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Semi-arid Crop Responses to Atmospheric Elevated CO_2

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ABSTRACT

Semi-arid tropics host most of the poor and small-holding farmers of the developing world. Global warming is seen largely as a consequence of continuous increase in the emission of carbon dioxide and other greenhouse gases into the atmosphere leading to unusual changes in global temperatures and rainfall patterns. This in turn is expected to increase the water scarcity in the environment, affecting plant growth and metabolism. In this context, we reviewed semi-arid crop responses to elevated CO_2 levels in terms of growth, yield components, physiological, biochemical and molecular changes. Predicted rise of carbon-dioxide in the atmosphere may benefit the plants by increasing the crop water use efficiency and net photosynthesis leading to greater biomass, yield and harvest index. C_3 and C_4 crop plants vary in their degree of response to elevated CO_2, which will likely affect the proportion of land area occupied by these crops in future. Stomatal conductance will probably be reduced at higher CO_2 concentrations reducing transpiration per unit leaf area and consequently increasing the leaf temperature. The high CO_2 is an ameliorative of the adverse effects of drought and acts by altering the plant, biochemical and molecular systems. Understanding of the direct effects of elevated CO_2 and its interactions with the other climate variables is needed in order to predict the impact of climate change scenarios on crop growth and food security in future.

Keywords: biochemical and molecular changes, climate change, elevated carbon dioxide, growth, semi-arid crops, yield

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INTRODUCTION

Atmospheric CO_2 concentration, which was about 280 µmol mol^{-1} before the industrial revolution, has in recent year's surpassed 380 µmol mol^{-1} due to human activities (IPCC 2007a, 2007b). Much of the changes in atmospheric CO_2 occurred over the last 50 years (1953 to 2003), and the increase was about 60–70 ppm (Krull *et al.* 2005; Keeling and Whorf 2005; Mizyed 2009). With this likely exponential pattern of increase, it is estimated to reach 605 to 755 ppm by 2070. The average mean warming is projected to be between 2.23 and 2.87 ºC by 2050 at the global level (Mizyed 2009). The increasing atmospheric CO_2 concentration and the associated predictions of global warming (IPCC 2007a, 2007b; Frank *et al.* 2010) have stimulated research programs to determine the likely effects of the future elevated CO_2 levels on agricultural productivity (Ziska *et al.* 2004) on the functioning of natural ecosystems (Körner 2006, Körner *et al.* 2007) after first human health (Loladze 2002) ultimately on food security (Long *et al.* 2005). However, as a mean to increase green house crop yields and as a part of global climatic change prediction, the effects of atmospheric CO_2 enrichment on growth and productivity of selected crop species have been studied for more than a century using greenhouses, controlled-environment chambers, open-top chambers, FACE and other experimental techniques (Drake *et al.* 1985). The results of these chamber-based experiments on CO_2 enrichment have been reviewed (Kimball 1983, 1986, 1993; Kimball and Idso 1983; Cure 1985; Cure and Acock 1986; Idso and Idso 1994, 2001; Curtis and Wang 1998; Wand *et al.* 1999; Nakagawa and Horie 2000; Kimball *et al.* 2002; Hovenden *et al.* 2006; Vanaja *et al.* 2006b; Uprety *et al.* 2007; Taub *et al.* 2008; Leakey *et al.* 2009a; Morgan *et al.* 2009a).

A direct effect of increased concentration of elevated CO_2 and other greenhouse gases has already resulted in warmer temperatures globally, a trend that is expected to continue. Changes in temperature are likely to alter precipitation worldwide, decreasing in many areas (Houghton *et al.* 2001; Mizyed 2009), although different prediction scenarios appear to agree only on an increase in temperature, but show large disagreement with regards to precipitation. Yet,

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Invited Review

it is likely that climate change could result in prolonged episodes of water deficit (Mizyed 2009). The semi-arid tropics are one of the world's most marginalized regions, plagued water scarcity, and land degradation. This ecosystem is characterized by extreme rainfall variability, recurrent and unpredictable droughts, flooding, warm temperatures and a fragile natural resource base with inherent low fertility soils. Due to these, agriculture is quite risky with distinct growing seasons, separated by hot and dry periods. As a result, crops that grow in semi-arid areas are has to face the challenges of climatic variables along with abiotic and botic stresses. Herein we review the empirical evidences, particularly on the semi-arid crop responses to elevated CO_2 in terms of changes in growth, flowering, yield components, biochemical and molecular changes.

GROWTH AND ADAPTATIONS

Many experimental studies have focused on the effects of CO_2 enrichment on biomass accumulation in plants. These experiments were carried out with agricultural and horticultural plants under more or less controlled conditions (*i.e.,* greenhouse, growth chamber, etc.) to maintain elevated CO_2 levels. Kimball (1983, 1986) reviewed on the basis of large number of studies, showed that C_3 plants responded with a higher average increment in biomass production than C_4 plants (Ghannoum *et al.* 2000; Vanaja *et al.* 2006a, 2008) in response to a doubling of CO_2 concentrations. One important lacuna in this area of research is the non-availability of response information to a gradient of CO_2 concentration. In most of the CO_2 enrichment experiments only one level of additional CO_2 was included (usually doubled current level), which permits no estimation of how plants will react to the gradual increase in CO_2 concentrations over several decades. It could be that adaptation and acclimation phenomena lead to a diminution or an increase of the relative CO_2-induced increase in biomass accumulation. CO_2-induced stimulation of net photosynthesis, and consequently of growth, is frequently found to be greatest in the early development stages of plants and then to level off gradually (Bloom *et al.* 2002; Reich *et al.* 2006). There have been few attempts to use long term experiments with several CO_2 levels as a means of estimating the stimulation of biomass production through elevated CO_2. With rising CO_2, the rate of biomass production gradually approaches a point of saturation, the exact CO_2 concentration at which the growth rate reaches a plateau is depend on species or variety or experimental condition (Idso 1989). Some crop plants only need relatively small rise in CO_2 for reaching their full potential in biomass production. Furthermore, plant species differ in their sensitivities to CO_2, with winners and losers emerging in studies designed to evaluate species responses to CO_2; this suggests that rising atmospheric CO_2 over the past hundred years may have already led to species shifts in native plant communities. Globally, C_3 shrubs are expanding into C_4 grasslands (Morgan *et al.* 2007, 2009).

Elevated CO_2 increases the root growth, root volume, root biomass as well as abundance of root hairs under drought stress. Under elevated CO_2, the density of root hair was larger, which is expected to help in faster and greater capture of water and nutrients (BassiriRad *et al.* 2001) from the soil. Rogers *et al.* (1994) demonstrated root dynamic changes under elevated CO_2. Since high CO_2 tends to increase the root/shoot ratio, it seems that the elevated CO_2 stimulation of root growth was relatively higher than the stimulation of shoot growth. Vanaja *et al.* (2006a, 2007) showed that under elevated CO_2 the root shoot ratio of cereals (sorghum and millet) was increased at initial stages under well watered condition, but in blackgram (*Vigna mungo* L. Hepper) such an increase occurred only under water stressed condition. Under normal conditions, the root/shoot dry weight ratio increases as plant water stress develops (Seneweera *et al.* 2001). The increase is mostly due to a relative reduction in shoot dry weight. However there were rare cases where an absolute amount of root dry weight increase was observed under drought stress (Sindhoj *et al.* 2004). Though these findings indicate that elevated CO_2 level may promote better root growth and drought adaptation, further research in these area is needed to ascertain crop-wise responses and crop species/genotype × environment interactions.

Leaf number and leaf elongation had been shown to increase substantially under CO_2 enriched conditions in many crop plants (Seneweera and Conroy 2004; Vu and Allen 2009). It has been reported that both cell expansion and cell production are sensitive to CO_2 concentration, but the effects appear to be highly dependent on the growth environment and genotype (Taylor *et al.* 2001). Ferris *et al.* (2001) suggested that the increased leaf size under elevated CO_2 was associated with faster rates of cell elongation. Another possible explanation for larger leaf blades at elevated CO_2 is that the duration of cell expansion could be longer. Leaf dry weight, leaf thickness and specific leaf weight were also increased under elevated CO_2, whereas leaf area was reduced under drought stress. Vanaja *et al.* (2006a) evaluated the leaf area of food (pulses and cereals) and oil seed crops for their response to elevated CO_2 at vegetative stage and observed that the pulse crop responded better than others under elevated CO_2 concentration. An increase in growth, leaf area and photosynthesis has also been reported in seedlings of *Syzyzium cumini* L. (Skeel), a tropical tree spices (Ratnakumar and Swamy 2003) under elevated CO_2. Elevated CO_2 has been shown to promote greater volume of foliage, higher number of siliqua and greater root growth in *Brassica juncea* (Uprety *et al.* 2008). An increase in leaf area under high CO_2 conditions could lead to a different pattern of water use of the crop canopy, and in particular quicker soil moisture depletion under the high CO_2 conditions. However, elevated CO_2 also causes partial stomatal closure and decreased stomatal which more often results in modest reduction in evapotranspiration, as will be discussed in a later section.

PHYSIOLOGICAL, BIOCHEMICAL AND MOLECULAR CHANGES

CO_2 effect on photosynthesis

It is well known that elevated CO_2 stimulates photosynthesis. Also important is whether or not the plants acclimate to the higher CO_2 by altering the biochemical makeup of their photosynthetic apparatus. Indeed, the internal CO_2 concentration in the stomatal chamber appears to be highly regulated and adaptation of that concentration may be expected after exposure to increased CO_2. The biochemical and molecular basis for such photosynthetic acclimation have been reviewed by Moore *et al.* (1999). **Table 1** express the percentage increase in photosynthesis is reported by several investigators for agricultural crops (Ainsworth *et al.* 2002; Kimball *et al.* 2002; Ainsworth and Long 2005; Rogers *et al.* 2006; Booker *et al.* 2007; Sujatha *et al.* 2008). At short time scales (hourly to daily), plant photosynthesis and transpiration respond nonlinearly to atmospheric CO_2 concentration and vapor pressure deficit, depending on plant water status and thus soil moisture (Manzoni *et al.* 2008). The CO_2 acclimation response is mainly due to RuBP carboxylase, *i.e.*, the initial carboxylation enzyme in photosynthetic process of C_3 plants. Investigators have reported varying degrees of activity for this enzyme from leaves of plant (peanut, soybean, and rice) acclimated to elevated CO_2 levels (Vu *et al.* 2007). Furthermore, the data suggest that activity of RuBPCase could be affected by stromal acidification. Indeed, it has been demonstrated with illuminated, intact chloroplasts and leaf slices that induced osmotic stress results in acidification of the stroma, with pH values dropping close to levels found in the dark. Lorimer *et al.* (2001) working with purified spinach RuBPCase, have shown that in the presence of 10 μM CO_2 and 20 mM Mg^{2+}, the activity of this enzyme decreases more than 4-fold with a pH change from 8.5 to 7.5. Stromal acidification under mode-

Table 1 Comparison of changes in net photosynthesis between short and long-term CO_2 (700ppm elevated CO_2 levels) experiments on globally important C_3 and C_4 semi-arid crops. (Sources: Cure and Acock 1986; Ghannoum *et al.* 2000; Leakey *et al.* 2003; Booker *et al.* 2007; Souza *et al.* 2008; Vu and Allen 2009).

Metabolic type	**Crop species**	**Percent change in net photosynthesis due to elevated CO_2**	
		Short-term effect <1 week	**Long-term effect >1 week**
C_3	Barley	+50	+14
	Cotton	+60	+13
	Soybean	+78	+42
	Peanut	--	+22
C_4	Maize	+26	---
	Millet	-3	+6
	Sugarcane	--	+30

rate to severe drought stress, producing a less active enzyme, could explain not only the decline of *in vivo* CO_2 fixation catalyzed by RuBPCase, but also the transient decline of initial *in vitro* activities observed with the extracted soybean enzyme. For upper leaves, the CO_2-induced of photosynthetic rate ranged from about 25 to 45% under ample water and high nitrogen for wheat, ryegrass, and cotton, which are C_3 photosynthetic crops. At low N, the values were somewhat lower for wheat, but, surprisingly, they were higher for ryegrass. For sorghum, which is C_4 crop, the stimulation was much less, only about 9%, in maize the photosynthesis was increase in dry climate and favorable well watered conditions the enhanced CO_2 would not affect the photosynthesis (Leakey *et al.* 2004). However, under water stress the sorghum had a larger response of about 23%, which was probably more due to the effect of elevated CO_2 on plant water relations than a direct stimulation of photosynthesis (Wall *et al.* 2001). Wheat ears responded somewhat more than the upper leaves (Wechsung *et al.* 2000).

Effect of CO_2 on the quantity of new sink and sources

An elevated level of CO_2 doubled the rate of accumulation of dry matter but had no effect on the acclimation of the photosynthesis rate or on levels of carbohydrates in radish leaves at dawn (Overdieck *et al.* 1988). The carbon needed to satisfy the demand for these newly generated sinks was met by new photosynthates produced during high CO_2 exposure rather than from stored carbohydrates. The continued high rate of photosynthesis contributed the growth and sub-satiability of the new sinks. Elevated CO_2 enrichment enhances flag leaf senescence in barley due to greater grain nitrogen sink capacity (Fangmeier *et al.* 2000) Elevated CO_2 alters many interacting forces such as canopy architecture and partitioning of photo assimilates (Uprety *et al.* 2000). So, part of the acclimation process might be related to having new sources (leaves) contributing to the overall biomass accumulation, thereby the need to down-regulate the overall machinery. However despite of acclimation photosynthetic capacity, carbon gain is markedly greater in plants grown at the CO_2 anticipated at the middle of this century (Leakey *et al.* 2009a).

High CO_2 and CO_2 concentration in the stomatal chamber

Photo-oxidative damages can be ameliorated with elevated CO_2 supply to the plants (Scarascia-Mugnozz *et al.* 1996). If it is assumed that under mild water deficits the restriction of water loss and CO_2 uptake by low stomatal conductance predominates, and then the elevated CO_2 ameliorates the plant performance by maintaining greater supply of CO_2 to the leaves and thereby maintaining the level of net photosynthesis. This would help maintain use of captured light energy for NADPH and ATP synthesis by providing more sink capacity and thus would diminish the accumulation of excitation energy in the photosynthetic pigments which is a major cause of photo-oxidatative damage (Able *et al.* 2003; Grantz *et al.* 2006). Elevated CO_2 should be acclamatory therefore be beneficial for plants in dry environments, offsetting some of the damaging consequences of global environmental change. However, acclamatory changes in the photosynthetic machinery after a long period of growth under elevated CO_2 may reduce the benefits also under water deficits, because it seems that, as we saw above, Rubisco activity decreases after some time of acclimation. Therefore, even greater light capture with greater capacity for synthesis of NADPH and ATP (an apparent benefit in elevated CO_2 for regeneration of ATP) would be in vain unless rubisco activity uses this pool of NADPH and ATP. Any decrease in rubisco activity would then again predispose plants to photo oxidative damage (Scarascia-Mugnozz *et al.* 1996).

When considering an individual leaf within a crop canopy, drastic changes have been shown in their response to elevated CO_2. Brooks *et al.* (2001) observed an increased net photosynthesis of the wheat canopy by about 19%, with ample nitrogen and water, by FACE (free air carbon dioxide enrichment), while it was a mere 9% when subjected to low nitrogen. Therefore, it seems that the extent of stimulation by FACE depends on the quantity of available N in the plant canopy and maybe with the N allocation variation from the old to the new leaves in the canopy. Confirming this, Hileman *et al.* (1994) found a similar stimulation in the upper leaf than in the whole canopy for cotton. Under drought conditions, elevated CO_2 would delay the onset of stress due to soil moisture depletion, and also counteract the reduction in photosynthesis resulting from lower *ci* caused by drought-induced reduction in stomatal conductance (Leakey 2009a).

Effect of CO_2 on product composition

Few existing studies on the composition of agricultural plant products grown under conditions of elevated CO_2 and these give no indication of significant changes in quality and composition (Fangmeier *et al.* 2002; Martre *et al.* 2003; Lynch and Clair 2004; De Graaff *et al.* 2006) ultimately its impact on human health (Loladze 2002). The percentage of fat, protein and raw fiber in soybean and maize were found to remain largely the same in a range (340−910 ppm) of CO_2 concentration (Rogers *et al.* 1983). The protein content of wheat grain from plants grown in elevated CO_2 concentration was unchanged (Hevelka *et al.* 1984). Elevated CO_2 did not influence composition, seedling emergence, or seedling vigor of seeds produced at two different temperatures in red kidney bean (Thomas *et al.* 2009). A Meta-analysis by Taub *et al.* (2008) suggests that the increasing carbon dioxide concentration of the 21st century are on the protein concentrations of major food crops, incorporating 228 experimental observations on barley, rice, wheat, soybean and potato. Each crop had lower protein concentrations when grown at elevated (540–958 $\mu mol\ mol^{-1}$) compared with ambient (315–400 $\mu mol\ mol^{-1}$) CO_2. For wheat, barley and rice, the reduction in grain protein concentration was 10–15% of the value at ambient CO_2. For potato, the reduction in tuber protein concentration was 14%. For soybean, there was a much smaller, although statistically significant reduction of protein concentration of 1.4%. However, the nitrogen content of the shoots of cereal plants grown in elevated CO_2 was lower than under normal CO_2, compared to roots (Jin 2007) while their grain showed no such change in nitrogen content (Rogers *et al.* 1994). This might indicate that, overall, the carbon fixation capacity of plants is relatively more enhanced by increased CO_2 than N uptake, either by at a short term effect on photosynthetic rate or because of an increase in the leaf area of plants under high CO_2. This would mechanically lead to a reduction in the nitrogen content, in particular under low N conditions.

Effect of high CO_2 on stomatal conductance – Relation to WUE

Elevated CO_2 causes partial stomatal closure, which reduces the stomatal conductance and the exchange of gases between the internal tissues of plants and the atmosphere. Under conditions of unlimiting water and nitrogen, FACE reduced the conductance of C_4 sorghum, by 37% (Wall *et al.* 2001). (Raschi *et al.* 1996) The reduction in wheat was nearly as much as 34%, while the reduction in the woody perennials was less, about 15%. Reductions in conductance due to FACE have also been reported for water-stress treatments, but these data are harder to interpret because of the combination of high CO_2 and water uptake deficit makes it difficult to compare with plants grown under normal CO_2. Ainsworth and Roger (2007) reported that FACE could reduce the mean of stomatal conductance, and it was not associated with a similar change in stomatal density.

Wall *et al.* (2001) report a slightly larger reduction in conductance for wheat (Wu *et al.* 2004) under low nitrogen compared to high nitrogen and we would expect also that the conductance under low N and normal CO_2 would also be lower than under high N. A greater reduction under low N (McDonald *et al.* 2002) is to be expected as low N causes reductions in Rubisco activity and concentration, which forces a reduction in stomatal conductance in order to maintain a constant C_i/C_a ratio (ratio of internal leaf CO_2 concentration to that of outside air), at least according to the Ecosys model by Grant *et al.* (2001).

Several studies on the effects of elevated CO_2 on stomatal conductance from chamber-based studies have reported similar results. Kimball and Idso (1983) extracted 46 observations of reductions in transpiration due to increasing CO_2 from 330 to 660 μmol mol^{-1}, and they calculated an average reduction of 34%, or of about 20% when scaled to the 190 μmol mol^{-1} increase in CO_2 being used. Wand *et al.* (1999) performed a meta-analysis on observations reported for wild C_3 and C_4 grass species. When there was no stress, elevated CO_2 (scaled to a 190 μmol mol^{-1} increase) reduced stomatal conductance by 21.3 and 16.0% for C_3 and C_4 species, respectively. Water and nutrient stresses did not significantly change the response of C_4 grasses. In their metaanalysis focusing on woody species, Curtis and Wang (1998) found a mean reduction of only 11% (scale to 6%), which was not significant at the 95% probability level. So, there are clear evidences that high CO_2 decreases stomatal conductance to maintain the C_i/C_a ratio, and this may be part of the long term acclimation that plants may undertake under increasing CO_2 conditions. This would still have a large benefit under water deficit, since a lower stomatal conductance would mechanically increase the water use efficiency.

From both the FACE and the chamber data already discussed, it appears that elevated CO_2 reduced the conductance of both C_3 and C_4 herbaceous species. Similarly also, the conductance of the woody species were affected much less than those of herbaceous species. Water and nutrient stress did not significantly change the response of C_4 grasses. In their meta-analysis focusing on woody species, Curtis and Wang (1998) found a mean reduction of only 11% (scale to 6%), which was not quite significant at the 95% probability level. However, FACE appears to have reduced stomatal conductance more than one and a half times the average reductions derived from chamber experiments. Of course, this may be due merely to the sparseness of the number of FACE experiments, or it may not have been appropriate to scale the data linearly.

Assessing effects of elevated CO_2 on evaporation with FACE technology

Free Air Carbon dioxide Enrichment (FACE) approach (Kimball *et al.* 2002; Long *et al.* 2004) is particularly advantageous for assessing the impacts of elevated CO_2 on microclimatic processes, such as evapotranspiration (ET), because there are no walls to alter the wind flow or to shade the plant canopies. Because elevated CO_2 causes a decrease in stomatal conductance, transpiration per unit leaf area is decreased while canopy temperature is increased. The increase in temperature raises the water vapor pressure inside the leaves, which tends to increase leaf transpiration, thereby negating some of the reduction due to the decrease in stomatal conductance (Kimball *et al.* 1993). Thus, the resultant effect of elevated CO_2 on ET is a combination of individual effects of the CO_2 on decreasing stomatal conductance, increasing leaf area, and increasing canopy temperature.

In experiments on cotton in Arizona, there was very little effect (< 2% reduction) on ET, as determined by soil water balance of stem flow gauges. Thus, the counteracting effects of CO_2 on conductance, leaf area, and canopy temperature must have compensated each other (Kimball *et al.* 2002). On the other hand, modest reductions in ET were observed in wheat. At ample water and nitrogen, for example, soil water balance determinations indicate ET reductions of about 3.6% (Hunsaker *et al.* 2000), while those from energy balance suggest a slightly larger reduction of about 7% (Kimball *et al.* 1993), while the estimates from soil water balance were much smaller (<2%) (Hunsaker *et al.* 2000). However, simulations with the ecosystem model by Grant *et al.* (2001) predicted a reduction in ET by 16% at low nitrogen, caused by reductions in rubisco activity (Vu *et al.* 2007) and concentration, which forced greater reductions in stomatal conductance in order to maintain a constant ci/ca ratio. In the case of sorghum, with ample water and nitrogen, somewhat larger reductions in ET (about 10%) have been observed by Conley *et al.* (2001). When seasonal water supply is severely growth limiting, one would expect plants to utilize all the water available to them, so that effects of elevated CO_2 on seasonal ET would be minimal, but a slower use (lower daily ET) would allow plants to last longer during their cycle (no forced maturity), which would give them more time for grain filling and probably a significant yield gain under water limited conditions. In other words, the major benefit of an increase in CO_2 level would be an increase in the WUE component, which would allow a more progressive use of the soil profile moisture.

Earlier studies have shown that leaves of tree seedlings grown in relatively short term experiments under elevated CO_2 caused reduction in the superoxide dismutase activities (Long and Naidu 2002). Superoxide dismutase (SOD) is an essential enzyme for survival of organisms in an oxygen-containing environment. The product of superoxide dismutase reaction, H_2O_2, is also toxic. In chloroplasts and in cytosol, H_2O_2 is detoxified by ascorbate and ascorbate peroxidase (APx) activities and in mitochondria and peroxisomes by catalase (CAT) activities. Superoxide dismutase and subsequent sequence of detoxifying reactions involving antioxidants such as ascorbate and glutathione (GT) serve to prevent the accumulation of such toxic oxygen species and protect cells from non-specific oxidative degradation of proteins, lipids or DNA. Increased rate of antioxidative enzymes i.e. SOD, CAT and APx was found in the foliage of groundnut (Ratnakumar *et al.* 2006) and soybean (Booker and Fiscus 2005) by the interaction of salinity and elevated CO_2. Therefore, this contradicts the previous work on tree seedlings (Polle *et al.* 1993), and suggests that more work would be needed to assess whether high CO_2 can interact with the anti-oxidative machinery.

Effect of high CO_2 on gene expression

Evidence suggests that regulation of the expression of photosynthetic genes, via increased soluble carbohydrate concentration, may lead to an acclimation of growth to elevated CO_2 (**Fig. 1**) and a down regulation of the photosynthetic machinery. Most recent research has focused on the effects of CO_2 enrichment on plant growth, leaf photosynthesis and biomass accumulation, but few studies (Ainsworth *et al.* 2006; Li *et al.* 2008; Souza *et al.* 2008; Cseke *et al.* 2009;

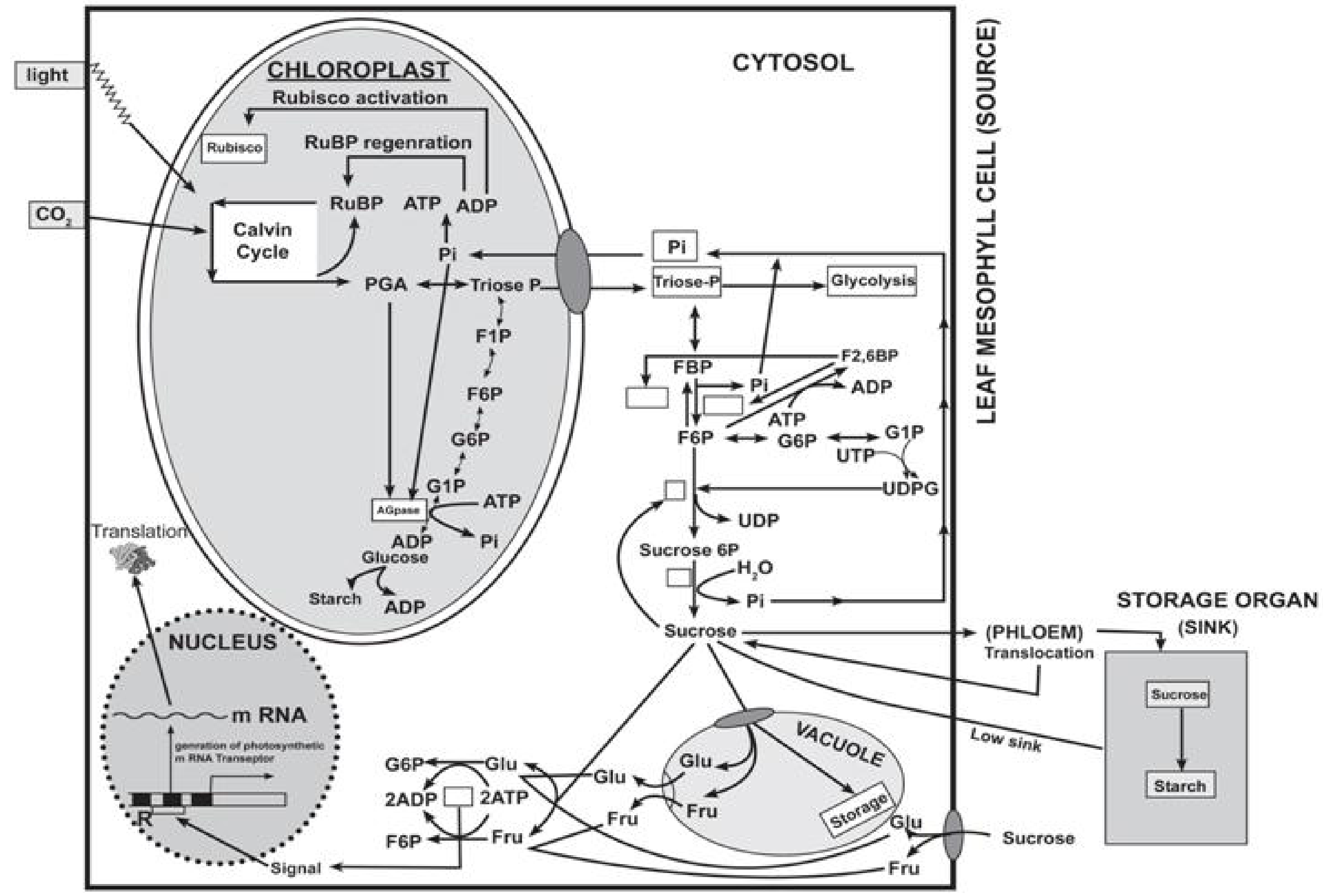

Fig. 1 Regulation of the photosynthetic machinery through increased soluble carbohydrate concentration may lead to an acclimation to elevated CO_2. Source: modified version of Sharma-Natu and Ghildiyal 2005.

Fukayama *et al.* 2009; Leakey *et al.* 2009b) have examined the effects of elevated CO_2 on gene expression in terrestrial plants. In controlled environments, a decrease of *rbcS* (gene encoding the smaller subunit of Rubisco) and *rbcL* (gene encoding the larger subunit of Rubisco) transcript levels at elevated CO_2 was found in tomato (vanOosten *et al.* 1994) and in wheat leaves (Nie *et al.* 1995). Ainsworth *et al.* (2006) are identified 1.146 transcripts that showed a significant change in expression in growing versus fully expanded leaves. However, it has not been shown that these decreases in transcript levels are apparent at all stages of crop development. Nie *et al.* (1995) found weak correspondence between increased soluble carbohydrate concentration and decreased levels for nuclear gene transcripts when they examined the spring wheat grown under different elevated CO_2 concentrations using FACE facility. Short-term growth at elevated CO_2 by FACE stimulated carbon gain irrespective of down regulations of plastid function and alerted expression of gene (Li *et al.* 2008) in *Arabidopsis*. Although few genes responded to long term exposure to elevated CO_2, the transcriptional activity of leaf elevated CO_2 responsive genes was distinctly different between the clones, differently impacting multiple pathways during both early and late growing seasons (Cseke *et al.* 2009). In a recent work Fukayama *et al.* (2009) identified that 46 genes were up-regulated (>1.5-fold) and 35 down-regulated (<0.68-fold) that included many signal transduction and transcription regulation related genes. By contrast, the expressions of most of the genes for primary metabolism were not significantly altered. Additionally, the transcript profile revealed that the expressions of genes for enzymes involved in CO_2 fixation (carbonic anhydrase, Rubisco, phosphoglycerate kinase and glyceraldehyde-3-phosphate dehydrogenase) were down-regulated, whereas that of genes encoding enzymes for RuBP regeneration (fructose bisphosphate phosphatase, fructose bisphosphate aldolase, sedoheptulose bisphosphate phosphatase and phosphoribulokinase) and starch synthesis (ADP-glucose pyrophosphorylase and starch synthase) were up-regulated under elevated CO_2. In sugarcane leaves, 35 genes (14 repressed and 22 induced) exhibited differential expression due to elevated CO_2 concentration and were reported to be related to photosynthesis and development (Souza *et al*. 2008).

YIELD

Because of the economic importance, there have been numerous observations over the past century of the effects of elevated CO_2 on the yield of agricultural crops (Poorter and Navas 2003), especially green-house crops (Kimball 1986; Miglietta *et al.* 1998; Amthor 2001; Jablonski *et al.* 2002; Nowak *et al*. 2004; Ziska *et al*. 2004; Long *et al.* 2006). More recently, several FACE experiments (Kimball *et al*. 2002; Ainsworth and Long 2005; Leakey *et al*. 2009a) have concentrated on open-field agricultural crops, with yield serving as an important economic parameter, to assess the effect of high CO_2 under more “natural” conditions.

In the biomass section dealt previously in this review, the responses of the forage crops such as ryegrass and clover in which shoot biomass is the economic yield were already presented. For wheat (Triboï *et al.* 2003; Hodson and White 2009) and rice (Nakagawa and Horie 2000), grain yield was increased by an average of 12% at ample N and water that is, to a similar extent to that of the shoot biomass. Under very high N, rice yields increased by an average of 11%; while at low N, wheat and rice yields increased up to 7% by elevated CO_2. The latter figure is somewhat higher than the average 3% increase for shoot biomass. When water was limiting, wheat yields were increased by 23%, which was significantly greater than the biomass stimulation (14%), and obviously was possible through an increased harvest index by elevated CO_2 (Kim-

Table 2 Percent response of different plant parts of semi-arid crop at different experimental conditions of elevated CO_2 (350 to 700 ppm).

Crop	Response of plant part	Experimental conditions	% Response	References
Cereals				
Triticum aestivum L. [Wheat]	Yield	High CO_2, temperature	10 to 20%	Hodson *et al.* 2009
	Diploid, tetraploid, hexaploid	FACE	6%,11%, 15%	Uprety *et al.* 2008
Zea mays L. [Corn]	whole plant	field	8%	Rogers *et al.* 1983
		open-top chamber	48%	Leakey *et al.* 2006
		FACE (Well Water)	No response	
		FACE (water stress)		
Sorghum bicolor (L.) Moench [Sorghum]	Whole plant (Seedling stage)	Open-top chambers	9.08%	Vanaja *et al.* 2006a
	Whole plant	FACE, adequate soil moisture	0%	Ottman 2001
		FACE, dry soil moisture	23%	
Pulses				
Glycine max (L.) Merr. [Soyabean]	Cultivar yield	Modified open-top chambers	35%	Ziska and Bunce 2000
	Plant growth, yield	Soy FACE	increased	Ainsworth *et al.* 2002; Long *et al.* 2006
Phaseolus vulgaris L. [Garden bean]	Whole plant	Growth chamber:	32%	Cowling and Sage 1998
	Seed yield	High temperature (36°C) Moderate temperature(25°C) chamber	95% 24%	Prasad *et al.* 2002
Vigna radiata (L.) R. Wilczek [Mungbean]	Whole plant	Open-top chambers: CO_2 exposure during days 0–20 and 21–40	55%, 8%	Das *et al.* 2002
Vigna unguiculata (L.) Walp. [Cowpea (or) Black-eyed pea)	Whole plant	Growth chamber: Pots (3.7 liter)	113%	Bhattacharya *et al.* 1985
		Pots (1 liter)	64 %	Overdieck *et al.* 1988
Vigna mungo (L.) Hepper [Blackgram]	Seedling	Open-top chambers and moisture stress	79.7%	Vanaja *et al.* 2006
	Whole plant	Open-top chambers	54%	Vanaja *et al.* 2007
	Yield		33.3%	
Oil seed				
Helianthus annuus L. [Sunflower]	Whole plant	Open-top chambers: Low, medium and high nitrogen	39%, 11%, 101%	Zerihun and BassiriRad 2000
Ricinus communis L. [Castor bean]	Leaves	Growth chambers At 0 hours light	68%	Grimmer *et al.* 1999
		And after 14 hours light	47%	Grimmer and Komor 1999
	Whole plant	Open-top chambers with 700 ppm	15.8%	Vanaja *et al.* 2008
Arachis hypogaea L. [Peanut]	Whole plant	Controlled environment chambers, irrigated and drought, temperature 32°C	41%, 29%	Clifford *et al.* 2000
	Leaf antioxidants	Open-top chambers with 600 ppm	increased	Ratnakumar *et al.* 2006
Fiber				
Gossypium hirsutum L. [Cotton]	Whole plant	FACE	128%	Hileman *et al.* 1994

ball *et al.* 2002). So, it appears that the major benefit of increased CO_2 would be under conditions of drought stress, and we hypothesize that elevated CO_2 would produce more biomass and seed yield through an increased water use efficiency. Yield components such as panicle length, grain number, and grain weight increased under high CO_2, but the general contribution of grain weight was less than the other two components (Kimball *et al.* 2002) because the husk physically limits and determines the size of the grain. The grain number has been shown to increase in rice (Uprety *et al.* 2000) and in blackgram (Vanaja et al 2007) under high CO_2 levels.

In the case of a C_4 grass, sorghum, there was a small average negative response (-5%) under ample water, but with a high variability (Kimball *et al.* 2002; Ottman *et al.* 2002). In contrast, at low water, the sorghum yielded about 25% more grain under FACE compared to the controls, which was probably due to the high-CO_2-induced partial stomatal closure, which reduced ET and enabled the FACE-grown plants to maintain photosynthesis and grow longer in each drought cycle, and fills the grains better.

Tuber yields from potato (Miglietta *et al.* 1998; Donnelly *et al.* 2001), a C_3 crop, increased substantially by 28% due to the FACE treatments, which stands in marked contrast to the average 21% decrease in shoot biomass. The latter appears related to effects of elevated CO_2 on the early onset of senescence (Bindi *et al.* 1999). Nevertheless, such a marked difference in response between shoots and tubers represents a major change in reallocation of resources leading to improvement of harvest index in this plant under high CO_2 (Heagle *et al.*2003).

Yield of woody perennial cotton were increased about 40% by FACE under both ample and low-water conditions, further examination of the lint fiber portion of the yield revealed it was increased even more, by about 54% (Pinter *et al.* 1996). All of these yield stimulations were slightly higher than the mean biomass stimulations and therefore reflect a slight and concurrent improvement in the harvest index.

Kimball (1986) assembled and analyzed 53 observations of the effects of elevated CO_2 on agricultural yields and obtained an average increase of 15% (scaled to an elevation of CO_2 = 550 μmol mol^{-1}). Yields of C_3 and C_4 crops were increased by 23 and 26%, respectively. Similarly, Cure (1985) and Cure and Acock (1986) conducted a literature survey and presented the results of response to a doubled CO_2 concentration (550 μmol mol^{-1}) on the yield of 10 major agricultural crops. They reported yield increases of 19, 8, 113 and 28% for wheat, rice, cotton, and potato, respectively, under ample water and nutrients. Nakagawa and Horie (2000) recently reviewed the responses of rice to elevated CO_2 and temperature, including several years' of their work with temperature-gradient tunnels. They concluded that under field conditions doubling of CO_2 increases rice yields by about 25% on an average, or about 14% when scaled to 550 μmol mol^{-1}. In contrast to the above results the maize production was unaffected by elevated CO_2 in absence of drought (Leakey *et al.* 2006).

In the case of wheat at ample water and nutrients, the average FACE value of about 15% is at the lower edge of the chamber values from the literature. Similarly for rice, the FACE values (10%) are slightly lower than the recent and fairly extensive review value (14%) of Nakagawa and

Horie (2000) derived from chambers and temperature-gradient tunnels. The average FACE potato yield increase of about 28% agrees exactly with the chamber mean value from Cure. In the case of cotton, Cure's (1985) early review induced only a single experiment, which suggested that cotton's response to CO_2 was dramatic. So the FACE value of about 38% may still seem lower, although it is still larger than that of most other species. In a series of open-top chamber experiments Kimball *et al.* (1993) found that elevated CO_2 at 650 μmol mol^{-1} increased cotton yields by about 60%, which scales to 395 μmol mol^{-1}, and is in close agreement with the FACE results.

The percentage increases in agricultural yield under water stressed conditions were plotted by Kimball *et al.* (1993) against the percentage increases under well-watered conditions for 25 experiments reported in the literature. Although some data reported by Lobell and Field (2008), Ried and Fiscus (2008) and that in **Table 2** tend to indicate that the benefit of increase CO_2 would be under water stress, it appears from this review that the responses under water stress were not significantly different from those of well-watered conditions. We hypothesize that it may depend on the type of stress that is considered. We could hypothesize that any drought stress during grain filling is crucial (terminal stress) and the crops would probably benefit more from increased CO_2 than under well-watered conditions. FACE-grown wheat and especially sorghum had larger yield increases due to elevated CO_2 under water-stressed compared to ample watered conditions. Kimball *et al.* (1993) similarly plotted the percentage increases for 19 observations obtained under nutrient stress, and the average response was only 49% of that observed with ample nutrients (Kimball *et al.* 2002). This low-nutrient result is consistent with the FACE, C_3 grain yield data, which show a mean 7% stimulation due to elevated CO_2 under low N compared to a 12% increase at ample N. This (Long *et al.* 2006) conclusion that yield responses from chambers are the same from chamber-based and FACE experiments are in marked contrast to the thesis of Ziska and Bunce (2007) suggestions focused on methodological disparities *per se*, improved projection of future food supply could be achieved by incorporation of projected changes in CO_2 and biotic/abiotic uncertainties into current crop models. Tubiello *et al.* (2007) suggested that the experimental and modeling steps are necessary to avoid confusion in future meta-analyses and comparisons of experimental and model data.

CONCLUSION

Based on results from various studies , it can visualized that the semi-arid crop productivity, water requirement, and land use patterns will moderately change in future in response to high CO_2. The predicted rise of atmospheric carbon dioxide alone is likely to benefit the semi-arid crop plants with a greater shoot biomass, yield, and harvest index through increased crop water use efficiency and net photosynthesis. Crops vary in the degree of their response to CO_2, especially between C_3 and C_4 photosynthetic types, which likely will affect the proportions of land area divided among the various crops in the future. Stomatal conductance will probably be reduced at higher CO_2 concentrations which reduce transpiration per unit leaf area and consequently increase the leaf temperature. The growth response to elevated CO_2 is large even under water stress conditions. High CO_2 ameliorates the adverse effects of drought by altering the plant physiological, biochemical, and molecular systems. As the solar radiation, temperature, rainfall and other climatic variables play a great role in plant growth and production, all these factors need to be accounted for while determining the direct effects of CO_2 its interactions with all these climate variables in order to predict the impact of increased CO_2 on the food and fodder crops under climate change scenarios.

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