Response of Respiration of Soybean Leaves Grown at Ambient and Elevated Carbon Dioxide Concentrations to Day-to-day Variation in Light and Temperature under Field Conditions

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● *Background and Aims* Respiration is an important component of plant carbon balance, but it remains uncertain how respiration will respond to increases in atmospheric carbon dioxide concentration, and there are few measurements of respiration for crop plants grown at elevated [CO_2] under field conditions. The hypothesis that respiration of leaves of soybeans grown at elevated [CO_2] is increased is tested; and the effects of photosynthesis and acclimation to temperature examined.
● *Methods* Net rates of carbon dioxide exchange were recorded every 10 min, 24 h per day for mature upper canopy leaves of soybeans grown in field plots at the current ambient [CO_2] and at ambient plus 350 µmol mol^{-1} [CO_2] in open top chambers. Measurements were made on pairs of leaves from both [CO_2] treatments on a total of 16 d during the middle of the growing seasons of two years.
● *Key Results* Elevated [CO_2] increased daytime net carbon dioxide fixation rates per unit of leaf area by an average of 48 %, but had no effect on night-time respiration expressed per unit of area, which averaged 53 mmol m^{-2} d^{-1} (1·4 µmol m^{-2} s^{-1}) for both the ambient and elevated [CO_2] treatments. Leaf dry mass per unit of area was increased on average by 23 % by elevated [CO_2], and respiration per unit of mass was significantly lower at elevated [CO_2]. Respiration increased by a factor of 2·5 between 18 and 26 °C average night temperature, for both [CO_2] treatments.
● *Conclusions* These results do not support predictions that elevated [CO_2] would increase respiration per unit of area by increasing photosynthesis or by increasing leaf mass per unit of area, nor the idea that acclimation of respiration to temperature would be rapid enough to make dark respiration insensitive to variation in temperature between nights.

Key words: *Glycine max* Merrill., carbon dioxide, respiration, temperature, acclimation.

INTRODUCTION

Respiration is an important component of plant carbon balance, with rapidly growing plants daily losing about one third of the carbon fixed in photosynthesis (McCree and Amthor, 1982). Predicting how plant carbon balance may be affected by the rising concentration of carbon dioxide in the atmosphere ([C_a]) is of importance both from a global carbon budget perspective and in predicting plant growth. While there are many measurements of responses of photosynthesis of plants to simulated increases in [C_a], and biochemical models that often provide a reasonable approximation of the observed photosynthetic responses, how respiration will respond to increases in [C_a] remains uncertain (Drake *et al*., 1999; Gonzalez-Meler *et al*., 2004).

Rising [C_a] is expected to increase leaf respiration in C_3 species by increasing photosynthesis (Amthor, 2000), because increased photosynthesis at elevated [CO_2] usually results in the accumulation of large amounts of non-structural carbohydrates, and these provide the respiratory substrates. Small carbohydrate concentrations have been found to decrease rates of dark respiration (e.g. Azcon-Bieto and Osmond, 1983; Hrubec *et al*., 1985; Noguchi and Terashima, 1997; Grimmer and Komor, 1999), but this is generally only apparent near the end of the night, when carbohydrates are depleted (Mullen and Koller, 1988;

Verklei and Challa, 1988). Because photosynthetic rates of mature leaves greatly exceed the plant's capacity to utilize carbohydrates (except when stresses strongly limit photosynthesis), higher photosynthesis at elevated [CO_2] also requires increased export of carbohydrates, which requires energy supplied by respiration. The energy required for translocation may represent a significant component of that produced by respiration of mature leaves (Bouma *et al*., 1995; Noguchi *et al*., 2001). In this study, respiration rates were measured on field-grown plants at the growth [CO_2], to avoid complications of potential short-term effects of measurement [CO_2] on respiration rates (Drake *et al*., 1999) and to maintain normal plant source–sink balance. It was hypothesized that growth at elevated [CO_2] would increase rates of respiration per unit of area by increasing photosynthesis.

There have been numerous measurements of respiration of plants grown at ambient and elevated [CO_2] in controlled environment chambers (e.g. Gifford *et al*., 1985; Poorter *et al*., 1988; Bunce and Caulfield, 1991; Baker *et al*., 1992; Thomas *et al*., 1993; Grimmer and Komor, 1999; Sakai *et al*., 2001), including soybean (e.g. Thomas and Griffin, 1994; Bunce, 1995; Bunce and Ziska, 1996; Griffin *et al*., 2001*b*), but diverse responses have been found. In most studies in controlled environment chambers, light and temperature were kept constant from day to day and often during days; the relevance of these observations to

respiration rates under field conditions is uncertain. One purpose of this study was to determine if the responses of respiration of soybean leaves to elevated [CO$_2$] in the field were similar to those found under controlled environment conditions. While leaf respiration of a few tree species grown outdoors at ambient and elevated [CO$_2$] has been studied (e.g. Wullschleger and Norby, 1992; Wullschleger *et al.*, 1992; Mitchell *et al.*, 1995; Kellomaki and Wang, 1998; Jach and Ceulemans, 2000; Hamilton *et al.*, 2001; Griffin *et al.*, 2001*a*; Zha *et al.*, 2001), there are few measurements of respiration of crop plants grown at elevated [CO$_2$] under field conditions. In summarizing responses for woody plants, Curtis and Wang (1998) found that elevated [CO$_2$] reduced respiration rates per unit of mass, although that conclusion has been questioned (Gonzalez-Meler *et al.*, 2004). Many of the studies on tree species have focused on expanding leaves to allow separation of growth and maintenance respiration, and therefore provide only limited data on responses of mature leaves, which in most systems will contribute the majority of leaf respiration. This study was restricted to fully expanded leaves.

Respiration of leaves often acclimates to temperature, such that after prolonged exposure to a range of temperatures, rates of respiration become nearly or completely independent of the exposure temperature (Atkin *et al.*, 2001). The rate of acclimation of respiration relative to the rate of change in temperature would control rates of respiration in natural environments. However, there have been few studies concerning rates of acclimation of respiration to temperature. Atkin *et al.* (2001) found that acclimation in eucalyptus was sufficiently rapid that rates of respiration per unit of mass were relatively independent of seasonal changes in night temperature. In two deciduous tree species, leaf respiration acclimated within a day or two to large changes in temperature (Bolstad *et al.*, 2003).

While measurements of whole-plant respiration rates would be desirable from a modelling or productivity perspective, experimental separation of plant from soil respiration remains problematic, and with regard to temperature acclimation, roots and shoots do not experience the same temperatures in the field. Therefore, the more specific hypotheses concerning responses of respiration to [CO$_2$] and temperature were addressed at the single-leaf rather than at the whole-plant level. Both Atkin *et al.* (2001) and Griffin *et al.* (2002) found that leaf respiration rates differed depending on whether diurnal changes in temperature occurred for the whole shoot or just for the measured leaf, and emphasized that accurate estimates of leaf respiration required that natural temperature patterns occurred for the whole shoot. Therefore, in this study, the measured leaf was held at the ambient air temperature to which the whole shoot was exposed. It was hypothesized that acclimation of respiration to temperature in leaves of soybean would be sufficiently rapid that day-to-day variation in night-time temperature would not affect respiration rates.

MATERIALS AND METHODS

With the recognized need to conduct respiration measurements throughout whole dark periods, and to include nights with a range of temperatures and prior photosynthesis, it was considered more important to have replication over dates than to measure multiple leaves per [CO$_2$] treatment on a given night. The potential drawback of this sampling design is that if the [CO$_2$] treatment effects on respiration were strongly affected by temperature or daily photosynthesis, it might be difficult to detect [CO$_2$] treatment effects using replication over time. The advantage is that any [CO$_2$] treatment effects detected would be relatively robust against variation in temperature, plant age, daily photosynthesis, and time of day. Furthermore, the data could be used to examine effects of temperature and prior photosynthesis on respiration more effectively than if measurements were confined to a few dates.

Soybeans, *Glycine max* Merrill. 'Kent' were grown at the South Farm of the Beltsville Agricultural Research Center in open top chambers, as previously described (Bunce and Sicher, 2001). Two chambers were flushed with ambient air, and two were flushed with ambient air to which pure carbon dioxide was added at a rate sufficient to increase the concentration to $350 \pm 50 \ \mu mol \ mol^{-1}$ above that of outside air. The [CO$_2$] of the ambient air averaged 370 $\mu mol \ mol^{-1}$ during the day and 450 $\mu mol \ mol^{-1}$ at night during this study. Soybeans were planted in June of 2000 and 2003 in rows 30 cm apart and thinned to a final density of 25 plants m^{-2}. Net carbon dioxide exchange rate measurements were made on a total of 16 d between July 18 and September 11. All plants were in the flowering to early pod-filling stages, and were producing new leaves throughout the measurement period. Thus all leaves measured were approximately the same age (about 2 weeks from unfolding) and none were senescent.

Net rates of carbon dioxide exchange were recorded every 10 min for 24 h for mature upper canopy leaves for one leaf from each [CO$_2$] treatment on each measurement date. Leaf cuvettes were made of clear acrylic, with water jackets on upper and lower surfaces, and contained a mixing fan. Entire terminal leaflets of mature upper canopy leaves were placed in the cuvettes and sealed around the petiole with caulk. Thermocouples were pressed against the undersides of leaflets to measure temperature, and a quantum sensor was mounted beside the leaflets inside each cuvette. Leaves were held nearly horizontal, and were not shaded by other leaves. Water kept at the temperature of the outside air was circulated through the water jackets of the cuvettes. Each cuvette was used as part of an open gas exchange system. A gas blending system provided air at 370 and 720 $\mu mol \ mol^{-1}$ [CO$_2$] to the two cuvettes. The dew point of air entering the cuvettes was controlled to a few degrees below the expected minimum night temperature in order to prevent condensation in spite of transpiration. Flow rates of air entering the cuvettes were measured using a mass flow meter. The difference in [CO$_2$] between air streams entering and leaving each cuvette and the flow rate entering each cuvette was determined by a differential CO$_2$ analyser (Li-6252, LI-Cor, Lincoln, Nebraska) and a mass flow meter switched sequentially between cuvette airstreams. The airstreams were dried before entering the differential CO$_2$ analyser. The sensitivity of the differential analyser was corrected for the absolute [CO$_2$], which was
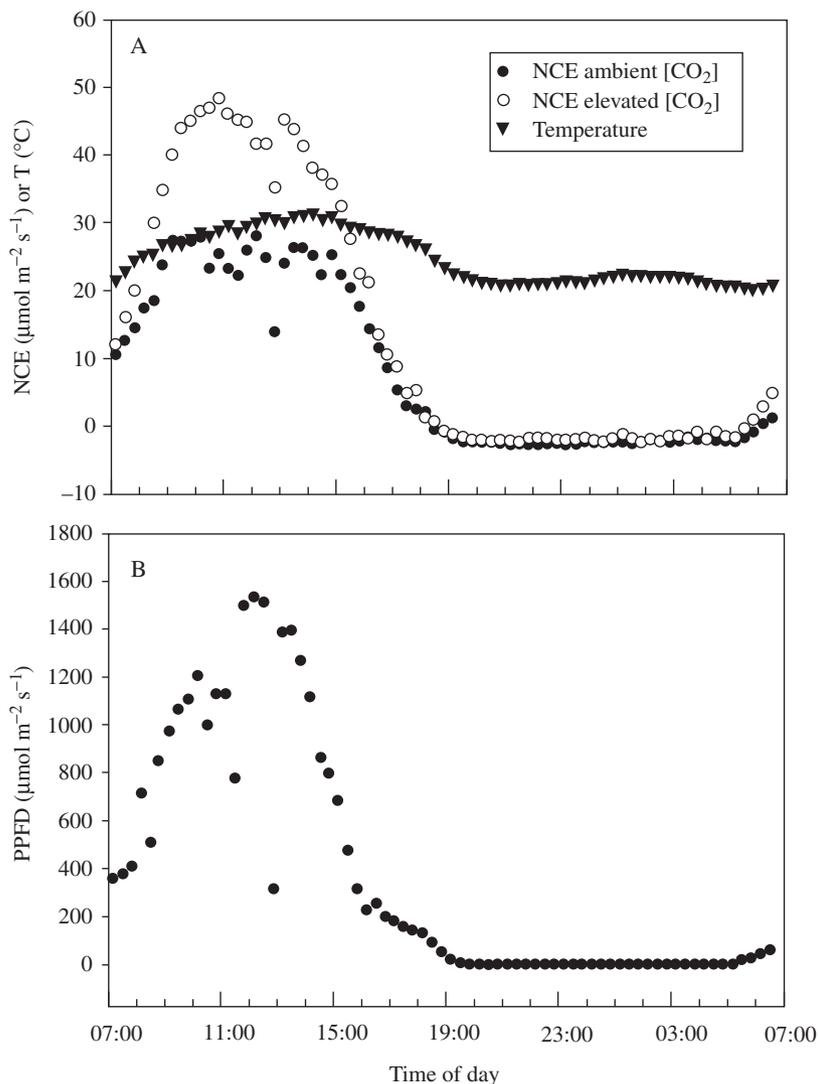
FIG. 1. (A) Rates of net carbon dioxide exchange and leaf temperature, and (B) PPFD for a 24 h period beginning on day 221, 2000, for soybeans leaves grown and measured at ambient and ambient +350 µmol mol^{-1} [CO$_2$]. Leaf temperature and PPFD are averaged across leaves, for clarity.

measured by an absolute CO$_2$ analyser (LI-6252). The zero drift of the differential analyser was automatically checked after each individual measurement, and calibration of the differential analyser at each background [CO$_2$] was checked daily. Similar leaves of randomly selected plants from either of two chambers per [CO$_2$] treatment were placed in the cuvettes early in the morning, and harvested to determine area and dry mass 24 h later. The rate of respiration of each leaf was summed for the entire night. 'Night' was defined as the time when the photosynthetic photon flux density was less than 5 µmol m^{-2} s^{-1}.

Statistical analysis

Using the leaves measured at ambient and elevated [CO$_2$] on the same day, paired *t*-tests were used to test for effects of [CO$_2$] treatment on photosynthesis and respiration rates per unit of leaf area, leaf mass per unit of area, and respiration rates per unit of mass. Linear regressions were used to test for relationships between daily photosynthesis and daily PAR, and between respiration and daily photosynthesis. Linear and exponential regressions were used to test for relationships between respiration and average night-time temperature. Multiple regressions were used to test for effects of daily photosynthesis on respiration after accounting for the response of respiration to temperature. Separate regressions were developed for the two [CO$_2$] treatments. When significant correlations between physiological parameters and environmental factors occurred, analysis of covariance was used to test for [CO$_2$] effects, using the environmental factor as a covariable. Statistical tests were implemented using JMP v. 5, SAS Institute, Cary, NC.

RESULTS

A typical daily pattern of net carbon dioxide exchange rate (NCE) is shown in Fig. 1 for a mostly clear day. Most of the

TABLE 1. *Mean values and ranges of daily photosynthesis and respiration of soybean leaves grown and measured at ambient and elevated [CO_2]*

Variable	Ambient		+350 μmol mol^{-1}		
	Mean	Range	Mean	Range	Probability
Photosynthesis per area (mmol m^{-2} d^{-1})	745	34–1310	1103	45–1670	0·001
Respiration per area (mmol m^{-2} d^{-1})	53	22–87	53	23–75	0·751
Respiration per mass (mmol g^{-1} d^{-1})	1·55	0·63–2·81	1·25	0·51–2·24	0·002

Means are for 24 h measurements on 16 days over two years, with a pair of leaves measured at both [CO_2] on a given day. Ranges indicate day-to-day differences in average values. 'Probability' is the probability of obtaining a larger t-value under the hypothesis of no [CO_2] treatment effect, using paired t-tests.
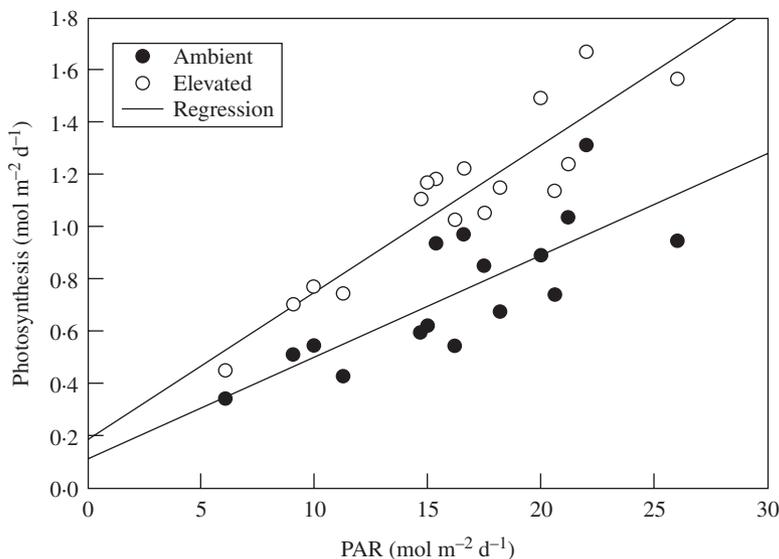

FIG. 2. Relationships between daily integrals of photosynthesis and the integral of photosynthetically active radiation on different measurement dates, for leaves of soybean grown and measured at ambient and ambient +350 μmol mol^{-1} [CO_2]. Linear regressions are shown for each [CO_2] treatment, and had r^2 values of 0·62 and 0·84 for ambient and elevated [CO_2], respectively.

scatter in NCE is in the daytime, and is related to intermittent cloudiness. NCE was higher at elevated [CO_2] throughout the daytime, although the difference was much less at low than at high PPFD. Averaged over all 16 measurement days, the elevated [CO_2] increased daytime NCE per unit of leaf area by an average of 48 % (Table 1). Daily photosynthesis per unit of area increased linearly with daily PAR for both [CO_2] treatments, and was greater at elevated [CO_2] at all values of daily PAR (Fig. 2). Respiration expressed per unit of area did not differ significantly between [CO_2] treatments (Table 1). Because leaf dry mass per unit of area was increased by an average of 23 % by elevated [CO_2], from 34 to 42 g m^{-2}, respiration per unit of mass was significantly lower at elevated [CO_2] (Table 1). There was no significant correlation between respiration and daily photosynthesis at either [CO_2] (not shown).

Respiration increased with average night temperature, increasing by a factor of 2·5 between 18 and 26 °C for both carbon dioxide treatments (Fig. 3). Exponential and linear regressions gave nearly the same r^2 values (Fig. 3), with higher r^2 values for respiration rates per unit of mass than for rates per unit of area. Analysis of covariance using temperature as a covariable indicated significantly lower

respiration per unit of mass at elevated [CO_2] (not shown) as did the paired t-test (Table 1), with no differences for respiration rates per unit of area.

Seasonal patterns of mean daily temperature are shown in Fig. 4, with the dates of NCE measurement indicated. Three of the measurement dates (day of year 214 and 221 in 2000 and day of year 218 in 2003) followed at least two days when mean temperatures were consistently substantially above average, and three measurement dates (day of year 208 and 234 in 2000 and day of year 255 in 2003) followed lower than normal temperatures (Fig. 4). These measurement dates were examined for evidence of acclimation of respiration to temperature by determining whether respiration rates on those dates were consistently higher or lower than predicted by linear regressions relating respiration to temperature with those six dates excluded. If warmer temperatures resulted in acclimation of respiration to a lower rate for a given temperature, then respiration rates measured after above average temperatures would be lower than predicted from the regression. Similarly, exposure to cooler temperatures for a few days would result in respiration rates higher than predicted from the regression. This did not occur for either the higher or lower temperatures, for
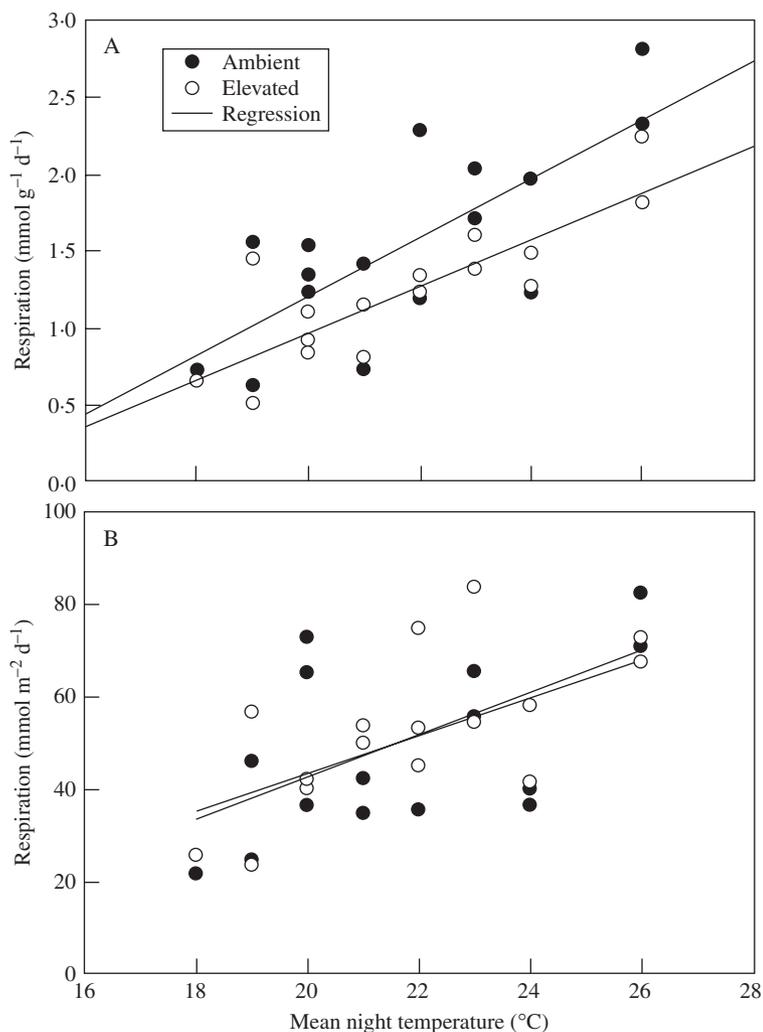
FIG. 3. Relationships between daily integrals of respiration per unit of mass (A) and per unit of area (B), and mean night-time temperature on different measurement dates, for soybeans leaves grown and measured at ambient and ambient +350 μmol mol^{-1} [CO$_2$]. For respiration rates per unit of mass, linear regressions had r^2 values of 0·57 and 0·69 for ambient and elevated [CO$_2$], respectively, and exponential relationships had r^2 values of 0·59 and 0·68 for ambient and elevated [CO$_2$], respectively. For respiration rates per unit of area, linear regressions had r^2 values of 0·27 and 0·50 for ambient and elevated [CO$_2$], respectively, and exponential relationships had r^2 values of 0·27 and 0·51, respectively.

either [CO2] treatment, as rates for those dates were nearly identical to the rates predicted by the regressions, which excluded those dates (Table 2).

Despite 2·5 fold ranges in daily photosynthesis between days for both carbon dioxide regimes, caused by cloudiness, multiple regression did not detect significant relationships (at $P = 0·05$) between daily photosynthesis and respiration expressed per unit of mass (Table 3) or per unit of area (not shown) for either carbon dioxide treatment, when temperature was also included in the regression.

DISCUSSION

The equal rates of respiration per unit of area and lower rates per unit of mass for plants grown and measured at elevated [CO$_2$] in this study are in agreement with one study of soybean leaf respiration in controlled environment chambers (Griffin *et al*., 2001*b*). Two other studies have found lower rates per unit of area at elevated [CO$_2$] (Bunce, 1995; Griffin *et al*., 1999) and one found higher rates (Thomas and Griffin, 1994). Rates per unit of mass have either been lower or not different at elevated [CO$_2$] in these studies. The lack of higher rates of respiration per unit of area at elevated [CO$_2$] in this study contradicts the hypothesis that higher photosynthetic rates would increase respiration by increasing translocation rates, or by providing more non-structural carbohydrates as substrates for respiration. Of these, only higher photosynthesis was actually measured in this study, but increased photosynthesis must result in either more rapid translocation of carbohydrates or an increased content of carbohydrates, or both. It is conceivable that more rapid translocation at elevated [CO$_2$] occurred during the day but not at night. However, this seems unlikely, because both Grimmer and Komor (1999) and Grodzinski *et al*. (1998) found that elevated [CO$_2$]
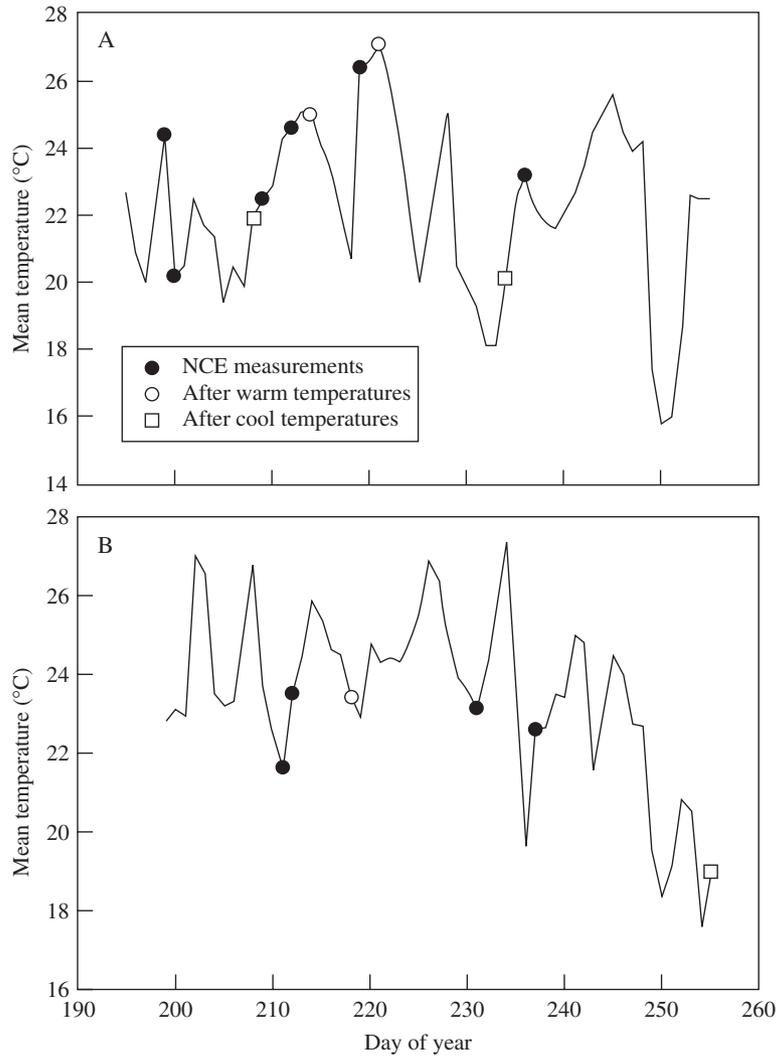
FIG. 4. Mean daily air temperatures for (A) 2000 and (B) 2003 at the South Farm of the Beltsville Agricultural Research Center, Beltsville, Maryland. Symbols indicate dates when leaf net carbon dioxide exchange was measured. Measurement dates when previous temperatures had been warmer or cooler than average are indicated by special symbols.

TABLE 2. *Respiration of soybeans leaves grown and measured at ambient and ambient +350 μmol mol^{-1} [CO_2] for six measurement dates which followed at least two days when mean temperatures were consistently substantially above or below average*

Following higher than average temperatures				Following lower than average temperatures			
Ambient [CO_2]		Elevated [CO_2]		Ambient [CO_2]		Elevated [CO_2]	
Actual	Predicted	Actual	Predicted	Actual	Predicted	Actual	Predicted
1·74	1·82	1·37	1·43	1·13	1·13	0·93	0·94

Actual rates were compared with rates predicted from the regressions relating respiration to temperature with the data for those six dates excluded. Each value is a mean for three measurement dates identified in the text. All values are mmol g^{-1} d^{-1}.

did not increase daytime translocation rates in C_3 species. Furthermore, elevated [CO_2] increased daytime starch and sucrose per unit of area by 86 % and 67 %, respectively, in another study using the same variety of soybeans in the same location (Bunce and Sicher, 2001).

A compensating reduction in maintenance respiration in leaves grown at elevated [CO_2] would be a possible explanation for the lack increase in respiration despite increased photosynthesis. Lower maintenance respiration at elevated [CO_2] has been suggested by a few other studies.

TABLE 3. *Multiple linear regressions relating respiration rate per unit of mass to temperature and photosynthesis of the previous day for soybean leaves grown and measured at ambient and ambient +350 μmol mol^{-1} [CO_2]*

Parameter	Ambient		Ambient + 350 μmol mol^{-1}	
	Coefficient	Probability	Coefficient	Probability
Intercept	-2.52 ± 1.10	0.039	-1.76 ± 0.61	0.017
Temperature	0.182 ± 0.061	0.011	0.119 ± 0.035	0.004
Photosynthesis	0.139 ± 0.573	0.812	0.358 ± 0.262	0.195

In some cases lower maintenance respiration in leaves grown at elevated [CO_2] could be attributed to lower protein content (e.g. Baker *et al*., 1992; Wullschleger *et al*., 1992; Drake *et al*., 1996; Kellomaki and Wang, 1998), but in other cases [CO_2] treatment effects on leaf protein content were either non-existent or insufficient to explain the observed lower respiration rates (e.g. Bunce, 1995; Jach and Ceulemans, 2000; Griffin *et al*., 2001*a*). In the present study it is unlikely that growth at elevated [CO_2] affected nitrogen content, because previous studies with this variety of soybean under similar conditions found no reduction in chlorophyll, ribulose bisphosphate carboxylase, or soluble protein per unit of area at elevated [CO_2] (Bunce and Sicher, 2001). Bunce (1995) and Griffin *et al*. (2001*b*) suggested that more mitochondrial respiration and maintenance processes might be shifted to the light period at elevated [CO_2]. However, because recent work has questioned the interpretation of estimates of daytime respiration (Pinelli and Loreto, 2003), this question is difficult to address experimentally. Clearly, growth at elevated [CO_2] reduced respiration in these mature soybean leaves compared with our expectations based on current understanding of respiration.

In this study, there was no detectable effect on respiration rates of even the 2·5 fold range of daily photosynthesis caused by cloudiness. Whitehead *et al*. (2004) found a dependence of respiration on daily photosynthesis in oak when comparing fully exposed upper canopy leaves with leaves deliberately shaded or lower in the canopy, but such a relationship was not evident for day-to-day variation in daily photosynthesis among fully exposed upper leaves. Thus, even within a [CO_2] treatment, relationships between respiration and daily photosynthesis are not always evident. When large changes in daily photosynthesis due to cloudiness have no detectable effect on respiration rates, perhaps it is not surprising that the smaller changes in photosynthesis caused by the elevated [CO_2] treatment also did not increase respiration.

The results indicating a large response of respiration rate averaged over the night to the mean temperature of the night do not support the idea that acclimation of respiration to temperature would be rapid enough to make dark respiration insensitive to variation in temperature between nights. In fact, the 2·5 fold change in respiration for the 8 °C range in mean night-time temperatures is at least as large as that typically observed for short-term temperature changes (reviewed in Tjolker *et al*., 2001). Neither the rate of acclimation of respiration to temperature, nor the signal controlling acclimation (e.g. night-time temperature, daily mean temperature, carbohydrate status or demand for respiration) is known for soybean, or for any species. The observed response of respiration to night temperature might indicate either a slow rate of acclimation or an inconsistent environmental cue. The latter is quite likely, because, at this time of year in this climate, there is often little correlation between the mean temperature of a given night and the temperature of the preceding day. In this data set, for example, the mean temperature of a given night was correlated with the prior 24 h mean temperature, and with the prior night temperature, with r^2 values of less than 0·25. However, even in examining days proceeded by at least two days with temperatures consistently above or below average, there was no evidence of acclimation of respiration to temperature. It is also possible that soybean has only limited potential for acclimation of respiration to temperature, since none was found in soybean cotyledons by Gonzalez-Meler *et al*. (1999). Possibly, acclimation of respiration to temperature in soybean is slower than in trees (Bolstad *et al*., 1993). For whatever reason, night-to-night variation in mean temperature strongly affected respiration rates of mature soybean leaves in the field.

In summary, the hypothesis that respiration rates would be increased by growth at elevated [CO_2], and the hypothesis that rates would be independent of night-time temperature were both rejected. The results for soybean were consistent with the generalization developed for woody species that growth at elevated [CO_2] does not affect leaf respiration rates per unit of area, but decreases respiration per unit of leaf mass by about 20 % (Curtis and Wang, 1998), in spite of increased photosynthesis. No influence of day-to-day variation in light or daily photosynthesis on respiration was detected, and respiration did not acclimate to variation in mean night temperature.

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