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The influence of increasing growth temperature and CO_2 concentration on the ratio of respiration to photosynthesis in soybean seedlings

LEWIS H. ZISKA and JAMES A. BUNCE
Climate Stress Laboratory, USDA-ARS, Bldg 046 A, 10300 Baltimore Avenue, Beltsville, MD 20705, USA.

Abstract

Using controlled environmental growth chambers, whole plants of soybean, cv. 'Clark', were examined during early development (7–20 days after sowing) at both ambient ($\approx$ 350 μL L^{-1}) and elevated ($\approx$ 700 μL L^{-1}) carbon dioxide and a range of air temperatures (20, 25, 30, and 35 °C) to determine if future climatic change (temperature or CO_2 concentration) could alter the ratio of carbon lost by dark respiration to that gained via photosynthesis. Although whole-plant respiration increased with short-term increases in the measurement temperature, respiration acclimated to increasing growth temperature. Respiration, on a dry weight basis, was either unchanged or lower for the elevated CO_2 grown plants, relative to ambient CO_2 concentration, over the range of growth temperatures. Levels of both starch and sucrose increased with elevated CO_2 concentration, but no interaction between CO_2 and growth temperature was observed. Relative growth rate increased with elevated CO_2 concentration up to a growth temperature of 35 °C. The ratio of respiration to photosynthesis rate over a 24-h period during early development was not altered over the growth temperatures (20–35 °C) and was consistently less at the elevated relative to the ambient CO_2 concentration. The current experiment does not support the proposition that global increases in carbon dioxide and temperature will increase the ratio of respiration to photosynthesis; rather, the data suggest that some plant species may continue to act as a sink for carbon even if carbon dioxide and temperature increase simultaneously.

Keywords: acclimation, elevated CO_2, respiration, R:P ratio, soybean, temperature

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Introduction

As atmospheric carbon dioxide and other anthropogenic trace gases increase, many global climate change models (GCMs) predict an increase in average surface temperature of 2–5 °C (See Houghton *et al.* 1996). For whole plant or canopy gas exchange, it has been theorized that autotrophic respiration (R, carbon loss) will be more sensitive to temperature than photosynthesis (P, carbon gain) with a subsequent reduction in carbon use efficiency (i.e. net carbon gain: gross carbon input) (Woodwell *et al.* 1983, Houghton & Woodwell 1989, Woodwell 1990, Ryan 1991).

However, the concept that plant respiration is highly temperature dependent is primarily based on short-term responses of plants (typically single leaves) to changes in the measurement temperature (see Gifford 1994 for a review). In a number of plant species, the increase in respiration observed when temperature is increased may be lost completely with acclimation (Rook 1969; Larigauderie & Korner 1995). In a study of seven diverse species for example, including two evergreen trees, Gifford (1994) demonstrated a $\approx$ 50% reduction in the sensitivity of respiration with growth temperature compared to measurement temperature.

In addition, there have been a number of studies (reviewed by Wullschleger *et al.* 1994) which demonstrate that elevated [CO_2] can alter respiration independently of photosynthesis. While some studies do show that elevated [CO_2] can stimulate respiration, an increasing number of investigations demonstrate an inhibition of leaf

Correspondence: Dr Lewis H. Ziska,
e-mail lziska@asrr.arsusda.gov, fax +1/301-504-6626

or whole plant respiration by elevated CO_2 concentrations (reviewed by Wullschleger *et al.* 1994). Since growth and photosynthesis are typically stimulated by elevated [CO_2], the overall effect of reduced respiration would be to further increase carbon use efficiency.

Although both temperature and carbon dioxide can alter respiration and are expected to increase concurrently, few studies have examined the interaction of both environmental parameters. Previous work with two herbaceous perennials, *Medicago sativa* and *Dactylus glomerata* as well as soybean (*Glycine max*) indicated a significant reduction in night-time respiration, primarily maintenance respiration, at the elevated (700 μL L^{-1}) CO_2 concentration and lower growth temperatures (15, 20 °C) used in these studies (Ziska & Bunce 1993; Bunce & Ziska 1996). However, none of these studies examined the effect of increasing CO_2 concentration and temperature on the ratio of respiration to photosynthesis. In the current experiment, our principle objective was to test the general question of whether the ratio of respiration to photosynthesis is affected by potential changes in growth temperature and CO_2 concentration using soybean as a test case. CO_2 and/or temperature induced modification in the ratio of R:P could alter the whole plant carbon balance and productivity of crop and native species with global climate change.

Materials and methods

Experiments were performed using controlled environment chambers located at the Climate Stress Laboratory, USDA-ARS, Beltsville, Maryland using soybean (*Glycine max*, cv 'Clark', maturity group IV). Seed for Clark was obtained from the USDA soybean germplasm collection in Urbana, Illinois.

For each controlled environment chamber (EGC, Chagrin Falls, Ohio), the carbon dioxide concentration was controlled by continuous flushing with CO_2 free-air, then re-injecting CO_2 to maintain the desired CO_2 concentration. Injection of CO_2 was controlled by an absolute infrared gas analyser (WMA-2, PP Systems, Haverhill, Mass.) which sampled air continuously. The set points for [CO_2] were 350 (ambient) and 700 μL L^{-1} (elevated). Actual CO_2 concentrations for an average 24 period were 356 + 13 and 699 + 2 μL L^{-1}. Since only one pair of chambers was available, the same experiment was repeated four times at constant day/night temperatures of 20, 25, 30 and 35 °C + 0.5 °C. To determine the effect of short-term changes in temperature on whole plant respiration, the 25 °C experiment was repeated with the ambient and elevated [CO_2] grown plants exposed to temperatures from 15 to 35 °C at approximate 5 °C intervals for a 2-hour period over 2 consecutive nights. Only data from the last hour of a given measurement temperature were used to determine the short-term response. In all experiments, plants received 14 h of 1.0 mmol m^{-2} s^{-1} photosynthetic photon flux (PPF) from a mixture of high pressure sodium and metal halide lamps. At temperatures between 20 and 35 °C, average daily relative humidity (RH) exceeded 60% (≈ 65%). Temperature, CO_2 concentration and relative humidity were monitored and recorded at one minute intervals by a EGC network datalogger (EGC Corp. Chagrin Falls, Ohio) in conjunction with a PC.

Two to three seeds were sown in 15-cm diameter plastic pots filled with 1.8 dm^3 of vermiculite. All pots were thinned to one seedling within 2–3 days following emergence. For each experiment at a given growth temperature, 20–25 pots were assigned to each CO_2 treatment. Pots were arranged to avoid mutual-shading. All pots were watered daily (twice daily at the 35 °C growth temperature) with complete nutrient solution.

Initiation of 24-h whole plant gas exchange for each experiment began at the same physiological stage with the unfolding of the first trifoliate. Age at this physiological stage differed depending on growth temperature and CO_2 concentration. To determine daily rates of gas exchange (i.e. both light and dark periods), whole plants, including pots, roots and vermiculite, were placed inside one of two ≈ 5 L mylar measurement chambers held at the respective growth temperature. Air of the same carbon dioxide concentration used during growth was obtained by mixing CO_2 free-air with pure carbon dioxide before passing through each measurement chamber. The air stream was humidified by bubbling through a water filled container to achieve RH values > 60%. Humidity, light and temperature within the smaller measurement chamber were set to match those of the entire growth chamber. Carbon dioxide efflux from pots maintained under treatment conditions but which contained no plants was checked at a given growth temperature prior to measurement of whole plant respiration to determine possible microbial respiration as described by Ziska & Bunce (1993). Low rates of CO_2 efflux, relative to the whole plant, were observed each time and were subtracted from the CO_2 efflux rate of plants with pots. A differential infrared carbon dioxide analyser (Li-Cor 6252, Lincoln, NE, USA) measured the net carbon dioxide exchange rate over a 7–9-day period across each of the smaller measurement chambers. The sensitivity of the analyser was corrected for the background carbon dioxide concentration. Data for chamber temperature, flow rate and CO_2 concentration were recorded using a micrologger (21X, Campbell Scientific, Logan, UT, USA) at 5 minute intervals.

At approximate 48 h intervals during the 7–9-day period, the two measured plants and 3–4 additional nonmeasured plants were harvested (0800–1000 hours) and a new set of plants placed within the measurement

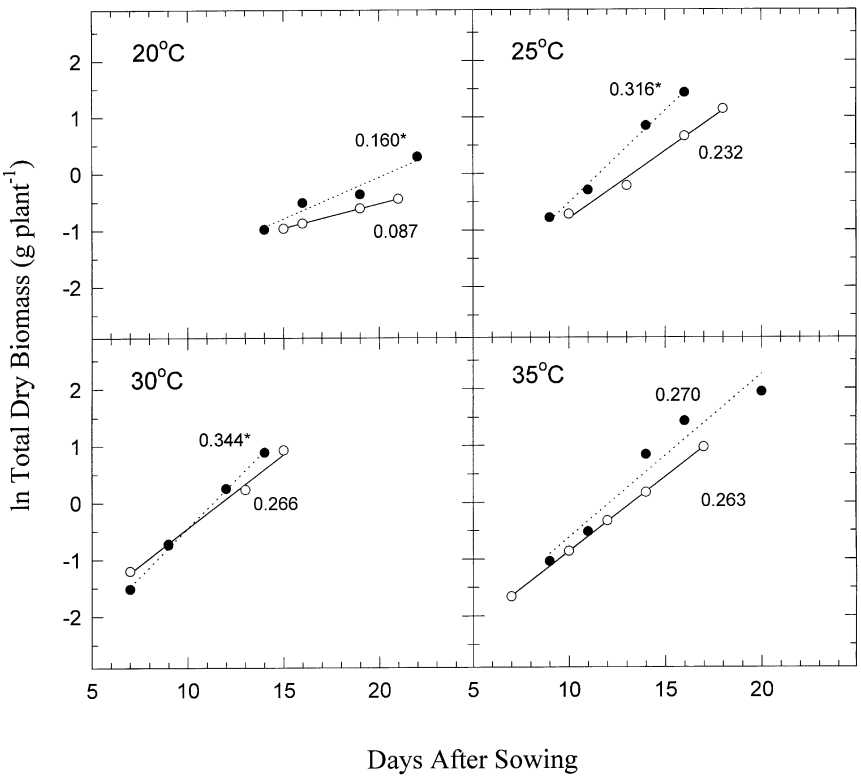

Fig. 1 Relative growth rates (based on 4 sampling periods) for soybean grown at ambient (350 μL L^{-1}, ○) and elevated (700 μL L^{-1}, ●) CO_2 at 4 different growth temperatures. First order regressions were used as the 'best-fit' for each CO_2 concentration at a given growth temperature. * indicates a significant difference ($P < 0.05$) between [CO_2] treatments for a given growth temperature (Students unpaired *t*-test). No linear response had an R^2 value of less than 0.95.

chambers. At each harvest, plants were separated into leaves, (including petioles), stems and roots. Each component was oven dried at 70 °C for 48–96 h depending on sample size. Leaf area was measured with a leaf area meter (Model 3100, Li-Cor). All remaining plants for all growth temperatures were harvested 21–22 days after sowing (DAS).

Since dark respiration may be dependent on the concentration of carbohydrates, leaf and root tissue were sampled from 3 to 4 plants at the beginning and end of the gas exchange period for each [CO_2] treatment and growth temperature. Carbohydrates were extracted from fresh tissue with 80% (v/V) ethanol, and starch and sucrose were analysed enzymatically as described by Ziska *et al.* (1995). Glucose liberated from starch and sucrose was measured spectrophotometrically in coupled enzyme assays as described by Bergmeyer *et al.* (1974).

Results

For soybean, the relationship between the natural log of whole plant biomass on a dry weight basis and time was essentially linear (i.e. $R^2 > 0.95$) at all CO_2 concentrations and growth temperatures, indicating a constant relative growth rate (RGR) over the sampling period (Fig. 1). Elevated [CO_2] significantly increased the RGR for soybean compared with ambient [CO_2] up to a growth temperature of 35 °C. However, the degree of stimulation of RGR by elevated [CO_2] was reduced with increasing growth temperature (e.g. a doubling of RGR at 20 °C, but a 29% increase at a growth temperature of 30 °C).

Whole plants of soybean at a growth temperature of 25 °C showed continual increases in night-time respiration as measurement temperature increased from 15 to 35 °C (Fig. 2a). A significant reduction in dark respiration was observed at elevated [CO_2] (relative to ambient [CO_2]) at measurement temperatures < 25 °C. For plants measured and compared at their respective growth temperatures, a significant reduction in dark respiration on a whole plant dry weight basis (i.e. roots, stems and leaves) was observed at elevated [CO_2] at growth temperatures of 20 and 25 °C. However, in contrast to measurement temperature, no further increase in night-time respiration was noted for the ambient and elevated [CO_2] treatments at growth temperatures above 25 °C (Fig. 2b).

Throughout the 7–9 day measurement period, dark respiration was either the same or lower at elevated CO_2 irrespective of growth temperature (Fig. 3). No significant interaction between CO_2 concentration and growth temperature was observed (Fig. 3). The reduction in respira-

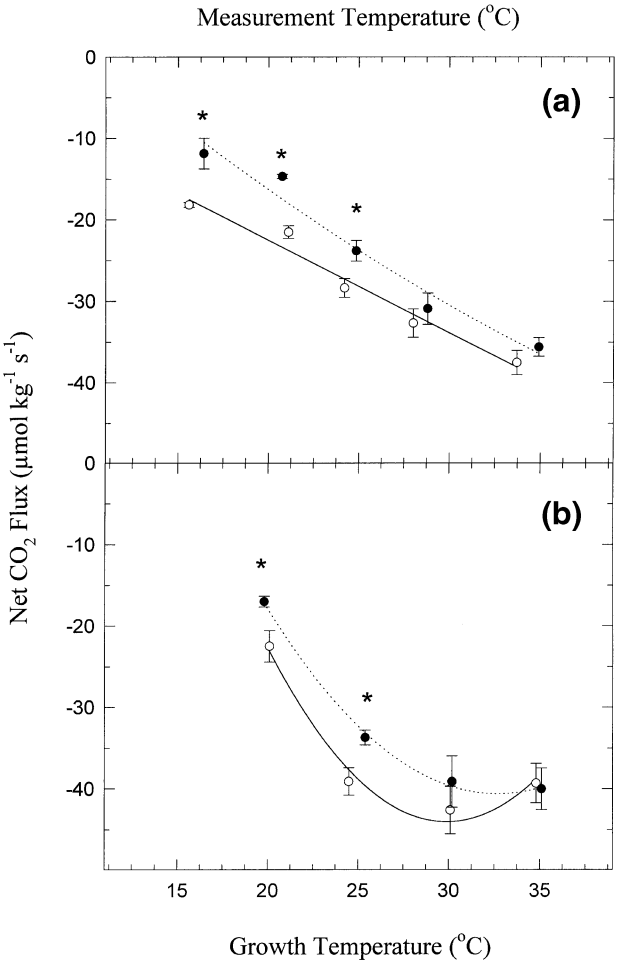

Fig. 2 Dark respiration on a unit whole plant dry weight basis, (i.e. leaves, stems and roots) determined as CO_2 efflux during the night (22.00–07.00 hours) for soybean grown at ambient (350 μL L^{-1}, ○) and elevated (700 μL L^{-1}, ●) [CO_2]. Respiration was determined for soybean grown at a constant day night temperature of 25 °C but measured over a range of measurement temperatures (a); or for soybean grown at constant day/night growth temperatures of 20, 25, 30 and 35 °C (b). * indicates a significant difference ($P < 0.05$) between [CO_2] treatments for a given growth or measurement temperature (Students unpaired *t*-test). For (a), each point is the mean of 12 measurements for a given measurement temperature. For (b), each point is the average of 60 measurements taken over a 7–12 day period. Bars are + SE

tion per unit dry weight observed at elevated relative to ambient CO_2 concentration was not associated with a reduction in carbohydrate concentration during the gas exchange period. Instead, elevated [CO_2] resulted in a significant increase (relative to ambient CO_2 concentration) at the end of the gas exchange period for leaf sucrose at 20, 25 and 35 °C and starch (all growth temperatures) (Table 1). Levels of sucrose and starch within the roots were small relative to leaf concentrations, and no significant effect of CO_2 concentration was observed (Table 1). No interactive effects between CO_2 concentration and temperature were observed for either sucrose or starch for either organ.

The ratio of respiration to photosynthesis (R:P) was plotted as a function of dry weight for whole plants (i.e. roots, stems and leaves) for all [CO_2] and temperature treatments. The R:P ratio increased as plants aged with no further change observed after a dry weight value of ≈ 1.0 g (Fig. 4). Little difference in the R:P ratio among plants grown at different temperatures was observed. However, plants grown at elevated [CO_2] demonstrated a consistent reduction in the R:P ratio at all growth temperatures when compared to the ambient [CO_2] treatment.

Discussion

The relative stimulation of soybean growth with elevated [CO_2] while significant, was reduced with increasing growth temperature. To date, a number of studies have shown that the relative enhancement of CO_2 assimilation in soybean exposed to elevated CO_2 concentrations is unchanged (Jones *et al.* 1985; Campbell *et al.* 1990; Baker & Allen 1993), or decreased with increasing temperature (Sionit *et al.* 1987). For the plants used in the current experiment, increasing temperature resulted in less stimulation of whole plant assimilation and total biomass production by elevated, relative to ambient, CO_2 concentration (see Tables 1 and 2, Ziska & Bunce 1997). Although vapour pressure deficit (VPD) increased from ≈ 0.9 to 2.0 kPa for the RH and growth temperatures used in this experiment, the response of soybean assimilation at ambient and elevated [CO_2] has been shown to be parallel for VPDs from 0.5 to 3.0 kPa (see Bunce 1993). Consequently, the decline in the growth response to elevated CO_2 with temperature cannot be attributed to a differential response of assimlation rate to VPD.

The reduction at high temperature in the magnitude of the enhancement of growth under the elevated CO_2 concentration did not appear to be a consequence of greater carbon loss as temperature increased. While respiration in the short term was quite sensitive to changing temperature at either CO_2 concentration, respiration acclimated to long-term temperatures exceeding ≈ 25 °C (i.e. respiration at a growth temperature of 25 °C was not significantly different than that at 35 °C, see Fig. 2).

Specific rates of dark respiration did not increase significantly at elevated relative to the ambient CO_2 treatment at any growth temperature. In fact, if respiration is considered in relation to RGR, then plants grown at elevated [CO_2] had a consistently lower rate of respiration per unit growth. That is, the amount of carbon lost by dark respiration per unit increase in dry weight was reduced at all but the highest growth temperature (data

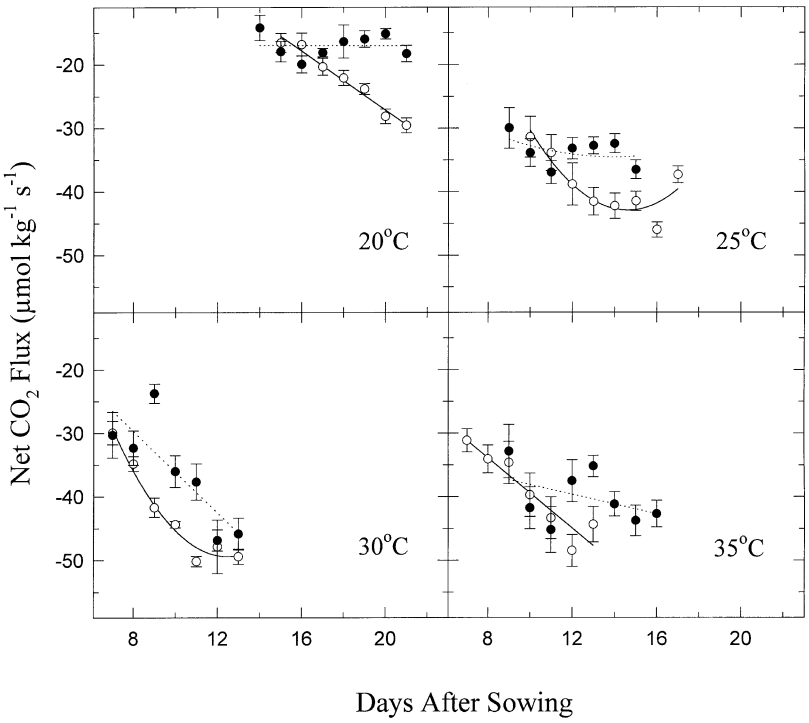

Fig. 3 Dark respiration on a unit whole plant dry weight basis, (i.e. leaves, stems and roots) determined as CO_2 efflux during the night (2200–2700) as a function of days after sowing for soybean grown at ambient (350 μL L^{-1}, ○) and elevated (700 μL L^{-1}, ●) [CO_2] at 4 different growth temperatures. Each point is the average of 50–60 measurements taken during the night period (22.00–07.00 hours).

not shown). Although expressing specific rates of dark respiration on a dry weight basis may magnify the difference between ambient and elevated [CO_2] grown plants due to increased leaf carbohydrate levels at elevated [CO_2], overall levels of starch were still low. Consequently, it should not be interpreted that the effects of [CO_2] on respiration were merely artifacts. The reduction in respiration per unit growth observed here was consistent with that observed previously for soybean over a similar range of temperatures (Bunce & Ziska 1996). Analogous results regarding respiratory inhibition by elevated [CO_2] have been reported for a number of different species (see Wullschleger *et al.* 1994, Poorter *et al.* 1992).

Although a number of studies have examined the effect of CO_2 concentration on respiration, few have examined the effect of increasing CO_2 concentration and temperature on the ratio of respiration to photosynthesis. Such information would be essential in determining if future increases in CO_2 concentration over a range of growth temperatures alter whole plant carbon balance. In an experiment with seven species grown over a range of temperatures (with presumably different RGRs), values of R:P were largely unaffected (Gifford 1994). Gifford (1995), has also demonstrated consistent R:P ratios over a wide range of temperatures (15–30 °C) and between ambient and elevated [CO_2] (710 μL L^{-1}) at a single growth temperature (20 °C) in wheat. Similarly, in the current experiment, the R:P ratio for soybean plants was unaffected over a 15 °C temperature range at a given CO_2 concentration, although the R:P ratios were much lower than those reported for wheat. In contrast to wheat, R:P ratios were consistently lower at the elevated CO_2 concentration relative to the ambient condition over a wide range of growth temperatures, suggesting a reduction in respiratory cost per unit tissue.

Respiration has frequently been modelled as a linear response to RGR with the slope indicative of growth (structural costs) and the intercept indicating maintenance (turnover costs) (See McCree 1982). In this interpretation, increased RGR would increase R, but decrease R:P, while increased temperature would be expected to increase maintenance respiration, and increase R:P (Amthor 1989). It is possible that simultaneous increases in RGR and temperature offset to produce a consistent R:P ratio.

In the current experiment, respiration per unit dry weight declined although RGR was constant. This has been observed previously for both soybean (Bunce 1990), *Plantago major* (Poorter *et al.* 1988), and wheat (Du Cloux *et al.* 1987). Although not fully understood within the context of the respiration model, these observed changes in respiration per unit dry weight at constant RGR would

Table 1 Changes in percentage starch and sucrose (w/w) in soybean leaves grown at ambient (350 μL L^{-1}) and elevated (700 μL L^{-1}) CO_2 concentration. Carbohydrate was determined for each CO_2 and temperature treatment at the beginning and end of gas exchange measurements. Gas exchange began with the unfolding of the first trifoliate, which varied with growth temperature. Net carbon exchange occurred over a 7–9 day period. See methods for additional details. n = 3–4 plants. * indicates a significant difference ($P < 0.05$) for either sucrose or starch between CO_2 treatments at a given growth temperature (Students unpaired t-test)

Temp. (°C)	CO_2 (μL L^{-1})	Sucrose Begin	End	Starch Begin	End
Leaves					
20	350	1.58	1.69	6.50	3.29
	700	2.14	2.44*	13.39*	12.57*
25	350	1.64	1.29	9.27	6.40
	700	1.24	3.04*	6.28	13.45*
30	350	1.46	2.13	6.50	1.78
	700	1.31	2.37	6.67	14.37*
35	350	0.77	1.35	1.30	1.26
	700	2.02	2.39	0.80	10.89*
Roots					
20	350	0.29	0.15	0.58	0.56
	700	0.27	0.24	0.65	0.60
25	350	0.71	0.35	1.00	0.89
	700	0.38	0.24	1.85	0.76
30	350	0.21	0.16	0.59	0.50
	700	0.23	0.31	0.64	0.79
35	350	0.52	0.33	0.80	0.54
	700	0.30	0.46	0.61	0.78

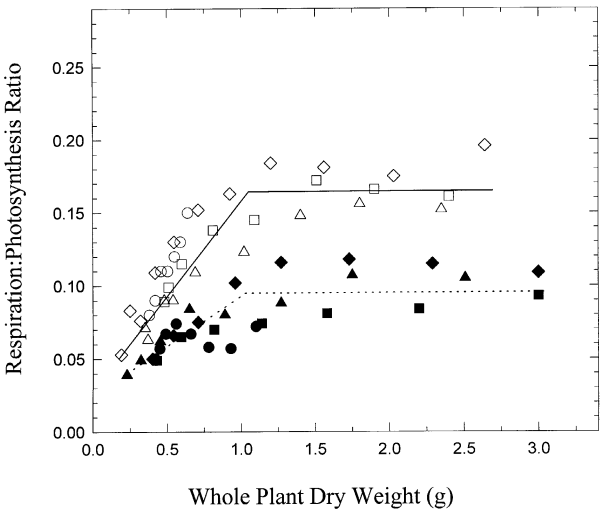

Fig. 4 The ratio of average night-time respiration rate (R) to average day-time photosynthetic rate (P) for soybean grown at ambient (350 μL L^{-1}, open symbols) and elevated (700 μL L^{-1}, closed symbols) CO_2 concentration at 4 different growth temperatures. Net carbon exchange occurred over a 7–9 day period. Each point represents the R:P ratio determined on a dry weight basis for a 24-h period for a given CO_2 concentration and growth temperature. See methods for additional details. Day/night growth temperatures were 20 °C (○, ●), 25 °C (□, ■), 30 °C (△, ▲) and 35 °C (◇, ◆). Lines were hand-drawn.

result in the early increase in R:P ratio observed in the current study.

Irrespective of changes in growth temperature, lower R:P ratio was consistently observed as a function of whole plant dry weight for the elevated [CO_2] treatment. Although elevated [CO_2] increased RGR at growth temperatures between 20 and 30 °C with a reduction in R:P ratio, no change in RGR between CO_2 concentrations was observed at 35 °C. However, R:P ratios were still lower for the elevated CO_2 concentration at this temperature. Amthor (1991) has suggested potential mechanisms by which elevated [CO_2] could modify respiration (aside from changes in RGR) and separated these into two general categories: short-term or direct effects which occur upon immediate exposure to elevated [CO_2], possibly through inhibition of respiratory enzymes; or long-term or indirect effects which would involve alterations in growth and/or maintenance respiration, possibly through changes in tissue composition. Previous work comparing the response of different soybean cultivars to temperature and CO_2 concentration demonstrated that the reduction in dark respiration at elevated [CO_2] was probably by the persistence of a direct effect rather than by a change in tissue composition (Bunce & Ziska 1996), consistent with a possible reduction in respiratory enzymatic activity (González-Meler *et al.* 1996).

The use of blank pots will underestimate microbial respiration since rhizodeposition will add substrate for microbial respiration. However, increased rhizodeposition should increase and not decrease microbial respiration in an elevated CO_2 environment. Consequently, any error associated with the presence of plants would be more likely to cause an overestimation and not an underestimation of R:P at elevated [CO_2].

In conclusion, soybean exhibited respiratory acclimation to increasing temperature with the same R:P ratio over a wide range of growth temperatures; consequently, high temperatures did not result in relatively higher rates of respiration. Elevated CO_2 concentration, on the other hand, reduced the ratio of R:P for soybean. Although additional data, especially with respect to woody species, are needed, these initial data with soybean do not support the idea that potential increases in carbon dioxide and temperature will increase the ratio of respiration to photosynthesis (Woodwell 1990, Gore 1992). Rather, the data suggest that plant species may continue to act as a sink for carbon as atmospheric carbon dioxide increases, even if temperature also increases concomitantly.

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