Reduced diurnal temperature range does not change warming impacts on ecosystem carbon balance of Mediterranean grassland mesocosms

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Abstract

Daily minimum temperature (T_{min}) has increased faster than daily maximum temperature (T_{max}) in many parts of the world, leading to decreases in diurnal temperature range (DTR). Projections suggest that these trends are likely to continue in many regions, particularly in northern latitudes and in arid regions. Despite wide speculation that asymmetric warming has different impacts on plant and ecosystem production than equal-night-and-day warming, there has been little direct comparison of these scenarios. Reduced DTR has also been widely misinterpreted as a result of night-only warming, when in fact T_{min} occurs near dawn, indicating higher morning as well as night temperatures. We report on the first experiment to examine ecosystem-scale impacts of faster increases in T_{min} than in T_{max}, using precise temperature controls to create realistic diurnal temperature profiles with gradual day–night temperature transitions and elevated early morning as well as night temperatures. Studying a constructed grassland ecosystem containing species native to Oregon, USA, we found that the ecosystem lost more carbon at elevated than ambient temperatures, but remained unaffected by the 3 °C difference in DTR between symmetric warming (constantly ambient + 3.5 °C) and asymmetric warming (dawn T_{min} = ambient + 5 °C, afternoon T_{max} = ambient + 2 °C). Reducing DTR had no apparent effect on photosynthesis, probably because temperatures were most different in the morning and late afternoon when light was low. Respiration was also similar in both warming treatments, because respiration temperature sensitivity was not sufficient to respond to the limited temperature differences between asymmetric and symmetric warming. We concluded that changes in daily mean temperatures, rather than changes in T_{min}/T_{max}, were sufficient for predicting ecosystem carbon fluxes in this reconstructed Mediterranean grassland system.

Keywords: asymmetric warming, carbon, diurnal temperature range, grassland, respiration

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Introduction

Mean temperatures have increased 0.10 to 0.16 °C per decade globally over the last 50 years, with faster increases in daily minimum temperature (T_{min}) than daily maximum temperature (T_{max}), a phenomenon commonly referred to as night-warming or asymmetric warming (Vose *et al.*, 2005; IPCC, 2007). Examinations of crop yields and natural ecosystem productivity over this period have shown reduced productivity in response to increased T_{min} (Stooksbury & Michaels, 1994; Nemani *et al.*, 2001; Peng *et al.*, 2004; Zheng *et al.*, 2009), presumably due to changes in the timing of the growing season or to changes in the balance of daytime photosynthesis and nighttime respiration. However, such studies provide no evidence that impacts of asymmetric warming differ from equal-night-and-day warming. Furthermore, experimentalists have widely interpreted the concept of asymmetric warming as meaning night-only warming, when in fact the coldest time of day occurs near dawn, suggesting that warming has probably accelerated morning as well as night temperatures (Amthor *et al.*, 2010). We report on the first experiment to examine ecosystem-scale impacts of faster increases in T_{min} than in T_{max}, using realistic diurnal temperature profiles with gradual day–night temperature transitions and elevated early morning as well as night temperatures.

Decreased diurnal temperature range (DTR, T_{max}–T_{min}) is a phenomenon thought to be caused by direct and indirect effects of aerosols and greenhouse gases that reduce daytime solar irradiance and increase nighttime long wave radiation (Dai *et al.*, 1997; Stone & Weaver, 2003; Wild *et al.*, 2007). Although global temperature trends showed widespread reductions in DTR from the 1950s to mid-1980s, since then, some climatic regions have experienced stable or increasing DTR,

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demonstrating that warming is impacted by a complexity of interactions among land use, regional climate regimes, and atmospheric chemistry (Zhou *et al.*, 2007, 2009; Makowski *et al.*, 2008). Several future climate scenarios, nevertheless, predict faster increases in T_{min} than in T_{max} to predominate, particularly for mid to northern latitudes and in arid regions (IPCC, 2007; Lobell *et al.*, 2007). This outlook of greater regional variability in the diurnal pattern of warming underscores the importance of understanding how changes in DTR, in addition to changes in mean temperature, impact plant growth and ecosystem carbon balance.

A major concern for both natural and managed ecosystems is that a reduction in DTR, or an increase, may alter the balance of photosynthesis and respiration. There are at least three factors that play in predictions of how the balance of photosynthesis and respiration could be impacted by greater-night-than-day warming. As photosynthesis only occurs during the day, greater-night-than-day warming could in principle increase nighttime respiratory costs to a greater extent than photosynthesis (Manunta & Kirkham, 1996). On the other hand, photosynthesis in C3 plants generally has a lower temperature optimum than respiration (Luo, 2007), so warming in the early morning could enhance photosynthetic gains and incur lower respiratory costs compared with warming in the afternoon (Dhakhwa & Campbell, 1998; Zheng *et al.*, 2009). Photosynthesis and respiration are also often closely coupled through carbon supply and demand feedbacks, which can regulate CO_2 exchange rates in addition to direct temperature effects (Turnbull *et al.*, 2002; Gifford, 2003; Atkin *et al.*, 2007; Wan *et al.*, 2009). These three factors lead to conflicting expectations and make it impossible to predict *a priori* whether plants and ecosystems should be more productive under symmetric or asymmetric warming, or perhaps equally productive under both.

In addition, assessing whether DTR is an important driver of photosynthesis and respiration may aid interpretation of prior whole-ecosystem warming studies, which exhibit divergent results that may be related to variability in how temperature treatments are applied (Luo, 2007). For example, some whole-ecosystem warming experiments have used passive radiation shields that trap heat at night or open-top chambers that experience most warming during the day (Aronson & McNulty, 2009). Other experiments are thermostatically controlled to impose a constant level of warming (Hanson *et al.*, 2011). Although several studies have examined the impacts of day vs. night warming, these have almost exclusively involved abrupt temperature changes at dawn and dusk (Manunta & Kirkham, 1996; Turnbull *et al.*, 2002; Zhang *et al.*, 2003; Frantz *et al.*, 2004; Volder *et al.*, 2004; Wolfe-Bellin *et al.*, 2006; Wan

et al., 2009), rather than realistic, sinusoidal diurnal temperature profiles (e.g., Fig. 1b). Using unrealistic diurnal temperature profiles may actually obfuscate potential warming impacts by imposing warming at incorrect times of day and forcing either larger or smaller changes in photosynthesis and respiration than would naturally occur.

To investigate the understudied and misrepresented phenomenon of asymmetric warming, we compared the impacts of asymmetrically elevated temperature profiles (dawn T_{min} = ambient + 5 °C, afternoon T_{max} = ambient + 2 °C), symmetrically elevated (ambient + 3.5 °C at all times), and ambient profiles on plant growth and whole-ecosystem CO_2 exchange of a constructed
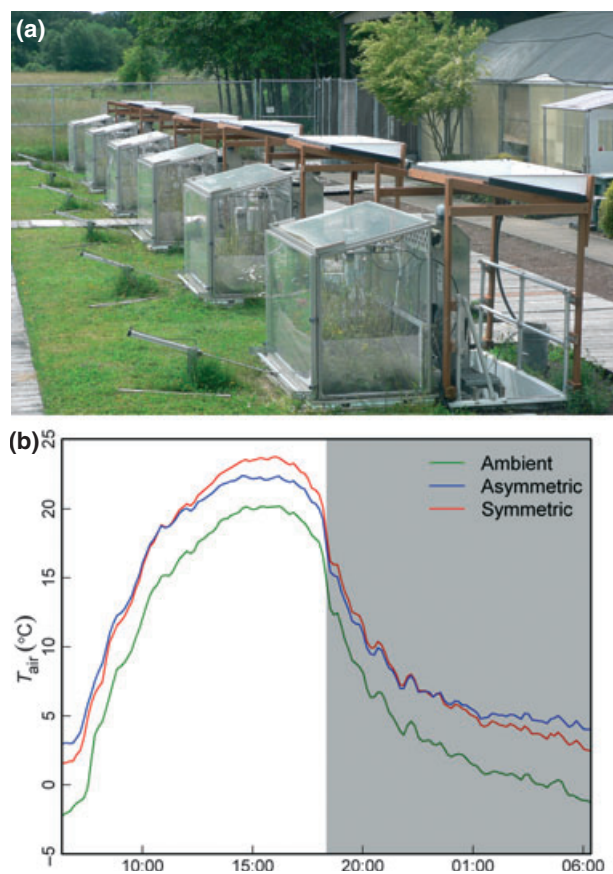

Fig. 1 Environmental chambers (terracosms) and temperature treatments. (a) One of two rows of terracosms ($N = 12$), with subsurface compartments containing 1 m soil profiles (not visible). Weather station in adjacent grassland provides set-point for ambient conditions. (b) Diurnal temperature profiles for ambient, asymmetric warming (T_{min} = ambient + 5 °C, T_{max} = ambient + 2 °C), and symmetric warming (continuously ambient + 3.5 °C) treatments, shown for March 16–17, 2010. Asymmetric and symmetric treatments differ in diurnal temperature range by 3 °C, with maximum temperature differences of 1.5 °C at T_{min} and T_{max}.

grassland ecosystem containing species native to the Willamette Valley, OR, USA (Fig. 1). Using sunlit, high-precision environmental chambers called 'terracosms' (Tingey *et al.*, 1996), we were able to simulate diurnal temperature profiles with realistic, gradual day–night transitions over 4 years of growth. Our main objectives were to determine (1) whether plant growth and whole-ecosystem carbon balance are greater, less, or equal under asymmetric warming compared with symmetric warming and (2) whether component fluxes of respiration and photosynthesis are impacted differently by symmetric and asymmetric warming.

Materials and methods

Terracosm description

This experiment was performed at the terracosm facility of the US Environmental Protection Agency Western Ecology Division, Corvallis, OR (44.565, −123.293, elevation 77 m). The 12 terracosms are sunlit chambers that provide complete climate control of an enclosed constructed native grassland plant community and soil system, and function as combined lysimeters and cuvettes to allow accounting of ecosystem carbon, nutrient, and water fluxes (Fig. 1a). Each terracosm has a ground surface area of 1×2 m, a soil compartment with a sloping bottom that ranges 1.0 to1.3 m deep, and an aboveground chamber with sloping roof that ranges in height from 1.5 to 1.7 m. The soil compartment is insulated with 15 cm thick foam (R value 60), which allowed elevated soil temperatures to be maintained in the warming treatments via heat transfer from the air, with natural diurnal and seasonal temperature variations (Fig. 3a). The aboveground chamber is constructed of transparent Teflon film on three sides and the roof and has instrumentation on the north side, with a minimum 89% transmission of solar radiation.

Soils were collected in 2005 from a local native grassland site that had not been disturbed in 100 + years. The soil was a moderately deep, well-drained, silty clay loam in the Dixonville series (Fillmore, 2009). The profile was excavated in 20 cm increments, sieved through 2.45 cm mesh, and repacked into the terracosms to 100 cm above a layer of drainage gravel. The top 5 cm of soil was steam-sterilized to prevent germination of the seed bank.

Common co-occurring native grassland plant species from the Willamette Valley (Campbell, 2004) were started from seed in the greenhouse, and 16 individuals per species were planted into the terracosm soil compartments on 10 cm centers in a replicated layout in spring 2006. The composition of the plant community included three annual forbs, eight perennial forbs (including one N-fixer), and three perennial grasses. This mixture of plant functional types was chosen to reflect the average composition of 'native' Willamette Valley grasslands, defined as areas containing at least 75% native species (data from Stanley *et al.*, 2008). The plants were allowed to establish in the terracosms under ambient conditions without aboveground chambers for 1 year, after which the annuals did
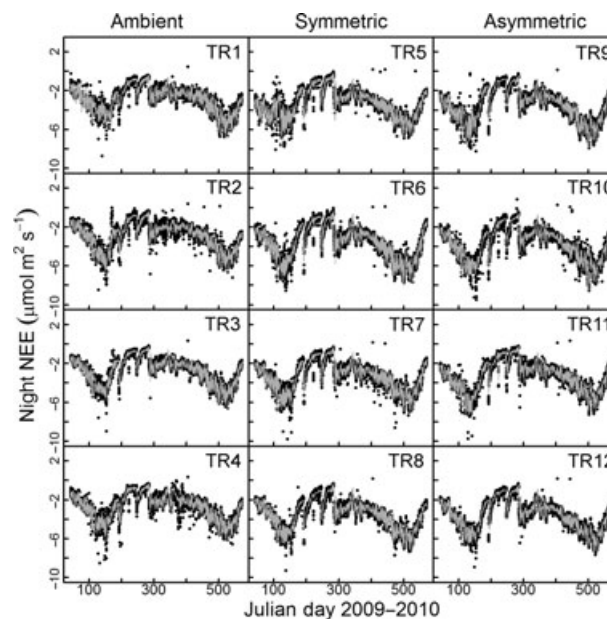

Fig. 2 Observed (points) and modeled (gray line) night R_{eco} based on air temperature and soil moisture in each terracosm, for partitioning net ecosystem CO_2 exchange.

not regenerate, leaving only perennial species for the remainder of the study. The aboveground chambers were installed and temperature treatments initiated on April 16, 2007, following the last winter frost, and continued until July 26, 2010, covering four spring growing seasons.

Terracosm temperatures, relative humidity, and CO_2 concentrations were controlled every minute based on measurements from an on-site weather station. Ambient terracosm T_{air} matched the weather station, and symmetric T_{air} was maintained continuously at ambient + 3.5 °C. Asymmetric T_{air} was ramped linearly between ambient + 5 °C at dawn and ambient + 2 °C in the mid-afternoon, at a time predetermined for each day of year as the average time of T_{max} from 40-year temperature records at Corvallis-Hyslop weather station. CO_2 concentration and relative humidity were maintained at ambient levels, and rainfall was collected from the roofs of the terracosms and added real-time with an automated irrigation system. Temperature and humidity were controlled by removing heat and moisture with chilled air radiators, then maintaining set-point conditions via strip heaters and humidifiers. CO_2 concentrations were measured continuously using LiCor-6262 infrared gas analyzers (Lincoln, NE, USA) located at each terracosm and the weather station. CO_2 was controlled during the day by injecting CO_2 into the air handler when concentrations fell below ambient levels and at night by opening dump valves to increase mixing with ambient air.

Plant production and ecosystem carbon exchange

Aboveground net primary production was measured nondestructively each spring for 4 years by summing the green surface area of individual species as they reached peak cover,

which was generally cued by the initiation of flowering. One-sided surface area was visually estimated by spreading plants across a 1 cm^2 grid to assess the area occupied. This technique produced replicable area measurements that were highly correlated with dry mass, based on harvested samples from about 72 individuals of each species across the terracosms and across years. Plant surface area was converted to g carbon using species-specific relationships among area, dry mass, and percentage carbon content. The carbon content was determined from subsamples of dried, ground leaves using a Costech ECS-4010 elemental analyzer (Valencia, CA, USA).

Whole-ecosystem CO_2 exchange rate was measured on an hourly basis beginning in February 2009, by determining the time required for a 10 ppm change in CO_2 concentration with CO_2 control and injection turned off, following chamber accumulation equations (Licor-Biosciences, 2004). These rates were corrected for nonbiological leaks of CO_2 into or out of the terracosm, calculated following Tingey *et al.* (2000). Leak rates were calculated as the product of the CO_2 concentration gradient from inside to outside the chamber, and a leak rate coefficient was determined from the rate of depletion of a non-biologically active SF_6 tracer gas, which we monitored every 3 weeks.

Daily and seasonal net ecosystem exchange (NEE) rate and annual net ecosystem production (NEP) were calculated from the cumulative sum of hourly CO_2 exchange rates. Less than 4% of hourly measurements were missing or omitted for technical failures. Missing data were gap-filled when possible by several methods. At night, when gas exchange rates reflected respiratory processes, gaps of less than 8 h were filled by linear interpolation following the assumption that respiration rates were mainly controlled by a gradual change in temperature. During the day, when gas exchange rates reflected both photosynthesis and respiration, 1-h gaps were filled by linear interpolation, and larger gaps were filled using the average of the remaining chambers from the same treatment when data were available. Hours in which data were missing for an entire treatment were omitted to maintain the same number of measurements across treatments.

In addition, fluxes in summer 2010 were modeled for 16 days after the treatments ended to complete carbon budgets for the longer-than-usual spring growing season. These fluxes were predicted by extrapolating regressions of NEE, gross photosynthesis (P_g), and whole-ecosystem respiration (R_{eco}, estimated as described below) vs. soil moisture and air temperature from the final 5 weeks of measurements.

To assess the relative impacts of warming treatments on whole-ecosystem gross photosynthesis and respiration, we partitioned daily NEE into estimated component fluxes. We estimated daytime R_{eco} based on regressions between nighttime R_{eco} and soil moisture and air temperature, following a modification of the procedure from Reichstein *et al.* (2005), with regression coefficients calculated in 15 day windows (each regression contained ~80–180 observations using original, not gap-filled data). The modeled estimates of night R_{eco} closely approximated observed values, with no apparent systematic biases in modeled-measured deviations across chambers, treatments, or seasons (Fig. 2). Regression coefficients

and daytime soil moisture and air temperature were then used to predict daytime R_{eco} for the middle 5 days of each window, leaving 10 days of overlap between windows. P_g was then estimated as the difference between daytime CO_2 exchange rate and estimated daytime R_{eco}. Despite the limitations of this flux-partitioning technique – including imperfect ability to predict night R_{eco} and extrapolation from nighttime to daytime respiration – this regression approach has been shown to produce similar results to other partitioning approaches (Desai *et al.*, 2007), and we used it only in conjunction with alternative, complementary analyses of directly measured day and night net CO_2 exchange rate.

Temperature–response curves

The temperature response of net photosynthesis (i.e., daytime CO_2 exchange rate) was measured in a short-term temperature manipulation under a clear sky on May 13, 2010, which approximately coincided with peak aboveground biomass in the asymmetric and symmetric warming treatments. Soil moisture was relatively high at this point in the growing season, averaging 0.35, 0.38, and 0.45 v/v in the asymmetric, symmetric, and ambient treatments, respectively. To examine the effects of temperature alone, measurements were made between 9:30 and 15:00 hours under saturating light conditions with CO_2 held constant at 380 ppm and relative humidity at 60%. In a separate light-response (constant temperature) manipulation in May 2009, we had established that photosynthesis was saturated when levels of photosynthetically active radiation (PAR) exceeded 1200 μmol m^{-2}s^{-1}. After PAR exceeded 1200 μmol m^{-2}s^{-1}, we increased air temperature in 3 °C increments every 30 min, starting from the lowest temperatures we could maintain (approximately 15 ° for ambient chambers, 18 °C for elevated chambers) up to 35 °C. The photosynthetic temperature response for each terracosm was determined by nonlinear regression of the following second-order equation (Gunderson *et al.*, 2010):

$$P = P_{opt} - b(T - T_{opt})^2, \qquad (1)$$

where P is the daytime CO_2 exchange rate at temperature T, P_{opt} is the rate at the temperature optimum, T_{opt}, and the parameter b defines the spread of the parabola.

We examined the temperature response of night R_{eco} within a window 10 days before and after the photosynthesis experiment (May 3–23, 2010). Relative temperature sensitivity was determined by calculating the Q_{10} as follows:

$$Q_{10} = \frac{R\{T\}}{R\{T + 10\}}, \qquad (2)$$

where $R\{T\}$ and $R\{T + 10\}$ are respiration rates at temperatures T and $T + 10$ °C, respectively. Q_{10} for each chamber was averaged for all possible $R\{T\}/R\{T + 10\}$ pairs. In numeric simulations, we found this arithmetic calculation of Q_{10} to be least biased by differences in temperature range, as also supported by Schindlbacher *et al.* (2010) and Sierra (2011). We also compared basal respiration rates at a common temperature of 10 ± 0.5 °C (R_{10}) for each treatment.

Using observed temperature-flux relationships, we then conducted sensitivity analyses to assess the theoretical differences in light-saturated photosynthesis and respiration under the three experimental temperature regimes and compared these with observed differences. Expected photosynthesis was calculated for light-saturated hours from May 3 to 23, 2010, using the aforementioned photosynthesis temperature–response curve (Eqn 1) with observed temperatures and average coefficients for each treatment. Expected R_{eco} was calculated for the same days, but focusing on predawn hours when temperatures were most different between asymmetric and symmetric treatments. Expected R_{eco} was calculated by fitting mean treatment Q_{10} and R_{10} values in a modified van't Hoff equation:

$$R = R_{10} \times Q_{10}^{\frac{T-10}{10}} \qquad (3)$$

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Statistical analysis

Treatment differences in seasonal and annual NEE, R_{eco}, P_{gross}, and NEP were assessed using analysis of variance. Seasons were analyzed separately due to large seasonal differences in the magnitude and variance of fluxes. To determine whether gas exchange rates from predawn, postdawn, and afternoon periods differed under symmetric and asymmetric warming, we analyzed each time of day within each season using a mixed-effects model, stipulating treatment as fixed effects and chamber as a random effect, with an auto-regressive variance–covariance structure to account for temporal autocorrelation. To assess treatment differences in photosynthetic temperature sensitivity (P_{opt}, T_{opt}, and b) and respiration Q_{10}, we analyzed fitted parameters from each terracosm using analysis of variance. Treatment differences in R_{10} were also determined with a mixed-effects model as described above.

Results

Seasonal growth patterns

Time series of daily NEE, and estimated partitioned fluxes for P_g and R_{eco}, showed that the bulk of ecosystem carbon uptake occurred during the spring and early summer (Fig. 3a and b). Net carbon losses began mid-summer as plants senesced and entered dry-season dormancy and continued through the fall and winter, despite the regreening of plants with the onset of fall rains. Fluxes tracked together for symmetric and asymmetric treatments across all seasons and exhibited no treatment differences in the summed flux for each season, or over a year from February 2009 to February 2010 (Fig. 3b and c).

Compared with ambient conditions, the timing of peak carbon uptake was accelerated by warming by approximately 2 and 4 weeks in 2009 and 2010, respectively. Earlier growth was followed by earlier senescence, however, with the result that warming had no affect on total aboveground plant growth in any of the

4 years of the study (Fig. 4). By contrast, whole-ecosystem production decreased with warming in 2009–2010 (Fig. 3c) from a near-neutral carbon balance under ambient temperatures to a net loss of carbon to the atmosphere at elevated temperatures (average ambient NEP = −102 g C m^{-2} yr^{-1}, 95% CI = −314 to 111; asymmetric NEP = −427 g C m^{-2} yr^{-1}, 95% CI = −713 to −149; symmetric NEP = −431 g C m^{-2} yr^{-1}, 95% CI = −760 to −93). The higher annual net loss of carbon at elevated temperatures appeared to be due to greater increases in annual respiration than photosynthesis. P_g was significantly higher under warming in the fall and winter seasons, but R_{eco} also increased with warming in all seasons except summer dormancy. Estimates of partitioned fluxes indicate that ecosystem respiration and photosynthesis were both sensitive to the 3.5 °C increase in daily mean temperature, but not to the 3 °C difference in DTR.

To further probe whether fluxes under asymmetric and symmetric warming differed within the diel time scale, we compared net CO_2 exchange rate during periods of the day when temperatures were most different: predawn, postdawn, and afternoon periods defined as when temperatures differed by 1–1.5, 0.75–1.5, and 1–1.5 °C, respectively (see Fig. 1b). Even during these periods of maximum temperature difference, however, we found no significant differences in CO_2 exchange rate under asymmetric and symmetric warming (Fig. 5). We found that using two different approaches to probe for potential impacts of reduced DTR – comparing estimated values for P_g and R_{eco}, and direct measurements of day and night net CO_2 exchange – both suggested there were no significant response of photosynthesis or respiration to reduced DTR at the ecosystem level.

To understand why photosynthesis and respiration seemed to be sensitive to the 3.5 °C mean temperature increase between ambient and elevated temperatures, but not to the dawn and afternoon temperature differences between asymmetric and symmetric treatments, we constructed temperature–response curves for net photosynthesis and night R_{eco} (i.e., day and night net CO_2 exchange rate) near the time of peak growth in May 2010 and conducted sensitivity analyses. We specifically examined whether the apparent lack of response to reduced DTR was due to: (1) differences in the temperature sensitivity between symmetric and asymmetric treatments, perhaps resulting from acclimation to growth under prolonged differences in DTR, or (2) limited sensitivity to temperature for both treatments, such that 0–1.5 °C temperature differences on either end of the day had no perceptible effects. For both photosynthesis and respiration, we found no evidence to support the first possibility (Fig. 6a and b).
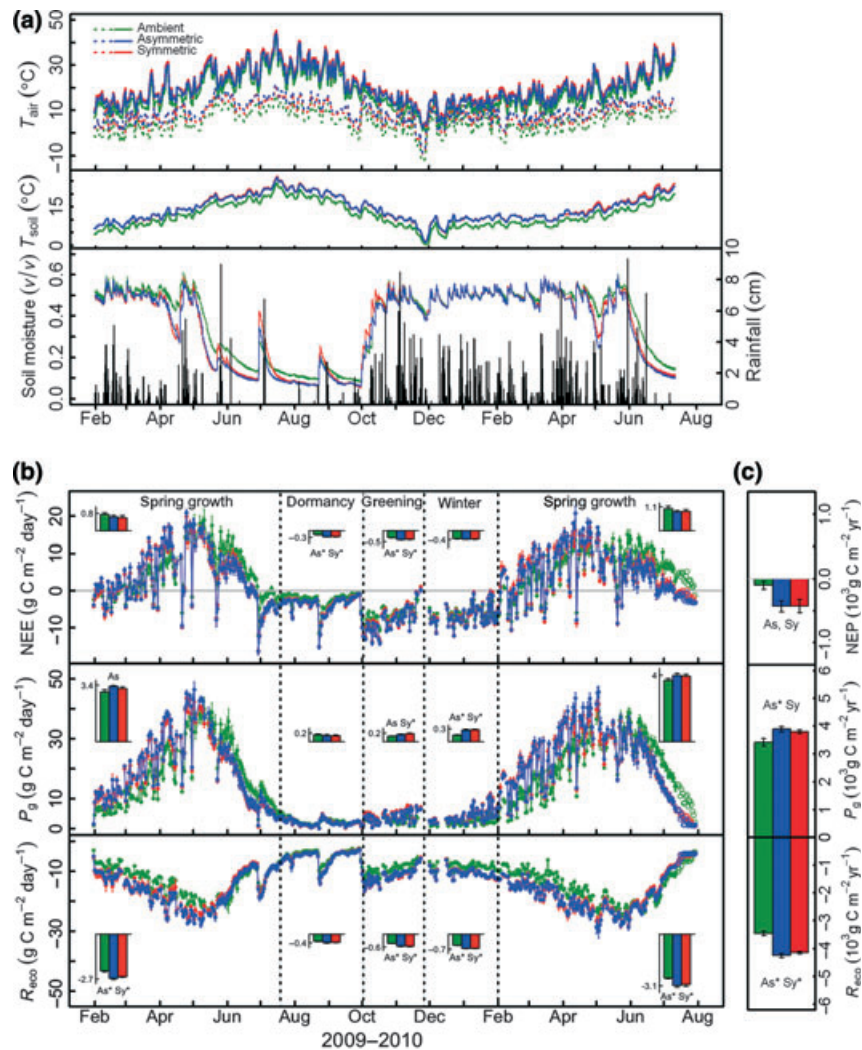
Fig. 3 Environmental conditions and whole-ecosystem CO_2 exchange from February 2009 to August 2010. (a) Top, daily air T_{min}/T_{max} at 1 m (dotted/solid lines); middle, daily average soil temperature at 5 cm depth; bottom, daily rainfall (black vertical lines) and average soil moisture at 0–30 cm depth (colored lines). (b) Daily total net ecosystem exchange (NEE, top) calculated from summing hourly CO_2 exchange rate measurements, partitioned fluxes for gross photosynthesis (P_g, middle), and ecosystem respiration (R_{eco}, bottom). Empty circles indicate modeled fluxes for 16 days after treatments ended (see Materials and methods). Floating bar plots show total fluxes for each season (10^3g C m^{-2}). As and Sy indicate significant differences between ambient vs. asymmetric and ambient vs. symmetric treatments, respectively, and there were no significant differences between the two elevated treatments. Asterisk indicates $P < 0.05$, otherwise $P < 0.1$. (c) Total annual CO_2 fluxes from February 2009 to February 2010. All error bars are SEM ($N = 4$ terracosms per treatment).

Asymmetric and symmetric treatments exhibited no differences in the photosynthetic temperature optimum (95% CI for difference = −1.2 to 3.8 °C) or maximum photosynthetic rates (95% CI for difference = −1.3 to 1.6 μmol m^{-2} leaf s^{-1}) and no difference in the Q_{10} for night R_{eco} (95% CI for difference = −0.1 to 0.1) or basal respiration rate, R_{10} (95% CI for difference = −0.6 to 0.5) (Fig. 6c and d). Although both warming treatments had significantly higher photosynthetic temperature optima than the ambient treatment, and reduced Q_{10} and R_{10} values, this apparent temperature acclimation

may have been due to the advanced stage of growth at elevated temperatures. When photosynthetic and respiration temperature responses were calculated for the ambient treatment as it reached peak biomass a month later, they were not significantly different from the elevated temperature treatments in May (data not shown).

Given that reduced DTR had no apparent impact on photosynthetic or respiratory temperature–response curves, we conducted analyses to assess whether these temperature sensitivities were sufficient to express dif-
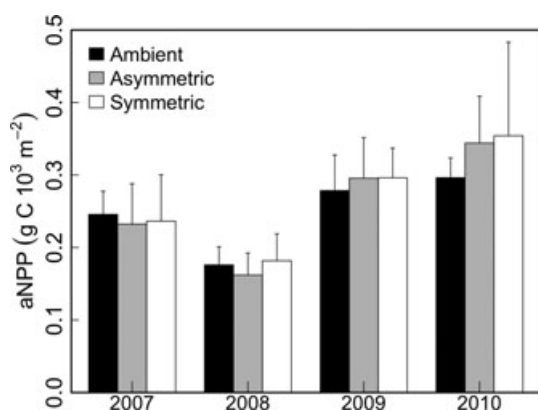
Fig. 4 Timeseries of aboveground annual net primary productivity aNPP). No significant differences occurred among treatments in any year. Error bars = 95% CI ($N = 4$ terracosms per treatment).
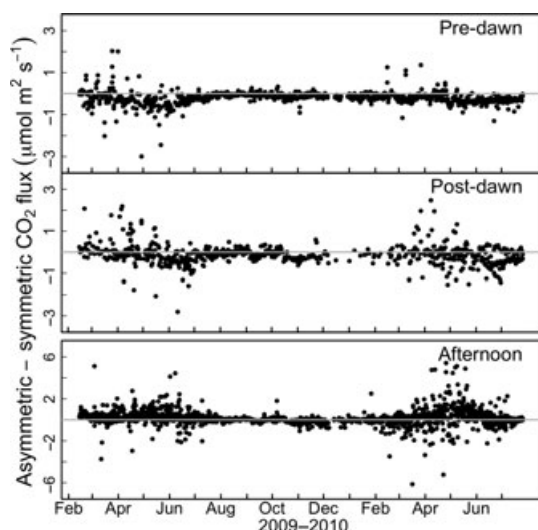

Fig. 5 Differences in CO_2 exchange rate between asymmetric and symmetric warming, during predawn, postdawn, and afternoon when temperatures differed by at least 1, 0.75, and 1 °C, respectively. No significant difference in CO_2 exchange rate was observed for any time of day, within any season.

ferences in light-saturated net photosynthesis or night R_{eco} under the experimental temperature regimes. We used average temperature response coefficients from each treatment (Fig. 6a and b) and observed temperatures to calculate expected light-saturated photosynthesis and predawn respiration rates for each treatment during the period of peak growth May 3–23, 2010 (Fig. 6c and d). For respiration, we show results for predawn hours when treatment temperatures were most different (≥ 1 °C), to optimize detection of flux differences ($N = 36$ h in 20 days). We calculated an expected

difference in cumulative predawn R_{eco} of only 0.2% between symmetric and asymmetric treatments, which agreed closely with the observed, although not significant, difference of 2.2%. This sensitivity analysis indicates that the Q_{10} of 1.5 observed in both symmetric and asymmetric treatments was not sufficient to express differences in R_{eco} that could be detected statistically, even during the time of day when temperatures were most different. By comparison, systems with Q_{10} values of 2.0, 2.5, or 3.0 experiencing these temperature regimes would have yielded higher predawn respiration rates in the asymmetric than symmetric treatment by 4.8%, 9.2%, or 13.3%, respectively.

For photosynthesis, we calculated expected cumulative net photosynthesis across light-saturated hours only ($N = 43$ h in 20 days), as a means for isolating the effects of temperature alone. Expected photosynthesis rates were calculated using the light-saturated temperature–response curves described above. Within these hours, we predicted 5.5% higher total photosynthesis for the asymmetric than symmetric treatment, which was similar to the observed, although not significant, difference of 4%. This small difference in net photosynthesis between the two elevated temperature treatments is consistent with the broad temperature–response curves that were measured, showing little change in net photosynthesis across temperatures from 15 to 28 °C in both treatments (Fig. 6a). After controlling for light level, photosynthesis appeared to be fairly insensitive to temperature changes across a large range typical of spring daytime temperatures.

Further consideration of light and temperature interactions suggests that differences in photosynthesis between the warming treatments may also have been minimized because photosynthesis was light-limited at times when temperature differences were the greatest. This could help explain why differences in NEE were not detected during postdawn hours (Fig. 5). During midday hours when light could reach saturating levels, temperatures differed by less than 1 °C between warming treatments. This means that assimilation was always comparatively low when treatment temperature differences were the greatest, a fact that contradicts the *a priori* expectation that asymmetric warming could augment morning photosynthesis compared with symmetric warming.

Discussion

Reducing DTR by 3 °C, a level that is consistent with predictions for the next century (Stone & Weaver, 2003; Lobell *et al.*, 2007) did not detectably alter warming impacts on plant and ecosystem carbon balance, nor on
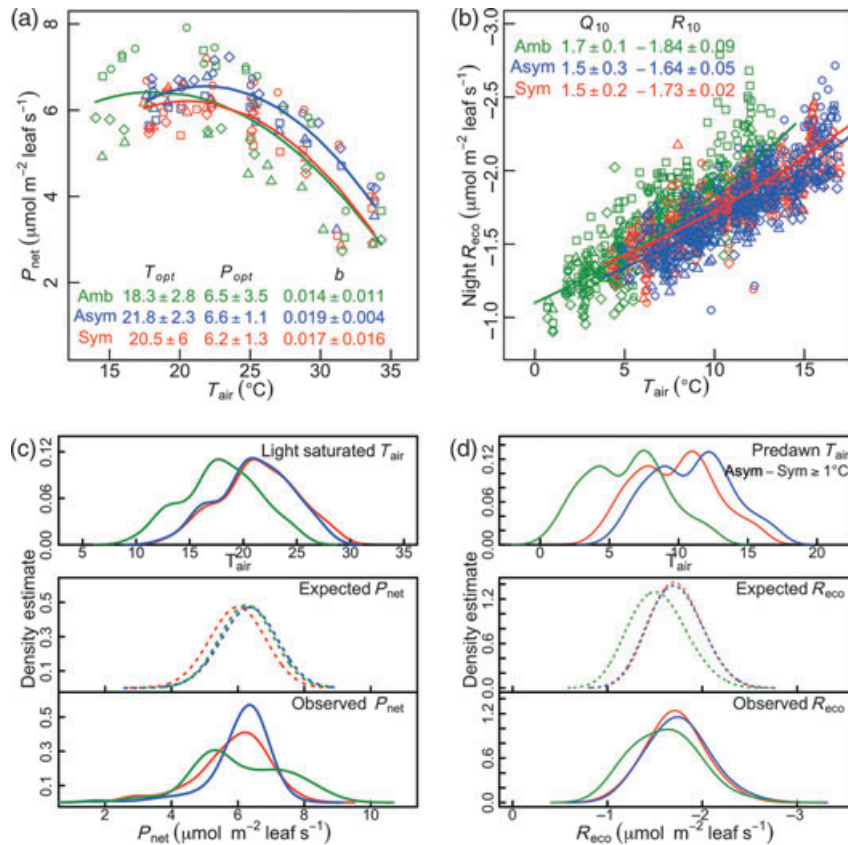
Fig. 6 Sensitivity evaluation of light-saturated net photosynthesis and night ecosystem respiration (R_{eco}) to treatment temperature differences. (a) Light-saturated P_{net} temperature response on May 13, 2010. Lines represent Eqn 1 fitted with mean treatment parameters (shown with 95%CI) (N = 8–12 per terracosm, 129 total, PAR >1200 μmol m^{-2}s^{-1}, soil moisture >0.35 v/v, P_{net} normalized by green plant surface area, one-sided, measured May 17–19, 2010). (b) Temperature response for night R_{eco} from May 3 to 23, 2010, also normalized by plant surface area. Lines represent Eqn 3 fitted with mean treatment parameters (reported with 95%CI) (N = 124–131 per terracosm, 1559 total). (c and d) Top panels: observed distribution of air temperatures during (c) light-saturated and (d) predawn hours, May 3–23, 2010 (N = 49 and 63 h, respectively). Middle panels: distribution of expected CO_2 exchange rates calculated from air temperatures and mean response curves in (a) or (b). Bottom panels: observed distributions of light-saturated P_{net} and predawn R_{eco}.

rates of photosynthesis and respiration. The expectation that asymmetric warming would increase night respiration was not met, nor was the expectation of increased morning photosynthesis. Our results instead indicate that reducing DTR in a realistic manner, with gradual day/night temperature transitions rather than step-changes at dawn and dusk, minimized temperature differences between asymmetric and symmetric warming regimes and had minimal impacts on both photosynthesis and respiration.

Average day and night temperatures are likely to be more similar under asymmetric and symmetric warming than has been recognized previously. The diurnal temperature profiles for asymmetric and symmetric treatments had maximum differences of 1.5 °C at T_{min} and T_{max}, but between those times approached zero difference, with the result that the asymmetric treatment was only 0.26 °C cooler over the entire day and only

0.31 °C warmer over the entire night when compared with the symmetric treatment. The fact that a fairly large 3 °C reduction in DTR could result in only small changes in average day and night temperatures has not been widely appreciated and suggests that the phenomenon of 'night warming' has been exaggerated. Although previous work has tended to focus on trends in T_{min} and T_{max}, these trends exceed average warming across the whole night and day because of gradual diurnal temperature transitions. Prior warming experiments with constant night/day temperature offsets thus tend to impose higher average night temperatures and lower day temperatures than realistic warming profiles.

In addition to the small differences in average day and night temperatures between symmetric and asymmetric warming, we found that both treatments had low sensitivity of respiration to temperature at the eco-

system scale, during the peak growing season ($Q_{10} = 1.5 \pm 0.3$ for May 2010). Although grassland systems have often been shown to have higher Q_{10} values, synthesis work has revealed that removing artifacts related to differences in temperature range leads to a global convergence in Q_{10} of 1.4 ± 0.1 across regions and vegetation types (Mahecha et al., 2010). Although forecasts of respiration based on Q_{10} values should be interpreted cautiously (Davidson et al., 2006), this low global Q_{10} combined with our results indicates a potentially limited influence of DTR on ecosystem responses to climate change. Systems that are less sensitive to temperature in general should be less impacted by changes in DTR (Dhakhwa & Campbell, 1998; Medvigy et al., 2010; Sierra et al., 2010).

Although the Q_{10} method of describing respiration temperature sensitivity can be criticized for simplifying physiological processes, it is notable that the responses of this complex plant and soil system, which had too many potential outcomes to predict a priori, appeared to have simple Q_{10} responses to the temperature treatments. For May 2010, we were able to explain treatment effects on respiration and photosynthesis fairly well with Q_{10} functions alone, without incorporating additional factors. This finding contrasts with results from at least two previous night-warming experiments, in which temperatures were changed abruptly at dawn and dusk. In these studies, compensatory feedbacks between photosynthesis and respiration were found to override the direct effects of temperature (Turnbull et al., 2002; Wan et al., 2009). Higher rates of photosynthesis occurred under night-warming than equal-day-and-night warming, which was suggested to be a response to nightly foliage carbohydrate depletion.

Although we found no evidence for compensatory effects in response to reduced DTR (but rather a lack of response entirely), we cannot completely rule out the possibility that close coupling between photosynthesis and respiration minimized DTR impacts. For instance, Atkin et al. (2007) have suggested that compensating mechanisms operate to maintain a constant ratio of respiration to photosynthesis in plants under small, but not large temperature increases. Homeostasis in response to small, but not large temperature changes could provide a partial explanation for our finding that an increase in mean temperature, but not the comparatively small change in temperature caused by reducing DTR, impacted rates of photosynthesis and respiration. Similarly, our findings may differ from prior night-only warming experiments because greater temperature forcing is imposed with constant in contrast to gradual nighttime temperature increases.

An additional explanation for the unresponsiveness of this system to reduced DTR may be the Mediterra-nean climate with mild winters and dry summers. The onset of spring growth for some species can be related to the date of last frost (Nemani et al., 2001); however, at this location, altering DTR had minimal effect on the date of last frost because ambient T_{min} on freezing nights was generally only slightly below 0 °C, so both warming treatments increased to temperatures above the frost threshold (number of nights per year below freezing, average for winters 2007–2010: AMB = 68, SYM = 16, ASYM = 11). Furthermore, most of the grassland species remained active throughout the winter and did not experience complete winter dormancy, so the onset of spring growth may have been less sensitive to minimum temperatures when compared with vegetation that hardens off in the winter. Although warmer temperatures resulted in earlier acceleration of spring growth for the warmer treatments (Fig. 4), total growing season length was insensitive to the number of frost-free days. In other ecosystems, earlier spring growth can also increase annual productivity and total growing season length (Schwartz & Reiter, 2000), but we found that growth in the elevated temperature treatments stopped sooner than in the ambient treatment, accompanying soil moisture depletion.

Our findings of decreased NEP and shifted timing of plant growth at elevated temperatures are consistent with several other grassland studies (Alward et al., 1999; Saleska et al., 1999; De Boeck et al., 2007). Results are varied, however, with others reporting increases or decreases in plant growth (Shaw et al., 2002; Wan et al., 2009), or an increase or no change in NEP (Grime et al., 2008) in response to warming. Although we cannot suggest that differences in DTR are responsible for the lack of consensus, other aspects of experimental design are important considerations, particularly manipulation of soil temperatures. One of the unique advantages of the terracosms was realistic soil warming conditions via heat transfer from air (Aronson & McNulty, 2009), which supported realistic respiration rates by maintaining diurnal and seasonal temperature variation and realistic vertical temperature profiles. One limitation of the study, however, is that soils were disturbed during installation, which may precondition soil responses to warming in unforeseeable ways and could have contributed to the observed higher respiration at elevated temperatures. Disturbance effects could be revealed by monitoring over additional growing seasons for evidence of system equilibration.

In conclusion, our finding that reduced DTR had no significant effects on photosynthesis, respiration, or NEP indicates that results from symmetric warming studies in some cases may also be relevant for predicting asymmetric warming impacts. Although historic changes in T_{min}/T_{max} have been used to infer changes

in night/day temperatures, it is important to recognize that T_{min} and T_{max} represent the extremes of night-and-day temperatures and are poor proxies for understanding changes in mean night/day temperatures. Night-warming studies that impose an exaggerated level of warming across the whole night may be less informative models for asymmetric warming than symmetric warming studies. The broad implication of these results is that for the Mediterranean grasslands, carbon models may have the ability to predict ecosystem carbon balance based on changes in mean temperatures alone without needing to also consider changes in DTR.

Acknowledgements

References

Alward RD, Detling JK, Milchunas DG (1999) Grassland vegetation changes and nocturnal global warming. *Science*, **283**, 229–231.

Amthor JS, Hanson PJ, Norby RJ, Wullschleger SD (2010) A comment on "Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality" by Aronson and McNulty. *Agricultral and Forest Meteorology*, **150**, 497–498.

Aronson EL, McNulty SG (2009) Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology*, **149**, 1791–1799.

Atkin OK, Scheurwater I, Pons TL (2007) Respiration as a percentage of daily photosynthesis in whole plants is homeostatic at moderate, but not high, growth temperatures. *New Phytologist*, **174**, 367–380.

Campbell BH (2004) *Restoring Rare Native Habitat in the Willamette Valley. A Land Owners' Guide for Restoring Oak Woodlands, Wetlands, Praries, and Bottomland Hardwood and Riparian Forests*. Defenders of Wildlife, West Linn, OR.

Dai A, Del Genio AD, Fung IY (1997) Clouds, precipitation, and temperature range. *Nature*, **386**, 665–666.

Davidson EA, Janssens IA, Luo Y (2006) On the variability of respiration in terrestrial ecosystems: moving beyond Q_{10}. *Global Change Biology*, **12**, 154–164.

De Boeck HJ, Lemmens CMHM, Vicca S et al. (2007) How do climate warming and species richness affect CO_2 fluxes in experimental grasslands? *New Phytologist*, **175**, 512–522.

Desai AR, Richardson AD, Moffat AM et al. (2007) Cross-site evaluation of eddy covariance GPP and RE decomposition techniques. *Agricultral and Forest Meteorology*, **148**, 821–838.

Dhakhwa GB, Campbell CL (1998) Potential effects of differential day-night warming in global climate change on crop production. *Climatic Change*, **40**, 647–667.

Frantz JM, Cometti NN, Bugbee B (2004) Night temperature has a minimal effect on respiration and growth in rapidly growing plants. *Annals of Botany*, **94**, 155–166.

Gifford RM (2003) Plant respiration in productivity models: conceptualisation, representation and issues for global terrestrial carbon-cycle research. *Functional Plant Biology*, **30**, 171–186.

Grime JP, Fridley JD, Askew AP, Thompson K, Hodgson JG, Bennett CR (2008) Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences*, **105**, 10028–10032.

Gunderson CA, O'Hara KH, Campion CM, Walker AV, Edwards NT (2010) Thermal plasticity of photosynthesis: the role acclimation in forest responses to a warming climate. *Global Change Biology*, **16**, 2272–2286.

Hanson PJ, Childs KW, Wullschleger SD, Riggs JS, Thomas WK, Todd DE, Warren JM (2011) A method for experimental heating of intact soil profiles for application to climate change experiments. *Global Change Biology*, **17**, 1083–1096.

IPCC (2007) Observations: surface and atmospheric climate change. In: *Climate Change 2007: The Physical Science Basis*, contribution of working group I to the fourth assessment report of the IPCC. (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL) pp. 235–336. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Licor-Biosciences (2004) *LI-8100 Automated Soil CO2 Flux System & LI-8150 Multiplexer Instruction Manual*.Licor-Biosciences, Lincoln, NE.

Lobell DB, Bonfils C, Duffy PB (2007) Climate change uncertainty for daily minimum and maximum temperatures: a model inter-comparison. *Geophysical Research Letters*, **34**, L05715.

Luo Y (2007) Terrestrial carbon-cycle feedback to climate warming. *Annual Review of Ecology and Systematics*, **38**, 683–712.

Mahecha MD, Reichstein M, Carvalhais N et al. (2010) Global convergence in the temperature sensitivity of respiration at ecosystem level. *Science*, **329**, 838–840.

Makowski K, Wild M, Ohmura A (2008) Diurnal temperature range over Europe between 1950 and 2005. *Atmospheric Chemistry and Physics*, **8**, 6483–6498.

Manunta P, Kirkham MB (1996) Respiration and growth of sorghum and sunflower under predicted increased night temperatures. *Journal of Agronomy and Crop Science*, **176**, 267–274.

Medvigy D, Wofsy SC, Munger JW, Moorcroft PR (2010) Responses of terrestrial ecosystems and carbon budgets to current and future environmental variability. *Proceedings of the National Academy of Sciences*, **107**, 8275–8280.

Nemani RR, White MA, Cayan DR, Jones GV, Running SW, Coughlan JC, Peterson DL (2001) Asymmetric warming over coastal California and its impact on the premium wine industry. *Climate Research*, **19**, 25–34.

Peng S, Huang J, Sheehy JE et al. (2004) Rice yields decline with higher night temperature from global warming. *Proceedings of the National Academy of Sciences*, **101**, 9971–9975.

Reichstein M, Falge E, Baldocchi D et al. (2005) On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biology*, **11**, 1424–1439.

Saleska SR, Harte J, Torn MS (1999) The effect of experimental ecosystem warming on CO_2 fluxes in a montane meadow. *Global Change Biology*, **5**, 125–141.

Schindlbacher A, de Gonzalo C, Días-Pinés E et al. (2010) Temperature sensitvity of forest soil organic matter decomposition along two elevation gradients. *Journal of Geophysical Research*, **115**, G03018.

Schwartz MD, Reiter BE (2000) Changes in North American spring. *International Journal of Climatology*, **20**, 929–932.

Shaw MR, Zavaleta ES, Chiariello NR, Cleland EE, Mooney HA, Field CB (2002) Grassland responses to global environmental changes upressed by elevated CO_2. *Science*, **298**, 1987–1990.

Sierra CA (2011) Temperature sensitivity of organic matter decomposition in the Arrhenius equation: some theoretical considerations. *Biogeochemistry*, doi: 10.1007/s10533-011-9596-9.

Sierra CA, Harmon ME, Thomann E, Loescher HW (2010) Amplification and dampening of soil respiration by changes in temperature variability. *Biogeosciences Discussions*, **7**, 8979–9008.

Stanley AG, Kaye TN, Dunwiddie P (2008) Regional strategies for restoring invaded praries: a multi-site, collaborative approach for controlling invasive species. *Native Plants Journal*, **9**, 247–254.

Stone DA, Weaver AJ (2003) Factors contributing to diurnal temperature range trends in twentieth and twenty-first century simulations of the CCCma coupled model. *Climate Dynamics*, **20**, 435–445.

Stooksbury DE, Michaels PJ (1994) Climate change and large-area corn yield in the southeastern United States. *Agronomy Journal*, **86**, 564–569.

Tingey DT, McVeety BD, Waschmann R, Johnson MG, Phillips DL, Rygiewicz PT, Olszyk DM (1996) A versatile sun-lit controlled-environment facility for studying plant and soil processes. *Journal of Environment Quality*, **25**, 614–625.

Tingey DT, Waschmann RS, Phillips DL, Olszyk DM (2000) The carbon dioxide leakage from chambers measured using sulfur hexafluoride. *Environmental and Experimental Botany*, **43**, 101–110.

Turnbull MH, Murthy R, Griffin KL (2002) The relative impacts of daytime and night-time warming on photosynthetic capacity in *Populus deltoides*. *Plant, Cell & Environment*, **25**, 1729–1737.

Fillmore (2009) *Soil survey of Benton County, Oregon, United States*. Department of Agriculture, Natural Resources Conservation Service, U.S. Govt Printing Office, 1449 pp.

Volder A, Edwards EJ, Evans JR, Robertson BC, Schortemeyer M, Gifford RM (2004) Does greater night-time, rather than constant, warming alter growth of managed pasture under ambient and elevated atmospheric CO_2? *New Phytologist*, **162**, 397–411.

Vose RS, Easterling DR, Gleason B (2005) Maximum and minimum temperature trends for the globe: an update through 2004. *Geophysical Research Letters*, **32**, 5.

Wan S, Xia J, Liu W, Niu S (2009) Photosynthetic overcompensation under nocturnal warming enhances grassland carbon sequestration. *Ecology*, **90**, 2700–2710.

Wild M, Ohmura A, Makowski K (2007) Impact of global dimming and brightening on global warming. *Geophysical Research Letters*, **34**, 4.

Wolfe-Bellin KS, He J-S, Bazzaz FA (2006) Leaf-level physiology, biomass, and reproduction of phytolacca americana under conditions of elevated carbon dioxide and increased nocturnal temperature. *International Journal of Plant Sciences*, **167**, 1011–1020.

Zhang C-J, de A. Prado CHB, Zu Y-G, Guo J-Q, Ronquim CC, Ferreira LL (2003) Effect of overnight temperature on leaf photosynthesis in seedlings of *Swietenia macrophylla* King. *Journal of Forestry Research*, **14**, 130–134.

Zheng HF, Chen LD, Han XZ (2009) The effects of global warming on soybean yields in a long-term fertilization experiment in Northeast China. *Journal of Agricultural Science*, **147**, 569–580.

Zhou L, Dickinson RE, Dirmeyer P, Min S-K (2009) Spatiotemporal patterns of changes in maximum and minimum temperatures in multi-model simulations. *Geophysical Research Letters*, **36**, 6.

Zhou L, Dickinson RE, Tian Y, Vose RS, Dai Y (2007) Impact of vegetation removal and soil aridation on diurnal temperature range in a semiarid region: application to the Sahel. *Proceedings of the National Academy of Sciences*, **104**, 17937–17942.