates as the consequences of clipping lasted for one month in 2000 (the end of July to the end of August) and 2 months in 2002 (the end of July to the end of September). The clipping effect on soil respiration was confounded by the two severe droughts in summer of 2001, leading to no obvious changes in soil respiration in the clipped comparing to unclipped subplots. Sometimes in spring and autumn when soil moisture was not limiting, soil respiration was greater in the clipped than unclipped subplots, which might have resulted from the higher soil temperature caused by clipping (Figure 5c).

[27] The main effect of warming on annual mean soil respiration was statistically significant only in 2001 (15.6%, p < 0.05, Figure 6). No effects of clipping or the interactions of warming and clipping on annual mean soil respiration were found in any of the 3 years. Across the 12-month period in 2002, neither warming nor clipping or their interactions had any effect on the annual averages of heterotrophic respiration (Figure 6). On average, heterotrophic respiration accounted for 62% of the annual mean soil respiration. This value was slightly lower than that (70%)

found in another experiment, in which plants were clipped weekly at the soil surface [Wan and Luo, 2003].

[28] During the 3-year experimental period from January 2000 to December 2002, annual mean soil respiration showed a positive linear correlation (p < 0.001) with total AGB in the same year across different subplots (Figure 7a). The warming responses (percent change in the warmed compared to control plots) of annual mean soil respiration showed a positive linear correlation (p < 0.05, Figure 7b) with the warming responses of total AGB during the 3 years. The slope in Figure 7b suggest that for one unit increase in total AGB, there was approximately 39% increase in annual mean soil respiration under warming compared to under control. Given that root respiration contributed approximately 38% to the annual mean soil respiration and that warming did not affect heterotrophic respiration (see above), the 39% stimulation of total soil respiration in response to one unit increment in AGB could be primarily ascribed to the enhanced root respiration under warming.

[29] Soil organic carbon content measured in November 2001 explained 53% (p < 0.001) of the variation of heterotrophic respiration in 2002 across different subplots (Figure 7c). The linear correlations between soil respiration and AGB and between heterotrophic respiration and soil organic C suggest that C substrate was the main factor in regulating soil C release across the spatial scale at our experimental site.

4. Discussion
## 4.1. Clipping Effect on the Tallgrass Prairie

[30] Clipping significantly reduced total AGB during all the 3 years whereas it had no consistent effect on green AGB. However, clipping stimulated total root biomass and increased the percentage of root biomass at the depth of 5–15 cm but decreased the percentage of root biomass at the depth of 0–5 cm, which suggested indirect effects of clipping on plant growth through affecting soil moisture (especially at the soil surface). The differential responses of the aboveground and belowground biomass to clipping might be caused by the shifts in the partition of photosynthate between plant roots and aboveground parts. The clipping effect on annual mean soil respiration was not statistically significant in any of the 3 years (Figure 6). However, soil respiration in the clipped subplots was found to be lower within 1 month in 2000 and 2 months in 2002 of the clipping treatment. By contrast, clipping increased soil respiration sometime in spring and autumn, largely caused by the higher soil temperature in the clipped subplots.

[31] Extrapolation of the short-term clipping effect on soil respiration observed in our study is imprecise. As shown in this study and in previous studies [Wan and Luo, 2003], C supply plays an important role in regulating soil respiration (including root and heterotrophic respirations) in the tallgrass prairie. Clipping removes aboveground plant materials and reduces the input of organic matter into soil from plant litter; thus it will eventually decrease soil organic carbon and heterotrophic respiration in the long term. In addition, clipping removes N (1.5 g m^{-2} yr^{-1}) from the ecosystem and reduces N release from decreased litter input, gradually
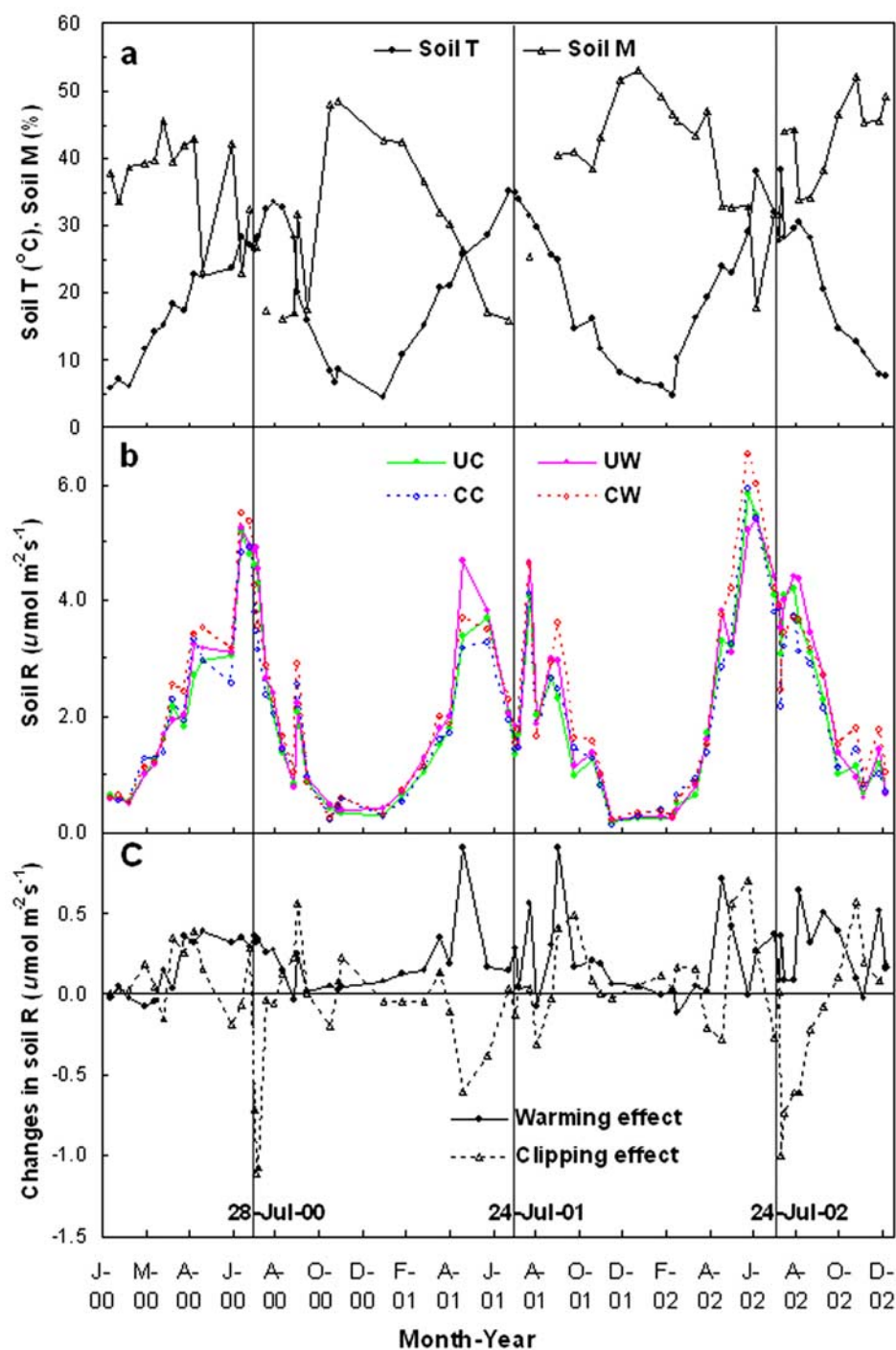
Figure 5. Seasonal dynamics of (a) soil temperature (line with solid cycles) and moisture (line with blank triangles) in the unclipped control subplots, (b) soil respiration under the four treatments, and (c) changes in soil respiration in response to warming (solid line with solid cycles) and clipping (dashed line with blank triangles) from January 2000 to December 2002. The three vertical black lines and the dates refer to the time when aboveground biomass was clipped. See Figure 1 for abbreviations.
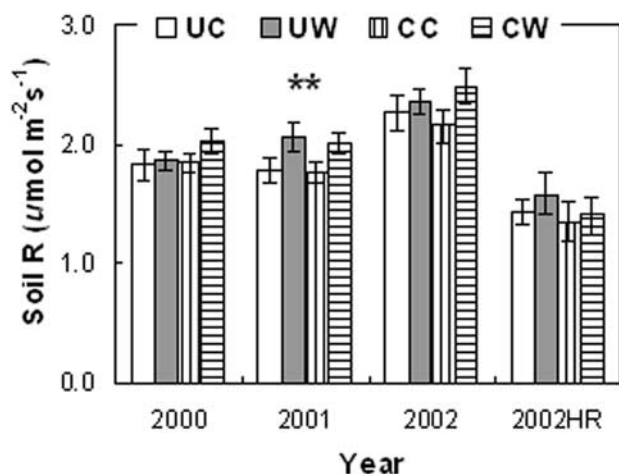
Figure 6. Warming and clipping effects on annual mean soil respiration from 2000 to 2002 and heterotrophic respiration in 2002 (mean ± 1 SE). See Figure 1 for abbreviations.

1999; *Norby and Luo*, 2004]. In a subalpine coniferous forest in Colorado, *Huxman et al.* [2003] found that increases in temperature have a positive effect on net ecosystem exchange during spring and a negative effect during middle summer. Similarly, growth of white spruce in Alaska shows a 40% decrease in summer and a 36% increase in spring as a result of long-term climate warming [*Wilmking et al.*, 2004]. The negative direct effects of elevated temperature on total AGB in summer offset the positive effects in spring and autumn, leading to less C
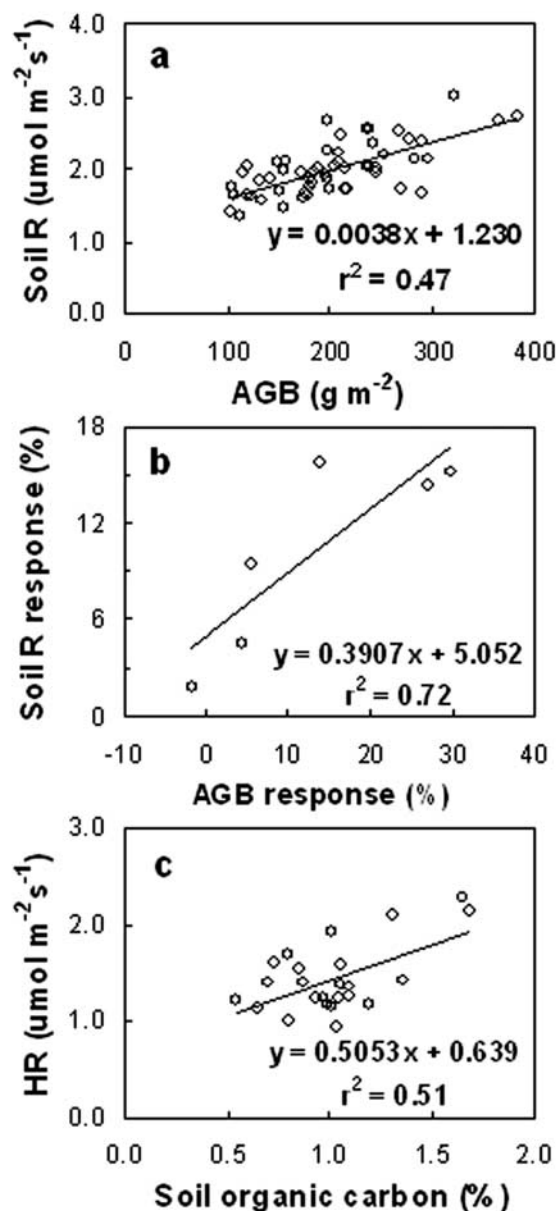
leading to lower soil N availability, plant growth, and NPP. The decreased plant growth and NPP will, in turn, cause lower root respiration.

4.2. Direct Warming Effects in Different Seasons

[32] Because the rates of many biological processes typically peak at some intermediate temperature, the direct effects of warming could vary with temperatures in different seasons [*Aber and Melillo*, 1991; *Lamber et al.*, 1998; *Shaver et al.*, 2000; *Rustad and Norby*, 2002]. Global warming reduces the likelihood that plants will be exposed to their lower thermal limits. Elevated temperature could directly enhance NPP because plant photosynthesis increases more than respiration when temperature is low, leading to a net carbon uptake in plants [*Aber and Melillo*, 1991; *Lamber et al.*, 1998]. Our results showed that green AGB in the warmed plots was significantly greater than in the control plots in spring and autumn and that, across different subplots, green AGB was positively correlated with the monthly mean soil temperature before each green biomass measurement.

[33] Global warming could also potentially increase the risk of plant exposure to the upper thermal limits in the summer. For plants and ecosystems that have adapted to regional climates, summer temperatures are near the optimal range or upper thermal limit of photosynthesis and growth for plants, which is inferred from the positive linear correlation between the temperature optimum for canopy CO_2 uptake and the mean summer temperatures in the forests across North America and Europe [*Baldocchi et al.*, 2001]. Therefore elevated temperatures in summer would decrease photosynthesis and increase respiration, resulting in a net carbon loss from plants and less AGB at the ecosystem scale [*Aber and Melillo*, 1991; *Ryan*, 1991; *Lamber et al.*, 1998]. Our observation that elevated temperature in summer caused less total AGB increment was consistent with other experiments [*Mitchell et al.*, 1993; *Gunn and Farrar*,

Figure 7. Linear correlations between (a) annual mean soil respiration and total AGB (from 2000 to 2002), (b) the warming responses of annual mean soil respiration and those of total AGB (from 2000 to 2002), and (c) annual mean heterotrophic respiration in 2002 and soil organic carbon measured in November 2001.

uptake in ecosystems. The opposite directions of warming effects on plant growth and AGB in spring and summer could make it more complicated to project the future changes in ecosystem C cycling.

4.3. Indirect Warming Effect Through Extending the Length of Growing Season

[34] Warming with infrared radiators extended the growing season by approximately 19 days in the Oklahoma tallgrass prairie (Table 2). Lengthened growing seasons under warming have also been found in other studies. In a field experiment with the same heating facility (infrared radiators) in a subalpine meadow, warming advanced the date of snowmelt by almost 1 week relative to controls [*Price and Waser*, 1998]. *Norby et al.* [2003] also found that a 4°C increase in air temperature manipulated with open top chamber extended the length of growing season by 2–3 weeks for tree seedlings in Tennessee. Increasing evidence has shown that global warming can extend the length of growing season across the different biomes on the Earth [*Post and Stenseth*, 1999; *Sparks and Carey*, 1995; *Price and Waser*, 1998; *Menzel and Fabian*, 1999; *Chmielewski and Rötzer*, 2001; *Menzel et al.*, 2001; *Peñuelas and Filella*, 2001; *Fitter and Fitter*, 2002; *Lucht et al.*, 2002; *Peñuelas et al.*, 2002; *Walther et al.*, 2002; *Root et al.*, 2002; *Parmesan and Yohe*, 2003] owing to greater warming in winter, spring, and autumn than in summer [*Houghton et al.*, 2001]. As a consequence, the threshold temperature for plant growth is reached earlier in spring and later in autumn, leading to an extended length of growing season.

[35] The extended growing season under warming could accelerate leaf emergence and unfolding in spring and delay leaf senescence in autumn. These phenological changes would result in a longer favorable period for plant photosynthesis and growth, leading to increased leaf area index and green biomass in spring and autumn [*Oberbauer et al.*, 1998; *Menzel and Fabian*, 1999; *Peñuelas and Filella*, 2001; *Peñuelas et al.*, 2002; *Myneni et al.*, 1997; *Norby et al.*, 2003; *Leinonen and Kramer*, 2002]. At our experimental site, we observed significant increases in the percent coverage and the number of living stems of western ragweed (*Ambrosia psilostachya* DC.) in spring and autumn, leading to an enhanced ragweed AGB in the warmed plots in comparison with the control plots [*Wan et al.*, 2002a]. Our results were consistent with those from other warming experiments. In the subarctic and arctic tundra ecosystems, the extended growing season caused an earlier leaf expansion in spring [*Chapin and Shaver*, 1996; *Oberbauer et al.*, 1998; *Arft et al.*, 1999; *Hartley et al.*, 1999] and a greater green leaf biomass of *Dryas* in autumn [*Welker et al.*, 1997].

[36] The phenological difference between the control and warmed plots could lead to enhanced gross photosynthesis [*Hobbie and Chapin*, 1998] and plant growth [*Norby et al.*, 2003], affecting ecosystem C cycling [*Keeling et al.*, 1996; *Myneni et al.*, 1997; *Schimel et al.*, 2001; *Lucht et al.*, 2002]. For example, a 5 to 10 day extension of growing season in autumn increased gross primary production by around 500 kg C ha^{-1} in a deciduous forest in Massachusetts [*Goulden et al.*, 1996]. Synthesis of results

from a global eddy flux network suggests that net CO_2 exchange of temperate broadleaved forests increased by about 5.7 g C m^{-2} d^{-1} with a 1-day extension of growing season [*Baldocchi et al.*, 2001]. A model simulation also showed that a 1-day change in the length of growing season would increase net ecosystem production by 1.6% and gross primary production by 0.5% in the eastern U.S. deciduous forests [*White et al.*, 1999]. At the global scale, *Keeling et al.* [1996] observed that the amplitude of the seasonal CO_2 cycle in the Northern Hemisphere had been increasing since the early 1960s and that the springtime decline in atmospheric CO_2 concentration had advanced by about 7 days, which were attributed to the lengthened growing season associated with global warming.

4.4. Indirect Warming Effect Through Enhancing Net N Mineralization

[37] Elevated temperatures have been shown to increase net N mineralization across different biomes [*Rustad et al.*, 2001; *Shaw and Harte*, 2001; *Melillo et al.*, 2002]. The enhanced net N mineralization and availability would stimulate plant N uptake and growth, leading to increased NPP. Our results showed that elevated temperature tended to increase net N mineralization in the first year (2000) but to decrease it in the second year (2001). In a subalpine meadow manipulated with the same warming facility, *Shaw and Harte* [2001] also found interannual variability in the warming effects on soil N mineralization depending on soil moisture and vegetation type. The interannual variability in net N mineralization observed in our study was not consistent with that found in the Harvard forests with soil warming, where net N mineralization rate in the warmed plots was constantly higher than in the control plots over a decade [*Melillo et al.*, 2002]. Interannual variations in warming-induced net N mineralization could affect plant N uptake and use and temporally change the coupling of C and N cycling in the tallgrass prairie.

4.5. Indirect Warming Effect Via Reducing Soil Moisture

[38] Stepwise multiple regression analyses were conducted to examine the potential effects of soil moisture on green and total aboveground biomass and annual mean soil respiration across different subplots. The results showed that soil moisture was never a significant factor in regulating AGB or annual mean soil respiration across the spatial scale in our experimental site. The statistically insignificant effects of soil moisture on AGB and annual mean soil respiration might have been attributed to two possible reasons. First, during the first 3 years, warming caused a small significant reduction (3.7%, $p < 0.05$) in soil moisture only in the third year. Second, shift in species composition under warming might help to explain. In another study (S. Wan et al., unpublished data, 2005], we found that the increased total AGB under warming primarily resulted from the enhanced growth, biomass productivity, and dominance of C_4 species whereas biomass of C_3 species did not change. In comparison with C_3 species, C_4 species have higher water use efficiency. The enhanced dominance of C_4 species

might have compensated for the negative warming effects through reducing soil moisture.

4.6. Response of Soil Respiration to Warming

[39] Warming did not affect annual mean soil respiration in the first [see *Luo et al.*, 2001] and third year in the tallgrass prairie. However, total soil respiration significantly increased in the second year in the warmed comparing to control plots. The warming responses of soil respiration showed a positive linear correlation with those of AGB across the 3 years, suggesting that the increased soil respiration largely resulted from enhanced belowground C allocation and root respiration. The proportional changes in soil respiration to those of AGB not only support our previous conclusion of C substrate regulation on soil respiration [*Wan and Luo*, 2003], but also indicate that there are coupled responses of ecosystem C uptake (AGB) and release (soil respiration) to warming. The proportional stimulation of soil respiration to that of AGB can limit the C sequestration capacity in the tallgrass prairie ecosystem under global warming.

4.7. Differential Responses of C and N Cycling to Warming

[40] Our results showed that warming tended to increase net N mineralization in the first year (2000) but to decrease it in the second year (2001). However, total AGB did not show any response to elevated temperature in 2000 but significantly increased in 2001. Total soil respiration showed proportional changes to those of total AGB. Therefore our results suggest temporally differential responses of C (AGB and soil respiration) and N (net N mineralization) processes to experimental warming in the short-term.

[41] The differential responses of C and N processes to warming in the first year of the experiment might result partly from the complex interactions between plants and microbes and partly from a delicate balance between microbial immobilization and mineralization. Plants in the grassland ecosystem are strongly N limited [*Vitousek and Howarth*, 1991; *Burke et al.*, 2002], which is implied by the significant linear correlation between AGB and soil available N in the first year (Figure 4, left). The direct effects of warming could not lead to a significant increase in total AGB in the first year. As a consequence, C allocation to rhizosphere processes might not change much either, leading to the statistically insignificant changes in annual mean soil respiration. On the other hand, the tallgrass prairie ecosystem in the southern Great Plains has a warm climate. N cycling is fast and the N pool sizes in plants and soils are relatively small, leading to the high turnover rates of N. Warming could accelerate N turnover in the ecosystems. In the tallgrass prairie ecosystem, microbes are mostly likely limited by C substrate [*Garcia and Rice*, 1994]. The faster N turnover under warming might not stimulate microbial immobilization, resulting in an enhanced net N mineralization in 2000.

[42] The increased N mineralization and availability in the first year might have stimulated plant N uptake. Most of the dominant C_4 plants in the ecosystem are perennial species with substantial rhizomes. The perennial species in the tallgrass prairie can store approximately 60% of their annual N in the belowground tissue at the end of growing season [*Adams and Wallace*, 1985]. The enhanced plant N uptake and storage in the first year could stimulate the canopy leaf area development and the leaf- and canopy-level photosynthesis [*Field and Mooney*, 1986] in the subsequent year, contributing to the stimulated plant growth and aboveground and belowground biomass. The enhanced NPP in 2001 would increase the belowground C inputs, which, on the one hand, stimulated soil respiration. On the other hand, the increased belowground C input alleviated the microbial C limitation, leading to enhanced microbial N immobilization and reduced net N mineralization in the second year. Thus net N mineralization decreased by 104% and 99% in 2001 in the unclipped and clipped subplots, respectively.

[43] Correlation analysis also supported the results that C and N processes differentially responded to elevated temperature. The significant linear correlations between AGB and N availability in the first year suggest that there was a limitation of available soil N on plant growth and total AGB irrespective of the enhanced net N mineralization in 2000. However, the enhanced plant N uptake and storage in the first year ameliorated the N stress and stimulated plant growth and total AGB in the second year. The stimulation of plant production by plant N accumulation was also shown in a Kansas tallgrass prairie under fire perturbation [*Blair*, 1997]. One-year time lags of biomass in response to a severe drought were also found in a Minnesota grassland [*Haddad et al.*, 2002] and a Kansas tallgrass prairie [*Briggs and Knapp*, 1995], which could be attributable to the feedback of litter and/or nutrient on primary production following drought.

[44] In conclusion, clipping significantly reduced total AGB and increased root biomass, but had no effect on net N mineralization and annual mean soil respiration. Experimental warming differentially affected the C (AGB and soil respiration) and N (mineralization) processes in the tallgrass prairie. The direct effect of warming on AGB could be both positive and negative depending on seasons. Warming had also indirect effects on AGB through extending growing season and changing soil N mineralization and availability. The linear correlation between the warming responses of soil respiration and those of AGB suggests coupled changes in the ecosystem C uptake and release, which might result in a limited C sequestration in the tallgrass prairie under global warming. Given the interannual variations in the warming responses of AGB, net N mineralization, and soil respiration observed in our study, long-term experiments are needed before generalizations and extrapolations can be made.

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