

Photosynthetic and Respiratory Acclimation to Experimental Warming for Four Species in a Tallgrass Prairie Ecosystem

Xuhui Zhou*, Xiaozhong Liu, Linda L. Wallace and Yiqi Luo

(Department of Botany and Microbiology, University of Oklahoma, Norman, Oklahoma 73019, USA)

Abstract

Global temperature has been increased by 0.6 °C over the past century and is predicted to increase by 1.4–5.8 °C by the end of this century. It is unclear what impacts global warming will have on tallgrass species. In the present study, we examined leaf net photosynthetic rate (P_n) and leaf respiration rate in darkness (R_d) of *Aster ericoides* (L.) Nesom, *Ambrosia psilostachya* DC., *Helianthus mollis* Lam., and *Sorghastrum nutans* (L.) Nash in response to experimental warming in a tallgrass prairie ecosystem of the Great Plains, USA, in the autumn (fall) of 2000 and through 2001. Warming has been implemented with infrared heaters since 21 November 1999. The P_n increased significantly in spring, decreased in early fall, and did not change in summer and late fall in the four species under warming compared with control. The R_d of the four species increased significantly until mid-summer and then did not change under warming. Measured temperature-response curves of P_n showed that warming increased the optimum temperature of P_n (T_{opt}) by 2.32 and 4.59 °C for *H. mollis* and *S. nutans*, respectively, in August, whereas there were no changes in May and September, and *A. ericoides* and *A. psilostachya* also showed no changes in any of the 3 months. However, P_n at optimum temperature (P_{opt}) showed downregulation in September and no regulation in May and August for all four species. The temperature-response curves of R_d illustrate that the temperature sensitivity of R_d , Q_{10} , was lower in the warmed plots compared with the control plots, except for *A. ericoides* in August, whereas there were no changes in May and September for all four species. The results of the present study indicate that photosynthetic and respiratory acclimation varies with species and among seasons, occurring in the mid-growing season and not in the early and late growing seasons.

Key words: acclimation; *Ambrosia psilostachya*; climatic warming; photosynthesis; respiration; *Sorghastrum nutans*; tallgrass prairie; temperature.

Zhou X, Liu X, Wallace LL, Luo Y (2007). Photosynthetic and respiratory acclimation to experimental warming for four species in a tallgrass prairie ecosystem. *J. Integr. Plant Biol.* 49(3), 270–281.

Available online at www.blackwell-synergy.com/links/toc/jipb, www.jipb.net

Received 19 Jan. 2006 Accepted 20 Mar. 2006

Supported by US National Science Foundation (NSF) (DEB 0078325, DEB 0092642, and DEB 0444518), and US Department of Energy (DE-FG03-99ER62800).

Publication of this paper is supported by the National Natural Science Foundation of China (30624808) and Science Publication Foundation of the Chinese Academy of Sciences.

*Author for correspondence.

Tel: +1 (405)325 8578;

Fax: +1 (405)325 7619;

E-mail: <zxuhui14@ou.edu>.

© 2007 Institute of Botany, the Chinese Academy of Sciences

doi: 10.1111/j.1672-9072.2006.00374.x

One of the predicted consequences of increasing emissions of carbon dioxide (CO₂) and other greenhouse gases is a rise in air temperature near the ground. The average surface temperature of the earth has increased by approximately 0.6 °C over the past century and is expected to increase by 1.4–5.8 °C over the period 1990–2100 (Intergovernmental Panel of Climate Change (IPCC) 2001). In the Great Plains, air temperature is predicted to increase by 2–4 °C with the doubling of current CO₂ concentration (Long and Hutchin 1991). This projected atmospheric warming, combined with the resulting climatic changes, may have marked ecological effects on terrestrial ecosystems, as well as on individual species (Peters and Darling 1985).

Both photosynthesis and respiration are temperature

dependent and among the most sensitive processes in response to global warming (Berry and Björkman 1980; Larigauderie and Körner 1995; Atkin et al. 2000c; Gunderson et al. 2000; Xiong et al. 2000; Jarvis et al. 2004). A change in temperature will result in an immediate alteration in the rates of each process (Berry and Björkman 1980; Atkin et al. 2000c, 2006). However, the short-term temperature sensitivity of photosynthesis typically differs from that of respiration in individual leaves, affecting carbon allocation within ecosystems and net carbon flux (Körner 1995; Atkin et al. 2005). In *Eucalyptus pauciflora*, for example, a decline in temperature from 25 to 15 °C reduces rates of leaf respiration and photosynthesis by 55% and 21%, respectively (Atkin et al. 2000a). If plants experience prolonged exposure to a new growth temperature, they may develop a variety of mechanisms to acclimate and/or adapt to the prevailing temperatures. As a result, a new balance between photosynthesis and respiration rates may be re-established in response to changes in temperature. When the new terrestrial carbon balance at leaf level is applied to ecosystem level, even to the global scale, it may exacerbate or mitigate the build-up of atmospheric CO₂ concentration owing to the differences in their temperature sensitivities in a warmer world. Nevertheless, most simulation models, such as Biome-BGC (Hunt et al. 1996), Century (Schimel et al. 1997), PnET (Aber and Federer 1992), and several dynamic vegetation models (White et al. 2000; Cramer et al. 2001), do not incorporate physiological acclimation potential for photosynthesis or respiration. To better model the effects of climatic warming on plant physiological performance, it is essential to understand photosynthetic and respiratory responses to rising temperature.

Acclimation of both photosynthesis and respiration has been reported in the literature when plants are exposed to changed temperatures (Edwards and Smith 1988; Larigauderie and Körner 1995; Battaglia et al. 1996; Atkin et al. 2000a, 2000b; Loik et al. 2000, 2004; Xiong et al. 2000; Bolstad et al. 2003; Lee et al. 2005; Yamori et al. 2005). For photosynthesis, the physiological acclimation is highly variable, ranging from fully acclimating with a pronounced shift in temperature optimum, a compensatory increase across all temperatures, or both to no change or a negative adjustment (Gunderson et al. 2000). Similarly, respiratory acclimation to temperature history is also not universal (Arnone and Körner 1997; Atkin et al. 2005). However, most evidence of photosynthetic and respiratory acclimation to rising temperature comes from laboratory studies with constant day/night temperatures for saplings or seedlings (e.g. Edwards and Smith 1988; Larigauderie and Körner 1995; Gunderson et al. 2000; Xiong et al. 2000; Bolstad et al. 2003; Yamori et al. 2005). Very few studies have been performed with small increases in temperature associated with global warming in the natural ecosystems (Bergh and Linder 1999; Loik et al. 2000, 2004; Llorens et al. 2004), where daily and seasonal temperatures vary greatly, and no tallgrass

species have been included in the previous studies.

The present study is part of a larger project to examine effects of the long-term warming plus yearly clipping on community structure and ecosystem processes in a tallgrass prairie ecosystem of central Oklahoma, USA (Luo et al. 2001; Wan et al. 2002, 2005; An et al. 2005; Zhou et al. 2006). In the present study, we examined the potential for temperature acclimation of photosynthesis and respiration in four native tallgrass species (*Aster ericoides*, *Ambrosia psilostachya*, *Helianthus mollis*, and *Sorghastrum nutans*). Infrared heaters were used to simulate climatic warming since 21 November 1999. The hypothesis was that plants exposed to experimental warming would exhibit less photosynthetic and respiratory gas exchange compared with control when their rates are measured in a similar leaf temperature. An additional objective of the present study was to investigate the differences in photosynthesis and respiration in response to experimental warming among the four species.

Results

Leaf net photosynthetic rate

Leaf net photosynthetic rates (P_n) of the four species are shown

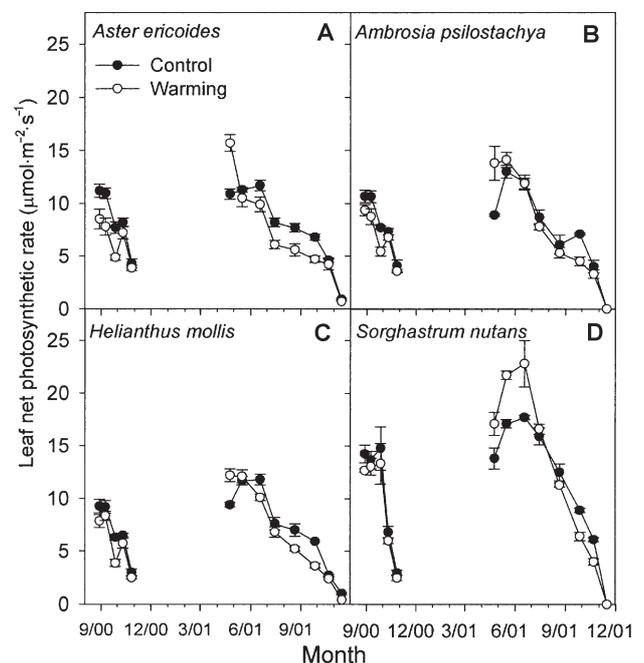


Figure 1. Seasonal variation of leaf net photosynthetic rate for four tallgrass species in the warming experiment in autumn (fall) 2000 and throughout 2001.

Data are the mean \pm SE ($n = 6$) from the control (solid circles) and warmed (open circles) plots.

in Figure 1 for both the control and warmed treatments. The P_n reached the maximum in April, May, or June (depending on the species), and then decreased until the end of the growing season in both 2000 and 2001. Warming increased the peak P_n of *A. ericoides* and *A. psilostachya*, shifted it from between May and June to April in *A. ericoides*, and extended the peak P_n time from May to between April and May in *A. psilostachya* (Figure 1A, B). In *H. mollis*, the peak P_n time was extended from between May and June to between April and May without changing peak P_n (Figure 1C). In the sole C_4 species (*S. nutans*), the peak P_n was significantly increased without a shift in timing (Figure 1D). The P_n increased significantly in spring ($P < 0.05$), decreased in early fall ($P < 0.05$), and did not change in summer and late fall ($P > 0.05$) in the four species under warming rela-

tive to the control (Figure 1). Warming resulted in a greater enhancement of P_n in *A. ericoides* and *S. nutans* than in the other two species in the early growing season. Leaf temperature did not differ between the control and warmed plots (data not shown; $P > 0.05$). In addition, the peak P_n tended to be greater in *S. nutans* (C_4 grass) than in the other three species (C_3 forbs) under either the control or warming treatments over the study period, but the difference was not statistically significant ($P > 0.05$).

Photosynthetic responses to temperature

The P_n versus leaf temperature curves of the four species in May, August, and September are shown Figure 2, and the P_n at

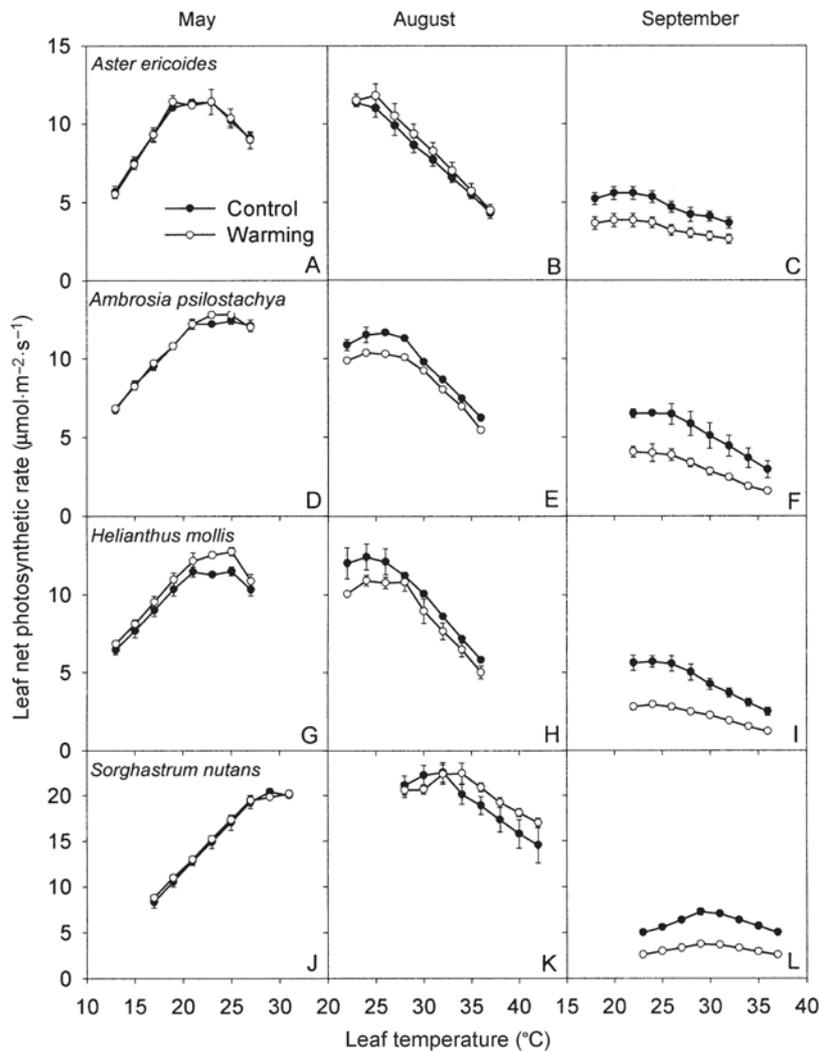


Figure 2. Leaf temperature response curves of net photosynthetic rate for the four species in three different seasons (May, August, and September).

Data are the mean \pm SE ($n = 6$) from the control (solid circles) and warmed (open circles) plots.

the temperature optimum (P_{opt}) and the temperature optimum (T_{opt}) derived from equation 1 (see Materials and Methods) are given in Table 1. These curves illustrate that P_n had different patterns in response to seasons, species, and treatments at respective temperature ranges. In early May, P_n increased with the measured temperature, reached a maximum, and then decreased. Warming did not significantly affect P_n , P_{opt} , or T_{opt} in any of the four species (Figure 2A, D, G, J; Table 1). In mid August, P_n initially leveled off and decreased with increasing temperatures in all four species (Figure 2B, E, H, K). Warming decreased P_{opt} by 1.10 and 1.59 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in *A. psilostachya* and *H. mollis*, respectively, and increased T_{opt} by 2.32 and 4.59 °C in *H. mollis* and *S. nutans*, respectively (Table 1). In late September, the temperature-response curves of P_n flattened out for all four species (Figure 2C, F, I, L) and warming

significantly reduced P_{opt} for the four species, although it did not vary T_{opt} (Table 1). A significant downward shift of photosynthesis under warming was detected for *A. psilostachya* and *H. mollis* in mid August ($P<0.05$) and for all four species in late September ($P<0.001$; Figure 2), resulting in photosynthetic acclimation.

Leaf respiration rate in darkness

The leaf respiration rate in darkness (R_d) displayed pronounced seasonal variations, which increased over time from spring, reached a maximum in summer, and then decreased until the end of the growing season in fall 2000 and through 2001 (Figure 3). Warming significantly increased R_d almost year-round in *H. mollis* ($P<0.05$; Figure 3C), whereas the other three species

Table 1. Photosynthetic temperature response parameters for the four species studied in early May, mid August, and late September in the warming experiment (eqn 1)

	Treatment	P_{opt} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	T_{opt} (°C)	b	R^2
May					
<i>Aster ericoides</i>	Control	11.31	21.66	0.078 ^a	0.984
	Warming	11.41	21.61	0.083 ^a	0.977
<i>Ambrosia psilostachya</i>	Control	12.38	24.88	0.041	0.989
	Warming	12.58	24.69	0.045	0.982
<i>Helianthus mollis</i>	Control	11.31	23.24	0.050	0.972
	Warming	12.22	23.32	0.055	0.951
<i>Sorghastrum nutans</i>	Control	21.41 ^a	35.36 ^a	0.040	0.989
	Warming	21.13 ^a	34.87 ^a	0.040	0.991
August					
<i>Aster ericoides</i>	Control	10.45	23.02	0.034	0.987
	Warming	11.10	23.36	0.039	0.988
<i>Ambrosia psilostachya</i>	Control	11.40	24.44	0.041	0.972
	Warming	10.30*	24.86	0.040	0.994
<i>Helianthus mollis</i>	Control	12.29	22.28	0.036	0.989
	Warming	10.70*	24.60*	0.046	0.968
<i>Sorghastrum nutans</i>	Control	21.90 ^a	27.96 ^a	0.040	0.942
	Warming	21.75 ^a	32.55 ^{*a}	0.059*	0.902
September					
<i>Aster ericoides</i>	Control	5.44	18.92	0.011	0.917
	Warming	3.80*	18.11	0.007	0.921
<i>Ambrosia psilostachya</i>	Control	6.65	20.70	0.016	0.989
	Warming	4.05*	20.47	0.011	0.984
<i>Helianthus mollis</i>	Control	5.86	19.36	0.013	0.982
	Warming	2.90**	20.80	0.008	0.985
<i>Sorghastrum nutans</i>	Control	6.89	30.02 ^a	0.042 ^a	0.922
	Warming	3.60**	29.92 ^a	0.022 ^{*a}	0.948

* $P<0.05$, ** $P<0.01$ for the effects of warming compared with control. ^aSignificantly different compared with the values for the same parameter obtained for the other three species ($P<0.05$).

P_{opt} , net photosynthetic rate (P_n) at the optimum temperature; T_{opt} , optimum temperature for P_n ; b , the relative spread of the parabola; R^2 is the determinant coefficient.

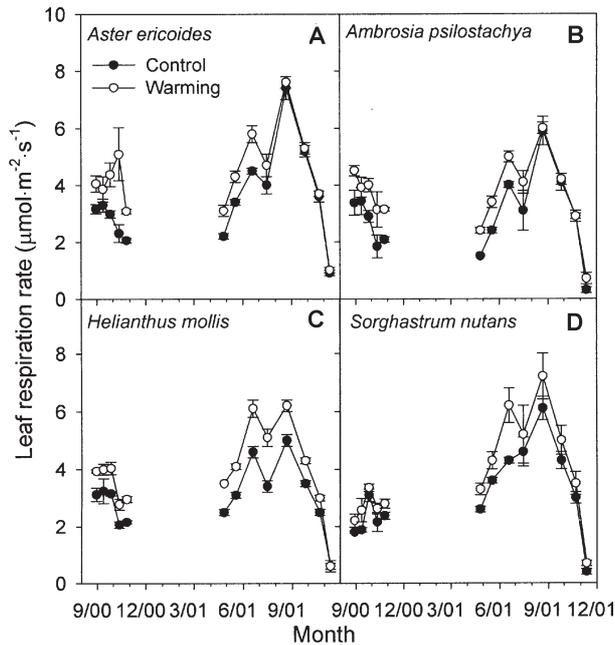


Figure 3. Seasonal variation of leaf respiration rate in darkness for four tallgrass species in the warming experiment in autumn (fall) 2000 and throughout 2001.

Data are the mean \pm SE ($n = 6$) from the control (solid circles) and warmed (open circles) plots.

increased R_d under warming until June 2001 ($P < 0.01$) and then there were no significant effects ($P > 0.05$; Figure 3A, B). On average, warming significantly increased the average R_d , with the greatest response in *H. mollis* (29.9%), an intermediate response in *A. ericoides* and *A. psilostachya* (24.4% and 25.3%, respectively), and the lowest response in *S. nutans* (21.8%) during the study period.

Respiratory responses to temperature

The R_d versus leaf temperature curves all showed similar patterns in response to seasons, species, and treatments (Figure 4). The R_d increased with the measured temperature in the three seasons studied (early May, mid August, and late September). Warming did not significantly affect R_d on the response curves for the different species ($P > 0.05$), except for *A. psilostachya* in late September ($P < 0.05$). The respiratory quotient (Q_{10}) derived from the exponential function showed that a lower Q_{10} in the warmed plots was found in August, except for *A. ericoides*, compared with that in the control plots, resulting in temperature acclimation of respiration, whereas there were no differences in all four species in May and September. The Q_{10} range was 2.52–2.91 in May, 1.86–2.36 in

August, and 1.97–2.59 in September, with the greatest values in *H. mollis*, intermediate values in *A. psilostachya* and *S. nutans*, and the lowest values in *A. ericoides* (Table 2).

Discussion

Plant physiological performance is highly sensitive to temperature and can acclimate to prevailing temperature at both short- and long-term temporal scales. Thus, prediction of ecosystem responses to climatic warming in a future world strongly relies on our understanding of plant physiological acclimation or adaptation. The present study showed that P_n exhibited at least partial temperature acclimation, which varied with species and seasons, either from seasonal variation of P_n or from its

Table 2. Estimated values of coefficients a and b in the equation $R_d = ae^{bT}$ for the respiration-temperature response curves and the temperature quotient $Q_{10} = e^{10b}$

		a	b	Q_{10}
May				
<i>Aster ericoides</i>	Control	0.287	0.093	2.52
	Warming	0.301	0.092	2.50
<i>Ambrosia psilostachya</i>	Control	0.176	0.098	2.66
	Warming	0.205	0.096	2.61
<i>Helianthus mollis</i>	Control	0.181	0.105	2.85
	Warming	0.187	0.107	2.91
<i>Sorghastrum nutans</i>	Control	0.240	0.100	2.71
	Warming	0.238	0.101	2.75
August				
<i>Aster ericoides</i>	Control	0.277	0.082	2.27
	Warming	0.312	0.082	2.26
<i>Ambrosia psilostachya</i>	Control	0.375	0.071	2.03
	Warming	0.501*	0.062	1.86*
<i>Helianthus mollis</i>	Control	0.179	0.086	2.36
	Warming	0.263*	0.078	2.17*
<i>Sorghastrum nutans</i>	Control	0.248	0.082	2.28
	Warming	0.400*	0.070	2.02*
September				
<i>Aster ericoides</i>	Control	0.369	0.068	1.97
	Warming	0.393	0.075	2.11
<i>Ambrosia psilostachya</i>	Control	0.280	0.077	2.17
	Warming	0.231	0.078	2.18
<i>Helianthus mollis</i>	Control	0.134	0.094	2.55
	Warming	0.130	0.095	2.59
<i>Sorghastrum nutans</i>	Control	0.284	0.077	2.16
	Warming	0.291	0.077	2.16

All determinant coefficients are greater than 0.95.

* $P < 0.05$ for the effects of warming compared with control. There were no significant differences among species for the derived parameters.

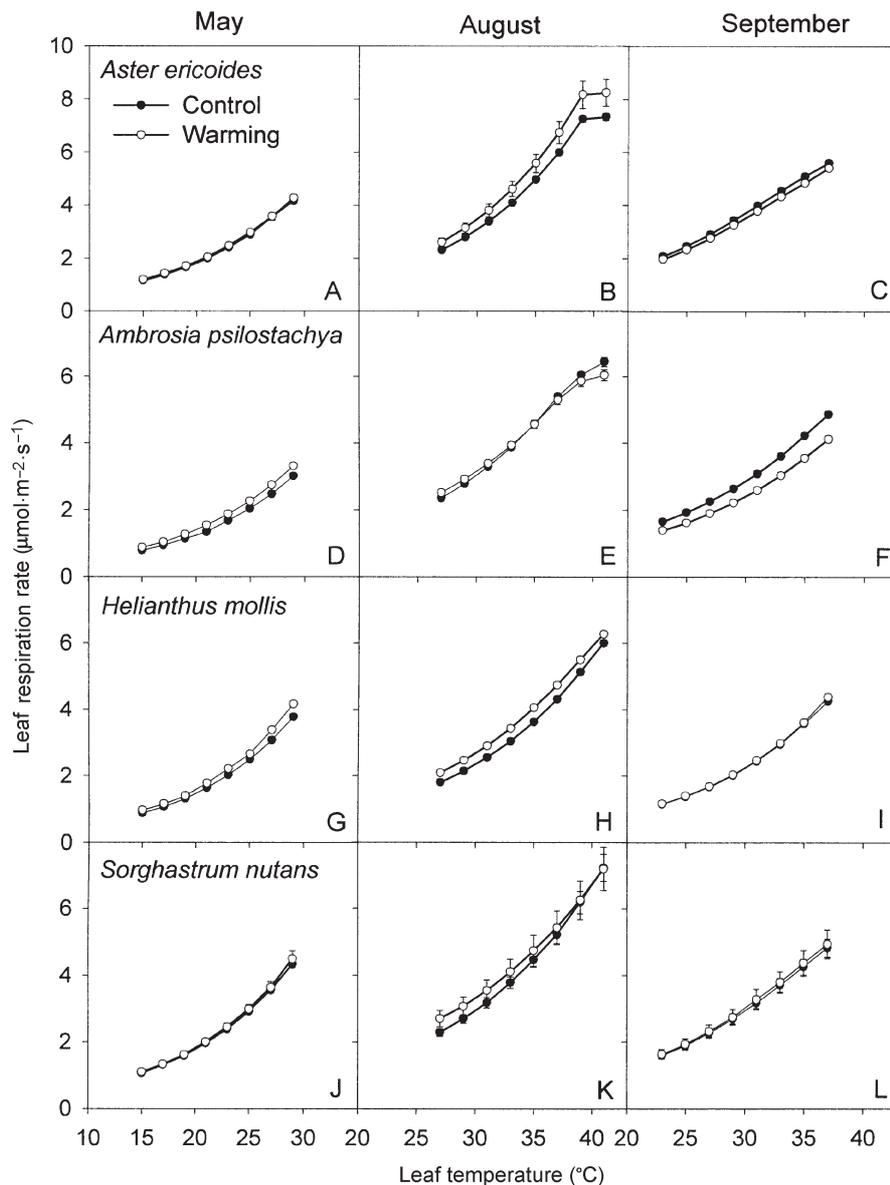


Figure 4. Leaf temperature-response curves of leaf respiration rate in darkness for the four species in three different seasons.

Data are the mean \pm SE ($n = 6$) from the control (solid circles) and warmed (open circles) plots.

temperature-response curves (Figures 1, 2; Table 1). Acclimation of R_d only occurred in August in *A. psilostachya*, *H. mollis*, and *S. nutans* from its temperature-response curves, whereas acclimation did not occur in *A. ericoides* in August and in any of the four species in May or September (Figures 3, 4; Table 2).

Photosynthetic acclimation is expressed as an increase or decrease in rates in response to lower or higher temperatures, respectively, when their rates are measured at a constant temperature. Based on this definition, our monthly results

showed photosynthetic acclimation only in early fall, whereas there was no acclimation in the other seasons (Figure 1). Previous studies of the effects of warming on photosynthesis have also reported contrasting results, which were increases (Chapin and Shaver 1996; Bergh and Linder 1999; Loik et al. 2004), decreases (Callaway et al. 1994; Roden and Ball 1996; Gunderson et al. 2000; He and Dong 2003), and no effects (Wookey et al. 1994; Nijs et al. 1996; Loik et al. 2000; Starr et al. 2000; Llorens et al. 2004). However, comparisons among

studies are difficult because of the different characteristics of warming treatments among the experiments and the various temperature sensitivities and optima for photosynthesis between species and ecotypes (Chapin et al. 1995; Shaw et al. 2000; Llorens et al. 2004). Furthermore, photosynthetic responses to temperature are often influenced by other interacting factors, such as drought, irradiance, water vapor deficit, leaf age, nutrient availability, and growing season (Chaves 1991; Ellsworth and Reich 1992, 1993; Gunderson et al. 2000; Llorens et al. 2004).

In the present study, experimental warming affected P_n in three modes during the entire growing season: increased P_n in spring, decreased P_n in early fall, and unchanged P_n in summer and at the end of growing season in comparison with that in control plots (Figure 1). The changes in the seasonal pattern of photosynthesis under warming might be related to: (i) direct effects of warming on enzymatically catalysed reactions and membrane processes of photosynthesis (Lambers et al. 2000); (ii) an interaction of temperature with other environmental factors, such as soil moisture, light, and nutrient availability (Shaver et al. 2000); and (iii) phenological changes caused by warming (Dunne et al. 2003; Sherry et al. 2007). Plant emergence is earlier in warmed plots than in control plots (Bowditch 2002). Because leaf photosynthesis varied with leaf age, light, water, and nutrient regimens, even at the similar leaf temperature, we can speculate that the warming treatment will shift the maximum photosynthesis rate as well as senescence to the earlier date. However, aboveground production in the warmed plots was greater than that in the control plots because senescence was delayed and plant productivity was stimulated for the C_4 grass species, including *S. nutans* (Wan et al. 2005). This phenomenon did not appear in the leaf photosynthesis rate of *S. nutans* owing to the loss of the photosynthetic dynamics if measurement was made once a month and the delay of senescence was less than a month.

In addition to temperature, soil moisture is also a key factor interacting with temperature limiting the biomass and functioning in tallgrass prairie ecosystems (Schimel et al. 1991). Warming decreased soil moisture in our experimental site and resulted in a seasonal drought in July and August 2001 (Wan et al. 2002). Therefore, soil drought in the warmed plots exacerbated water limitation on leaf photosynthesis in the summer. During the early growing season with enough soil moisture, temperature predominated photosynthesis before daily air temperature reached optimum. In the mid growing season, leaf temperature reached optimum or extra-optimum levels with limited moisture, but warming decreased the photosynthesis rate. In the late growing season, early senescence occurred in the warmed plots and temperature effects would be less important. However, the results of Loik et al. (2000) show that soil moisture appears to more significantly affect leaf photosynthesis

than temperature, most likely resulting from a short experimental period (i.e. 2 weeks) when soil water content was scarce.

Experimental warming affected the patterns of P_n , which varied among the four species, especially in the early growing season (Figure 1). These results indicate that the species response to warming was complicated. The shift of peak P_n time under warming can be explained by the optimum temperature (T_{opt}), which was lowest in *A. ericoides* (21.6 °C), highest in *S. nutans* (35.0 °C), and intermediate for *A. psilostachya* (24.8 °C) and *H. mollis* (23.3 °C; Table 1). The respective daily average and highest temperatures at the experimental site were 17 and 24 °C in April and 21 and 27 °C in May. Therefore, warming stimulated the P_n of all four species in April when air temperature was below the optimum temperature (T_{opt}). In May, air temperature in the warmed plots reached or exceeded T_{opt} for *A. ericoides*, fell within the optimum temperature range for *A. psilostachya* and *H. mollis*, and was still below optimum for *S. nutans*. Therefore, P_n showed a decrease in *A. ericoides*, an increase in *S. nutans* and *A. psilostachya*, and no change in *H. mollis*. The increment of P_n was between 15.1% and 27.4% in the four species compared with the control in early growing season, which corresponds to Q_{10} of 2.0 and 3.4, respectively. This Q_{10} value is similar to data reported earlier (Berry and Björkman 1980).

Acclimation may also be modeled by an increase (or decrease) in optimum temperature of P_n (T_{opt}) when plants are grown at a higher (or lower) temperature (relative acclimation; Berry and Björkman 1980) or by a shift in the photosynthetic temperature response, which P_n is consistent at the new growth temperature relative to the original one (absolute acclimation; Xiong et al. 2000). Temperature acclimation of photosynthesis has been reported mostly from laboratory experiments for grasses, forbs, and shrubs (Atkin et al. 2000a, 2000b), Antarctic vascular plants (Xiong et al. 2000), and other species (Anderson et al. 1990; Gunderson et al. 2000; Yamori et al. 2005). The results of the present study showed that T_{opt} shifted to higher for *S. nutans* and *H. mollis* in August, whereas there was no change for *A. psilostachya* and *A. ericoides* in August, and for all four species in May and September (Figure 2; Table 1). In spring, when temperature is below or around its optimum temperature, plants do not yet need to undergo acclimation. However, in August, when temperature is above the optimum temperature, temperature acclimation occurred to response to high temperature stress. In September, photosynthetic downregulation for the four species appeared because fewer new leaves were developed during this growing stage than before and earlier senescence occurred in warmed plots. These results indicate photosynthetic acclimation to a high temperature in some of these native tallgrass species. Moreover, we found that *S. nutans* still grew to a greater extent than the other three forbs and delayed its senescence. Therefore, C_4 grasses exhibit higher competitive ability in response to a warmer environment

with higher biomass (Wan et al. 2005).

Photosynthesis and respiration are interdependent, with respiration relying on photosynthesis for substrate, whereas photosynthesis depends on respiration for a range of compounds, such as carbon skeletons for protein synthesis and ATP for sucrose synthesis and repair of photosynthetic proteins (Krömer 1995; Atkin et al. 2000a). The temperature-mediated differences in leaf respiration are tightly linked to concomitant differences in leaf photosynthesis (Turnbull et al. 2001; Atkin et al. 2005). Like photosynthetic acclimation, plants exposed to a change in temperature can result in respiratory acclimation, which is the adjustment of leaf respiration rates to compensate for a change in temperature (Atkin et al. 2000c).

Numerous studies in the laboratory have shown that many plants, but not all taxa, appear to acclimate to changes in temperature conditions by adjusting their respiration-temperature responses (Pearcy 1977; Larigauderie and Körner 1995; Atkin et al. 2000b; Griffin et al. 2002; Loveys et al. 2003; Lee et al. 2005). The ability for acclimation of R_d varies with species, climate, plant N, leaf position within a canopy, season, and growth temperature (Atkin et al. 2005). Rapid temperature acclimation of leaf respiration has been reported in some studies, ranging from several hours to days (Larigauderie and Körner 1995; Tjoelker et al. 2001; Bolstad et al. 2003; Lee et al. 2005), most likely responding to substrate availability, the demand for ATP, and/or reducing the production of reactive oxygen species (Atkin et al. 2005). The responses of respiration to long-term changes in temperature are highly dependent on the effect of temperature on plant development and on the interactive effects of temperature with other abiotic factors (e.g. irradiance, drought, and nutrient availability; Atkin et al. 2005). It is very common for plants in cold environments to show R_d acclimation, whereas in warm climates the acclimation of R_d is poorly understood.

In the present study, the temperature quotient for respiration, Q_{10} , was lower in the warmed plots than that in the control plots, except for *A. ericoides* in August (Table 2); there were no changes in May or September. As a result, respiratory acclimation appeared to reduce respiratory carbon losses in mid-summer or during episodic high temperature events (Gunderson et al. 2000), mitigate the impact of environmental warming on the three species, and weaken positive feedback through the warming-respiration-atmospheric CO_2 concentration connection. Estimated Q_{10} values in the literature typically range from 1.2 to 4.0 (Ryan 1991; Tjoelker et al. 2001; Bolstad et al. 2003). Our estimates of Q_{10} (1.86–2.91) were well within the range. This respiratory acclimation was consistent with photosynthesis acclimation in August, which may be related to its physiological function as providing energy and intermediate products for growth and maintenance respiration, especially during droughts (Paulsen 1994). Therefore, the acclimation suggests that photosynthesis and respiration models should not

assume a constant relationship, but should include an appropriate potential component of acclimation with seasonal changes (Wythers et al. 2005).

However, surprisingly, warming increased the average leaf respiration in darkness (R_d) for all four species. We excluded the reasons resulting from leaf nitrogen (N) content and soil drought, because soil moisture and leaf N concentration were both lower in the warmed plots than in control plots (Wan et al. 2002; An et al. 2005) and warming should reduce leaf respiration (Ryan 1995; Tjoelker et al. 1999). Thus, other factors may have affected respiration responses to temperature in the present study. Leaf maintenance respiration is known to increase in response to rising temperature (Long 1991) because the processes of protein synthesis and replacement, membrane repair, and maintenance of gradients of ions and metabolites vary exponentially with temperature. This likely resulted in an increase in leaf respiration in the warmed plots in the early and middle growing seasons (Figure 3). Other mechanisms also may contribute to the increase, such as differential effects of night versus day temperatures (Wan et al. 2002), leaf-area expansion, stem elongation, and phenological development. However, further work is needed to examine the mechanisms.

Conclusions

The present study investigated photosynthetic and respiratory acclimation of four species to global warming in the tallgrass prairie of central Oklahoma, USA. The photosynthetic response to experimental warming was different among species and with seasons in fall 2000 and throughout 2001. Leaf respiration was consistently stimulated by warming until mid summer and then did not change. Temperature acclimation of photosynthesis and respiration largely varied with species and seasons, in which acclimation occurred in the mid growing season and not in the early and late growing seasons. Thus, ecosystem carbon balance and respiration models should incorporate an acclimation response with a seasonal change. In the present study, an increase in respiration relative to photosynthesis was greater at higher temperatures, which would result in carbon loss from ecosystems.

Materials and Methods

Field site description

The study was conducted at the Great Plains Apiaries in McClain County, Oklahoma (34°59' N, 97°31' W), approximately 40 km southwest of the Norman campus of the University of Oklahoma, USA. The field site is an old-field tallgrass prairie abandoned from agriculture 30 years ago without grazing for

25 years. The grassland is dominated by three C₄ grasses, *Schizachyrium scoparium*, *S. nutans*, and *Eragrostis curvula*, and two C₃ forbs, *Ambrosia psilostachya* and *Xanthocephalum texanum*. Mean annual temperature is 16.3 °C, with monthly air temperature ranging from 3.3 °C in January to 28.1 °C in July. Mean annual precipitation is 915 mm, with monthly precipitation ranging from 30 mm in January to 135 mm in May (average values from 1948 to 1998; Oklahoma Climatological Survey). A silt loam soil in the grassland includes 35.3% sand, 55.0% silt, and 9.7% clay (A. Subedar and Y. Luo, unpubl. data, 2003). Soil carbon content is 1.42% on a mass basis (Luo et al. 2001). The soil belongs to part of the Nash-Lucien complex with neutral pH, high available water capacity, and a deep, moderately penetrable root zone (US Department of Agriculture 1979).

Experimental design

The experiment used a paired, nested design with warming as the main factor and clipping as a secondary factor. Twelve 2 × 2 m plots were divided into six pairs of control (i.e. unwarmed) and warmed plots. In each warmed plot, one 165 × 15 cm infrared heater (Kalglo Electronics, Bethlehem, PA, USA) was suspended in the middle of each plot at a height of 1.5 m above the ground. The heating is operated year round, 24 h/day and 365 days/year in the field. To simulate shading effects of heaters, we installed one “dummy” heater made of metal flashing with the same shape and size as the heating device over each control plot. Each 2×2 m plot was divided into four 1×1 m subplots. Plants in two diagonal subplots were clipped at the height of 10 cm above the ground yearly, usually in July. After clipping, plants were allowed to regrow until the next clipping. The other two were the unclipped control subplots. Because the present study focused on ecophysiological responses to warming, we did not sample plants in clipped subplots. A previous study by Wan et al. (2002) documented that warming increased daily mean air temperature at 25 cm above the ground by 1.1 °C and soil temperature at the 2.5 cm depth by 2.0 °C. Further details of the study site have been described in Wan et al. (2002, 2005).

Photosynthesis and respiration measurements

Four perennial species, namely *A. ericoides*, *A. psilostachya*, *H. mollis*, and *S. nutans*, were chosen to examine the temperature response of gas exchange to experimental warming because of their various characteristics. *Aster ericoides* is little consumed by livestock and may lower the quality of prairie hay. *Ambrosia artemisiifolia* is a dominant forb in grassland whose pollen causes severe allergic reactions in late summer and fall to some people. *Helianthus mollis* is highly nutritious and palatable to all grazing animals. *Sorghastrum nutans* is one of the most important native tall grasses in the Great Prairie,

which is fairly tolerant to drought conditions and very tasty for animals (Great Plains Flora Association 1986; Ladd 1995). The first three species are C₃ forbs and the last one is C₄ grass.

Six individuals (one plant per plot) of each species were randomly selected in both the control and warmed plots. Measurements were made at midday between 10:00 and 15:00 hours (local time) on clear days every other week from August to October 2000 and monthly from April to November 2001. Net photosynthetic rate (P_n) and respiration rate in darkness (R_d) of the most recently fully expanded leaves for the four species were measured using an open-model portable photosynthesis system (LI-6400; Li-Cor, Lincoln, NE, USA). Leaf temperature was initially measured, the cuvette was applied to the leaf, and then temperature was held constant at the measured ambient level using the thermoelectric block within the cuvette. To avoid differences due to the changing photosynthetic photon flux density (PPFD) levels during the year, leaves were illuminated at 1 000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ using the light-emitting diode (LED) system. Other environmental conditions within the cuvette were controlled to match the ambient conditions.

When leaf respiration rate in darkness (R_d) was measured, the LED light source in the cuvette was off. All other conditions were the same as photosynthetic measurement. Data were logged when respiratory gas exchange had equilibrated. This condition was typically achieved within 1–3 min. Each measurement of photosynthesis and respiration was the average of three values logged at 30 s intervals. Although the respiration rate in darkness (R_d) is generally 20%–30% higher than night dark respiration rate (Wang et al. 2001), this measurement is more practical in the field and these numbers reflect CO₂ release of leaf respiration in the daytime.

Temperature response curves of P_n and R_d

To further examine acclimation of photosynthesis and respiration, the temperature response curves of P_n and R_d were determined in three months. In order to shorten the measuring period, we only randomly chose three plants for each species to measure the curve continuously from low to high temperatures. In early May, mid August, and late September, the measurements of P_n and R_d were made by manually setting leaf temperature of the cuvette to eight set points (i.e. ambient air temperature (AT; 1 point), three points below AT, and four points above AT), bracketing the ambient air temperature by 2 °C, and recording the steady state P_n and R_d as determined by maintaining a total coefficient of variation <1%. Because temperature equilibration of the leaf and gas-exchange system typically required 10–15 min (Griffin et al. 2002), data were recorded only after equilibration had taken place and a graph of photosynthesis and respiration as a function of time was observably stable. The wide range of measuring temperature used (15–42 °C) unavoidably resulted in variation in leaf-to-air vapor pressure

deficit (VPD) between measurements. By keeping air humidity high at the high measuring temperatures, this effort resulted in VPD between approximately 0.3 and 2.0 kPa because this range had little significant effects on stomatal conductance and photosynthetic rates (Day 2000).

Data analysis

Gas exchange data (P_n and R_d) in fall 2000 and throughout 2001, separated by different sections, were analyzed by repeated-measures analysis of variance (RM-ANOVA) for effects of warming treatments (SAS Institute, Cary, NC, USA). Differences were considered significant if probabilities (P) were less than 0.05. Treatment means were compared by the least significant difference (LSD) to determine whether means of the dependent variable were significantly different at the 0.05 probability level.

The photosynthesis and respiration data from temperature-response curves in early May, mid August, and late September were used to determine the temperature acclimation. To estimate optimum temperature and maximum photosynthesis rate, photosynthetic-temperature response curves were fitted with a quadratic equation (Battaglia et al. 1996; Gunderson et al. 2000):

$$P_n = P_{opt} - b(T - T_{opt})^2 \quad (1)$$

where P_n represents the mean net photosynthetic rate at temperature T in °C and P_{opt} is the net photosynthetic rate at the temperature optimum (T_{opt}). The term b describes the relative spread of the parabola (a small value of b indicates a wider parabola than does a large b). For temperature response curves of respiration, an exponential function was applied:

$$R_d = ae^{bT} \quad (2)$$

where R_d is the mean leaf respiration rate in darkness at temperature T in °C. The estimated coefficient, a , describes the basal respiration rate when temperature is zero and b represents the temperature sensitivity of respiration. The values of Q_{10} (i.e. the respiratory quotient as the respiration rate increases with a 10 °C increase in temperature) were determined for mean respiration rates by regression of natural logarithm (ln) of respiration on leaf temperature as $Q_{10} = e^{(10 \times b)}$.

Acknowledgements

The authors thank Dr Edwin Kessler for the donation of his farm to the University of Oklahoma for the research.

References

- Aber JD, Federer CA (1992). A generalized, lumped parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystem. *Oecologia* **92**, 463–474.

- An Y, Wan S, Zhou X, Subeda AA, Wallace LL, Luo Y (2005). Plant nitrogen concentration, use efficiency, and contents in a tallgrass prairie ecosystem under experimental warming. *Global Change Biol.* **11**, 1733–1744.
- Anderson J, McCollum G, Roberts W (1990). High temperature acclimation in pepper leaves. *HortScience* **25**, 1272–1274.
- Arnone JA, Körner C (1997). Temperature adaptation and acclimation potential of leaf dark respiration in two species of *Ranunculus* from warm and cold habitats. *Arctic Alpine Res.* **29**, 122–125.
- Atkin OK, Evans JR, Ball MC, Lambers H, Pons TL (2000a). Leaf respiration of snow gum in the light and dark: Interactions between temperature and irradiance. *Plant Physiol.* **122**, 915–923.
- Atkin OK, Holly C, Ball MC (2000b). Acclimation of snow gum (*Eucalyptus pauciflora*) leaf respiration to seasonal and diurnal variations in temperature: The importance of changes in the capacity and temperature sensitivity of respiration. *Plant Cell Environ.* **23**, 15–26.
- Atkin OK, Edwards EJ, Loveys BR (2000c). Response of root respiration to changes in temperature and its relevance to global warming. *New Phytol.* **147**, 141–154.
- Atkin OK, Bruhn D, Hurry VM, Tjoelker MG (2005). The hot and the cold: Unraveling the variable response of plant respiration to temperature. *Funct. Plant Biol.* **32**, 87–105.
- Atkin OK, Scheurwater I, Pons TL (2006). High thermal acclimation potential of both photosynthesis and respiration in two lowland *Plantago* species in contrast to an alpine congeneric. *Global Change Biol.* **12**, 500–515.
- Battaglia M, Beadle C, Loughhead S (1996). Photosynthetic temperature responses of *Eucalyptus globules* and *Eucalyptus nitens*. *Tree Physiol.* **16**, 81–89.
- Bergh J, Linder S (1999). Effects of soil warming during spring on photosynthetic recovery in boreal Norway spruce stands. *Global Change Biol.* **5**, 245–253.
- Berry J, Björkman O (1980). Photosynthetic response and adaptation to temperature in higher plants. *Annu. Rev. Plant Physiol.* **31**, 491–543.
- Bolstad PV, Reich P, Lee T (2003). Rapid temperature acclimation of leaf respiration rates in *Quercus alba* and *Quercus rubra*. *Tree Physiol.* **23**, 969–976.
- Bowdish S (2002). *The Effects of Warming and Land-use on Species Composition in the Tallgrass Prairie*. MS Thesis. University of Oklahoma, Norman, OK, USA.
- Callaway RM, DeLucia EH, Thomas EM, Schlesinger WH (1994). Compensatory responses of CO₂ exchange and biomass allocation and their effects on the relative growth rate of ponderosa pine in different CO₂ and temperature regimes. *Oecologia* **98**, 159–166.
- Chapin III FS, Shaver GR (1996). Physiological and growth

- responses of arctic plants to a field experiment simulating climatic change. *Ecology* **77**, 822–840.
- Chapin III FS, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA** (1995). Responses of arctic tundra to experimental and observed changes in climate. *Ecology* **76**, 694–711.
- Chaves MM** (1991). Effects of water deficits on carbon assimilation. *J. Exp. Bot.* **42**, 1–16.
- Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, Brovkin V et al.** (2001). Global response of terrestrial ecosystem structure and function to CO₂ and climate change: Results from six dynamic global vegetation models. *Global Change Biol.* **7**, 357–374.
- Day ME** (2000). Influence of temperature and leaf-to-air vapor pressure deficit on net photosynthesis and stomatal conductance in red spruce (*Picea rubens*). *Tree Physiol.* **20**, 57–63.
- Dunne JA, Harte J, Taylor KJ** (2003). Subalpine meadow flowering phenology responses to climate change: Integrating experimental and gradient methods. *Ecol. Monogr.* **73**, 69–86.
- Edwards JA, Smith RL** (1988). Photosynthesis and respiration of *Colobanthus quitensis* and *Deschampsia antarctica* from the maritime Antarctica. *Br. Antarct. Surv. Bull.* **81**, 43–63.
- Ellsworth DS, Reich PB** (1992). Water relations and gas exchange of *Acer saccharum* seedlings in contrasting natural light and water regimes. *Tree Physiol.* **10**, 1–20.
- Ellsworth DS, Reich PB** (1993). Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* **96**, 169–178.
- Great Plains Flora Association** (1986). *Flora of the Great Plains*. University Press of Kansas, Lawrence.
- Griffin KL, Turnbull M, Murthy R, Lin G, Adams J, Farnsworth B et al.** (2002). Leaf respiration is differentially affected by leaf vs. stand-level night-time warming. *Global Change Biol.* **8**, 479–485.
- Gunderson CA, Norby RJ, Wullschlegel SD** (2000). Acclimation of photosynthesis and respiration to stimulated climatic warming in northern and southern populations of *Acer saccharum*: Laboratory and field evidence. *Tree Physiol.* **20**, 87–96.
- He WM, Dong M** (2003). Plasticity in physiology and growth of *Salix matsudana* in response to simulated atmospheric temperature rise in the Mu Us Sandland. *Photosynthetica* **41**, 297–300.
- Hunt ER, Piper Jr SC, Nemani R, Keeling CD, Otto RD, Running SW** (1996). Global net carbon exchange and intra-annual atmospheric CO₂ concentrations predicted by an ecosystem process model and three-dimensional atmospheric transport model. *Global Biogeochem. Cycles* **10**, 431–456.
- Intergovernmental Panel of Climate Change** (2001). *Climate Change 2001: The Scientific Basis*. Cambridge University Press, New York.
- Jarvis AJ, Stauch VJ, Schulz K, Young PC** (2004). The seasonal temperature dependency of photosynthesis and respiration in two deciduous forests. *Global Change Biol.* **10**, 939–950.
- Körner C** (1995). Towards a better experimental basis for upscaling plant responses to elevated CO₂ and climate warming. *Plant Cell Environ.* **18**, 1101–1110.
- Krömer S** (1995). Respiration during photosynthesis. *Annu. Rev. Plant Physiol. Mol. Biol.* **46**, 45–70.
- Ladd D** (1995). *Tallgrass Prairie Wildflowers: A Nature Conservancy Book*. Falcon Press Publishing, Helena.
- Lambers H, Chapin III FS, Pons TL** (2000). *Plant Physiological Ecology*. Springer-Verlag, New York.
- Larigauderie A, Körner C** (1995). Acclimation of leaf dark respiration to temperature in alpine and lowland plant species. *Ann. Bot.* **76**, 245–252.
- Lee TD, Reich PB, Bolstad PV** (2005). Acclimation of leaf respiration to temperature is rapid and related to specific leaf area, soluble sugars and leaf nitrogen across three temperature deciduous tree species. *Funct. Ecol.* **19**, 640–647.
- Llorens L, Peñuelas J, Beier C, Emmett B, Estiarte M, Tietema A** (2004). Effects of an experimental increase of temperature and drought on the photosynthetic performance of two Ericaceous shrub species along a north–south European gradient. *Ecosystems* **7**, 613–624.
- Loik ME, Redar SP, Harte J** (2000). Photosynthetic response to acclimation-warming manipulation for contrasting meadow species in the Rocky Mountains, Colorado, USA. *Funct. Ecol.* **14**, 166–175.
- Loik ME, Still CJ, Huxman TE, Harte J** (2004). *In situ* photosynthetic freezing tolerance for plants exposed to a global warming manipulation in the Rocky Mountains, Colorado, USA. *New Phytol.* **162**, 331–341.
- Long SP** (1991). Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: Has its importance been underestimated? *Plant Cell Environ.* **14**, 729–739.
- Long SP, Hutchin PR** (1991). Primary production in grasslands and coniferous forests with climate change: An overview. *Ecol. Appl.* **1**, 139–156.
- Loveys BR, Atkinson LJ, Sherlock DJ, Roberts RL, Fitter AH, Atkin OK** (2003). Thermal acclimation of leaf and root respiration: An investigation comparing inherently fast- and slow-growing plant species. *Global Change Biol.* **9**, 895–910.
- Luo Y, Wan S, Hui D, Wallace L** (2001). Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* **413**, 622–625.
- Nijs I, Teughels H, Blum H, Hendrey G, Impens I** (1996). Simulation of climate change with infrared heaters reduces the productivity of *Lolium perenne* L. in summer. *Environ. Exp. Bot.* **36**, 271–280.
- Paulsen GM** (1994). High temperature responses of crop plants. In: Boote KJ, Bennett JM, Sinclair TR, Paulsen GM, eds. *Physiology and Determination of Crop Yield*. American Society of Agronomy, Madison. pp. 365–389.
- Pearcy RW** (1977). Acclimation of photosynthetic and respiratory carbon dioxide exchange to growth temperature in *Atriplex*

- lentiformis* (Torr.) Wats. *Plant Physiol.* **59**, 795–799.
- Peters RL, Darling JD** (1985). The greenhouse effect and nature reserves. *Bioscience* **35**, 707–715.
- Roden JS, Ball MC** (1996). The effect of elevated [CO₂] on growth and photosynthesis of two eucalyptus species exposed to high temperatures and water deficits. *Physiol. Planta.* **111**, 909–919.
- Ryan MG** (1991). Effects of climate change on plant respiration. *Ecol. Appl.* **1**, 157–167.
- Ryan MG** (1995). Foliar maintenance respiration of subalpine and boreal trees and shrubs in relation to nitrogen content. *Plant Cell Environ.* **18**, 765–772.
- Schimel DS, Kittel TGF, Knapp AK, Seastedt TR, Parton WJ, Brown VB** (1991). Physiological interactions along resource gradients in a tallgrass prairie. *Ecology* **72**, 672–684.
- Schimel DS, VEMAP Participants, Braswell BH** (1997). Continental scale variability in ecosystem processes, models, data and the role of disturbance. *Ecol. Monogr.* **67**, 251–271.
- Shaver GR, Canadell J, Chapin III FS, Gurevitch J, Harte J, Henry G et al.** (2000). Global warming and terrestrial ecosystems: A conceptual framework for analysis. *Bioscience* **50**, 871–882.
- Shaw MR, Loik ME, Harte J** (2000). Gas exchange and water relations of two Rocky Mountain shrub species exposed to climate change manipulation. *Plant Ecol.* **146**, 197–206.
- Sherry RA, Zhou X, Gu S, Arnone III JA, Schimel DS, Verburg PS et al.** (2007). Divergence of reproductive phenology under climate warming. *Proc. Natl. Acad. Sci. USA* **104**, 198–202.
- Starr G, Oberbauer SF, Pop EW** (2000). Effects of lengthened growing season and soil warming on the phenology and physiology of *Polygonum bistorta*. *Global Change Biol.* **6**, 357–369.
- Tjoelker MG, Reich PB, Oleksyn J** (1999). Changes in leaf nitrogen and carbohydrates underlie temperature and CO₂ acclimation of dark respiration in five boreal tree species. *Plant Cell Environ.* **22**, 767–778.
- Tjoelker MG, Oleksyn J, Reich PB** (2001). Modeling respiration of vegetation: Evidence for a general temperature-dependent Q₁₀. *Global Change Biol.* **7**, 223–230.
- Turnbull MH, Whitehead D, Tissue DT, Schuster WSF, Brown KJ, Griffin KL** (2001). Responses of leaf respiration to temperature and leaf characteristics in three deciduous tree species vary with site water availability. *Tree Physiol.* **21**, 571–578.
- US Department of Agriculture** (1979). *Soil Survey of McClain County*. Soil Conservation Survey, Stillwater, OK, USA.
- Wan S, Luo Y, Wallace LL** (2002). Changes in microclimate induced by experimental warming and clipping in tallgrass prairie. *Global Change Biol.* **8**, 754–768.
- Wan S, Hui D, Wallace LL, Luo Y** (2005). Direct and indirect warming effects on ecosystem carbon processes in a tallgrass prairie. *Global Biogeochem. Cycles* **19**, GB2014.
- Wang X, Lewis JD, Tissue DT, Seemann JR, Griffin KL** (2001). Effects of elevated atmospheric CO₂ concentration on leaf dark respiration of *Xanthium strumarium* in light and in darkness. *Proc. Natl. Acad. Sci. USA* **98**, 2479–2484.
- White A, Cannell MGR, Friend AD** (2000). The high-latitude terrestrial carbon sink: A model analysis. *Global Change Biol.* **6**, 227–245.
- Wookey PA, Welker JM, Parsons AN, Press MC, Callaghan TV, Lee JA** (1994). Differential growth, allocation and photosynthetic responses of *Polygonum viviparum* to simulated environmental change at a high arctic polar semi-desert. *Oikos* **70**, 131–139.
- Wythers KR, Reich PB, Tjoelker MG, Bolstad PB** (2005). Foliar respiration acclimation to temperature and temperature variable Q₁₀ alter ecosystem carbon balance. *Global Change Biol.* **11**, 435–449.
- Xiong FS, Mueller EC, Day TA** (2000). Photosynthetic and respiratory acclimation and growth responses of Antarctic vascular plants to contrasting temperature regimes. *Am. J. Bot.* **87**, 700–710.
- Yamori W, Noguchi K, Terashima I** (2005). Temperature acclimation of photosynthesis in spinach leaves: Analyses of photosynthetic components and temperature dependences of photosynthetic partial reactions. *Plant Cell Environ.* **28**, 536–547.
- Zhou X, Sherry B, An Y, Wallace LL, Luo Y** (2006). Main and interactive effects of warming, clipping, and doubled precipitation on soil CO₂ efflux in a grassland ecosystem. *Global Biogeochem. Cycles* **20**, GB1003.

(Handling editor: Li-Xin Zhang)