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Responses of Respiration to Increases in Carbon Dioxide Concentration and Temperature in Three Soybean Cultivars

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The purpose of this experiment was to determine how respiration of soybeans may respond to potential increases in atmospheric carbon dioxide concentration and growth temperature. Three cultivars of soybeans (*Glycine max* L. Merr.), from maturity groups 00, IV, and VIII, were grown at 370, 555 and 740 $cm^3 m^{-3}$ carbon dioxide concentrations at 20/15, 25/20, and 31/26 °C day/night temperatures. Rates of carbon dioxide efflux in the dark were measured for whole plants several times during exponential growth. These measurements were made at the night temperature and the carbon dioxide concentration at which the plants were grown. For the lowest and highest temperature treatments, the short term response of respiration rate to measurement at the three growth carbon dioxide concentrations was also determined. Elemental analysis of the tissue was used to estimate the growth conversion efficiency. This was combined with the observed relative growth rates to estimate growth respiration. Maintenance respiration was estimated as the difference between growth respiration and total respiration. Respiration rates were generally sensitive to short term changes in the measurement carbon dioxide concentration for plants grown at the lowest, but not the highest carbon dioxide concentration. At all temperatures, growth at elevated carbon dioxide concentrations decreased total respiration measured at the growth concentration, with no significant differences among cultivars. Total respiration increased very little with increasing growth temperature, despite an increase in relative growth rate. Growth respiration was not affected by carbon dioxide treatment at any temperature, but increased with temperature because of the increase in relative growth rate. Values calculated for maintenance respiration decreased with increasing carbon dioxide concentration and also decreased with increasing temperature. Calculated values of maintenance respiration were sometimes zero or negative at the warmer temperatures. This suggests that respiration rates measured in the dark may not have reflected average 24-h rates of energy use. The results indicate that increasing atmospheric carbon dioxide concentration may reduce respiration in soybeans, and respiration may be insensitive to climate warming.

Key words: *Glycine max* L. (Merr.), carbon dioxide, respiration, temperature, climate change.

INTRODUCTION

Much of the research on plant responses to global change factors such as atmospheric carbon dioxide concentration and temperature has focused on responses of photosynthesis. Because respiration is a large component of plant carbon balance, reliable predictions of how plant growth may be affected by changes in atmospheric carbon dioxide and climate also require information on the response of respiration. It has long been known that respiration is not simply a constant fraction of photosynthesis (McCree, 1970), and respiration responds to carbon dioxide concentration and temperature quite differently than the response of photosynthesis.

The rate of respiration by plants increases substantially with short-term increases in temperature, often doubling with a 10 °C increase in temperature. This has led some to speculate that higher global temperatures resulting from elevated atmospheric carbon dioxide concentrations would stimulate respiration (e.g. Woodwell *et al.*, 1983). However, this suggestion does not take into account acclimation of respiration to temperature or the response of respiration to carbon dioxide concentration.

Despite a large short-term response of respiration rate to temperature, respiration often acclimates to growth temperature so that respiration rates measured in the growth environment remain constant across a range of growth temperatures (e.g. Rook, 1969; Billings *et al.*, 1971). Temperature acclimation of respiration has been primarily examined in mature leaves, and its relationship to the growth and maintenance model of whole-plant respiration (Amthor, 1989) remains unclear. Analysis of whole plant respiration using the growth and maintenance model has indicated that growth respiration varies with temperature only as relative growth rate varies, but that maintenance respiration increases with increasing growth temperature (McCree and Silsbury, 1978; McCree and Amthor, 1982).

Increasing carbon dioxide concentration can affect respiration rates both directly and indirectly. Direct effects of the carbon dioxide concentration during the measurement on the rate of respiration have been found in several species

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(e.g. Gale, 1982; Bunce, 1990; Amthor, Koch and Bloom, 1992; Ziska and Bunce, 1994), including soybean (Bunce, 1990, 1995; Thomas and Griffin, 1994). Respiration rates generally are lower at elevated carbon dioxide concentrations. Indirect effects of growth carbon dioxide concentration on respiration rate may result from changes in relative growth rate or from changes in tissue composition (Ryan, 1991; Ziska and Bunce, 1994), but they have seldom been separated from direct effects (Bunce, 1995).

While numerous studies have shown increased or decreased rates of respiration in plants grown at elevated carbon dioxide (Poorter *et al*., 1992), the interaction between increased carbon dioxide concentration and increased temperature has received little experimental attention. Ziska and Bunce (1993, 1994) found that respiration of single leaves and whole plants increased with growth temperature both at ambient and elevated carbon dioxide in alfalfa, and at elevated carbon dioxide in orchard grass. In both species, growth at warmer temperatures eliminated the decrease in respiration at elevated carbon dioxide which occurred at cool temperatures. However, these studies did not separate direct and indirect effects of carbon dioxide concentration on respiration for whole plants. In the present paper, we have compared the responses of whole plant respiration to increased carbon dioxide concentration and temperature in three cultivars of soybean adapted to regions differing in temperature regime, examined direct and indirect effects of carbon dioxide on respiration, and separated the effects of carbon dioxide on respiration into the responses of growth and maintenance respiration.

MATERIAL AND METHODS

Experiments were conducted on three soybean cultivars: Maple Glen, Clark and CNS (maturity groups 00, IV and VII, respectively) grown in controlled-environment chambers. The carbon dioxide concentrations were maintained by flushing the chambers with carbon-dioxide-free air and by injecting carbon dioxide. Injection of carbon dioxide was controlled by absolute infrared gas analysers (MSA Instruments, Pittsburgh, PA, USA) attached to each chamber, which sampled air continuously. The set points for carbon dioxide were 370, 555 and 740 $cm^3\ m^{-3}$. Actual carbon dioxide concentrations ($\pm$s.d.) were 373 ± 12, 557 ± 25 and $735 \pm 27\ cm^3\ m^{-3}$. Because only three controlled environment chambers were available, the same experiment was repeated three times at day/night temperatures of 20/15, 25/20 and $31/26 \pm 1$ °C. In all experiments, plants received 14 h of 0·6 $mmol\ m^{-2}\ s^{-1}$ photosynthetic photon flux density (PPFD) from a mixture of incandescent and cool-white fluorescent lamps. At each day/night condition, the dew point temperature was adjusted to maintain a relative humidity $> 50\%$. Temperature and carbon dioxide concentration were recorded every 20 min with a data logger.

Plants were grown one plant per 3·5 l plastic pot, with pots rearranged biweekly to avoid self-shading. Vermiculite was used as the rooting medium to facilitate the harvesting of roots and because it contains no organic carbon. Twenty to 25 pots per cultivar were randomly assigned to each of the three growth chambers. At planting, pots with vermiculite but without plants were also placed in each chamber. All pots were flushed twice daily with a complete nutrient solution. When necessary, plant main stems were supported by staking.

Whole plant gas exchange was determined within a few hours of the end of the dark period at approximately weekly intervals beginning 14–28 days after emergence (DAE; depending on temperature). Whole plants were placed inside a plastic 42 l cylindrical chamber with an internal fan, which was placed inside a controlled environment chamber. Gas exchange of pots without plants was determined first to obtain a baseline value of carbon dioxide efflux. Carbon dioxide uptake was determined using a differential infrared carbon dioxide analyser (Li-Cor 6252, Lincoln, Nebraska, USA) in an open system attached to the cylindrical chamber. Temperature and humidity within the cylindrical chamber were set to match those of the night-time growth conditions. The gas stream entering the cylindrical chamber was humidified by bubbling it through a water bath at a controlled temperature and humidity was monitored by a dew point hygrometer (Hygro M-1, General Eastern Co., Cambridge, Massachusetts, USA). Mass flow controllers were used to mix dry, carbon-dioxide-free air with pure carbon dioxide to obtain the desired carbon dioxide concentration within the cylindrical chamber. The differential carbon dioxide analyser signal was calibrated over a range of background carbon dioxide concentrations to account for changes in sensitivity. For the 20/15 and 31/26 °C temperature treatments, the short term response of respiration rate to the measurement carbon dioxide concentration was also determined by exposing the plants to each of the three growth carbon dioxide concentrations for about 2 h.

The timing of the initial harvest was based on plant size, and was dependent primarily on temperature and to a lesser extent on cultivar. Following the initial harvest, plants were harvested at 7–10 d intervals. Final harvest for all cultivars was determined by the timing of early pod fill in the Maple Glen cultivar (which flowered at all temperatures and carbon dioxide concentrations). The final harvests for all three cultivars at each temperature were approximately 57, 50 and 41 DAE for the day/night temperatures of 20/15, 25/20 and 31/26 °C, respectively. At each harvest, three replicate plants per cultivar, temperature and carbon dioxide concentration were separated into roots, stem, leaves and pods (if any) and oven dried at 65 °C for 48–96 h (depending on sample size). Leaf area was measured with a photoelectric leaf area meter (Li-Cor, Model 3100, Lincoln, Nebraska, USA). Relative growth rate of plants for each treatment was calculated from the slope of the regression of the natural log of total dry mass on time.

Carbon, hydrogen and nitrogen contents of each plant from the final harvest of each treatment (a total of 81) were determined by the State of Maryland Soil Testing Lab. Sulphur and ash contents of a subsample of these plants ($n = 28$) were also determined by the same laboratory. A subsample was used for these two parameters since it was found that the sulphur content was $0{\cdot}0625 \pm 0{\cdot}0011$ times

the nitrogen content, and that the ash content was 13·2 ± 0·17 %, and because growth conversion efficiencies are quite insensitive to this degree of uncertainty in these parameters. Theoretical growth conversion efficiencies were calculated from carbon, hydrogen, nitrogen, sulphur and ash contents using the method of McDermitt and Loomis (1981). The substrates for nitrogen assimilation were assumed to be nitrate and ammonium in the same proportion as in the nutrient solution, 4·4 : 1, respectively.

Effects of carbon dioxide, temperature, cultivar and their interactions on respiration rate measured under the growth conditions were tested using a three-way ANOVA, combining data for four measurement times per treatment. Similar three-way ANOVAs were used to examine variation in elemental composition and calculated growth conversion efficiency based on data from the final harvests. These analyses used data from one chamber run for each carbon dioxide and temperature treatment. However, we repeated the treatments in other chambers and measurements of respiration of three plants at each of two sampling times per treatment per cultivar produced essentially the same results (see Results section).

Total respiration was separated into growth and maintenance components by estimating growth respiration from the growth conversion efficiency and the relative growth rate, and obtaining maintenance respiration from the difference (Bunce, 1995). The assumptions required when using this approach have been detailed by Amthor (1989), and some are discussed later. Growth respiration was calculated from the population relative growth rate for each cultivar for each treatment. In order to obtain a statistical comparison of carbon dioxide and temperature effects, the three cultivars were used as replicates in the analysis of growth and maintenance respiration. There was no significant variation among cultivars in total respiration (see Results). Respiration was measured at the night temperature and total daily respiration was calculated by assuming that the higher day temperature increased respiration exponentially, with a Q_{10} of 2·0 (McCree and Amthor, 1982), for 14 h out of 24.

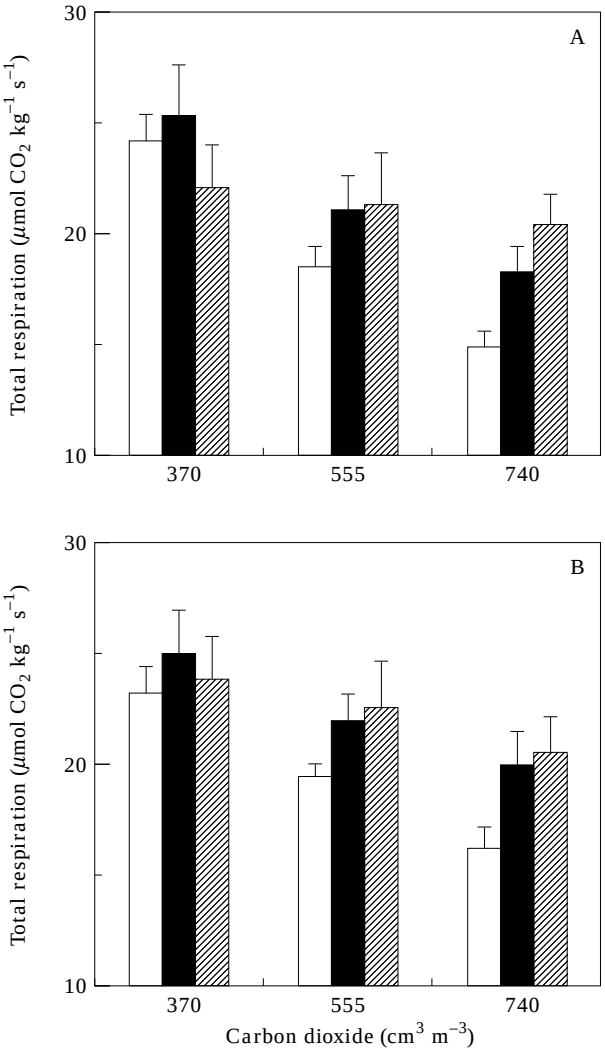

FIG. 1. Whole plant total respiration rate measured at the night-time growth condition, as a function of growth temperature and growth carbon dioxide concentration. Rates are means for three cultivars of soybeans averaged over four measurement times (A), or two measurement times in a repeat experiment using different growth chambers (B). Vertical lines indicate s.e. Growth temperatures: □, 20/15; ■, 25/20; ▨, 31/26 °C.

RESULTS AND DISCUSSION

Total respiration rates measured at the night-time growth conditions decreased with increasing growth carbon dioxide concentration especially at the cooler temperatures (Fig. 1), but there were no overall significant effects of growth temperature, nor were any interaction terms significant (Table 1). Respiration rates in the repeat experiment using different growth chambers were very similar to those in the main experiment (Fig. 1). There were no significant differences among the three cultivars, in spite of significant variation in the response of biomass production to these treatments (Ziska and Bunce, 1995). These results do not support the view that climate warming as atmospheric carbon dioxide concentration rises would increase plant respiration. Possible reasons for this result, as discussed later, are that respiration acclimated to increased growth temperature by reducing maintenance respiration, and that elevated carbon dioxide did not persistently increase relative growth rate but had the direct effect of reducing respiration.

Although not detected as a significant interaction term, the mean values of respiration rate of CNS and Clark were not lower at elevated carbon dioxide at the warmest growth regime. This is similar to the pattern observed in orchard grass and alfalfa (Ziska and Bunce, 1993) under similar treatments, where warm growth conditions eliminated the decrease in respiration caused by growth at elevated carbon dioxide concentrations.

Plant nitrogen content decreased with increasing carbon dioxide concentration and with increasing temperature, and differed among cultivars (Table 2). Carbon and hydrogen content varied relatively less than did nitrogen (statistical analysis not shown). Mean carbon content ranged only from 41·0 to 43·2 % (by dry mass) across all treatments, and

TABLE 1. *Respiration rates of three soybean cultivars grown at three carbon dioxide concentrations and three temperature regimes, and analysis of variance. Respiration rates were measured at the night temperatures and carbon dioxide concentrations. Rates are averages of single measurements on each of three plants at each of four measurement times per treatment for each cultivar*

CO_2 ($cm^3\ m^{-3}$)	Temperature (°C) day/night	Respiration rate (μmol $CO_2\ kg^{-1}\ s^{-1}$)		
		Maple Glen	Clark	CNS
370	20/15	24·3	24·5	23·7
370	25/20	25·6	24·3	26·5
370	31/26	25·0	19·7	21·6
555	20/15	17·2	19·1	19·1
555	25/20	20·0	21·2	21·9
555	31/26	16·5	19·5	28·2
740	20/15	14·5	15·0	15·4
740	25/20	19·1	16·9	18·9
740	31/26	18·1	20·5	22·9

Main effect means:	CO_2		Temperature		Cultivar	
	370	23·9	20/15	19·2	Maple Glen	20·1
	555	20·3	25/20	21·6	Clark	20·1
	740	17·9	31/26	21·3	CNS	22·0

ANOVA:

Source	df	Mean square	*F*-value	*P*-value
CO_2	2	977·9	10·87	0·0001
Temperature	2	187·5	2·08	0·1262
Cultivar	2	137·7	1·53	0·2181
CO_2 × Temperature	4	141·7	1·58	0·1810
CO_2 × Cultivar	4	91·7	1·02	0·3975
Temperature × Cultivar	4	58·6	0·65	0·6266
CO_2 × Temperature × Cultivar	8	55·3	0·62	0·7651
Residual	297	90·0		

hydrogen content ranged from 6·0 to 6·7%. Growth conversion efficiencies calculated from the elemental composition varied with carbon dioxide concentration or among cultivars by only 0·01 compared to the mean value of 0·68, although the differences were statistically significant (Table 3). Similar small effects of growth at elevated carbon dioxide on conversion efficiency have been reported in loblolly pine leaves, using calorimetry (Griffin, Thomas and Strain, 1993). The results indicate that the often reported decrease in nitrogen content of plants grown at elevated carbon dioxide (e.g. Larigauderie, Hilbert and Oechel, 1988; Sage, Sharkey and Seemann, 1989) may not necessarily have a substantial effect on the growth conversion efficiency. Although nitrogenous compounds are energetically expensive to synthesize (Penning de Vries, Brunstig and Van Laar, 1974), the 24% lower nitrogen content of soybean plants at doubled carbon dioxide resulted in only a 1% increase in the growth conversion efficiency in this study. Presumably this reflects compensating changes in other classes of compounds. In fact, the growth conversion efficiency was more closely predicted by carbon content than by nitrogen content in these samples, and carbon content was poorly correlated with nitrogen content (Table 4).

Averaged across cultivars, relative growth rate was not significantly affected by carbon dioxide concentration, and increased at the warmest temperature (Fig. 2). It is common for long-term relative growth rate to be unaffected by carbon dioxide concentration (e.g. Callaway *et al.*, 1994) in spite of an initial increase in relative growth rate and consistently higher biomass. This occurred because elevated carbon dioxide decreased leaf area ratio sufficiently to approximately compensate for increased net assimilation rate (Ziska and Bunce, 1995). The cooler temperatures used were suboptimal for growth of this warm-climate species. This was true for all three cultivars, although CNS, which is grown in warmer climates than the other cultivars, had the largest sensitivity of RGR to temperature (Ziska and Bunce, 1995).

Growth respiration increased at the warmest growth temperature, but there was no significant effect of carbon dioxide concentration (Fig. 3). Changes in growth respiration simply reflected the environmental effects on relative growth rate, because no substantial changes occurred in the growth conversion efficiency. This was expected for the temperature treatments (McCree and Silsbury, 1978; McCree and Amthor, 1982), but elevated carbon dioxide has sometimes been reported to decrease growth respiration (Wullschleger and Norby, 1992; Ziska and Bunce, 1993). However, previous studies estimated growth respiration from regressions of respiration on relative growth rate rather than from elemental composition, as used here.

Maintenance respiration decreased with increasing carbon

TABLE 2. *Nitrogen percentages of whole plants of three soybean cultivars grown at three carbon dioxide concentrations and three temperature regimes, and analysis of variance. Nitrogen contents are averages of three plants per treatment for each cultivar*

CO_2 ($cm^3\ m^{-3}$)	Temperature (°C) day/night	Nitrogen (% dry mass)		
		Maple Glen	Clark	CNS
370	20/15	4·3	5·0	5·6
370	25/20	4·2	5·1	5·1
370	31/26	4·0	3·7	4·0
555	20/15	3·7	3·9	4·5
555	25/20	3·9	4·1	4·3
555	31/26	3·6	3·6	3·8
740	20/15	2·9	3·1	4·0
740	25/20	3·9	3·6	4·1
740	31/26	3·9	2·9	3·5

Main effect means:	CO_2		Temperature		Cultivar	
	370	4·6	20/15	4·1	Maple Glen	3·8
	555	3·9	25/20	4·2	Clark	3·9
	740	3·5	31/26	3·7	CNS	4·3

ANOVA:

Source	df	Mean square	*F*-value	*P*-value
CO_2	2	5·103	35·79	0·0001
Temperature	2	14·439	101·20	0·0001
Cultivar	2	3·751	26·31	0·0001
CO_2 × Temperature	4	3·250	11·40	0·0001
CO_2 × Cultivar	4	3·399	11·92	0·0001
Temperature × Cultivar	4	1·576	5·53	0·0008
CO_2 × Temperature × Cultivar	8	0·797	1·40	0·2190
Residual	54	3·850		

TABLE 3. *Growth conversion efficiencies of three soybean cultivars grown at three carbon dioxide concentrations and three temperature regimes, and analysis of variance. Values were obtained from elemental analysis of tissue samples, and are averages of three plants per treatment for each cultivar*

CO_2 ($cm^3\ m^{-3}$)	Temperature (°C) day/night	Conversion efficiency		
		Maple Glen	Clark	CNS
370	20/15	0·702	0·696	0·704
370	25/20	0·661	0·651	0·652
370	31/26	0·699	0·719	0·685
555	20/15	0·691	0·701	0·695
555	25/20	0·665	0·676	0·658
555	31/26	0·689	0·689	0·678
740	20/15	0·717	0·711	0·686
740	25/20	0·680	0·684	0·668
740	31/26	0·678	0·711	0·700

Main effect means:	CO_2		Temperature		Cultivar	
	370	0·685	20/15	0·700	Maple Glen	0·687
	555	0·682	25/20	0·666	Clark	0·693
	740	0·693	31/26	0·694	CNS	0·681

ANOVA:

Source	df	Mean square	*F*-value	*P*-value
CO_2	2	0·000802	9·060	0·0004
Temperature	2	0·008996	101·646	0·0001
Cultivar	2	0·001027	11·610	0·0001
CO_2 × Temperature	4	0·000577	6·519	0·0002
CO_2 × Cultivar	4	0·0000686	0·775	0·5462
Temperature × Cultivar	4	0·000223	2·513	0·0521
CO_2 × Temperature × Cultivar	8	0·000426	4·809	0·0002
Residual	54	0·0000885		

TABLE 4. *Regressions between growth conversion efficiency and nitrogen and carbon contents, and between nitrogen and carbon contents for whole plant tissue samples of three cultivars of soybeans grown at three carbon dioxide concentrations and three temperature regimes.* (n = *81 for each regression*)

Variables					
Dependent	Independent	Intercept (±s.e.)	Slope (±s.e.)	RMS residual	r^2
Efficiency	% nitrogen	0·743 (0·012)	−0·014 (0.003)	0·018	0·213
Efficiency	% carbon	1·875 (0·044)	−0·028 (0·001)	0·006	0·901
% nitrogen	% carbon	−5·925 (4·501)	0·236 (0·107)	0·657	0·058

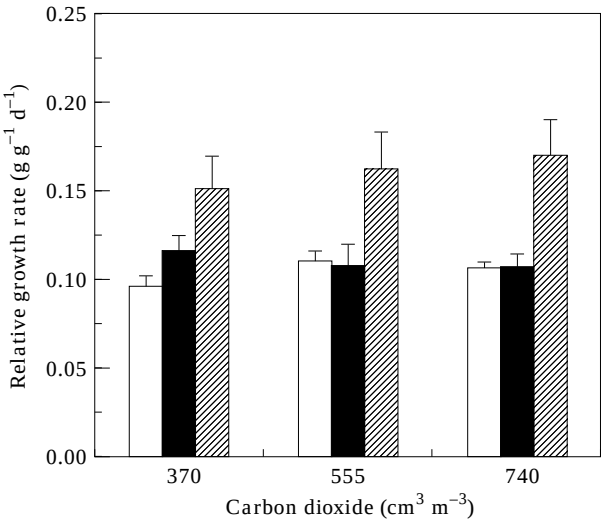

FIG. 2. Relative growth rate as a function of growth temperature and growth carbon dioxide concentration. Rates are means for three cultivars of soybeans. Vertical lines indicate s.e. The effect of temperature was significant ($P = 0·0001$); the effect of carbon dioxide was not significant ($P = 0·7430$). Growth temperatures: □, 20/15; ■, 25/20; ▨, 31/26 °C.

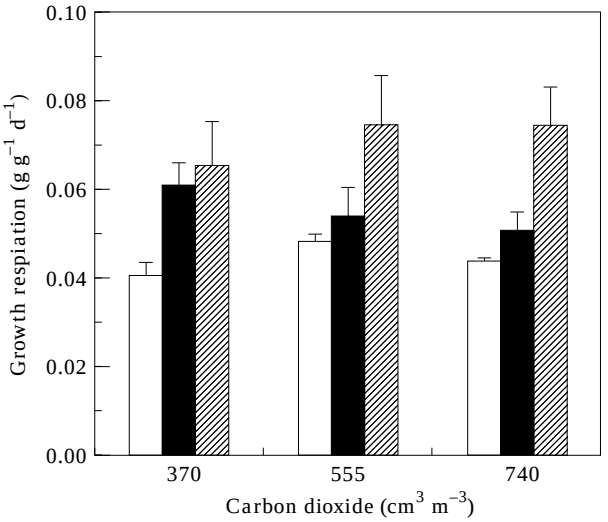

FIG. 3. Growth respiration rate as a function of growth temperature and growth carbon dioxide concentration. Rates are means for three cultivars of soybeans averaged over four measurement times. Vertical lines indicate s.e. The effect of temperature was significant ($P = 0·0004$); the effect of carbon dioxide was not significant ($P = 0·7984$). Growth temperatures: □, 20/15; ■, 25/20; ▨, 31/26 °C.

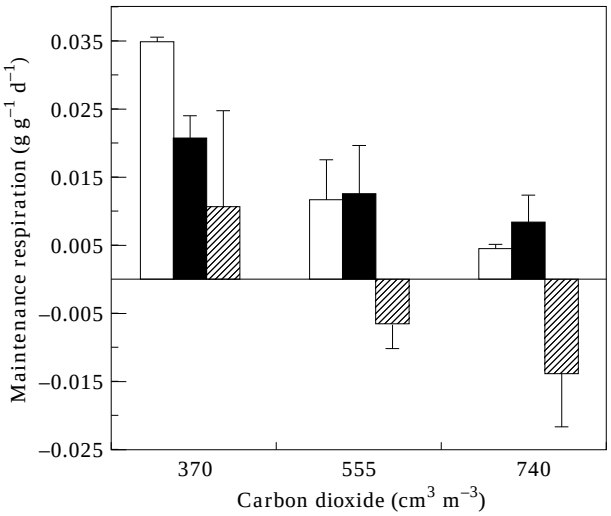

FIG. 4. Maintenance respiration rate as a function of growth temperature and growth carbon dioxide concentration. Rates are means for three cultivars of soybeans averaged over four measurement times. Vertical lines indicate s.e. The effect of temperature was significant ($P = 0·0027$) and the effect of carbon dioxide was also significant ($P = 0·0014$). Growth temperatures: □, 20/15; ■, 25/20; ▨, 31/26 °C.

dioxide concentration, and decreased at the warmest temperature (Fig. 4). Decreases in maintenance respiration with increasing carbon dioxide concentration have been reported for soybean leaves (Bunce, 1995) using the same techniques as used here, and for other species, using other techniques (e.g. Bunce and Caulfield, 1991; Wullschleger and Norby, 1992; Wullschleger, Norby and Gunderson, 1992; Ziska and Bunce, 1993).

Negative calculated values of maintenance respiration at elevated carbon dioxide, as sometimes found here, also occurred in soybean leaves (Bunce, 1995) in spite of the fact that respiration was measured for the whole dark period and there was no day/night temperature change in that study. Thus it is unlikely that the assumed short-term temperature response or sampling of respiration near the end of the dark period in this study caused the negative values. If the plants were preferentially using ammonium as the nitrogen substrate, the growth conversion efficiencies would be higher than assumed here, and calculated values of maintenance respiration would be higher. However, to eliminate negative values of maintenance respiration it would need to be assumed that the plants were assimilating no nitrate despite its predominance in the nutrient solution.

TABLE 5. *Respiration rate relative to the rate at 370 cm^3 m^{-3} carbon dioxide concentration for soybeans grown at three carbon dioxide concentrations and two temperature regimes. Responses are the means of three plants per cultivar per growth condition.* * *Indicates a significant effect* ($P = 0.05$) *of measurement carbon dioxide concentration on respiration rate using analysis of variance on absolute values of respiration rates*

Growth CO_2 (cm^3 m^{-3})	Temperature (°C) day/night	Cultivar	Respiration (relative values)	
			Measurement CO_2 (cm^3 m^{-3})	
			555	740
370	20/15	Maple Glen	0·79	0·71*
555	20/15	Maple Glen	0·94	0·88*
740	20/15	Maple Glen	1·00	1·00
370	20/15	Clark	0·84	0·81*
555	20/15	Clark	0·94	0·72*
740	20/15	Clark	0·92	0·89
370	20/15	CNS	0·90	0·84*
555	20/15	CNS	0·87	0·80*
740	20/15	CNS	0·84	0·81
370	31/26	Maple Glen	0·89	0·80*
555	31/26	Maple Glen	0·86	0·79*
740	31/26	Maple Glen	0·89	0·84
370	31/26	Clark	0·58	0·56*
555	31/26	Clark	0·78	0·85*
740	31/26	Clark	1·02	1·10
370	31/26	CNS	0·71	0·62*
555	31/26	CNS	0·81	0·64*
740	31/26	CNS	0·95	0·99

This would still leave the unreasonable result of zero maintenance respiration in some samples. Negative values of calculated maintenance respiration were taken to indicate that respiration measured at night underestimated the average 24-h rate of energy expenditure in growth and maintenance processes (Bunce, 1995). This could occur if growth and maintenance processes were more rapid in the light than in the dark. It is possible for photochemical energy to substitute for energy derived from respiration (Raven, 1976), for example in nitrate reduction (Johnson, 1990). Surplus photochemical energy is suggested by the apparent suppression of mitochondrial respiration in the light (e.g. Brooks and Farquhar, 1985; Villar, Held and Merino, 1994). Availability of photochemical energy might be greater at elevated carbon dioxide because of the suppression of photorespiration and subsequent conservation of photochemical energy, and therefore elevated carbon dioxide could increase the discrepancy between respiration measured at night and the average rate of growth and maintenance processes.

The decrease in maintenance respiration at the warmest growth temperature was unexpected, based on the increase with temperature observed in other species (McCree and Silsbury, 1978; McCree and Amthor, 1982), and the idea that maintenance costs such as protein turnover might be expected to increase with temperature. Additionally, maintenance respiration has sometimes been found to increase with relative growth rate (McCree, 1982; Bunce, 1989), and relative growth rate increased at the warmest temperature in these experiments. The decrease in maintenance respiration with temperature in these experiments caused total respiration to be essentially the same at all growth temperatures, i.e. it resulted in nearly complete acclimation of respiration to temperature. Similar complete acclimation of respiration rate to growth temperature was also found in orchard grass plants grown at ambient carbon dioxide (Ziska and Bunce, 1993).

Respiration consistently decreased with short-term increase in measurement carbon dioxide concentration in plants grown at the lower two carbon dioxide concentrations, but usually did not change significantly with measurement concentration in the plants grown at the highest concentration (Table 5). Similar differential sensitivity depending on growth carbon dioxide concentration occurred in amaranth (Bunce, 1990) and soybeans (Bunce, 1990; Thomas and Griffin, 1994), and alfalfa and orchard grass leaves (Ziska and Bunce, 1994). Azconbieto *et al.* (1994) found that long-term exposure to elevated carbon dioxide decreased the activity of cytochrome-c oxidase in some species. We speculate that the smaller increase in respiration rate, when the measurement carbon dioxide concentration is reduced below the growth concentration in plants grown at elevated carbon dioxide, may result from insufficient respiratory machinery as a result of acclimation to elevated carbon dioxide.

CONCLUSIONS

Our data indicate that long-term growth at elevated carbon dioxide reduced maintenance respiration of soybeans, probably by persistence of the direct effect of carbon dioxide concentration on respiration, rather than by change in

composition. Warmer growth temperatures did not increase specific respiration rate, because maintenance respiration decreased enough to compensate for the increase in growth respiration caused by increased relative growth rate. These data suggest that long-term stimulation of carbon uptake as carbon dioxide concentration rises may not necessarily be limited by increased respiration as temperature increases.

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