C$_4$ Plants Adaptation to High Levels of CO$_2$ and to Drought Environments

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1. Introduction

1.1 General features of the C$_4$ cycle

All plants use the Photosynthetic Carbon Reduction (PCR or Calvin-Benson) cycle for CO$_2$ 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$_3$ cycle. Plants utilizing this pathway are often named as C$_3$ species. A major problem with the C$_3$ 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$_4$ photosynthesis is an adaptation of the C$_3$ 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$_4$ species originate from warmer climates than C$_3$ species (Sage & Monson, 1999). Most C$_4$ plants are native to the tropics and warm temperate zones with high light intensity and high temperature. Under these conditions, C$_4$ 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$_4$ perennial grass in the central Amazon, which achieves a net production of 100 t (dry matter) ha^{-1} year^{-1} (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$_4$ plants. In addition, the most troublesome weeds like nutgrass, crabgrass and barnyard, are also C$_4$ species. Although C$_4$ 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$_4$-grass-lands (Ehleringer et al., 1997). Approximately half of the ˜10,000 grass and sedge species have C$_4$ 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
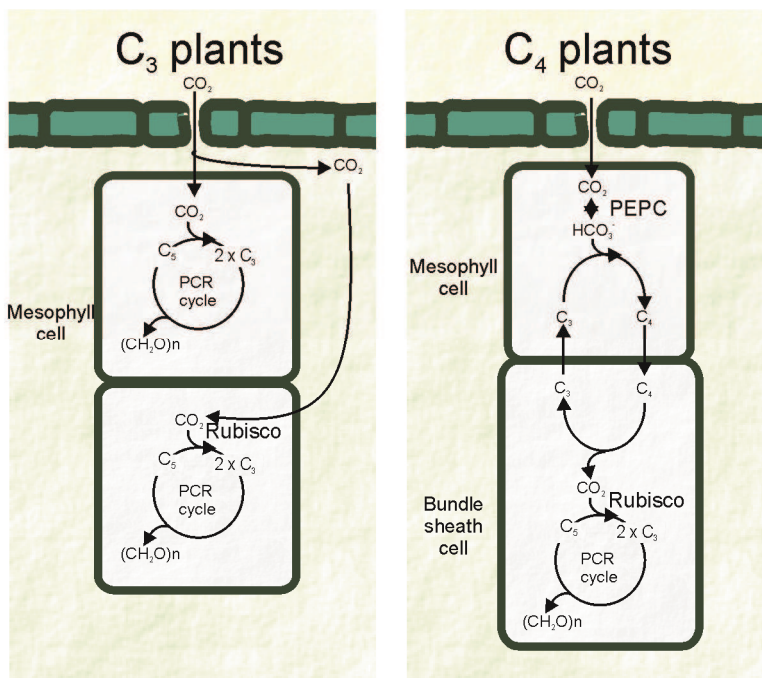

Fig. 1. Simplified scheme of carbon fixation pathways operating in C_3 and C_4 plants. Abbreviations: C_3, three-carbon organic acids; C_4, four-carbon organic acids; C_5, ribulose-1,5-bisphosphate; PCR, Photosynthetic Carbon Reduction Cycle; PEPC, phosphoenolpyruvate carboxylase; Rubisco, Ribulose-1,5-bisphosphate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

Hatch-Slack pathway, after the first scientists that postulated the metabolic pathway. However, they used the name *C$_4$ dicarboxylic acid pathway of photosynthesis*. Due to current use, the name has been shortened to *C$_4$ photosynthesis*, *C$_4$ pathway*, *C$_4$ syndrome* or *C$_4$ metabolism*. The plants that perform this type of photosynthesis are then called *C$_4$ plants*.

This general scheme is common among the C$_4$ 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$_4$ plants have been traditionally grouped into three biochemical subtypes depending on the major decarboxylase used (C$_4$-NADP-ME subtype; C$_4$-NAD-ME subtype or C$_4$-PEP-CK subtype). Each C$_4$ 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$_3$ *vs* C$_4$ species

C$_4$ species have evolved in a high CO$_2$ environment. This increases both their nitrogen and water use efficiency compared to C$_3$ species. C$_4$ plants have greater rates of CO$_2$ assimilation than C$_3$ 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$_4$ compared to C$_3$ plants, the range in leaf nitrogen concentration per unit dry mass is similar for both C$_4$ and C$_3$ species. Even though leaf nitrogen is invested into photosynthetic components into the same fraction in both C$_3$ and C$_4$ species, C$_4$ plants allocate less nitrogen to Rubisco protein and more to other soluble protein and thylakoids components. In C$_3$ 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$_4$ species (Evans & von Caemmerer, 2000; Sage et al., 1987). The lower nitrogen requirement of C$_4$ plants results from their CO$_2$-concentrating mechanism, which raises the bundle sheath CO$_2$ concentration, saturating Rubisco in normal air and almost eliminating photorespiration. Without this mechanism, Rubisco in the C$_3$ 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$_4$ plants, C$_3$ leaves must therefore invest more heavily in Rubisco and have a greater nitrogen requirement. Because the Rubisco specificity for CO$_2$ decreases with increasing temperature (Long, 1991), this difference between the C$_3$ and C$_4$ photosynthetic nitrogen-use efficiency is greatest at high temperatures (Long, 1999). The high photosynthetic nitrogen-use efficiency of C$_4$ plants is partially offset by the nitrogen-requirement for CO$_2$-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$_4$ plants is due to both higher photosynthetic rates per unit leaf area and lower stomatal conductance, with the greater CO$_2$ assimilation contributing to a major extent (Ghannoum et al., 2011).

The advantages of greater nitrogen use efficiency and water use efficiency of C$_4$ relative to C$_3$ photosynthesis are fully realized at high light and temperature, where oxygenase reaction of Rubisco is greatly increased. It is worth noting, although in C$_4$ 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 µmol 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_2, 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_2 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_2 increase in the atmosphere. C_4 plants are directly affected by all major global change parameters, often in a manner that is distinct from that of C_3 plants. In the present chapter, we will focus on the effect of increased CO_2, and its relation to temperature and drought, on C_4 plants. Understanding how plants have and will respond to the rapid change in CO_2 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 CO₂ response

In theory, increases in atmospheric levels of CO_2 above current levels can increase photosynthesis by decreasing photorespiration (fixation of O_2 rather than CO_2 by Rubisco), which increases with temperature and is higher in C_3 than C_4 and crassulacean acid metabolism (CAM) plants (Sage & Monson, 1999). In addition, rising CO_2 generally stimulates C_3 photosynthesis more than C_4. Doubling of the current ambient CO_2 concentration stimulated the growth of C_4 plants to the tune of 10–20% whereas that in C_3 plants was about 40–45% (Ghannoum et al., 2000).

C_3 photosynthesis is known to operate at less than optimal CO_2 levels and can show dramatic increase in carbon assimilation, growth and yields. As Rubisco is substrate-limited by the current atmospheric CO_2 levels, this enzyme has the potential to respond to increases in CO_2 concentration; and have a metabolic control to alter the CO_2 flux during carbon assimilation (Bernacchi et al., 2003; Long et al., 2004). On the contrary, photosynthetic carbon assimilation in the C_4 species is saturated or almost CO_2-saturated a low ambient pCO_2. The reason is that PEP-carboxylase utilizes HCO_3^- as substrate rather than CO_2; in consequence, the enzyme is insensitive to changes in the ratio of CO_2: O_2 due to lack of binding of O_2 to the catalytic site of PEP-carboxylase. Therefore, if plants were grown under elevated CO_2, carbon fixation would be little affected. This assumption that the inherent CO_2 concentrating mechanism in C_4 plants renders these plants insensitive to elevated CO_2 atmosphere is reflected in the lack of interest that it has been attributed to the study of the C_4 plants response to elevated CO_2 levels. To show this, Reddy et al. (2010) performed an exhaustive fifteen year- literature survey on the influence of elevated CO_2 among certain C_3, C_4 and CAM species. The authors provided information for forty C_3 plants and for only two C_4 species and three CAM plants. Most of the C_3 plants presented a significant positive response to photosynthetic acclimation, *Sorghum* and *Panicum* (C_4 plants) exhibited negative response, whereas *Ananas*, *Agave* and *Kalanchoe* (CAM plants) showed positive responses to increased CO_2 concentration during growth. In view of this survey, it is then evident, that responses to elevated CO_2 have been little investigated in C_4 species. Moreover, conflicting reports on plant responses to elevated CO_2, 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.

Leaky et al. (2009) proposed that the potential for increased growth and yield of C_4 plants at elevated CO_2 concentrations relays 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
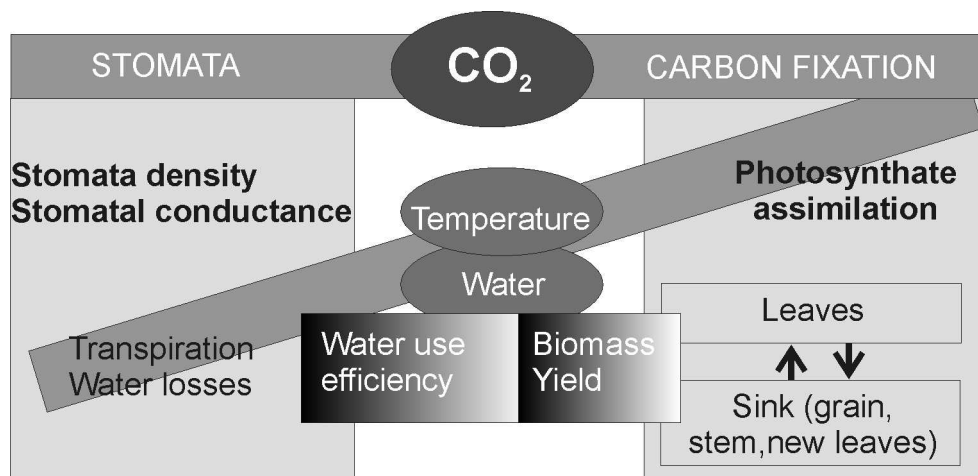
Fig. 2. Summary of the main factors involved in the response of plants to elevated CO_2

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_2 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_2 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_2 concentration is not unique to C₄ plants. Decreased stomatal conductance at elevated concentration of CO_2 in a C₃ soybean canopy also led to a significant reduction in canopy evapo-transpiration (Bernacchi et al., 2007). Therefore, interactive effects of CO_2 and water availability may alter the relative performance of C₃ and C₄ species. At stated before, at current CO_2 levels, C₄ species (particularly dicots) generally require less water than C₃ because of the higher CO_2 uptakes rates and greater stomatal resistance to water loss (Ehleringer et al., 1997). Under conditions of drought and elevated CO_2, based on comparative studies using model C₃ and C₄ plants, Ward et al. (1999) postulated that C₃ species would be more competitive than C₄ species as results of decreased water loss through transpirations and higher CO_2 rates that would decrease the relative advantage of C₄ plants under drought conditions.

3.1.2 Increased CO₂ and temperature

Global increases in temperature and CO_2 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_2 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_2 on photosynthetic heat tolerance were recently investigated in a comparative study including C_3 and C_4 species and they can be summarized as follows: (i) in C_3 species, elevated CO_2 typically increases heat tolerance of photosynthesis, except for plants grown at supra-optimal growing temperature, then elevated CO_2 may provide no benefit or even decrease photosynthesis; (ii) in C_4 species, elevated CO_2 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_3 and C_4 plants experience reductions of similar magnitude in stomatal conductance with increasing CO_2 (e.g., 20%–50% with a doubling of CO_2) (Sage, 1994; Reich et al., 2001; Wang et al., 2008), the lower stomatal conductance of C_4 plants at any given CO_2 level means lower average transpiration and higher leaf temperatures in C_4 plants, which may increase heat related damage in C_4 plants compared with C_3 plants in the same habitat. On the other hand, elevated CO_2 increases leaf size (Morison & Lawlor, 1999), and this should increase leaf temperatures during heat stress more in C_3 than C_4 species, given the greater average stimulation of growth in elevated CO_2 in C_3 species (Poorter & Navas, 2003).

3.1.3 Other considerations

Finally, to have a deeply understanding of the performance of C_4 plants under increased CO_2 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_2/O_2 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_3 species and found that plants grown under elevated CO_2 usually had lower nutrient concentrations, which reduced the growth rate of herbivores feeding on that plant material. Contrasting C_4 and C_3 species, C_4 grasses are a less nutritious food resource than C_3 grasses, both in terms of reduced protein content and increased carbon/nitrogen ratios. The abundance of C_3 and C_4 plants (particularly grasses) are affected by atmospheric carbon dioxide. There is an indication that as C_4-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_3 *versus* C_4 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_3 *versus* C_4) changes (Ehleringer et al., 2002).

Regarding plant-plant interactions using C_3 species, Wang (2007) showed that the growth response of mixed-species communities to elevated CO_2 was less than the response of single-species populations. In addition, the relative importance of these and other factors should be established for C_4 species grown under elevated CO_2.

4. Conclusion

C$_4$ plants are directly affected by all major global change parameters, often in a manner that is distinct from that of C$_3$ plants. Although an ongoing effort has been dedicated to the study of the response of C$_4$ plants to CO$_2$ enrichment, the literature regarding the response of C$_4$ plants is still under-represented when comparing to that of C$_3$ species. An understanding of C$_4$ plants responses to ambient variables such as temperature, CO$_2$, nutrients and water is essential for predictions of how agricultural and wild C$_4$ populations will respond to climate variations such as those predicted to occur with global climate change (Intergovernmental Panel on Climate Change, IPCC, 2001).

5. Acknowledgment

6. References

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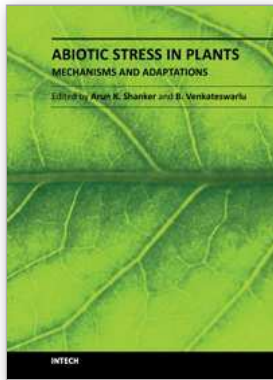
Abiotic Stress in Plants - Mechanisms and Adaptations

Edited by Prof. Arun Shanker

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 dived 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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