

## The effect of the build-up of carbon dioxide in the atmosphere on crop productivity

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### Introduction: global changes, their relative magnitudes and certainties

#### *The atmosphere past and present*

Over the last one or two billion years, the biosphere has been responsible for depleting the atmospheric CO<sub>2</sub> content from at least 10 to 30 times its present partial pressure to a mere 0.03% of the atmospheric volume (1) despite continuous emissions of CO<sub>2</sub> from volcanoes and other leakage points mostly associated with movements of tectonic plates. In consequence, carbon has accumulated in reduced form as coal and hydrocarbons in sedimentary rocks, and in the oxidised form of shell-carbonates in chalk and limestone. At the same time photosynthesis has been responsible for building up oxygen from virtually zero to 21% of the atmosphere. This O<sub>2</sub> concentration now seems to be in dynamic equilibrium between its generation by vegetation and its removal in the course of oxidising minerals exposed by weathering (1). More recently in the 160,000 years before industrialization started, the CO<sub>2</sub> concentration in the atmosphere has varied between about 180 ppm and about 340 ppm in association with ice-ages and interglacials (2). In fact, during the entire glacial era, atmospheric CO<sub>2</sub> concentration may have been around 200 ppm for many tens of thousands of years. So land-plant metabolism may well be adapted to substantially lower CO<sub>2</sub> concentrations than those into which we are now moving. Agriculture started about 10,000 years ago, soon after CO<sub>2</sub> concentration increased rapidly from 200 ppm to almost 300 ppm during the last glacial retreat.

Before industrialization started last century, the atmospheric CO<sub>2</sub> concentration was about 280 ppm (3). Now, following the razing of 15-20% of the world's forests (4) and the large-scale burning of fossil fuels, the CO<sub>2</sub> concentration has increased 25% to over 350 ppm. It is currently increasing by about 1.5 ppm per annum, although last year the concentration increase suddenly jumped to an unprecedented 2.4 ppm p.a.(5). The reason for that current surge of increase is unknown (at the time of writing, 20 May 1989).

#### *Relative rates of atmospheric change for plant productivity*

To state the current rate of CO<sub>2</sub> increase in terms appropriate to photosynthetic productivity of crops, we must recognise that net CO<sub>2</sub> uptake is positive only above the CO<sub>2</sub> compensation point of 50 to 60 ppm for C<sub>3</sub> plants. Thus the growth-effective CO<sub>2</sub> concentration is increasing by  $1.5/(350-50) = 0.5\%$  per annum.

How does this compare with the rate of increase in temperature owing to the greenhouse effect? According to the general circulation models, each doubling of CO<sub>2</sub> concentration will cause a temperature increase of about 3°C ? 1.5°C (6). The relationship is logarithmic and amounts to a temperature increase of 0.013 ? 0.006°C per ppm CO<sub>2</sub> at the present concentration of 350 ppm. Now considering both CO<sub>2</sub> and the other radiatively active trace gases like chlorofluorocarbons, methane, nitrous oxide and tropospheric ozone, the annual increase of greenhouse-effect gases is currently equivalent to about 2.2 ppm (CO<sub>2</sub> equivalents) p.a.

Thus the model-based estimate of current temperature increase owing to the combined anthropogenic greenhouse effect gases is 0.029 ? 0.013°C p.a. on a global average basis. To compare this rate, in terms of plant effectiveness, we need to use a base temperature for plant growth and development and an average temperature at which plants are growing. The average annual temperature over vegetated land is about 18°C. In Australia it varies from about 24°C in Cairns, 17°C in Perth, to 12°C in Hobart. The daily base temperature for C<sub>3</sub> plant growth and development is often taken in the 0 to 3°C range though it can be higher for species adapted to warmer climates. But the annual average base temperature is lower than the daily average base temperature during the growing season. One can readily appreciate

the reason by considering places like the tundra and boreal coniferous forests which grow at annual average temperatures of -12 to 0°C. Of course, the base temperature for an adapted species tends to increase with the annual average temperature of the place to which it is adapted. For the purposes of broad comparison let us make the plausible assumption that Australian crops generally grow in places that are between 10 and 20°C above their annual average base temperature. Then the annual rate of "phytotemperature" increase owing to the greenhouse effect warming is in the range in 0.29 ? 0.13% p.a. to 0.15 ? 0.06% p.a. Overall then, combining the extremes of these ranges, plant-effective temperature is increasing by 0.26 ? 0.16%p.a. This is less than the 0.5% p.a. increase in CO<sub>2</sub> concentration over the last decade. Furthermore, whereas the CO<sub>2</sub> increase is absolutely certain everywhere, the temperature increase is not certain even on a globally averaged basis. In any specific region greenhouse-dependent temperature change is nowhere near predictable yet.

How fast might rainfall be changing in response to greenhouse gases? This is more tenuous than temperature change, but the current general circulation models suggest a 5-12% increase in global average precipitation for a CO<sub>2</sub> doubling. Again including the non-CO<sub>2</sub> trace gas increases; this is equivalent to a current rate of increase of annual average rainfall of 0.02 to 0.05% p.a. That is, the actual rate of increase of plant effective CO<sub>2</sub>, at 0.5% p.a., is at least 10x greater than the predicted rate of increase in rainfall, 0.05% p.a. or less. Of course, we hear much about overall predicted rainfall increase being unevenly distributed, with some places even getting a decrease in rainfall. This is probably true, but the precision of such predictions is still far too low to develop predictive models of impact for any specific region like S.W. Australia, say.

While the general circulation model results suffer from low credibility for any specific region, their prediction of overall increased rainfall in concert with warming is nevertheless strongly supported by palaeo-climatic correlations. That is, palaeo-botanical evidence indicates that there is a strong positive relationship between global temperature and rainfall. As temperature rose in the geological record so did rainfall.

Concurrently, grasslands gave way to encroachment by forest. The opposite applied during cooling periods (7).

These broad comparisons of rates of change, and of levels of certainty in such changes, have implications for modelling and prediction of impacts of climate change. By the time temperature and rainfall have changed sufficiently to be discernible against the background of normal variability, the atmospheric CO<sub>2</sub> concentration will be substantially higher than it is now. For example, CO<sub>2</sub> concentration has increased by over 20% since World War 2 while global average phytotemperature has only increased by 1 to 3 % (0.2-0.3°C) in that time owing to an intervening cooling period. Crop and ecosystem models that might be used for predicting the impact of any change in rainfall and temperature on productivity have been constructed on the basis of observations made on plants growing in CO<sub>2</sub> concentrations of 300-340ppm not the higher concentrations that will be expected. So if CO<sub>2</sub> concentration has any influence on plant growth, it will also have influence on the functional relationships between plant productivity and temperature and rainfall. Furthermore, if CO<sub>2</sub> concentration interacts with temperature and water on plant growth, the equations will require even more modification to be applicable. Parenthetically, I should add that since vegetation plays a significant part in energy and momentum exchange at the Earth's surface, global vegetation response to the increasing CO<sub>2</sub> will also play a part in modulating climate. Unfortunately the amount we know about the impact of changes in CO<sub>2</sub>, temperature and rainfall on crop production ranks in reverse order to the magnitude and certainty of these changes. That is, we know much about how field productivity responds to rainfall, something about response to temperature, and relatively little about the responsiveness to CO<sub>2</sub>.

#### *Plant/ CO<sub>2</sub> relationships - a "broad-brush" view*

The acquisition of carbon by plants for reduction to carbohydrates by photosynthesis involves three big compromises that underpin how I view the role of CO<sub>2</sub> concentration in productivity. First evolution has been unable to come up with a differentially permeable outer skin for plants that is permeable to CO<sub>2</sub> but

impermeable to water vapour. Instead it invented stomata. Whenever  $\text{CO}_2$  is allowed into a plant, loss of water is inevitable. The price of  $\text{CO}_2$  diffusion across the air-plant interface is loss of water.

Second, the enzyme that fixes  $\text{CO}_2$  into organic matter requires, in common with all proteins, nitrogen for its structure. It so happens that after about 4 billion years of evolution this enzyme, RUBISCO, is still remarkably inefficient as enzymes go. There has to be a lot of it; so much so that at least a quarter of the plant's N is tied up in this one enzyme. Since most of the non-fertilizer soil N available to vegetation was fixed using energy from the oxidation of organic matter created by RUBISCO in the first place, this is a high price on the inherently inefficient C-acquisition system of the biosphere.

Thirdly, not only is RUBISCO catalytically ineffective as a carboxylase, it is also unable to distinguish between its key substrate,  $\text{CO}_2$ , and the key photosynthetic product,  $\text{O}_2$ . The reaction RUBISCO catalyses with oxygen as substrate produces phosphoglycolate, a metabolite that requires the machinery of the photorespiration cycle to convert into useable form, with the concomitant loss of some  $\text{CO}_2$  thereby wasting some of the energy fixed by the light reactions.

As the biosphere has slowly impoverished the atmosphere of  $\text{CO}_2$ , while poisoning itself with its accumulating waste product,  $\text{O}_2$ , plants have had to adapt metabolically, physiologically, morphologically and developmentally to this less and less bountiful atmospheric environment for plant growth.

Now that man is releasing some of the accumulated reduced carbon back into the atmosphere as  $\text{CO}_2$  derived from fossil fuels, we should expect in principal that the increasing concentration of  $\text{CO}_2$  has the potential to increase biosphere productivity by alleviating the constraints imposed by those three big compromises.

However, it is one thing for there to be a potential and another thing for such a potential to be realised. It could be, for example, that in gradually evolving to cope with diminishing  $\text{CO}_2$  and rising  $\text{O}_2$  levels, plants under field conditions can no longer respond to the suddenly increased atmospheric  $\text{CO}_2$  level to which man is now subjecting the biosphere. Perhaps, plants need further evolution to take advantage of the increasing  $\text{CO}_2$  concentration. If so, then in agriculture, with our capability to accelerate evolution through purposeful breeding, we may have the chance to capitalise on the changes that are occurring. But, in fact, I believe that, even without breeding, many field crops should already be responding positively to the increasing atmospheric  $\text{CO}_2$  concentration.

#### *Plant responses to $\text{CO}_2$ - some details and problems of interpretation*

While the short-term sensitivity of leaf photosynthesis and stomatal conductance is well-established, this knowledge is insufficient to allow prediction of crop yield response to atmospheric  $\text{CO}_2$  increase for several reasons.

- Photosynthesis and stomatal conductance may not be the only primary  $\text{CO}_2$ -sensitive aspects of plant biochemistry and physiology.
- Any positive feedback of leaf area increase, in response to  $\text{CO}_2$  enrichment, cannot be predicted solely from knowledge of  $\text{CO}_2$  effects on photosynthesis.
- The long-term seasonal response of photosynthesis, stomatal conductance and any other  $\text{CO}_2$  dependent phenomena may differ from short term responses (days) on account of acclimation processes.
- Any stimulation of primary production owing to  $\text{CO}_2$  enrichment may not necessarily be partitioned into economic yield.
- The other co-limiting variable factors in crop production, notably water, radiation, nitrogen and phosphorus, temperature, water-logging, soil compaction, acidity etc may attenuate or eliminate the potential productivity gains from  $\text{CO}_2$  enrichment.
- Altered competitive relations between weeds, pest and disease organisms and crops as a result of  $\text{CO}_2$  enrichment may alter the impact on commercial yield.
- Product quality and nutritional value may change in response to  $\text{CO}_2$  enrichment.

- If the predicted greenhouse effect warming comes about, then such secondary changes (and any further repercussions on local climate patterns) would be likely to further modify the primary CO<sub>2</sub> responses.

The state of evidence relating to all these considerations is rather fragmentary and neither available evidence nor space permits full development of all those topics here. Instead I shall develop a selection of specific aspects. I perceive a prevailing view among many agronomists and ecologists imbued with Leibigian concepts of single limiting factors, that most crop and natural vegetation will not exhibit long term response to changed CO<sub>2</sub> concentration because productivity is limited by other factors like water nitrogen or temperature. My research has led me to another view, namely that in many circumstances the efficiency of utilization of scarce plant inputs is limited by carbon availability to plants (8). Detailed reasons for this can be complex but may involve in part the operation of CO<sub>2</sub> sensitive plant processes other than photosynthetic CO<sub>2</sub> fixation.

#### *Non-photosynthetic effects of carbon dioxide*

There are many carboxylases in plant metabolism. Presumably then, there is at least the possibility of non-photosynthetic CO<sub>2</sub> effects on much of plant metabolism. Notably, CO<sub>2</sub> is involved with ethylene formation and action (9). It has long been known that very high CO<sub>2</sub> concentrations (e.g. 10% by vol.) can be used to improve fruit storage. Its effect is probably via inhibiting ethylene production by the fruit (10). But even at normal ambient levels of CO<sub>2</sub>, variation in its concentration can affect ethylene production and action. In leaves, modest increases in CO<sub>2</sub> concentration increase the rate of ethylene production in both C<sub>3</sub> (11,12) and C<sub>4</sub> leaves (13,14). Since ethylene is a potent plant growth regulator, one might expect CO<sub>2</sub> to have developmental or other non-photosynthetic effects. For example, perhaps the observation that sorghum plants grown in 2x normal CO<sub>2</sub> concentration exhibit a slow-down in the rate of flower development (15) might be explained by this mechanism. Perhaps also interference with ethylene production or action in leaves might explain in part the increase in leaf area observed in CO<sub>2</sub>-enriched plants, even in C<sub>4</sub> plants that did not gain a photosynthetic advantage at the leaf level from high CO<sub>2</sub> concentration (16).

Another possibility is that modest levels of CO<sub>2</sub> enrichment may reduce respiration rates in plants just as very high levels of CO<sub>2</sub> inhibit fruit respiration (9). Although the conventional physiological judgement would be that plants grown at high CO<sub>2</sub> levels would probably exhibit enhanced respiration (17) under the stimulus of high levels of tissue carbohydrates, there are several reports of reduced respiration rates of leaves or plants measured in high CO<sub>2</sub> concentrations. Such reports date back as far as 1915 (18), although the earlier work was for high concentrations up to several percent by volume, which is not necessarily pertinent to our present concerns. However, there is a smattering of papers over the last three decades which contain data indicating an inverse relation between dark respiration of leaves or whole plants and CO<sub>2</sub> during measurement. However such data were not the theme of the papers concerned and it was not until 1984 that the phenomenon was explicitly investigated. Then three papers almost concurrently addressed the question. Reuveni and Gale (19) found up to a 38% reduction in dark acclimated respiration of lucerne plants by measuring them in 950ppm CO<sub>2</sub> instead of the 350ppm CO<sub>2</sub> in which they grew. They were even able to demonstrate up to 20% increase in the growth rate of plants grown with 1200ppm CO<sub>2</sub> during the 16 hour night only, with normal air during the day.

In another study (20) the maintenance respiration coefficient of intact subterranean clover plants was reduced by about 25% for plants that had been exposed for several days to 1000ppm rather than 320ppm CO<sub>2</sub>. Similarly Gifford, Lambers and Morison (21) found reduced rates of respiration in wheat plants and wheat roots from plants grown throughout their lives at elevated CO<sub>2</sub> concentration. In the case of the roots, respiration was assessed by oxygen electrode at standard CO<sub>2</sub> concentration. Thus the effect was a feature of the concentration in which the plants grew rather than of the immediate CO<sub>2</sub> environment during measurement. It was found to be attributable to less engagement of the alternative pathway of respiration. This pathway is a seemingly wasteful one that is almost universally present in plant tissues to some degree or other though usually not fully operative.

In our current investigations to evaluate the generality and quantitative significance of this respiratory suppression by high CO<sub>2</sub> to the diurnal carbon balance of diverse species, we are concluding that it is a

common phenomenon which in some species will need to be taken into account in productivity models under elevated carbon dioxide (22).

#### *Interaction between CO<sub>2</sub> and other growth limiting external factors*

With the possibility of CO<sub>2</sub> affecting other processes that photosynthesis, such as photorespiration, dark respiration and aspects of development it is not surprising that there are complex interactions between CO<sub>2</sub> and other co-limiting environmental factors.

#### *Water*

The expectation, based on the water loss/ CO<sub>2</sub> gain compromise faced by plants, that high CO<sub>2</sub> concentration increases water use efficiency of dry matter production, is confirmed experimentally for diverse species such as wheat (23,24), Pinus species (25,26), and many other species including C<sub>4</sub> species (27,28). However, quantification of this phenomenon under open field conditions for which direct large scale experimentation is infeasible is being held up by our inability to quantify the feedbacks that impinge on broad-acre transpiration when stomatal conductance is reduced by higher atmospheric CO<sub>2</sub> concentration.

#### *Nitrogen*

Experimental evidence also supports the theoretical expectation that high CO<sub>2</sub> concentration may increase nitrogen use efficiency of plant growth that is restricted by nitrogen nutrient supply. For example, this has been shown for cotton (29), perennial ryegrass, and potato (30), nodulated legumes such as soybean (31). However, there remains doubt about the field applicability of such controlled environment studies for several reasons. For example, in many studies nutrient availability to experimental plants is restricted by regularly supplying various low concentrations (as opposed to amounts) of nutrient. However, in the field it may be closer to reality that a certain total amount of nitrogen nutrient comes available through the growing season (by organic-N mineralization possibly supplemented by fertilizer) and that most of this available N is consumed by the crop. If so, the concentration of soluble N may not be so relevant. It seems that under that type of N restriction, crop growth is still increased by CO<sub>2</sub> supplementation though by a lesser proportion than when N-nutrient supply is not restrictive (32). However, a corollary of this is that the carbon to nitrogen ratio of the biomass, and hence the organic litter deposited on and in the soil, would be expected to increase. An untested repercussion of this, at least for perennial, little fertilized systems like some permanent pastures, may be that the rate of mineralization is slowed down and nitrogen is even less available for future seasons' growth.

#### *Phosphate*

A theoretical basis for predicting the character of the interaction between growth-limiting phosphate levels and CO<sub>2</sub> does not exist. Data is sparse and conflicting. In some studies phosphate-restricted plant growth has been unresponsive to CO<sub>2</sub>. However, for other species, or genotypes of a single species, phosphate deficiency has not appreciably altered the percent increase of growth under enriched CO<sub>2</sub> conditions relative to high phosphate control (30,33,34). This interaction is in need of much more work.

#### *Temperature*

Details of the interaction between CO<sub>2</sub> and temperature during growth are also confused in the literature, partly because of the high demand for experimental controlled plant growth facilities to set up factorial CO<sub>2</sub> x temperature combinations.

Several reviewers have ventured generalizations about the character of the CO<sub>2</sub> x temperature interaction in plant growth. Strain and Cure (17) and Warrick and Gifford (35), based on growth experiments and extrapolating from theory and experiments with C<sub>3</sub> leaf net photosynthesis (36), suggested that the relative enhancement due to high CO<sub>2</sub> would increase progressively with temperature even beyond the

temperature optimum for growth. It was not specified, however, at how low a temperature growth response to CO<sub>2</sub> enrichment would be zero. However, Kimball (37) concluded that the relative growth enhancement owing to high CO<sub>2</sub> concentration is fairly constant across the normal range of crop growth temperatures. Aeock and Allen (38) expressed another view that when temperature is above or below the broad rather flat-topped optimum range for net photosynthesis, growth is insensitive to increased CO<sub>2</sub> concentration. Thus as, under that model, one considers progressively warmer conditions starting from base temperature, CO<sub>2</sub> responsiveness starts at zero, changes fairly abruptly to a substantial positive value and then changes back to zero responsiveness above the optimal temperature for net photosynthesis.

Those are three markedly different models each offered tentatively in the absence of adequate data. In support of the first model (progressive increase of responsiveness with increasing temperature), Idso et al., (39) published evidence using open-topped field chambers indicating that the "CO<sub>2</sub> modification factor" (i.e. unity = no CO<sub>2</sub> effect on growth rate) increased linearly with temperature using a composite data set for carrot, radish, cotton, water hyacinth and water fern. Remarkably the straight line relationship crossed the zero CO<sub>2</sub> response line at 18.5°C for pooled data (39). However, for separate studies of carrot and radish alone the intercept was at 11-12°C (40). This means, taking these results on face value, that for such plants growing at below 18.5°C or 12°C, increasing CO<sub>2</sub> concentration would decrease yield. The relationship was steep such that plants growing, for the pooled data (39), at 12°C would experience 50-60% reduction in growth rate, while plants growing at 30°C would have a 100% growth enhancement when growing at 640 ppm CO<sub>2</sub> instead of 340 ppm. If this were true and general, these results would have profound negative implications for future agriculture in cool environments like Tasmania, but strongly positive implications of CO<sub>2</sub> increase for tropical agriculture. To some extent any greenhouse-effect warming would mitigate the problem in cool areas.

However, there is no obvious physiological explanation of the negative effect of high CO<sub>2</sub> on growth at cool temperatures and there is other evidence that plants growing under cool conditions can respond positively to CO<sub>2</sub>. For example in wheat we have found that communities growing at 12°C (8) and at an average of 15°C (32) can certainly respond by 20-30% increased growth and yield under twice normal CO<sub>2</sub>. And in a diverse range of other crop species grown as individual plants at 19/14°C we have found doubling the CO<sub>2</sub> concentration increased growth by 44-132% (27).

For chilling sensitive species there is an unexplained phenomenon: growth at high CO<sub>2</sub> appears to buffer plants against the photosynthetic impact of chilling. The C<sub>4</sub> grass *Echinochloa crus-galli* grown at 28/22°C suffers a marked reduction in net photosynthesis rate following a 7°C night chill. It takes 4-5 days for the plant to recover normal photosynthetic rates. However, plants that had been grown under 675 ppm CO<sub>2</sub> exhibited no such set-back after a 7°C night (41). Furthermore, low latitude ecotypes of that C<sub>4</sub> species grown under a severely growth restricting low temperature of 21°/15°C, was significantly enhanced in growth after 48d at 675 ppm CO<sub>2</sub> compared with normal CO<sub>2</sub>. In contrast, the same ecotypes grown at 28°/22°C had no further growth enhancement from CO<sub>2</sub> enrichment as is expected theoretically for a C<sub>4</sub> species (42). This result differs from all three generalizations mentioned above. Similarly for the chilling sensitive C<sub>3</sub> dicot, okra (*Abelmoschus esculentus*), increasing the CO<sub>2</sub> concentration during growth up to 675 or 1000 ppm reduced the temperature regime below which no growth and yield occurred from 26°/20° to 20°/14°C (43).

Turning to supra-optimal temperatures, the generalizing models offer two diametrically opposed options for growth response to CO<sub>2</sub> a) a zero response to CO<sub>2</sub> or b) the strongest response exceeding direct proportionality with the CO<sub>2</sub> increment. Surely this one can be resolved. Unfortunately data is minimal. One test came about in experiments on heat-treating grape vine plants to rid them of viruses (44). Plants of *Vitis vinifera* and of a tropical vine *Leea brunoniana* grew poorly at the supra-optimal temperatures of 37-40°C used in the heat treatment experiments. However by increasing the CO<sub>2</sub> concentration to about 1200ppm during growth, dry weight increase was more than doubled. The effect was especially pronounced for the roots where dry weight increased many-fold under CO<sub>2</sub> enrichment for grape. These results are inconsistent with the notion that at high temperature extremes plant growth becomes insensitive to CO<sub>2</sub> enrichment.

There are good reasons to explain such response of plant growth that is restricted by high temperature. First, solubility of gases in water decreases as temperature rises. So there is less dissolved CO<sub>2</sub> at the carboxylation surface at higher temperatures. Furthermore, the solubility decline with temperature increase is steeper for CO<sub>2</sub> than for O<sub>2</sub>. Thus the ratio of oxygenation to carboxylation may increase with temperature, thereby increasing the ratio of photorespiration to photosynthesis. Increasing the CO<sub>2</sub> concentration is therefore relatively more effective at increasing net photosynthesis at high temperature than at lower temperature. Another reason is that the temperature response of the kinetic constants of the carboxylase and the oxygenase reactions of RUBISCO happen to be such that photorespiration is favoured over photosynthesis more as temperature increases (45). At high temperature, plants are more likely to encounter water stress than at lower temperatures. Therefore the stomatal closing effect of high CO<sub>2</sub> is likely to be of greater value for sustaining growth of plants at high temperature than for plants at moderate temperature. Another aspect relates to source-sink interrelationships as a function of temperature. Within the normal physiological range, photosynthesis is commonly found to have a fairly flat-topped temperature response curve in many species, whereas sink demand progressively increases with temperature at least until it reaches damaging values. Thus at high temperatures sink growth can become short of assimilate supply to meet potential sink growth. Then CO<sub>2</sub>-stimulated photosynthesis would be effective at meeting that high potential. In summary there are many reasons for doubting the Acock and Allen model (38) for zero CO<sub>2</sub> sensitivity of growth at high

temperature. Clearly, more detailed controlled environment studies are required on the CO<sub>2</sub> x temperature interaction.

### **Concluding comments**

I have discussed the CO<sub>2</sub>-temperature interactions in some detail to highlight several points. First, that the concept that when growth is restricted by other environmental factors it cannot also be CO<sub>2</sub>-dependent is false. Second, that in the case of some environmental limitations growth is relatively more CO<sub>2</sub>-dependant than when the other factor is optimally available. Third, that as the global temperature increases plant productivity may become relatively more CO<sub>2</sub> sensitive. However, this last possibility will be countered by the fact that as CO<sub>2</sub> concentration increases photosynthesis moves up its hyperbolic response curve closer to the saturation point. Fourth, that as CO<sub>2</sub> concentration increases, the optimum temperature for net photosynthesis of C<sub>3</sub> species is likely to increase too. And fifth, there is little point in models of the impact of global change being developed far ahead of the experimental results on which they must be based. We have a long way to go in understanding and quantitatively describing CO<sub>2</sub> and climate change effects on productivity and inter-species competition. However effective progress would be accelerated if modellers of the impact of climate change and experimentalists studying pertinent phenomena could work more closely together.

Finally, a main thrust of this paper has been to demonstrate that direct CO<sub>2</sub> effects are likely to be of considerable significance to the agricultural impact of global atmospheric change, at least as great as that of average temperature and rainfall change. However, whereas the increase in CO<sub>2</sub> is uniform, smooth, steady and relatively predictable, change in temperature and rainfall patterns and other climatic attributes is unlikely to be specially uniform, smooth and steady and is as yet unpredictable in any given region. While overall warmer wetter conditions are expected, in any one location drier and even cooler conditions and different seasonal patterns are possible. Therefore surprises, and not necessarily welcome ones, may be in store for agricultural systems superimposed on the potential productivity gains from the carbon dioxide fertilizing effect.

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