Effects of Prolonged Darkness on the Sensitivity of Leaf Respiration to Carbon Dioxide Concentration in C_3 and C_4 Species

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Predicting responses of plant and global carbon balance to the increasing concentration of carbon dioxide in the atmosphere requires an understanding of the response of plant respiration to carbon dioxide concentration ($[CO_2]$). Direct effects of the carbon dioxide concentration at which rates of respiration of plant tissue are measured are quite variable and their effects remain controversial. One possible source of variation in responsiveness is the energy status of the tissue, which could influence the control coefficients of enzymes, such as cytochrome-c oxidase, whose activity is sensitive to $[CO_2]$. In this study we compared responses of respiration rate to $[CO_2]$ over the range of 60 to 1000 µmol mol^{-1} in fully expanded leaves of four C_3 and four C_4 herbaceous species. Responses were measured near the middle of the normal 10 h dark period, and also after another 24 h of darkness. On average, rates of respiration were reduced about 70 % by the prolonged dark period, and leaf dry mass per unit area decreased about 30 %. In all species studied, the relative decrease in respiration rate with increasing $[CO_2]$ was larger after prolonged darkness. In the C_3 species, rates measured at 1000 µmol mol^{-1} CO_2 averaged 0·89 of those measured at 60 µmol mol^{-1} in the middle of the normal dark period, and 0·70-times when measured after prolonged darkness. In the C_4 species, rates measured at 1000 µmol mol^{-1} CO_2 averaged 0·79 of those at 60 µmol mol^{-1} CO_2 in the middle of the normal dark period, and 0·51-times when measured after prolonged darkness. In three of the C_3 species and one of the C_4 species, the decrease in the absolute respiration rate between 60 and 1000 µmol mol^{-1} CO_2 was essentially the same in the middle of the normal night period and after prolonged darkness. In the other species, the decrease in the absolute rate of respiration with increase in $[CO_2]$ was substantially less after prolonged darkness than in the middle of the normal night period. These results indicated that increasing the $[CO_2]$ at the time of measurement decreased respiration in all species examined, and that this effect was relatively larger in tissues in which the respiration rate was substrate-limited. The larger relative effect of $[CO_2]$ on respiration in tissues after prolonged darkness is evidence against a controlling role of cytochrome-c oxidase in the direct effects of $[CO_2]$ on respiration.   © 2001 US Government

Key words: Carbon dioxide, respiration, *Abutilon theophrasti* (L.), *Amaranthus retroflexus* (L.), *Amaranthus hypochondriacus* (L.), *Datura stramonium* (L.), *Helianthus annuus* (L.), *Solanum melongena* (L.), *Sorghum bicolor* (L. Moench), *Zea mays.*

INTRODUCTION

The current rapid rise in the concentration of carbon dioxide ($[CO_2]$) in the atmosphere has several potentially important implications for plants. In terms of direct effects, increases in photosynthesis and growth and reductions in stomatal conductance are the most well known. It was thought that increased atmospheric $[CO_2]$ would increase plant respiration because it increases plant growth rates and concentrations of carbohydrates, both of which have been found to influence rates of respiration (Poorter *et al.*, 1992). However, a decrease in the respiration rate of plant tissue grown and measured at elevated $[CO_2]$ is the common experimental outcome (Poorter *et al.*, 1992; Curtis and Wang, 1998; Drake *et al.*, 1999), and this unexpected result has stimulated interest in understanding responses of plant respiration to $[CO_2]$. Besides affecting plant carbon balance, plant respiration is also a major term in the global carbon balance (Gifford, 1994). An understanding of responses of plant respiration to elevated $[CO_2]$ is thus important to

understanding plant and ecosystem responses to rising atmospheric $[CO_2]$.

One simple explanation of the lower respiration rates of plants grown at elevated $[CO_2]$ is that these plants may contain tissue whose composition is such that it requires less respiration to synthesize. However, recent studies have generally ruled this out as a significant factor in the lower respiration rates of plants grown at elevated $[CO_2]$ (Griffin *et al.*, 1993; Amthor *et al.*, 1994; Bunce, 1995a; Bunce and Ziska, 1996; Poorter *et al.*, 1997). Another idea is that lower protein content in tissue developed at elevated $[CO_2]$ reduces rates of maintenance respiration (Baker *et al.*, 199; Wullschleger *et al.*, 1992). However, in several cases, a rapid reversibility of the inhibition of respiration by elevated $[CO_2]$ suggested that the effect of long-term exposure to elevated $[CO_2]$ on respiration rates measured under the growth conditions was accounted for by the persistence of an apparent direct effect of $[CO_2]$ on respiration (e.g. Mousseau, 1993; Bunce, 1995a; Tesky, 1995; Baker *et al.*, 2000). It has been suggested that there may be no direct effect of $[CO_2]$ on respiration, but that the gas exchange results are artefacts of leaks or errors due to

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interference of water vapour in CO_2 exchange measurements (Amthor, 2000). On the other hand, the observation that the activity of cytochrome-c oxidase can be inhibited by elevated $[CO_2]$ (Gonzalez-Meler *et al.*, 1996) provides a possible mechanism for a direct response of respiration to $[CO_2]$. This paper focuses on the direct response of respiration rate to short-term (minutes) changes in the measurement $[CO_2]$. We have attempted to minimize known experimental errors and examined several species for evidence of a direct effect of $[CO_2]$ on respiration, and have tested whether the patterns of response to prolonged darkness are consistent with control of the direct response to $[CO_2]$ by cytochrome-c oxidase.

The control that cytochrome-c oxidase exerts on the rate of respiration is expected to vary with the energy status of the tissue, with little control expected in tissue depleted of respiratory substrates (Gonzalez-Meler and Siedow, 1999). In contrast to this, Reuveni and Gale (1985) reported a larger relative effect of increased $[CO_2]$ on respiration in tissue grown under lower light conditions. We tested whether depletion of respiratory substrates changes the sensitivity of respiration to $[CO_2]$ in several species. To reduce complications due to plant development under different environmental conditions, respiratory substrates were reduced by prolonging the normal dark period, rather than by growing plants continually in dimmer light. Reuveni and Gale (1985) also noted that the absolute change in respiration rate with measurement $[CO_2]$ was equal for the two light regimes, and suggested that some fixed component of respiration might be affected by $[CO_2]$. The work reported here tests whether this pattern of a larger relative but equal absolute response of respiration to $[CO_2]$ in tissue depleted of respiratory substrates also occurs in other species.

MATERIALS AND METHODS

Plants of four C_3 species [*Abutilon theophrasti* (L.), *Datura stramonium* (L.), *Helianthus annuus* (L.) and *Solanum melongena* (L.)] and four C_4 species [*Amaranthus retroflexus* (L.), *Amaranthus hypochondriacus* (L.), *Sorghum bicolor* (L. Moench) and *Zea mays* (L.)] were grown in a controlled environment chamber. The chamber air temperature was 25 ± 0.2 °C, the dew point temperature was 18 ± 2 °C, $[CO_2]$ was 360 ± 20 µmol mol^{-1}, and there were 14 h per day of light at a photosynthetic photon flux density of 1.0 mmol m^{-2} s^{-1} from a mixture of high pressure sodium and metal halide lamps. Plants were grown in pots filled with vermiculite and watered daily with a complete nutrient solution containing 14.5 mM nitrogen (Robinson, 1984).

A specially designed gas exchange system was used to reduce three types of potential errors in the measurement of net CO_2 efflux in darkness: low signal to noise ratio; interference of water vapour in infrared analysis of CO_2; and leaks. The open system employed used an absolute infrared analyser (LI-6262, LiCor, Inc., Lincoln, Nebraska, USA) to measure the CO_2 and water vapour concentration of air provided by a gas blending system, a differential infrared gas analyser (LI-6252) and a chilled-mirror dew point hygrometer (M1, General Eastern, Cambridge MA,

USA) to determine the change in carbon dioxide and water vapour concentrations across the leaf cuvette, respectively, and a mass flow meter to measure flow into the leaf cuvette. The absolute $[CO_2]$ in the reference air stream was input into the differential CO_2 analyser, and the system software was used to correct the sensitivity of the differential measurement for the reference $[CO_2]$. The accuracy of this correction was checked by use of four pairs of calibration gases near 60, 360, 700 and 1000 µmol mol^{-1} CO_2. The analyser software correction was found to be accurate. No correction for water vapour was used in the system software of the differential CO_2 analyser. Differentials were determined both with air streams taken directly from before and after the leaf cuvette, and also after these air streams were dried by passing through columns of magnesium perchlorate. The CO_2 differentials of the dried air streams were used for the calculation of respiration rates. Because the water content of both sample and reference air streams was measured, the theoretical correction for dilution of CO_2 by water vapour could be calculated for comparison with the observed effect of the difference in water vapour concentration on the differential indicated by the carbon dioxide analyser. Additional water vapour in the sample cell compared with the reference cell—caused by transpiration—would reduce $[CO_2]$ in the sample cell, with the dilution being proportional to the difference in water vapour pressure between the cells relative to the total pressure. For example, with a 1.0 Pa higher water vapour pressure in the sample cell, a total pressure of 10^5 Pa, and a reference $[CO_2]$ of 1000 µmol mol^{-1}, a CO_2 analyser insensitive to water vapour should indicate lower $[CO_2]$ in the sample cell by 10 µmol mol^{-1}.

To eliminate leaks into the air lines to and from the leaf cuvette and from the cuvette itself, this part of the system was deliberately pressurized to 200 Pa above the ambient air pressure. The water-jacketed cuvette was made of clear acrylic, coated with teflon film, and had an internal volume of about 500 cm^3. A 1 cm wide strip of closed cell foam was used to seal the edges of the cuvette, and petioles were inserted through a groove and sealed with calk. A mixing fan and motor were completely enclosed in the cuvette. Leaks were tested for by placing the empty cuvette inside a controlled environment chamber, increasing the $[CO_2]$ in the chamber to 6000 µmol mol^{-1} and determining that there was no $[CO_2]$ differential across the cuvette. Similarly, this test was performed with each leaf in place in the cuvette, to determine that the $[CO_2]$ differential did not change when the $[CO_2]$ of the air in the controlled environment chamber was increased from about 500 to 6000 µmol mol^{-1}.

The signal to noise ratio of the whole system was increased by choosing species with large leaves, so that in all cases >100 cm^2 of leaf was enclosed in the cuvette, and by using low air flow rates. The air flow into the cuvette was between 1 and 4 dm^3 per minute, and $[CO_2]$ differentials exceeded the peak to peak noise of the differential CO_2 analyser by a factor of at least 30, but typically about 100. The output of the differential CO_2 analyser with reference gas in each cell was adjusted immediately before each differential measurement to eliminate errors due to drift of the analyser zero.

For each species, three leaves were measured near the middle of the normal dark period, i.e. after about 5 h of darkness, and three different leaves of each species were measured after an additional 24 h of darkness. Leaves selected for measurement had reached full area expansion a few days prior to sampling and had been fully exposed to chamber light the day prior to measurement. Each leaf was first measured at a $[CO_2]$ of 360 ± 25 μmol mol^{-1} at the growth temperature about an hour after being sealed into the gas exchange cuvette. The leaf to air water vapour pressure difference was 1.5 ± 0.2 kPa. Subsequent measurements were made at 700 ± 50, 60 ± 5, 1000 ± 70, and again at 360 ± 25 μmol mol^{-1} CO_2. The $[CO_2]$ reached each new set point in about 10 min, and rates of respiration were determined about 10 min later. After respiration rates were measured over this sequence, the leaf was harvested for determination of area and dry mass after drying at 70 °C, and leaf mass per unit area was calculated for individual leaves.

RESULTS

For all of the C_4 species, rates of respiration calculated from the $[CO_2]$ differential of the dried air streams were indistinguishable from rates calculated using the differential measured before the air streams were dried (e.g. Fig. 1). For C_3 species, respiration rates were progressively lower at higher $[CO_2]$ if calculations were based on the $[CO_2]$ differential before drying compared with rates calculated from the $[CO_2]$ differential of the dried air streams (e.g. Fig. 1). This difference between the C_3 and C_4 species was caused by smaller differences in water vapour concentration between the sample and reference air streams for the C_4 species. This occurred because the conductances to water vapour for the C_4 species ranged from 0.007 to 0.025 mol m^{-2} s^{-1}, while for the C_3 species conductances ranged from 0.06 to 0.10 mol m^{-2} s^{-1}. Applying the theoretical correction for dilution of $[CO_2]$ by water vapour to the $[CO_2]$ differentials of the air streams before drying would have progressively overestimated respiration rates as measurement $[CO_2]$ increased, compared with the results obtained with dried air streams. This over-correction for dilution would have resulted in essentially no change in respiration rate with $[CO_2]$ over the range of 350 to 700 μmol mol^{-1} in the C_3 species measured after 5 h of darkness, when respiration rates were relatively less responsive to $[CO_2]$ (Table 1). Using this erroneous correction would still have resulted in respiration rates decreasing with increasing $[CO_2]$ in the C_4 species and in all species when measured after prolonged darkness.

For every individual leaf measured, dark CO_2 efflux rates decreased with increasing $[CO_2]$, at least over the range of 60 to 700 μmol mol^{-1}. Rates measured at 360 μmol mol^{-1} CO_2 at the beginning and end of each measurement sequence never differed substantially, and mean values were used. Data for the two species with the largest and smallest relative responses are presented in Fig. 2. The responses illustrated in Fig. 2 are also typical in suggesting a decrease in slope with increasing $[CO_2]$.
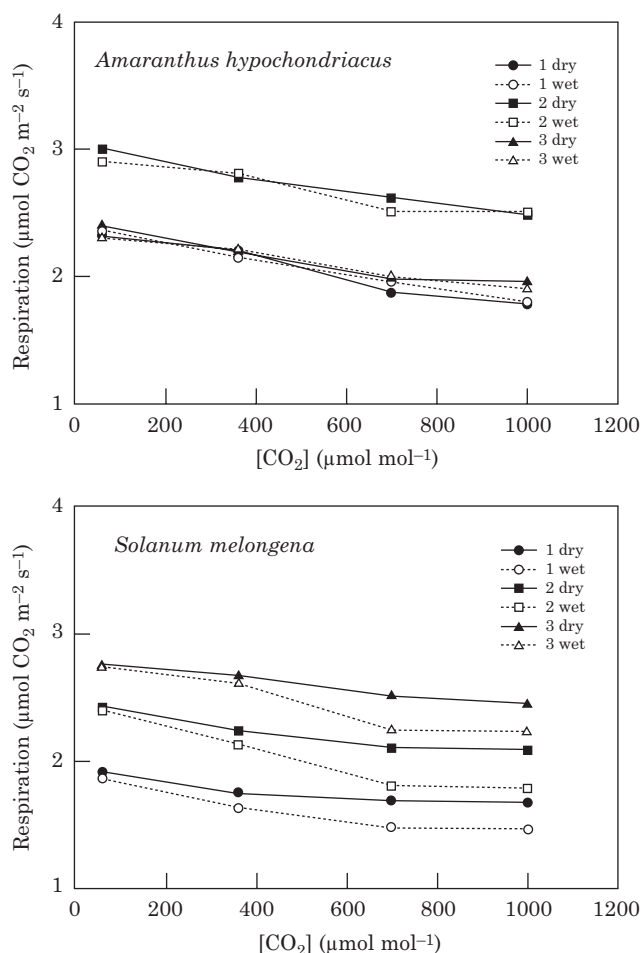

FIG. 1. Respiration rates as a function of measurement carbon dioxide concentration for individual leaves of *Amaranthus hypochondriacus* and *Solanum melongena* after 5 h of darkness, calculated from CO_2 differences across the leaf cuvette measured while the air streams were wet or after drying the air streams.

TABLE 1. *Relative changes ($\pm s.d.$) in respiration rate (R) for measurement carbon dioxide concentrations ($[CO_2]$) of 350 and 700 μmol mol^{-1}, after 5 h of darkness in leaves of four C_3 species, calculated from changes in $[CO_2]$ of dried air streams, or calculated changes measured for wet air streams and applying the theoretical correction for dilution of CO_2 by the measured differences in water vapour concentration of the air streams*

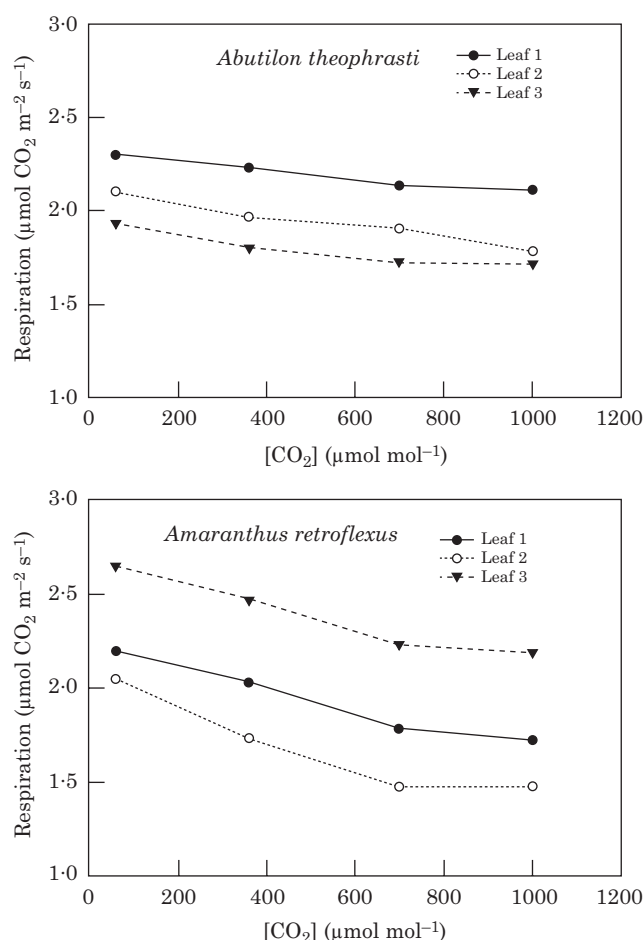|	R at 700/R at 350	
Species	Dry air streams	Theoretical correction for water vapour
A. theophrasti	0.95 ± 0.03	0.97 ± 0.03
S. melongena	0.95 ± 0.02	0.99 ± 0.02
D. stramonium	0.96 ± 0.02	1.04 ± 0.03
H. annuus	0.95 ± 0.02	0.98 ± 0.02

FIG. 2. Respiration rates as a function of measurement carbon dioxide concentration for individual leaves of *Abutilon theophrasti* and *Amaranthus retroflexus* after 5 hr of darkness. Respiration rates were calculated from carbon dioxide differences across the leaf cuvette measured after drying the air streams. Of the species examined, these species had the smallest and largest responses, respectively, of respiration rate to $[CO_2]$.

For all species, rates of efflux measured after about 29 h of darkness were lower than rates measured after about 5 h of darkness (Table 2). When measured at the growth $[CO_2]$ of 360 μmol mol^{-1}, mean rates after prolonged darkness ranged from about 10 to 50 % of those measured in the middle of the normal dark period (Table 2). Leaf dry mass per unit area was $30 \pm 7\%$ lower after the 29 h dark period compared with the 5 h dark period, for all species.

The values of respiration at a measurement $[CO_2]$ of 1000 μmol mol^{-1} relative to those at 60 μmol mol^{-1} were smaller on average in the C_4 than in the C_3 species, both when measured in the middle of the normal dark period and also when measured after prolonged darkness (Table 2). For both C_3 and C_4 species, the ratio of respiration at 1000 μmol mol^{-1} measurement CO_2 to that at 60 μmol mol^{-1} was reduced after 29 h of darkness compared with 5 h of darkness (Table 2). In three of the C_3 species (*A. theophrasti*, *S. melongena* and *D. stramonium*) and one of the C_4 species (*A. retroflexus*), the absolute magnitude of the decrease in respiration rate between 60 and 1000 μmol mol^{-1} was nearly the same after 5 and 29 h of darkness (Table 2). In the remaining species, the decrease was substantially less after prolonged darkness.

DISCUSSION

An effect of measurement $[CO_2]$ on plant respiration, assayed as the net rate of CO_2 efflux in darkness, remains somewhat controversial. This results, in part, from the inconsistency of the response across species and tissue types. For example, reported responses to increasing the measurement $[CO_2]$ from 350 to 700 μmol mol^{-1} range from decreases in excess of 50 % to slight increases, with many cases of undetectable change in rate (reviewed in Gonzalez-Meler and Siedow, 1999; Baker *et al.*, 2000). Some of this inconsistency may result from measurement errors, because the rates of respiration are often smaller compared with errors in the measurement systems than is the case, for example, with photosynthetic rates. In the results reported here, respiration rate in all species was decreased by increasing $[CO_2]$, despite efforts to minimize three known types of measurement error. A direct effect of $[CO_2]$ on respiration is consistent with observations of significant effects of night-time $[CO_2]$ on plant growth (e.g. Reuveni and Gale, 1985; Bunce, 1995*b*; Reuveni *et al.*, 1997; Griffin *et al.*, 1999;

TABLE 2. *Relative and absolute changes ($\pm$s.d.) in respiration rate (R) for measurement carbon dioxide concentrations ($[CO_2]$) of 60 and 1000 μmol mol^{-1}, after either 5 and 29 h of darkness in leaves of four C_3 and four C_4 species. Also given are the rates of respiration measured at 350 μmol mol^{-1} $[CO_2]$ after 29 h of darkness relative to rates after 5 h of darkness*

| Species | R at 1000/R at 60 | | R at 60 − R at 1000 | | R at 29 h/R at 5 h |
	5 h	29 h	5 h $\quad$ 29 h (μmol m^{-2} s^{-1})		
A. theophrasti	0.90 ± 0.03	0.76 ± 0.05	0.21 ± 0.03	0.18 ± 0.05	0.30
S. melongena	0.87 ± 0.02	0.61 ± 0.04	0.29 ± 0.04	0.23 ± 0.06	0.27
D. stramonium	0.89 ± 0.02	0.63 ± 0.06	0.25 ± 0.07	0.24 ± 0.03	0.31
H. annuus	0.89 ± 0.02	0.79 ± 0.05	0.27 ± 0.06	0.14 ± 0.05	0.27
A. retroflexus	0.75 ± 0.04	0.50 ± 0.07	0.45 ± 0.03	0.58 ± 0.08	0.50
A. hypochondriacus	0.83 ± 0.04	0.28 ± 0.17	0.53 ± 0.04	0.25 ± 0.06	0.09
S. bicolor	0.83 ± 0.07	0.67 ± 0.06	0.30 ± 0.07	0.14 ± 0.05	0.23
Z. mays	0.76 ± 0.06	0.57 ± 0.07	0.38 ± 0.08	0.19 ± 0.06	0.21

Ziska and Bunce, 1999), although it has not been proven that changes in respiration mediate these effects.

Of the errors in measuring respiratory CO_2 flux, the potential error caused by water vapour still requires careful attention, despite 'water vapour correction' features of infrared CO_2 analysers. The infrared carbon dioxide analyser used here did not respond to dilution of air by water vapour to the extent predicted theoretically. This was exemplified by the data for the C_3 species measured after 5 h of darkness, where correction of the analyser output for the theoretical dilution effect would have resulted in essentially no change in respiration rate between 350 and 700 μmol mol^{-1} CO_2, rather than the decrease obtained using dried air streams. It is possible that broadening of the infrared absorption band for carbon dioxide by the presence of water vapour could account for this discrepancy. Because different versions of infrared carbon dioxide analysers respond to water vapour in different ways (e.g. Bunce and Ward, 1985), it is necessary to test how the particular analyser being used responds, or else to ensure equal water contents of the air streams before analysis of carbon dioxide differentials.

All species showed a large decrease in respiration rate after an additional 24 h of darkness. This was probably due to depletion of respiratory substrates to the point where they limited the rate of respiration. Many studies have shown that most of the diurnal changes in leaf mass per unit area in mature leaves are accounted for by starch and soluble carbohydrates (e.g. Warrington *et al.*, 1977; Sicher *et al.*, 1984). The reduction in leaf mass per unit area during the 24 h of darkness is consistent with carbohydrate depletion.

Cytochrome-c oxidase has been identified as a respiratory enzyme that is inhibited by carbon dioxide in the appropriate concentration range (Gonzalez-Meler *et al.*, 1996). Amthor (2000) concluded that the small, but consistent, reduction in respiration with increased carbon dioxide concentration he observed in tree leaves was compatible with control by cytochrome-c oxidase. Similarly, the magnitude of change in respiration rate we observed would not exclude an effect mediated by cytochrome-c oxidase. However, the expectation of little control of respiration by cytochrome-c oxidase in tissue depleted of respiratory substrates (Gonzalez-Meler and Siedow, 1999) contrasts with our observations and with data for alfalfa (Reuveni and Gale, 1985). The consistent finding that the direct effects of measurement carbon dioxide concentration are relatively larger in tissue depleted of respiratory substrates is evidence that cytochrome-c oxidase may not be the primary site of carbon dioxide effects on respiration.

For about half of the species examined, the results found here were consistent with the results obtained by Reuveni and Gale (1985) in alfalfa: the absolute change in respiration rate with carbon dioxide concentration was nearly the same for tissue before and after prolonged darkness, while the relative change was larger for tissue depleted of respiratory substrates. This was not clearly related to photosynthetic pathway, as it occurred in three of the C_3 species and one of the C_4 species. However, equal absolute reductions in respiration rate for tissue differing in energy status apparently does not imply that some fixed component of respiration is reduced by elevated carbon dioxide in all cases, since the other species examined here, the absolute change in rate was substantially less after leaves had been kept in prolonged darkness. An alternative explanation of larger [CO_2] effects on respiration in tissue depleted of respiratory substrates is that [CO_2] affects maintenance respiration, which is a larger fraction of total respiration in depleted tissue (Reuveni and Gale, 1985). This idea is consistent with other data suggesting that maintenance respiration may be the primary target of effects of growth at elevated [CO_2] on respiration (Baker *et al.*, 1992; Wullschleger and Norby, 1992; Bunce, 1995*a*; Bunce and Ziska, 1996). The distinction between [CO_2] effects on maintenance *vs.* growth respiration is important to crop and ecosystem modelling, but understanding the functional significance of direct [CO_2] effects on respiration will require evidence of [CO_2] effects on physiological processes driven by respiration, and biochemical information about the mechanism of the effect.

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