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GRADUATE COLLEGE

RESPONSES OF A TALLGRASS PRAIRIE TO EXPERIMENTAL WARMING

A dissertation

SUBMITTED TO THE GRADUATE FACULTY

In partial fulfillment of the requirement for the degree of

DOCTOR OF PHILOSOPHY

By

SHIQIANG WAN

Norman, Oklahoma

2002

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RESPONSES OF A TALLGRASS PRAIRIE TO EXPERIMENTAL WARMING

A Dissertation Approved for the Department of Botany and Microbiology

By

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To my lovely daughter, JIAN YUAN,

and her generation

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ABSTRACT

This comprehensive research project was designed to examine the potential responses of a tallgrass prairie in the US Great Plains to global warming under two land use scenarios. A factorial design was used with warming as the primary factor nested with clipping. Infrared heaters were used to simulate climatic warming and clipping was used to mimic mowing for hay or grazing.

Changes in microclimate were quantified with an attempt to address the effectiveness of infrared heaters in simulating climatic warming in the real world. The warming treatment significantly increased daily mean and minimum air temperatures by 1.1 °C and 2.3 °C, respectively, but had no effect on daily maximum air temperature, resulting in a reduced diurnal air temperature range. Infrared heaters substantially increased daily maximum (2.5 and 3.5 °C), mean (2.0 and 2.6 °C), and minimum (1.8 and 2.1 °C) soil temperatures in both the unclipped and clipped subplots. Clipping also significantly increased daily maximum (3.4 and 4.3 °C) and mean (0.6 and 1.2 °C) soil temperatures, but decreased daily minimum soil temperature (1.0 and 0.6 °C in the control and warmed plots, respectively). Daily maximum, mean, and minimum soil temperatures in the clipped, warmed subplots were 6.8, 3.2 and 1.1°C higher than those in the unclipped, control subplots. Infrared heaters caused a reduction of 11.0% in soil moisture in the clipped subplots but not in the unclipped subplots. Clipping reduced soil moisture content by 17.7% and 22.7% in the control and warmed plots, respectively. Experimental warming and clipping interacted to exacerbate soil moisture loss (26.7%). Overall,

infrared heaters simulated climate warming well by enhancing downward infrared radiation and by reducing the diurnal air temperature range.

Differentiating between the direct and indirect effects of elevated temperature on net primary production will substantially improve our understanding of the mechanisms by which global warming affects carbon (C) cycling in terrestrial ecosystems. Experimental warming in the tallgrass prairie significantly increased green aboveground biomass (AGB) in early spring and late autumn when temperatures were low, resulting from both the positive direct effect on the ratio of plant photosynthesis to respiration and the positive indirect effect through extending the growing season. On the contrary, elevated temperature had a negative direct effect on peak AGB in summer when temperatures were high, offsetting the positive effect. Our observations, for the first time, provided experimental evidence on the counterbalance effects of elevated temperature on biomass accumulation at low and higher temperature ranges.

C and nitrogen (N) processes interact to substantially influence ecosystem function under climatic warming. I also examined the potential responses of C and N processes to elevated temperature. Warming increased net N mineralization by 1885% and 87% in the first year but reduced it by 81% and 34% in the second year in the unclipped and clipped subplots, respectively. Elevated temperature did not affect peak AGB in 2000, but significantly increased the peak AGB 13% and 27% without and with clipping in 2001. The results suggest that there was a time lag between the response of peak AGB and that of net N mineralization. The differential responses and a negative feedback between C and N processes could lead to the interannual variability of net primary production and limit long-term C uptake by ecosystems.

Climatic warming has social-economic impacts. The responses of an allergenic species, western ragweed (*Ambrosia psilostachya* DC.), to experimental warming and clipping were investigated from 1999 to 2001. Warming increased ragweed stems by 88% when not clipped and 46% when clipped. Clipping increased ragweed stems by 75% and 36% in the control and warmed plots, respectively. In 2001, warming resulted in a 105% increase in ragweed AGB, and the ratio of ragweed AGB to total AGB increased by 79%. Dry mass per ragweed stem in the warmed plots was 37% and 38% greater than that in the control plots in 2000 and 2001, respectively. Although warming caused no difference in pollen production per stem, total pollen production increased by 84% ($P < 0.05$) because there were more ragweed stems. Experimental warming significantly increased pollen diameter from 21.2 μm in the control plots to 23.9 μm in the warmed plots (a 13% increase). The results from our experiment suggest that global warming could aggravate allergic hazards and thereby jeopardize public health.

Chapter One

Introduction

Atmospheric concentrations of greenhouse gases such as CO_2, CH_4, and N_2O, have increased dramatically since the beginning of the industrial revolution largely due to human activities such as fossil fuel combustion and land-use change (IPCC 2001). These gases have the capability to trap heat in the atmosphere by absorbing infrared radiation reflected by the earth's surface. Considerable evidence is now available showing that global warming due to the elevated concentrations of these greenhouse gases have increased the earth's surface temperature by about 0.6 °C over the past century (Houghton *et al.* 2001, IPCC 2001). Current predictions based on general circulation models indicate that the global mean temperature will increase by an additional 1.4-5.8 °C in the 21st century (IPCC 2001).

The unprecedented changes in global mean temperature could profoundly alter the structure and function of ecosystems. During the past two decades, the ecosystem responses to global warming have attracted great research efforts. A number of warming experiments have been conducted to simulate climatic change in the real world (Shaver et al. 2000, Rustad et al. 2001, Rustad and Norby 2002). Ecosystem warming experiments

hold a great potential for providing insights into mechanisms underlying responses of terrestrial ecosystems to climatic change in coming decades. A network of Ecosystem Warming Studies (NEWS) under the auspices of Global Change and Terrestrial Ecosystems (GCTE) has been established recently (Rustad and Norby 2002). The GCTE-NEWS initially includes 32 experimental warming sites, representing four broadly defined biomes: high tundra, low tundra (including a temperate peat bog), forest, and grassland. However, it is impossible for those 32 warming sites to include all the major biomes on the earth. More and more warming sites are being established to fill the gaps of the GCTE-NEWS in representing the major vegetation types.

A warming experiment has been conducted in an Oklahoma tallgrass prairie since November 1999. This warming site provides a geographical reference point in the US Great Plains. Grasslands are one of the major biomes at both regional and global scales and occupy 47% of the earth's land area (Williams et al. 1968) and 54% of the conterminous United States (USDA 1974). Changes in the structure and function of the tallgrass prairie, one of the major vegetation types in the US Great Plains, could have substantial influence on the regional ecological and social-economic systems.

Global warming happens by enhancing the downward infrared radiation, which is dissipated through one or a combination of three major energy pathways: sensible heat, latent heat and soil conductive heat fluxes. The three energy pathways are responsible for warming of the air, increases in evapotranspiration, and heating of the soil (Shaver *et al.* 2000). Different heating facilities have been used to manipulate air and/or soil temperatures in the field. These facilities include: (1) greenhouses and open-top chambers (Chapin and Shaver 1985; Havström *et al.* 1993, Kennedy 1995a, b, Norby et al. 1997,

Oechel *et al.* 1998, Richardson *et al.* 2000), (2) above- and belowground electric-resistance wires and pipes (Rybost *et al.* 1975 a, b, Chapin and Bloom 1976, Van Cleve *et al.* 1990, Peterjohn *et al.* 1993, Bergh and Linder 1999, Hillier *et al.* 1994), (3) infrared reflectors (Zeiher *et al.* 1994, Luxmoore *et al.* 1998), and (4) infrared heaters (Harte *et al.* 1995, Nijs *et al.* 1996, Bridgham *et al.* 1999). Depending on their heating mechanisms, these facilities may vary in manipulating the three energy pathways and hence have different effects on the three aspects of microclimate (e.g., air temperature, soil temperature, and soil moisture). Quantification of microclimate changes will not only help compare different warming facilities but also facilitate interpretation and comparison of warming effects on ecosystems across different habitats (Shaver *et al.* 2000, Rustad *et al.* 2001). Therefore, the first study in this thesis was conducted to examine the effectiveness of infrared heaters used in the experiment in simulating global warming in the real world.

With its potential effects on almost all the physical, chemical, and biological processes, temperature can directly and indirectly influence various ecosystem processes. One of the processes, carbon (C) cycling, has attracted substantial attention from scientists, politicians and the public because changes in the C fluxes [e.g., net primary production (NPP) and heterotrophic respiration] between the biosphere and the atmosphere may impact future climatic change positively or negatively. Elevated temperature could increase or decrease NPP directly through affecting the ratio of plant photosynthesis to respiration (Aber and Melillo 1991, Lamber *et al.* 1998). Global warming also could affect NPP indirectly by extending the length of the growing season (Shaver *et al.* 2000, Rustad *et al.* 2001, Rustad and Norby 2002). Much evidence

hasshown increasing length of the growing season with rising global mean temperature (Post and Stenseth 1995, Sparks and Carey 1995, Menzel and Fabian 1999, Chmielewski and Rötzer 2001, Menzel *et al.* 2001, Peñuelas and Filella 2001, Peñuelas *et al.* 2002, Walther *et al.* 2002) due to greater warming in winter, spring and fall than in summer (Houghton *et al.* 2001). The direct and indirect effects of experimental warming on green aboveground biomass (AGB) in a tallgrass prairie were investigated in the second study.

Elevated temperature could also influence C cycling indirectly through alteration in nitrogen (N) cycling. N is the most limiting nutrient on NPP in natural terrestrial ecosystems (Binkley 1986, Chapin et al. 1986, Vitousek and Howarth 1991). The coupled C and N cycling can form a positive or negative feedback loop, leading to divergence or convergence of NPP across different ecosystems (Hobbie 1992, Tateno and Chapin 1997, Knops et al. 2002). Model simulations have shown that the warming effect on global C cycling is sensitive to these feedbacks (Schimel et al. 1994, McGuire et al. 1997, Den Elzen et al. 1997). However, it is unclear how temperature-induced changes in C and N processes responding at different timescales contribute to the overall pattern in ecosystem responses. Therefore, the third studies was designed to elucidate the coupling of C and N cycles in the tallgrass prairie and their responses to global warming.

The ecosystem responses to elevated temperature would not only affect the global climate by influencing C cycling, but also have potential impacts on public health. For example, it has been found that allergies among the general population have been increasing during the past half century, coinciding with the dramatic changes in the global environment since the 1950s (Platt-Mills and Carter 1997, Woolcock and Peat 1997, AAAAI 2000). Allergic diseases affect approximately 50 million people and cost

have health care cost about 18 billion dollars each year in the United States alone (AAAAI 2000). Ragweed pollen is the number one cause of human allergy in autumn (AAAAI 2000). Previous studies have shown that elevated atmospheric CO_2 concentration and land use change could stimulate pollen production of ragweed (Russell 1980, Emberlin 1994, Ziska, and Caulfield 2000a, b, Wayne *et al.* 2002). However, it has not been examined whether elevated temperature could lead to increased pollen production of ragweed. The fourth and last study in this work was used to detect the potential response of western ragweed (*Ambrosia psilostachya* DC.), an allergenic species, and its pollen production to experimental warming.

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Chapter Two

Changes in microclimate induced by experimental warming and clipping

ABSTRACT

To facilitate interpretation and comparison of warming effects on ecosystems across different habitats, it is imperative to quantify changes in microclimate induced by warming facilities. This paper reports observed changes in air temperature, soil temperature and soil moisture content under experimental warming and clipping in a tallgrass prairie in the US Great Plains. A factorial design was used with warming as the primary factor nested with clipping as the secondary factor. Infrared heaters were used to simulate climatic warming and clipping to mimic mowing for hay or grazing. The warming treatment significantly increased daily mean and minimum air temperatures by 1.1 °C and 2.3 °C, respectively, but had no effect on daily maximum air temperature, resulting in reduced diurnal air temperature range. Infrared heaters substantially increased daily maximum (2.5° and 3.5 °C), mean (2.0° and 2.6 °C), and minimum (1.8° and 2.1 °C) soil temperatures in both the unclipped and clipped subplots. Clipping also significantly increased daily maximum (3.4° and 4.3 °C) and mean (0.6° and 1.2 °C) soil temperatures, but decreased daily minimum soil temperature (1.0° and 0.6 °C in the control and warmed plots, respectively). Daily maximum, mean, and minimum soil temperatures in the clipped, warmed subplots were 6.8°, 3.2° and 1.1°C higher than those in the unclipped, control subplots. Infrared heaters caused a reduction of 11.0% in soil moisture in the clipped subplots but not in the unclipped subplots. Clipping reduced soil moisture content by 17.7% and 22.7% in the control and warmed plots, respectively. Experimental warming and clipping interacted to exacerbate soil moisture loss (26.7%). Overall, infrared heaters simulated climate warming well by enhancing all the three energy pathways and by reducing the diurnal air temperature range.

Keywords: clipping, climate warming, infrared heater, soil moisture, solar radiation, tallgrass prairie, temperature, vapor pressure deficit, wind speed.

INTRODUCTION

Climate warming has increased global mean temperature by about 0.6 °C over the past century and will continue to increase it by 1.4° to 5.8 °C in the 21st century (Houghton *et al.* 1995, 1996, IPCC 2001). Substantial efforts have been made to study the potential impacts of climate warming on terrestrial ecosystems by manipulating temperature in the field with a variety of warming facilities. Those facilities include: (1) greenhouses and open-top chambers (OTCs) (Chapin and Shaver 1985, Havström *et al.* 1993, Oechel *et al.* 1998, Richardson *et al.* 2000), (2) soil-heating pipes/wires, such as buried fluid pipes (Rybost *et al.* 1975 a, b, Chapin and Bloom 1976), buried electric-resistance wires (Van Cleve *et al.* 1990, Peterjohn *et al.* 1993, Bergh and Linder 1999), and aboveground electric-resistance wires (Hillier *et al.* 1994), (3) infrared reflectors (Zeiher *et al.* 1994, Luxmoore *et al.* 1998), and (4) infrared heaters (Harte *et al.* 1995, Nijs *et al.* 1996, Bridgham *et al.* 1999). It has not been carefully examined, however, how effectively these facilities simulate patterns of climate warming that are occurring in the real world. The patterns revealed by historical records and predicted by General Circulation Models (GCMs) include: (1) greater warming in winter than in summer, (2) a greater increase in daily minimum than maximum air temperature, leading to a reduction in the diurnal temperature range, and (3) decreased soil moisture in summer in mid-latitude regions (Mitchell *et al.* 1990, Maxwell 1992, King 1994, Smith *et al.* 1996, Houghton 1997, IPCC 2001).

In order to evaluate the effectiveness of warming facilities, the microclimatic parameters (e.g., air temperature, soil temperature, and soil moisture) in experimental

plots are needed to be compared with those predicted for climate warming. Climate warming happens by enhancing downward infrared radiation, which is dissipated through one or a combination of three major energy pathways: sensible heat, latent heat and soil heat fluxes. The three energy pathways are responsible for warming of the air, increases in evapotranspiration, and heating of the soil (Shaver *et al.* 2000). Depending on their heating mechanisms, different warming facilities may have different effects on the three microclimatic parameters. Quantification of microclimate changes will not only help compare different warming facilities but also facilitate interpretation and comparison of warming effects on ecosystems across different habitats (Shaver *et al.* 2000, Rustad *et al.* 2001).

Among the above warming facilities, infrared heaters most closely simulate processes of climate warming by enhancing downward infrared radiation (Harte and Shaw 1995). Changes in soil temperature and soil moisture under infrared heaters have been reported in a Rocky Mountain subalpine meadow in Colorado (Harte *et al.* 1995) and in Minnesota wetlands, USA (Bridgham *et al.* 1999). However, air temperatures have not been described for these sites, leaving a possibility for speculation that infrared heaters may warm the surface of plants and soils but not the surrounding air (Schulze *et al.* 1999, Shen and Harte 2000). Actually, air temperature manipulated with infrared heaters was once reported to increase in Eschikon, Switzerland (Nijs *et al.* 1996). Unfortunately, this experiment only lasted for three weeks and was largely neglected. In addition, it hasn't been reported in the literature how the heaters or other facilities affect daily maximum and minimum air/soil temperatures. Daily maximum and minimum temperatures are

important parameters for evaluation of warming facilities relative to the patterns of climate warming.

As a concurrent phenomenon of climate warming, human-caused land-use/cover change can alter regional and global budgets of energy and water fluxes through changes in vegetation coverage and albedo of the earth's surface (Walker *et al.* 1999). Reduced vegetation coverage through mowing or grazing may change the boundary layer near the soil surface, increase energy absorbed and emitted by the soil, and amplify the diurnal soil temperature range. Plant removal can have opposite effects on evaporation (positive) and transpiration (negative), resulting in an unpredictable net effect on soil moisture (Dahlgren and Driscoll 1994). Climate warming and land-use/cover change may play an interactive role in affecting microclimate (Vitousek 1992, Shaver *et al.* 2000).

This study was designed to characterize changes in microclimate under experimental warming and clipping. It is a part of a comprehensive warming experiment in a tallgrass prairie in the Great Plains, USA, where infrared heaters were used to mimic climate warming and clipping to simulate mowing for hay, which is a wide land-use practice in tallgrass prairie in the US Great Plains (Luo *et al.* 2001). Specific objectives are to evaluate: (1) the effectiveness of infrared heaters in altering air and soil temperatures and soil moisture, (2) the differences between observed microclimate changes achieved with infrared heaters and climatic warming patterns predicted by GCMs, (3) the interactions of experimental warming with clipping in terms of microclimate changes in tallgrass prairie, and (4) the roles of environmental factors in affecting the responses of air and soil temperatures.

MATERIALS AND METHODS

Experimental site, design and warming facility

The experimental site is located at the Great Plain Apiaries (34°58'54"N, 97°31'14"W), 25 miles from the Norman campus of the University of Oklahoma. This site hasn't been grazed for the past twenty years. The grassland is dominated by C_4 grasses (*Schizachyrium scoparium*, *Sorghastrum nutans* and *Eragrostis spp.*) and C_3 forbs (*Ambrosia psilostachya* and *Xanthocephalum texanum*). Mean annual temperature is 16.0 °C with a 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 experiment uses a paired factorial design with warming as the main factor nested with clipping. There are five 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 is the control. One 165 × 15 cm infrared heater (Kalglo Electronics Inc, Bethlehem, PA, USA) has a radiation output of about 100 watts/m^2 and is suspended 1.5 m above the ground in each warmed plot. In the control plot, one "dummy" heater with the same shape and size as the infrared heater is 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 is approximately 5 m to avoid heating the control plot by infrared heater. The distances between the individual sets of paired plots vary from 20 to 60 m.

Each 2 × 2 m plot is divided into four 1 × 1 m subplots. Two diagonal subplots in each plot were clipped 10 cm above the ground on 15 November 1999 and 28 July 2000, the other two are the unclipped control. Clipping removed about 85% of the aboveground biomass (unpublished data). After clipping, plants were allowed to grow until next clipping. The four treatments in the experiment are unclipped control (UC), unclipped warmed (UW), clipped control (CC), and clipped warmed (CW).

Air and soil temperature measurements

At the center of each plot, a T-type thermocouple was used to monitor air temperature at the height of 25 cm above the ground, thus only the effect of warming on air temperature was considered. Thermocouples were sheltered using perforated PVC tubes with open ends (15 cm in length, 5 cm in diameter). The PVC tubes were horizontally fastened on wood stacks. Thermocouples were put into the PVC tubes through a small hole at the middle part and positioned so they would not touch the wall of the PVC tubes. This design avoids the direct heating effect of upward and downward radiation on the sensor and keeps the air immediately surrounding the sensor at the same temperature level with the canopy air inside the plots.

At the centers of each clipped subplot and each unclipped subplot, thermocouples were used to measure soil temperature at the depth of 2.5 cm. All the thermocouples were connected to a CR10 datalogger (Campbell Scientific Inc., Utah, USA). Air and soil temperatures were measured every ten minutes, and then averages within one hour

were stored in an SM196 Storage Module. Daily maximum and minimum values for air and soil temperatures and the times at which they occurred were also recorded.

On 29 December 1999, soil temperatures at three depths (0, 5, and 10 cm) were measured using a 51 K/J thermometer (Fluke Co., Everett, WA, USA) in all subplots of paired plots 2 and 3. On 4 January 2000, the spatial pattern of surface soil temperature was measured on a 30 cm grid in paired plots 2, 3, and 4 using a Dew Point Microvoltmeter (Wescor Inc., Utah, USA).

Soil moisture measurement

Soil moisture content was measured gravimetrically twice a month. 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.

Statistical analysis

All the temperature and soil moisture data in this paper were collected from the experimental plots within the first year (1 December 1999 – 30 November 2000) of the warming study. Solar radiation, wind speed, and vapor pressure deficit (VPD) data were derived from a MESONET station 500 m north of our experimental site (Oklahoma Climatological Survey). Statistical significance of warming and clipping treatments were evaluated by analysis of variance (ANOVA). To test the spatial evenness of soil surface

temperature, a two-way ANOVA was applied using x and y coordinates as main effects. Multiple regression analysis was used to analyze the relationships of changes in air and soil temperature as well as their diurnal ranges with solar radiation, wind speed, VPD, and soil moisture. All significant factors were selected into models using a stepwise method. Path coefficients were calculated in order to compare the relative importance of different factors in affecting the response of air and soil temperatures. All the statistical analyses were performed using SAS (SAS Institute Inc. 1989-1996, NC, USA).

RESULTS AND DISCUSSIONS

Air temperature

Warming effects of infrared heaters on air temperature were greater at night than during the daytime. Hourly air temperature increased by nearly 2 °C at midnight in the warmed plots but there was essentially no increase due to warming at noon (Fig.1). Experimental warming enhanced daily mean air temperature more in the summer than in the winter (Fig.2a, b). Measured daily mean air temperature in the warmed plots was, over the experimental period of one year, 1.1 °C higher than those in the control plots (Table 1).

Daily minimum air temperature in the warmed plots significantly increased by 2.3 °C compared to that in the control plots (Fig.2b, Table1). Experimental warming had no significant effect on daily maximum air temperature in the warmed plots in comparison

to that in the control plots. The differential responses of daily maximum and minimum air temperatures to the infrared heaters resulted in a reduction in the diurnal air temperature range (the difference between daily maximum and minimum temperatures). The diurnal air temperature range in the warmed plots decreased by 2.2 °C ($p < 0.001$) compared to that in the control plots (Fig.2d).

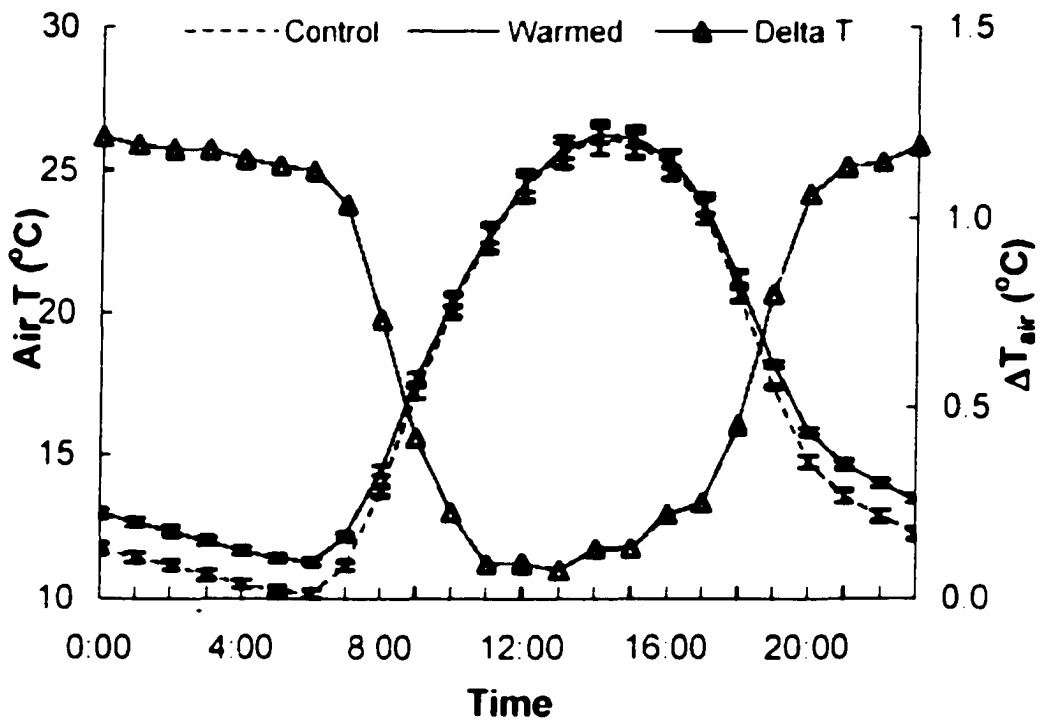

Figure 1. Hourly values of air temperature (mean ± 1SE) in and the difference between the control and warmed plots. Each value is the annual average from 1 December 1999 to 30 November 2000).

Table 1. Annual averages of air and soil temperatures and their increases (°C).

Air temperature	Maximum	Mean	Minimum
Control	28.2(1.48)	16.8(0.27)	7.7(0.40)
Warming	28.3(0.75)	17.9(0.24)	10.0(0.28)
Difference	0.1[0.0978]	1.1[0.0002]	2.3[0.0004]
Soil temperature			
Unclipped Control	20.8(1.33)	17.3(0.29)	14.7(0.35)
Unclipped Warming	23.3(1.97)	19.3(0.55)	16.5(0.37)
Clipped Control	24.2(1.14)	17.9(0.33)	13.8(0.23)
Clipped Warming	27.6(1.25)	20.5(0.28)	15.9(0.21)
UW–UC	2.5[0.0804]	2.0[0.0009]	1.8[0.0028]
CW–CC	3.5[0.0027]	2.6[0.0002]	2.1[0.0000]
CC–UC	3.4[0.0240]	0.6[0.0353]	–1.0[0.0181]
CW–UW	4.3[0.0049]	1.2[0.0166]	–0.6[0.0082]
CW–UC	6.8[0.0033]	3.2[0.0002]	1.1[0.0026]

Notes: UW–UC = Unclipped Warmed minus Unclipped Control, CW–CC = Clipped Warmed minus Clipped Control, CC–UC = Clipped Control minus Unclipped Control, CW–UW = Clipped Warmed minus Unclipped Warmed, CW–UC = Clipped Warmed minus Unclipped Control. Values in parentheses are standard deviations, n = 5; values in brackets are significance levels of ANOVA.

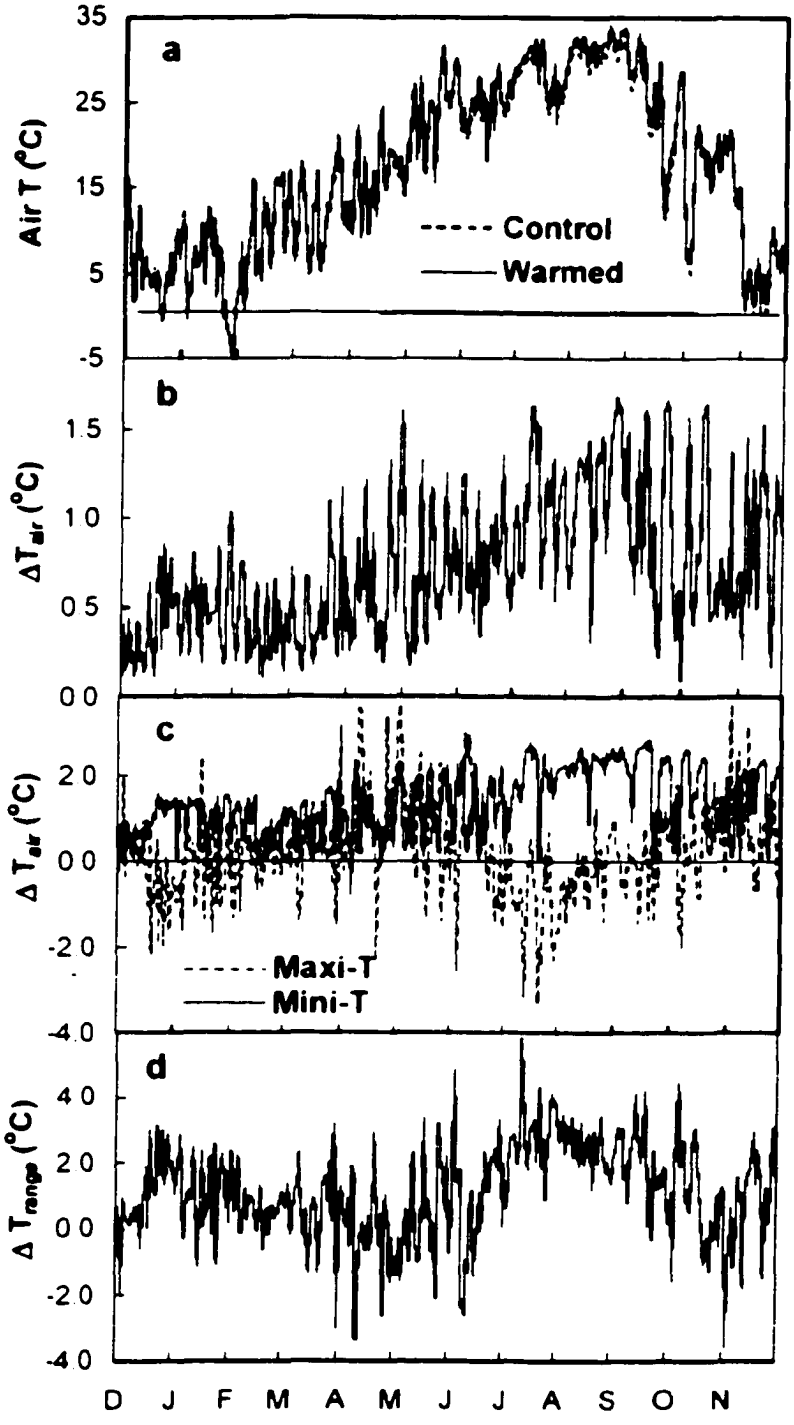

Figure 2. Daily mean air temperatures in the control and warmed plots (a) and heater-induced increases in (b) daily mean air temperature, (c) daily maximum and minimum air temperatures, and (d) the diurnal air temperature range.

The effects of environmental factors (solar radiation, vapor pressure deficit (VPD) and wind speed) on the responses of air temperature to experimental warming varied with different temporal scales. Multiple regression analysis showed that wind speed (WS, m s^{-1}), solar radiation (SR, J m^{-2} s^{-1}), and VPD (kPa) had significant effects on the hourly values of heater-induced increments in air temperature ($\Delta T_{hourly\ air}$ = 2.5883 – 2.2405WS –0.00227SR + 1.0219VPD, r^2 = 0.957, $p < 0.0001$) with path coefficients of –0.7508, –0.7048, and 0.6906, respectively. Increases in daily mean air temperature were primarily affected by wind speed with a path coefficient equaling –0.6406 (Fig.3a, b), then by daily mean VPD (path coefficient = 0.3004), and daily total solar radiation (path coefficient = 0.1346), yielding $\Delta T_{daily\ air}$ = 1.7008 – 1.1720WS – 0.2627VPD + 0.0000399SR, r^2 = 0.646, $p < 0.0001$. Increases in monthly mean air temperature were under the influence of wind speed (path coefficient = –0.5914) and VPD (path coefficient = 0.4387) but not solar radiation ($\Delta T_{monthly\ air}$ = 2.4980 – 1.9124WS + 0.2998VPD, r^2 = 0.8690, $p < 0.0001$) (Fig.3c).

The reduced diurnal air temperature ranges caused by infrared heaters are consistent with the effects of climate warming predicted by GCMs. A likely explanation for the reduced diurnal temperature range under climate warming is increases in cloud cover, which tend to obstruct daytime sunshine and to reduce the escape of terrestrial radiation at night (Houghton 1997, IPCC 2001). At the plot scale in our experimental site, the reduction in the diurnal temperature range is probably related to wind speed, VPD, and the relative contributions of infrared radiation from heaters to total energy flux. Wind blows the energy from infrared heaters away from the warmed plots, resulting in a lower increase in air temperature. When VPD is higher, more energy from the heaters is

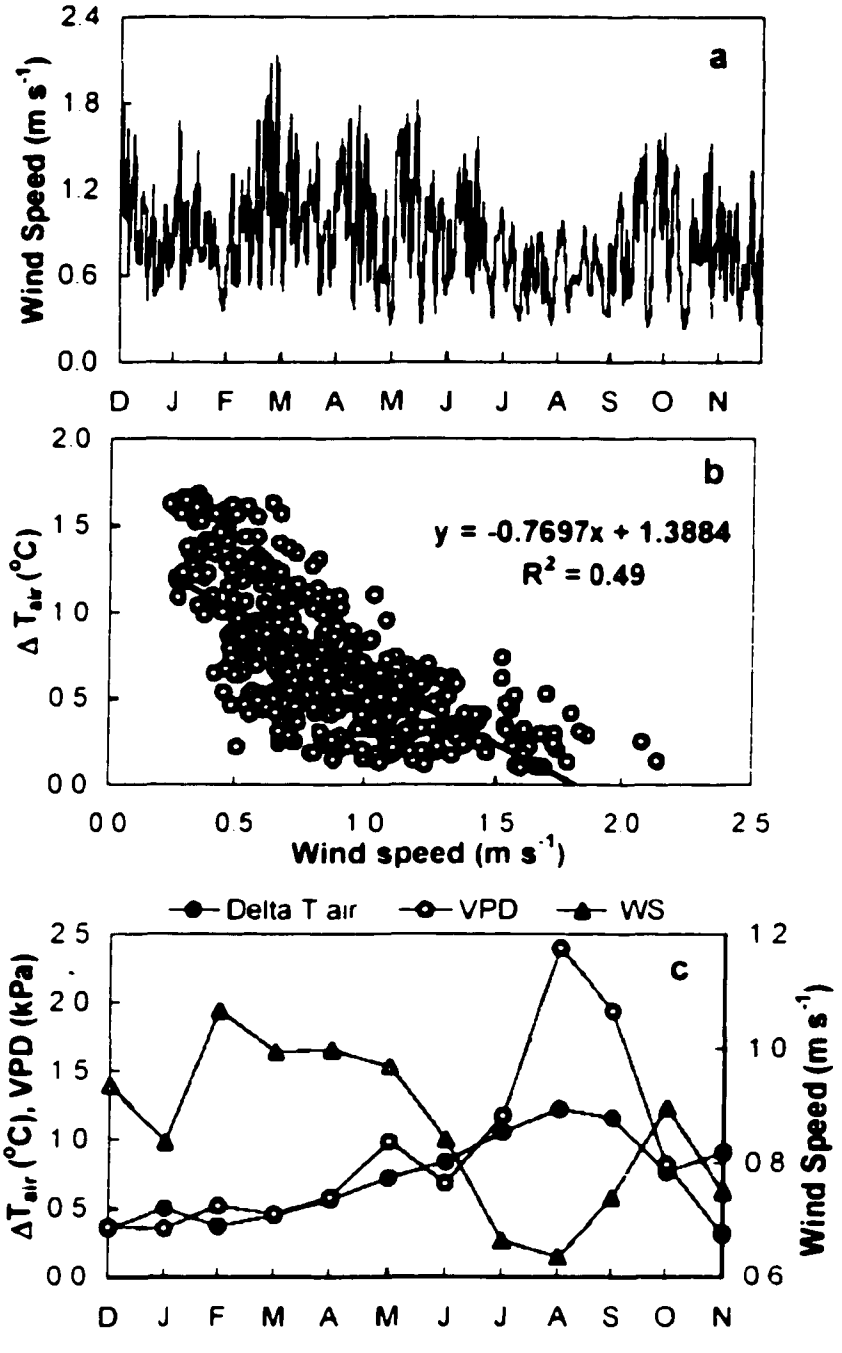

Figure 3. (a) Seasonal variations in daily mean wind speed. (b) Linear relationship between heater-induced increases in daily mean air temperature daily mean wind speed. (c) Monthly mean values of VPD, wind speed, and heater-induced increases in air temperature

converted to sensible heat, resulting in a greater air temperature increase. During the daytime, the added energy from infrared heaters is small relative to the total energy fluxes, causing little increases in daily maximum air temperature. At night, the additional energy from the heater accounts for a large fraction of the total energy flux, leading to a large increase in daily minimum air temperature.

Infrared heaters in our experimental plots amplified the seasonal variation in daily means air temperature whereas GCMs predict the opposite (Walker *et al.* 1999). In Oklahoma, wind speed is greater in winter than in summer, resulting in a reduced effect on air temperature in winter due to the negative correlation as shown in Figure 3. In addition, because of severe drought and a large VPD in the summer of 2000, a large portion of added energy from the heaters is dissipated as sensible heat, leading to larger increases in air temperature in summer than winter.

Soil temperature

Infrared heaters caused relatively constant increases in hourly values of soil temperature in the warmed plots in comparison to that in the control plots without clipping. With clipping, heater-induced increases in soil temperature were greater during the daytime than at night with a peak at noon (Fig.4). Clipping increased soil temperature during the daytime but decreased soil temperature at night in both the control and warmed plots. Soil temperature increased by nearly 6.5 °C in midday and 1.3 °C in

predawn in the warmed, clipped subplots as compared to values in the unclipped, control subplots.

Infrared heaters increased the yearly averages of soil temperature by 2.0° and 2.6 °C in the unclipped and clipped subplots, respectively (Table 1). Clipping elevated the annual averages of soil temperature by 0.6° and 1.2 °C in the control and warmed plots, respectively. Annual averages of soil temperature increased by 3.2 °C in the clipped, warmed subplots as compared to the unclipped, control subplots. Increases in soil temperature varied with seasons with peaks in summer during a severe drought (Fig. 5).

Infrared heaters differentially affected daily maximum versus minimum soil temperatures. Daily maximum soil temperature in the warmed plots increased by 2.5

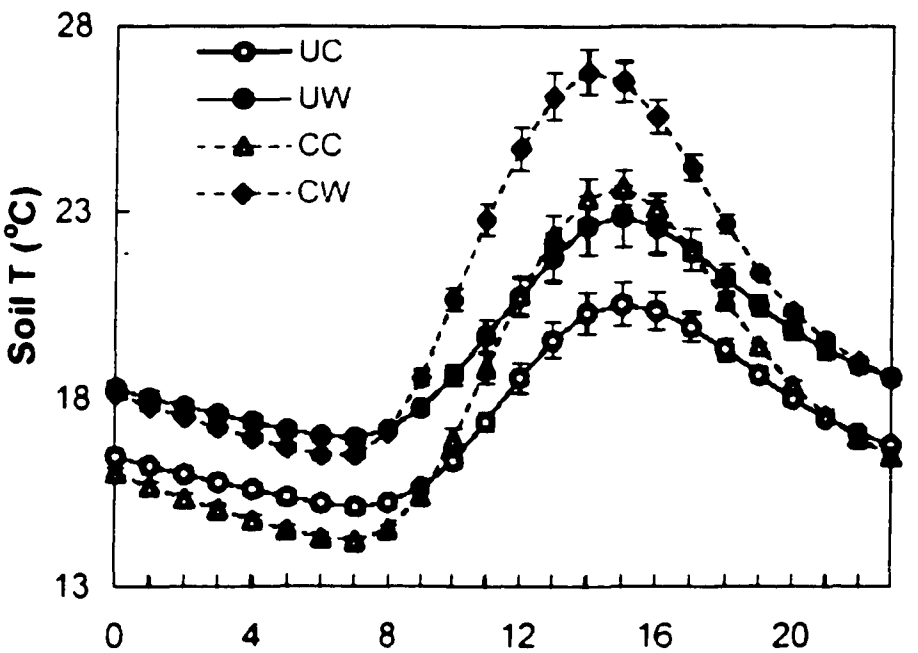

Figure 4. Hourly soil temperatures (mean ± 1 SE) in the unclipped control (UC), unclipped warmed (UW), clipped control (CC) and clipped warmed (CW) subplots. Each value is the annual average from 1 December 1999 to 30 November 2000.

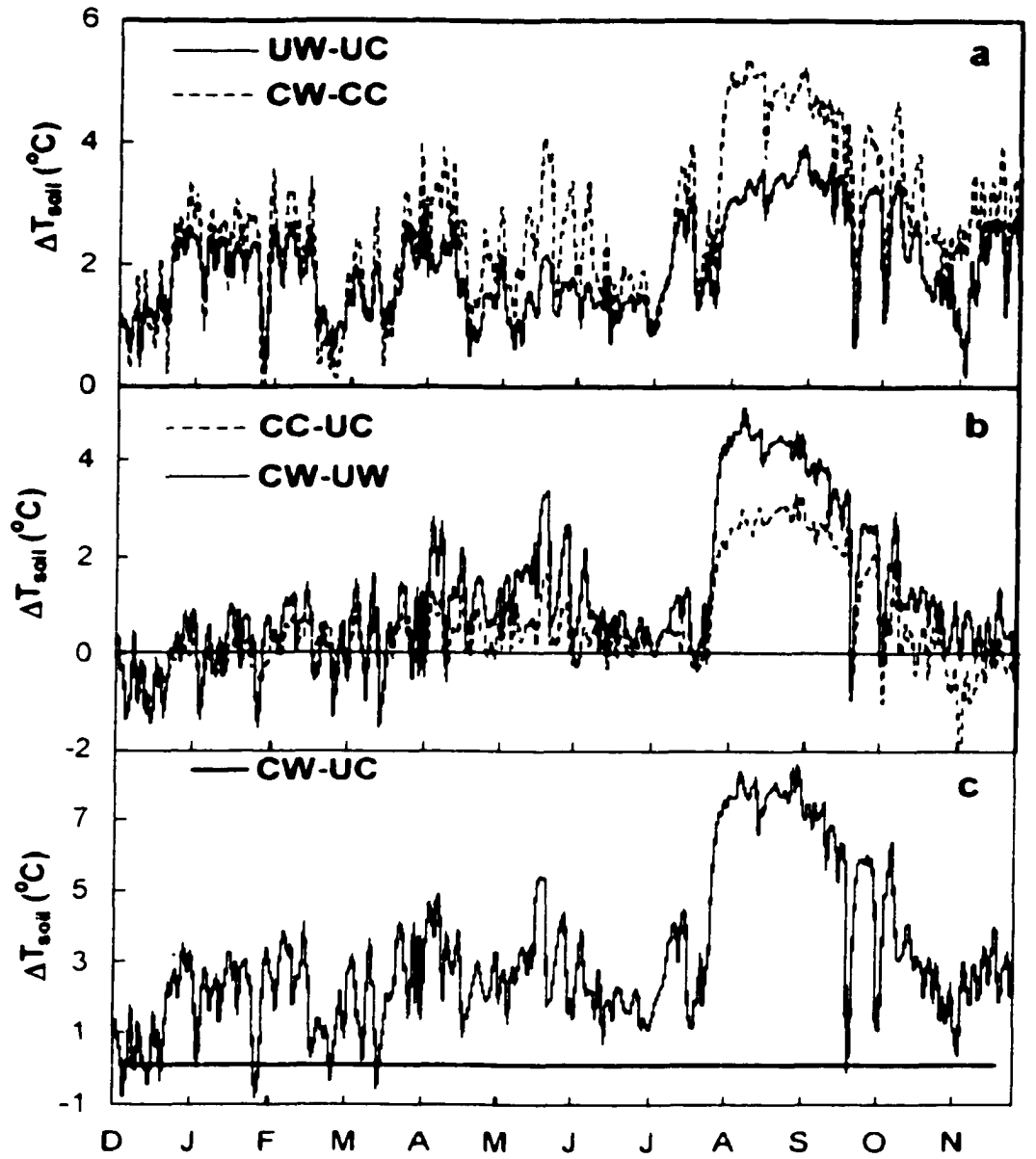

Figure 5. Increases in daily mean soil temperature because of (a) warming, (b) clipping, and (c) interaction of warming and clipping. UW–UC = Unclipped Warmed (UW) minus Unclipped Control (UC), CW–CC = Clipped Warmed (CW) minus Clipped Control (CC), CC–UC: Unclipped Control minus Clipped Control, CW–UW = Clipped Warmed minus Unclipped Warmed, CW–UC = Clipped Warmed minus Unclipped Control.

without clipping and by 3.5 °C with clipping relative to controls (Table 1). Infrared heaters enhanced daily minimum soil temperature by 1.8°C without clipping and 2.1 °C with clipping. Clipping increased daily maximum soil temperature by 3.4° and 4.3 °C, but decreased daily minimum soil temperature by 1.0° and 0.6 °C in the control and warmed plots, respectively. Daily maximum and minimum soil temperatures in the clipped, warmed subplots increased by 6.8° and 1.1 °C, respectively, compared to the unclipped, control subplots.

The differential responses of daily maximum and minimum soil temperatures to warming and clipping resulted in amplifications of the diurnal soil temperature range (Fig. 6). Warming increased the diurnal soil temperature range by 0.7 °C without clipping and by 1.4 °C with clipping (Fig.6a). Clipping elevated the diurnal soil temperature range by 4.3° and 5.0 °C in the control and warmed plots, respectively (Fig.6b). The diurnal soil temperature range in the clipped warmed subplots increased by 5.7 °C in comparison to that in the unclipped control subplots (Fig.6c).

Soil moisture content affected the responses of daily mean soil temperature. Increases in daily mean soil temperature due to warming are negatively correlated with soil moisture content ($r^2_{UW\text{-}UC} = 0.263$, $r^2_{CW\text{-}CC} = 0.259$, $p < 0.05$, Fig.7a). Similarly, changes in daily mean soil temperatures induced by both clipping ($r^2_{CC\text{-}UC} = 0.519$, $r^2_{CW\text{-}UW} = 0.431$, $p < 0.001$, Fig.7b) and the interaction of warming and clipping ($r^2 = 0.1380$, $p > 0.05$, Fig.7c) also showed negative correlations with soil moisture content. Our results are consistent with that in a subalpine meadow in Colorado, USA with the same type of warming facility (Harte *et al.* 1995). In that study, increases in soil temperature were

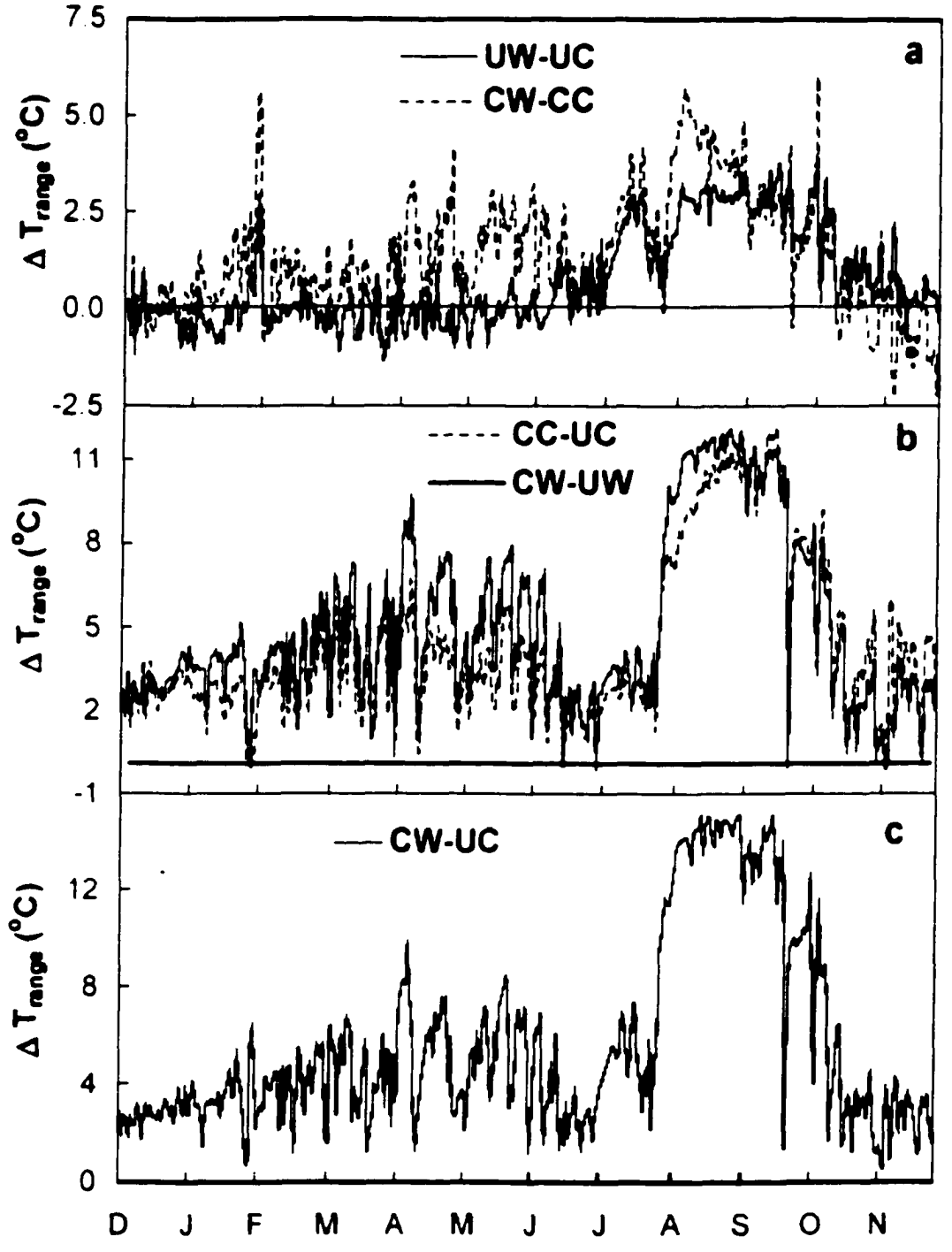

Figure 6. Changes in the diurnal soil temperature range associated with (a) warming, (b) clipping, and (c) interaction of warming and clipping. See Fig. 5 for abbreviations.

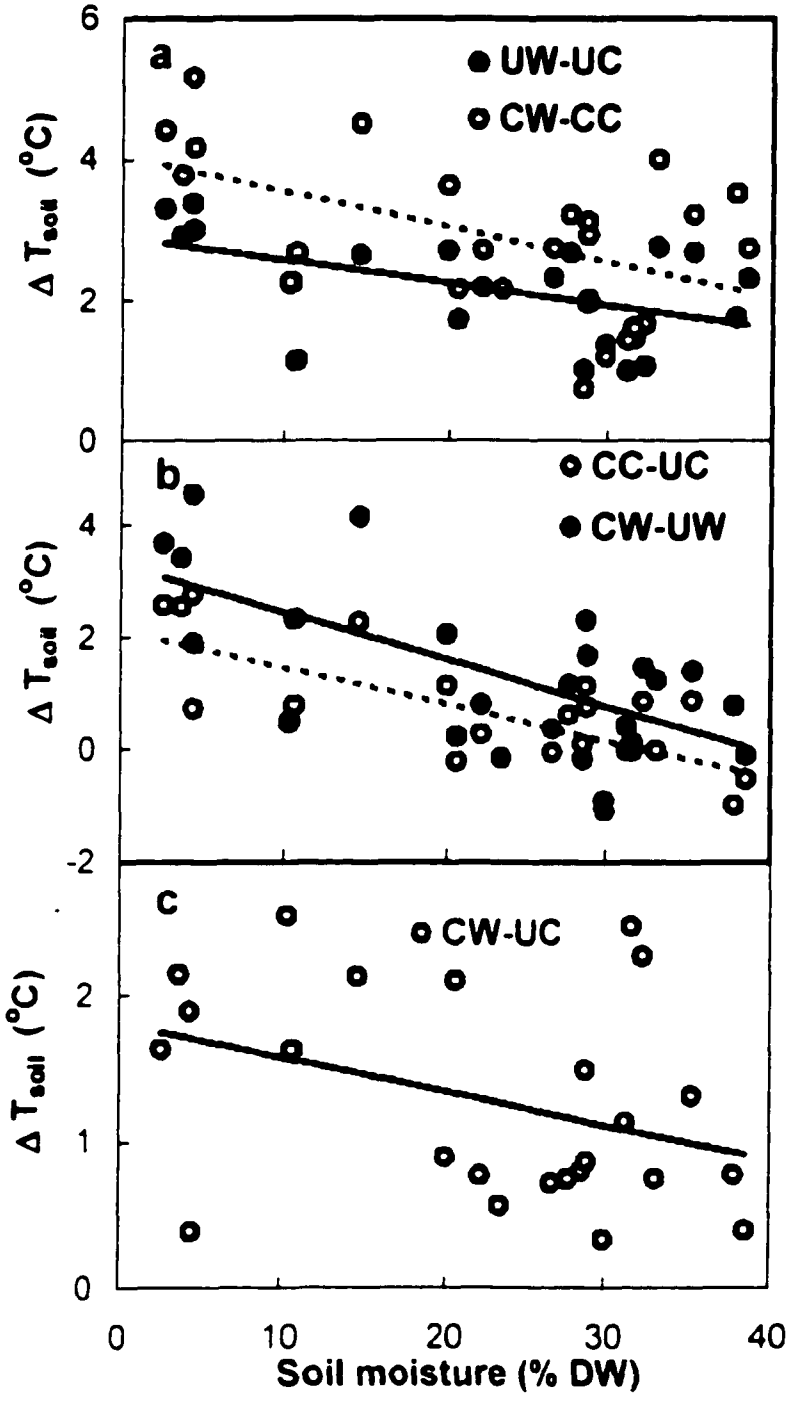

Figure 7. Effect of soil moisture on the response of soil temperature to (a) warming, (b) clipping, and (c) their interactions. See Fig. 5 for abbreviations.

Table 2. Path coefficients* and R^2 of stepwise multiple regression analyses between the hourly, daily, and monthly increases in soil temperature with vapor pressure deficit (VPD), solar radiation, and wind speed.

	VPD	Solar Radiation	Wind Speed	R^2
Hourly ΔT_{Soil}				
UW–UC	–0.3871	+0.8320	+0.4398	0.9429
CW–CC	+0.5620	+1.0973	–0.6962	0.9692
CC–UC		+0.9347	+0.5478	0.9096
CW–UW		+1.0108	+0.3327	0.9590
CW–UC		+1.0178	+0.3154	0.9699
Daily ΔT_{Soil}				
UW–UC	+0.7408	–0.2043	–0.3647	0.5879
CW–CC	+0.6915		–0.3339	0.6524
CC–UC	+0.7925	+0.0835		0.7170
CW–UW	+0.7452	+0.1395	–0.0624	0.7226
CW–UC	+0.7854		–0.1885	0.6927
Monthly ΔT_{Soil}				
UW-UC	+1.3430	–0.6563		0.8903
CW-CC	+0.8726			0.7615
CC-UC	+1.1264		+0.2618	0.9659
CW-UW	+0.9478			0.8983
CW-UC	+0.9468			0.8965

***: The absolute values of path coefficients represent the relative importance of different factors in affecting the responses of air and soil temperature. The signs (+ and –) stand for positive or negative roles of these factors in influencing the responses of air and soil temperature.**

greater in the study area with lower soil moisture content (0.93 °C in 1991 and 0.87 °C in 1992) than those in the study area with higher soil moisture content (0.00 °C in 1991 and 0.17 °C in 1992). Higher soil moisture content might cause more infrared radiation from heaters dissipated as latent heat and less as soil heat flux, resulting in smaller increases in daily mean soil temperature.

Multiple regression analysis indicated that solar radiation was the dominant factor affecting increases in hourly values of soil temperature whereas VPD was the primary factor influencing daily and monthly increases in average soil temperatures (Table 2). These factors may alter energy exchange between the warmed plots and the ambient environment, alter heat fluxes among the three energy pathways, change the proportion of enhanced infrared radiation to the total energy budget, and affect soil moisture content.

Increases in soil temperature caused by infrared heaters in our study are higher than those for a subalpine ecosystem in Rocky Mountains (Harte *et al.* 1995) and similar to those in Minnesota wetlands (Bridgham *et al.* 1999) using the same type of heating facility. The results from this study suggest that seasonal changes in plant canopy coverage may not affect responses of soil temperature to infrared heaters.

Infrared heaters had relatively even effects on soil temperature along the soil profile from 0 to 10 cm. Soil temperatures in the warmed plots were significantly higher than

those in the control plots at all three depths either without (Fig.8a) or with clipping (Fig.8b).

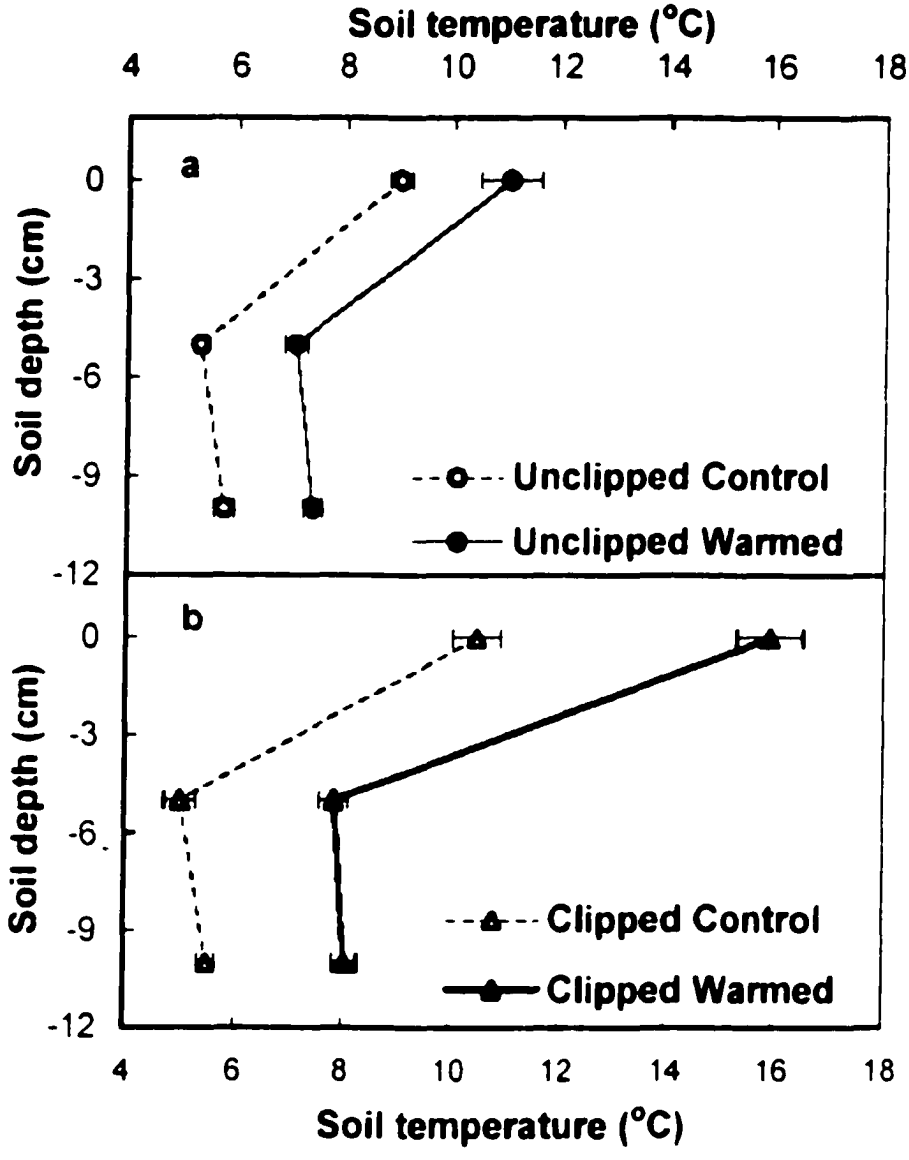

Figure 8. Soil temperatures (mean ± 1SE) at three depths in the (a) unclipped and (b) clipped subplots showed constant increases along the soil profiles. Measurements were taken on 29 December 1999.

We also measured spatial distributions of temperature at the soil surface. Results of two-way ANOVA showed no significant difference of soil surface temperature between any two rows or columns in any subplots (Fig. 9). The even distribution of heating effects over the plot surface resulted from parabolic reflectors above the heating rod that uniformly deliver infrared radiation over the plot (Loik and Harte 1997).

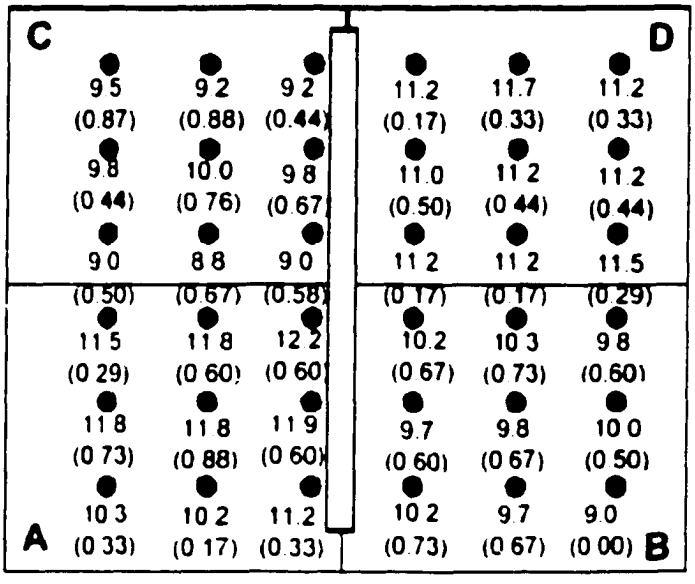

Figure 9. Spatial pattern of soil surface temperature (mean ± 1SE) in the warmed plots measured on 4 January 2000. Subplot A and D are the clipped subplots, B and C are the unclipped subplots. The dark rectangle in the center part is the footprint of the infrared heater.

Differential responses of air and soil temperatures

Our results indicate that air temperature responded less to experimental warming than did soil temperature, probably because of fast lateral exchange of energy between the

warmed plots and ambient atmosphere. However, infrared heaters reduce the diurnal range of air temperature but amplify the diurnal range of soil temperature. Under climate warming, the difference between increases in air and soil temperatures may be less than that in our experimental plots (Kane *et al.* 1992). Since air and soil temperatures affect different ecosystem processes, the differential increases in air and soil temperatures caused by infrared heaters may result in different experimental outcomes (Shaver *et al.* 2000). For example, changes in air temperature mainly affect ecophysiological processes in the aboveground plant tissues, such as plant photosynthesis and respiration. Changes in soil temperature influence processes occurring in the soil, such as plant root respiration and microbial activities. The large increase in soil temperature may stimulate more carbon release whereas small increases in air temperature will have little effect on photosynthesis. Thus the net effects of the differential increases in air and soil temperature may result in decreases in net ecosystem productivity.

Soil Moisture

Soil moisture content in the warmed plots relative to that in control plots was not significantly altered by infrared heaters without clipping ($p > 0.10$), but significantly decreased by 11.0 % ($p < 0.05$) with clipping. Clipping significantly decreased soil moisture by 17.7 % ($p < 0.001$) and 22.7 % ($p < 0.001$) in the control and warmed plots, respectively. Soil moisture content in the clipped, warmed subplots was reduced by 26.7% ($p < 0.001$, Fig.10) compared to the unclipped, control subplots.

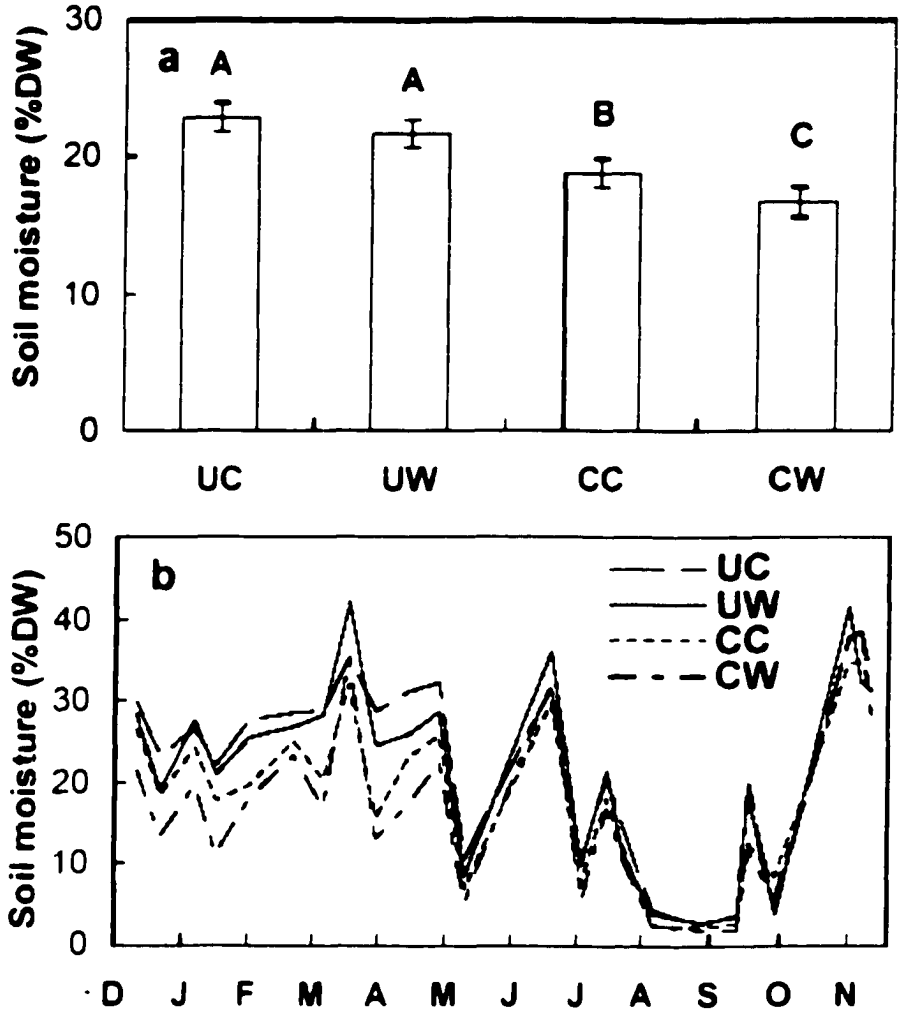

Figure 10. (a) Annual averages (Mean ± 1SE) and (b) seasonal variations of soil moisture contents. See Fig. 4 for abbreviations.

In a Rocky Mountain subalpine meadow ecosystem, summer soil water content was significantly decreased by 25 % with the same type of heating facility (Harte *et al.* 1995, Loik and Harte 1997). Extra energy provided by infrared heaters in the warmed plots was partially dissipated as latent heat, resulting in more evapotranspiration and decreased soil moisture content. Although it may reduce plant transpiration by removing aboveground biomass, clipping may increase evaporation from the soil surface due to less

plant coverage and boundary layer resistance and increases in soil temperature. Loss of soil moisture would decrease latent heat flux, leading to more energy dissipated as sensible heat (air warming) and soil heat flux (soil warming). Our data support this mechanism in that soil temperature increase is negatively correlated to soil moisture content. For plants exposed to soils with low water content under experimental warming, plant water potential may decrease, leading to reductions in stomatal conductance and photosynthetic CO_2 fixation (Loik and Harte 1997, Loik *et al.* 2000).

Comparison with other warming facilities

Infrared heaters used in our experimental site increased daily mean and minimum air temperatures, did not affect daily maximum air temperature, and decreased the diurnal air temperature range. Infrared heaters also increased daily maximum, mean and minimum soil temperatures and the diurnal soil temperature range. However, air and soil temperatures showed differential responses to enhanced infrared radiation, with air temperature responding less than soil temperature. The effect of infrared heaters on soil moisture depended on land use patterns as mimicked by clipping. Environmental factors, such as solar radiation, wind speed, VPD, and soil moisture affected the responses of air and soil temperatures to infrared heaters in our study.

Greenhouses (GHs) and open-top chambers (OTCs) are widely used at different habitats across the world to manipulate temperature in field (Chapin and Shaver 1985, Havström *et al.* 1993, Marion *et al.* 1997, Richardson *et al.* 2000). Within a day, GHs/OTCs increase air temperature in the daytime when there is incoming solar radiation

and decrease air temperature at night (Wookey *et al.* 1993, Kennedy 1995a, b, Marion *et al.* 1997, Suzuki and Kudo 1997, Werkman *et al.*1999), leading to an amplification of the diurnal air temperature range (Debevec and MacLean 1993, Havström *et al.* 1993, Hollister and Webber 2000). Over the seasons, GHs/OTCs elevate daily mean air temperature more in the summer than in the winter (Kennedy 1995b, Marion *et al.* 1997, Stenström *et al*, 1997). In addition, GHs/OTCs, especially those in the Arctic, Subarctic, Antarctic, and alpine regions, are often used in summer and are not operational in winter due to severe weather (Kennedy 1995a). Summer studies may be adequate for understanding plant responses but miss an important period of predicted large increases in temperature, which is critical for quantifying annual budgets of carbon and other biogeochemical compounds. Reported changes in soil temperatures in GHs/OTCs are inconsistent, being unchanged (Havström *et al.* 1993, Suzuki and Kudo 1997, Hobbie *et al.* 1999) or experiencing increased daily mean and maximum soil temperatures and decreased daily minimum soil temperature (Wookey *et al.* 1993, Michelsen *et al.* 1996, Robinson *et al.* 1998, Oechel *et al.* 1998, Shaver *et al.* 1998, Day *et al.* 1999). In general, GHs/OTCs cause much greater increases in air temperature than in soil temperature (Havström *et al.* 1993, Robinson *et al.* 1995, Suzuki and Kudo 1997, Jones *et al.* 1998, Day *et al.* 1999, Welker *et al.* 2000) and have no effects on soil moisture in some studies (Chapin and Shaver 1985, Shaver *et al.* 1986, Havström *et al.* 1993, Robinson *et al.* 1998). Although GHs/OTCs do not generate microclimates similar to predicted climate warming, they require no electricity supply and are convenient for use in remote regions (Karl *et al.* 1991, Kennedy 1995a).

Soil heating pipes/wires can keep constant increases in soil temperature (2.5–10 °C) in the heated plots compared to the control plots (Rykbost *et al.* 1975a, b, Van Cleve *et al.* 1990, Hillier *et al.* 1994, McHale *et al.* 1998, Hartley *et al.* 1999). These facilities generate soil temperature gradients away from pipes and/or wires (Verberg *et al.* 1999) and hardly affect air temperature unless they are combined with other facilities (i.e., GHs or OTCs) (Hartley *et al.* 1999). Without changes in air temperature, plants experience change only in their root systems and will therefore react differently to what is expected under climate warming. Soil moisture content has been reported to decrease by soil heating pipes/wires (Peterjohn *et al.* 1994, Hantschel *et al.* 1995, Rustad and Fernandez 1998). Overall, soil heating pipes/wires create a novel thermal environment in the rhizosphere for roots and microbes while the aerial environment for the aboveground part of plant remains unchanged.

Infrared reflectors only act at night and raise the nighttime and minimum air temperatures. They usually have no effect on daytime air temperature. As a consequence, infrared reflectors may cause an increase in plant respiration and no change in plant photosynthesis. Indeed, it has been reported that plant growth and primary productivity are reduced in the plots under infrared reflectors in comparison to those under control (Zeiher *et al.* 1994, Luxmoore *et al.* 1998). Infrared reflectors are supposed to affect both air and soil temperatures although no report has been published on the changes in soil temperature so far (Zeiher *et al.* 1994, Luxmoore *et al.* 1998).

CONCLUSIONS

Infrared heaters add a constant amount of downward infrared radiation that is dissipated through the three pathways of energy dissipation, i.e., sensible heat to warm the air, latent heat to increase evapotranspiration and soil conductive heat flux to warm the soil (Shaver *et al.* 2000). Contrary to the speculation that infrared heaters do not warm the air (Schulze *et al.* 1999, Shen and Harte 2000), our experimental results have shown that infrared heaters significantly increase daily mean and minimum air temperatures and adequately simulate the diurnal pattern of air temperature under climate warming. Infrared heaters can manipulate both air and soil temperatures without the need to combine with other warming facilities. However, infrared heaters have only been used in a few ecosystems with low-stature plants so far. With the advantages of non-perturbation to gas composition, precipitation, light, wind speed, and pollination and no physical disturbance to soil, infrared heaters may have a broad application across different habitats where electricity supply is available.

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Chapter Three

Direct and indirect effects of elevated temperature on aboveground biomass

ABSTRACT

Differentiating between the direct and indirect effects of elevated temperature on net primary production will substantially improve our understanding of the mechanisms by which global warming affects carbon cycling in terrestrial ecosystems. Experimental warming in a tallgrass prairie significantly increased green aboveground biomass in early spring and late autumn when temperature was low, resulted from both the positive direct effect on the ratio of plant photosynthesis to respiration and the positive indirect effect through extending the growing season. On the contrary, elevated temperature had a negative direct effect on peak aboveground biomass in summer when temperature was high, offsetting the positive effect. Our observations, for the first time, provided experimental evidences on the contradictory effects of elevated temperature on biomass accumulation at low and higher temperature ranges.

Keywords: aboveground biomass, global warming, growing season, soil temperature, tallgrass prairie

INTRODUCTION

Global warming has increased the Earth's surface temperature by 0.6 °C during the last century and is predicted to increase it by 1.4-5.8 °C in the 21st century (Houghton *et al.* 2001). Scientists, politicians and the public are most concerned with the response of global carbon (C) budget because changes in the major C fluxes (net primary production and heterotrophic respiration) between the biosphere and the atmosphere may put a positive or negative feedback to future climatic change. Elevated temperature has the potential to directly or indirectly influence net primary production (NPP) and heterotrophic respiration because temperature is related to almost all the physical, chemical and biological activities. The effect of elevated temperature on C cycling will also depends on the initial temperature at a specific location because the rate of many biological processes in relation to temperature typically peaks at some intermediate temperature (Shaver *et al.* 2000, Rustad *et al.* 2001, Rustad and Norby 2002).

Elevated temperature could increase or decrease net primary production (NPP) directly through affecting the ratio of plant photosynthesis to respiration depending on the temperature ranges because photosynthesis is more sensitive to temperature than respiration when temperature is low whereas respiration is more sensitive than photosynthesis at the high temperature range (Aber and Melillo 1991, Lamber *et al.* 1998). Elevated temperature could also affect NPP indirectly by extending the length of growing season (Shaver *et al.* 2000, Rustad and Norby 2002). Much evidence has shown increasing length of the growing season with rising global mean temperature (Post and Stenseth 1995, Sparks and Carey 1995, Menzel and Fabian 1999, Chmielewski and

Rötzer 2001, Menzel *et al.* 2001, Peñuelas and Filella 2001, Peñuelas *et al.* 2002, Walther *et al.* 2002) due to greater warming in winter, spring and fall 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 advanced leaf emergence and unfolding in spring, delayed leaf senescence and fall in autumn (Menzel and Fabian 1999, Peñuelas and Filella 2001, Peñuelas *et al.* 2002), and prolonged vegetative activity (Myneni *et al.* 1997). These phonological changes result in a longer leaf life span and favorable period for plant photosynthesis and growth. Therefore, an extended growing season could substantially influence NPP in terrestrial ecosystems (Goulden *et al.* 1996, White *et al.* 1999, Baldocchi *et al.* 2001, Schimel et al. 2001) and the atmospheric CO_2 concentration (Keeling *et al.* 1996). However, little research effort has been made to differentiate and quantify the direct or indirect effects of elevated temperature on NPP at different temperature ranges so far, which will likely to improve the projection of the potential responses of global C cycling to climatic warming.

As a part of a comprehensive warming experiment in an Oklahoma tallgrass prairie in the Great Plains, USA (Luo *et al.* 2001, Wan *et al.* 2002a,b), this study was designed to examine the potential direct and indirect effects of global warming on NPP in grassland ecosystems. Soil temperature, green aboveground biomass (AGB) in spring and autumn and peak AGB in summer was monitored.

MATERIAL AND METHODS

The experimental site is located at the Great Plain Apiaries (34°58'54"N, 97°31'14"W), 25 miles from the Norman campus of the University of Oklahoma. This site hasn't been grazed for the past twenty years. The grassland is dominated by C_4 grasses (*Schizachyrium scoparium*, *Sorghastrum nutans* and *Eragrostis spp.*) and C_3 forbs (*Ambrosia psilostachyia* and *Xanthocephalum texanum*). Mean annual temperature is 16.0 °C with a 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 Nash-Lucien complex, which is characterized as having a low permeability rate, high available water capacity and deep and moderate penetrable root zone (National Cooperative Soil Survey).

The experiment uses a paired factorial design with warming as the main factor nested with clipping. There are 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 is the control. One 165 × 15 cm infrared heater (Kalglo Electronics Inc, Bethlehem, PA, USA) has a radiation output of about 100 watts/m^2 and is suspended 1.5 m above the ground in each warmed plot. In the control plot, one "dummy" heater with the same shape and size as the infrared heater is 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 is approximately 5 m to avoid heating the control plot by infrared heater. The distances between the individual sets of paired plots vary from 20 to 60 m.

Each 2 × 2 m plot is 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 are the unclipped controls. Clipping removed about 85% of the aboveground biomass (unpublished data). After clipping, plants were allowed to grow until next clipping. The four treatments in the experiment are unclipped control (UC), unclipped warmed (UW), clipped control (CC), and clipped warmed (CW).

At the centers of each clipped subplot and each unclipped subplot, type-T thermocouples were used to measure soil temperature at the depth of 2.5 cm. All the thermocouples were connected to a CR10 datalogger (Campbell Scientific Inc., Utah, USA). Soil temperatures were measured every ten minutes, and then averages within one hour were stored in an SM196 Storage Module.

The point quadrat method was used to measure green aboveground biomass in April and November and peak aboveground biomass in the unclipped subplots in July. Plants were clipped annually from two diagonal subplots in July to calculate peak aboveground biomass.

One-tailed paired t test was used to examine the statistical significance of warming effects. All statistical analyses were conducted using SAS software (SAS Institute).

RESULTS AND DISCUSSIONS

Experimental warming manipulated with infrared heaters significantly increased mean soil temperature by 2.0° and 2.6 °C in 2000 and 1.7 and 2.7 °C in 2001 in the unclipped and clipped subplots, respectively (Wan *et al.* 2002b).

Green AGB significantly increased in April and November over the two and one-half years (Fig. 1). In early spring, AGB in the warmed plots was, on average, 23% and 24% higher than that in the control plots without and with clipping. In late autumn, warming significantly increased green AGB by 60% and 23% in the unclipped and clipped subplots, respectively. On average, peak AGB in summer enhanced by 5% without clipping and 20% with clipping in the warmed plots compared with in the control plots (data not shown).

These results suggest that the extended growing season could have contributed to the enhanced plant growth and green AGB in early spring and late autumn. Unfortunately, there was no data for the plant phenology, which make it difficult to relate changes in green AGB with extended growing season. However, since plant phenology is closely related to temperature, soil temperature was used as a proxy for the estimate of the growing season length. The growing season was defined as the time period between the first day in early spring and the last day in late autumn when soil temperature was continually above 10 °C for 5 days. Heating manipulation extended the growing season, on average, by 18 days with an advance of 12 days in early spring and a delay of 6 days in late autumn (Table 1). Extended growing season was also found in other warming

experiments. A 4 °C increase in air temperature manipulated with open top chamber extended the length of growing season by 2-3 weeks (Norby *et al.* 1998).

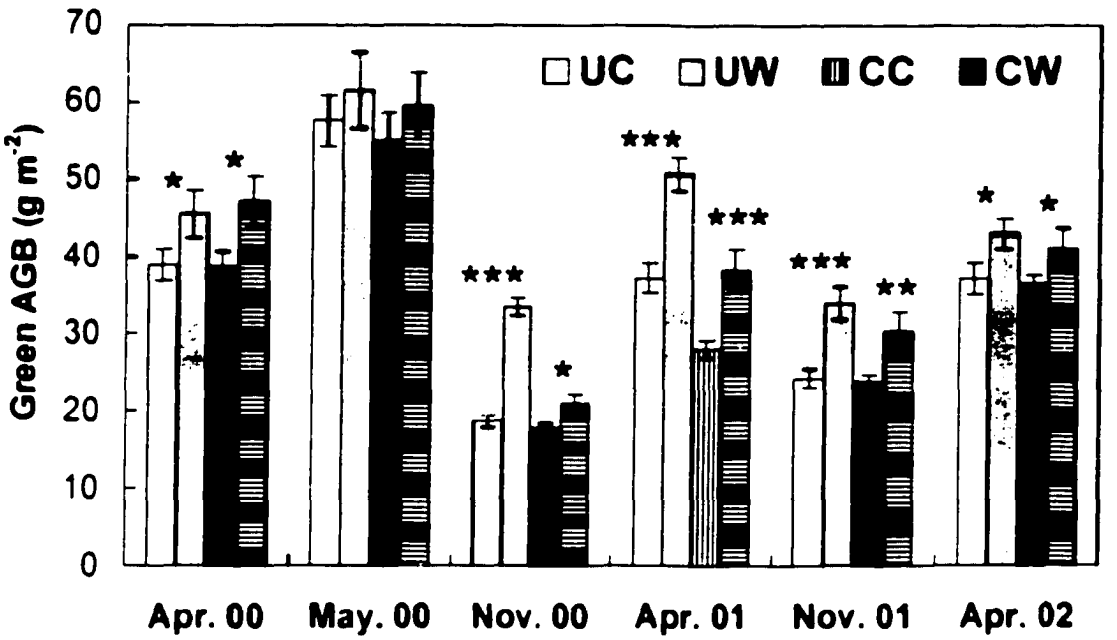

Figure 1. Warming effects on green aboveground biomass (mean ± 1 SE). UC: Unclipped control, UW: Unclipped warmed, CC: Clipped control, CW: Clipped warmed. One-tailed paired *t* test was used to examine warming effects on AGB in the unclipped and clipped subplots. *statistically significant at confidence level of 95%, ** statistically significant at confidence level of 99%, ***statistically significant at confidence level of 99.9%.

The extended growing season could stimulate leaf emergence in early spring and delay leaf senescence in late autumn, leading to an increased leaf area index, lengthened the favorable period for plant photosynthesis and, enhanced plant growth and green biomass in spring and autumn (Norby *et al.* 1998, 2002). Significant increases in percent

coverage and number of living stems of western ragweed (*Ambrosia psilostachya* DC.) were observed in early spring and late autumn, leading to an enhanced peak ragweed AGB in the warmed plots (Wan *et al.* 2002a). Our results were consistent with those from other warming experiments. In the arctic tundra ecosystems, the extended growing season caused an earlier leaf expansion in early spring (Chapin and Shaver 1996) and a greater green leaf biomass of *Dryas* in late autumn (Welker *et al.* 1997). In a US deciduous forest, temperature elevation increased aboveground growth rates in young *Acer rubrum* and *A. saccharum* trees mainly through its effect on tree phenology, i.e., earlier buds opening in spring and longer leaf retention in autumn (Norby *et al.* 1998).

Table 1. Experimental warming extended the length of the growing season. 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 the growing season shown as calendar dates below. Figures in parentheses are the number of days the season was advanced in spring and delayed in autumn in warmed plots compared with control plots.

	Year	UC	UW	CC	CW
Spring	2000	02/21	02/15 (7)	02/21	02/13 (8)
	2001	03/10	03/04 (6)	03/10	03/02 (8)
	2002	03/12	02/19 (21)	03/12	02/18 (22)
Fall	2000	11/06	11/07 (1)	11/06	11/07 (1)
	2001	11/26	12/07 (11)	11/26	12/07 (11)

UC: Unclipped control, UW: Unclipped warmed, CC: Clipped control, CW: Clipped warmed.

The enhanced plant growth and green AGB due to the extended growing season could have substantially contributed to the C fluxes between terrestrial ecosystems and the atmosphere (Keeling *et al.* 1996, Myneni 1997, Schimel *et al.* 2001). A 5 to 10 day extension of the growing season in autumn increased gross primary production by around 500 kg C ha^{-1} in a deciduous forest in Massachusetts, USA (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} day^{-1} with a 1-day extension of the growing season (Baldocchi *et al.* 2001). A model simulation also showed that a 1-day change in the length of the growing season would increase net ecosystem production by 1.6% and gross primary production by 0.5% in the eastern US deciduous forests (White *et al.* 1999). 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.

To examine the direct effect of elevated temperature on AGB, AGB in different subplots was plotted against monthly mean soil temperature 30 days before each biomass measurement. The results showed that green AGB was positively correlated with monthly mean soil temperature in early spring (April, $p< 0.001$) and late autumn (November, $p<0.001$). On the contrary, peak AGB was negatively correlated with monthly mean soil temperature (July, $p< 0.0001$) in summer (Fig. 2). The results suggest that higher temperature caused greater green AGB in spring and less peak AGB in summer in different subplots.

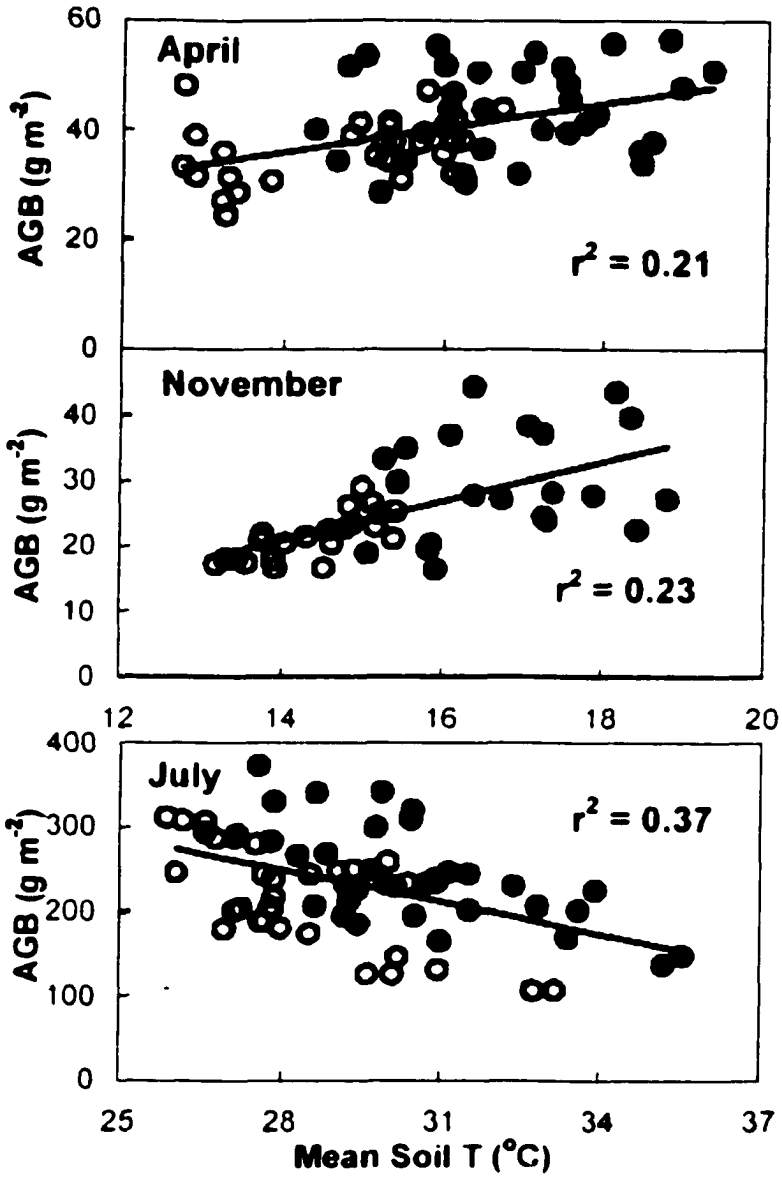

Figure 2. AGB showed positive correlations with monthly mean soil temperatures in spring (upper panel) and fall (middle panel) but a negative correlation in summer (lower panel). Each data point stands for the average AGB of the two unclipped or clipped subplots in each control (open circle) or warmed (solid circle) plot.

The relationship between AGB increment and the elevation of soil temperature in each paired (control vs. warmed) plot showed similar patterns, i.e., positive in spring ($p< 0.01$) and negative in summer ($p<0.05$) (Fig.3). However, no such relationship was found in autumn ($r^2=0.017$, $p>0.05$, data not shown), possibly because there were only two years' of autumn data compared to three years' data for spring and summer. Soil water availability might act as a potential confounding factor, but our data show no significant correlation between AGB and soil moisture ($p>0.05$). The results suggest that elevated temperatures enhanced green AGB in early spring and late fall but lead to less increase in peak AGB in summer.

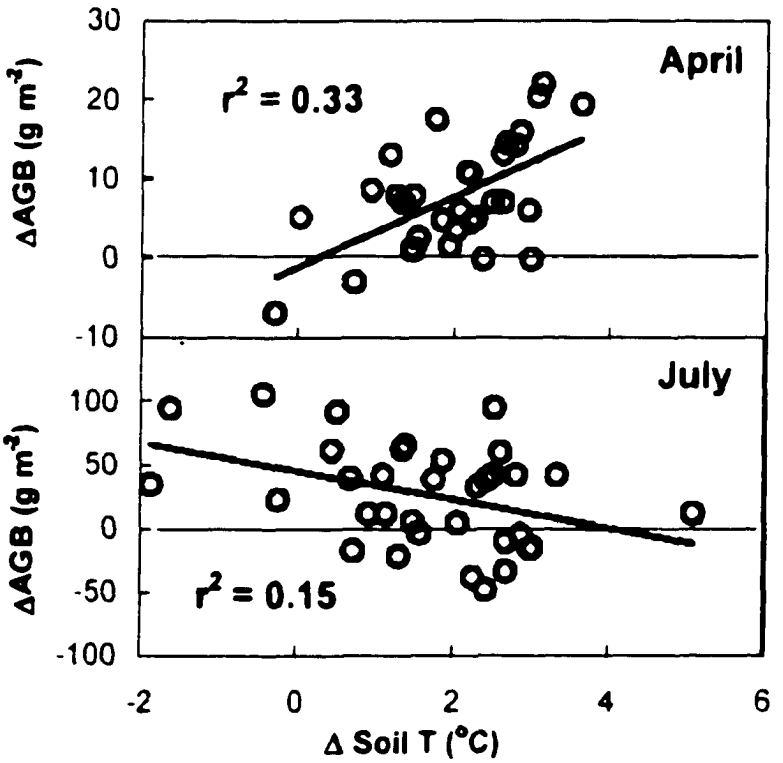

Figure 3. Linear correlations between AGB increment and soil temperature increase in early spring (upper panel) and summer (lower panel).

Global warming reduces the likelihood that plants will be exposed to their lower thermal limits. Elevated temperature could directly enhance NPP because photosynthesis increases more than respiration when temperature is low, leading to a net C uptake in plants (Aber and Melillo 1991, Lamber *et al.* 1998). Results from warming experiments in tundra ecosystems showed that photosynthesis in the warmed plots significantly increased compared with that in the control plots in early spring (Hobbie and Chapin 1998) and in late autumn (Chapin and Shaver 1996) when temperature was low. Combined with the indirect effect through the lengthened growing season, the direct effect of elevated temperature would cause substantial increases in the ratio of plant photosynthesis to respiration, leading to enhanced NPP (Chapin and Shaver 1996, Goulden *et al.* 1996, Oberbauer *et al.* 1998, White *et al.* 1999, Baldocchi *et al.* 2001) and affecting the atmospheric CO_2 concentration (Keeling *et al.* 1996).

During the growing season, the effects of elevated temperature on plant growth are diminished because temperature is no longer a limiting factor for plant growth. In May 2000, there was no significant difference in AGB between the control and warmed plots (Fig. 1). The decline in the warming-control difference in AGB over the season may have resulted from plant growth in the controls "catching up" to that under warming (Chapin and Shaver 1996).

Global warming could also potentially increase the risk of plants exposure to the upper thermal limits in summer. For plants and ecosystems that have evolved under and 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 not affect or even decrease photosynthesis but would increase respiration, resulting in a net C loss from plants and less AGB at the ecosystem scale (Aber and Melillo 1991, Ryan 1991, Lamber *et al.* 1998). Results of warming experiments in an arctic tundra ecosystem (Chapin and Shaver 1996) and a subalpine meadow ecosystem in Rocky Mountains, Colorado, USA (Loik *et al.* 2000) showed no direct effects of elevated temperature on photosynthesis in the middle of the growing season. Based on eddy-covariance measurements, Goulden *et al.* (1996) found that the response of forest photosynthesis to temperature varied little from summer to summer in a deciduous forest in Massachusetts, USA. Norby *et al.* (1998) also found that elevated temperature in a hot, dry summer had a negative effect on dry matter accumulation of *A. saccharum* but its effect on *A. rubrum* was smaller and not significant because *A. rubrum* has a more southerly distribution and a higher optimum temperature range. Our observation that elevated temperature in summer caused less peak AGB increment was also supported by the results from other experiments (Mitchell *et al.* 1993, Gunn and Farrar 1999), in which plant dry mass was decreased at high temperature ranges. The negative direct effects of elevated temperature on peak AGB in summer offset the positive effects in spring and autumn, leading to less C uptake in ecosystems.

The above observations from our experiment and other experiments show that the elevated temperature could have negative direct effects on biomass accumulation in summer and positive direct and indirect effects in spring and autumn, leading to a net C uptake at low temperature and a net C loss at high temperature (Aber and Melillo 1991, Ryan 1991, Lamber *et al.* 1998, Shaver *et al.* 2000). Our results indicate that AGB in

cold regions would have a greater response to climate change than in warm regions because greater warming and lengthening of the growing season are predicted to occur at high latitudes than at low latitudes (Houghton *et al.* 2001). At the global scale, NDVI (Normalized Difference Vegetation Index) in colder ecosystems responds to temperature anomalies directly and positively, leading to an assumption that temperature may have direct negative effects on plant growth in semiarid ecosystems (Braswell *et al.* 1997). This phenomenon was also shown by a model prediction (White *et al.* 1999) and a synthesis of experimental results from Global Change and Terrestrial Ecosystems Network of Ecosystem Warming Studies (Rustad *et al.* 2001), in which AGB showed a greater positive response to warming in colder ecosystems. Further studies are needed to examine the other indirect effects of elevated temperature, including altered moisture regime, nutrient mineralization and availability, litter decomposition, and species composition, on NPP in order to predict the long-term response of the tallgrass prairie to global warming.

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Chapter Four

Differential responses of carbon and nitrogen cycles to experimental warming

ABSTRACT

Carbon and nitrogen processes interact to substantially influence the ecosystem function under global warming. The objective of this study was to examine the potential responses of carbon and nitrogen cycling to elevated temperature in an Oklahoma tallgrass prairie. Warming increased net N mineralization by 1885% and 87% in the first year but reduced it by 81% and 34% in the second year in the unclipped and clipped subplots, respectively. Elevated temperature under experimental warming did not affect peak AGB in 2000, but significantly increased the peak AGB 13% and 27% without or with clipping in 2001. The results suggest that there was a time lag between the response of peak aboveground biomass and that of net nitrogen mineralization. The differential responses and a negative feedback between carbon and nitrogen cycling could lead to the interannual variability of net primary production and limit long-term C uptake by ecosystems.

Keywords: Aboveground Biomass, carbon cycling, C:N ratio, net nitrogen mineralization, tallgrass prairie, warming.

INTRODUCTION

In natural terrestrial ecosystems, carbon (C) cycling is generally coupled with nitrogen (N) cycling because N is the most limiting nutrient on net primary production (NPP) (Binkley 1986, Chapin et al. 1986, Vitousek and Howarth 1991). The coupled C and N cycling can form a positive or negative feedback loop, leading to divergence or convergence of NPP across different ecosystems (Hobbie 1992, Tateno and Chapin 1997, Knops et al. 2002). Model simulations have shown that the warming effect on global C cycling is sensitive to these feedbacks (Schimel et al. 1994, McGuire et al. 1997, Den Elzen et al. 1997). However, it is unclear how temperature-induced changes in C and N processes responding at different timescales contribute to the overall pattern in ecosystem responses. Here I provide an experimental evidence to show that C and N cycling in terrestrial ecosystems may be differentially affected by elevated temperature.

MATERIALS AND METHODS

In situ net N mineralization was measured for two years (from November 1999 to December 2001) using an incubation method. The incubations were performed on "undisturbed" soil in 15 cm long perforated PVC tubes with a diameter of 4 cm. Paired PVC tubes were inserted into the soil adjacently within 15 cm apart. One tube was removed immediately while the other one was taken as the control treatment and left in the field for approximately two months. A plastic film was used to cover the upper end of the treatment tube to avoid leaching of NO_3. In the first half-year from November 1999 to May 2000, soil cores were taken from all the subplots. Afterwards only half of the subplots were considered in order to reduce disturbance to the experimental sites.

Ammonium and nitrate were determined at the Soil, Water and Forage Analytical Laboratory of Oklahoma State University. Net N mineralization was calculated from the net change in available N ($NH_4^+ + NO_3^-$) between control and incubated samples. Soil organic C and N were measured using soil samples taken in November 2000 and December 2001.

The point quadrat method was used to measure aboveground biomass in the unclipped subplots. Plants were clipped annually in July from two diagonal subplots to calculate aboveground biomass. In December 2001, soil cores with a diameter of 5.2 cm were taken from one unclipped and one clipped subplots in each plot and washed to measure root biomass.

Soil respiration was measured once or twice a month using LiCor 6400 Portable Photosynthesis System with an attachment of LiCor 6400-9 soil chamber. A PVC collar (80 cm^2 in area and 5 cm in height) was installed permanently at the center of each subplot for measurement of total soil respiration. A PVC tube (80 cm^2 in area and 70 cm in length) was used to replace the PVC collar at the center of one unclipped and one clipped subplot to measure "root-free" respiration in October 2001.

RESULTS AND DISCUSSIONS

Warming increased net N mineralization by 1885% and 87% in the first year but reduced it by 81% and 34% in the second year in the unclipped and clipped subplots, respectively (Fig. 1a). The change in the net N mineralization was statistically significant only in the unclipped subplots ($p < 0.05$) in both years. Elevated temperature under experimental warming did not affect peak AGB in 2000, but significantly increased the peak AGB in 2001, both without (13%, $p < 0.05$) and with clipping (27%, $p < 0.01$) (Fig. 1b). Warming also enhanced root biomass by 20% and

24% without and with clipping in 2001, but the difference between the control and warmed plots was statistically significant only in the clipped subplots ($p < 0.05$, data not shown). In the third year, peak AGB in the warmed plots was 5% ($p>0.05$) and 30% ($p<0.001$) higher than that in the control plots without and with clipping, respectively. From these observations, it appears that there was a time lag between the response of peak AGB and that of net N mineralization to elevated temperature.

Though the enhanced net N mineralization in the present study lasted only for one year, increased net N mineralization and N availability under warming has widely been found in different biomes across the world (Rustad et al. 2001). The observed differential responses of net N mineralization and peak AGB to elevated temperature in the present study could be due to two possible reasons. First, most plant species in the tallgrass prairie community are perennial species. The enhanced N availability due to increased N mineralization in the first year might have been readily taken up by plants in that year but stored for use in the subsequent years (Vukicevic et al. 2001). The enhanced plant N uptake and storage will increase canopy leaf area index and leaf-level photosynthesis (Field et al. 1986) in the subsequent year, leading to the stimulated plant growth and above- and below-ground biomass. Contrary to this, the reduced N mineralization in the second year (but not N availability) should have caused a lowered peak biomass increment in the unclipped warmed plots in the second year. Second, the tallgrass prairie has both C_3 and C_4 species. C_4 species have higher N use efficiency (NUE) and low N requirement (Lamber et al. 1998), hence the increased net N mineralization and availability might not have benefited growth of C_4 species. On the other hand, growth and biomass accumulation of C_3 species would be stimulated by enhanced N availability as these species have

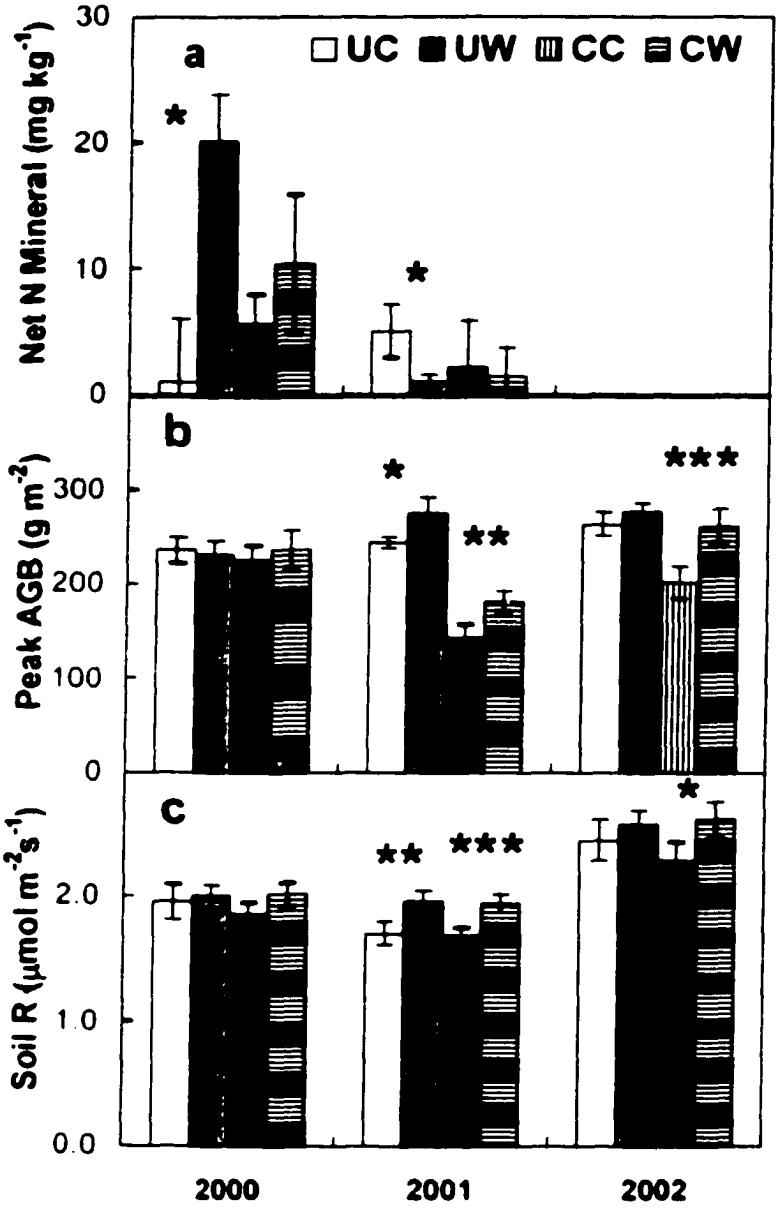

Figure 1. Annual total net N mineralization (a), peak AGB (b), and annual mean soil respiration (c) in the four subplots (mean ± 1SE). UC: Unclipped Control, UW: Unclipped Warmed, CC: Clipped Control, CW: Clipped Warmed; * statistically significant at the confidence level of 95%; ** statistically significant at the confidence level of 99%, * statistically significant at the confidence level of 99.9%.**

lower NUE and higher N requirement and show a positive response to N fertilization (Hunt and Bazzaz 1980, Vitousek 1983). In another study on the same warming site, significant responses in one of the C_3 species, western ragweed (*Ambrosia psilostachya* DC.) was observed. Stem numbers, dry mass per stem, AGB per unit ground area, and the ratio of ragweed AGB to total AGB of western ragweed in the warmed plots were significantly higher than those in the control plots in the second year, but only the dry mass per stem showed significant changes in the first year (Wan et al. 2002). In the third year, none of the four variables in the warmed plots were significantly different from those in the control plots, reflecting the effects of reduced N mineralization in the previous year.

The differential response in net N mineralization and biomass accumulation observed in the present study are in agreement with other reports. In wet sedge tundra, Shaver et al. (1998) found significant increase in net N mnieralization under warming, but the corresponding increase in plant biomass were proportionally smaller and marginally significant in that year. A study by Day et al. (1999) on growth and reproduction of two vascular plants in the Antarctic also found improved growth due to warming in *Colobanthus quitensis* (Caryophyllaceae). However, warming had few effects on growth in *Deschampsia antarctica* (Gramineae). In the present study, elevated temperature caused increase in net N mineralization in the first year, which in turn stimulated plant growth and peak AGB in the second year. The enhanced primary production put a negative feedback to N cycling by increasing C input into the soil, stimulating microbial N immobilization, and reducing net N mineralization in the second year.

Soil respiration showed a concomitant response with that of peak AGB during the three years (Fig. 1c). In the first year, there was no significant difference in soil respiration between the warmed and control plots ($p > 0.05$) (Luo et al. 2001). In the second year, soil respiration in the

warmed plots was significantly greater than that in the control plots without (15%, $p < 0.01$) and with clipping (16%, $p < 0.001$). In the third year, total soil respiration increased by 5% ($p>0.05$) and 15% ($p < 0.05$) in the unclipped and clipped subplots, respectively. Root-free respiration in the warmed plots was slightly, but insignificantly ($p>0.05$), higher than in the control plots without (5%) and with (2%) clipping.

It is assumed that C input (NPP) and output (soil respiration) in terrestrial ecosystems may have different responses to global warming because these two processes are supposed to have different temperature sensitivities. However, data in the present study showed that the changes in soil respiration occurred concurrently with the changes in NPP. Rhizosphere respiration (including root respiration and mycorrhizal microbial respiration) contributes approximately 30% to annual total soil respiration in the tallgrass prairie (Wan and Luo 2003). On one hand, enhanced NPP under warming caused an increase in belowground C allocation through root exudates, mucilage and root litter, leading to an increase in rhizosphere and total soil respiration in the second year. In support of this, significant increase in soil respiration under warming occurred in early spring and late autumn when the green biomass in the warmed plots was significantly greater than that in the control plots (Wan et al. unpublished data). On the other hand, heterotrophic respiration from soil organic matter with long turnover time might not respond much to the elevated temperature. The insignificant change of root-free respiration in the third year confirmed this assumption (see above).

Further analyses also supported the previous results that C and N differentially responded to elevated temperature. Plotting peak AGB against available N six months before each biomass measurement in the unclipped and clipped subplots in each plot showed positive linear correlations between peak AGB and N availability across the seasons in 2000 ($p < 0.01$, 0.01,

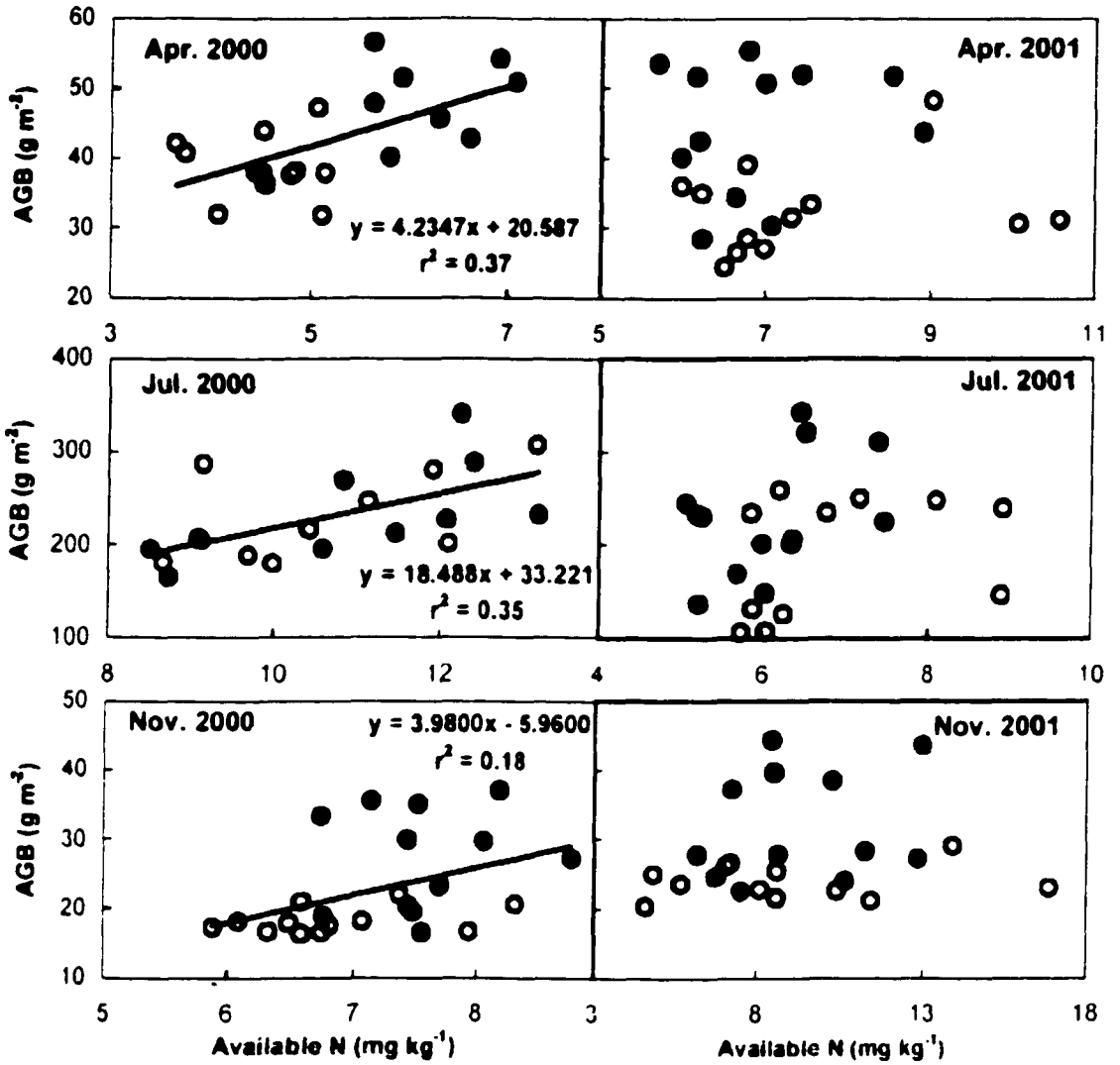

Figure 2. The relationship between AGB and soil N availability. The positive correlation between AGB and available N six months before AGB measurements was statistically significant only in the first year ($p < 0.01$, 0.01, and 0.05 for April, July, and November, respectively). Each data point was the average AGB in the two unclipped or clipped subplots in each control (open circle) and warmed (solid circle) plot.

and 0.05 for April, July, and November, respectively). However, this correlation disappeared in the second year ($p > 0.05$) (Fig. 2). The enhanced available N from increased net N mineralization was taken up and stored but did not result in significant increase in peak AGB in the first year, leading to observed N limitation in 2000. The increased plant N uptake mitigated the N limitation and stimulated plant growth and biomass accumulation in the second year.

A growing C accumulation in plant biomass on land over the last decades could be attributable to the warming-enhanced N mineralization (Hungate et al. 1997). It helps balance the global C cycle and helps account for the "missing sink". In the US Central grasslands, nutrient enhancement caused an increase in NPP, demonstrating that nutrient interactions are a major control over vegetation response to climate change (Schimel et al. 1990). Globally, there appears to be a net C release to the atmosphere during warm and dry years, and a net uptake during subsequent cooler years, reflecting a lagged effect of enhanced N mineralization on NPP (Braswell et al. 1997, Vukicevic et al. 2001).

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Chapter Five

Response of an allergenic species, *Ambrosia psilostachya* (Asteraceae), to experimental warming and clipping: Implications for public health

ABSTRACT

This study was designed to examine the responses of an allergenic species, western ragweed (*Ambrosia psilostachya* DC.), to experimental warming and clipping. The experiment was conducted from 1999 to 2001. Warming increased ragweed stems by 88% when not clipped and 46% when clipped. Clipping increased ragweed stems by 75% and 36% in the control and warmed plots, respectively. In 2001, warming resulted in a 105% increase in ragweed aboveground biomass (AGB), and the ratio of ragweed AGB to total AGB increased by 79%. Dry mass per ragweed stem in the warmed plots was 37% and 38% greater than that in the control plots in 2000 and 2001, respectively. Although warming caused no difference in pollen production per stem, total pollen production increased by 84% ($P < 0.05$) because there were more ragweed stems. Experimental warming significantly increased pollen diameter from 21.2 μm in the control plots to 23.9 μm in the warmed plots (a 13% increase). The results from our experiment suggest that global warming could aggravate allergic hazards and thereby jeopardize public health.

Key words: aboveground biomass; allergy; *Ambrosia psilostachya* (Asteraceae); global warming; Oklahoma; pollen; ragweed; tallgrass prairie.

INTRODUCTION

There are increasing risks to public health associated with global warming and changes in land use. Assessment of such risks poses a major challenge to scientists and policy makers. A main concern for public health highlighted in the *Third Assessment Report of the Intergovernmental Panel on Climate Change* (McCarthy *et al.* 2001) is allergic diseases, which each year affect more than 50×10^6 people and cost about 18×10^9 dollars for health care in the United States alone (AAAAI 2000). Further, allergic diseases have increased among the general population over the last 50 years (Platt-Mills and Carter 1997, Woolcock and Peat 1997, AAAAI 2000), an increase that coincides with the unprecedented changes in the global environment since the 1950s. The prime cause of human allergies during the autumn is airborne ragweed (*Ambrosia*) pollen (Meggs *et al.* 1996), and the abundance of ragweed pollen is closely related to meteorological conditions (Buck and Levetin 1982), suggesting that global warming may increase the amount of ragweed pollen and therefore human allergies. The responses of allergenic species, in particular their pollen production, to global warming, however, have not been carefully studied.

This study was designed to examine the effects of experimental warming and clipping on western ragweed (*Ambrosia psilostachya* DC.), an allergenic species. It is a part of a comprehensive warming experiment in a tallgrass prairie in the U.S. Great Plains (Luo *et al.* 2001, Wan *et al.* 2002). Infrared heaters were used to mimic climate warming, and clipped to simulate mowing for hay, a widespread land-use practice in the tallgrass prairie of the Great Plains.

MATERIALS AND METHODS

Site description

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. The site has not been grazed for the past 20 yr. The grassland is dominated by C_4 grasses (*Schizachyrium scoparium* (Michx.) Nash-Gould, *Sorghastrum nutans* (L.) Nash, and *Eragrostis curvula* (Schrad.) Nees) and C_3 forbs (*Ambrosia psilostachya* and *Aster ontarionis* Wieg.). Mean annual temperature is 16.3°C with a monthly mean temperature of 3.3°C in January and 28.2°C in July. The annual precipitation is 967 mm. The soil is part of the Nash-Lucien complex, which is characterized by having a low permeability, high available water capacity, and deep, moderately penetrable root zone (USDA Soil Conservation Service and Oklahoma Agricultural Experiment Station, 1963).

Experimental design

The experiment used a paired factorial design, with warming as the main factor nested with clipping. There were five pairs of 2 × 2 m plots. One plot in each pair had been warmed continuously with infrared heaters since 21 November 1999, and the other plot was the control. In each warmed plot, a single 165 × 15 cm infrared heater (Kalglo Electronics, Bethlehem, Pennsylvania, USA) was suspended 1.5 m above the ground. The heater had a radiation output of approximately 100 W/m^2. In the control plot, a "dummy" heater of the same shape and size as the infrared heater was suspended 1.5 m above the ground to simulate the shading effects of the heater. The distance between the control

and warmed plots in each pair was approximately 5 m to prevent heating of the control plot by the infrared heater. The distances between the individual sets of paired plots varied from 20 to 60 m.

Each 2 × 2 m plot was divided into four 1 × 1 m subplots. Two diagonal subplots in each plot were clipped to 10 cm above the ground on 15 November 1999, 28 July 2000, and 24 July 2001; the other two were the unclipped control subplots. Clipping removed approximately 85% of the aboveground biomass. After clipping, plants were allowed to grow until the next clipping. The four treatments in the experiment were (1) unclipped unwarmed, (2) unclipped warmed, (3) clipped unwarmed, and (4) clipped warmed.

Stem number, aboveground biomass, percent coverage

Ragweed stems were counted in the field on 25 August 1999 and 19 July 2001 and in the plant material clipped in 2000 and 2001. On 20 November 2001, living stems were counted in the unclipped subplots.

After clipping, plants were separated into ragweed, other forbs, and grasses, and each group was oven dried at 60°C for 48 h and then weighed. Ragweed aboveground biomass (AGB), the ratio of ragweed AGB to total AGB, and the dry mass per ragweed stem were measured and calculated.

In November 2000 and in April and June 2001, the percent coverage of ragweed was estimated using the point count method (Floyd and Anderson 1987). A one-tailed paired *t* test was used in statistical analysis.

Pollen analysis

In September and October 2001, six ragweed stems in the unclipped, unwarmed subplots and the unclipped, warmed subplots in each pair were randomly selected for pollen sampling. Ragweed pollen was sampled once every 3 days from 21 September to 20 October 2001. Ragweed flowers were put into 17 × 20 cm zip-lock plastic bags (S.C. Johnson & Son, Racine, Wisconsin, USA) and shaken for 20 s. Pollen was washed from each bag with 20 mL of water. The pollen solution was put into culture plates with a diameter of 8.65 cm. The pollen in each sample was counted 15 times using an ocular micrometer under a light microscope (200×). The diameters of 42 pollen grains sampled on 6 October 2001 from both unwarmed and warmed plots were measured with an objective micrometer (320×). Pollen production for each date was calculated by multiplying the mean value of pollen counted within the range of the ocular micrometer by the quotient of the area of culture plate and the area of the ocular micrometer. Pollen production per stem was the quotient of the sum of pollen production for all sampling dates and the number of stems sampled. Total pollen production per subplot was calculated by multiplying the average pollen production per stem in the unwarmed and warmed plots by stem numbers in each subplot.

RESULTS AND DISCUSSION

Experimental warming significantly increased daily mean air temperature (up 1.2°C) and daily mean soil temperatures (up 1.8° and 2.7°C without and with clipping,

respectively). Clipping also increased daily mean soil temperatures by 0.4° and 1.2°C in the unwarmed and warmed plots, respectively.

Experimental warming progressively increased the number of ragweed stems. Before the treatments in 1999, stem numbers were similar in the four subplots. Warming increased the number of stems slightly, but not significantly, in the clipped subplots (37%, $P > 0.10$) in 2000. By 2001 the number of stems in the warmed plots was significantly higher both without clipping (88%, $P < 0.05$) and with clipping (46%, $P < 0.05$) than in the unwarmed plots. Clipping also increased stem numbers by 75% ($P < 0.05$) in the unwarmed plots and by 36% ($P < 0.10$) in the warmed plots in 2001 (Fig. 1).

Biomass production of ragweed was also stimulated by experimental warming. Dry mass per ragweed stem in the warmed plots increased significantly (by 37% and 38% in 2000 and 2001, respectively) compared with that in the unwarmed plots. Increased stem

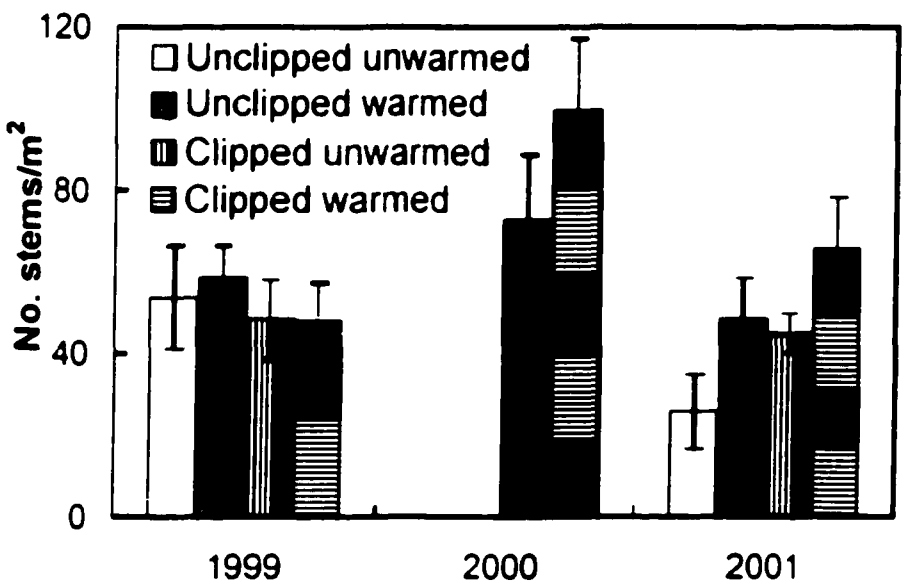

Figure 1. Warming and clipping effects on the number of western ragweed (*Ambrosia psilostachya*) stems (means ± 1 SE).

Table 1. Effects of warming on western ragweed (*Ambrosia psilostachya*) characteristics (mean ± 1 SE) in the clipped subplots.

Characteristic	1999	2000	2001
Dry mass per stem (g)			
Unwarmed	0.57 ± 0.179	0.54 ± 0.054	0.37 ± 0.052
Warmed	0.41 ± 0.121	0.75 ± 0.078	0.52 ± 0.066
t test	0.2455	0.0343*	0.0288*
Aboveground biomass (AGB, g/m^2)			
Unwarmed	22.0 ± 5.89	43.3 ± 13.4	17.2 ± 2.77
Warmed	21.6 ± 8.70	69.0 ± 7.45	35.2 ± 8.29
t test	0.4887	0.1082	0.0150*
Ragweed AGB/total AGB (%)			
Unwarmed	4.31 ± 0.66	17.3 ± 3.39	12.2 ± 2.72
Warmed	4.99 ± 2.36	27.2 ± 4.34	21.9 ± 5.41
t test	0.3927	0.1131	0.0096**

*Statistically significant at confidence level of 95%.

**Statistically significant at confidence level of 99%.

numbers and dry mass per stem in 2001 led to substantial increases in ragweed AGB per unit ground area (105%) and in the ratio of ragweed AGB to total AGB (79%) in the warmed plots compared with those in the unwarmed plots (Table 1).

Percent coverage of ragweed was 195% and 136% higher in the warmed plots than in the unwarmed plots in April and June 2001, respectively. A severe frost in November

2000 killed all ragweed stems in the unwarmed plots, whereas most stems survived in the warmed plots (Fig. 2a). After the first frost in November 2001, the number of living stems was significantly greater (239%) in the warmed plots (18.7 stems/m^2) than in the unwarmed plots (5.5 stems/m^2, Fig. 2b). The increase in percent coverage likely resulted from stimulated emergence and growth in spring and enhanced survivorship in fall under warming, suggesting an increase in the length of the growing season.

Increased stem numbers, biomass production, and percent coverage of ragweed in tallgrass prairie under warming may be attributable to several factors. First, well adapted to disturbed, dry, warm areas, ragweed has a higher photosynthetic rate than other forbs, partly because its taller stature gives it an advantage in light competition (Abul-Fatih and Bazzaz 1979a, b, Bazzaz and Carlson 1979). Second, experimental warming and increased light level at the soil surface due to clipping may stimulate germination of ragweed (Pickett and Baskin 1973), resulting in increased stem numbers. Third, warming extends growing-season length, enhances survivorship, and promotes growth of ragweed. Fourth, ragweed has a high nitrogen requirement and shows a positive response to nitrogen fertilization (Hunt and Bazzaz 1980, Vitousek 1983). Thus, increased nitrogen availability under experimental warming (Rustad *et al.* 2001) may also indirectly enhance growth of ragweed. Moreover, the root exudates, leaf leachate, and decomposed litter of western ragweed release secondary metabolites that inhibit other species, such as *Andropogon ternarius* (Neill and Rice 1971). Experimental warming may augment such an allelopathic effect. Interactions of the above physiological and ecological processes may provide ragweed with a competitive advantage over other species in the tallgrass prairie community.

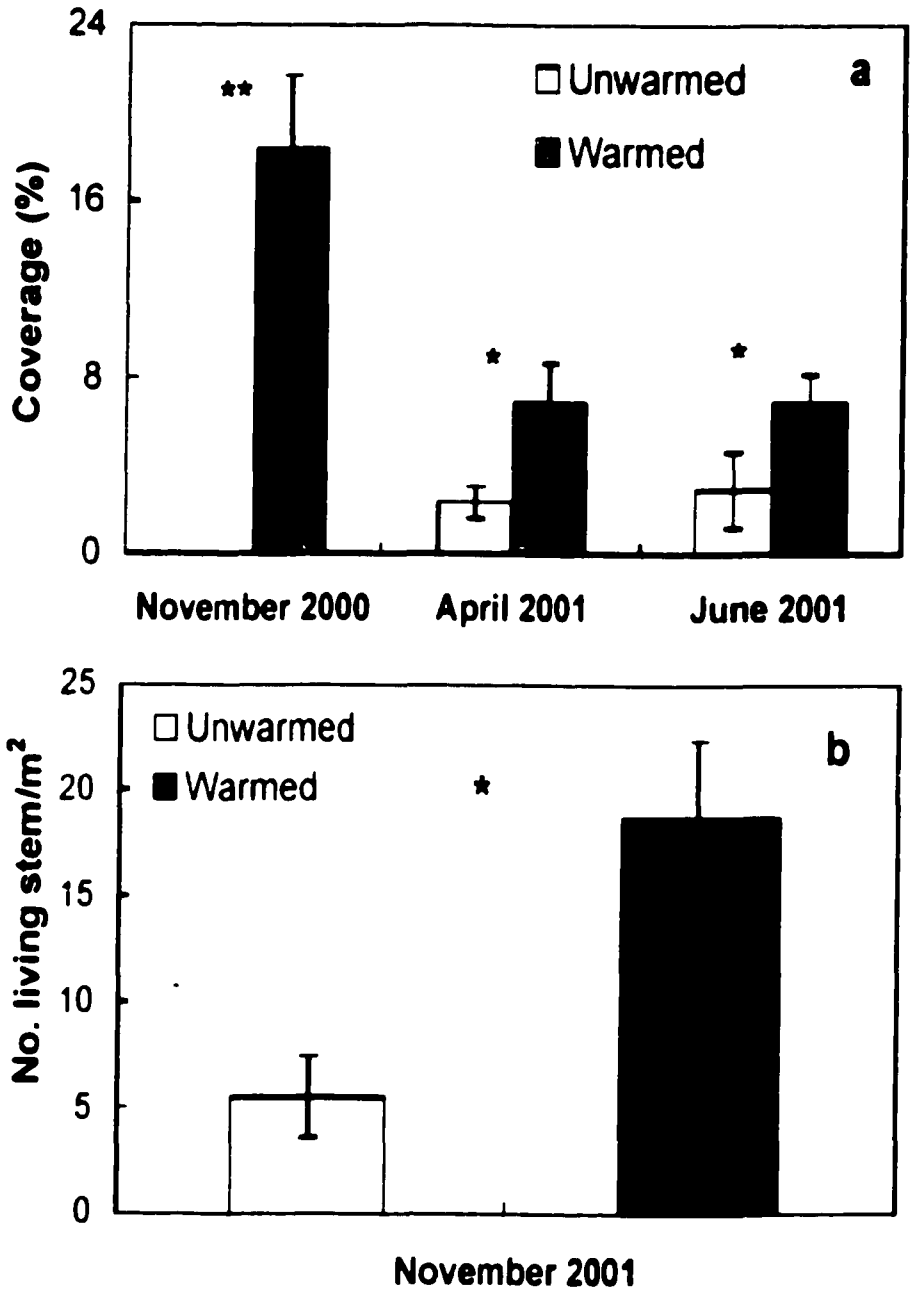

Figure 2. Warming effect on (a) the percent coverage (means ± 1 SE) and (b) the number (means ± 1 SE) of living western ragweed stems in the unclipped subplots. *Statistically significant at confidence level of 95%, **statistically significant at confidence level of 99%.

The diameter of the pollen grains was significantly greater (13%) in the warmed plots (23.9 μm) than in the unwarmed plots (21.2 μm, Fig. 3a). Allergenic proteins are located in both pollen walls (Howlett *et al.* 1979) and cytoplasm (Grote 1991, 1999, Rodríguez-Garcia *et al.* 1995, Staff *et al.* 1999). As a result, larger pollen grains could presumably carry more allergenic proteins than smaller ones. In addition, previous studies indicated that higher temperature increases protein and allergen content of pollen grains (Van Herpen 1981, Hjelmroos *et al.* 1995). Thus, enhanced pollen size and allergen content could lead to an increased allergic effect in humans. However, larger pollen grains may sink faster and travel shorter distances than smaller ones.

Total pollen production per unit of ground area increased significantly (84%, Fig. 3b) with warming, even though there was no difference in pollen production per stem between the warmed and unwarmed plots (data not shown). The increase in pollen production in the warmed plots resulted primarily from the increase in stem numbers. Our results are corroborated by palynological studies in which ragweed pollen abundance from lake sediment cores increased in dry, warm intervals during the postglacial period (Davis 1969) and over the past 50 000 years (Grimm *et al.* 1993).

Unprecedented changes in the global environment since the 1950s have coincided with increases in allergies among the general population (Platt-Mills and Carter 1997, Woolcock and Peat 1997, AAAAI 2000), suggesting that global change might already be increasing the production of ragweed pollen. During the past 50 yr, atmospheric CO_2 concentration has increased by more than 20% (McCarthy *et al.* 2001). When the concentration of CO_2 was elevated experimentally from 280 to 370 ppm, ragweed pollen production increased by 131%; elevation of CO_2 from 370 to 600 ppm yields 90% more

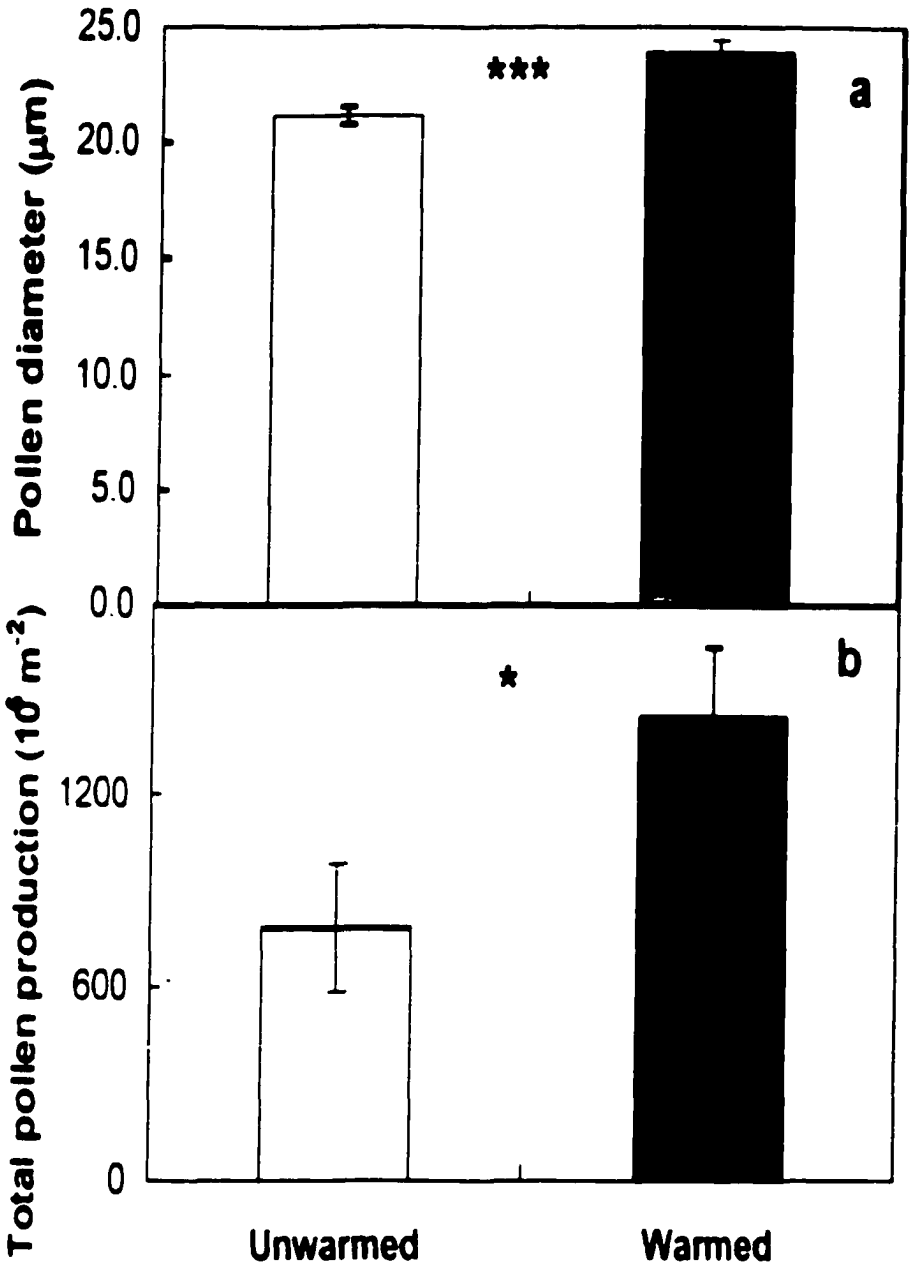

Figure 3. Warming effects on (a) the diameter (means ± 1 SE) of pollen grains and (b) the total pollen production (means ± 1 SE) of western ragweed in the unclipped subplots. ***Statistically significant at confidence level of 99.9%, *statistically significant at confidence level of 95%.

pollen (Ziska and Caulfield 2000a, b). A recent study also showed that a doubling of the atmospheric CO_2 concentration from 350 to 700 ppm stimulated ragweed pollen production by 61% (Wayne *et al.* 2002). In addition to an increase in atmospheric CO_2 since the 1950s, global mean temperature has risen by approximately 0.5°C and extended the growing season by about 3 wk (Peñuelas and Filella 2001). A 1.2°C increase in air temperature and its associated change in the length of the growing season enhanced ragweed pollen production by 84%, suggesting that an intensified and lengthened allergic season might result. Elevated temperature increases not only allergic pollen production but also protein and allergen content of pollen grains (Van Herpen 1981, Hjelmroos *et al.* 1995). Land use has also changed greatly in the past 50 years (McCarthy *et al.* 2001). Data from a palynological study (Russell 1980) and a model simulation (Emberlin 1994) indicate that land use change affects ragweed pollen abundance. Our results also show that clipping, which mimics harvesting hay, stimulates growth, stem numbers, and total pollen production of ragweed. In short, the three concurrent driving forces of global change—rising atmospheric CO_2 concentration, global warming, and land use change—may augment pollen production of ragweed and intensify cross-reactive allergies with other pollens and air pollutants (Staff *et al.* 1999, AAAAI 2000, Epstein 2000, Cifuentes *et al.* 2001, Fernandez *et al.* 2001).

Global change has the potential not only to exacerbate human allergies but also to increase the incidence of other diseases related to heat waves, flooding, drought, air pollution, and reduced food supply, as well as vector-, food-, and water-borne infections (Cohen 2000, Epstein 2000, Cifuentes *et al.* 2001, Fernandez *et al.* 2001, McCarthy *et al.* 2001). With a continuing increase in global mean temperature, airborne pollen

abundance and other health risk factors will likely increase further. Our results and those from previous studies (Van Herpen 1981, Hjelmroos *et al.* 1995, Ziska and Caulfield 2000a, b, Wayne *et al.* 2002) point to the urgency of reducing the emission of greenhouse gases. Mitigation of greenhouse gases will not only slow global warming but also substantially benefit public health (Cifuentes *et al.* 2001).

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