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Scope, Options and Approaches to Climate Change

Increase Crop Yield Potential Through the Understanding of Genetic Control of Plant Responses to Increased Carbon Dioxide

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6.1 Introduction

Carbon dioxide [CO_2] concentration in the atmosphere increased from less than 300 μmol CO_2 mol^{-1} before the industrial revolution to 387 μmol CO_2 mol^{-1} by 2009, further increasing at a rate of 1.9 μmol CO_2 mol^{-1} per year since 2000 (IPCC, 2007). This increase in atmospheric [CO_2], along with other greenhouse gases such as methane, nitrous oxide, and halocarbons, is likely to increase the atmospheric temperature (Carter et al., 2007). The IPCC 2007 emissions scenario A1B predicts that the atmospheric [CO_2] concentration could reach 550 μmol CO_2 mol^{-1} by 2050 (Carter et al., 2007). For a similar increase in radiative force, the atmospheric temperature is expected to increase by 1.4 to 4.5°C in 2100 (IPCC, 2007). The climatic perturbations that result from the changes in the atmospheric composition are expected to have strong regional effects (Carter et al., 2007; Vadez et al., 2012). There is growing evidence suggesting that many plants of the C_3 biochemical type will respond positively to increased atmospheric CO_2 concentration under optimum growth conditions (Fitzgerald et al., 2016; Long et al., 2004; Sankaranarayanan et al., 2010; Seneweera et al., 2005), but the beneficial effect of elevated CO_2 could be offset by other climatic stress factors, such as high temperatures and periodic drought (Ahuja et al., 2010; Fernando et al., 2014; Fitzgerald et al., 2016).

Plant growth at elevated CO_2 is mediated through increase in photosynthetic capacity (increased carbon gain) and reduction in stomatal conductance (improved plant water use efficiency) (Ainsworth and Rogers, 2007; Thilakarathne et al., 2015). Increased photosynthesis at elevated CO_2 is largely due to a reduction in photorespiration and is directly associated with decrease in O_2/CO_2 ratio at the site of the CO_2 fixation (Bowes, 1991). Elevated CO_2 also reduces the stomatal conductance by 30-40% at double the CO_2 concentration, which leads to improved efficiency of plant water use (Leakey et al., 2012; Seneweera et al., 2001). Elevated CO_2 also substantially increases radiation use efficiency by reducing photorespiration, which is likely to offset the yield loss resulting from high temperature and drought stress. For C_4 plants, elevated CO_2 is likely to have a much lesser impact on photosynthesis. However, C_4 crops benefit from elevated CO_2 under water stress conditions because stomatal conductance is reduced which leads to reduced transpiration (McMurtrie et al., 2008; Seneweera et al., 2001).

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There is a significant amount of literature available on plant response to elevated CO_2 and its influence on plant growth, productivity, and physiological and biochemical processes. Elevated CO_2 also influences the changes in the biochemical composition of grains and their nutritional quality (Conroy et al., 1998; Hogy et al., 2009; Seneweera et al., 1996). Fundamental understanding of these responses is essential to improve grain quality under future climate change conditions. Crop production needs to be increased by 60% in order to sustain a global population increase from today's 7 billion to 9 billion by 2050 (Rosegrant and Cline, 2003). Thus, feeding the growing population will be the biggest challenge in the 21st century. Simultaneously, changes in the atmospheric composition will be an additional challenge for crop production, as it will significantly modify the crop production environment. Therefore, the challenges that arise from climate change provide opportunities to apply biotechnology to improve crop yield and quality. In plant breeding or genetic engineering programs for increased crop production, photosynthesis will be one of the key targets, as the main resource for photosynthesis, CO_2, will increase unless consistent effort is tended by the global community to reduce carbon emissions. Three major targets identified for photosynthesis improvement are: the increase in efficiency of photosynthetic radiation us; reduction of photorespiration; and redesigning C_3 photosynthesis with C_4 traits. If Ribulose bisphosphate carboxylase/oxygenase (RuBisCO) can be engineered to completely suppress photorespiration, theoretically, the potential yield of C_3 crops can be increased by up to 45% (Long et al., 2006). There have been a number of attempts to introduce more efficient C_4 photosynthetic traits into C_3 plants; though the progress has been limited (Matsuoka et al., 1994; Miyao and Fukayama, 2003; Sheehy et al., 1996). In this paper , an overview of plant responses to elevated CO_2 concentrations, as well as the underlying causes of those responses will be discussed. Possible strategies that can be adopted to address global food security under a changing climate will also be discussed.

6.2 Impact of CO_2 and climate stress on growth and yield of agricultural crop

The increase in CO_2 concentration to 550 μmol CO_2 mol^{-1}, as projected to occur by the middle of the 21st century (IPCC, 2007), is likely to increase the essential resources for plant growth and development as never experienced in the recent past (Pearson and Palmer, 2000). Using over 400 experimental findings, (Kimball and Idso, 1983) Kimbal and Idso (1983) have shown that elevated CO_2 can increase the yield of agricultural crops. The mean stimulation of C_3 plant growth was 26% for an increase in the CO_2 concentration from 340 to 660 μL CO_2 L^{-1}. In contrast, (Ainsworth et al., 2008) Ainsworth et al. (2008) showed a 14% grain yield increase in the Free AIR CO_2 Enrichment (FACE) experiment as compared to a 31% increase in enclosure studies when CO_2 was raised from 373 to 570 μmol CO_2 mol^{-1}. These responses are much lower than previously estimated. It is still unclear whether FACE studies are underestimating or enclosure systems are overestimating the response to elevated CO_2. Thus, the true magnitude of the positive "fertilization" effect of elevated CO_2 is still uncertain. It has also been demonstrated that there is a large intra-specific variability in growth response to elevated CO_2. For example, plants that have large vegetative sink strength, such as woody crops have showed a 42% biomass enhancement at elevated CO_2, while wheat and rice yield will be increased only by 15%. Understanding the physiological and molecular basis of these discrepancies in response to elevated CO_2 is essential in order to prepare effectively for the inevitable future changes in climate.

6.3 The Primary Mechanisms of Plants Respond to Elevated CO_2

The direct response of plants to elevated CO_2 results from an increase in the photosynthetic rate and a reduction in stomatal conductance. Increases in photosynthetic rates occur only in C_3 species. This response to elevated CO_2 is partly due to an increase in CO_2 concentration at the site of fixation and the suppression of photorespiration. These responses can be easily explained by the kinetic data of RubisCO, which is the rate-limiting enzyme in the photosynthetic carbon reduction cycle (Bowes, 1991; Long et al., 2006). Meta analysis of a large number of FACE experimental data shows a 31% increase in light-saturated leaf photosynthesis and a 28% increase in diurnal photosynthetic carbon assimilation (Ainsworth and Long, 2005). However, the initial stimulation of C_3 photosynthesis is not always maintained. Long-term exposure of plants to elevated CO_2 reduces the potential photosynthetic rates, an adjustment known as "photosynthetic acclimation" (Moore et al., 1998; Seneweera et al., 2005; Seneweera and Norton, 2011). The majority of vascular plants uses the C_3 carbon assimilation pathway and respond well to elevated CO_2. About 2–3% of plants, such as maize, sorghum, and sugar cane, belong to the C_4 type, while 6–7% use Crassulacean Acid Metabolism (CAM). For C_4 and CAM plants, the plant-water use efficiency is improved at elevated CO_2 through the lowering of the stomatal conductance. However, the physiological mechanism of this response is still not well understood (Keel et al., 2007; Seneweera et al., 2001).

6.4 Interaction of Rising CO_2 With Other Environmental Factors – Temperature and Water

The positive gain from rising CO_2 could be negated by rising atmospheric temperature and thereby compromise, and challenge, global food security. To address this issue, it is important to understand the interactions of these environmental signals both at the cellular and whole plant level. It has been widely reported that the optimum growth temperature for several plants has already been shown to substantially increase at elevated CO_2 (Taub et al., 2000; Zhu et al., 1999). For example, optimum growth temperature will increase by 5°C when plants are grown at 700 μmol CO_2 mol^{-1} concentration (Long, 1991). The underlying physiological mechanism that improves the temperature tolerance of plants under elevated CO_2 is likely to be directly or indirectly linked to photosynthesis and photorespiration (Sage and Kubien, 2007). Improved kinetic properties of RuBisCO due to increases in temperature at elevated CO_2 can also contribute to increased photosynthesis (Sage and Kubien, 2007). For example, in an oxygen (O_2) rich atmosphere, as at present, the specificity of RuBisCO for CO_2 is relatively low. However, under elevated CO_2 conditions, the oxygenation of RuBisCO decreases as a result of the decrease in the O_2/CO_2 ratio at the in-site of the CO_2

fixation, leading to a significant reduction in photorespiration. Photorespiration is a wasteful reaction and hence, the suppression of this reaction at elevated CO_2 can further improve photosynthetic carbon gain, translating into increased growth and yield.

Most of the C_3 plants, which account nearly 95% of the plant species on earth, will increase their photosynthetic capacity and biomass production in future CO_2 rich atmosphere. However, water stress will be common under climate change conditions and thus future crop productivity will depend on the availability of soil water (Ghannoum, 2009; Lawlor and Tezara, 2009). At elevated CO_2, plants produce large root volumes, an adaptive response to access more water at elevated CO_2. For example, (Wechsung et al., 1999) Wechsung et al. (1999) observed a 70% increase in the dry weight of water-stressed wheat when the plants are exposed to 550 μmol CO_2 mol^{-1}. With C_4 species, the growth response to elevated CO_2 concentrations is usually maintained or even increased under mild water stress (Samarakoon and Gifford, 1996, Seneweera et al., 2001), but under severe drought, the response is much smaller (Seneweera et al., 2001). Other interactions, such as nutrient cycling, set the ultimate limit to a carbon driven, long-term stimulation of plant production (Finzi et al., 2006, Hungate et al., 2006). Increasing evidence shows that progressive nitrogen (N) limitation (i.e. mineral N declining over time) is one of the key responses to elevated CO_2 concentrations. No new N input can lead to dynamic changes in both natural and managed ecosystems. It is likely that elevated CO_2 can change the dynamics of nutrient turnover; thus, interdisciplinary approaches that manage this nutrient are essential, particularly to ensure food and ecosystem security in the future.

6.5 Impact of Climate Change on Crop Quality

Rising CO_2 concentration effects crop and pasture quality by changing the plant metabolism of carbon and nitrogen at both cellular and whole plant level (Seneweera et al., 2005). As wheat and rice are the world's most important food sources, special focus will be given to these two crops. For rice, it is generally consumed as a cooked whole grain, the properties of the grain itself, rather than the flour, determine the quality. The main quality traits in rice are average grain weight, amylose concentration, relative paste viscosity, and nutrient concentration. The other major characteristics of rice are the appearance, milling, and cooking quality (Juliano, 1992). An increase in the atmospheric CO_2 is likely to increase the firmness of the cooked grain because elevated CO_2 increases the grain amylose content of rice (Seneweera et al., 1996). The amylose content in rice endosperm, one of the key traits that determine the grain firmness, is closely linked to the post-transcriptional regulation of the waxy (*Wx*) gene. Rice cultivars with higher amylose content produce large amounts of *Wx* mRNA and Wx protein (Wang et al., 1995); thus, an understanding of the regulation of the waxy gene under elevated CO_2 is important to maintain the cooking quality of rice in future climate. In addition, elevated CO_2 reduces a wide range of nutrients that are essential for human and animal health (Seneweera, 2011, Seneweera and Conroy, 1997). These nutrients include protein, micronutrients, amino acids, fatty acids, carbohydrate and phytate (Högy and Fangmeier, 2008; Seneweera and Conroy, 1997). In fact, zinc (Zn) and iron (Fe) deficiency has been recognized as one of the major risk factors by the World Health Organization, with Zn being the fifth leading risk factor for disease in the developing world. One-third of the world's population is at risk of Zn deficiency, ranging from 4 to 73% of a country's population, depending on the area. Detailed understanding of the impact of elevated CO_2 on grain protein and micronutrients, such as Zn and Fe is essential, in order to improve the nutrient quality of grain.

Unlike rice, wheat is mainly consumed as a processed product; thus, its nutritive value and rheological characteristics determine wheat quality. Elevated CO_2 increases grain starch content, which is closely associated with improved carbohydrate translocation to the grain. Similar to rice, changes in the amylose-amylopectin ratio are documented at elevated CO_2 levels (Blumenthal et al., 1996; Hoegy and Fangmeier, 2008). Lipid concentration, which plays an important role in bread making, is also reduced at elevated CO_2. Reduction in the protein concentration at elevated CO_2 is also significant, with the quality of gluten proteins being largely affected (Fernando et al., 2015). These proteins are closely associated with the binding of gliadin and glutenin in gluten, as well as the binding of gluten to starch in the dough, ultimately determining the rheological characteristics of the flour. Similar to rice, mineral nutrients such as Zn and Fe are also significantly reduced in grain produced at elevated CO_2, suggesting that climate change could lead to a hidden global famine of micronutrients, unless otherwise if we do not address these issue immediately.

6.6 Climate Change, Crop Improvement, and Future Food Security

Rising CO_2 concentrations are likely to improve the potential grain yield of most of the C_3 crop plants, but accompanying changes in atmospheric temperature and periodic drought are likely to have a negative impact on the growth and yield of crops (Ghannoum, 2009; Seneweera et al., 1994; Seneweera et al., 2002). Based on the current growth rate, the world population is expected to reach 9 billion by 2050. To meet the higher food demands, crop production will need to be increased by at least 50%. Over the past decade, annual grain yields from cereal breeding programs have reached a plateau (FAO-Stat, 2008). This yield stagnation is exacerbated by population growth, land limitation, and the uncertainty of climate change, all of which are likely to lead to a global food production crisis.

To address this problem, it is necessary to understand the underlying cause of this yield stagnation. There is mounting evidence that yield potentials of many crops are limited by the capacity to exploit sufficient carbon during their lifecycles (Fischer et al., 1998). In the past, higher grain yield was achieved through the introduction of semidwarf "Green Revolution" gene that encodes a mutant enzyme involved in Gibberellic Acid (GA) synthesis (Fischer et al., 1998; Okawa et al., 2002). For rice, it is very clear that source capacity is the limiting factor for high yield (Peng et al., 2008), as shown by the higher number of unfilled grains in new breeding lines. There is strong evidence that photosynthesis source capacity is strongly correlated with yield potential (Fischer et al., 1998; Poorter, 1993; Thilakarathne et al., 2015). It has been suggested that photosynthetic carbon gain can be improved by engineering rate-limiting steps in photosynthesis, thereby increasing the photosynthesis per unit leaf area. For this, it is necessary to understand the major factors controlling the photosynthetic carbon flux. The major limitations identified in C_3 photosynthesis are limitations by RuBisCO and its kinetic properties; limitations by "regeneration," the rate of recycling of the sugar phosphate acceptor, Ribulose bisphosphate (RuBP), (or sugar synthesis and export limitation). Improvement in photosynthesis could also be achieved by introducing a CO_2 concentrating mechanism to C_3 plants. In addition, there is a considerable genotypic variation in photosynthetic capacity and the maximum photosynthetic rate in leaf material at a given phonological stage under well-watered conditions. However, only a limited number of studies have been conducted regarding the breeding of crop lines for increase in photosynthesis in source organs. Thus, an understanding of the function of the photosynthetic machinery and its environmental interactions will help to manipulate plants under a changing climate in the future.

6.7 Intra-specific Variation in Crop Response to Elevated [CO_2] - Current Germplasm Versus Wild Relatives

The responsiveness to elevated [CO_2] is varied with crop species and even within the species and considerable variation is observed. A large intra-specific variation has been reported in many economically important C_3 crop species such as rice (Krishnan et al., 2011; Mohammed and Tarpley, 2010; Yang et al., 2009) and wheat (Tausz et al., 2013; Thilakarathne et al., 2012; Ziska, 2008). Thus, there is an intense interest in understanding mechanisms of how elevated [CO_2] mediates such differential growth response within same crop species. Plant growth and yield response to elevated [CO_2] is also dependent on the environmental and genotype interaction. Basic understanding of interaction between environment and genotype has been extensively used in plant breeding programs to increase crop yield potential (Tausz et al., 2013). This led to make major breakthrough in crop yield barriers in the recent past when background [CO_2] was rapidly increasing (Parry and Hawkesford, 2012; Seneweera and Norton, 2011). In general, to increase the yield potential, appropriate characteristics must be selected from broad genetic background. Broadly, morphological/growth, biochemical and molecular and eco-physiological traits should be considered for such breeding experiments. These traits can be targeted to improve various component of plant process, e.g. improving yield potential (Reynolds et al., 2011), quality (Shewry et al., 2009), nutrient use efficiency (Foulkes et al., 2009), or transpiration efficiency (Richards et al. 2010). Therefore, identification of new physiological traits that can capture the response to CO_2 and other environmental factors are immensely important to increase the crop productivity or improve crop quality under changing climate conditions.

6.8 Identification of New QTLs for Plant Breeding

Crop yield and stress responsiveness are complex traits and normally controlled by quantitative trait loci (QTLs), and are strongly influenced by the environment. Understanding the mechanisms of plant responses to elevated [CO_2] are important and QTL analysis is a powerful tool to dissect complex traits into single chromosome loci and to characterize them. Genotypic (based on molecular markers) and phenotypic data from a segregating population derived from experimental crosses of contrasting lines are used for QTL analysis. Coarse QTLs are mapped by identifying marker loci correlating with the phenotype. After this primary mapping, QTL will be identified within a chromosome region of 10-30 cM, which usually contains several hundred genes. To characterize the function of coarsely mapped QTL and to proceed for fine mapping, selection of near isogenic lines (NILs), that harbors only target QTL allele at the short chromosome segment on a single chromosome, will be required. NILs allow physiological testing evaluating the precise effect of target QTL without the effect of other segregating QTLs. Further, NILs suitable for fine-mapping of QTL region after backcrossing with parental line, called advanced backcross QTL analysis (AB-QTL). After this step, QTL will be finely mapped within a chromosome region of <1 cM. When the target QTL region approaches cM level, genetic map is anchored to the physical map, and genomic sequencing and bioinformatics approaches such as gene prediction and annotation and/or transcriptional profiling approaches will be useful for the identification of responsible gene after transgenic validation of candidate gene. The information of gene-of-interest or nearest marker to fine-mapped QTL will be available for breeding approaches by genetic engineering or marker-assisted selection (MAS), respectively. So far, limited numbers of studies have been reported in the cloning of QTLs regulating source function of crop species, and no studies reporting the cloning of QTLs involving the response to elevated [CO_2]. The phenotype (P) is not only determined by the genetics (G) and environmental factors (E), but also their interactions (G x E). To analyze QTLs involving the [CO_2] responsiveness, it requires comparing the phenotypes of mapping population under both ambient and elevated [CO_2] conditions, the growth facility and intensive labor will be the limiting factors.

6.9 Association Mapping for Large Germplasm Screening

Association mapping (Genome wide association study, GWAS) is an alternative approach to positional cloning . Association mapping analyzes the statistical association between genotypic and phenotypic data data using a set of germplasm accessions or cultivated varieties. Compared to QTL analysis, association mapping doesn't require the production of mapping populations, and enables to survey more diverse alleles with high genetic resolution because a set of genotypes potentially harbor wide natural variations of haplotypes due to accumulation of recombination events occurred during past generations. However, the level of linkage disequilibrium (LD) among the tested genotypes affects the resolution of mapping. When testing low LD panels with high density single nucleotide polymorphisms (SNPs), it is potentially high enough to narrow down the associated region to a few genes without additional fine-mapping. So far, no study has been reported on GWAS involving the response to elevated [CO_2]. However, the large genetic variation of [CO_2] responsiveness have been reported, more attention should be directed in adopting GWAS to find useful genetic alleles from wide natural variation, that would contribute to increase the crop productivity or improve crop quality under changing climate conditions.

6.10 Genetic Engineering of CO_2 Responsive Traits

One of the biggest threats in climate change is addressing the crop productivity issues with increasing food demand for growing population. Research have been undertaken to increase the crop productivity through conventional breeding under elevated [CO_2] levels. However, genetic engineering could be used as a tool to introduce new traits that are not possible through conventional breeding (Jauhar, 2006). Elevated [CO_2] has directly increased the net photosynthetic rate of C_3 crops due to increased carboxylation and reduced photorespiration by Rubisco enzyme (Ainsworth and Rogers, 2007; Long et al., 2004). However, this initial increased photosynthetic rate in C_3 crops is only temporal as a result of photosynthesis acclimation (Long et al., 2004). This is due to prolonged exposure of plants to high CO_2 which affects the balance of photosynthetic machinery interms of activity of Rubisco and RuBP regeneration (Sage et al., 1989). This can be overcome by engineering the Rubisco affinity to CO_2 by introducing Rubisco from a nongreen algae with lower specificity and higher catalytic rate (Zhu et al., 2004; Ainsworth et al., 2008). Decrease in grain protein content in C_3 plants grown under elevated CO_2 have been reported (Myers et al., 2014). This is majorly due to large investment of nitrogen (about 6% leaf nitrogen) in Rubisco synthesis at elevated CO_2, due to decrease in Rubisco content (Parry et al., 2003). This nitrogen acquisition gap can be eliminated by engineering nonleguminous C_3 plants to fix atmospheric nitrogen (Ainsworth et al., 2008). Elevated [CO_2] also reduces stomatal conductance (Ainsworth et al., 2008). Due to this responsive trait, C_4 plants are vulnerable to drought stress (Leakey 2009). Manipulating the expression of epidermal patterning factor (*EFP2*) for decreased stomatal density and increased stomatal size has proved beneficial for future CO_2 concentrations in Arabidopsis (Doheny-Adams et al., 2012). Similarly engineering C_4 plants for modifying the stomatal density and size can be beneficial for optimal growth at elevated [CO_2] levels in future. Addressing the inverse effects of elevated [CO_2] in crop plants by genetic engineering approach can be effective and efficient.

6.11 Conclusions

There is now adequate evidence that the CO_2 fertilization effect is occurring due to improved photosynthetic efficiency and will continue for C_3 plants at least until the [CO_2] reaches 750 μmol/mol C_4 plants are less likely to respond, but in C_3 plant, radiation, water and N use efficiencies all are expected to increase with the outcome as increased growth and yield, and ultimately food security. The final outcome will be moderated by water, temperature and N supply as well as O_3 and various ecosystem level impacts that are now starting to be understood.

It is apparent that current breeding strategies are not necessarily selecting genotypes that are responsive to e[CO_2] (Ziska et al. 2004) so a fresh approach will be needed using the rapidly advancing capabilities in functional genomics, genetic transformation and synthetic biology, targeting traits that will provide cultivars able to exploit what was – in evolutionary terms – scarce atmospheric carbon. The challenge to develop new cultivars will require a revised strategy evaluating hundreds or thousands of genotypes rather than the current four or five. This evaluation should consider these responses across a broad range of environmental conditions, in experiments designed to test interactions between e[CO_2] and other factors such as temperature, water and O_3. Ainsworth et al. (2008) proposed a new generation of large FACE experiments that would contribute to the challenge of understanding, and then adapting to the challenges of a carbon rich future.

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