
Keynote Speech

Opportunities and Challenges to Crop Improvement Through Photosynthesis Under Changing Climate

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Abstract

Crop production is seriously threatened by global climate change and recent demands for the growth of crops to produce bio-fuels. On the other hand, population growth will exert an immense pressure on food demand in the coming years. By 2050, food production will need to increase by 50% to feed the growing population. The most feasible option is to increase the crop yield potential through increasing the photosynthetic capacity per leaf area. Raising the atmospheric CO₂ concentration from the current concentration of 390 to 550 L CO₂ L⁻¹ (year 2050 CO₂ concentration in the atmosphere), caused an increase in photosynthesis by (31%), while photorespiration and stomatal conductance decreased by ~50% and ~22% respectively. This increase in photosynthesis at elevated CO₂ will promote a grain yield of up to 45% for some cereal cultivars suggesting that yield enhancement is possible through increasing photosynthesis.

Introduction

Inevitable climate change coupled with an increase in world population, from a current population of 7 billion to 10 billion by 2050, will increase the demand for food. In the middle of the last century, advances in plant breeding led to the Green Revolution through which large improvements in grain production occurred (Woodhouse, 1989). However, in recent years, plant breeders have failed to systematically increase the yield in line with population growth (Zhu et al. 2010). Now, it is estimated that the world's cereal production must increase by 50% by 2050 to meet the projected food demand (Royal Society, 1999). Rice and wheat are the two most commercially important cereal crops, accounting for more than 70% of the global food supply and plays a major role in global food security (Long et al. 2005; Seneweera and Norton, 2011). The predictions suggest that the grain yield of these crops needs to be increased by more than 50% to feed the world's growing population.

Food production is further challenged by climate change, which is likely to reduce the world cereal production by up to 10-15% by the middle of this century. The magnitude of the response is largely dependent on geographical location, environmental interaction and crop species (Rothstein, 2007). Rising CO₂ is the major cause for climate change, contributing to more than 70% of global warming (IPCC, 2007). On

the other hand, CO₂ is also the primary substrate for photosynthesis, and most C₃ plants are not yet photosynthetically saturated at current atmospheric CO₂ concentration. Photosynthesis will substantially increase with increasing CO₂ concentration leading to large increases in grain yield (Seneweera et al., 2005), however it is still a matter of debate whether this yield stimulation under elevated CO₂ would be sustained as other environmental factors such as high temperature and periodic drought negatively impact photosynthesis (Ainsworth et al. 2002).

Development of adaptation strategies to mitigate climate change will not fully address the issue of global food security as food production *needs* to increase by 50% by the middle of this century, and this is much larger than the expected reduction in food production under future climate conditions. Global food security can only be achieved by a sizeable investment in research and development, particularly in the area of transformational research in cereal breeding technologies. For example, in the middle of the last century, huge increments in cereal yield were achieved through the introduction of GA-insensitive dwarfing genes through traditional breeding programs. The "Green Revolution" was made possible by increasing the harvest index (HI) driven by the increase in grain number (Peng et al., 2008). Crossing Dee-Geo-woo-

gen and Peta (rice) produced the miracle breeding line of IR8, which increased the yield potential by almost 100% (Peng et al. 2008). A similar breakthrough in the yield barrier is currently required to meet future food demand. Massive global starvation is inevitable in the coming years if this important issue is not addressed effectively.

Among the major limiting factors for plant growth are the carbon assimilation capacity and radiation use efficiency, which affects the yield potential in many agronomically important crops, including rice and wheat (Sheehy et al. 2000). This was supported by theoretical calculations and observations made from Free Air CO₂ Enrichment (FACE) research. This argument was further supported by observation that the fertile grain number had declined in recent breeding lines of rice and wheat, despite an increase in total grain number (Fischer et al., 1998; Krishnan et al., 2011; Seneweera et al. 2010). In my presentation, I will discuss (1) agriculture and food security in global and regional context (2) food production under a changing climate, which we have learned from Free Air CO₂ Enrichment research (3) how genetic engineering research can be used to manipulate photosynthesis and yield potential and (4) how genetic variability in photosynthesis can be utilised to improve yield potential.

Agriculture and food security

World food production needs to increase by 50% to meet population demand by 2050. As rice and wheat are the two main cereals crops that contribute to more than 70% of the food requirement globally, improvement of their productivity is essential. Current yearly increases in cereal yields due to conventional breeding methods have dropped to less than a third of the annual gains seen between 1960 and 1988 (Fischer et al. 2009). This yield stagnation is further compounded by competition for agricultural land from urbanisation and bio-fuel feed stocks, increasing fuel and fertiliser costs and the uncertainty of climate change. The first significant step towards increasing food security has been taken in the breeding of "golden rice" (Rothstein, 2007) in which genetic engineering has been used to enhance vitamin A concentration.

Crop production under changing climate - what we have learned from FACE research

The projected increase in CO₂ concentration (550 μmol CO₂ mol by the middle of the 21st Century), will contribute to more than 70% of climate change (IPCC, 2007). This will have a profound influence on other atmospheric physical processes. For example, temperature will rise everywhere and, all year round, the mean annual temperature is expected to increase by 0.5-1.0°C (IPCC, 2007), with most of the change occurring in summer and the least in winter. Evapotranspiration is expected to increase by 2-4%, which will have a major impact on both rain-fed and winter-cropping systems. Precipitation will be more erratic, and will have a large impact on the growth cycle of agricultural crops.

On the other hand, CO₂ is the primary substrate for photosynthesis and an increase of its concentration is likely to increase the resources for photosynthesis and thus for plant growth (Pearson and Palmer, 2000). Elevated CO₂ increased cereal yield by 14% when CO₂ concentration was raised from ~ 373 to ~ 570 μmol CO₂ mol under field conditions, Free Air CO₂ Enrichment (FACE). The primary mechanism that promotes plant growth is through stimulation of photosynthetic rates and a reduction in photorespiration and stomatal conductance (Bowes, 1991); all these processes work positively under elevated CO₂. However, the initial stimulation of C₃ photosynthesis is not always maintained when plants are exposed to elevated CO₂ for a longer period, reducing the potential photosynthetic rates. This adjustment is known as "photosynthetic acclimation" (Moore et al., 1998; Seneweera et al., 2005; Seneweera et al., 2011) and this process may limit the realisation of full yield potential (Seneweera et al. 2002).

A majority of vascular plants use the C₃ carbon assimilation pathway and respond well to elevated CO₂. Compared to the C₃ plants, about 2-3% species such as maize, sorghum, and sugar cane, belong to the C₄ type, and 6-7% use the Crassulacean Acid Metabolism (CAM). These species show little response to high CO₂ (Long et al. 1975). The advantages of the C₄ pathway over C₃ photosynthesis (at least at higher

temperatures) are evidenced by the fact that 11 out of the 12 most productive plant species on the planet are C_4 (Furbank, 1998). Further, C_4 plants are well adapted to various abiotic stresses such as water limitation, high temperature and nutrient deficiencies, which will be very common under future climate-change scenarios. Thus, managing the crops between C_3 and C_4 families may play an important role in maintaining global food security.

Genetic manipulation of photosynthesis is the key target to increase yield potential

Improving the photosynthetic capacity per given leaf area is likely to be an achievable target to improve crop productivity. Most of the important grain crops (rice, wheat, barley, canola, soybean, pulses), tuber crops (potato, cassava, yams, sweet potato) and vegetable crops (tomato, carrots, cabbages, etc) utilise C_3 photosynthesis, capturing CO_2 directly from the substomatal air spaces of the leaf via Rubisco. The efficiency of CO_2 assimilation in C_3 crop plants is severely compromised by photorespiratory activity (Zhu *et al.*, 2008). In C_3 plants under current atmospheric CO_2 condition, one-third of Rubisco is involved in the incorporation of oxygen rather than CO_2 and the subsequent processing and recycling of the product of this reaction, phosphoglycolate, requires both energy and the loss of CO_2 (Bowes, 1991).

C_4 plants have evolved a complex biochemical mechanism to concentrate CO_2 at the site of Rubisco. In C_4 photosynthesis, photorespiration is eliminated and Rubisco operates at close to its theoretical maximum velocity (Von Caemmerer and Furbank, 2003). The efficiency of conversion of total solar energy to grain in a C_4 plant is approximately 2.2% while in a C_3 cereal, this figure is only 1.4% (Zhu *et al.*, 2008). This 60% increase in photosynthetic efficiency, if translated into yield, with the compounded N-use efficiency and water-use efficiency of C_4 crops, makes the installation or modification of C_4 photosynthesis in C_3 plants an attractive proposition to increase the yield potential of cereals.

A number of strategies have been employed to improve photosynthesis. Three of the strategies aim to increase the CO_2 concentration around C_3 Rubisco, (1) improving CO_2 diffusion into the chloroplast and its site of the fixation; (2) introducing C_4 like characteristics into C_3 cells, introducing CO_2/HCO_3^- pump protein to the chloroplast membrane from cyanobacteria (Price *et al.*, 2008) or by introducing a new catabolic pathway into plastid that bypasses the energy-expensive photorespiration by recycling the Rubisco oxygenation product, 2-phosphoglycolate (Kebeish *et al.*, 2007). (3) The other avenue is to increase or improve the efficiency of Rubisco by having better kinetic characteristic (K_{ca}). Each of these strategies involves unique genetic engineering challenges.

Genetic diversity and future directions for plant breeding

Genetic variation across species for light saturated photosynthesis has been well documented for a number of species, including rice and wheat (Thilakarathne *et al.*, 2012; Evans, 1989; De Costa *et al.*, 2003). It is more likely that even more extensive variation may be found within the same species, if we extend our investigation into the wild relatives (Austin *et al.*, 1989). For example, wild relatives of wheat and rice have higher chlorophyll a:b ratios with greater adaptation to a high light environment. However, the major factor that limits the progress of germplasm screening for such specific traits is phenotyping capabilities. Recent advancement in several ground-based sensors offers the promise of screening of the canopy photosynthesis and leaf N status with higher precision, including measuring spectral reflectance, chlorophyll content and leaf photosynthetic activity. Other key questions regarding genetic variation in photosynthesis which remain to be answered are: which genes are involved and whether this trait is controlled by variation in a multitude of genes or just a few genes? Fulfilment of these knowledge gaps is vitally important to improve the photosynthesis and yield potential of agronomically important crops

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