Effect of Elevated Levels of Carbon Dioxide on the Activity of RuBisCO and Crop Productivity

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Abstract Atmospheric CO_2 concentration is now higher than it was at any time in the past 26 million years and is expected to nearly double during this century. This trend is of concern to agriculture because elevated atmospheric carbon dioxide levels have been shown to decrease the rates of photorespiration. Rubisco, the key enzyme in photosynthesis and photorespiration, exhibits dual activity and is known to be regulated by relative CO_2/O_2 ratio of the atmosphere. Terrestrial plants with a C_3 photosynthetic pathway respond in the short term to increased CO_2 concentration via increased net photosynthesis and decreased transpiration. Recent empirical evidence suggests that the warming may only be about 0.25 °C, so the primary effects on agriculture are likely to be the beneficial increases in crop yields and water use efficiency. However, researchers have shown that elevated levels of carbon dioxide inhibit nitrate assimilation in wheat and *Arabidopsis* plants. Another important implication of this study is the effect of elevated levels of carbon dioxide on the nutritional quality of the crop. Under elevated CO_2 most plant species show higher rates of photosynthesis, increased growth, decreased water use, and lowered tissue concentrations of nitrogen and protein. Rising CO_2 over the next century is likely to affect both agricultural production and food quality.

Keywords CO_2 concentration • Rubisco • Carboxylation • Oxygenation • Photosynthesis • FACE • Plant nutrition • Hidden hunger • Meta-analysis approach

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1 Introduction

All over the globe there is a concurrent increase in population and it is expected to exceed nine billion (Godfray et al. 2010), hence the requirement for food is constantly increasing (FAOSTAT 2013). Consequently, hordes of human activities such as deforestation for arable land, fossil fuel burning, and attempts to increase crop productivity are occurring in order to feed the growing population. Due to these anthropogenic activities elevation of atmospheric CO_2 and consequently temperature increase has been recorded globally. According to the fifth report of the IPCC, global warming is unequivocal (DTE Annual 2014), its effects are quite visible, the atmosphere and oceans have warmed, the amount of snow and ice have diminished, sea levels are rising, there is loss of biodiversity, fluctuating crop yields, and increase in the concentration of the greenhouse gases are observable universally. The World Meteorological Organization in its (2013) report stated that there are increases of 39 %, 158 %, and 20 %, respectively, in global average concentration of CO_2, CH_4, and N_2O since the start of the industrial era in 1750. Atmospheric CO_2 concentration is now higher than it was at any time in the past 26 million years. The current annual rate of increase in CO_2 concentration is expected to bring the levels to far above 600 ppm by the end of the current century (Schimel et al. 1996). Since 1960 the amount of CO_2 in the atmosphere has risen from 315 to 378 ppm (approximately 20 %). An elevated level of CO_2 is directly related to global warming which means an increase in the global mean temperature. Among the environmental factors, temperature is a major factor that affects growth, development, and yield of crops (Luo 2011). A warmer global climate change will result in the change in agricultural patterns by shifting food growing areas, changes in crop yields, increase in irrigation demands, and an increase in pests, crop diseases, and weeds in warmer areas. The World Bank estimates that by the mid-twenty-first century, crop yield would decrease by up to 30 % in South Asia due to climate change. The region is already experiencing warming, increasing variability of the monsoon rainfall, heavier downpours, and an increase in the frequency of drought and floods. Recent devastating floods of Jammu and Kashmir (2014) and Uttarakhand (2013) regions of India and Pakistan along eastern Afghanistan (2013), and the recent Hudhud cyclone (2014) at the southern coast of India are remarkable examples of climate change.

This trend of accelerated carbon emissions is of concern to agricultural production and food quality because elevated atmospheric carbon dioxide levels have shown strong diversified effects on crops. The quality of crops is a multifaceted and complex subject and involves different stages of growth and development including pre- and post-harvest and environmental and technological aspects. It also involves nutritional, elemental (zinc, iodine, etc.), and macromolecular (protein) composition in plant tissues (DaMatta et al. 2010; Taub et al. 2008; Hay and Porter 2006). There is growing evidence suggesting that many crops, notably C3 crops, may respond positively to increased atmospheric CO_2 in the absence of other stressful conditions (Long et al. 2004). However, the beneficial direct impact of elevated CO_2 can be offset by the effects of climate change, such as elevated temperatures, higher ozone levels, and altered patterns of precipitation (Easterling et al. 2000; Trenberth 2011). During early evolution the atmosphere was of high CO_2 concentration (4–5 times the present value) and that is the time when plants originated. During the last 25–30 million years CO_2 concentration has stabilized at a relatively low value.

The effects of elevated CO_2 are not uniform; some species, particularly those that utilize the C_4 variant of photosynthesis, show less response to elevated CO_2 than do other types of plants. Rising CO_2 is therefore likely to have complex effects on the growth and composition of natural plant communities. The preliminary effects of elevated CO_2 levels in most crop plants, particularly C3 plants, include biomass accumulation, development, and reproduction (Kimball 1983; Kimball et al. 1993; Poorter and Navas 2003). However, it has been observed in various studies that initial stimulation of the net photosynthesis rate is temporal and plants are not able to sustain the maximal stimulation, a phenomenon known as photosynthesis acclimation. In other words, plants on prolonged exposure to high CO_2 concentration exhibit reduced photosynthetic rates. Sucrose is known to interfere in the transcription of genes encoding proteins involved in CO_2 fixation and electron transport activity (Moore et al. 1999) and therefore photosynthesis slows down. Plants respond to these projected future levels of CO_2 from various types of enclosure studies conducted over the past three decades. Among these studies the most notable are Open Top Chambers (OTC) and Free Air CO_2 Enrichment (FACE) studies (Lewin et al. 1994; Hendry and Miglietta 2006). These studies revealed that photosynthetic carbon uptake is enhanced by elevated CO_2 despite acclimation of photosynthetic capacity (Leakey et al. 2009).

In a group of plants with or without phylogenetic relatedness such as C_4 or legumes showing acclimation, there is larger potential for the stimulation of photosynthetic carbon uptake because elevated CO_2 increases the carboxylation rate of Rubisco and decreases the rate of photorespiration (Long et al. 2004; Ainsworth and Rogers 2007). Genetic factors are known to play an important role in photosynthetic response to elevated CO_2 as shown by the PopFACE experiment (Scarascia-Mugnozza et al. 2006). Poplars exported more than 90 % of their photosynthate during the day and stored the rest of the overflow photosynthate as starch (Davey et al. 2006) which enabled the trees to avoid acclimation of photosynthetic potential and maintain maximal stimulation of photosynthetic carbon uptake at elevated CO_2.

In the era of global warming, it is very important to understand the impact of CO_2 enrichment, temperature, and other climatic changes on food crops to estimate future food production. This chapter primarily focuses on the expected elevated levels of CO_2 in the future, its effect on the activity of Rubisco, and the quality of crops. The apprehensions regarding the negative impact of elevated levels of CO_2 in times to come also lead to a short discussion on the direction of research to combat the problem.

2 Rubisco and Its Role in Photosynthesis

Ribulose 1,5bisphosphate Carboxylase Oxygenase (Rubisco) is a major soluble protein present in the plant cell. It is responsible for photosynthesis and photorespiration. Rubisco is one of the key enzyme proteins in the biosphere and accounts for half of total leaf proteins. It is a multisubunit enzyme having molecular weight of about 560,000 Da. It comprises two subunits, large and small. Small subunits are coded by the nuclear genome whereas the large subunit by the chloroplast genome. These subunits are associated to form the complex functional holoenzyme. It is located in the chloroplast stroma and is activated by an increase in pH and Mg^{2+} ion (Taiz and Zeiger 2006). It is a unique enzyme catalyzing carboxylation of RuBP to form two molecules of PGA and oxygenation of RuBP to form PGA and phosphoglycolic acid. The PGA is further metabolized by the C_3 cycle whereas phosphoglycolic acid is metabolized via photorespiratory or C_2 cycle (Kajala et al. 2011). Thus this protein exhibits dual enzymatic activity, carboxylation, and oxygenation of RuBP. The property of carboxylase/oxygenase is regulated by the relative CO_2/O_2 ratio of the atmosphere. If this ratio is high carboxylase activity is favored whereas a low ratio favors the oxygenase property. It has also been noted that during high temperature RuBP carboxylase loses its affinity for CO_2 and acts as RuBP oxygenase. However, the global increase in CO_2 levels has been shown to be linked with global warming. Therefore it is very important to discover the effect of CO_2 enrichment on crop productivity when environmental temperature is also increasing.

2.1 *Effect of Elevated Levels of CO_2 on Photosynthesis*

The study pertaining to the effect of elevated CO_2 on crop productivity was developed in the late 1970s and 1980s. During the early days the data were mainly obtained from use of indoor growth chambers through outdoor growth chambers, greenhouses, and later on studies were undertaken in open top chambers (OTC) to Free Air CO_2 Enrichment (FACE) studies. Under certain circumstances (Arp 1991; Ronchi et al. 2006; Stafford 2008) the results of greenhouses and OTCs were debated in the scientific world because of their limitations. Plants grown in the above-mentioned systems were not exposed to changing environmental conditions such as temperature, humidity, and wind (Ross et al. 2004; Long et al. 2006). In OTCs the conditions are warmer than the adjacent unenclosed fields and plants in them showed edge effect. It also gave limited access to pests and diseases but if they gain contact, high humidity and warmer temperature may worsen epidemics (Long et al. 2006). FACE acts as an alternative to the OTC and can minimize as far as possible lacunas associated with small pots and confined systems. It apparently mimics realistic future agricultural conditions (Dodd 2013; Ainsworth et al. 2008a). FACE studies have been conducted worldwide on a large number of plant communities including crops such as wheat, rice, sorghum, potato, grapes, cotton (Kimball et al. 2002), natural grasslands of Tasmania (Hovenden et al. 2006), and plantation forests of *Pinus* and *Populus* spp. (Norby et al. 2005).

In spite of all the advantages the main limitation of FACE is the cost of the large amounts of CO_2 that must be released during the experiments (estimated costs around US$1 million over a year) excluding the additional cost of the investigation (DaMatta et al. 2010). In addition to cost, other key points such as CO_2 versus temperature interaction evaluations and testing CO_2 above 550 ppm are rarely performed using the current FACE technology (Tubiello et al. 2007; Ainsworth et al. 2008b).

Drake et al. (1997) reported limitations in photosynthesis, when plants were first grown at a given CO_2 concentration and then transferred to different CO_2 concentrations. The first limitation was referred to as the limitation due to supply and utilization of CO_2. The second limitation was the supply and utilization of light, and the third refers to the utilization of triose phosphate. Several theoretical models have predicted that the doubling of atmospheric CO_2 concentration will increase the Earth's temperature by 2.5 °C to 4.3 °C, which could seriously disrupt agricultural production (IPCC 2007). The temperature response of crop growth and yield, respectively, must be considered to predict the CO_2 effects on the crops (Ziska and Bunce 1997; Porter and Semenov 2005). High temperatures reduce the net carbon gain in C_3 species by increasing photorespiration at ambient CO_2 levels. At elevated levels of CO_2, photorespiration reduces, thereby increasing photosynthesis and hence carbon gain (Badger and Price 2003). More recent empirical evidence suggests that the warming may only be about 0.25 °C, so the primary effects on agriculture are likely to be beneficial increases in crop yields and water-use efficiency. However, grain yield is known to increase marginally under increased CO_2 concentration. Apart from the tropical grasses, which constitute only 3–4 % of all known plant species, the rest of the plant species termed C3 plants lack optimal CO_2 concentration. This recent increase in CO_2 concentration will significantly stimulate growth, development, and reproduction in a wide variety of C3 plants (Kimball 1983; Kimball et al. 1993; Poorter and Navas 2003). The impact of increasing CO_2 concentration on plants has been lauded by some as “a wonderful and unexpected benefit from the industrial revolution” (Robinson and Robinson 1997). With the increasing human population, the major challenge is the demand for food. Several studies have indicated that two of the major crops, wheat and rice, show a positive response to elevated levels of atmospheric CO_2 (Mandersheid and Weigel 1997; Horie et al. 2000). Such an effort holds significant promise that cereal yields can be potentially increased as per the demand of the growing population. In a FACE experiment Ainsworth et al. (2008c) reported that elevated CO_2 increases photosynthesis, resulting in increased dry matter accumulation, leaf area, and plant height in trees and shrubs and to some extent in C_3 plants. Jablonski et al. (2002) evaluated 79 crop and native species at CO_2 enriched conditions and reported a 31 % increase in overall biomass of the plants. Yang et al. (2009) in a FACE study at 570 ppm of CO_2 reported there is an 8 % increase in number of panicles per unit area, 10 % increase in number of spikelets per panicle, and 4 % increase in grain biomass, and all of them taken together led to a 30 % increase in grain yield. De Souza et al. (2008) in an OTC-based study with an elevated CO_2 (380–740 ppm) on sugarcane reported 50 % increase in biomass and 29 % increase in sucrose accumulation. Similarly there have been many studies that have quantified the effect of increased CO_2 concentration and N utilization (Lam et al. 2012a). They further reported that elevated CO_2 concentration increases crop production by supplying an adequate amount of N either from soil, fertilizer, or biological N-fixation.

2.2 Effect of CO_2 Concentration on the Activity of Rubisco and Nitrogen Assimilation

Rubisco is the rate limiting enzyme in photosynthesis and its activity is largely affected by atmospheric CO_2 and nitrogen availability. It is mandatory to emphasize that maintenance of the C/N ratio is pivotal for various growth and development processes in plants governing yield and seed quality. It is therefore of prime importance to maintain the optimum levels of C and N within plants as well as externally in soil for proper growth and development (Paul and Driscoll 1997; Martin et al. 2002; Malamy 2005). In C_3 plants, Rubisco is the key photosynthetic enzyme involved in carbon assimilation and it is the major storage protein and source of nitrogen, which is utilized by the plants' reproductive components when Rubisco undergoes degradation during leaf senescence. Thus the effect of elevated CO_2 on plants is twofold: because of the decline in levels of Rubisco the process of photosynthesis becomes rate limiting, and there is reduction in the available nitrogen pool. Bloom et al. (2012, 2014)have shown that elevated CO_2 directly inhibits plant nitrogen metabolism, especially the assimilation of nitrates into proteins in leaves of C_3 plants. An optimum C/N ratio suggests increased CO_2 levels with lower nitrogen levels resulting in lower protein content. In leaf tissue, the ratio of nitrate to total nitrogen concentration and the stable isotope ratios of organic nitrogen and free nitrate clearly exhibited that nitrate assimilation was slower under elevated than ambient CO_2. Under CO_2-enriched conditions plants grow larger and dilute the amount of protein within their tissues (Ellsworth et al. 2004; Reich et al. 2006); there is also accumulation of carbohydrates within leaves, downregulation of Rubisco (Long et al. 2004), and carbon-enriched rhizosphere limits available N to plants (Reich et al. 2006). Recently several meta-analysis data indicated enriched CO_2 inhibits the assimilation of nitrates (Cheng et al. 2012; Pleijel and Uddling 2012; Myers et al. 2014). It further leads to reduced sink protein concentration because N supply to sinks during filling occurs from catabolized protein from senescing photosynthetic tissues (Hay and Porter 2006). This adversely affects grain quality particularly in cereal crops. It has also been observed that plant growth is slower under elevated than ambient CO_2 when nitrate serves as the sole nitrogen source and faster when ammonia is the only source of nitrogen (Matt et al. 2001; Bloom et al. 2002; Lekshmy et al. 2013). The detailed study on nitrate assimilation confirmed that elevated CO_2 inhibited leaf nitrate assimilation in field-grown wheat. It was observed that the percentage of total nitrogen that remained as unassimilated nitrate was higher under elevated than ambient CO_2 over a period of time. There is ubiquitous evidence supporting the above concept (Jablonski et al. 2002; Ziska et al. 2004). Several research groups have demonstrated that under elevated CO_2 conditions the protein concentrations in wheat grain, rice grain, potato, and barley decline by 8 %, whereas these crops, respectively, are the source of 21, 13, 2, and 0.3 % of the protein in the human diet (Myers 2014; Kimball et al. 2001; Erbs et al. 2010). This may result in diminishing the amounts of protein available for human consumption by about 3 % as atmospheric CO_2 reaches the levels anticipated during the next few years. Apart from N, other elements in grains are also filled by mobilization from vegetative pools (Hay and Porter 2006). Loladze (2002) reported that increase in photosynthesis under elevated CO_2 may be associated with increased plant requirements for P but decreased for N. Fangmeier et al.(1999) reported that elevated CO_2 may change the concentrations of different elements that respond similarly to N, such as S, Mg, Ca, K, and Zn. In order to achieve food security in times to come sophisticated strategies with respect to nitrogen fertilization are required in order to increase not only the grain yield but also the protein yields under elevated CO_2 levels.

2.2.1 Effect of Nitrogen Fertilizers

The scientists suggest that, as global climate change intensifies, it will be critical for farmers to manage nitrogen fertilization carefully in order to prevent losses in crop productivity and quality. The reversed N management practices may include greater use of legume intercropping or legume cover crops apart from fertilizers (Lam et al. 2012b; WUWT 2010). The probable effect of the increasing global atmospheric CO_2 concentration on agricultural yields was evaluated in a large number of species grown with CO_2 enrichment. A lot has been learned about the response of plants to elevated CO_2 levels from various sorts of enclosure studies conducted during the last three decades (Leakey et al. 2006, 2009). Open fields might respond less than greenhouses or growth chambers to increased CO_2 because nutrient levels in general worldwide agriculture are lower than those in the indoor studies, or open fields might respond more because the light levels are generally higher. However, keeping these limitations of the data in mind, the analysis showed that yields probably will increase by 33 % with a doubling of atmospheric CO_2 concentrations.

Legumes are important components of cropping systems and are major sources of vegetable oil and protein for human and animal consumption. They provide about 20 % of the world's protein for the human diet, and one fourth of the world's fats and oils (Harlan 1992). Legumes also help to enrich soil through their unique capability to form symbiotic relationships with nitrogen-fixing bacteria that capture atmospheric nitrogen and make it available for crop growth. In addition, legumes are traditionally used as green manure and cover crops in crop rotation to improve physical conditions of the soil. Legumes, too, are capable of responding to elevated CO_2 with increased photosynthesis and growth (Rogers et al. 2009). For most plants, growth under elevated CO_2 can alter the internal balance between carbon (gained via enhanced photosynthesis) and nitrogen (either unaffected or taken up in decreased amounts due to decreased uptake of water). In contrast, most legume species participate in close mutualistic relationships with bacteria that live in nodules formed on the plant's roots. These bacteria are able to "fix" atmospheric nitrogen, chemically reducing it to a form that can be taken up and used by plants. Under elevated CO_2 conditions, legumes may be able to shunt excess carbon to root nodules where it can serve as a carbon and energy source for the bacterial symbionts. In effect, legumes may be able to exchange the excess carbon for nitrogen and thereby maximize the benefits of elevated atmospheric CO_2. Many studies in controlled environments have shown that, compared to other plant species, legumes show greater enhancement of photosynthesis and growth by elevated CO_2 (Rogers et al. 2009).

Decreases in tissue nitrogen concentrations under elevated CO_2 are also smaller for legumes than for other C_3 species (Cotrufo et al. 1998; Jablonski et al. 2002; Taub et al. 2008). In FACE experiments, soybeans (a legume) show a greater response to elevated CO_2 than wheat and rice in photosynthesis and overall growth, although not in harvestable yield (Long et al. 2006). C_4 plants use a biochemical pump to concentrate CO_2 at the locations within the leaf where the Rubisco enzyme mediates incorporation of CO_2 by the Calvin–Benson photosynthetic cycle. Because CO_2 concentrations are already high within the bundle sheath cells, increasing atmospheric CO_2 concentrations above current levels has little direct effect on photosynthetic rates for C_4 species. C_4 species respond to elevated CO_2 by decreasing stomatal conductance; this may lead to some indirect enhancement of photosynthesis by helping avoid water stress under drought conditions (Leakey et al. 2009). Thus, increased stomatal closure under conditions of high CO_2 will result in reduced loss of latent heat there by increasing leaf temperature (Kimball and Bernacchi 2006). However, a new dimension was added to this study by the work of Rogers et al. (1998) in swards of perennial rye grass grown under conditions of additional 240 ppm CO_2. The study did not exhibit any reduction in the amounts of Rubisco as long as they received high levels of nitrogen from the soil. Under conditions of low soil nitrogen these plants displayed a 25 % reduction in the levels of Rubisco. Researchers removed a large portion of leaf from these plants and continued growing them under conditions of low nitrogen. The results showed increased levels of Rubisco to facilitate greater carbon uptake to repair the damage caused by removal of the major portion of the leaf. These and several other observations led to the conclusion that plants grown under conditions of elevated CO_2 levels require less nitrogen . This gives them the opportunity to reallocate some of the extra nitrogen to other metabolic processes required for optimal growth and development together with the required carbon gains through photosynthesis.

Effect of Elevated Levels of CO_2 on Photorespiration

Rubisco is a bifunctional enzyme possessing carboxylase as well as oxygenase activity. We have thus far discussed the effect of elevated CO_2 on the carboxylase activity thereby affecting photosynthesis. The oxygenase activity is responsible for the process of photorespiration, a metabolic pathway leading to loss of carbon from the plant. The question therefore is the effect of increased levels of CO_2 on the oxygenase activity and the associated implications of any potential changes in the quality and content of nutrition in the crops with a suggested futuristic increase in the levels of atmospheric CO_2.

Voluminous experimental data demonstrate that atmospheric CO_2 enrichment favors carboxylation over oxygenation, thereby increasing photosynthetic rates with concomitant reductions in photorespiratory rates (Taiz and Zeiger 2002). The rising CO_2 content of the air thus invariably leads to greater rates of net photosynthesis and a more efficient process of carbon fixation. Hence, less Rubisco is needed to obtain the carbon required for plant growth and development under CO_2-enriched conditions. *Arabidopsis thaliana* was grown at atmospheric concentrations of 1000 ppm of CO_2 for 40 days (Cheng et al. 1998); in this study the foliar Rubisco was found to be 34 % lower in concentration compared with the controls. However, the contents of glucose and fructose were enhanced more than 2-fold by elevated CO_2, and starch concentrations were increased more than 3.5-fold. Thus, although elevated CO_2 reduced the amount of Rubisco in leaves, photosynthetically derived sugars and starch still accumulated to tremendous values. Studies on *Leucadendron* species revealed a 30 % reduction in the activity of Rubisco when grown under a twice-ambient concentration of CO_2 (Midgley et al. 1999).

Several studies reported 40 % greater rates of net photosynthesis in the plants grown in a CO_2-enriched environment when compared with the plants grown under ambient CO_2 conditions. Similar results were reported in chalk grassland species exposed to CO_2 concentration of 600 ppm for 14 months (Bryant et al. 1998). In this study elevated levels of CO_2 caused an average reduction in Rubisco activity of 32 % while still exhibiting 28 % higher rates of photosynthesis compared with the controls at ambient CO_2 concentration. Similarly, work on grassland species for a period of two years by Davey et al. (1999) under elevated CO_2 concentration of 700 ppm showed a decline in Rubisco activity by an average of 27 % with a simultaneous increase in photosynthetic rates from 12 to 74 %.

One of the most consistent effects of elevated atmospheric CO_2 on plants is an increase in the rate of photosynthetic carbon fixation by leaves. Across a range of FACE experiments, with a variety of plant species, growth of plants at elevated CO_2 concentrations of 475–600 ppm increases leaf photosynthetic rates by an average of 40 % (Ainsworth and Rogers 2007). In FACE experiments, stimulation of photosynthesis by elevated CO_2 in C4 plants is only about one third of that experienced by C3 species. C4 plants also show little or no enhancement of growth (dry matter production) in these studies (Ainsworth and Long 2005). The very limited data available also show no increase in C4 crop yield in FACE studies (Long et al. 2006). Although there is little FACE data available on the effects of elevated CO_2 on plant nitrogen and protein concentrations, data from chamber experiments show C4 plants to be much less responsive than C3 plants in this regard (Cotrufo et al. 1998). The picture that emerges is that C4 plants are in general relatively unresponsive to an elevation of atmospheric CO_2 above current ambient levels.

3 Elevated CO_2 and Effects on Food Quality

Another important implication of this study is the effect of elevated levels of carbon dioxide on the nutritional quality of the crop. A CO_2-enriched environment stimulates higher photosynthesis and an increased growth rate. However, enhanced growth rate does not exhibit any correlation with the nutrient availability and elemental nutrient (Kant et al. 2012). As compared to preindustrial times, today plants are experiencing a global elemental imbalance (Loladze 2002). Plants are the foundation of the major food supply to the human population. The low concentrations of several essential micronutrients, such as iron, iodine, and zinc in modern crops contribute to the problem of micronutrient malnutrition popularly known as hidden hunger and are affecting the economy and health of more than 50 % of the world population (Loladze 2002).

Photosynthesis and stomatal behavior are crucial to carbon and water metabolism, therefore growth of plants under elevated CO_2 leads to a large variety of secondary effects on plant physiology. The availability of additional photosynthate enables most plants to grow faster under elevated CO_2. The FACE experiments have shown increased dry matter production on an average by 17 % for the aboveground and more than 30 % for the belowground portions of plants (Ainsworth and Long 2005; de Graaff et al. 2006). This increased growth is also reflected in the harvestable yield of crops, with wheat, rice, and soybean all showing increases in yield of 12–14 % under elevated CO_2 in FACE experiments (Ainsworth 2008a; Long et al. 2006). Increased levels of CO_2 also lead to changes in the chemical composition of plant tissues. Due to increased photosynthetic activity, carbohydrates (sugars and starches) per unit leaf area increase on an average by 30–40 % under FACE-elevated CO_2 (Ainsworth 2008a; Ainsworth and Long 2005). Leaf nitrogen concentrations in plant tissues typically decrease in FACE under elevated CO_2 with nitrogen per unit leaf mass decreasing on average by 13 % (Ainsworth and Long 2005). This decrease in tissue nitrogen is likely due to several factors such as dilution of nitrogen from increased carbohydrate concentration, decreased uptake of minerals from the soil as stomatal conductance decreases (Taub and Wang 2008), and decrease in rate of assimilation of nitrate into organic compounds (Bloom et al. 2010). This in turn is likely to affect human nutrition as well. In FACE experiments, protein concentrations in grains of wheat, rice, and barley as well as potato tubers decrease by 5–14 % under increased CO_2 (Taub et al. 2008). The elevated CO_2 may also affect the concentrations of calcium, magnesium, and phosphorous in the crop plants (Loladze 2002; Taub and Wang 2008).

Recently Hamada et al. (2014) reported the effects of extreme climate on the chemical composition of temperate grassland species under ambient and elevated CO_2. In an enriched CO_2 environment different C_3 and C_4 plant species show reduced forage quality through a lower crude protein content (Wand et al. 1999), whereas in combination with high temperature, fiber content increased in *Medicago sativa* and as a result digestibility was reduced (Sanz-Sáez et al. 2012). In another report elevated CO_2 induced an increased C/N ratio in soybean (Ainsworth et al. 2002) and tannin accumulation in *Lotus corniculatus* (Carter et al. 1999). The changes in plant chemical composition in response to global climate change are very complicated because these effects are species dependent. It can be seen at the carbohydrate level (Fisher et al. 2002; Oliveira et al. 2013). In legumes under elevated CO_2, the C:N ratio is lower, C:P ratio is higher, and N:P ratio is higher than in nonleguminous plants (Lee et al. 2003)

4 Conclusion and Future Prospects

Under the conditions of continuous consumption of fossil fuels, CO_2 concentration will rise; simultaneously economic growth and development will result in increase in other greenhouse effect gases such as methane, nitrous oxides, chloro-fluorocarbons, and their substitutes. In this scenario, elevated CO_2 is increasing crop productivity in plants which is the demand of the time in order to feed the global population. However, plant responses to climate change are very complicated and species-group-specific. Interactions between elevated CO_2 and extremes of climatic conditions were observed in many cases. It has been found that elevated CO_2 amplified or reduced the impact of the extreme climatic condition. It has further been found that the nutritional quality of crops grown in elevated CO_2 will lead to hidden hunger and affect the economy as well as the health of the global population. The need of the hour is a multidimensional approach to the problem of crop productivity and its nutritional quality. The meta-analysis approach including FACE, proteomics, and genomics along with metabolomics will give us insight to overcome the problem of micronutrient malnutrition as a consequence of elevated levels of atmospheric CO_2. Adaptation to gradual changes in climate is possible, however, sudden changes would be more serious and therefore mitigation strategies need to be followed.

1. Selections of plants that exhibit higher reproduction capacity under elevated CO_2
2. Germplasm selection that can grow under conditions of elevated CO_2 and high temperature and incorporation of these traits into desirable crop production cultivars to improve flowering and seed set
3. Change in planting schedule and other crop management procedures to optimize yields under changed climatic conditions
4. Selection of species that grow under conditions of high temperature and require less water for growth
5. Altered irrigation strategies to overcome conditions of drought

References

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. New Phytol 165:351–372

Ainsworth EA, Rogers A (2007) The response of photosynthesis and stomatal conductance to rising [CO2]: mechanisms and environmental interactions. Plant Cell Environ 30:258–270

Ainsworth EA, Davey PA, Bernacchi CJ, Dermody OC, Heaton EA, Moore DJ et al (2002) A meta-analysis of elevated [CO2] effects on soybean (*Glycine max*) physiology, growth and yield. Global Change Biol 8:695–709

Ainsworth EA, Beier C, Calfapietra C, Ceulemans R, Durand-Tardif M, Farquhar GD et al (2008a) Next generation of elevated [CO2] experiments with crops: a critical investment for feeding the future world. Plant Cell Environ 31:1317–1324

Ainsworth EA, Leakey ADB, Ort DR, Long SP (2008b) FACE-ing the facts: inconsistencies and interdependence among field, chamber and modelling studies of elevated [CO_2] impacts on crop yield and food supply. New Phytol 179:5–9

Ainsworth EA, Rogers A, Leakey ADB (2008c) Targets for crop biotechnology in a future high-CO2 and high-O_3 world. Plant Physiol 147:13–19

Arp WJ (1991) Effects of source–sink relations on photosynthetic acclimation to elevated CO_2. Plant Cell Environ 14:869–875

Badger MR, Price GD (2003) CO_2 concentrating mechanisms in cyanobacteria: molecular components, their diversity and evolution. J Exp Bot 54:609–622

Bloom AJ, Smart DR, Nguyen DT, Searles PS (2002) Nitrogen assimilation and growth of wheat under elevated carbon dioxide. Proc Natl Acad Sci USA 99:1730–1735

Bloom AJ, Burger M, Asensio JSR, Cousins AB (2010) Carbon dioxide enrichment inhibits nitrate assimilation in wheat and *Arabidopsis*. Science 328:899–903

Bloom AJ et al (2012) CO_2 enrichment inhibits shoot nitrate assimilation in C_3 but not C_4 plants and slows growth under nitrate in C_3 plants. Ecology 93:355–367

Bloom AJ, Burger M, Kimball BA, Pinter PJ Jr (2014) Nitrate assimilation is inhibited by elevated CO_2 in field-grown wheat. Nat Clim Chang 4:477–480

Bryant J, Taylor G, Frehner M (1998) Photosynthetic acclimation to elevated CO_2 is modified by source: sink balance in three component species of chalk grassland swards grown in a free air carbon dioxide enrichment (FACE) experiment. Plant Cell Environ 21:159–168

Carter EB, Theodorou MK, Morris P (1999) Responses of *Lotus corniculatus* to environmental change. Effect of elevated CO_2, temperature and drought on tissue digestion in relation to condensed tannin and carbohydrate accumulation. J Sci Food Agric 79:1431–1440

Cheng SH, Moore B, Seemann JR (1998) Effects of short and long term elevated CO_2 on the expression of ribulose-1,5-bisphosphate carboxylase/oxygenase genes and carbohydrate accumulation in leaves of *Arabidopsis thaliana* (L.) Heynh. Plant Physiol 116:715–723

Cheng L et al (2012) Arbuscular mycorrhizal fungi increase organic carbon decomposition under elevated CO_2. Science 337:1084–1087

Cotrufo MF, Ineson P, Scott A (1998) Elevated CO_2 reduces the nitrogen concentration of plant tissues. Glob Change Biol 4:43–54

DaMatta FM, Grandis A, Arenque BC, Buckeridge MS (2010) Impacts of climate changes on crop physiology and food quality. Food Res Int 7:1814–1823

Davey PA, Parsons AJ, Atkinson L, Wadge K, Long SP (1999) Does photosynthetic acclimation to elevated CO_2 increase photosynthetic nitrogen-use efficiency? A study of three native UK grassland species in open-top chambers. Funct Ecol 13:21–28

Davey PA, Olcer H, Zakhleniuk O, Bernacchi CJ, Calfapietra C, Long SP, Raines CA (2006) Can fast-growing plantation trees escape biochemical down-regulation of photosynthesis when grown throughout their complete production cycle in the open air under elevated carbon dioxide? Plant Cell Environ 29:1235–1244 de Graaff MA, Van Groenigen KJ et al (2006) Interactions between plant growth and soil nutrient cycling under elevated CO_2: a meta-analysis. Glob Change Biol 12:2077–2091

De Souza AP, Gasper M, Silva EA, Ulian EC, Waclawovsky AJ et al (2008) Elevated CO_2 increases photosynthesis, biomass and productivity and modifies gene expression in sugarcane. Plant Cell Environ 31:1116–1127

Dodd M (2013) Elevated CO_2 impacts on grazed pasture: long-term lessons from the New Zealand FACE. Climate change impacts on grassland production, composition, distribution and adaptation Proceedings of the 22nd international grassland congress, pp 1279–1284

Drake BG, Gonzalez-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO2? Annu Rev Plant Physiol Plant Mol Biol 48:609–639

DTE Annual (2014) http://www.cseindia.org/dteannual/Climate-change-spread-big.jpg

Easterling DR, Evans JL, GroismanPYa KTR, Kunkel KE, Ambenje P (2000) Observed variability and trends in extreme climate events: a brief review. Bull Am Meteorol Soc 81:417–425

Ellsworth DS et al (2004) Photosynthesis, carboxylation and leaf nitrogen responses of 16 species to elevated pCO_2 across four free-air CO_2 enrichment experiments in forest, grassland and desert. Glob Change Biol 10:2121–2138

Erbs M et al (2010) Effects of free-air CO_2 enrichment and nitrogen supply on grain quality parameters and elemental composition of wheat and barley grown in a crop rotation. Agric Ecosyst Environ 136:59–68

Fangmeier A, De Temmerman L, Mortensen L, Kemp K, Burke J, Mitchell R et al (1999) Effects of nutrients on grain quality in spring wheat crops grown under elevated CO_2 concentrations and stress conditions in the European multiple-site experiment 'ESPACE-wheat'. Eur J Agric 10:215–229

FAOSTAT (2013) Food supply, crops primary equivalent. http://faostat3.fao.org/faostat-gateway/go/to/download/C/CC/E

Fisher DS, Mayland HF, Burns JC (2002) Variation in ruminants preference for tall fescue hays cut either at sundown or at sunup. J Anim Sci 77:762–768

Godfray HCJ, Beddington JR, Crute IR, Haddad L, Lawrence D, Muir JF, Pretty J, Robinson S, Thomas SM, Toulmin C (2010) Food security: the challenge of feeding 9 billion people. Science 327:812–818

Hamada AE, Peshev D, Zinta G, Van den Ende W, Janssens IA, Asard H (2014) Climate extreme effects on the chemical composition of temperate grassland species under ambient and elevated CO_2: a comparison of fructan and non-fructan accumulators. PLoS One 9(3), e92044

Harlan JR (1992) Crops and man. American Society of Agronomy & Crop Science Society of America, Madison, WI

Hay RKM, Porter JR (2006) The physiology of crop yield, 2nd edn. Blackwell, Oxford

Hendry GR, Miglietta F (2006) FACE Technology: past, present, and future. In: Nosberger J, Long SP, Norby RJ, Stitt M, Hendry GR, Blum H (eds) Managed ecosystems and CO_2. Springer, Berlin, pp 15–43

Horie T, Baker JT, Nakagawa H, Matsui T, Kim HY (2000) Crop ecosystem responses to climatic change: rice. In: Reddy KR, Hodges HF (eds) Climate change and global crop productivity. CAB International, Wallingford, pp 81–106

Hovenden MJ, Miglietta F, Zaldei A, Vander Schoor JK, Wills KE, Newton PCD (2006) The TasFACE climate change impacts experiment: design and performance of combined elevated CO_2 and temperature enhancement in a native Tasmanian grassland. Aust J Bot 54:1–10

Hudhud Cyclone (2014) http://www.downtoearth.org.in/content/phailin-hudhud-year-extreme-weather-events

IPCC (2007) Climate change: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, pp 11–18

Jablonski LM, Wang X et al (2002) Plant reproduction under elevated CO_2 conditions: a meta-analysis of reports on 79 crop and wild species. New Phytol 156:9–26

Jammu and Kashmir (2014) http://www.downtoearth.org.in/content/urban-floods-lessons-jammu-kashmir

Kajala K, Covshoff S, Karki S, Woodfield H, Tolley BJ, Dionora MJA, Mogul RT, Mabilangan AE, Danila FR, Hibberd JM, Quick WP (2011) Strategies for engineering a two-celled C4 photosynthetic pathway into rice. J Exp Bot 62:3001–3010

Kant S, Seneweera S, Rodin J, Materne M, Burch D, Rothstein SJ, Spangenberg G (2012) Improving yield potential in crops under elevated CO2: integrating the photosynthetic and nitrogen utilization efficiencies. Front Plant Sci 3:1–9

Kimball BA (1983) Agric Water Manage 7(1–3):55–72

Kimball BA, Bernacchi CJ (2006) Evapotranspiration, canopy temperature and plant water relations. In: Nösberger J, Long SP, Norby RJ, Stitt M, Hendrey GR, Blum H (eds) Managed ecosystems and CO_2. Springer, Berlin, pp 311–324

Kimball BA et al (1993) Effects of increasing atmospheric CO_2 on vegetation. Vegetation 104/105: 65–75

Kimball BA et al (2001) Elevated CO_2, drought and soil nitrogen effects on wheat grain quality. New Phytol 150:295–303

Kimball BA, Kobayashi K, Bindi M (2002) Responses of agricultural crops to free-air CO_2 enrichment. Adv Agron 77:293–368

Lam SK, Chen D, Norton R, Armstrong R (2012a) Nitrogen demand and the recovery of 15N-labelled fertilizer in wheat grown under elevated carbon dioxide in southern Australia. Nut Cyc Agroecosys 92:133–144

Lam SK, Chen D, Norton R, Armstrong R, Mosier AR (2012b) Nitrogen dynamics in grain crop and legume pasture systems under elevated atmospheric carbon dioxide concentration: a meta-analysis. Glob Change Biol 18:2853–2859

Leakey ADB, Uribelarrea M, Ainsworth EA, Naidu SL, Rogers A, Ort DR, Long SP (2006) Photosynthesis, productivity, and yield of maize are not affected by open-air elevation of CO_2 concentration in the absence of drought. Plant Physiol 140:779–790

Leakey ADB, Ainsworth EA, Bernacchi CJ, Rogers A, Long SP, Ort DR (2009) Elevated CO_2 effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. J Exp Bot 60:2859–2876

Lee TD, Reich PB, Tjoelker MG (2003) Legume presence increases photosynthesis and N concentrations of co-occurring non-fixers but does not modulate their responsiveness to carbon dioxide enrichment. Oecologia 137:22–31

Lekshmy S, Jain V, Khetarpal S, Pandey R (2013) Inhibition of nitrate uptake and assimilation in wheat seedlings grown under elevated CO_2. Indian J Plant Physiol 18(1):23–29

Lewin KF, Hendrey GR, Nagy J, Lamorte RL (1994) Design and application of a free air carbon dioxide Enrichment facility. Agric For Meteorol 1–4:15–29

Loladze I (2002) Rising atmospheric CO_2 and human nutrition: toward globally imbalanced plant stoichiometry? Trends Ecol Evol 17:457–461

Long SP, Ainsworth EA, Rogers A, Ort DR (2004) Rising atmospheric carbon dioxide: plants FACE the future. Annu Rev Plant Biol 55:591–628

Long SP, Ainsworth EA et al (2006) Food for thought: lower-than-expected crop yield stimulation with rising CO_2 concentrations. Science 312:1918–1921

Luo Q (2011) Temperature thresholds and crop production: a review. Clim Change 109:583–598

Malamy JE (2005) Intrinsic and environmental response pathways that regulate root system architecture. Plant Cell Environ 28:67–77

Mandersheid R, Weigel HJ (1997) Photosynthetic and growth responses of old and modern spring wheat cultivars to atmospheric CO_2 enrichment. Agric Ecosyst Environ 64:65–71

Martin T, Oswald O, Graham IA (2002) Arabidopsis seedling growth, storage lipid mobilization, and photosynthetic gene expression are regulated by carbon: nitrogen availability. Plant Physiol 128:472–481

Matt P et al (2001) Elevated carbon dioxide increases nitrate uptake and nitrate reductase activity when tobacco is growing on nitrate, but increases ammonium uptake and inhibits nitrate reductase activity when tobacco is growing on ammonium nitrate. Plant Cell Environ 24:1119–1137

Midgley GF, Wand SJE, Pammenter NW (1999) Nutrient and genotypic effects on CO_2-responsiveness: photosynthetic regulation in *Leucadendron* species of a nutrient-poor environment. J Exp Bot 50: 533–542

Moore BD, Cheng SH, Sims D, Seemann JR (1999) The biochemical and molecular basis for photosynthetic acclimation to elevated atmospheric CO2. Plant Cell Environ 22:567–582

Myers SS et al (2014) Rising CO_2 threatens human nutrition. Nature 510:139–142

Norby RJ, DeLucia EH, Gielen B et al (2005) Forest response to elevated CO_2 is conserved across a broad range of productivity. Proc Nat Acad Sci USA 102:18052–18056

Oliveira VF, Silva EA, Zaidan LBP, Carvalho MAM (2013) Effects of elevated CO_2 concentration and water deficit on fructan metabolism in *Viguiera discolour* Baker. Plant Biol 15:471–482

Pakistan and Afghanistan (2013) http://www.weather.com/news/heavy-rains-kill-53-pakistan-20130805

Paul MJ, Driscoll SP (1997) Sugar repression of photosynthesis: the role of carbohydrates in signalling nitrogen deficiency through source: sink imbalance. Plant Cell Environ 20:10–116

Pleijel H, Uddling J (2012) Yield vs quality trade-offs for wheat in response to carbon dioxide and ozone. Glob Change Biol 18:596–605

Poorter H, Navas ML (2003) Plant growth and competition at elevated CO_2: on winners, losers and functional groups. New Phytol 157:175–198

Porter JR, Semenov MA (2005) Crop responses to climatic variation. Philos Trans R Soc Lond B Biol Sci 360(1463):2021–2035

Reich PB et al (2006) Nitrogen limitation constrains sustainability of ecosystem response to CO_2. Nature 440:922–925, 2006

Robinson A, Robinson Z (1997) Science has spoken, global warming is a myth. The Wall Street Journal, December 4

Rogers A, Fischer BU, Bryant J, Frehner M, Blum H, Raines CA, Long SP (1998) Acclimation of photosynthesis to elevated CO_2 under low-nitrogen nutrition is affected by the capacity for assimilate utilization. Perennial ryegrass under free-air CO_2 enrichment. Plant Physiol 118:683–689

Rogers A, Ainsworth EA, Leakey ADB (2009) Will elevated carbon dioxide concentration amplify the benefits of nitrogen fixation in legumes? Plant Physiol 151:1009–1016

Ronchi CP, DaMatta FM, Batista KD, Moraes GABK, Loureiro ME, Ducatti C (2006) Growth and photosynthetic down-regulation in *Coffea arabica* in response to restricted root volume. Funct Plant Biol 33:1013–1023

Ross DJ, Newton PCD, Tate KR (2004) Elevated CO_2 effects on herbage production and soil carbon and nitrogen pools and mineralization in a species-rich, grazed pasture on a seasonally dry sand. Plant Soil 260:183–196

Sanz-Sáez Á, Erice G, Aguirreolea J, Muñoz F, Sánchez-Díaz M et al (2012) Alfalfa forage digestibility, quality and yield under future climate change scenarios vary with Sinorhizobium meliloti strain. J Plant Physiol 169:782–788

Scarascia-Mugnozza G et al (2006) Responses to elevated [CO2] of a short rotation, multispecies Poplar plantation: the POPFACE/EUROFACE Experiment. Ecological Studies, vol 187

Schimel D et al (1996) Radiative forcing of climate change. In: Houghton JT et al (eds) Climate change 1995: the science of climate change. Cambridge University Press, Cambridge

Stafford N (2008) The other greenhouse effects. Nature 448:526–528

Taiz L, Zeiger E (2002) Plant physiology, 3rd edn. Sinauer Associates, Sunderland

Taiz L, Zeiger E (2006) Plant physiology, 4th edn. Sinauer Associates, Sunderland

Taub DR, Wang XZ (2008) Why are nitrogen concentrations in plant tissues lower under elevated CO_2? A critical examination of the hypotheses. J Integr Plant Biol 50:1365–1374

Taub D, Miller B et al (2008) Effects of elevated CO_2 on the protein concentration of food crops: a meta-analysis. Glob Change Biol 14:565–575

Trenberth KE (2011) Changes in precipitation with climate change. Clim Res 47:123–138

Tubiello FN, Soussana J-F, Howden SM (2007) Crop and pasture response to climate change. Proc Natl Acad Sci USA 104:19686–19690

Uttarakhand (2013) http://www.downtoearth.org.in/content/man-made-reasons-uttarakhand-disaster

Wand SJE, Midgley GF, Jones MH, Curtis PS (1999) Responses of wild C4 and C3 grass (Poaceae) species to elevated atmospheric CO_2 concentration: a meta- analytic test of current theories and perceptions. Glob Change Biol 5:723–741

World Meteorological Organization (2013) http://www.wmo.int/pages/meetings/documents/Final_2013PTC_Report.pdf

WUWT (2010) http://wattsupwiththat.com/2010/05/14/now-its-more-co2-that-will-threaten-crops/

Yang L, Wang H, Liu Y, Zhu J, Huang J, Liu G et al (2009) Yield formation of CO_2-enriched inter-subspecific hybrid rice cultivar Liangyoupeijiu under fully open-air field condition in a warm sub-tropical climate. Agric Ecosyst Environ 129:193–200

Ziska LH, Bunce JA (1997) Influence of increasing carbon dioxide concentration on the photosynthetic and growth stimulation of selected C4 crops and weeds. Photo Res 54:199–208

Ziska LH et al (2004) Quantitative and qualitative evaluation of selected wheat varieties released since 1903 to increasing atmospheric carbon dioxide: Can yield sensitivity to carbon dioxide be a factor in wheat performance? Glob Change Biol 10:1810–1819