Respiration in a future, higher-CO$_2$ world

J. S. AMTHOR School of Forestry and Environmental Studies, Yale University, New Haven, CT, U.S.A.

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Abstract. Apart from its impact on global warming, the annually increasing atmospheric [CO$_2$] is of interest to plant scientists primarily because of its direct influence on photosynthesis and photorespiration in C$_3$ species. But in addition, ‘dark’ respiration, another major component of the carbon budget of higher plants, may be affected by a change in [CO$_2$] independent of an increase in temperature. Literature pertaining to an impact of [CO$_2$] on respiration rate is reviewed. With an increase in [CO$_2$], respiration rate is increased in some cases, but decreased in others. The effects of [CO$_2$] on respiration rate may be direct or indirect. Mechanisms responsible for various observations are proposed. These proposed mechanisms relate to changes in: (1) levels of nonstructural carbohydrates, (2) growth rate and structural phytomass accumulation, (3) composition of phytomass, (4) direct chemical interactions between CO$_2$ and respiratory enzymes, (5) direct chemical interactions between CO$_2$ and other cellular components, (6) dark CO$_2$ fixation rate, and (7) ethylene biosynthesis rate. Because a range of (possibly interactive) effects exist, and present knowledge is limited, the impact of future [CO$_2$] on respiration rate cannot be predicted. Theoretical considerations and types of experiments that can lead to an increase in the understanding of this issue are outlined.

Key-words: carbon budget; carbon dioxide; respiration.

Introduction

Earth’s atmospheric [CO$_2$] is increasing on an annual basis due to human activities, and it is expected that the present annual mean concentration (ca. 350 cm$^{-3}$ m$^{-2}$) will be doubled during the next century. This increase has obvious consequences for plant metabolism and growth since CO$_2$ is the carbon substrate of photosynthesis and CO$_2$ inhibits photorespiration. In addition to effects on photosynthesis and photorespiration, especially in C$_3$ species, available evidence (summarized herein) indicates that CO$_2$ at atmospheric levels can affect respiration, although present knowledge of the impacts of an increase in [CO$_2$] on respiration is scant. It is important to better understand this issue since respiration supports the growth and maintenance processes and is a large component of the carbon budget of higher plants; estimates indicate that about half the carbon fixed in photosynthesis (less photorespiration) is eventually ‘lost’ to respiration (Kira, 1975; Amthor, 1989).

An increase of a few degrees Celsius in the annual mean surface temperature of the Earth will probably accompany the increase in concentration of CO$_2$ (and other infra-red absorptive gases) during the coming century (Woodwell, 1989). Although respiration rate responds strongly to temperature in the short term, acclimation to moderate changes in temperature occurs (e.g. Rook, 1969; Woleadge & Jewiss, 1969; Chatterton, McKell & Strain, 1970; Billings et al., 1971; Pearcy, 1977; McNulty & Cummins, 1987; Korner & Larcher, 1988, Fig. 10). Thus, a small, gradual change in temperature need not alter respiration rate, although it is a common assumption that an increase in temperature will directly increase plant respiration. The temperature change might modify other plant processes (e.g. developmental) resulting in changes in respiration, and patterns of cloud cover and precipitation are likely to change as a consequence of an altered atmosphere, and these could affect many aspects of plant metabolism, including respiration. A review of the potential effects of climate change on respiration is beyond the scope of this paper, however (see Ryan [1991] for such a review); rather, effects of [CO$_2$] on respiration that are independent of climate change are considered. Further, the physiology of higher, terrestrial plants exposed to 0–1000 cm$^{-3}$ CO$_2$ m$^{-3}$ in the aerial environment is emphasized.

Due to a lack of critical experiments and theory, some of what follows is speculative, with the intent of stimulating new thought on the topic. The specific goals of this communication are to (1) review existing data, (2) suggest mechanisms that may be responsible for effects of [CO$_2$] on respiration, and (3) outline types of additional data that could clarify this issue, irrespective of the fact that techniques available for conducting some of the experiments suggested are problematic.

1Glycolysis, the oxidative pentose phosphate pathway (network), the TCA cycle, mitochondrial electron transport, and related metabolism is here considered as respiration, which may occur in light or in darkness. Typical measures of respiration are CO$_2$ generation and O$_2$ consumption in the dark, but other metabolic reactions can generate and consume these gases, and such gas fluxes may be called apparent respiration.
Types of respiratory response to CO₂

It is often difficult to make meaningful comparisons of apparent respiration rates from different studies, or extrapolate beyond one system of measurement to another. Measurements may be made on isolated cells, individual organs, whole plants, or plant communities, and those organs or plants may be actively growing (high specific respiration rate) or largely mature (low specific respiration rate). Area-based measurements may refer to ground area for a plant community or the area of a leaf for individual leaves. Mass based measurements usually apply to dry (versus wet or fresh) mass, but total dry mass includes nonstructural compounds and the levels of nonstructural matter are in constant flux in the intact plant. In addition, the process measured (CO₂ efflux or O₂ uptake) is a factor that may influence conclusions, and respiration itself is a function of the environmental history of the plant, which differs among studies.

Indirect versus direct effects

Both indirect and direct effects of [CO₂] on respiration rate have been observed (citations below). The distinction between direct and indirect is of the temporal relationship between a change in [CO₂] and a change in respiration rate, irrespective of the initial, specific molecular effect of CO₂ on metabolism; indirect effects are due to the [CO₂]-history of the plant, whereas direct effects result from the [CO₂] at the time of a respiration measurement.

In a future world, it is likely that both indirect and direct effects of [CO₂] on respiration rate will occur. Moreover, there may be interactions between the two types of effect (e.g. the previous [CO₂] of the plant’s environment might modify the magnitude of direct effects). In present studies, however, the relative significance of indirect and direct effects is a function of the experimental protocol, and the ability to discern such effects will depend in part on the methods used to measure and express respiration.

Respiratory control

Respiratory responses to [CO₂] can be considered within the context of those that relate to the respiratory control theory and those that do not. Respiratory control might be outlined as follows (Beevers, 1970; Dry, Bryce & Wiskich, 1987). Respiration generates carbon skeletons, CO₂, NAD(P)H, ATP, and water from reduced carbon (mostly carbohydrates), NAD(P), ADP, Pi, and O₂. Except in very young cells, the enzymes catalysing respiratory reactions are generally present in excess of the amounts required for observed rates of respiration. Thus, fine control of the enzymes and the availability of substrates are usually the brakes on respiration. Without the regeneration of ADP [and NAD(P)] during the course of growth, maintenance, transport, and other processes, respiration will be ‘held in check’, whereas respiration rate will ‘increase in synchrony’ with an increase in the utilization of ATP (and NAD(P)H in such processes (Beevers, 1974) when quantities of reduced carbon, O₂, and enzymes are not limiting respiration. Thus, the rate of respiration can be regulated by the need for respiration, and when [CO₂] affects processes consuming ATP, the resulting effects on respiration rate can be interpreted within the context of respiratory control.

Respiration and the regeneration of ADP are not always linked to growth and maintenance, however, since hydrolysis of ATP not coupled to useful processes and futile cycling can also occur. In addition, activity of the alternative pathway (cyanide-resistant mitochondrial electron transport from ubiquinone to oxygen not contributing to an electrochemical gradient across the inner mitochondrial membrane) reduces, but does not eliminate, the control of respiration rate by the availability of ADP (Dry et al., 1987). Moreover, respiration supplies carbon skeletons for biosynthesis, in addition to ATP and reductant, and respiration rate should not be controlled by ATP turnover alone.

Indirect effects of [CO₂] on respiration

Plants (or organs) from CO₂-enriched (500–1000 cm³ m⁻³) environments may have increased rates of apparent respiration when measured at any given [CO₂] (Ludwig, Charles-Edwards & Withers, 1975; Gifford, 1977; Azcon-Bieto & Osmond, 1983; Gifford, Lambers & Morison, 1985, Helianthus annuus roots; Hrubec, Robinson & Donaldson, 1985; Poorter, Pot & Lambers, 1988; Nijs, Impens & Behaeghe, 1989; Bunce, 1990). Conversely, decreased rates of respiration (at a given [CO₂]) have also been observed following CO₂-enrichment (Gifford et al., 1985, Triticum aestivum; Spencer & Bowes, 1986; B. G. Drake, personal communication). Both cases imply that the [CO₂]-history of a plant alters that plant in such a way as to affect respiratory metabolism. Several factors could be involved.

Carbohydrate pool size

In C₃ species, an increase in [CO₂] is often accompanied by an asymptotic increase in photosynthesis (Pearcy & Bjorkman, 1983). This typically results in an increase in nonstructural carbohydrate levels, which can lead to an increase in respiration rate (Farrar, 1985). Increased respiration due to increased carbohydrate levels will be limited to tissues in which additional carbohydrates accumulate. Moreover, the intra- and inter-cellular compartmentation of carbohydrates with respect to sites of respiration is important.

An increase in respiration rate due to increased carbohydrate levels implies that ADP regeneration is not regulating respiration rate, which is counter to the general idea of respiratory control by such recycling. Therefore, it is important to consider the mechanisms whereby increased carbohydrate content might lead to
increased respiration and growth since this can clarify the strong relationship between carbohydrate content or photosynthesis and whole-plant respiration (Farrar, 1985).

In young, actively growing cells, respiration rates might proceed up to those allowed by full engagement of the respiratory machinery. Then, carbon-substrate availability may be the limiting factor since ATP is consumed (and ADP is regenerated) in growth processes as rapidly as it is synthesized. Under such conditions, respiration is source-limited as opposed to the sink-limited case in which ADP recycling limits carbohydrate oxidation. Meristematic regions have only poorly developed phloem, and because of this, rapid transport of sugars (and amino acids etc.) to dividing and growing cells requires large concentration gradients. An increase in the concentration of sugars near such regions might have an appreciable impact on the transport of carbon to the areas of vigorous growth.

A link between carbohydrate level and respiration rate via ADP recycling may also exist. For example, processes dependent on respiration (growth, maintenance, translocation, nutrient uptake and assimilation, etc.) might respond directly to carbohydrate levels; respiratory substrates might be positive effectors (modulators) of a rate limiting reaction in those processes, and additional growing points might be initiated as a result of elevated sugar concentration. The increased rate of ATP use in those processes would then lead to increased respiration rate.

High carbohydrate levels may also increase alternative pathway activity (Lambers, 1985). This activity might be more extensive under elevated \([\text{CO}_2]\), as has been observed in some cases (Steingrover [cited by Lambers, 1982]; Musgrave, Strain & Siedow, 1986), but not in others (Gifford et al., 1985; n.b. sugar levels were not increased by elevated \([\text{CO}_2]\) in these experiments). A better understanding of the interactions among \([\text{CO}_2]\), carbohydrate levels, and respiration rate may emerge when the role(s) of the alternative pathway in physiology and growth, and its regulation, have been more fully elucidated.

A goal of respiration research is to develop a unified theory of the effects of both ADP (and NADP[P]) regeneration and carbohydrate levels on respiration rate. That goal (see Farrar, 1985; Dry et al., 1987) is beyond the scope of this paper, but whatever the actual controls may be for a given set of circumstances, tissue respiration rate is often positively correlated with carbohydrate levels (Farrar, 1985; Lambers, 1985; Amthor, 1989). Thus, it is not surprising that increased \([\text{CO}_2]\) during the day can lead to increased respiration rate at night (e.g. Hrubec et al., 1985; Nijs et al., 1989), although decreases in respiration following growth in a \([\text{CO}_2]\)-enriched environment (e.g. Spencer & Bowes, 1986) are perhaps surprising.

In future \([\text{CO}_2]\)-enrichment experiments, carbohydrate levels should be measured concomitantly with respiration rate in order to determine if the two responses are correlated, as has already been done for a few species (Azcon-Bieto & Osmond, 1983; Gifford et al., 1985; Hrubec et al., 1985). In addition, more estimates of alternative pathway activity as a function of \([\text{CO}_2]\) are needed. Finally, effects of \([\text{CO}_2]\) assimilation rate versus \([\text{CO}_2]\) during previous photosynthesis might be ascertained by varying \([\text{CO}_2]\), \([\text{CO}_2]\) assimilation, and substrate level independently. Some such experiments have revealed interesting relationships (Ludwig et al., 1975), but more data are needed.

**Growth rate**

Whole-plant growth is often accelerated by \([\text{CO}_2]\)-enrichment (compare previous section), especially in C₃ species, and an increase in growth will generally be accompanied by an increase in both growth and maintenance respiration. When growth is increased, growth respiration will increase to supply carbon skeletons, ATP and reductant needed for additional biosynthesis (Penning de Vries, van Laar & Chardon, 1983). Increased growth results in larger plants, and larger plants require more respiration for maintenance since there is then more phytomass to be maintained, although whole-plant specific maintenance respiration rate may decrease as plant size increases (Amthor, 1989).

A strong, positive relationship between specific (or area based) respiration rate and growth \([\text{CO}_2]\) may exist in young, growing organs or plants, but be less apparent or nonexistent in older ones (Hrubec et al., 1985; Poorter et al., 1988). This suggests that growth and growth respiration rates are limited by substrate level and increased \([\text{CO}_2]\) assimilation diminishes this limitation, while maintenance (mature tissue) respiration rate is independent of substrate level, i.e. maintenance respiration is regulated by ATP use in maintenance processes.

The relationship between growth and total respiration is summarized in the growth efficiency (ratio of growth to growth plus respiration or photosynthesis [Tanaka & Yamaguchi, 1968; Yamaguchi, 1978]), which is a measure of the overall efficiency of respiration, and which has been increased as a result of whole-plant \([\text{CO}_2]\)-enrichment (Silisbury & Stevens, 1984; Du Cloux et al., 1987; Poorter et al., 1988; Drake et al., 1989; Gaudillere & Mousseau, 1989). These results are for ‘long term’ exposures to elevated \([\text{CO}_2]\) and indicate an increase in the efficiency of assimilate retention (but see Nijs et al. [1989] for the opposite response). Interpreting available data is difficult because structural growth rate and composition estimates (see following section) are not available; that is, enhanced photosynthesis can lead to an increase in total plant dry mass without a proportional increase in structural tissue, and it is the structural tissue that requires respiration for growth and then maintenance. A meaningful measure of respiration is on a structural mass (or protein) basis, and structural growth and respiration rates should be measured concomitantly to distinguish effects of growth per se from other \([\text{CO}_2]\) effects on respiration.
Phytomass composition

Elevated [CO$_2$] can result in a change in phytomass composition (e.g. Norby, O’Neill & Luxmoore, 1986) which can lead to changes in respiratory requirements. Growth rate is one determinant of growth respiration rate, but phytomass composition is another. The amount of growth respiration required for the synthesis of a unit mass of tissue decreases as the fraction of expensive compounds (e.g. proteins and lipids) in that tissue decreases (Penning de Vries et al., 1983). Similarly to growth respiration, maintenance respiration rate is related to phytomass composition. Specific maintenance respiration rate is positively related with tissue growth rate is one determinant of growth respiration. Specific respiration rate of a unit mass of tissue decreases as the fraction of amount of growth respiration required for the synthesis and phytomass composition is an indicator of maintenance requirements.

Algebraically, a 20% increase in the dry mass of a mature organ due to starch accumulation under CO$_2$- enrichment would result in a decrease in specific respiration rate of nearly 17% if other factors were not affected and starch storage incurred insignificant respiratory costs. Such an alteration in respiration rate would occur without, in fact, any real change in respiration or its functions. Experimentally, Spencer & Bowes (1986) found a 59% decrease in Eichhornia crassipes leaf protein content when grown at a [CO$_2$] of 600 compared to 330 cm$^3$ m$^{-3}$. Specific respiration rate (derived from their Tables III and V) was reduced by a similar fraction, 62%, in plants grown at 600 versus 330 cm$^3$ m$^{-3}$ (when measured at 330 cm$^3$ m$^{-3}$). Consequently, when expressed on a protein basis, leaf respiration rate was the same for plants grown at the different CO$_2$ levels. In future experiments, concomitant measures of phytomass composition and respiration rate may provide explanations for indirect effects of [CO$_2$] on specific respiration rate.

In summarizing indirect effects, the following might be observed for a plant community growing under elevated [CO$_2$]: (1) On a ground area basis, respiration rate might be higher, due to increased phytomass (increased growth and maintenance respiration requirements). (2) On a dry phytomass basis, respiration rate might be lower, due to compositional changes (particularly an increase in the C:N). (3) On a protein content basis, respiration rate might be unaffected. Other plausible scenarios can be envisaged, and the level of soluble carbohydrates at any point in time may influence respiration rate. Nonetheless, this hypothetical example shows that the expression of data may be crucial to an understanding of the mechanisms responsible for indirect effects of [CO$_2$] on apparent respiration rate. Moreover, when respiration rate is measured at different CO$_2$ levels, the possibility of direct effects of CO$_2$ on respiration must be considered.

Direct effects of [CO$_2$] on respiration

In the [CO$_2$] range relevant to the present discussion (up to 1000 cm$^3$ m$^{-3}$), leaf and seedling apparent respiration rate can be directly inhibited by CO$_2$ in the dark (Holmgren & Jarvis, 1967; Begg & Jarvis, 1968; Cornic & Jarvis, 1972; Kaplan, Gale & Poljakoff-Mayber, 1977, for a CAM species; Reuveni & Gale, 1985; Bunce, 1990; G. W. Koch, A. J. Bloom & J. S. Amthor, unpublished data for Rumex crispus). For Rumex at least, the inhibition of respiration rate by CO$_2$ is readily reversible.

Intercellular [CO$_2$]

Direct effects of CO$_2$ on respiration are likely to be mediated through intercellular [CO$_2$], $C_a$, and a knowledge of the relationships between ambient [CO$_2$] and $C_a$ are needed. In the dark, CO$_2$ is added to the interior of a leaf (or other organ) by respiration and by the diffusion of CO$_2$ from the atmosphere through the boundary layer and leaf surface, while CO$_2$ exits a leaf by diffusion in the opposite direction. The change of $C_a$ with time is described by:

$$\frac{dC_a}{dt} = R/tz + kC_a z - kC_a z,$$

where $C_a$ is the atmospheric [CO$_2$]; $R$ is apparent respiration rate (cm$^3$ CO$_2$ m$^{-2}$ leaf [one side] s$^{-1}$), which is assumed to be constant; $z$ is leaf thickness (m); and $k$ is leaf surface and boundary layer conductance to CO$_2$ diffusion (m s$^{-1}$).

Equation 1 can be integrated with respect to time yielding:

$$C_a(t) = \frac{R}{k} + C_a + ae^{-kt/z},$$

where $a$ is determined by initial conditions. With $t = 0$ when $C_a = C_i$, which is near the start of the dark period in growth chambers, $a = -R/k$. Realistic combinations of $k$ and $z$ for leaves result in $ae^{-kt/z}$ approaching zero within a few seconds to a few minutes, at which time $C_a$ is stable and equal to $C_a + R/k$. For example, with $R = 0.05$ cm$^3$ m$^{-2}$ s$^{-1}$ and $k = 0.0002$ m s$^{-1}$, eqn 2 yields $C_a = C_i + 250$ cm$^3$ m$^{-3}$ within a few minutes. If under these conditions, $C_a$ were increased 100%, from 300 to 600 cm$^3$ m$^{-3}$, $C_i$ would be increased by 55%, from 550 to 850 cm$^3$ m$^{-3}$ (effects of [CO$_2$] on stomatal aperture, possibly a result of altered respiration rate in guard cells [Raghavendra & Vani, 1989; Shaish, Roth-Bejerano & Itai, 1989], are ignored here). At mitochondria, [CO$_2$] could be higher than these estimates of $C_a$, but it may be similarly affected by changes in $C_a$. When measuring apparent respiration rate by leaves as a function of $C_a$, estimates of $C_i$ should be made so that differences in $k$ among experiments are taken into account.

For bulky organs and tissues with much lower surface conductances or poor internal aeration, a small change in $C_i$ is not likely to have an appreciable impact on $C_a$ (see also, Solomos, 1987). A corollary is that moderate changes in $C_i$ are not likely to have a direct impact on respiration in organs other than leaves; that is, within the context of atmospheric CO$_2$ buildup, direct effects of [CO$_2$] on respiration rate will be limited to well-aerated tissues, whereas indirect effects may be realized in all tissues. Nonetheless, because changes in $C_i$ expected
Can CO₂ affect respiratory enzymes?

Direct effects of [CO₂] on respiration rate could be due to direct effects of CO₂ on respiratory enzymes. Available evidence, primarily from studies with fruits and seeds, indicates that CO₂ (at quite high concentrations) can indeed have direct effects on respiratory biochemistry (references below). Direct effects of CO₂ at reasonable concentrations (<1000 cm⁻³) on the biochemistry of leaf respiration have not been studied.

Monning (1983) suggested that glycolysis was slowed in *Malus* mature fruit slices treated with 50000 cm⁻³ CO₂ m⁻³. High [CO₂] inhibited O₂ uptake and inactivated both ATP:phosphofructokinase and PFP:fructose 6-phosphate 1-phosphotransferase in *Pyrus communis* mature fruit, whereas other glycolytic enzymes were apparently unaffected (Kerbel, Kader et al., 1988).

At [CO₂]’s of 100000 cm⁻³ and higher, activity of succinate dehydrogenase was inhibited in mitochondria isolated from *Ricinus communis* endosperm (Ranson, Walker & Clarke, 1960). At higher [CO₂], activity of the mitochondrial pyruvate dehydrogenase complex and/or citrate synthase was also inhibited, but other mitochondrial enzymes were not affected. Storage of *P. communis* fruit in elevated [CO₂] prevented the increase in succinate dehydrogenase amount and/or activity observed during storage in normal air (Frenkel & Patterson, 1973). In *Malus* fruits, CO₂ inhibited succinate (but not malate) metabolism (Shipway & Bramlage, 1973; Monning, 1983), while Miller & Hsu (1965) concluded that for *Brassica oleracea*, mitochondrial ‘dehydrogenases in general’ are CO₂-sensitive, although their results were also for very high [CO₂]. In sum, succinate dehydrogenase may be particularly sensitive to high [CO₂].

Possible bases for direct effects of CO₂ on respiration

A change in C may alter intracellular pH, which in turn could affect many components of metabolism, including respiratory enzyme activity. According to the review by Bown (1985), however, moderate changes in ambient [CO₂] are unlikely to perturb intracellular pH. In many of the experiments involving very high [CO₂] cited earlier, pH was controlled, so effects of pH on respiratory activity can be discounted.

Respiratory (and other) enzymes may be most sensitive to CO₂ outside the concentration range normally experienced by the enzymes. This is supported by the fact that only small changes in ambient [CO₂] are required for effects on leaf respiration, whereas root and rhizome respiration rate may be unaffected by much higher [CO₂], as long as it remains within the range normal for that tissue (Bown, Boulter & Coult, 1968; Palta & Nobel, 1989), and bulky fruit respiration may be unaffected by [CO₂] on the order of 10000 cm⁻³, which is, however, below concentrations accumulating within such fruits during normal metabolism (e.g. Solomos, 1987). When [CO₂] is increased above levels normally experienced by roots, rhizomes and fruits, respiration in those organs is affected. But what might explain the tissue-specificity?

Respiratory enzymes potentially exist in multiple forms or isoenzymes (succinate dehydrogenase/Complex II is a good candidate due to its complex structure) and different isoenzymes may be dominant in different tissues, i.e. leaves, rhizomes, roots and bulky fruits. Moreover, the enzymes involved could be allosteric, and CO₂ could be a negative effect at concentrations above those normal for that tissue (isoenzyme). Specifically, CO₂ could be reversibly bound to the enzyme(s) in the formation of a carbamate (reaction of CO₂ with an amine). Mitz (1979) and Lorimer (1983) discuss the formation of carboxamates and the potential regulation of metabolism by CO₂. Note that Rubisco is activated in part by the reaction of CO₂ and a lysine residue in the formation of a carbamate (Lorimer, 1983), and that this occurs at [CO₂]’s below atmospheric (i.e. the [CO₂] in chloroplasts). It is suggested that respiratory enzymes could be inactivated at similar [CO₂]’s. Evidence for direct effects of CO₂ on respiratory enzymes could be found in the inhibition of uncoupled respiration, but such experiments have not been reported.

Direct interactions between CO₂ and respiratory enzymes are outside the realm of respiratory control by ADP recycling or carbohydrate level, but direct effects of CO₂ on respiration that are consistent with respiratory control can also be considered. For example, carboxamate formation could modify mitochondrial nucleotide translocase (ADP-ATP antiport), representing a direct effect on respiratory control. Direct effects could be on maintenance and growth processes, not respiratory enzymes. Membranes may be readily affected by CO₂ (Mitz, 1979), which could result in altered rates of transport and gradient maintenance processes, leading to altered respiration rate through respiratory control mechanisms.

Dark CO₂ fixation

Dark fixation of CO₂ into organic acids, a common phenomenon even in non-CAM plants, could be enhanced by increased C. An increase in dark fixation would decrease the CO₂ efflux rate and could be interpreted as a decrease in respiration rate if some independent measure of respiration or dark fixation were not made. The rate of dark fixation might be affected for reasons other than an increase in C, however. For example, if the nitrogen metabolism of a plant is altered by elevated-CO₂, dark fixation could change appreciably (Hammel, Cornwell & Bassham, 1979).

Results of the experiments by Gale (1982) indicate that not all (or perhaps any) of the decrease in CO₂
efflux caused directly by elevated \([CO_2]\) is due to enhanced dark \(CO_2\) fixation, but that respiration (and its functions) is indeed inhibited. Concomitant measurements of apparent respiration and dark fixation under varying \(C\) (in the relevant range) are needed. During such experiments, close attention should be paid to the nitrogen status of the tissues involved.

Interactions between temperature and direct effects

The direct effect of \([CO_2]\) on apparent respiration rate may be temperature dependent. As temperature was increased from 30 to 45°C, the relative, direct inhibition of respiration by \(CO_2\) diminished in \(Stylosanthes humilis\) (Begg & Jarvis, 1968) due to a loss of respiratory sensitivity to temperature above 40°C in \(CO_2\)-free air. Reuveni & Gale (1985) observed a smaller percentage inhibition of \(Medicago sativum\) shoot respiration by \(CO_2\) at 25 compared to 19°C. Contrary to these results, respiration was stimulated by \(CO_2\) (comparing 140, 300 and 520 cm\(^3\) m\(^{-3}\)) in \(Pisum sativum\) at and below 30°C but was inhibited at and above 36°C (Hellmuth, 1971). (Hellmuth’s paper is apparently the only one to report a direct stimulation of respiration by increased \([CO_2]\) near atmospheric levels.) Because data are limited, and contradictory, interactive effects of temperature and \([CO_2]\) on respiration deserve study, especially since warming will occur through the next century.

In summary, there is evidence that a moderate change in \([CO_2]\) at near atmospheric levels can directly affect apparent respiration rate. Mechanisms potentially responsible for these effects include: (1) altered intracellular pH; (2) direct interactions between \(CO_2\) and respiratory enzymes (e.g. the formation of carbonates); (3) direct interactions between \(CO_2\) and processes consuming respiratory products, perhaps involving membrane changes; and (4) increased dark \(CO_2\) fixation. Firm evidence for or against any of these mechanisms, within the context of increasing atmospheric \([CO_2]\), is lacking.

Ethylene biosynthesis

In addition to the effects discussed thus far, \(CO_2\) could also influence respiration rate via effects on ethylene biosynthesis. Although the biochemical bases for respiratory responses to ethylene are unclear, for the present purposes it is sufficient to know that ethylene is a strong promoter of respiration, and that \(CO_2\) can affect ethylene biosynthesis. As with effects of \(CO_2\) on respiration rate, the study of \(CO_2\) effects on ethylene biosynthesis have involved a range of \([CO_2]\)’s, methodologies, and tissues, and have produced a range of results (e.g. Bassi & Spencer, 1982; Philosoph-Hadas, Aharoni & Yang, 1986; Chevery et al., 1988; Sisler & Wood, 1988). Whether increasing atmospheric \([CO_2]\) will alter ethylene biosynthesis in the coming century is unknown.

\(CO_2\), respiration and stress

Carbon dioxide is only one component of the fossil fuel problem. Air pollutants arising from fossil fuel use are likely to increase in concentration and geographic distribution in the future. Since respiration may be required for the repair of air pollution injury (Amthor, 1988; Coleman, Mooney & Gorham, 1989), any direct inhibition of respiration by elevated \([CO_2]\) could exacerbate air pollution damage. Conversely, increased carbohydrate levels under elevated \([CO_2]\) might result in enhanced repair of air pollution injury (Sutton & Ting, 1977).

With respect to heat stress, Gale (1982) has shown that a direct inhibition of \(Xanthium strumarium\) leaf respiration by elevated \([CO_2]\) (640 versus 320 cm\(^3\) m\(^{-3}\)) during a high temperature treatment in the dark resulted in physiological damage. This was probably the result of a decrease in the production or use of respiratory products required in repair (maintenance) processes.

Implications for the present

Respiration in a future world is the focus of this paper, but the topic of \([CO_2]\) effects on respiration has implications for the present. A technique not uncommon for estimating respiration rate is to monitor \(CO_2\) efflux into \(CO_2\)-free air in the dark (e.g. Gifford, 1977; Hrubec et al., 1985). This method probably overestimates the rate of respiration under ambient \([CO_2]\). Measurements of \(O_2\) consumption in solution allow buildup of dissolved \(CO_2\) from respiration, which could itself inhibit respiration (see Bown [1985] for a related discussion). During the dark period in growth chambers and glasshouses, \([CO_2]\) often becomes elevated, a fact that is relevant to physiological and growth studies carried out in such environments. Moreover, plants may be exposed to ‘elevated \(CO_2\)’ in the field at the present time; during the night when wind speed is low \([CO_2]\) may be several hundred cm\(^3\) m\(^{-3}\) above daytime levels (Reicosky, 1989).

Concluding remarks

Available data suggest that moderate changes in atmospheric \([CO_2]\) can have an appreciable impact on the rate of higher plant respiration. This is an important issue with regard to increasing atmospheric \([CO_2]\) and the global carbon budget since respiration is a large component of the carbon balance of plants.

Indirect and direct effects of \([CO_2]\) on respiration are apparent, although data are limited. Increases and decreases in respiration rate have resulted from an increase in \([CO_2]\), and effects of \([CO_2]\) on respiration vary among species (Cournic & Jarvis, 1972; Gifford et al., 1985; Bunce, 1990; B. G. Drake, personal communication), highlighting the need for experiments involving a range of ecologically significant species. The interactive effects of other environmental factors (e.g.
temperature) with respiratory responses to $[\text{CO}_2]$ are largely unknown and deserve study.

In a future, higher-$\text{CO}_2$ world, it is the balance among respiratory responses to $[\text{CO}_2]$ that will be important. That balance cannot be predicted with present knowledge. Thus, whole-plant carbon budgets in a higher-$\text{CO}_2$ world are also not predictable; much additional research is needed.

References


