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## Review

# Rising atmospheric carbon dioxide concentration and the future of C<sub>4</sub> crops for food and fuel

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Crops with the C<sub>4</sub> photosynthetic pathway are vital to global food supply, particularly in the tropical regions where human well-being and agricultural productivity are most closely linked. While rising atmospheric [CO<sub>2</sub>] is the driving force behind the greater temperatures and water stress, which threaten to reduce future crop yields, it also has the potential to directly benefit crop physiology. The nature of C<sub>4</sub> plant responses to elevated [CO<sub>2</sub>] has been controversial. Recent evidence from free-air CO<sub>2</sub> enrichment (FACE) experiments suggests that elevated [CO<sub>2</sub>] does not directly stimulate C<sub>4</sub> photosynthesis. Nonetheless, drought stress can be ameliorated at elevated [CO<sub>2</sub>] as a result of lower stomatal conductance and greater intercellular [CO<sub>2</sub>]. Therefore, unlike C<sub>3</sub> crops for which there is a direct enhancement of photosynthesis by elevated [CO<sub>2</sub>], C<sub>4</sub> crops will only benefit from elevated [CO<sub>2</sub>] in times and places of drought stress. Current projections of future crop yields have assumed that rising [CO<sub>2</sub>] will directly enhance photosynthesis in all situations and, therefore, are likely to be overly optimistic. Additional experiments are needed to evaluate the extent to which amelioration of drought stress by elevated [CO<sub>2</sub>] will improve C<sub>4</sub> crop yields for food and fuel over the range of C<sub>4</sub> crop growing conditions and genotypes.

**Keywords:** climate change; photosynthesis; CO<sub>2</sub> fertilization; maize; sorghum; food security

## 1. INTRODUCTION

Climate change in the twenty-first century will impact many aspects of the human and natural world (IPCC 2007), but our well-being will arguably be most influenced by the effects of climate change on agriculture (Cline 1992). This problem will compound the current challenges to food supply, which led to approximately 825 million people being undernourished in 2006 (Food and Agriculture Organization of the United Nations (FAO), <http://faostat.fao.org/>). Spikes in food prices during 2007–2008 occurred in large part because of (i) increasing demand from a growing global population, (ii) increasing demand for meat and therefore grain to feed livestock, (iii) rising energy and fertilizer prices, and (iv) increased demand for crops to produce biofuels (MacKenzie 2008; World Bank 2008a). As a result, a further 44 million people are projected to become undernourished during 2008, with long-term consequences resulting from the reduced health and education of children in the poorest households (World Bank 2008b). It is important to have reliable estimates of how climate change will impact crop yields so that the necessary action can be taken to minimize the negative consequences and maximize the benefit from any positive consequences of climate change on crop yield. Taking action through traditional breeding or biotechnology to develop crops that are better adapted to future growing conditions will be aided by understanding the mechanisms driving crop responses to climate change (Ainsworth *et al.* 2008a).

Rising concentrations of CO<sub>2</sub> ([CO<sub>2</sub>]) in the atmosphere are driving the global warming and climate change that will negatively impact crop yields in many parts of the world this century. However, elevated [CO<sub>2</sub>] in and of itself also has beneficial physiological effects on crops. The response of C<sub>4</sub> species to many factors of climatic and atmospheric changes, including temperature, precipitation, elevated [CO<sub>2</sub>] and land use, was comprehensively reviewed by Sage & Kubien (2003). This paper aims to highlight the uncertainty about how C<sub>4</sub> crops will be impacted by rising [CO<sub>2</sub>] in the future and review new knowledge on this subject arising from free-air CO<sub>2</sub> enrichment (FACE) studies under field conditions. This topic deserves greater attention because C<sub>4</sub> crops (i) contribute a significant fraction of global food supply, (ii) are particularly important to food production in hot, dry countries where undernourishment is already a problem, and (iii) are playing an increasingly important global role as a biofuel feedstock.

## 2. THE CURRENT AND FUTURE IMPORTANCE OF C<sub>4</sub> CROPS TO FOOD AND FUEL SUPPLY

Currently, the most important C<sub>4</sub> crops are maize (*Zea mays* L.), sorghum (*Sorghum bicolor* [L.] Moench), millets (mainly *Pennisetum glaucum* [L.] R. Br., *Setaria italica* [L.] P. Beauvois, *Panicum miliaceum* L., *Eleusine coracana* L.) and sugar cane (*Saccharum officinarum* L.). C<sub>4</sub> crops were responsible for 40 per cent (approx. 800 million metric tonnes) of the world's grain harvest in 2006 (United States Department of Agriculture, Foreign Agricultural Service (USDA-FAS), [www.fas.usda.gov/wap/current/toc.asp](http://www.fas.usda.gov/wap/current/toc.asp)), which indicates the global significance of future climate

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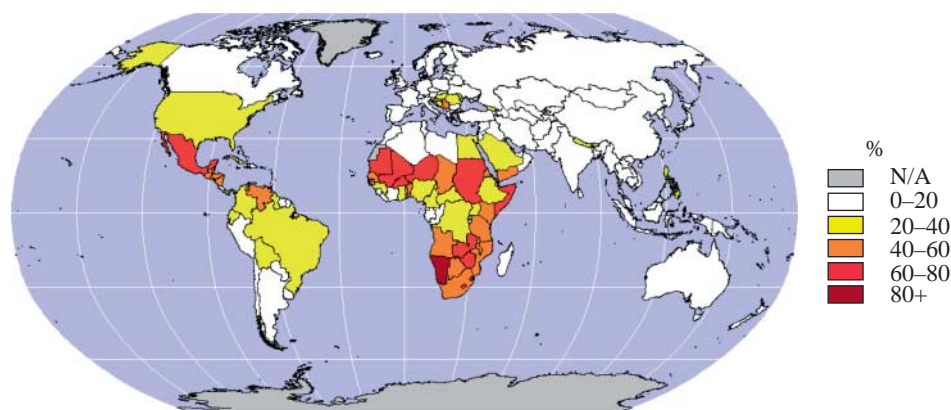


Figure 1. Percentage of agricultural land used for the production of C<sub>4</sub> crops in 2006. Estimates of national C<sub>4</sub> crop production area were taken from the ProdSTAT database, FAO (<http://faostat.fao.org>) (grey, n.a.; white, 0–20%; yellow, 20–40%; orange, 40–60%; red, 60–80%; dark red, +80%).

change impacts on production from C<sub>4</sub> crops. However, there are substantial regional and country-to-country differences in the importance of C<sub>4</sub> crops to food production (figure 1). The largest fraction of the world's C<sub>4</sub> grains is produced in the fertile Midwest region of the USA (approx. 34% in 2006; USDA-FAS), using intensive agricultural practices. However, the countries that will probably be most affected by the response of C<sub>4</sub> crops to climate change are in Africa and Central America (figure 1). More than 25 countries in these regions devote 50–88 per cent of their agricultural land to the production of C<sub>4</sub> crops. The less favourable production environment along with socio-economic challenges in these regions limit productivity, with the yields for maize in Ethiopia (2.30 tonnes per hectare), Mexico (3.03 tonnes per hectare), Nigeria (1.66 tonnes per hectare) and Zimbabwe (0.56 tonnes per hectare) being merely 6–32 per cent of that in the USA in 2006 (9.36 tonnes per hectare; USDA-FAS). Critically, agricultural productivity and human well-being are most tightly linked in the poorest countries, many of which are found in Africa and Central America (Rosegrant *et al.* 2006). In these poor countries, any reductions in C<sub>4</sub> crop productivity resulting from climate change will have direct and substantial negative consequences. This is emphasized by The World Bank identifying increased agricultural production in the world's poorest tropical nations as an essential component of meeting the time-bound targets of the Millennium Development Goals to: eradicate extreme poverty and hunger; achieve universal primary education; empower women; reduce child mortality; improve maternal health; and combat HIV and malaria, while ensuring environmental sustainability (Rosegrant *et al.* 2006).

Maize is by quantity the most important C<sub>4</sub> grain crop (approx. 712 million metric tonnes in 2006), with production occurring in more than 160 countries (FAO 2008). Sorghum and millet are less important on a global scale, but are very important to human well-being, contributing significant fractions (20–50%) of grain production in arid countries such as Sudan, Niger and Burkina Faso. In addition to these grain crops, sugar cane is a C<sub>4</sub> crop that is used for both food and fuel. Approximately 60 per cent of the world's sugar cane is produced in Brazil, India, China and Thailand (FAO). In Brazil, approximately half of the crop is used for food and the other half is used to produce approximately 16 billion litres of ethanol per year, which accounts for

approximately 40 per cent of liquid fuels within the country (Goldemberg 2007). Meanwhile, 13 per cent of the US maize crop was used to produce a similar volume of ethanol in 2005 (Somerville 2006). The use of sugar cane and maize as sources of fuel in addition to food has brought an increase in the area of land planted with these C<sub>4</sub> crops (Searchinger *et al.* 2008).

It is highly likely that both food and biofuel production in the future will be more dependent on C<sub>4</sub> crops than today. By 2020, global demand for maize as a food supply is projected to exceed that for wheat and rice, making it the world's most important crop (Pingali 2001). The production of ethanol from sugar cane in Brazil and maize in the USA is now being followed by proposals to use C<sub>4</sub> perennial grasses as cellulose feedstocks for energy generation. This has the potential to substantially increase the contribution of C<sub>4</sub> crops to agriculture. For instance, over 12 million hectares of land are expected to be available for biomass crop production in the 25 European Union countries in 2010 (European Environmental Agency 2007), and converting approximately 22 million hectares of land to perennial crops in the USA could help to produce the approximate 1 billion tons of biomass needed to produce enough cellulosic ethanol to replace 30 per cent of petroleum consumed each year (Perlack *et al.* 2005). On a global scale, there are 385–472 million hectares of abandoned agricultural land that could be used for production of biofuel crops without removing land from food production or causing deforestation (Campbell *et al.* 2008). The C<sub>4</sub> grasses switchgrass (*Panicum virgatum*; Lemus *et al.* 2002) and Miscanthus (*Miscanthus × giganteus*; Heaton *et al.* 2008) have been proposed as good candidates to grow on these lands as biofuel crops. Even if only half of the available abandoned land (190–235 million acres) was used to grow such crops, this would nearly double the global land area of C<sub>4</sub> crops.

### 3. ELEVATED [CO<sub>2</sub>] AS AN IMPORTANT ELEMENT OF CLIMATE CHANGE IMPACTS ON CROP YIELDS

The production environment for crops in the future will be altered by climate change in numerous ways, including greater atmospheric [CO<sub>2</sub>], greater temperatures, altered timing and quantity of water availability, greater tropospheric [O<sub>3</sub>] and altered incidence of pests, diseases and pollinators. These factors will combine with agricultural management decisions, improved agronomy, new germ

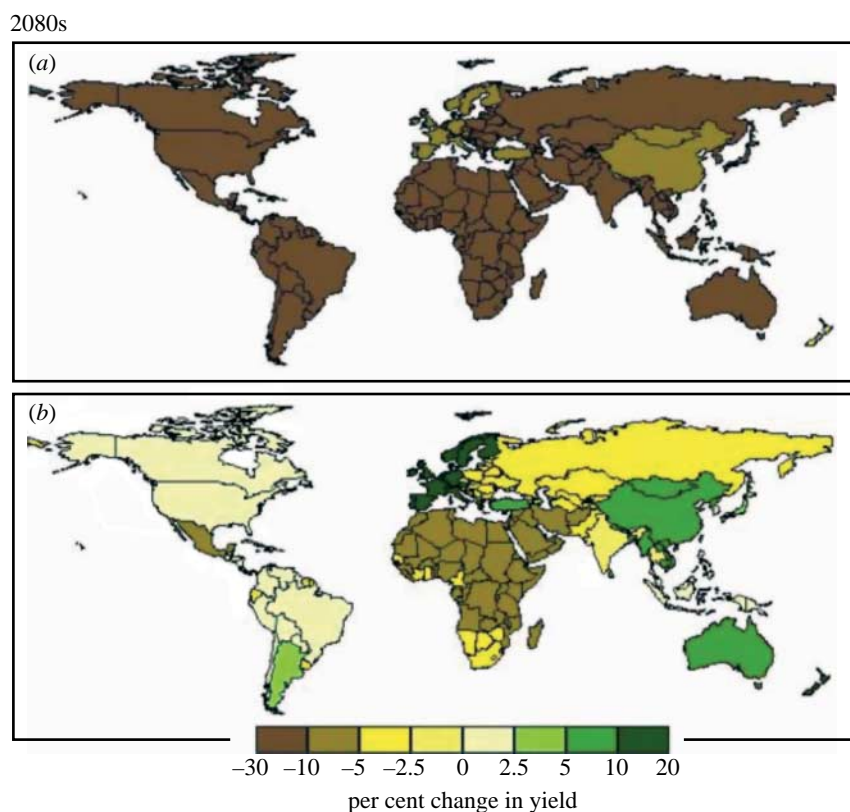


Figure 2. Percentage changes in national cereal yields for the 2080s compared with 1990 under the HadCM3 SRES A2b scenario, (a) with and (b) without the direct effects of elevated [CO<sub>2</sub>]; reprinted with permission from Parry *et al.* (2004).

plasm and economic factors to determine future crop yields (Easterling *et al.* 2007). Information on the nature and extent of crop responses to various climate change factors has been synthesized in a number of process-based crop models to provide projections of future crop yields. These assessments combine the use of the crop models with projections of future climatic conditions from global circulation models run under different socio-economic scenarios (e.g. Parry *et al.* 2004). Overall, the projections indicate that crop yields will decline as a result of climate change by the second half of this century, and that the effects will be felt earlier and more strongly at lower latitudes (Easterling *et al.* 2007). The impact of elevated [CO<sub>2</sub>] on crop yields is so fundamental to the outcome that model projections are often presented for scenarios of ‘climate change without CO<sub>2</sub> effects on crop physiology’ (figure 2a) and of ‘climate change plus CO<sub>2</sub> effects on crop physiology’ (figure 2b). A common prediction has been that crop yields will be reduced under the scenario of climate change without CO<sub>2</sub> effects on crop physiology (figure 2a; Parry *et al.* 2004). However, crop yields are projected to decline less everywhere, and even increase in some regions, when the positive effects of elevated [CO<sub>2</sub>] on crop physiology are also considered (figure 2b; Parry *et al.* 2004).

Given the pivotal role that the CO<sub>2</sub> fertilization effect has on the direction as well as the magnitude of changes in crop yields as a result of climate change, it is important to estimate it accurately and then simulate it correctly in the models. There is a strong consensus that elevated [CO<sub>2</sub>] is capable of eliciting two direct physiological responses in plants, enhanced rates of photosynthesis and reduced stomatal conductance (Peart *et al.* 1989; Ainsworth & Long 2005). Greater photosynthesis allows greater carbon gain and biomass accumulation, while reduced stomatal

conductance leads to lower transpiration and lower soil moisture depletion, which can forestall or even prevent the onset of drought stress. There is consensus that both mechanisms operate in the vast majority of C<sub>3</sub> species (Ainsworth & Long 2005). However, while C<sub>4</sub> species consistently display lower stomatal conductance at elevated [CO<sub>2</sub>], the nature of their photosynthetic responses to elevated [CO<sub>2</sub>] is under debate.

It is notable that the results of more work on C<sub>4</sub> crop responses to elevated [CO<sub>2</sub>] will also be relevant to C<sub>3</sub> crops, since the contribution of reduced stomatal conductance to stimulation of yield in C<sub>3</sub> crops at elevated [CO<sub>2</sub>] is difficult to estimate and may explain some of the recent debate surrounding the most accurate way to parametrize the CO<sub>2</sub> fertilization factors used for them in crop models (Long *et al.* 2006; Tubello *et al.* 2007a,b; Ainsworth *et al.* 2008b).

#### 4. RESEARCH OUTPUT ON CLIMATE CHANGE AND THE WORLD'S MAJOR CROPS

In general, the proportion of published studies about the responses to climate change of each of the world's six most important crops corresponds well to the proportion of agricultural land area each crop occupies (figure 3). It is not surprising that the greatest research effort has been targeted towards the most widely planted crops, whether it has considered individual elements of climate change or their combined effects. However, the distribution of research output among the major crops does deviate from this general pattern in a number of notable ways. First, wheat has been the subject of a disproportionately large number of studies on all subjects, while rice has been the subject of disproportionately few. This may reflect the greater importance of wheat production in the developed countries of North America and Europe, which support

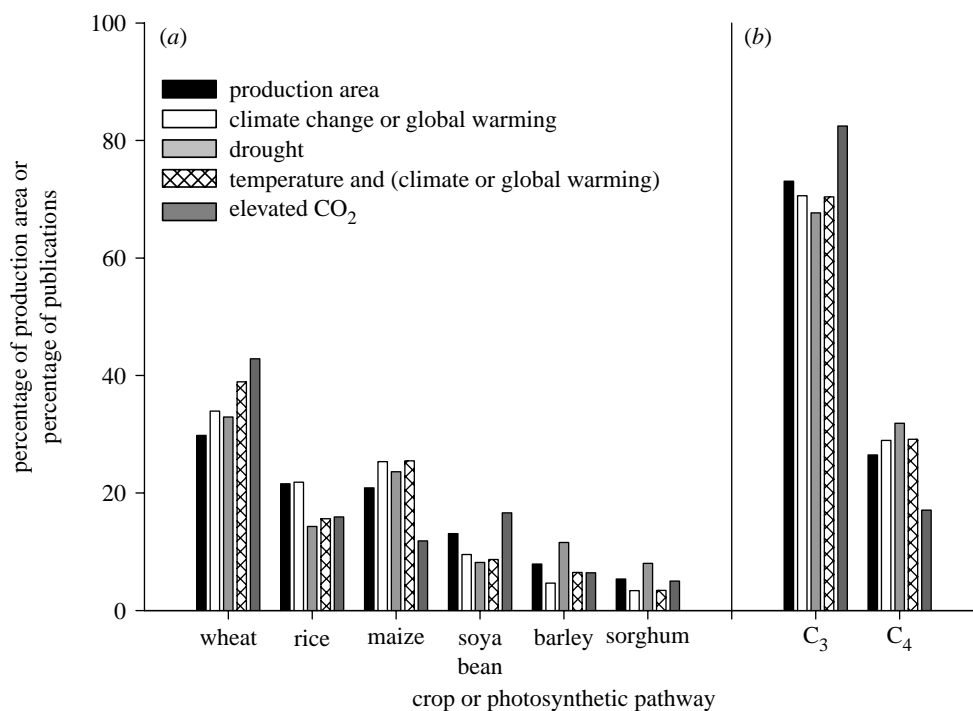


Figure 3. Percentage of global crop production area (black bars) and percentage of peer-reviewed publications listed in the web of science citation database (ISI, Thomson Inc., Philadelphia, PA) with the following search terms: climate change or global warming (white bars), drought (light grey bars), temperature and climate change or global warming (hatched bars) and elevated CO<sub>2</sub> (dark grey bars) for (a) the six most widely grown crops and (b) C<sub>3</sub> (wheat, rice, soya bean and barley) and the C<sub>4</sub> (maize and sorghum) crops.

relatively large government and industrial agricultural research programmes, versus the greater importance of rice production in tropical, developing countries. Second, while maize responses to drought, temperature and generalized climate change have been studied extensively, it has been the subject of only approximately half as many studies on elevated [CO<sub>2</sub>] as its large area of production would merit. The smaller number of C<sub>4</sub> crops relative to C<sub>3</sub> crops means that if the research output for the two photosynthetic pathways is compared, there is a major disparity, with the result that we have a generally poorer understanding of, and ability to predict, C<sub>4</sub> responses to climate change. Most concerning is the disproportionate lack of attention that C<sub>4</sub> crop responses to elevated [CO<sub>2</sub>] have received.

## 5. PHYSIOLOGICAL RESPONSES OF C<sub>4</sub> SPECIES TO GROWTH AT ELEVATED [CO<sub>2</sub>]

### (a) Does elevated [CO<sub>2</sub>] stimulate photosynthesis directly?

Analysis of photosynthetic CO<sub>2</sub> response ( $A/c_i$ ) curves provides a practical and conceptual basis on which to understand the mechanism by which growth at elevated [CO<sub>2</sub>] impacts photosynthesis in both C<sub>3</sub> and C<sub>4</sub> plants. In C<sub>3</sub> plants, an increase in the atmospheric [CO<sub>2</sub>] from today's ambient [CO<sub>2</sub>] of 385 to the 550 ppm projected for 2050, or 700 ppm projected for 2100, leads to a rise in the intercellular [CO<sub>2</sub>] ( $c_i$ ) from approximately 270 to 385 or 490 ppm, respectively (figure 4a). In this example from soya bean, the result is the direct stimulation of photosynthesis by 29 per cent under 2050 conditions or 39 per cent under 2100 conditions. There is a biochemical basis for this effect, in which greater [CO<sub>2</sub>] around the enzyme Ribulose-1,5-BISphosphate Carboxylase

Oxygenase (Rubisco) instantaneously accelerates the carboxylation reaction that captures CO<sub>2</sub> and inhibits the competing oxygenation reaction that causes carbon loss through photorespiration (Bowes 1991). In C<sub>4</sub> plants, the initial slope of the  $A/c_i$  curve is much steeper and photosynthesis becomes saturated by CO<sub>2</sub> at a lower  $c_i$  (figure 4b). This is because (i) C<sub>4</sub> plants use a different primary carboxylase, phosphoenolpyruvate carboxylase, which has a higher affinity for HCO<sub>3</sub><sup>-</sup> and for which O<sub>2</sub> is not a competitive substrate and (ii) they concentrate CO<sub>2</sub> around Rubisco to more than five times ambient [CO<sub>2</sub>] in specialized bundle sheath cells, which saturates or nearly saturates the carboxylation reaction and inhibits photorespiration (Furbank & Hatch 1987). Consequently, in C<sub>4</sub> plants, an increase in atmospheric [CO<sub>2</sub>] from 385 to 550 or 700 ppm also leads to greater  $c_i$ , but in this example from maize there is essentially no ( $\leq 1\%$ ) direct stimulation of photosynthesis (figure 4b). This theory would not hold for C<sub>4</sub> plants in two situations. First, if the operating  $c_i$  of photosynthesis under ambient [CO<sub>2</sub>] was below the inflexion point of the  $A/c_i$  curve. Second, if growth at elevated [CO<sub>2</sub>] caused a biochemical or physical change within the leaf that altered the shape of the  $A/c_i$  curve in such a way that photosynthesis became sensitive to increases in  $c_i$ .

Even if C<sub>4</sub> photosynthesis is saturated at ambient [CO<sub>2</sub>] and no acclimation occurs to change the shape of the  $A/c_i$  curve, C<sub>4</sub> crop photosynthesis and productivity could still be stimulated by elevated [CO<sub>2</sub>] in times and places of drought stress. Drought is any situation in which the supply of water to the plant is exceeded by the demand for water by the plant, leading to stress and reduced productivity. This can result from either inadequate soil water content, high atmospheric vapour pressure deficits or a combination of these two factors. Under such

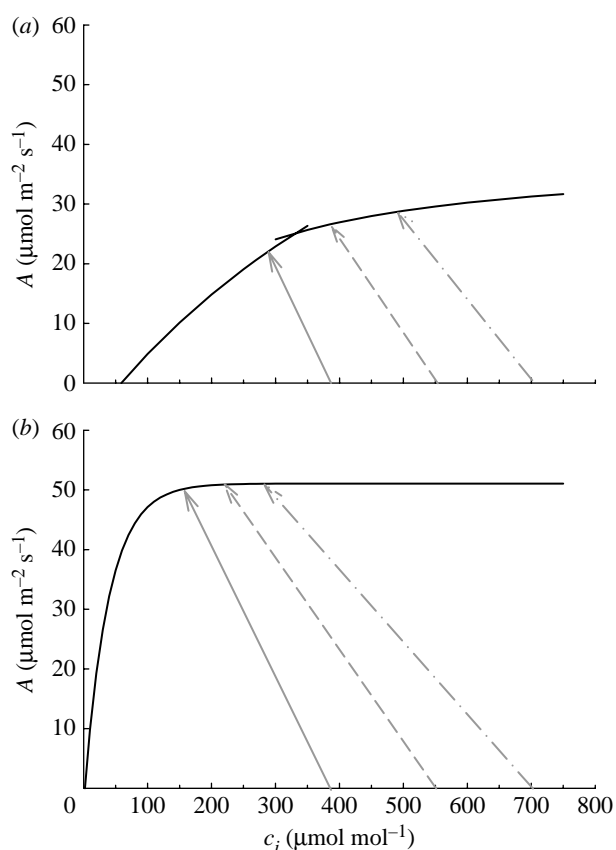


Figure 4. The response of photosynthesis ( $A$ ) to intercellular  $\text{CO}_2$  concentration ( $c_i$ ) under saturating light. (a) Representative  $A/c_i$  response of *Glycine max* (soya bean), as predicted from the C<sub>3</sub> leaf biochemical model of photosynthesis of Farquhar *et al.* (1980). The grey lines illustrate the supply function for  $\text{CO}_2$ , starting at the atmospheric  $[\text{CO}_2]$  and ending at the operating  $c_i$  of photosynthesis. This is illustrated for the current atmospheric  $[\text{CO}_2]$  (385 ppm, solid line), elevated  $[\text{CO}_2]$  anticipated for 2050 (550 ppm, dashed line), and elevated  $[\text{CO}_2]$  anticipated for 2080 (700 ppm, dashed and dotted line). (b) Representative  $A/c_i$  response of *Zea mays* (maize) fitted with the model equations for C<sub>4</sub> photosynthesis (von Caemmerer 2000); adapted from Leakey *et al.* (2006). Grey lines indicate the supply function for photosynthesis, as described above.

conditions, stress can be delayed or reduced by lower water use under elevated  $[\text{CO}_2]$  conserving soil moisture resources. The reduction in leaf photosynthetic  $\text{CO}_2$  uptake due to lower stomatal conductance under drought can also be ameliorated by greater  $c_i$  under elevated  $\text{CO}_2$  (figure 5). The situation where rising  $[\text{CO}_2]$  only benefits C<sub>4</sub> plants in times or places of drought stress is cause for concern when compared with existing model projections of future C<sub>4</sub> crop yields, which may be overoptimistic as a result of assuming a consistent  $\text{CO}_2$  fertilization effect for C<sub>4</sub> crops across all times and growing conditions (e.g. 7%), albeit a smaller  $\text{CO}_2$  fertilization effect than for C<sub>3</sub> crops (e.g. 25%, Rosenzweig & Iglesias 1994).

Since the late 1960s experiments have been done using enclosures to expose C<sub>4</sub> plants to varying  $[\text{CO}_2]$ . Elevated  $[\text{CO}_2]$  did not directly stimulate C<sub>4</sub> photosynthesis in some studies (Hocking & Meyer 1991; Ziska *et al.* 1991; Samarakoon & Gifford 1996; Ghannoum *et al.* 1998). However, stimulation of C<sub>4</sub> photosynthesis under elevated  $[\text{CO}_2]$  was observed in other studies, even when plants were well watered and drought stress was not intended to occur

(Knapp *et al.* 1993; Amthor *et al.* 1994; Poorter *et al.* 1996; Wand *et al.* 1999; Anderson *et al.* 2001; De Souza *et al.* 2008). Various studies have attributed direct stimulation of photosynthesis at elevated  $[\text{CO}_2]$  to the operating  $c_i$  of photosynthesis under ambient  $[\text{CO}_2]$  being below the inflexion point of the  $A/c_i$  curve (Wong 1979; Watling & Press 1997; Ziska & Bunce 1997), or one of three different acclimation responses altering the relationship between photosynthesis and  $c_i$ : (i) altered bundle sheath leakiness (Saliendra *et al.* 1996; Watling *et al.* 2000), (ii) direct  $\text{CO}_2$  fixation in the bundle sheath (Moore *et al.* 1986), and (iii) C<sub>3</sub>-like photosynthesis in young C<sub>4</sub> leaves (Dai *et al.* 1995; Ziska *et al.* 1999). These findings were reviewed in detail by Ghannoum *et al.* (2000), who concluded that C<sub>4</sub> photosynthesis could only be stimulated by elevated  $[\text{CO}_2]$ : (i) directly, when the operating  $c_i$  of photosynthesis under ambient  $[\text{CO}_2]$  was below the inflexion point of the  $A/c_i$  curve or (ii) indirectly, when reduced stomatal conductance stimulated photosynthesis via altered water relations or energy balance. These questions are revisited here, focusing on evidence from recent FACE studies. FACE studies are of particular value because they impose fully open-air treatments of elevated  $[\text{CO}_2]$  in the field, which uniquely allow investigation of  $\text{CO}_2$  sensitivity in large plots of plants with an undisturbed plant–soil–atmosphere continuum, i.e. with unlimited rooting volume and realistic micrometeorological controls on water relations and energy balance, and without the changes in microclimate caused by growth in chambers.

Three large-scale FACE experiments with treatment plots of more than 100 m<sup>2</sup> have featured C<sub>4</sub> species. It is challenging under field conditions to consistently and unequivocally separate the direct effects of elevated  $[\text{CO}_2]$  from responses mediated by altered water relations. Nonetheless, the data are consistent with elevated  $\text{CO}_2$  having little or no direct effect on either the rate of C<sub>4</sub> photosynthesis or photosynthetic enzyme capacity. Sorghum was grown in 1998 and 1999 at ambient (approx. 370 ppm) and elevated  $[\text{CO}_2]$  (approx. 570 ppm), under ample irrigation (complete replacement of evapotranspiration) or drought stress (flood irrigations only post-planting and mid-season) in Maricopa, AZ, USA. Despite some evidence for stimulated photosynthesis at elevated  $[\text{CO}_2]$  in young tissue and leaves (Cousins *et al.* 2001, 2003), investigators at the site reported that the direct effects of elevated  $[\text{CO}_2]$  on photosynthesis were ‘nominal’ (Wall *et al.* 2001). In the amply irrigated plots, there was no significant effect of elevated  $[\text{CO}_2]$  on *in vivo* photosynthetic rate of  $\text{CO}_2$  uptake by the youngest fully expanded leaf at midday on 13 of 17 measurement dates, across the two growing seasons (Wall *et al.* 2001). Elevated  $[\text{CO}_2]$  was reported to stimulate photochemical light energy usage, but only during drought or at midday when short-term water stress developed under high atmospheric vapour pressure deficits and temperatures (Cousins *et al.* 2002). Therefore, when observed, stimulation of photosynthesis by elevated  $[\text{CO}_2]$  was most likely due to amelioration of water stress, rather than by direct stimulation of C<sub>4</sub> photosynthesis. Even if photosynthesis in young leaves of C<sub>4</sub> crops was directly stimulated by elevated  $[\text{CO}_2]$ , it did not have a measurable impact on biomass accumulation or yield under well-watered conditions (Ottman *et al.* 2001).

The C<sub>4</sub> grass *Paspalum dilatatum* was grown at ambient (approx. 360 ppm) and elevated  $[\text{CO}_2]$  (approx.

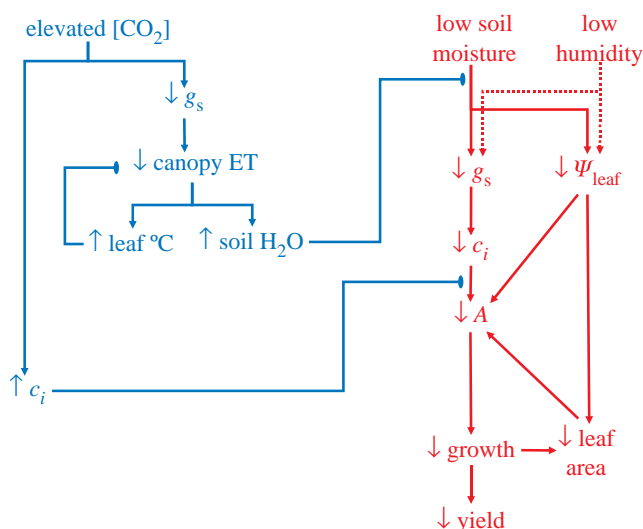


Figure 5. Schematic of the interacting effects of elevated [CO<sub>2</sub>] (blue lines) and drought (red lines) on C<sub>4</sub> plant function. *A*, photosynthesis; *g<sub>s</sub>*, stomatal conductance; canopy ET, evapotranspiration;  $\psi_{\text{leaf}}$ , leaf water potential. Enhancing effects are represented as arrows, suppressing effects are represented as flat-headed lines. The decrease in stomatal conductance of C<sub>4</sub> species observed at elevated [CO<sub>2</sub>] reduces whole-plant water use, which in turn conserves soil moisture and increases leaf temperature. In the absence of water stress, increased leaf temperature may slightly stimulate photosynthesis, but otherwise there would be no effect on plant carbon relations. Under drought conditions, soil or atmospheric water deficits cause reduced stomatal conductance and leaf water potential, which restrict photosynthesis, leading to lower growth and yield. Under such conditions, elevated [CO<sub>2</sub>] would delay the onset of stress due to soil moisture depletion, and also counteract the reduction in photosynthesis resulting from lower *c<sub>i</sub>* caused by drought-induced reduction in stomatal conductance.

475 ppm) as part of a mixed species, managed grassland FACE experiment in New Zealand. Measurements of *A/c<sub>i</sub>* curves in 1999 indicated that plants growing at both ambient and elevated [CO<sub>2</sub>] were operating at or close to saturating *c<sub>i</sub>*, and therefore did not display different rates of photosynthesis (von Caemmerer *et al.* 2001). While changes in the shape of the *A/c<sub>i</sub>* curve in C<sub>3</sub> plants grown at elevated [CO<sub>2</sub>] were observed, there was no evidence of photosynthetic acclimation in the C<sub>4</sub> species.

Maize was grown in 2002 and 2004 at ambient (approx. 370 ppm) and elevated [CO<sub>2</sub>] (approx. 550 ppm) in the US Corn Belt, at SoyFACE, Urbana IL. Diurnal courses of gas exchange in the youngest fully expanded leaf were measured at five developmental stages in each season. On 7 of the 10 dates of measurements, when the crop was not experiencing drought stress, there was no CO<sub>2</sub> effect on photosynthesis (Leakey *et al.* 2004, 2006). In the 2004 season, this absence of a direct CO<sub>2</sub> effect on photosynthesis was corroborated by *A/c<sub>i</sub>* curve data, indicating that the *c<sub>i</sub>* measured *in vivo* in both ambient and elevated [CO<sub>2</sub>] treatments was above the inflexion point of the curve and that photosynthesis was CO<sub>2</sub> saturated in both treatments. In addition, there was no acclimation of photosynthesis to elevated [CO<sub>2</sub>], with no CO<sub>2</sub> effect on *in vivo* or *in vitro* estimates of photosynthetic enzyme capacity, leaf carbohydrates or leaf N (Leakey *et al.* 2006). Consistent with the well-watered treatment of sorghum in Arizona, USA, when there was no drought stress at any

stage of the season, maize grown at ambient and elevated [CO<sub>2</sub>] produced the same final biomass and yield.

What could explain the direct effects of elevated [CO<sub>2</sub>] that have been observed in some enclosure studies, but not in others and not in FACE experiments? Maize, sorghum and millet roots commonly extend to depths of 1–2 m under field conditions, in order to meet the water requirements of the shoot (Allen *et al.* 1998; Carcova *et al.* 2000). This allows water extraction from a much larger soil volume than the pots used in some enclosure experiments (e.g. 3.5 l in Ziska & Bunce 1997; Ziska *et al.* 1999; 5 l in Wong 1979; Maroco *et al.* 1999). Therefore, even if pots are well watered, there may not be sufficient root surface available to absorb water to fully meet the requirements of the shoot. Even if sufficient water is available, the mechanical barrier presented by the pot wall is likely to feedback and alter plant development (Masle *et al.* 1990). Growth at elevated [CO<sub>2</sub>] could reduce water requirements and alleviate this stress—giving the impression that elevated [CO<sub>2</sub>] directly stimulates carbon gain. Other enclosure studies have avoided this problem by growing plants in open-top chambers (OTCs) with unrestricted rooting depths of 2 m (Amthor *et al.* 1994). However, under high light conditions (more than 1600  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), air temperature and vapour pressure deficit within OTCs can be up to 4.3°C and 0.8 kPa greater than outside the enclosure (Whitehead *et al.* 1995). This is likely to promote water stress in the shoot around midday and reduce photosynthesis. This could be alleviated by reduced stomatal conductance and water use at elevated [CO<sub>2</sub>] and be easily misinterpreted as a direct stimulation of photosynthesis by elevated [CO<sub>2</sub>]. In most studies, the growth [CO<sub>2</sub>] of the ambient treatment is not controlled. Canopies of large C<sub>4</sub> crops can have high rates of photosynthetic CO<sub>2</sub> uptake and can draw down the [CO<sub>2</sub>] during the day. For example, Watling *et al.* (2000) report that sorghum in a controlled environment cabinet reduced the atmospheric [CO<sub>2</sub>] from 350 to 330 ppm. This may be sufficient to reduce *c<sub>i</sub>* to values below the inflexion point of the *A/c<sub>i</sub>* curve. In this case, carbon gain would be lower in plants growing at ambient than at elevated [CO<sub>2</sub>]. However, the result would reflect the direct effect of sub-ambient [CO<sub>2</sub>], not elevated [CO<sub>2</sub>], on carbon gain. In earlier studies, ambient [CO<sub>2</sub>] was naturally lower than today, which may explain some reports of direct stimulation of photosynthesis by elevated [CO<sub>2</sub>]. For the example, in *A/c<sub>i</sub>* curves measured for maize at 30°C (figure 4), increasing [CO<sub>2</sub>] from an ambient concentration of 320–550 ppm would stimulate photosynthesis by almost 4 per cent. This suggests that some direct stimulation of C<sub>4</sub> photosynthesis may have occurred due to rising [CO<sub>2</sub>] over the last 50 years, but that no additional benefit will be gained in the future. Differences in the developmental stage, treatment [CO<sub>2</sub>] and genotype under study may also play a role in the varied response of C<sub>4</sub> plants to growth at elevated [CO<sub>2</sub>]. However, the FACE studies on both maize and sorghum thoroughly characterized photosynthesis, reporting measurements made at multiple times of day and 5–10 developmental stages over each growing season. FACE experiments have investigated the effects of elevated [CO<sub>2</sub>] approximately 1.5 times ambient [CO<sub>2</sub>], while cabinet studies have imposed elevated [CO<sub>2</sub>] treatments with higher [CO<sub>2</sub>] (Maroco *et al.* 1999;

Watling *et al.* 2000). The difference in observed effects could then only be explained by a threshold [CO<sub>2</sub>] necessary to see direct stimulation of C<sub>4</sub> photosynthesis and no such mechanism has been proposed. Each of the three FACE experiments investigated only one C<sub>4</sub> species. Maize, sorghum and *Paspalum dilatatum* all possess NADP-malic enzyme type C<sub>4</sub> photosynthesis. While there is evidence from enclosure studies for differences in N use efficiency among C<sub>4</sub> subtypes (Ghannoum *et al.* 2005), there is no clear pattern in sensitivity to growth at elevated [CO<sub>2</sub>] (Wand *et al.* 1999). Further studies, in the field, are needed to confirm the consistency of C<sub>4</sub> responses to elevated [CO<sub>2</sub>].

In summary, results from FACE experiments extend the evidence presented by Ghannoum *et al.* (2000) suggesting that C<sub>4</sub> photosynthesis is not directly stimulated by elevated [CO<sub>2</sub>]. This has two important implications. First, projections of C<sub>4</sub> crop yield in the future that applied a consistent CO<sub>2</sub> fertilization effect across all growing conditions will have likely overestimated future yields. Second, developing quantitative understanding of the changes in water relations of C<sub>4</sub> plants at elevated [CO<sub>2</sub>] is essential to predicting their future performance, and also adapting C<sub>4</sub> crops to future growing conditions (Ainsworth *et al.* 2008a).

**(b) Does elevated [CO<sub>2</sub>] improve C<sub>4</sub> plant water relations, and then indirectly enhance photosynthesis, growth and yield by delaying and ameliorating drought stress?**

Ghannoum *et al.* (2000) proposed a conceptual model of the main mechanisms by which C<sub>4</sub> plants respond to elevated [CO<sub>2</sub>]. A modified version of the model is presented here incorporating the subsequent findings from FACE experiments (figure 5). The decrease in stomatal conductance of C<sub>4</sub> species consistently observed at elevated [CO<sub>2</sub>] reduces whole-plant water use, which in turn conserves soil moisture and increases leaf temperature. In the absence of water stress, increased leaf temperature may slightly stimulate photosynthesis, but otherwise there would be no effect on plant carbon relations. Under drought conditions, soil or atmospheric water deficits cause reduced stomatal conductance and leaf water potential, which restrict photosynthesis, leading to lower growth and yield. Under such conditions, elevated [CO<sub>2</sub>] would delay the onset of stress due to soil moisture depletion, and also counteract the reduction in photosynthesis resulting from lower *c<sub>i</sub>* caused by drought-induced reduction in stomatal conductance.

Enclosure studies have provided evidence for this mechanism, with reduced water use reported at elevated [CO<sub>2</sub>] compared to ambient [CO<sub>2</sub>] in maize (−25 to 30%; Samarakoon & Gifford 1996), *Panicum coloratum* (−17%; Seneweera *et al.* 1998), *Bouteloua gracilis* (Morgan *et al.* 1998) and sugar cane (Vu & Allen 2009). In all three of these cases, plant water status under drought conditions was improved, resulting in greater photosynthesis and biomass accumulation. In addition, there have been a number of studies in which C<sub>4</sub> plants showed greater stimulations of biomass accumulation in response to elevated [CO<sub>2</sub>] under drought stress compared to well-watered conditions (Owensby *et al.* 1997; Seneweera *et al.* 1998). Growth at elevated [CO<sub>2</sub>] has also been shown to alleviate inhibition of shoot growth by water stress under

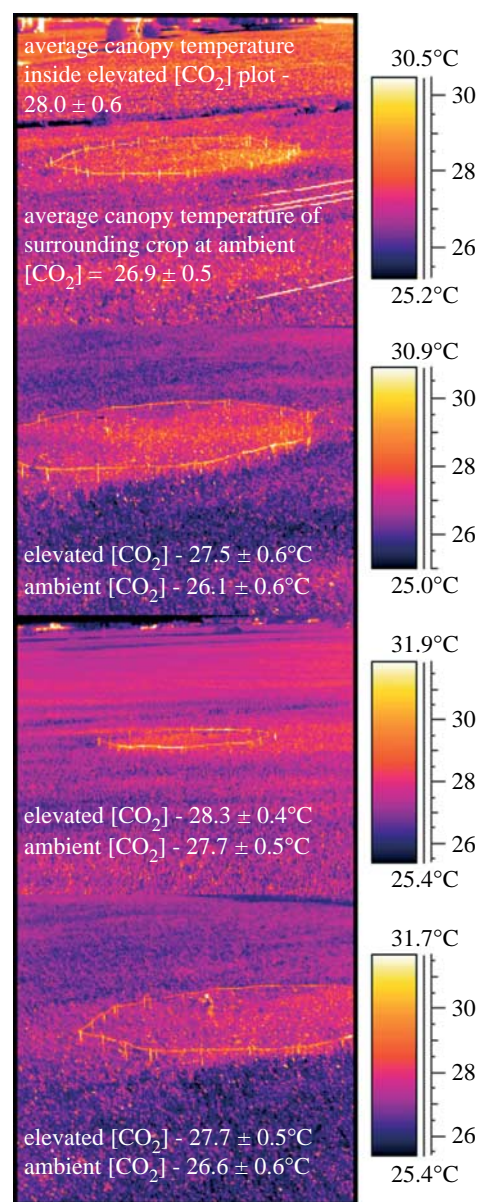


Figure 6. Infrared image showing that maize growing inside an elevated [CO<sub>2</sub>] plot was warmer than maize growing under ambient [CO<sub>2</sub>] outside the plot at 15.30 h on 15 July 2004. At that time, the average canopy temperature inside the four elevated [CO<sub>2</sub>] plots at SoyFACE was  $27.9 \pm 0.2^\circ\text{C}$ , significantly higher than the canopy temperatures under ambient [CO<sub>2</sub>] outside the plots ( $26.8 \pm 0.3^\circ\text{C}$ ;  $p = 0.03$ ).

conditions of atmospheric water deficit. Growth of leaves in *P. coloratum* was greater when elevated [CO<sub>2</sub>] decreased stomatal conductance and transpiration under high vapour pressure deficit conditions, even though soil water content was maintained at 100 per cent (Seneweera *et al.* 1998).

A number of mechanisms may operate to modify the amelioration of water stress by elevated [CO<sub>2</sub>] in the field, compared to enclosure studies. First, whole-plant transpiration can become, at least partially, uncoupled from stomatal conductance (Jarvis & McNaughton 1986; Collatz *et al.* 1991; Meinzer *et al.* 1997). In enclosure studies, forced air circulation and the restricted scale of plant canopies reduces the likelihood that canopy size and structure will interact with the microclimate to impose significant canopy resistance to water flux (McLeod & Long 1999). Second, when superimposed upon



heterogeneous water availability in time and space in the field, relatively subtle changes in whole-plant transpiration at elevated [CO<sub>2</sub>] may not significantly impact plant water status and therefore carbon gain. Plants grown in pots and subjected to drought treatments typically experience rapid soil water depletion and relatively severe decreases in shoot water potential. By comparison, the larger rooting zone of field-grown crops ensures a slower progression into drought stress, which favours root exploration to access water deeper in the soil and also osmoregulation within shoot tissues to withstand decreasing soil water availability. Thus, there is a particular need to test changes in plant water relations under elevated [CO<sub>2</sub>] under fully open-air field conditions.

Midday stomatal conductance of upper canopy leaves of sorghum grown under FACE was lower under elevated [CO<sub>2</sub>] by 32 per cent with ample irrigation and by 37 per cent under severe drought stress (Wall *et al.* 2001). The effect of elevated [CO<sub>2</sub>] on whole-plant water use was smaller, but still significant. Averaged over 2 years, growth of sorghum at elevated [CO<sub>2</sub>] decreased soil water depletion by 10 per cent under ample irrigation and by 4 per cent under severe drought stress (Conley *et al.* 2001). This was generally corroborated by decreases in latent heat flux from the canopy under elevated [CO<sub>2</sub>] (Triggs *et al.* 2004). Even with ample irrigation, the semi-desert growing conditions in Maricopa, Arizona caused transient drought stress, particularly at midday (Cousins *et al.* 2002). This stress was ameliorated by growth at elevated [CO<sub>2</sub>], leading to 9 per cent greater midday leaf photosynthetic uptake of amply irrigated sorghum, on average over the two growing seasons (Wall *et al.* 2001). By contrast, sorghum under severe drought stress responded to elevated [CO<sub>2</sub>] with regular improvements in water potential and this amelioration of stress enhanced midday photosynthesis by 23 per cent over two seasons.

Maize was grown at SoyFACE in 2002 and 2004, allowing comparison between an 'average' year (2002) that included periods of insufficient soil water for the crop versus an 'atypical' year (2004) in which the crop experienced ideal growing conditions with plentiful soil water at all times (Leakey *et al.* 2006). Stomatal conductance of the youngest fully expanded leaf of maize over the diurnal period was lower under elevated [CO<sub>2</sub>], by 23 per cent on average in 2002 and by 29 per cent on average in 2004. As with sorghum, this translated into a smaller, but still significant, decrease in whole-plant water use. Soil moisture under elevated [CO<sub>2</sub>] was up to 31 per cent greater between 5 and 25 cm depth, and up to 11 per cent greater between 25 and 55 cm depth (Leakey *et al.* 2006). This corresponded with measurements of a C<sub>3</sub> soya bean canopy in which lower stomatal conductance at elevated [CO<sub>2</sub>] directly led to a smaller but significant reduction in canopy evapotranspiration (Bernacchi *et al.* 2007). Early in the 2002 growing season, the maize crop experienced drought stress. At the same time, maize displayed greater rates of photosynthesis under elevated [CO<sub>2</sub>] than ambient [CO<sub>2</sub>]. This was consistent with conserved soil water under elevated [CO<sub>2</sub>] ameliorating drought stress and increasing carbon gain.

Lower stomatal conductance can increase canopy temperatures inside elevated [CO<sub>2</sub>] plots relative to outside the plots where plants are growing at ambient

[CO<sub>2</sub>]. Occasional surveys with an infrared camera suggest that the effect is more prevalent on windy days, presumably when canopy conductance is high and stomatal conductance is the primary control of transpiration (A. D. B. Leakey, D. R. Ort & S. P. Long 2002–2005, unpublished data). At 15.30 h on 15 July 2004, canopy temperature at elevated [CO<sub>2</sub>] was 1.1°C greater than under ambient [CO<sub>2</sub>] (figure 6). This compared with average maximum temperature differences between ambient and elevated [CO<sub>2</sub>] grown plants of 1.47 and 1.85°C in well-watered treatments of sorghum in Maricopa, AZ (Triggs *et al.* 2004). Increased leaf temperature will increase transpiration and counteract the effect of reduced stomatal conductance at elevated [CO<sub>2</sub>] to some extent. Ghannoum *et al.* (2000) observed that an increase in leaf temperature of 1°C increased photosynthesis by 2.0 μmol m<sup>-2</sup> s<sup>-1</sup>. However, in the absence of drought stress in 2004 at SoyFACE, elevated [CO<sub>2</sub>] was estimated, on average, to only increase leaf temperature by 0.26°C and photosynthesis by 0.3 μmol m<sup>-2</sup> s<sup>-1</sup>, and had no apparent effect on the diurnal course of photosynthesis or end of season biomass (Leakey *et al.* 2006). An additional important factor is that increases in [CO<sub>2</sub>] beyond that, which saturate photosynthesis, can continue to decrease stomatal conductance and increase leaf temperature, at least to 1200 ppm CO<sub>2</sub> (Siebke *et al.* 2002). Clearly, direct observations under open-air field conditions are needed to evaluate the importance of this mechanism more rigorously.

There is clear potential for growth of C<sub>4</sub> plants at elevated [CO<sub>2</sub>] to decrease water use and reduce drought stress, leading to greater photosynthesis. On average, in FACE experiments at 550 ppm, CO<sub>2</sub> stomatal conductance of C<sub>4</sub> species is 25 per cent lower than at ambient [CO<sub>2</sub>] (Ainsworth & Long 2005). However, the consequences of this response at the whole-plant scale under open-air field conditions have been intensively assessed only in two species (maize and sorghum), each in only one location (IL, USA and AZ, USA). More open-air studies are needed to test the wider applicability of the finding that elevated [CO<sub>2</sub>] does not directly stimulate C<sub>4</sub> photosynthesis but can enhance productivity by ameliorating drought stress. Topics that need to be addressed include determining the threshold levels of water stress at which (i) photosynthesis is increased sufficiently by elevated [CO<sub>2</sub>] to alter growth or harvestable yield and (ii) improved water relations under elevated [CO<sub>2</sub>] are insufficient to prevent lethal crop failure. More broadly, improvements are needed in understanding how elevated [CO<sub>2</sub>] will combine with other factors of climate change to determine C<sub>4</sub> plant performance in the future. For instance, greater temperatures have been observed to increase the sensitivity of leaf photosynthetic CO<sub>2</sub> uptake to elevated [CO<sub>2</sub>] in some cases (Sage 2002), but not in others (Kim *et al.* 2007). These uncertainties must be addressed to improve understanding of how elevated [CO<sub>2</sub>], and climate change in general, will impact the world's most vulnerable agricultural regions.

## 6. CONCLUSION

Crops with the C<sub>4</sub> photosynthetic pathway are currently very important to global food supply and are becoming increasingly important to fuel production. They are

especially important in the tropical regions where climate change is expected to have its greatest negative impacts and where C<sub>4</sub> crops dominate agricultural production and most directly impact human well-being. While rising atmospheric [CO<sub>2</sub>] is the major driving force behind the greater temperatures and water stress that will reduce future crop yields, it also has the capacity to directly benefit crop physiology. Elevated [CO<sub>2</sub>] enhances C<sub>3</sub> crop yield through stimulated photosynthesis, reduced photorespiration and lower stomatal conductance. The nature of C<sub>4</sub> plant responses to elevated [CO<sub>2</sub>] has been more controversial. Recent evidence from FACE experiments supports the argument that elevated [CO<sub>2</sub>] does not directly stimulate C<sub>4</sub> photosynthesis. Stomatal conductance is lower in all plants at elevated [CO<sub>2</sub>] compared to ambient [CO<sub>2</sub>], and this can delay and ameliorate drought stress. However, this means that unlike C<sub>3</sub> crops, C<sub>4</sub> crops will benefit only from elevated [CO<sub>2</sub>] in times and places of drought stress. Current projections of future crop yields have assumed that CO<sub>2</sub> will directly enhance photosynthesis in all situations and, therefore, are likely to be overly optimistic. The effect of elevated [CO<sub>2</sub>] on C<sub>4</sub> crops has received a disproportionate lack of attention compared to the effects of other elements of climate change on C<sub>3</sub> and C<sub>4</sub> plants. Consequently, adequate data are not available to reliably estimate the extent to which amelioration of drought stress at elevated [CO<sub>2</sub>] will improve yields over the range of C<sub>4</sub> crop growing conditions and genotypes. The increasing importance of C<sub>4</sub> crops for production of food, and more recently biofuels, should make this a priority for further study.

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