

## Substrate regulation of soil respiration in a tallgrass prairie: Results of a clipping and shading experiment

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[1] Changes in soil respiration, one of the major fluxes of global carbon cycling, could significantly slow down or accelerate the increase in atmospheric CO<sub>2</sub>, with consequent feedbacks to climate change. It is critical to understand how substrate availability regulates soil respiration in projecting the response of carbon cycling to changed climate. We conducted a clipping and shading experiment for 1 year in a tallgrass prairie of the Great Plains, United States, to manipulate substrate supply to soil respiration. Our results showed that reduced substrate supply under clipping and/or shading significantly decreased soil respiration at all the timescales (diurnal, transient, and annual) irrespective of the minor concurrent changes in soil temperature and moisture. Annual mean soil respiration decreased significantly by 33, 23, and 43% for the clipping, shading, and clipping plus shading treatments, respectively. Temperature sensitivity of soil respiration decreased from 1.93 in the control plots to 1.88, 1.75, and 1.83 in the clipped, shaded, and clipped plus shaded plots, respectively. Rhizosphere respiration, respiration from decomposition of aboveground litter, and respiration from oxidation of soil organic matter and dead roots accounted for 30, 14, and 56% of annual mean soil respiration, respectively. Rhizosphere respiration was more sensitive to temperature than the other two components. Our results suggest a critical role of substrate supply in regulating soil respiration and its temperature sensitivity. *INDEX TERMS*: 1615 Global Change: Biogeochemical processes (4805); 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; *KEYWORDS*: carbon substrate, clipping, rhizosphere respiration, shading, tallgrass prairie, temperature sensitivity

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### 1. Introduction

[2] As one of the major carbon (C) fluxes between terrestrial ecosystems and the atmosphere, soil respiration releases about 68 Pg C [Raich and Schlesinger, 1992] to 80 Pg C [Raich *et al.*, 2002] to the atmosphere each year, which is more than 10 times the current rate of fossil fuel combustion [Schlesinger, 1997]. A small change in soil respiration could significantly slow down or accelerate the increase in atmospheric CO<sub>2</sub>, with consequent feedbacks to climate change [Raich and Schlesinger, 1992; Rustad *et al.*, 2000]. Substantial research efforts on soil respiration have been made during the past several decades. However, there are still uncertainties about the roles of environmental factors in regulating soil respiration and its temperature sensitivity and the relative contributions of different components to total soil respiration.

[3] Rates of soil respiration strongly vary with soil temperature and moisture availability [Kucera and Kirkham, 1971; Singh and Gupta, 1977; Schlenter and Van Cleve, 1985; Carlyle and Ba Than, 1988; Lloyd and Taylor, 1994; Rustad *et al.*, 2000]. Diurnal and seasonal variations in soil microclimate result in substantial differences in soil respiration within sites. Differences in soil respiration rates across spatial scales have also been associated with climate differences [Raich and Potter, 1995; Atkin *et al.*, 2000]. As a result, soil temperature and moisture are frequently considered as the major factors regulating soil respiration in global C cycling models [Raich *et al.*, 2002]. However, since release of CO<sub>2</sub> from soils requires C sources, substrate quantity and quality may play a critical role in controlling soil respiration [Singh and Gupta, 1977; Boone *et al.*, 1998; Raich and Tufekcioglu, 2000].

[4] Substrate supply of soil respiration comes from at least three sources, including (1) rhizosphere labile C supply from photosynthesis, (2) aboveground litter, and (3) soil organic matter (SOM) and dead roots [Wiant, 1967; Högberg *et al.*, 2001]. Partitioning the total soil respiration to its components (i.e., rhizosphere respiration, microbial respiration from aboveground litter and microbial respiration from

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SOM and dead roots) is another critical issue in understanding C cycling at ecosystem and global scales. On one hand, different sources of substrate supply have different magnitudes and turnover rates and may respond differently to perturbations. Thus the relative contributions from different components will determine the rate of soil respiration and its response to environmental change [Hanson *et al.*, 2000; Schlesinger and Andrews, 2000; Högberg *et al.*, 2001]. On the other hand, it is crucial, but very difficult, to separate the role of seasonal variation of substrate supply from those of the concurrently seasonal variations of soil temperature and moisture in regulating soil respiration. There is a stronger seasonal variation of the rhizosphere labile C supply from photosynthesis than those of aboveground litter or SOM and dead roots. The former contributes 10–90% to total soil respiration depending on the seasons of the year [Hanson *et al.*, 2000; Raich *et al.*, 2002]. Therefore precise estimates of the contribution of different components to soil respiration need at least year-around data.

[5] The differences in the turnover rates, magnitudes, and seasonal patterns of the three substrate sources result in different responses of the three components of soil respiration to temperature. As a consequence, the temperature sensitivity ( $Q_{10}$ ) may differ among the three components [Holland *et al.*, 2000]. While most simulation models of regional and global C cycling generally use a single, fixed  $Q_{10}$  coefficient for the exponential function between soil respiration and temperature, experimental studies have found that  $Q_{10}$  of soil respiration and SOM and litter decomposition decreases under elevated temperature [Kirschbaum, 1995; Liski *et al.*, 1999; Giardina and Ryan, 2000; Luo *et al.*, 2001]. Therefore better understanding of the interdependence between substrate supply and the temperature sensitivities of the three components will be helpful in projection of the feedbacks between climate change and global C cycling.

[6] To examine the regulation of substrate supply on soil respiration and its temperature sensitivity, we conducted a 1-year manipulative experiment in a tallgrass prairie with the following specific objectives: (1) examining the responses of soil respiration and its temperature sensitivity to reduced substrate supply, (2) partitioning the total soil respiration into different components, and (3) determining the temperature sensitivities of the three components.

## 2. Material and Methods

### 2.1. Site Description and Experiment Design

[7] The field study was conducted on a tallgrass prairie, 3 km east of Norman campus of the University of Oklahoma (latitude 35.2°N, longitude 97.4°W). The soil was Vernon clay loam and vegetation was dominated by *Panicum virgatum*, *Schizachyrium scoparium*, *Andropogon gerardii*, *Sorghastrum nutans*, *Ambrosia psilostachya*, *Xanthocephalum texanum*, *Bromus japonicus*, and *Eragrostis spp.*

[8] We used randomized complete block design with four treatments, namely, control, clipping, shading, and clipping plus shading, each replicated five times. The plot size was 1 × 1 m. Distance among plots was 1.5 m. Field facilities were set up on 21 June 2001. In the clipped and clipped plus

shaded plots, plants were clipped at the soil surface once a week and removed from the plots. The shaded plots were manipulated with double layer black cloth that provided a 100% percent reduction in light intensity.

### 2.2. Field Measurements

[9] To measure soil respiration, a PVC collar (80 cm<sup>2</sup> in area and 5 cm in height) was put 2–3 cm into the soil at the center of each plot. Living plants inside the soil collars were clipped at the soil surface 1 day before each measurement of soil respiration. The clipped plant material was left in the collars for the control and shaded plots or removed from the collars for the clipped and clipped plus shaded plots. In the first two months, soil respiration was measured 1 day before and 1, 2, 3, 4, 5, 7, 10, 15, 20, 25, 30, 35, 38, 39, 43, 53 days after clipping and/or shading to quantify its transient responses. In the rest of the experiment, soil respiration was measured twice a month. Soil respiration was measured using a LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, Nebraska, USA) attached with a LI-6400-09 soil CO<sub>2</sub> flux chamber. In order to minimize the temperature difference among the four treatments, measurement of soil respiration began at 0800 LT (local time) in the early morning of each measuring date except for 20 June (1200 LT) and 22 June (1000 LT) 2001. Two diurnal cycles of soil respiration were measured at 2-hour time intervals 4 days (from 0800 LT 25 June 2001 to 0800 LT 26 June 2001) and 1 year (from 0800 LT 20 June 2002 to 0800 LT 21 June 2002) after the manipulation.

[10] Soil moisture (percent volumetric) at the depth of 15 cm was measured twice a month using time domain reflectometry (Soilmoisture Equipment Corp., Santa Barbara, California). Soil temperature at the depth of 5 cm was measured adjacent to each PVC collar at the time of the soil respiration measurement using a thermocouple connected to LI-6400. One soil core (25 cm in depth and 60 cm<sup>2</sup> in area) was sampled at the center of each plot to measure root biomass by the end of the experiment (21 June 2002).

### 2.3. Statistical Analysis

[11] On the basis of the whole year data, we established exponential and polynomial functions to describe the relationship between soil respiration and soil temperature and between soil respiration and soil moisture:

$$R = \alpha e^{\beta T}, \quad (1)$$

$$R = \chi M^2 + \delta M + \varepsilon, \quad (2)$$

where  $R$ ,  $T$ , and  $M$  are soil respiration, temperature, and moisture, respectively.  $\alpha$ ,  $\beta$ ,  $\chi$ ,  $\delta$ , and  $\varepsilon$  are constant coefficients. The temperature sensitivity ( $Q_{10}$ ) of soil respiration was calculated as  $Q_{10} = \exp(10 \times \beta)$ . According to equation (2), we calculated a constant,  $M_0$ , as:  $M_0 = -\delta/2\chi$ .  $M_0$  was the soil moisture content at which soil respiration was highest.

[12] Clipping and shading manipulations affected soil temperature and soil moisture in our study. Altered soil temperature and soil moisture, in turn, influenced soil respiration. In order to eliminate the effects of concurrently

changed soil temperature and moisture on soil respiration, we established a third equation by combining equations (1) and (2) to describe the interactive effects of soil temperature and moisture on soil respiration:

$$R = \alpha \times e^{\beta T} \frac{\chi M^2 + \delta M + \varepsilon}{\chi M_0^2 + \delta M_0 + \varepsilon} \quad (3)$$

On the basis of year-around data, an equation was developed for each of the clipped and/or shaded plots. Then we used the soil temperature and moisture data in the control plots to calculate soil respirations in the clipped and/or shaded plots and compared with soil respiration in the control plots.

[13] In comparison with the control, clipping cut off the substrate supply from photosynthesis to roots and rhizosphere microbes and from aboveground litter to microbes and thus suppressed rhizosphere respiration and microbial respiration from aboveground litter (Figure 1). Shading cut off substrate supply from photosynthesis to plant roots and rhizosphere microbes and blocked rhizosphere respiration. Therefore, with the respiration from the shaded plots used as a proxy for the sum of respiration from SOM and dead roots and from aboveground litter, we estimated rhizosphere respiration as the difference in soil respirations between the control and shaded plots. Microbial respiration from aboveground litter was calculated by subtracting soil respiration in the clipped plus shaded plots from that in the shaded plots. Microbial respiration from SOM and dead roots was the average of the soil respiration in the clipped and clipped plus shaded plots.

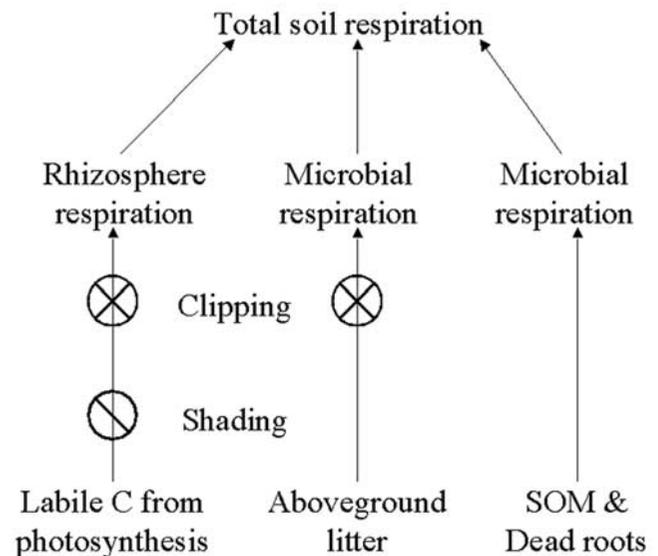
[14] Statistical significance of treatment effects was evaluated by analysis of variance (ANOVA). All the statistical analyses were performed using SAS (SAS Institute, Inc., 1989–1996, North Carolina, USA).

### 3. Results and Discussions

#### 3.1. Diurnal Cycle

[15] Within the diurnal cycles, clipping significantly increased soil temperature, whereas shading and clipping plus shading decreased soil temperature compared to the control plots (Figure 2, top). The temperature differences between the control plots and the clipped and/or shaded plots were highest in the early afternoon and lowest in the early morning. However, the measured soil respirations in the clipped and/or shaded plots reduced significantly in comparison with that in the control plots within the diurnal cycles ( $P < 0.05$ , Figure 2, middle). Soil respiration rates on 25 June 2002 were much higher than on 21 June 2001, which was caused by the early summer drought in 2001. The diurnal pattern of soil respiration in our experiment, i.e., a peak in the middle afternoon and a lowest rate at predawn, was similar to those observed in other studies [Witkamp, 1969; Davidson *et al.*, 1998; Xu and Qi, 2001a].

[16] We also took into account the concern that the concurrent changes in soil temperature and moisture under clipping and/or shading manipulation might affect the rate of soil respiration. Since soil moisture would not change much within 24 hours, we corrected the diurnal soil

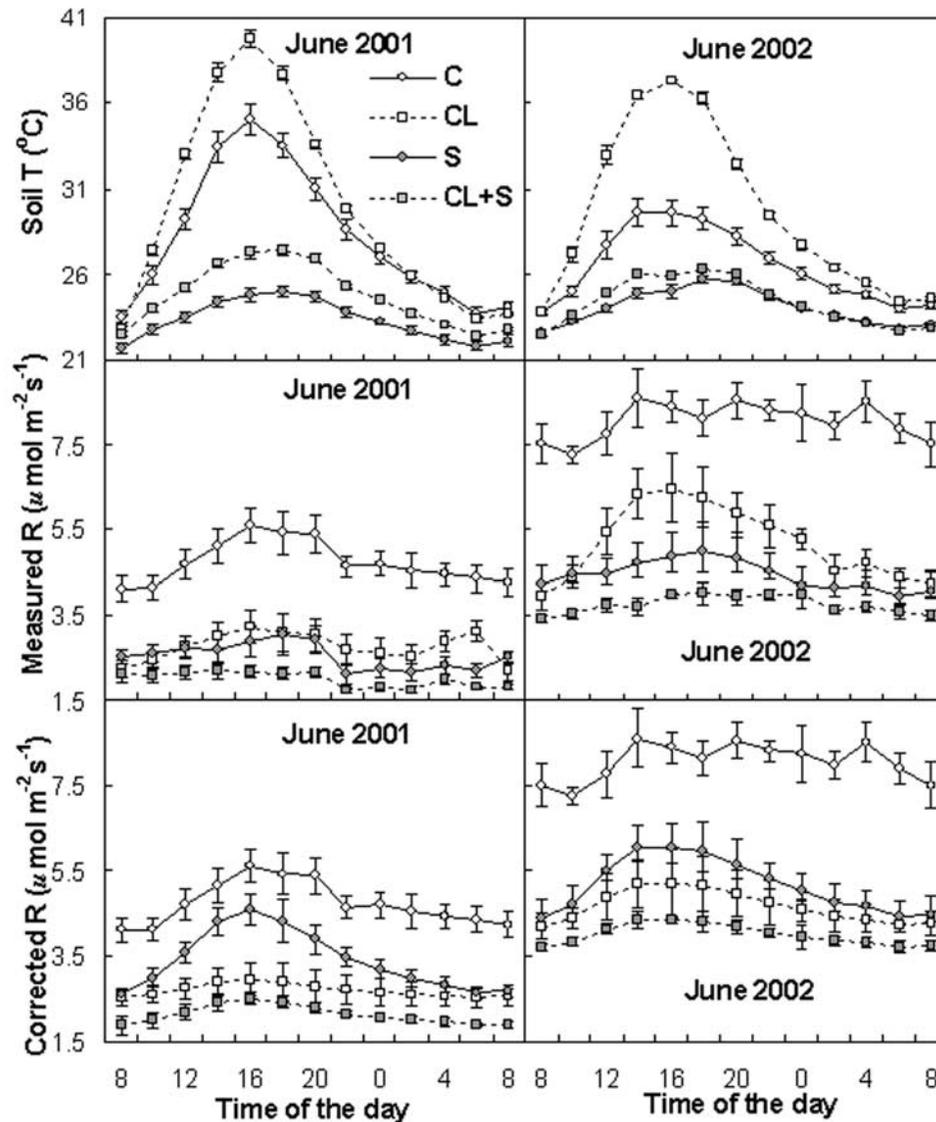


**Figure 1.** Conceptual model of soil respiration, showing different components and their substrate sources. Clipping cuts off carbon supply from photosynthesis and from aboveground litter thus suppresses rhizosphere respiration and microbial respiration from aboveground litter. Shading cuts off carbon supply from photosynthesis and blocks rhizosphere respiration.

respirations in the clipped, shaded and clipped plus shaded plots based on the soil temperature in the control plots. First, linear functions between soil respiration and soil temperature were established using data in the clipped and/or shaded plots. The linear functions had higher correlation coefficients than the exponential functions in describing the diurnal variation of soil respiration. Then, soil respirations in the shaded, clipped, and clipped plus shaded plots were calculated using soil temperature in the control plots based on the linear function for each plot. Thus the effects on soil respiration of concomitantly changed soil temperature due to clipping and/or shading manipulation were minimized.

[17] The measured soil respirations in the clipped plots were always highest among the clipped and/or shaded plots (Figure 2, middle) due to the high soil temperatures in the clipped plots (Figure 2, top). On the contrary, the corrected soil respirations in the shaded plots were the highest among the clipped and/or shaded plots (Figure 2, bottom), indicating the effects of substrate availability on soil respiration because substrate supply in the shaded plots included both aboveground litter and SOM and dead roots, whereas substrate supply in the clipped and clipped plus shaded plots was SOM and dead roots.

[18] Daily mean soil temperatures in the clipped plots were 1.6 and 3.2°C higher than those in the control plots in year 2001 and 2002, respectively. In comparison with the control treatment, shading decreased daily mean soil temperatures by 4.9 and 2.5°C, whereas clipping plus shading reduced daily mean soil temperatures by 3.4 and 2.2°C in year 2001 and 2002, respectively (Figure 3, top). Four days after manipulation, daily averages of the meas-

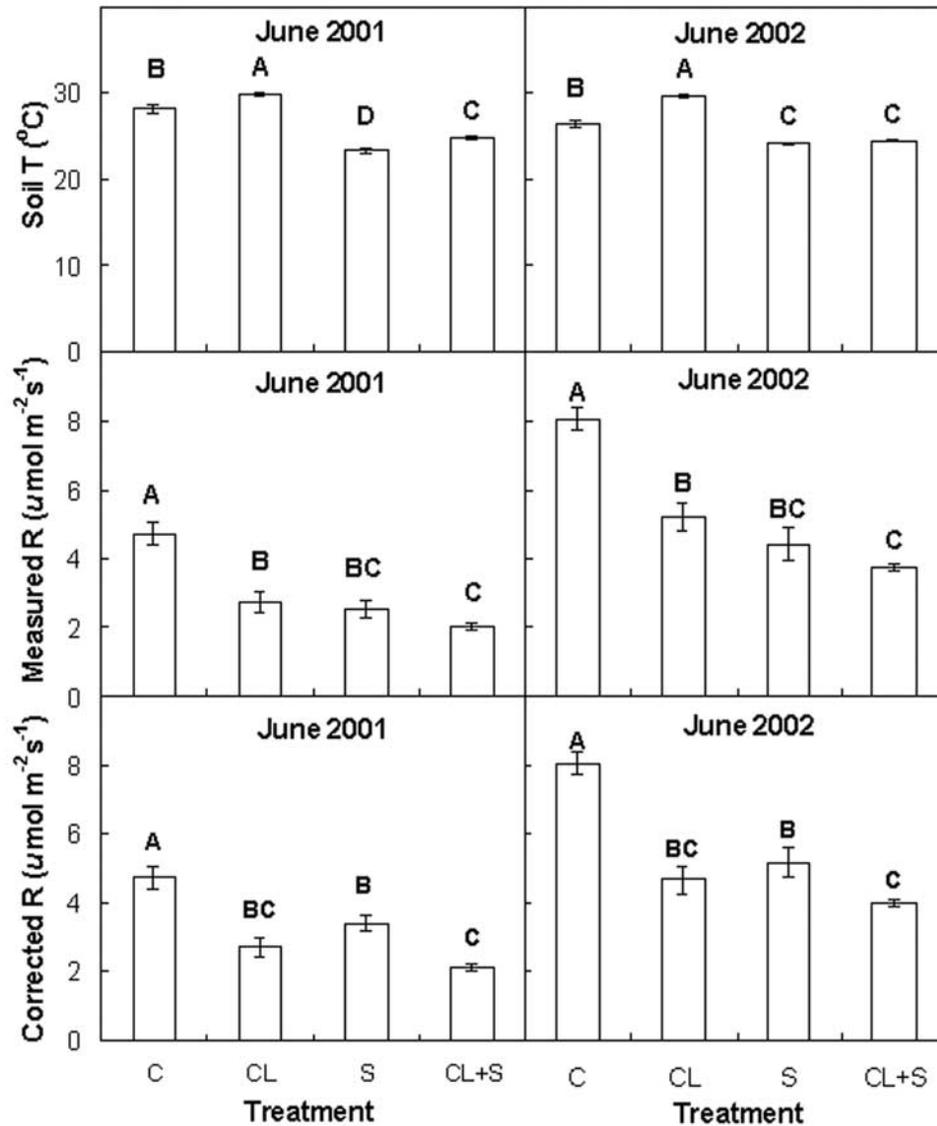


**Figure 2.** (top) Diurnal variations of soil temperatures and (middle) measured and (bottom) corrected soil respirations 4 days (June 2001, left) and 1 year (June 2002, right) after treatment (mean  $\pm$  1 SE). Abbreviations are as follows: C, the control plots; CL, the clipped plots; S, the shaded plots; and CL + S, the clipped plus shaded plots.

ured soil respirations in the clipped, shaded, and clipped plus shaded plots were 42, 46, and 58% lower, respectively, than that in the control plots. One year later, daily averages of the measured soil respiration decreased by 36, 45, and 53% for the clipping, shading, clipping plus shading treatments, respectively. The sequence of the measured soil respirations was as follows: Control plots were greater than clipped plots, which were greater than shaded plots, which were greater than clipped plus shaded plots in both days nearly 1 year apart (Figure 3, middle). The sequence of the measured soil respiration in the clipped and/or shaded plots was affected by the concurrent changes in soil temperature and confounded the effects of substrate supply on soil respiration.

[19] After correction, the sequence for the daily averages of soil respirations, i.e., control plots greater than shaded plots greater than clipped plots greater than clipped plus shaded plots (Figure 3, bottom), clearly showed the effects of substrate supply on soil respiration. Daily averages of the corrected soil respirations in the clipped, shaded, and clipped plus shaded plots were 43, 28, and 55% in 2001 and 42, 36, and 50% in 2002 lower than in the control plots, respectively.

[20] The substrate supply in the clipped plots and the clipped plus shaded plots was the same. The measured soil respirations in the clipped plots were significantly higher than those in the clipped plus shaded plots because of the higher soil temperature in the clipped plots (Figure 3,



**Figure 3.** (top) Daily averages of soil temperatures and (middle) measured and (bottom) corrected daily mean soil respirations 4 days (June 2001, left) and 1 year (June 2002, right) after treatment (mean  $\pm$  1 SE). Characters above the bars are the results of analysis of variance; different characters between any two bars stand for statistical significance at confidence level of 95%. See Figure 2 for abbreviations.

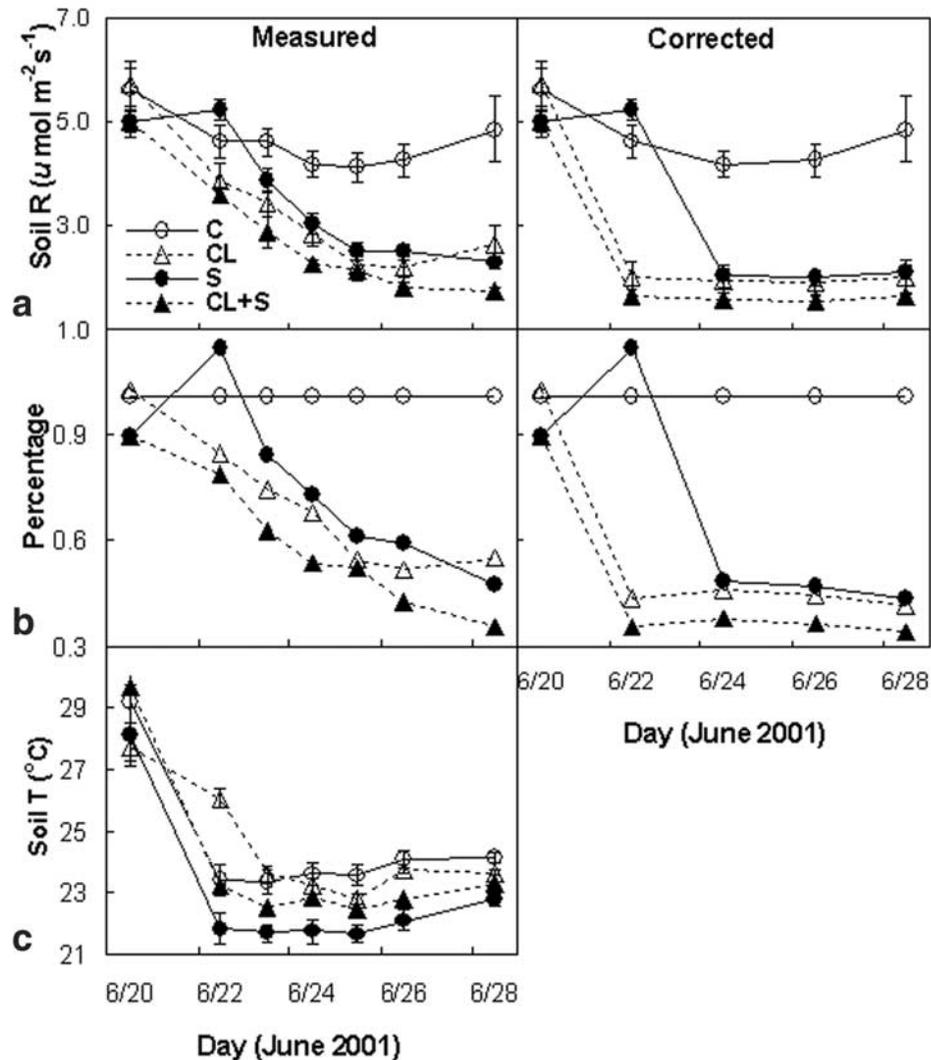
middle). However, there was no significant difference in the corrected soil respirations between the two treatments (Figure 3, bottom).

[21] Diurnal variations in soil respirations 4 days and 1 year after treatment showed that manipulation with clipping and/or shading significantly reduced soil respiration because of the reduced substrate supply (i.e., photosynthesis and aboveground litter) irrespective of the concurrent changes in soil temperature.

### 3.2. Transient Response

[22] To illustrate transient responses to the abrupt reduction in substrate supply, we made intense measurements of soil respiration in the first week before and after treatment.

There were no significant differences in soil respirations or temperatures among the four treatments before clipping and shading manipulation (20 June 2001). The measured soil respirations in the clipped and clipped plus shaded plots decreased sharply 1 day after manipulation in comparison with that in the control plots. However, the measured soil respiration in the shaded plots did not change the first day after shading and began to decrease in the second day after shading. The results suggested that clipping affected soil respiration more rapidly than shading because clipping cut off substrate supply from photosynthesis immediately. Within the first week after manipulation, both the measured and corrected soil respirations in the clipped and/or shaded plots were significantly lower than that in the control plots

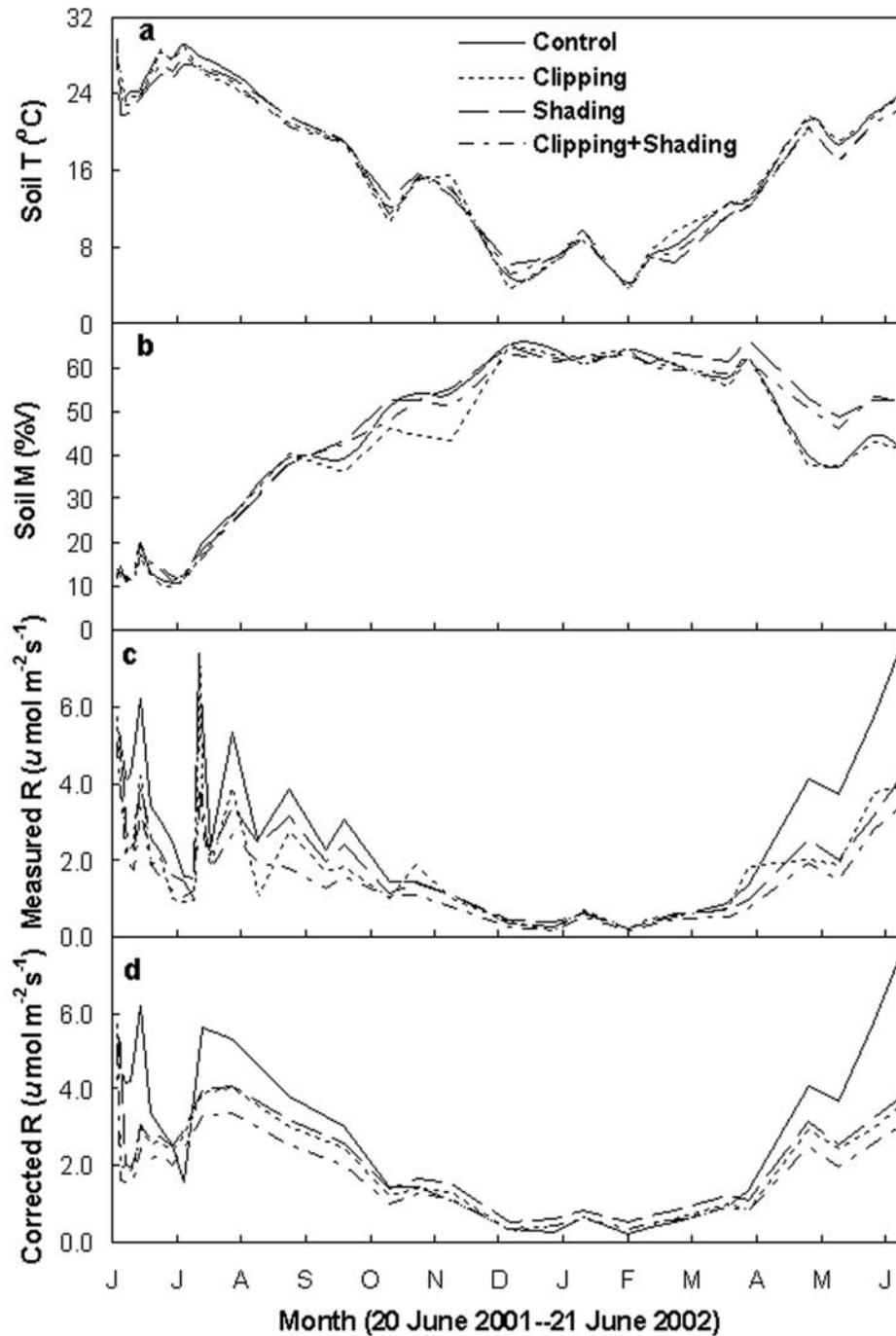


**Figure 4.** (a) Transient responses of the measured (left) and corrected (right) soil respirations (mean  $\pm 1$  SE). (b) Relative magnitudes of soil respirations in the clipped and/or shaded plots to that in the control plots. (c) Measured soil temperatures (mean  $\pm 1$  SE) to manipulation with clipping and/or shading. Measurement before treatment (20 June 2001) began at 1200 LT, which caused the high soil temperatures in Figure 4c; measurements after treatment began at 0800 LT except on 22 June 2001 (1000 LT). See Figure 2 for abbreviations.

except for the shaded plots on 22 June 2001 (Figure 4a). The measured soil respirations in the clipped and/or shaded plots showed a gradual decrease in comparison with the control plots (Figures 4a and 4b, left). However, the corrected soil respirations in the clipped and/or shaded plots reduced sharply and stabilized at low levels compared to the control plots (Figures 4a and 4b, right), suggesting rapid loss of substrate supply from photosynthesis and above-ground litter. Seven days after manipulation, the measured soil respiration in the clipped, shaded, and clipped plus shaded plots decreased by 45, 53, and 64% (Figure 4b, left), respectively, in comparison with that in the control plots. After correction, soil respirations in the clipped and/or shaded plots were 58, 57, and 66% lower than that in the control plots (Figure 4b, right).

[23] The shaded plots had the highest respiration rates (both measured and corrected) among the clipped and/or shaded plots irrespective of their lowest soil temperature (Figure 4c). This was caused by the fact that shading only cut off substrate supply from photosynthesis, whereas clipping and clipping plus shading cut off substrate supply from both photosynthesis and aboveground litter.

[24] Our results were consistent with the results from other experiments. In a Kansas tallgrass prairie, soil respiration reduced by 21–49% 2 days after clipping even though clipping increased soil temperature [Bremer *et al.*, 1998]. Similarly, the rate of rhizosphere respiration in planted barrel (*Medicago truncatula* Gaertn. Cv. Paraggio) decreased immediately after defoliation [Crawford *et al.*, 2000]. In a Minnesota grassland, shading for 2 days caused



**Figure 5.** (a) Seasonal variations of soil temperature, (b) soil moisture, and (c) measured and (d) corrected soil respirations.

a 40% reduction in soil respiration, while clipping reduced soil respiration by 19% [Craine *et al.*, 1999]. The reductions for both treatments were independent of soil temperature. Rhizosphere respiration of wheat plants was 50% lower than the control 5–6 days after shading manipulation [Kuzyakov and Cheng, 2001]. A girdling experiment in a Scots pine forest in Sweden showed that soil respiration reduced by 27–37% 5 days after treatments [Högberg *et al.*,

2001]. Results from our experiment and other experiments indicate that reduced substrate supply leads to an almost immediate decrease in soil respiration.

### 3.3. Seasonal Variation and Annual Average

[25] The seasonal variation in soil temperature showed no clear pattern of the effect of clipping on soil temperature, whereas shading and clipping plus shading decreased soil

temperature for most of the measuring dates (Figure 5a). Clipping slightly, but insignificantly, decreased soil moisture during most measuring dates except for November 2001. Shading and clipping plus shading did not affect soil moisture in 2001 and in the first 4 months in 2002 but significantly increased soil moisture in May and June 2002 (Figure 5b). The seasonal variations of both the measured and corrected soil respirations were similar with that of soil temperature but opposite to that of soil moisture during most time of the 1-year experimental period (Figures 5c and 5d). However, the summer drought in 2001 caused low soil respiration rates irrespective of the high soil temperatures. The seasonal variation of soil respiration in the tallgrass prairie was inconsistent with that in California grasslands, where the seasonal pattern of soil respiration was similar to that of soil moisture and opposite to that of soil temperature [Luo *et al.*, 1996]. The results suggested an interactive role of soil temperature and moisture in affecting the seasonal variations of soil respiration.

[26] During the growing seasons, both the measured and corrected soil respirations in the clipped and/or shaded plots were significantly lower than those in the control plots. There were no clipping and/or shading effects on soil respirations during the nongrowing season (Figures 5c and 5d). After correcting for soil temperature and moisture, soil respiration in the shaded plots was always highest among the clipped and/or shaded plots (Figure 5d), which could be attributable to different substrate supply in the shaded plots and in the clipped and clipped plus shaded plots. The larger differences in soil respirations between the control and treated plots during the growing seasons were also observed in harvested [Edwards and Ross-Todd, 1983; Nakane *et al.*, 1996] and girdled [Högberg *et al.*, 2001] forest ecosystems. These results indicated that there were substantial contributions of photosynthesis to total substrate supply and of rhizosphere respiration to total soil respiration.

[27] There was no significant effect of clipping on annual mean soil temperature, whereas shading and clipping plus shading significantly reduced soil temperature by 0.9 and 0.7°C, respectively (Figure 6a). Clipping slightly decreased annual mean soil moisture, whereas shading and clipping plus shading slightly increased annual mean soil moisture, but neither the decreases nor the increases were statistically significant (Figure 6b). Annual averages of the measured soil respirations in the clipped, shaded, and clipped plus shaded plots were 34, 31, and 48% lower than that in the control plots, respectively (Figure 6c). After correction, soil respirations reduced by 33, 23 and 43% in the clipped, shaded, and clipped plus shaded plots, respectively, in comparison with that in the control plots (Figure 6d). The reduction in annual mean soil respiration due to clipping in our experiment was much higher than that in a Kansas tallgrass prairie (17–18%), where the plants were clipped 3 times a year [Bremer *et al.*, 1998].

[28] The shaded plots and the clipped plus shaded plots had similar annual mean soil temperature and moisture. However, annual averages of both the measured and corrected soil respirations in the shaded plots were significantly higher than those in the clipped plus shaded plots, which was attributed to the fact that shading only cut off substrate

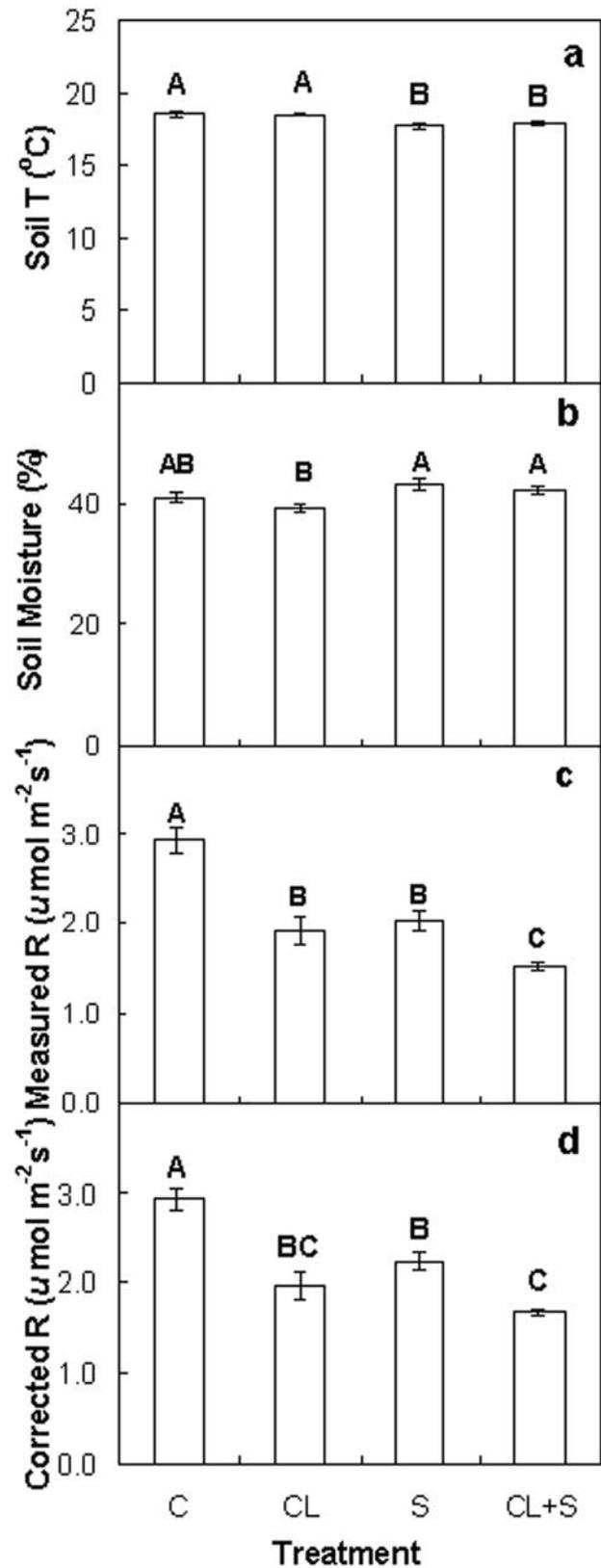


Figure 6. (a) Annual averages of soil temperature, (b) soil moisture, and (c) measured and (d) corrected soil respirations (mean  $\pm$  1 SE). See Figure 2 for abbreviations.

supply from photosynthesis, whereas clipping plus shading cut off substrate supply from both photosynthesis and aboveground litter. The measured soil respiration in the clipped plots was statistically significantly higher than that in the clipped plus shaded plots, which resulted from the differences in soil temperatures between the two treatments (Figure 6a). However, there was no significant difference in soil respirations in the two treatments after correction (Figure 6d), suggesting that they had the same substrate supply.

[29] We quantified the possible changes in soil respiration rates due to the concurrent changes in soil temperature in the clipped and/or shaded plots. We used the exponential function between soil respiration and soil temperature in the control plots ( $R = 0.8182e^{0.0657T}$ ) and calculated respiration rates in the four treatments using the annual mean soil temperature for each treatment (19.86, 19.74, 18.99, and 19.13°C). The results showed that calculated annual mean soil respirations in the clipped ( $2.99 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), shaded ( $2.85 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), and clipped plus shaded plots ( $2.88 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) were only 0.8, 5.6, and 5.0% lower, respectively, than that in the control plots ( $3.02 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). The decreases in the calculated annual mean soil respirations due to the concurrent changes in soil temperature were much less than those of the measured (34, 31, and 48%) and corrected (33, 23 and 43%) soil respirations, indicating that the reductions in soil respirations for the three treatments were mostly attributed to the decline in the substrate supply.

[30] Plants control autotrophic and heterotrophic respiration via their control over substrate availability [Zak *et al.*, 1994; Janssens *et al.*, 2001; Kuzyakov and Cheng, 2001]. For example, soil respirations are positively correlated with aboveground net primary productivity in grassland and litter production in forests, which are related to the quantity of C supplied to soil [Raich and Nadelhoffer, 1989; Raich and Schlesinger, 1992; Luo *et al.*, 1996; Raich and Tufekcioglu, 2000]. On the basis of eddy covariance data, Janssens *et al.* [2001] hypothesized that differences in soil respiration among 18 European forests are likely to depend more on productivity than on temperature. All the diurnal, transient, and seasonal results in our experiment showed that reduced substrate supply manipulated with clipping and/or shading lead to significant decreases in soil respiration, irrespective of the concurrent changes in physical environment (temperature and moisture). Our results were consistent with those of similar experiments in Minnesota [Craine *et al.*, 1999] and Kansas [Bremer *et al.*, 1998] grasslands. A tree-girdling experiment in a boreal forest also confirmed that the relative aboveground and belowground allocation of net primary productivity (NPP) was one of the critical factors to influence the rate of soil respiration [Högberg *et al.*, 2001].

### 3.4. Changes in Temperature Sensitivity ( $Q_{10}$ )

[31] Substrate supply not only affected the rate of soil respiration but also had effects on other aspects of soil respiration. Temperature sensitivity ( $Q_{10}$ ) of soil respiration governs the response of soil C efflux to elevated temperature.  $Q_{10}$  varies with soil temperature, soil moisture, and the seasons [Kirschbaum, 1995; Liski *et al.*, 1999; Giardina and Ryan, 2000; Luo *et al.*, 2001; Xu and Qi,

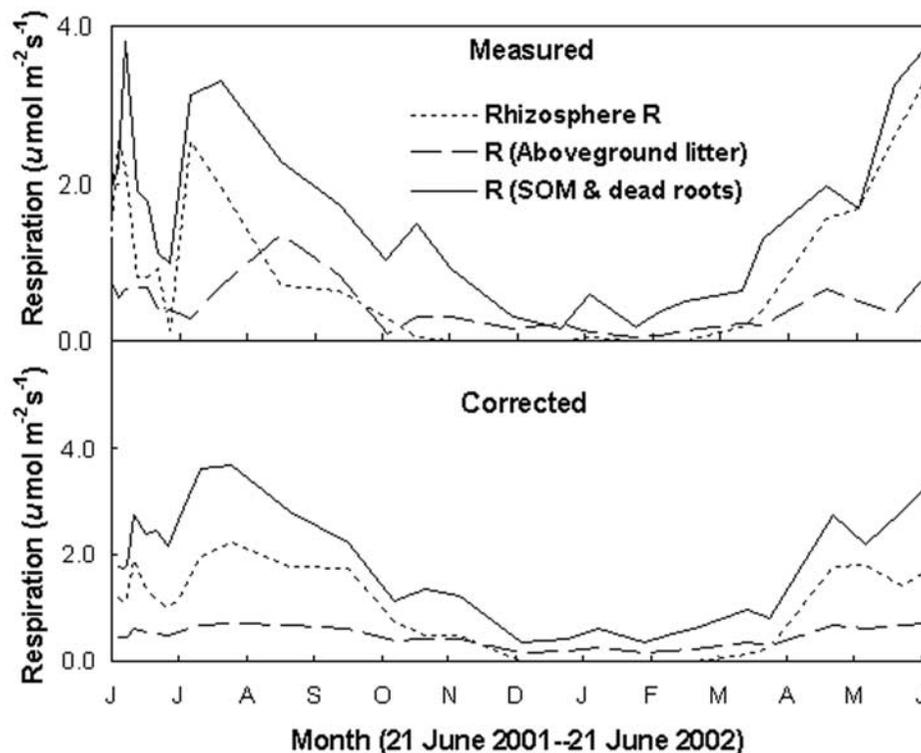
2001b]. During the 1-year experimental period,  $Q_{10}$  of soil respiration was substantially lowered by summer drought in 2001 in comparison with that in 2002 for all the treatments (see below).

[32] Within the 1-year experimental period,  $Q_{10}$  of the corrected soil respiration decreased from 1.93 in the control plots to 1.88, 1.75, and 1.83 in the clipped, shaded, and clipped plus shaded plots, respectively, suggesting regulation of substrate supply on temperature sensitivity of soil respiration. Summer drought in 2001 confounded the effects of reduced substrate supply on  $Q_{10}$ . There were no consistent changes in  $Q_{10}$  in 2001 (1.65, 1.72, 1.60, and 1.70 for the control, clipped, shaded, and clipped plus shaded plots, respectively). However,  $Q_{10}$  in 2002 in the clipped and/or shaded plots (3.19, 2.77, and 3.00) substantially declined compared to that in the control plots (3.78).

[33] The results of our experiment that clipping and shading substantially reduced  $Q_{10}$  of soil respiration were supported by the other experiments. Townsend *et al.* [1997] reported a slight but insignificant decline in  $Q_{10}$  in their laboratory examination of the temperature dependence of the slow and active SOM pools. Boone *et al.* [1998], Holland *et al.* [2000], and Atkin *et al.* [2000] also described reductions in  $Q_{10}$  with decreasing substrate availability. Declines in soil respiration and  $Q_{10}$  in response to reduced substrate supply indicate that ecosystems with low NPP and soil C content may be less responsive to global warming than ecosystems with high NPP and soil C content in terms of soil respiration. It has been found that  $Q_{10}$  of soil respiration decreases under higher temperature ranges [Kirschbaum, 1995; Liski *et al.*, 1999; Giardina and Ryan, 2000; Luo *et al.*, 2001]. However, our results showed that  $Q_{10}$  of soil respiration reduced under manipulation, independent of increases (the clipped plots) or decreases (the shaded and the clipped plus shaded plots) in soil temperature.

### 3.5. Contributions From Different Components

[34] Across the 1-year time period, rhizosphere respiration had a similar seasonal pattern with but was almost always lower than microbial respiration from SOM and dead roots, whereas microbial respiration from aboveground litter was the lowest (Figure 7). Rhizosphere respiration, microbial respiration from aboveground litter, and microbial respiration from SOM and dead roots accounted for, on average, 31, 15, and 54% of the measured total soil respiration, respectively. After correction, rhizosphere respiration, microbial respiration from aboveground litter, and microbial respiration from SOM and dead roots attributed 30, 14, and 56% to total soil respiration, respectively. However, rhizosphere respiration accounted for up to 48% of total soil respiration during the growing season. Our estimate of the contribution of rhizosphere respiration to total soil respiration was very close to those of a Missouri tallgrass prairie (30%) [Herman, 1977], a temperate mixed hardwood forest (33%) [Bowden *et al.*, 1993], and nonforest vegetations (36.7%) [Hanson *et al.*, 2000] but was much lower than that of planted wheat (75%) [Kuzyakov and Cheng, 2001]. The higher contribution of rhizosphere respiration to total soil respiration in planted wheat was based on a short-term laboratory experiment during the



**Figure 7.** Seasonal variations of rhizosphere respiration, microbial respiration from aboveground litter, and microbial respiration from soil organic matter (SOM) and dead roots calculated using the (top) measured and (bottom) corrected soil respirations in the four treatments.

early growing season [Kuzyakov and Cheng, 2001]. It was noteworthy that there was a big difference in the estimates of the contribution of rhizosphere respiration during the growing season and across the whole year time period in our experiment. Therefore the contribution of rhizosphere respiration might be overestimated if based only on the growing season data. A substantial contribution of rhizosphere respiration to total soil respiration indicates that changes in environmental factors that influence plant photosynthesis and belowground C allocation, such as elevated  $\text{CO}_2$  and elevated temperature, could lead to substantial responses of rhizosphere and total soil respirations [Luo *et al.*, 1996; Hungate *et al.*, 1996; Zak *et al.*, 2000; Rustad *et al.*, 2001]. In an Oklahoma tallgrass prairie, response of total soil respiration to experimental warming varied concurrently with that of aboveground biomass (S. Wan *et al.*, manuscript in preparation, 2003).

[35] We were interested not only in the relative contributions of different components to total soil respiration but also in their responses to elevated temperature. There was a great interannual variation in  $Q_{10}$  of the three components.  $Q_{10}$  of rhizosphere respiration, microbial respiration from aboveground litter, and microbial respiration from SOM and dead roots were 1.60, 1.33, and 1.70 in 2001 and 4.13, 2.15, and 3.10 in 2002, respectively, which could have resulted from the summer drought in 2001. During the 1-year period,  $Q_{10}$  was 1.97, 1.48, and 1.86 for rhizosphere respiration, microbial respiration from aboveground litter, and microbial

respiration from SOM and dead roots, respectively. In another experiment in 2000, we found soil respiration was significantly restricted by low soil moisture [Liu *et al.*, 2002]. We deleted several data points in summer 2001;  $Q_{10}$  of rhizosphere respiration, microbial respiration from aboveground litter, and microbial respiration from SOM and dead roots were 2.20, 1.46, and 2.02 in 2001 and 2.51, 1.63, and 2.16, respectively, for the whole year period. The results suggested that rhizosphere respiration was more sensitive to temperature than the other two components. Boone *et al.* [1998] also found that  $Q_{10}$  value of rhizosphere respiration was higher than that of mineral soil at the Harvard forest in Massachusetts. Higher  $Q_{10}$  for rhizosphere respiration indicates that the potentially enhanced NPP and belowground C allocation under elevated atmospheric  $\text{CO}_2$  and global warming may be offset by the rapid increase in rhizosphere respiration, leading to less C storage in the soil.

### 3.6. Root Biomass

[36] We were concerned that there was a possible lateral C movement through rhizomes due to the relative small and nontrenched plots in our experiment. To minimize the possible influence of lateral C movement, we measured soil respiration at the center of each plot. Another concern was that reduced substrate supply from photosynthesis might stimulate root death and decomposition in the clipped and/or shaded plots, leading to biased estimates of the relative contributions of different components to total soil respira-

tion. We measured total root biomass (including living and dead roots) by the end of the experiment. The result showed that clipping, shading, and clipping plus shading significantly decreased total root biomass by 24, 38, 45%, respectively, in comparison with the control, which could possibly have resulted from both the stimulated root decomposition in the clipped and/or shaded plots and the growth of new roots in the second year in the control plots. We were unable to quantify the magnitude of the stimulated root decomposition because we did not separate the dead roots from the living roots.

#### 4. Conclusions

[37] Our 1-year manipulative experiment provided a unique data set to examine the effect of reduced substrate supply on soil respiration and its temperature sensitivity and to quantify the relative contributions of different components to total soil respiration. We have demonstrated that substrate supply is one of the major factors in regulating soil respiration and its temperature sensitivity. The regulation of substrate supply on soil respiration and the high temperature sensitivity of rhizosphere respiration indicate that the interannual variability in soil respiration may be largely attributable to the variability in C fixation through photosynthesis and belowground C allocation.

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