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# C<sub>4</sub> Plants Adaptation to High Levels of CO<sub>2</sub> and to Drought Environments

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## 1. Introduction

### 1.1 General features of the C<sub>4</sub> cycle

All plants use the Photosynthetic Carbon Reduction (PCR or Calvin-Benson) cycle for CO<sub>2</sub> fixation in which Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) catalyzes the first step producing a three-carbon compound, phosphoglycerate (3-PGA). For this reason this process is referred to as the C<sub>3</sub> cycle. Plants utilizing this pathway are often named as C<sub>3</sub> species. A major problem with the C<sub>3</sub> cycle is that the enzyme Rubisco catalyzes two competing reactions: carboxylation and oxygenation (Portis & Parry, 2007). The oxygenation reaction directs the flow of carbon through the photorespiratory pathway, and this can result in losses of between 25% and 30% of the carbon fixed. Environmental variables such as high temperature and drought can result in an increase in the oxygenase reaction. Therefore, reducing the Rubisco oxygenase reaction has the potential to increase carbon assimilation significantly and would represent a step change in photosynthesis (up to 100% depending on temperature; Long et al., 2006).

The C<sub>4</sub> photosynthesis is an adaptation of the C<sub>3</sub> pathway that overcomes the limitation of the photorespiration, improving photosynthetic efficiency and minimizing the water loss in hot, dry environments (Edwards & Walker, 1983). Generally, C<sub>4</sub> species originate from warmer climates than C<sub>3</sub> species (Sage & Monson, 1999). Most C<sub>4</sub> plants are native to the tropics and warm temperate zones with high light intensity and high temperature. Under these conditions, C<sub>4</sub> plants exhibit higher photosynthetic and growth rates due to gains in the water, carbon and nitrogen efficiency uses. Indeed, the highest known productivity in natural vegetation is for a C<sub>4</sub> perennial grass in the central Amazon, which achieves a net production of 100 t (dry matter) ha<sup>-1</sup> year<sup>-1</sup> (Piedade et al., 1991; Long, 1999). Some of the world's most productive crops and pasture, such as maize (*Zea mays*), sugar cane (*Saccharum officinarum*), sorghum (*Sorghum bicolor*), amaranth, paspalums (*Paspalum notatum* and *P. urvillei*), bermudagrass (*Cynodon dactylon*), blue grama (*Bouteloua gracilis*) and rhodes grass (*Chloris gayana*) are C<sub>4</sub> plants. In addition, the most troublesome weeds like nutgrass, crabgrass and barnyard, are also C<sub>4</sub> species. Although C<sub>4</sub> plants represent only a small portion of the world's plant species, accounting for only 3 % of the vascular plants, they contribute about 20% to the global primary productivity because of highly productive C<sub>4</sub>-grass-lands (Ehleringer et al., 1997). Approximately half of the ~10,000 grass and sedge species have C<sub>4</sub> photosynthesis, but fewer than 2,000 of the dicotyledonous species exhibit

$C_4$  photosynthesis. Given their disproportionate influence on global productivity,  $C_4$  plants have attracted much attention by the ecophysiological and ecosystem communities (Sage & Monson, 1999).

In  $C_4$  plants, the photorespiration is suppressed by elevating the  $CO_2$  concentration at the site of Rubisco though suppressing the oxygenase activity of the enzyme. This is achieved by a biochemical  $CO_2$  pump and relies on a spatial separation of the  $CO_2$  fixation and assimilation. In general, these species have a particular anatomy (Kranz anatomy), where mesophyll and bundle sheath cells cooperate to fix  $CO_2$  (Figure 1). Differentiation of these two cell types is essential for the operation of  $C_4$  photosynthesis, although special cases for the operation of the  $C_4$  cycle within only one type of photosynthetic cell have been found (Edwards et al., 2004; Lara et al., 2002; Lara & Andreo, 2005).

Basically, carboxylation of phosphoenolpyruvate (PEP) by the phosphoenolpyruvate carboxylase (PEP-carboxylase) produces four-carbon organic acids in the cytosol of mesophyll cells. This so-called  $C_4$  compounds are transported to the bundle sheath cells and decarboxylated to yield  $CO_2$  which is assimilated by Rubisco in the Photosynthetic Carbon Reduction (PCR) cycle (Hatch, 1987). The decarboxylation reaction also produces three-carbon organic acids ( $C_3$ ) that return to the mesophyll cells to regenerate PEP in a reaction catalyzed by the enzyme pyruvate orthophosphate dikinase (PPDK). This process called

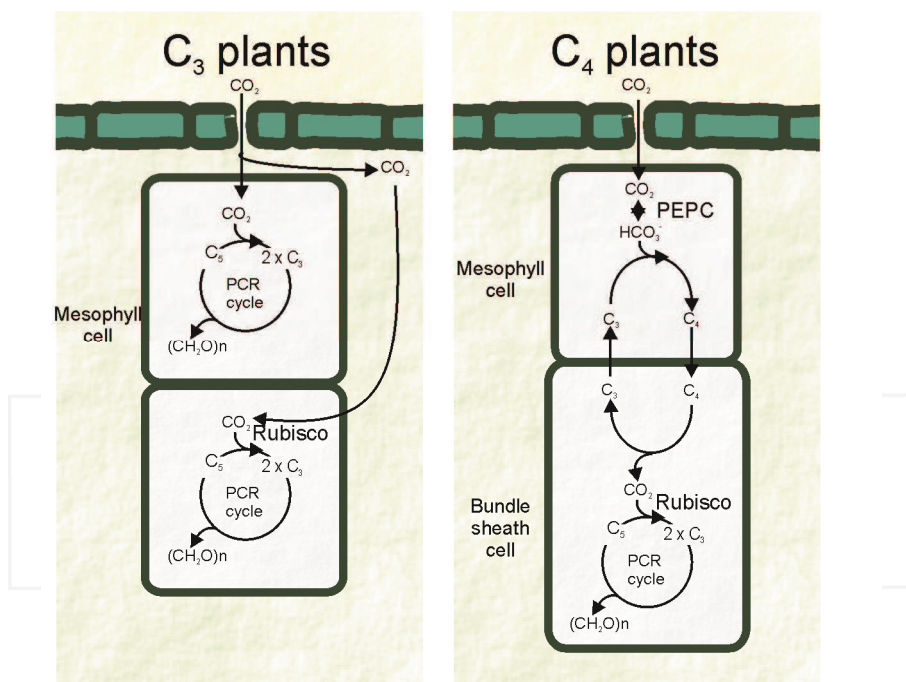


Fig. 1. Simplified scheme of carbon fixation pathways operating in  $C_3$  and  $C_4$  plants. Abbreviations:  $C_3$ , three-carbon organic acids;  $C_4$ , four-carbon organic acids;  $C_5$ , ribulose-1,5-bisphosphate; PCR, Photosynthetic Carbon Reduction Cycle; PEPC, phosphoenolpyruvate carboxylase; Rubisco, Ribulose-1,5-bisphosphate carboxylase/oxygenase.

*Hatch-Slack pathway*, after the first scientists that postulated the metabolic pathway. However, they used the name *C<sub>4</sub> dicarboxylic acid pathway of photosynthesis*. Due to current use, the name has been shortened to *C<sub>4</sub> photosynthesis*, *C<sub>4</sub> pathway*, *C<sub>4</sub> syndrome* or *C<sub>4</sub> metabolism*. The plants that perform this type of photosynthesis are then called *C<sub>4</sub> plants*.

This general scheme is common among the C<sub>4</sub> species; however, there are variations to this basic pathway that include diverse decarboxylation enzymes as well as different transported metabolites. Thus, the decarboxylation process occurs in three diverse ways, mainly using one of the following enzymes: NADP-malic enzyme (NADP-ME), NAD-malic enzyme (NAD-ME) or phosphoenolpyruvate carboxykinase (PEP-CK). Therefore, C<sub>4</sub> plants have been traditionally grouped into three biochemical subtypes depending on the major decarboxylase used (C<sub>4</sub>-NADP-ME subtype; C<sub>4</sub>-NAD-ME subtype or C<sub>4</sub>-PEP-CK subtype). Each C<sub>4</sub> subgroup possesses particular structural features, biochemistry and physiology, and also differences in the mechanism used to regenerate phosphoenolpyruvate (PEP), the substrate of PEP-carboxylase in mesophyll cells. Nevertheless, it is now becoming apparent that, in several cases, more than one decarboxylase operates at the same time (Drincovich et al., 2011).

## 1.2 C<sub>3</sub> vs C<sub>4</sub> species

C<sub>4</sub> species have evolved in a high CO<sub>2</sub> environment. This increases both their nitrogen and water use efficiency compared to C<sub>3</sub> species. C<sub>4</sub> plants have greater rates of CO<sub>2</sub> assimilation than C<sub>3</sub> species for a given leaf nitrogen when both parameters are expressed either on a mass or an area basis (Ghannoum et al., 2011). Although the range in leaf nitrogen content per unit areas is less in C<sub>4</sub> compared to C<sub>3</sub> plants, the range in leaf nitrogen concentration per unit dry mass is similar for both C<sub>4</sub> and C<sub>3</sub> species. Even though leaf nitrogen is invested into photosynthetic components into the same fraction in both C<sub>3</sub> and C<sub>4</sub> species, C<sub>4</sub> plants allocate less nitrogen to Rubisco protein and more to other soluble protein and thylakoids components. In C<sub>3</sub> plants, the photosynthetic enzyme Rubisco accounts for up to 30% of the leaf nitrogen content (Lawlor et al., 1989), but accounts for only 4–21% of leaf nitrogen in C<sub>4</sub> species (Evans & von Caemmerer, 2000; Sage et al., 1987). The lower nitrogen requirement of C<sub>4</sub> plants results from their CO<sub>2</sub>-concentrating mechanism, which raises the bundle sheath CO<sub>2</sub> concentration, saturating Rubisco in normal air and almost eliminating photorespiration. Without this mechanism, Rubisco in the C<sub>3</sub> photosynthetic pathway operates at only 25% of its capacity (Sage et al., 1987) and loses ca. 25% of fixed carbon to photorespiration (Ludwig & Canvin, 1971). To attain comparable photosynthetic rates to those in C<sub>4</sub> plants, C<sub>3</sub> leaves must therefore invest more heavily in Rubisco and have a greater nitrogen requirement. Because the Rubisco specificity for CO<sub>2</sub> decreases with increasing temperature (Long, 1991), this difference between the C<sub>3</sub> and C<sub>4</sub> photosynthetic nitrogen-use efficiency is greatest at high temperatures (Long, 1999). The high photosynthetic nitrogen-use efficiency of C<sub>4</sub> plants is partially offset by the nitrogen-requirement for CO<sub>2</sub>-concentrating mechanism enzymes, but the high maximum catalytic rate of PEP-carboxylase means that these account for only ca. 5% of leaf nitrogen (Long, 1999). Improved leaf and plant water use efficiency in C<sub>4</sub> plants is due to both higher photosynthetic rates per unit leaf area and lower stomatal conductance, with the greater CO<sub>2</sub> assimilation contributing to a major extent (Ghannoum et al., 2011).

The advantages of greater nitrogen use efficiency and water use efficiency of C<sub>4</sub> relative to C<sub>3</sub> photosynthesis are fully realized at high light and temperature, where oxygenase reaction of Rubisco is greatly increased. It is worth noting, although in C<sub>4</sub> plants energy loss

due to photorespiration is eliminated, and additional energy is required to operate the  $C_4$  cycle (2 ATPs per  $CO_2$  assimilated). In dim light, when photosynthesis is linearly dependent on the radiative flux, the rate of  $CO_2$  assimilation depends entirely on the energy requirements of carbon assimilation (Long, 1999). The additional ATP required for assimilation of one  $CO_2$  in  $C_4$  photosynthesis, compared with  $C_3$  photosynthesis, increases the energy requirement in  $C_4$  plants (Hatch, 1987). However, when the temperature of a  $C_3$  leaf exceeds ca. 25 °C, the amount of light energy diverted into photorespiratory metabolism in  $C_3$  photosynthesis exceeds the additional energy required for  $CO_2$  assimilation in  $C_4$  photosynthesis (Hatch, 1992; Long, 1999). This is the reason why at temperatures below ca. 25–28 °C,  $C_4$  photosynthesis is less efficient than  $C_3$  photosynthesis under light-limiting conditions. It is interesting to note, that while global distribution of  $C_4$  grasses is positively correlated with growing season temperature, the geographic distribution of the different  $C_4$  subtypes is strongly correlated with rainfall (Ghannoum et al., 2011).

On the contrary,  $C_4$  plants are rare to absent in cold environments. Although there are examples of plants with  $C_4$  metabolisms that show cold adaptation, they still require warm periods during the day in order to exist in cold habitats (Sage et al., 2011). In consequence,  $C_4$  species are poorly competitive against  $C_3$  plants in cold climates (Sage & McKown, 2006; Sage & Pearce, 2000). The mechanisms explaining the lower performance of  $C_4$  plants under cold conditions have not been clarified (Sage et al., 2011). Among early plausible explanations were the low quantum yield of the  $C_4$  relative to the  $C_3$  pathway (Ehleringer et al., 1997), and enzyme lability in the  $C_4$  cycle, most notably around PEP metabolism (PEP-carboxylase and pyruvate orthophosphate dikinase) (Matsuba et al., 1997). Both hypothesis are insufficient since maximum quantum yield differences do not relate to conditions under which the vast majority of daily carbon is assimilated and there cold-adapted  $C_4$  species that have cold stabled forms of PEP-carboxylase and pyruvate orthophosphate dikinase, and synthesize sufficient quantity to overcome any short term limitation (Du et al., 1999; Hamel & Simon, 2000; Sage et al., 2011). The current hypothesis is that  $C_4$  photosynthesis is limited by Rubisco capacity at low temperatures. Even in cold-tolerant  $C_4$  species, Rubisco capacity becomes limiting at low temperature and imposes a ceiling on photosynthetic rate below 20 °C (Kubien et al., 2003; Pittermann & Sage, 2000; Sage, 2002).

## 2. Climate change

According to the Intergovernmental Panel on Climate Change (IPCC), the current atmospheric  $CO_2$  level of 384  $\mu\text{mol l}^{-1}$  (800 Gt) is predicted to rise to 1000 Gt by the year 2050. Only this time humans are the drivers of these changes and not glacial-interglacial cycles. Human-caused increases in atmospheric  $CO_2$  concentration are thought to be largely responsible for recent increases in global mean surface temperatures and are projected to increase by 1.4 to over 5 °C by 2100 (Intergovernmental Panel on Climate Change, 2001, 2007). Increase in global average temperatures would further result in drastic shifts in the annual precipitation with a 20% reduction per year, and about 20% loss in soil moisture (Schiermeier, 2008). Regarding plants, higher atmospheric  $CO_2$  levels tend to reduce stomatal conductance and transpiration, thereby lowering latent heat loss and causing higher leaf temperatures (Bernacchi et al., 2007). Thus, in the future, plants will likely experience increases in acute heat and drought stress, which can impact ecosystem productivity (Cias et al., 2005) and biodiversity (Thomas et al., 2004). The sensitivity of photosynthesis to each of the environmental variables including high temperature, low

water availability, vapor pressure deficit and soil salinity, associated with the inevitable rise in atmospheric CO<sub>2</sub>, has not been well documented in assessing plant responses to the new changing environment (Reddy et al., 2010). How plant growth responds to the rising CO<sub>2</sub> concentration will not only affect ecosystem productivity in the future, but also the magnitude of C sequestration by plants and, consequently, the rate of CO<sub>2</sub> increase in the atmosphere. C<sub>4</sub> plants are directly affected by all major global change parameters, often in a manner that is distinct from that of C<sub>3</sub> plants. In the present chapter, we will focus on the effect of increased CO<sub>2</sub>, and its relation to temperature and drought, on C<sub>4</sub> plants. Understanding how plants have and will respond to the rapid change in CO<sub>2</sub> concentration, together with developing knowledge about their capacity to adapt, is an essential initial step in understanding the full impact that the multiple interacting factors of global change (e.g. drought, temperature, ozone) will have on terrestrial ecosystems. These ecosystems produce services upon which we are dependent for food, fuel, fiber, clean air, and fresh water (Leakey et al., 2009).

### 3. The CO<sub>2</sub> response

In theory, increases in atmospheric levels of CO<sub>2</sub> above current levels can increase photosynthesis by decreasing photorespiration (fixation of O<sub>2</sub> rather than CO<sub>2</sub> by Rubisco), which increases with temperature and is higher in C<sub>3</sub> than C<sub>4</sub> and crassulacean acid metabolism (CAM) plants (Sage & Monson, 1999). In addition, rising CO<sub>2</sub> generally stimulates C<sub>3</sub> photosynthesis more than C<sub>4</sub>. Doubling of the current ambient CO<sub>2</sub> concentration stimulated the growth of C<sub>4</sub> plants to the tune of 10–20% whereas that in C<sub>3</sub> plants was about 40–45% (Ghannoum et al., 2000).

C<sub>3</sub> photosynthesis is known to operate at less than optimal CO<sub>2</sub> levels and can show dramatic increase in carbon assimilation, growth and yields. As Rubisco is substrate-limited by the current atmospheric CO<sub>2</sub> levels, this enzyme has the potential to respond to increases in CO<sub>2</sub> concentration; and have a metabolic control to alter the CO<sub>2</sub> flux during carbon assimilation (Bernacchi et al., 2003; Long et al., 2004). On the contrary, photosynthetic carbon assimilation in the C<sub>4</sub> species is saturated or almost CO<sub>2</sub>-saturated a low ambient pCO<sub>2</sub>. The reason is that PEP-carboxylase utilizes HCO<sub>3</sub><sup>-</sup> as substrate rather than CO<sub>2</sub>; in consequence, the enzyme is insensitive to changes in the ratio of CO<sub>2</sub>: O<sub>2</sub> due to lack of binding of O<sub>2</sub> to the catalytic site of PEP-carboxylase. Therefore, if plants were grown under elevated CO<sub>2</sub>, carbon fixation would be little affected. This assumption that the inherent CO<sub>2</sub> concentrating mechanism in C<sub>4</sub> plants renders these plants insensitive to elevated CO<sub>2</sub> atmosphere is reflected in the lack of interest that it has been attributed to the study of the C<sub>4</sub> plants response to elevated CO<sub>2</sub> levels. To show this, Reddy et al. (2010) performed an exhaustive fifteen year- literature survey on the influence of elevated CO<sub>2</sub> among certain C<sub>3</sub>, C<sub>4</sub> and CAM species. The authors provided information for forty C<sub>3</sub> plants and for only two C<sub>4</sub> species and three CAM plants. Most of the C<sub>3</sub> plants presented a significant positive response to photosynthetic acclimation, *Sorghum* and *Panicum* (C<sub>4</sub> plants) exhibited negative response, whereas *Ananas*, *Agave* and *Kalanchoe* (CAM plants) showed positive responses to increased CO<sub>2</sub> concentration during growth. In view of this survey, it is then evident, that responses to elevated CO<sub>2</sub> have been little investigated in C<sub>4</sub> species. Moreover, conflicting reports on plant responses to elevated CO<sub>2</sub>, and several such differential photosynthetic responses, could be attributed to differences in experimental technologies, plant species used for the experiments, age of the plant as well as duration of the treatment (Sage, 2002).

Nevertheless,  $C_4$  species still exhibit positive responses (Fig. 2), particularly at elevated temperature and arid conditions where they are currently common and under nutrient-limited situations as well (Ghannoum et al., 2000; Sage & Kubien, 2003). High  $CO_2$  aggravates nitrogen limitations and in doing so may favor  $C_4$  species, which have greater photosynthetic nitrogen use efficiency (Sage & Kubien, 2003). On the other hand, elevated  $CO_2$  can also increase water use efficiency, in part by decreasing stomatal conductance and transpiration (Ainsworth et al., 2002). The irradiance is also a paramount factor; enhanced photosynthesis under elevated  $CO_2$  conditions was observed in  $C_4$  plants grown under high irradiance, while there was not much response when grown under low irradiance (Ghannoum et al., 2000).

Differences in the conductance of the bundle sheath cells to  $CO_2$  (varying with the decarboxylating subtype and also associated with changes in the ratio of Rubisco:PEP-carboxylase activity) were proposed to be responsible for different rates of  $CO_2$  leakage (Brown & Byrd, 1993; Ehleringer & Pearcy, 1983; Hattersley, 1982; Saliendra et al., 1996). Nevertheless, further studies showed that the stimulation of leaf photosynthesis at elevated  $CO_2$  was not associated with  $CO_2$  leak rates from the bundle sheath or with changes in the ratio of activities of PEP-carboxylase to Rubisco (Ziska et al., 1999).

Another aspect of plant metabolism which may vary under exposure to increased  $CO_2$  is the respiration. As highlighted by Reddy and colleagues (2010) in  $C_4$  plants little is known about the impact of elevated  $CO_2$  on the respiratory rates, which are reduced in  $C_3$  species and thus, probably contributing to increase biomass yield.

Neither  $C_3$  nor  $C_4$  species show acclimation responses that are directly linked to  $CO_2$  level. Instead, the  $CO_2$  effect on the photosynthetic biochemistry is largely mediated by carbohydrate accumulation in leaves under conditions where carbon sinks in the plant are also experiencing high carbon supply (Sage & McKown, 2006). The effectiveness with which increases in  $CO_2$  can be translated into growth benefits is depending in the sink-source balance and is affected by various plant and environmental factors. Depending on the growing conditions, these changes may or not conduct to increases in leaf area (Ghannoum et al., 2001; Leakey et al., 2006; Morison & Lawlor, 1999). For plants grown under optimal growth conditions and elevated  $CO_2$ , photosynthetic rates can be more than 50% higher than for plants grown under normal  $CO_2$  concentrations. This reduces to 40% higher for plants grown under the average of optimal and suboptimal conditions, and over the course of a full day, average photosynthetic enhancements under elevated  $CO_2$  are estimated to be about 30%. The 30% enhancement in photosynthesis is reported to increase relative growth rate by only about 10%. This discrepancy is probably due to enhanced carbohydrate availability exceeding many plants' ability to fully utilize it due to nutrient or inherent internal growth limitations. Consequently, growth responses to elevated  $CO_2$  increase with a plant's sink capacity and nutrient status (Kirschbaum, 2010).

### **3.1 Responses to increased $CO_2$ levels are dependent on other environmental factors**

#### **3.1.1 Increased $CO_2$ and drought**

Global circulation models have predicted that, together with increases in the  $CO_2$  concentration, in the future some regions will have increases in the frequency and severity of droughts.

Leakey et al. (2009) proposed that the potential for increased growth and yield of  $C_4$  plants at elevated  $CO_2$  concentrations relies on the decrease in water use and reduction of drought stress, and not by a direct effect of increased photosynthesis. In this respect, some  $C_4$  plants

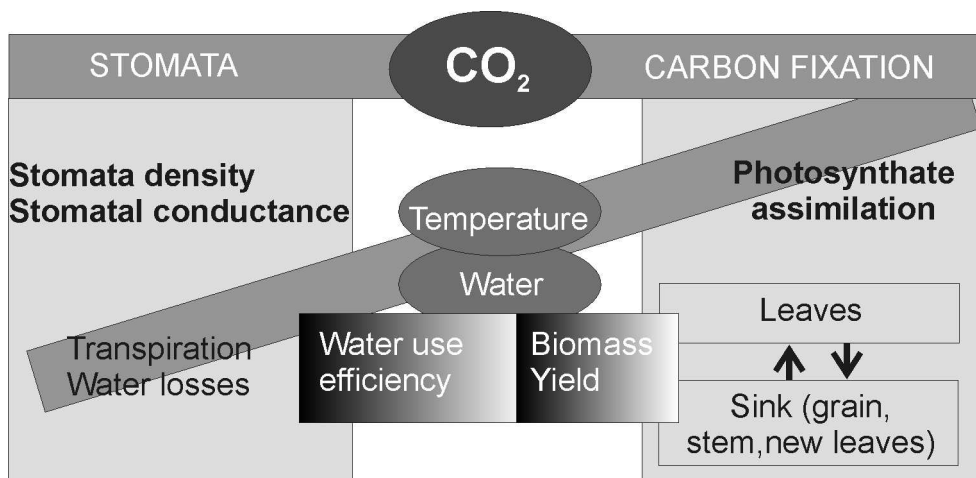


Fig. 2. Summary of the main factors involved in the response of plants to elevated CO<sub>2</sub>

grown under Free-Air Carbon dioxide Enrichment (FACE) exhibited increased photosynthetic rates only during drought or under the conditions of atmospheric vapor pressure deficits (Cousins, et al., 2002; Leakey et al., 2009). Elevated CO<sub>2</sub> reduced midday stomatal conductance of FACE-grown sorghum by 32% with irrigation and by 37% under drought stress (Wall et al., 2001). The effect of elevated CO<sub>2</sub> concentration on whole plant water use was smaller, but still significant (Conley et al., 2001). It is worth mentioning, that this indirect mechanism of enhanced carbon uptake by elevated CO<sub>2</sub> concentration is not unique to C<sub>4</sub> plants. Decreased stomatal conductance at elevated concentration of CO<sub>2</sub> in a C<sub>3</sub> soybean canopy also led to a significant reduction in canopy evapo-transpiration (Bernacchi et al., 2007). Therefore, interactive effects of CO<sub>2</sub> and water availability may alter the relative performance of C<sub>3</sub> and C<sub>4</sub> species. As stated before, at current CO<sub>2</sub> levels, C<sub>4</sub> species (particularly dicots) generally require less water than C<sub>3</sub> because of the higher CO<sub>2</sub> uptakes rates and greater stomatal resistance to water loss (Ehleringer et al., 1997). Under conditions of drought and elevated CO<sub>2</sub>, based on comparative studies using model C<sub>3</sub> and C<sub>4</sub> plants, Ward et al. (1999) postulated that C<sub>3</sub> species would be more competitive than C<sub>4</sub> species as results of decreased water loss through transpirations and higher CO<sub>2</sub> rates that would decrease the relative advantage of C<sub>4</sub> plants under drought conditions.

### 3.1.2 Increased CO<sub>2</sub> and temperature

Global increases in temperature and CO<sub>2</sub> may have interactive effects on photosynthesis. On one hand, negative effects of heat stress on plants are well known, since photosynthesis is thought to be among the most thermosensitive aspects of plant function. Both the light (electron transport) and dark (Calvin cycle) reactions of photosynthesis have thermolabile components, especially photosystem II (PSII) in the light reactions (Berry & Björkman, 1980; Heckathorn et al., 1998, 2002; Santarius 1975; Weis & Berry, 1988) and Rubisco activase in the Calvin cycle (Crafts-Brandner & Salvucci, 2002). Therefore, limiting processes controlling photosynthesis at elevated temperature could be either declining capacity of electron transport to regenerate ribulose-1,5-bisphosphate, or reductions in the capacity of Rubisco activase to maintain Rubisco in an active configuration (Sage et al., 2008).



Since, studies examining the effects of elevated CO<sub>2</sub> and increased growth temperature (typically 3–5 °C) had yield positive (Faria et al., 1996, 1999; Ferris et al., 1998; Huxman et al., 1998; Taub et al., 2000), negative (Bassow et al., 1994; Roden & Ball, 1996), and no effects (Coleman et al., 1991) on photosynthetic and plant tolerance to acute heat stress. Again, growing conditions and type of carbon assimilation pathways are need to be discriminated. General effects of elevated CO<sub>2</sub> on photosynthetic heat tolerance were recently investigated in a comparative study including C<sub>3</sub> and C<sub>4</sub> species and they can be summarized as follows: (i) in C<sub>3</sub> species, elevated CO<sub>2</sub> typically increases heat tolerance of photosynthesis, except for plants grown at supra-optimal growing temperature, then elevated CO<sub>2</sub> may provide no benefit or even decrease photosynthesis; (ii) in C<sub>4</sub> species, elevated CO<sub>2</sub> frequently decreases photosynthetic thermotolerance, at near-optimal growing temperature as well as supra-optimal growing temperature (Wang et al. 2008; Hamilton et al., 2008). Although both C<sub>3</sub> and C<sub>4</sub> plants experience reductions of similar magnitude in stomatal conductance with increasing CO<sub>2</sub> (e.g., 20%–50% with a doubling of CO<sub>2</sub>) (Sage, 1994; Reich et al., 2001; Wang et al., 2008), the lower stomatal conductance of C<sub>4</sub> plants at any given CO<sub>2</sub> level means lower average transpiration and higher leaf temperatures in C<sub>4</sub> plants, which may increase heat related damage in C<sub>4</sub> plants compared with C<sub>3</sub> plants in the same habitat. On the other hand, elevated CO<sub>2</sub> increases leaf size (Morison & Lawlor, 1999), and this should increase leaf temperatures during heat stress more in C<sub>3</sub> than C<sub>4</sub> species, given the greater average stimulation of growth in elevated CO<sub>2</sub> in C<sub>3</sub> species (Poorter & Navas, 2003).

### 3.1.3 Other considerations

Finally, to have a deeply understanding of the performance of C<sub>4</sub> plants under increased CO<sub>2</sub> conditions other factors besides water availability, soil nutrition and temperature, should be considered. One aspect to be included in the analysis should be pests and diseases.

Changes in the ratio of CO<sub>2</sub>/O<sub>2</sub> in the atmosphere affects plant metabolism in ways that ultimately influence the quality of leaves as a food resource for animals. To herbivores, the decreased leaf protein contents and increased carbon/nitrogen ratios common to all leaves under elevated atmospheric carbon dioxide imply a reduction in food quality. Stiling and Cornelissen (2007) analyzed plant-herbivore interactions using C<sub>3</sub> species and found that plants grown under elevated CO<sub>2</sub> usually had lower nutrient concentrations, which reduced the growth rate of herbivores feeding on that plant material. Contrasting C<sub>4</sub> and C<sub>3</sub> species, C<sub>4</sub> grasses are a less nutritious food resource than C<sub>3</sub> grasses, both in terms of reduced protein content and increased carbon/nitrogen ratios. The abundance of C<sub>3</sub> and C<sub>4</sub> plants (particularly grasses) are affected by atmospheric carbon dioxide. There is an indication that as C<sub>4</sub>-dominated ecosystems expanded 6–8 Ma b.p., there were significant species-level changes in mammalian grazers. Today there is evidence that mammalian herbivores differ in their preference for C<sub>3</sub> *versus* C<sub>4</sub> food resources, although the factors contributing to these patterns are not clear. Elevated carbon dioxide levels will likely alter food quality to grazers both in terms of fine-scale (protein content, carbon/nitrogen ratio) and coarse-scale (C<sub>3</sub> *versus* C<sub>4</sub>) changes (Ehleringer et al., 2002).

Regarding plant-plant interactions using C<sub>3</sub> species, Wang (2007) showed that the growth response of mixed-species communities to elevated CO<sub>2</sub> was less than the response of single-species populations. In addition, the relative importance of these and other factors should be established for C<sub>4</sub> species grown under elevated CO<sub>2</sub>.

## 4. Conclusion

C<sub>4</sub> plants are directly affected by all major global change parameters, often in a manner that is distinct from that of C<sub>3</sub> plants. Although an ongoing effort has been dedicated to the study of the response of C<sub>4</sub> plants to CO<sub>2</sub> enrichment, the literature regarding the response of C<sub>4</sub> plants is still under-represented when comparing to that of C<sub>3</sub> species. An understanding of C<sub>4</sub> plants responses to ambient variables such as temperature, CO<sub>2</sub>, nutrients and water is essential for predictions of how agricultural and wild C<sub>4</sub> populations will respond to climate variations such as those predicted to occur with global climate change (Intergovernmental Panel on Climate Change, IPCC, 2001).

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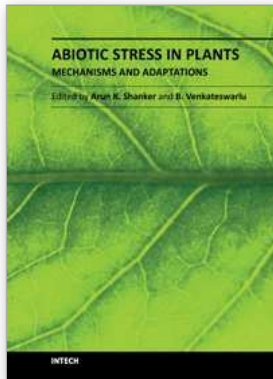
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## **Abiotic Stress in Plants - Mechanisms and Adaptations**

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World population is growing at an alarming rate and is anticipated to reach about six billion by the end of year 2050. On the other hand, agricultural productivity is not increasing at a required rate to keep up with the food demand. The reasons for this are water shortages, depleting soil fertility and mainly various abiotic stresses. The fast pace at which developments and novel findings that are recently taking place in the cutting edge areas of molecular biology and basic genetics, have reinforced and augmented the efficiency of science outputs in dealing with plant abiotic stresses. In depth understanding of the stresses and their effects on plants is of paramount importance to evolve effective strategies to counter them. This book is broadly divided into sections on the stresses, their mechanisms and tolerance, genetics and adaptation, and focuses on the mechanic aspects in addition to touching some adaptation features. The chief objective of the book hence is to deliver state of the art information for comprehending the nature of abiotic stress in plants. We attempted here to present a judicious mixture of outlooks in order to interest workers in all areas of plant sciences.

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