



Review

FACE-ing the global change: Opportunities for improvement in photosynthetic radiation use efficiency and crop yield

Jindong Sun^{a,b,*}, Lianxin Yang^c, Yulong Wang^c, Donald R. Ort^{a,b,d}

^a Institute for Genomic Biology, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA

^b Department of Plant Biology, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA

^c Key Laboratory of Crop Genetics & Physiology of Jiangsu Province, Yangzhou University, Yangzhou 225009, China

^d Photosynthesis Research Unit, USDA-ARS, Urbana, IL 61801, USA

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ABSTRACT

The earth is rapidly changing through processes such as rising [CO₂], [O₃], and increased food demand. By 2050 the projected atmospheric [CO₂] and ground level [O₃] will be 50% and 20% higher than today. To meet future agricultural demand, amplified by an increasing population and economic progress in developing countries, crop yields will have to increase by at least 50% by the middle of the century. FACE (Free Air Concentration Enrichment) experiments have been conducted for more than 20 years in various parts of world to estimate, under the most realistic agricultural conditions possible, the impact of the CO₂ levels projected for the middle of this century on crops. The stimulations of crop seed yields by the projected CO₂ levels across FACE studies are about 18% on average and up to ~30% for the hybrid rice varieties and vary among crops, cultivars, nitrogen levels and soil moisture. The observed increase in crop yields under the projected CO₂ levels fall short of what would be required to meet the projected future food demand, even with the most responsive varieties. Crop biomass production and seed yield is the product of photosynthetic solar energy conversion. Improvement in photosynthetic radiation use efficiency stands as the most promising opportunity allowing for major increases in crop yield in a future that portends major changes in climate and crop growing environments. Our advanced understanding of the photosynthetic process along with rapidly advancing capabilities in functional genomics, genetic transformation and synthetic biology promises new opportunities for crop improvement by greater photosynthesis and crop yield. Traits and genes that show promise for improving photosynthesis are briefly reviewed, including enhancing leaf photosynthesis capacity and reducing photorespiration loss, manipulating plant hormones' responses for better ideotypes, extending duration of photosynthesis, and increasing carbon partitioning to the sink to alleviate feedback inhibition of photosynthesis.

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* Corresponding author at: Institute for Genomic Biology, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA. Tel.: +1 217 244 2996; fax: +1 217 244 2057.
E-mail address: jindong.sun@gmail.com (J. Sun).

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1. Introduction

Human activities are driving rapid changes in the global environment. Among the significant global changes is increasing human population, which by 2050 is projected to surpass 9 billion compared to 6.7 billion people that populate the earth today (<http://www.census.gov>). However, because economic capacity is also rapidly increasing in developing parts of the world, feeding 9 billion people possessing the economic means to be better nourished will create a demand on agriculture that will require 50% or more increase in crop productivity [1–3].

Human activities are also causing rapid changes in the atmosphere and climate that directly impact production agriculture. Atmospheric and climate change began accelerating after the industrial revolution. CO₂ concentrations which averaged about 270 ppm prior to the industrial revolution, have now surpassed 380 ppm, and will exceed 550 ppm by 2050 [4]. A potentially positive benefit of rising [CO₂] is the stimulation of photosynthesis in C₃ crops as the higher [CO₂] in future atmospheres will relieve Rubisco limitation on photosynthesis and suppress photorespiratory loss [4,5]. For example, a highly validated biochemical model of photosynthesis [5] suggests that the increase in atmospheric [CO₂] from 372 ppm to 550 ppm has the potential to increase Rubisco-limited photosynthesis by 36% at 25 °C [4,5]. However, increasing [CO₂] is also responsible for more than 60% of the phenomenon known as “greenhouse” effect [7] that is driving global warming and is predicted to cause changes in precipitation and weather patterns that are expected to have negative consequences for agriculture.

While ozone in the stratosphere is naturally occurring and protects the earth’s surface from UV radiation, ground-level or tropospheric ozone is present primarily as a pollutant where it is toxic to crops. In contrast to CO₂, the ground-level ozone is geographically heterogeneous with highest levels occurring near metropolitan cities and developed agricultural areas where volatile emissions from automobiles, factories and other sources are high. Pollutant ozone is formed primarily by the reaction of sunlight, NO_x and volatile organic hydrocarbons in the troposphere [7,8]. By 2050, ground-level [O₃] is projected to increase by 20% [6]. The accumulated doses of ozone exposure above a selected threshold (generally 40 ppb) or the dose actually taken up into the plants above the threshold have been used to determine and predict ozone damage to vegetation [9]. In various parts of the world, crops already frequently experience [O₃] above the damage threshold. Ozone enters plant leaves through the stomata where it can react to produce variety of reactive oxygen species, causing damage to plant cells through ethylene and jasmonate dependent signaling and other mechanisms [9,10]. The estimated crop yield loss due to current ozone damage is significant, range from 10 to 20% for a number of crops in many areas of the world [9,11].

More studies assessing future crop production are especially important, and solutions to meeting increased agriculture demand via new crops with improved photosynthetic radiation use efficiency and better adapted to current and future atmospheric and climate conditions need to be considered as early as possible. Except for corn and sorghum, the world’s major food crops are C₃ plants for which elevated [CO₂] has the potential to substantially increase radiation use efficiency, thereby helping offset the yield loss resulting from ozone pollution, global warming and drought stress. Elevated [CO₂] would have much less impact on C₄ crops,

but would benefit C₄ crops in drought conditions due to reduced water use [4].

Plant responses to elevated CO₂ have been studied for many years. Enclosure facilities (growth chambers, greenhouses and open top chambers) and lately FACE facilities (Free Air Concentration Enrichment, in which crops can be grown in the field under the elevated CO₂ levels) have been used to study the responses. All of these methods show positive CO₂ effects on plant photosynthesis, growth and seed yield [12–16]. However, the various methods vary in the relative responses of crop yield to elevated CO₂ when compared with the ambient control. Thus it has been debated whether these methods are consistent in the responses of crop yield to elevated CO₂ [13–16]. It was concluded that the responses of crop yield to elevated CO₂ were lower in FACE studies than the enclosure studies [13,24]; whereas others argued that the responses of crop yield were similar between FACE studies and enclosure studies if extrapolated with similar ambient and elevated [CO₂] [15,16]. Ainsworth et al. [14] later limited the comparisons of FACE and enclosure studies to those with similar ambient and elevated [CO₂] and concluded that the elevated CO₂ stimulation in FACE experiments was indeed significantly lower than that in enclosure studies. There are big differences between enclosure method and FACE method. The advantages of the enclosure method are that the cost is low, the studies can be conducted almost in any places and at any time, and the levels of temperature, humidity, and irrigation can be more easily controlled than the FACE method. The disadvantages of enclosure method are that enclosure facilities generally had much smaller plot sizes, loosely controlled plant density, larger edge effect, often limited root growth when grown in pots, and thus greater variations than the FACE method. The meaningful crop yield is the harvested sink tissues (seeds, fruits or tubers) per unit area land under natural field conditions. The data from a study where plants were grown in pots and the plant density was loosely controlled or from a study under artificial environmental conditions that are significantly different from the field conditions would hardly be translated into meaningful crop yield. CO₂ stimulation would be higher for a low density population than for a high density population since a low density population would be less limited by light. Some chamber studies did not strictly control the plant density and reported the responses on single plant basis, could have much high responses (some are >90% response to elevated CO₂, see [14]). For example, the transgenic tomato plants over-expressing sucrose-p synthase yielded 70–80% more fruits in open top chambers but only 20–30% more fruit in 2-year field trials compared with the untransformed control [60]. FACE facilities are closer to natural field conditions than open top chambers, which, in turn, are closer than growth chambers, thus better method for studying responses of crop yield to elevated CO₂. While the enclosure studies have been enormously important in conducting well controlled experiments to investigate mechanisms, FACE studies that are conducted under realistic agricultural conditions provide the best quantitative information about the response of yield to elevated CO₂ where interactions with other factors such as weeds, insects, pathogens, microorganisms and microclimates are in play [4]. FACE experiments have more than a 20-year history and have been conducted on a range of crops in several geographical locations around the world. A great deal of important information has been learned and a great deal of

new results of hybrid rice and winter wheat has been recently published from FACE which is the primary focus of this review.

Crop production has been substantially enhanced over the past half century as new varieties were developed with improved harvest indices, higher planting densities and better responsiveness to fertilizers and better management of weeds and disease was achieved. These new traits and management practices were the basis of the so-called “green revolution” but do not seem to be capable of doubling crop productivity required to meet the projected agricultural demand later this century. The harvest index for major crops may already be close to the maximum potential (*i.e.* 0.5–0.60) and have seen little increase in the past decade [1]. Though the average crop yield increases with each year due to the increase in inputs of fertilizers, herbicides, fungicides and irrigations, the maximum yield for major crops is no longer increasing [1]. Crop yield responses to these inputs are not linear and further increases in these inputs would not raise the maximum yield potentials. Another breakthrough, or second “green revolution”, is needed to meet the rising food demand [1,2]. Crop biomass production and seed yield are the products of photosynthetic solar energy conversion. The theoretical maximum potential to convert solar energy into biomass, the broad mean solar radiation use efficiency (RUE), is estimated at about 4.6% for C_3 plants and 6% for C_4 plants at 30 °C and current 380 ppm $[CO_2]$, and the advantage of C_4 over C_3 will largely disappear as the $[CO_2]$ nears 700 ppm late in this century [17]. With the photosynthetic solar energy conversion efficiencies of all the crops far lower than these maximum theoretical values, improving photosynthetic efficiency will need to play an important role if a substantial increase in productivity is to be achieved.

2. How do crops respond to FACE elevated $[CO_2]$?

2.1. Soybean responses to elevated $[CO_2]$

Since 2001, experiments on soybean responses to elevated CO_2 have been conducted at SoyFACE (<http://www.soyface.uiuc.edu>). The $[CO_2]$ in the atmosphere just above the FACE plots was raised to 550 ppm, as projected for the year 2050, and a computer-controlled system maintained the $[CO_2]$ within $\pm 10\%$ of the target for >90% of the time across the duration of the growing season. The FACE designs in China, Japan and other places are similar to SoyFACE design [18–20]. Some aspects in soybean responses to elevated $[CO_2]$ have been reviewed [4,18,21] and are summarized here in Table 1.

Table 1

Average percent change in various traits with elevation of CO_2 to 550 ppm versus ambient in SoyFACE (Champaign, IL, USA).

Trait	% Change ^a	Ref
Seed yield	13% ^e	[13,18]
Primary production (biomass above-ground)	18% ^c	[24]
Harvest index	–3% ^c	[24]
Plant height	13% ^c	[24]
Branch	20% ^b	[24]
Maturity days	3% ^c	[18,24]
Nodes	17% ^c	[24]
Maximum leaf area index (LAI)	15% ^b	[22,23]
Integral daily CO_2 uptake (A')	25% ^b	[25]
Light saturated CO_2 uptake (A_{sat})	20% ^b	[25,26]
Stomatal conductance (g_s)	–10% ^b	[26]
Stomatal limitation (l)	–7% ^b	[26]
Respiration (night)	37% ^a	[27]
Maximum rate of Rubisco carboxylation (V_{cmax})	–6% ^b	[26]
Leaf starch	70% ^d	[25,27]
Leaf sucrose	50% ^d	[25,27]
Leaf glucose	100% ^d	[25,27]
Leaf fructose	70% ^d	[25,27]

^a Common cultivar pioneer 93B15 or Pana was used. ^{a,b,c,d,e} indicate analysis across 1, 2, 3, 4, and 5 years, respectively.

The results showed significant effects of CO_2 treatments on soybean biomass and seed yield. On average, the elevated $[CO_2]$ enhanced the above-ground biomass and seed yield by 18% and 13%, respectively, compared with the ambient control (Table 1). The SoyFACE experiment also included a seasonal 25% elevation of ozone which decreased both the above-ground soybean biomass and seed yield by 11% [22]. It was further shown that elevating $[CO_2]$ to 550 ppm largely reversed the inhibition of 25% increase in $[O_3]$ with the biomass and seed yield similar to the elevated $[CO_2]$ alone [22].

The stimulation of biomass and yield of soybean by elevated $[CO_2]$ involved several components. Growth at elevated $[CO_2]$ stimulated node production by 17% and maximum leaf area index by 15% [22–24]. The integral daily CO_2 uptake increased 25% and light-saturated CO_2 uptake increased 20% on average under elevated $[CO_2]$ compared with the ambient [25,26]. Elevated $[CO_2]$ not only stimulated photosynthesis, but also stimulated respiration by 37% [27] and decreased stomatal conductance by 10% [26]. Lower stomata conductance resulted in higher water use efficiency and in lower seasonal water use even though the elevated $[CO_2]$ canopy was nearly 15% larger than the ambient canopy [28].

Soybean leaves grown at elevated $[CO_2]$ had significantly increased content of non-structural carbohydrate and other metabolites at mid-day (Table 1). Elevated $[CO_2]$ increased leaf starch by 70% and sugars (sucrose fructose and glucose) by 50–100%. Elevated $[CO_2]$ also increased leaf pinitol, malate, betaine and proline (data not shown). There are some advantages for plants to use pinitol as the major osmolyte rather than sucrose because pinitol is less metabolically reactive, thus preventing it from potential down-regulation of photosynthesis through sugar sensing [29]. The increased osmolytes are consistent with the leaf osmotic potential, leaf water potential, relative water content and leaf mass area under elevated $[CO_2]$ compared with the ambient control (J. Sun, unpublished).

The SoyFACE results show several interesting findings that are useful for future soybean crop improvement. First, the results indicate that the seed yield of the current soybean cultivars is limited by photosynthesis (“source”) under current ambient CO_2 levels. Elevated $[CO_2]$ significantly enhanced photosynthesis and therefore enhanced biomass and seed yield (“feed-forward” regulation of sink by photosynthesis). The seed yield positively correlated with biomass ($R = 0.9144$). Enhanced light interception (ϵ_i) due to an increase in leaf area index and enhanced conversion of intercepted radiation energy into primary production (ϵ_c) due to increase in Rubisco-limited photosynthesis contribute $\sim 20\%$ and $\sim 80\%$, respectively, to the increase in above-ground biomass and seed yield under elevated $[CO_2]$ in SoyFACE [22]. Rubisco is limited by current CO_2 levels and elevated $[CO_2]$ stimulates Rubisco-limited photosynthesis under field conditions. The increased integral daily CO_2 uptake (25%) and light-saturated CO_2 uptake (20%) are consistent with the increase in biomass under elevated $[CO_2]$ (Table 1).

Second, the results suggest that the seed yield of the current soybean cultivars will be more limited by photosynthate-utilization “sink” in the future due to rising CO_2 levels. Regulation of photosynthesis by sink has been demonstrated by a sink-limited determinate isoline and a non-nodulating isoline of a soybean cultivar [30]. In elevated $[CO_2]$, the determinate isoline and the non-nodulating isoline showed more down-regulation of photosynthesis and the maximum rate of Rubisco carboxylation (V_{cmax}), and higher total non-structural carbohydrate (TNC) content compared with the indeterminate and nodulating control. The increase in seed yield was lower than theoretical estimate and lower than the increase in the biomass under elevated $[CO_2]$ [4,13,16], indicating the limitation of carbon partitioning into sink. The significant rise in leaf glucose and fructose is another

indication of the limitation of photosynthate utilization. The maximum rate of Rubisco carboxylation decreased 6–13%, again indicating the limitation of photosynthate-utilizing sinks. Limited photosynthate-utilizing sink would impose feedback inhibition on photosynthesis, possibly through sugar sensing [29]. In addition, elevated [CO₂] stimulation of biomass is much lower than that of nighttime respiration (37%, CO₂ efflux 1.8 μmol m⁻² s⁻¹ vs. 1.3 μmol m⁻² s⁻¹) [27], indicating a substantial portion of the increased respiration is used for maintenance respiration rather than growth respiration since the accumulated biomass is highly correlated with the accumulated nighttime respiration [31]. To keep up with the increased photosynthesis, the sink has to be increased accordingly (“feedback” regulation of photosynthesis by sink). For seed crops, the number of seeds per unit area is the most important and is the final sink for carbon partitioning and photosynthate utilization.

Third, 550 ppm [CO₂] largely offsets the negative effect of a 25% increase above ambient ozone on biomass and seed yield. Both biomass and seed yield were reduced by 11% under elevated ozone. The biomass and seed yield under the combination of elevated [CO₂] plus ozone were similar to that under elevated [CO₂] alone. Elevated [CO₂] decreased integral daily stomatal conductance by 10% [20], and thus reduced the ozone flux into leaves through stomata and alleviated some of the negative ozone effects. The negative ozone effects on leaf area index, leaf lifespan and conversion of intercepted radiation energy into biomass (ϵ_c), tend to be offset by elevated [CO₂] [22]. However, it is likely that the impact of higher levels of ozone on soybean would not be fully offset by 550 ppm [CO₂].

2.2. Why do the responses of C₃ crops to elevated [CO₂] vary?

The responses of C₃ crop yield to elevated [CO₂] not only varied between FACE studies and enclosure studies such as open top

chambers and growth chambers [13–16], but also varied among FACE studies. Analysis of different FACE studies may help to explain the variations.

The responses of crop yield to elevated [CO₂] in various FACE studies on C₃ crops are summarized in Table 2. The measured responses of crop yield to elevated [CO₂] varied among years, crops, cultivars, nitrogen levels and soil moisture conditions. Seed yield in C₃ crops increased 18% on average, ranging from 3 to 35% under elevated [CO₂] (Table 2). One important factor that should be noted is the differences among varieties. The hybrid cultivars have much higher responses to elevated [CO₂] than the conventional open pollinated varieties. The rice FACE studies showed that the seed yield increased 13% on average for a few conventional open pollinated japonica cultivars and 32% on average for two hybrid cultivars under elevated [CO₂] across 3 years, indicating a significant difference in crop yield response to elevated [CO₂] between the conventional open pollinated varieties and the hybrid varieties [32–34]. The various cultivars of the conventional open pollinated varieties showed different responses to elevated [CO₂] in FACE. The elevated [CO₂] stimulation of yield varied from 3 to 18% among four conventional open pollinated rice cultivars [35]. Winter wheat Ningmai 9 appeared to have a higher seed yield in response to elevated [CO₂] (24%) than other C₃ conventional open pollinated varieties including a spring wheat cultivar (13%). The greater CO₂ responsiveness of Ningmai 9 is likely due to the longer growing season for the winter wheat. In addition, it appeared that the rice indica ecotype has a higher yield response to elevated CO₂ than the rice japonica ecotype, ~24% versus 13%, respectively (L. Yang and Y. Wang, Yangzhou University, unpublished). Different cultivars used for various studies may partially explain the difference in stimulation of seed yield by elevated [CO₂].

Another important factor is the effect of nitrogen nutrition. CO₂ stimulation of crop yield positively correlates with nitrogen levels,

Table 2
Percent (%) increase in crop yield with elevation of CO₂ in various FACE studies.

FACE	Crop	Cultivar	CO ₂	N	%	AVG	No. years	Ref	
Champaign, IL, USA (40°02'N, 88°14'W)	Soybean	Pioneer 93B15	550	0	13	13	5 (2001–2006)	Table 1 this review	
		Shanyou 63	570	125	33	32	3 (2004–2006)	[33]	
Yangzhou, Jiangsu, China (32°36'N, 119°42'E)	Rice Hybrid indica			250	35				
		Liangyoupei 9	570	125	28		3 (2004–2006)	[34]	
				250	32				
Shizukuishi, Iwate, Japan (39°38'N, 140°57'E)	Rice Japonica	Akitakomachi	560	40	7	13	3 (1998–2000)	[20]	
				80	14				
				120	15				
		Akitakomachi	570	80	6		2 (2003–2004)	[35]	
		Kakehashi			3				
Wuxi, Jiangsu, China (31°37'N, 120°28'E)	Wuxiangging 14		557	150	11		3 (2001–2003)	[32]	
				250	12				
				350	18				
	Winter wheat	Ningmai 9		570	108	15	24	2 (2001–2003)	[40]
					180	21			
					250	35			
Maricopa, AZ, USA (33°4'N, 111°59'W)	Spring Wheat	Yecora Rojo	550	70	9	13	2 (1996–1997)	[37]	
				350	16				
Braunschweig, Germany (52°18'N, 10°26'E)	Winter Barley	Yecora Rojo	550	277	10 ^a		2 (1993–1994)	[37]	
					23 ^b				
Stuttgart, Germany (48°43'N, 9°11'E)	Rapeseed	Campino	500	130	17	17	1 (2007)	[38]	
		Primura	560	252	20 ^c	20	1 (1995)	[39]	

CO₂, ppm; N, nitrogen fertilizer (kg/ha); %, percent increase in crop yield; AVG, average.

^a Wet soil—unlimited water.

^b Dry soil—limited water.

^c Tuber yield.

and crop yield is higher under sufficient nitrogen than limited nitrogen for many crops such as wheat and rice (Table 2). There are positive interactions between CO₂ and nitrogen levels in rice and wheat [20,40]. The stimulation of crop yield in rice and wheat at elevated [CO₂] was at least 50% higher under sufficient nitrogen than limited nitrogen. Elevated [CO₂] would generally require more nitrogen availability for optimum crop production. The hybrid rice cultivars appeared to respond much less to nitrogen fertilizer than conventional open pollinated varieties for CO₂ stimulation of seed yield, perhaps indicating better nitrogen use efficiency and better adaptation in hybrid rice plants compared to the conventional open pollinated varieties.

In addition, soil moisture also affects CO₂ response. Stimulation of crop yield at elevated [CO₂] was twice as large under water stress (23%) compared to well-watered conditions (10%) in wheat FACE [37] (Table 2), indicating a positive interaction between levels of CO₂ and levels of water stress on crop yield. Elevated [CO₂] decreases stomatal conductance thus decreasing water loss under drought conditions [26]. The increased osmolytes such as pinitol, sucrose, hexose, glycine betaine and proline under elevated [CO₂] may also explain the increased drought tolerance for crops by osmotic adjustments.

Seed yield was also strongly influenced by other environmental conditions and varied from year to year and from study to study. A yield test generally requires relatively large areas of field, many years and multiple locations to get an accurate estimate of the effects of varieties. Due to resource limitations, FACE studies are currently limited to a few locations in a few countries with limited cultivars. Different varieties as well as treatment variations may influence the estimates of the response of crop yield to CO₂. Using the average response helps to maximize the statistical power for the estimate of the elevated CO₂ effects. With continual experiments occurring throughout several years at multiple locations and utilizing multiple cultivars, cultivar effects can be separated from the experiment errors; thus, with the joint efforts of plant breeding, better projections can be made using the best varieties of crops.

Based on Farquhar's biochemical model, which assumes that plant leaf photosynthesis is generally limited by Rubisco under ambient [CO₂] and by RuBP-regeneration under high [CO₂] when light is not limiting [5], the increase in atmospheric [CO₂] from 372 ppm to 550 ppm would increase Rubisco-limited photosynthesis by 36% at 25 °C and by nearly 50% at 30 °C, or RuBP-limited photosynthesis by 18–22% between 25 and 30 °C [4]. However, light may often limit photosynthesis in a crop canopy in the field. Detailed analysis of canopy photosynthesis would be useful to accurately assess the response. The average responses of the crop yields to the projected elevated [CO₂] are lower than the potential of Rubisco-limited photosynthesis, indicating some other limitations. Light or RuBP limitation for a crop canopy, sink limitation and excess respiration loss are the likely causes for the difference. This gap is one of the opportunities for further improvement and is discussed in the following section.

3. Can photosynthetic radiation use efficiency be improved?

For many crops, improved harvest index played a large role in improved crop yields. However, harvest index in the world's most important crops may already be close to the maximum potential and further increases in crop yield will have to involve increase in crop biomass [1]. Biomass is directly proportional to the integral of net photosynthesis, implying that improvement in net photosynthesis would contribute to greater crop biomass and crop yield. Although a correlation between crop yield and leaf photosynthesis is frequently absent [41], this is to be expected as biomass and seed yield should correlate with integrated canopy photosynthesis

rather than single leaf light-saturated photosynthesis. Integrated canopy photosynthesis can be difficult to measure as it is strongly influenced by environmental conditions and varies with diurnal and developmental time. The leaves in a crop population experience various light conditions over time such that photosynthesis alternates between Rubisco-limited and light-limited conditions. Elevated CO₂ FACE experiments have unequivocally demonstrated that enhanced photosynthesis does result in biomass increase which in turn leads to enhanced seed yield with unchanged or even decreased harvest index. Biomass, or primary production, is the function of available incident solar radiation across the season, the efficiency of light interception by the crop and the efficiency of conversion of absorbed energy into biomass. Improvement of photosynthetic radiation use efficiency has been an interest for crop improvement [17,42–49]. C₄ grasses such as *Miscanthus* have among the highest annual primary production, producing 50% more biomass than C₄ corn because *Miscanthus* has substantially longer canopy duration and a higher leaf area index (LAI) [50]. Thus *Miscanthus* plants out perform corn plants due to greater light interception even though the photosynthetic solar energy conversion efficiency of these two C₄ grasses is similar (F.G. Dohleman & S.P. Long, personal communications). Thus improvement of primary production can potentially come from numerous sources such as the reduction of losses from photorespiration and respiration, the manipulation of plant hormone responses for better ideotypes, the extension of the duration of photosynthesis, the enhancement of nutrient uptake and use efficiency and the amplification of sink strength and carbon partitioning into sink or improvement of photosynthetic solar energy conversion efficiency (Fig. 1). In some cases improvements may be possible by manipulating one or a few genes, in other cases by substantially redesigning photosynthesis.

3.1. New opportunities for enhancing leaf photosynthesis

While rising [CO₂] will stimulate C₃ photosynthesis, other elements of pending climate change may be beneficial to photosynthetic productivity in some circumstances and detri-

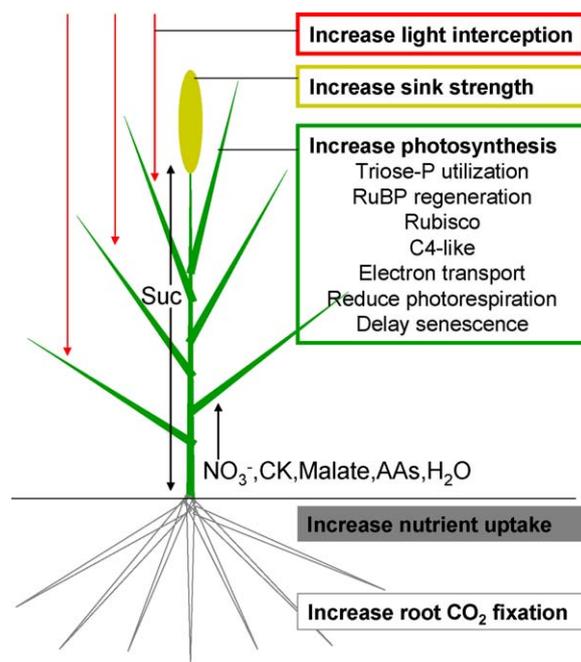


Fig. 1. Plant source-sink relation and the areas for improvement in photosynthetic radiation use efficiency and crop yield. Suc, sucrose; CK, cytokinin; AAs, amino acids.

metabolites and maximal activities of enzymes were obtained from the published literature. In the “evolutionary” algorithm, the total amount of protein-nitrogen is assumed to be fixed, and the percentage of each enzyme is allowed to vary to select the higher light-saturated photosynthesis to seed for the next generation. After 1500 generations, photosynthesis increases by 60%, indicating the possibility for improvement in photosynthetic capacity. The results indicate that under current atmospheric $[\text{CO}_2]$ more investment is needed in sedoheptulose-1,7-bisphosphatase, fructose-1,6-bisphosphatase (FBPase), Rubisco and ADP-glucose pyrophosphorylase (AGPase) at the expense of the photorespiratory enzymes.

Leaf photosynthetic capacity is seriously impaired in *Arabidopsis* starch mutants with low ADP-glucose pyrophosphorylase activity, a key enzyme for starch synthesis [57], whereas photosynthesis is enhanced in transgenic wheat plants over-expressing deregulated ADP-glucose pyrophosphorylase that is less inhibited by phosphate (Pi) and stimulated by low 3-PGA levels under high light [58]. Sucrose phosphate synthase is a key enzyme for sucrose synthesis and is regulated by phosphorylation and metabolites with Pi as inhibitor and Glc-6-p as stimulator. The transgenic potato plants over-expressing maize sucrose phosphate synthase increased tuber sucrose and starch contents and tuber yield by at least 20% in the field [59]. Transgenic tomato plants over-expressing maize sucrose phosphate synthase also displayed higher tomato yield, which appeared associated with enhancing sucrose phosphate synthase activity to optimum levels [60]. Interestingly, the transgenic sugarcane plants over-expressing a bacterial sucrose isomerase (SI) gene that converts sucrose into isomaltulose, which is not metabolized by plants but is digested by human with health benefits over sucrose, had doubled the stored sugar content due to accumulation of isomaltulose without any decrease in stored sucrose concentration and showed enhanced photosynthesis [61].

Some non-regulated enzymes of the Calvin cycle catalyzing reversible reactions, such as aldolase and transketolase, exert significant control over carbon flux and RuBP regeneration [55]. Transgenic tobacco plants over-expressing sedoheptulose-1,7-bisphosphatase, or fructose-1,6-bisphosphatase or dual function fructose-1,6-bisphosphatase/sedoheptulose-1,7-bisphosphatase had increased leaf photosynthesis by 6–27% and biomass by 15–50% [62–64]. It appears that sedoheptulose-1,7-bisphosphatase is more limiting than fructose-1,6-bisphosphatase and there is an additive effect for sedoheptulose-1,7-bisphosphatase and fructose-1,6-bisphosphatase on photosynthesis in tobacco plants. It remains to be investigated if sedoheptulose-1,7-bisphosphatase and fructose-1,6-bisphosphatase are limiting photosynthesis in crop plants under agricultural field conditions.

3.1.2. Engineering C_3 crops with C_4 -like photosynthesis

C_4 plants have higher photosynthesis, water use efficiency and crop productivity than C_3 plants under current $[\text{CO}_2]$ because C_4 plants have special $[\text{CO}_2]$ concentrating mechanism through using phosphoenolpyruvate carboxylase as the primary CO_2 fixing enzyme, which is not oxygen sensitive, and a bundle sheath cell C_4 acid decarboxylase to concentrate CO_2 around Rubisco. While over-expressing C_4 genes in C_3 crops is successful [2,65], the difficulty remains in the generation of the Kranz anatomy within C_3 , thereby allowing for effective CO_2 concentrating around Rubisco. Some species have C_4 photosynthesis in single cells such as the aquatic plant *Hydrilla* and the terrestrial *Chenopodiaceae*, indicating a possible alternative to engineering C_3 plants to perform Kranz-type C_4 photosynthesis without having to engineer a dual-cell Kranz system although the photosynthetic rates in organisms are quite low [66,67]. Since C_4 photosynthesis generally requires 20% (NADP malic enzyme and NAD malic enzyme types)

or 10% (phosphoenolpyruvate carboxykinase type) more ATP energy for CO_2 concentrating than C_3 photosynthesis, the question is whether C_4 photosynthesis in a single C_3 cell system is cost effective. The theoretical analysis by van Caemmerer [68] indicates that engineering C_4 photosynthesis in a single C_3 cell system is inefficient but may have some advantages in ameliorating internal CO_2 diffusion limitation under high light and especially when stomata are closed. The rising $[\text{CO}_2]$ at 2050 (550 ppm) would already theoretically benefit C_3 plants with 36% enhancement in photosynthesis at 25 °C without additional energy cost [4] and would increase hybrid rice yield by 32% as shown in FACE studies (Table 2). Further increase in $[\text{CO}_2]$ in C_3 chloroplasts by the C_4 CO_2 -concentrating mechanism would hardly enhance additional photosynthesis if counting 10–20% more energy needed for CO_2 concentrating although C_4 plants would maintain a water use efficiency advantage over C_3 . However, Hibberd and Quick [69] found that C_4 photosynthesis does exist to some extent in some C_3 plants especially in the stems and leaf petioles. In Hibberd and Quick’s model the CO_2 elevated around the roots in the soil is fixed through phosphoenolpyruvate carboxylase to form malate which is transported through vascular tissues to the stems and leaf petioles where decarboxylation supplies CO_2 for Rubisco. CO_2 is concentrated there since bundle sheath cells have a high resistance to CO_2 diffusion in the stems and leaf petioles. Stems, leaf petioles and other non-foliar tissues substantially contribute to the total carbon fixation and may account for up to 40% of the carbon fixed in the seeds or fruits [70]. It may be possible to substantially improve photosynthesis by engineering non-foliar tissues with more efficient photosynthesis with the enhancement of root CO_2 fixation by phosphoenolpyruvate carboxylase.

3.1.3. Minimizing photorespiratory loss

Photorespiratory loss is significant in C_3 plants (Fig. 2). For plant photorespiratory cycle, the recycling of two glycolate molecules costs the equivalent of about 11 ATP, including one CO_2 loss that costs about 9 ATP (assume two NADPH and three ATP are required for one CO_2 fixation), one ATP for NH_3 recycle, and one ATP for converting glycerate into 3-PGA. Britto et al. (2004) proposed to over-express phosphoenolpyruvate carboxylase, pyruvate orthophosphate dikinase and glutamine synthetase together in the C_3 leaf to create a metabolic cycle to reduce CO_2 loss and NH_4^+ loss from photorespiration [71]. It is unclear whether this approach is cost effective since extra energy would be needed to recycle CO_2 using phosphoenolpyruvate carboxylase, and CO_2 may be only slightly concentrated due to low resistance for CO_2 diffusion without the “Kranz” structure. Over-expressing glutamine synthetase does decrease NH_3 loss from photorespiration and increases N use efficiency [72]. It appears more efficient to manipulate plant photorespiratory cycle by engineering the *E. coli* glycolate catabolic pathway into C_3 plants [73], in which glycolate is converted into glycerate through glycolate dehydrogenase complex, glyoxylate carboligase and tartronic semialdehyde reductase in the chloroplast. Compared with the plant photorespiratory cycle, the bacterial pathway has 36% less energy cost for converting two glycolate molecules into 3-PGA, which produces one extra NADH and saves one ATP that is used for NH_3 recycling in photorespiratory cycle. In addition, CO_2 released in the chloroplast by *E. coli* glyoxylate carboligase effectively concentrates CO_2 at Rubisco, further reducing the photorespiratory loss. Transgenic *Arabidopsis* plants with enhanced bacterial glycolate catabolic activity had increased photosynthesis, ~70% more shoot biomass and twice the root biomass under ambient CO_2 conditions [73], indicating that a substantial amount of glycolate bypassed the plant photorespiratory cycle. Knocking out the chloroplast glycolate transporter might further improve photosynthesis by forcing more of the Rubisco oxygenase glycolate flux through the redesigned biosyn-

thetic pathway. The bacterial glycolate pathway would more likely work in other C_3 species since photorespiration is conserved in all of the C_3 plants. This pathway provides a new opportunity for substantially reducing photorespiratory loss and enhancing net photosynthesis. Though the rising $[CO_2]$ would partially offset the advantage of the bypass pathway, the bypass pathway remains advantageous especially when stomata are closed and CO_2/O_2 ratio is low.

3.1.4. Improving the efficiency of light reaction

The rate of electron transport may co-limit photosynthesis [55]. The rising $[CO_2]$ would affect the balance between the light reaction and the dark reaction of photosynthesis. Hybrid rice plants have a larger response to elevated $[CO_2]$ than conventional open pollinated varieties in seed yield (Table 2). Heterosis studies showed many genes involved in light reactions such as chlorophyll *a/b* binding protein, cytochrome *b/f* complex and some components of photosystems were up-regulated in the super hybrid rice Liangyoupeijiu (LYP9) compared with its conventional open pollinated parents [74]. Engineering a more efficient light reaction may have potential for improving photosynthetic radiation use efficiency especially under elevated $[CO_2]$. The solar radiation use efficiency in green alga *Chlamydomonas reinhardtii* was improved ~3-fold using truncated light-harvesting chlorophyll antenna (*tla1*) mutation [75]. The *tla* alga mutant has a smaller light-harvesting chlorophyll antenna size and thus works to alleviate the excess light absorption that leads to the saturation of photosynthesis and the need to dissipate excess excitation energy through photoprotective mechanisms and at the same time permits more light penetration into deep layers of alga population. The *tla* gene is nuclear-coded, which makes it technically applicable to plants by modification of plant genome by down-regulation of *tla*. More studies are needed to validate the hypothesis as to whether down-regulation of *tla* can be applied to plants' light-colored leaves, would allow more light to penetrate into the deep layers within the leaf and allow for more sun-lit leaf area, accommodate more leaf area per unit area land and increase radiation use efficiency for a crop canopy. However, lower absorbing leaves would be lower canopy photosynthesis early in the season when LAI values are low. Development of a canopy photosynthesis model in which the impact of changes in chlorophyll concentration on season long carbon gain could be evaluated would be important in determining the overall potential in chlorophyll manipulation.

3.2. Manipulation of plant hormone responses for better ideotypes

For many monocot crops the erect leaf type is one of the most important ideotype traits for light interception and canopy photosynthesis. Canopy photosynthesis is well correlated with sun-lit leaf area index rather than the single leaf light-saturated photosynthesis. The leaf orientations of cereal crops are critical for their canopy light interception and photosynthesis [48,76]. Two extreme leaf orientations, horizontal and vertical, are compared for their sun-lit leaf area index and canopy photosynthesis (Fig. 3). Compared to the canopy with horizontal leaves, the canopy with vertical leaves has higher sun-lit leaf area index and higher gross and net photosynthesis. The canopy with vertical leaves has higher optimum leaf area index for high net photosynthesis than the canopy with horizontal leaves. Both the leaf orientation and plant height strongly influence the sun-lit leaf area index. Moderately high sun-lit leaf area index and moderate plant height would be desirable for high light interception. For example, *Miscanthus* plants, have peak leaf area index at about 10 and are 3 m high or greater. However, higher leaf area index and taller plants would increase the risk of lodging. Lodging would significantly decrease sun-lit leaf area index, light interception and crop yield. For cereal

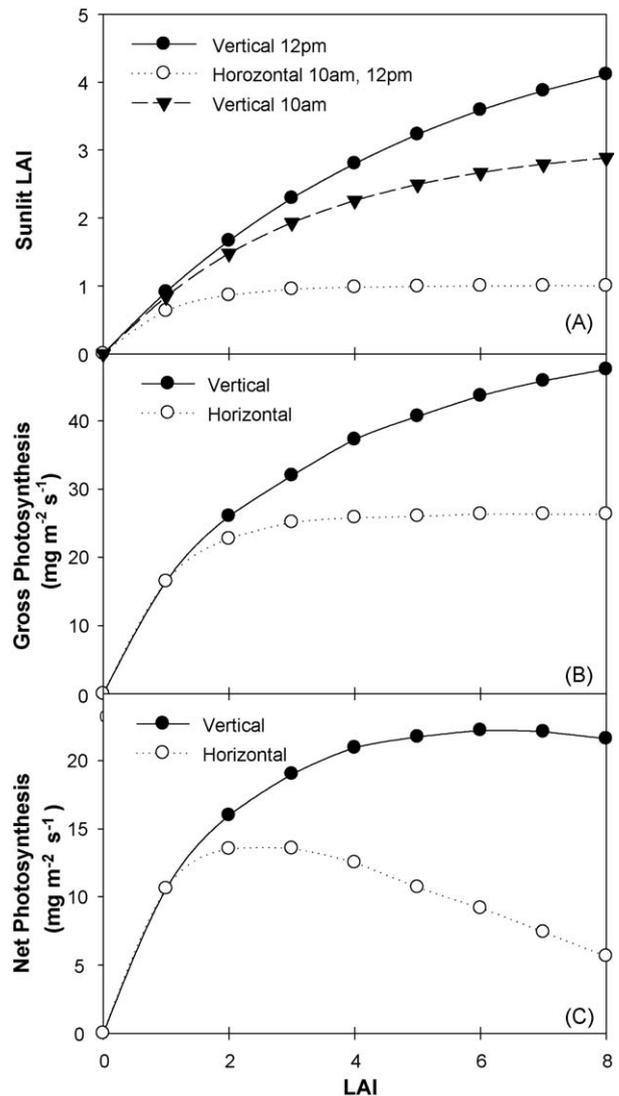


Fig. 3. Simulation of the effects of leaf orientation (vertical or horizontal) and leaf area index (LAI) on sun-lit leaf area index, canopy gross photosynthesis and net photosynthesis on June 22 at 40°N. Sun-lit leaf area, gross and net photosynthesis was calculated according to Campbell (1977) [77].

crops, it would be desirable to have shorter basal internodes and longer top internodes for lodging resistance and bearing more seeds. The pulvini of many dicots move leaves, which track the sun and maximize light interception of the upper leaves, which is undesirable in a crop as it tends to exacerbate saturation losses.

The modulation of plant hormones is a potential target for genetic improvement of plant stature, leaf orientation, and crop yield. The “green revolution” genes were primarily the suppression of gibberellic acid (GA) response pathway, either reduced in GA responses or defective in GA biosynthesis, which led to new varieties with erect leaves, short statures, lodging resistance, high seed yield and high harvest index [78,79]. The reduced GA response in wheat is due to mutation of one of the reduced height loci (*rht-1*), which are orthologues of *Arabidopsis* transcription factor GA insensitive (*delta GAI*) and associated with GA signaling pathway. The transgenic rice plants containing the *delta GAI* gene possess morphological changes such as short statures [78]. The semidwarf 1 (*sd1*) in rice is due to mutation of *GA20ox*, a key enzyme for GA synthesis [79].

Brassinosteroids (BR), the growth-promoting steroidal hormones, are also possible alternative targets for modification of leaf

erectness and potentially other processes such as photomorphogenesis, cell elongation and stress tolerance in plants [80]. A high-yielding semidwarf barley cultivar was associated with the missense mutation of *uzu* gene, an ortholog of *Arabidopsis* brassinosteroid insensitive1 (BRI1) [81]. Transgenic rice plants over-expressing a brassinosteroid-deficient dwarf4 have erect leaf phenotype and higher seed yield in dense planting [82,83]. Transgenic rice plants over-expressing sterol C-22 hydroxylases which up-regulate the levels of brassinosteroid (BR) hormone intermediates downstream 6-deoxo-cathasterone using a promoter that is specific only to the stems, leaves and roots showed higher CO₂ assimilation, more tillers, increased biomass and seed yield by 14–44% [84].

Phytochromes (Phy), the red (R) and far-red (FR) light-absorbing photo-receptors, play important roles in plant photomorphogenesis and shade avoidance as well as germination, elongation growth, apical dominance and flowering time mainly through cross-talk with plant hormones such as GA and ABA [85]. Potato plants over-expressing *Arabidopsis* phytochrome B gene were reported to have short stems, high CO₂ uptake, more branches, more tubers and higher tuber yield [86,87]. Transgenic rice plants over-expressing *Arabidopsis* phytochrome A using *rbcS* promoter were shorter with decreased internodes length, more panicles and a 6–21% increase in seed yield [88]. The active phytochromes interact with phytochrome-interacting factors (PIFs) or phytochrome-interacting factor-like (PILs) for signaling transduction [85]. Phytochrome-interacting factors and phytochrome-interacting factor-like, which are transcription factors, are also likely targets for crop improvement and for better photosynthesis through improved plant architecture.

Different from modern rice cultivars, the wild rice plants are prostrate and less productive. The prostrate stature can be manipulated with the genes of prostrate growth 1 (*prog1*), lazy prostrate phenotype (*lazy1*) and tiller angle control 1 (*tac1*) [89–91]. Mutation of prostrate growth 1 or tiller angle control 1 resulted in stem erectness phenotype and increased seed yield in rice [89,90]. Expression of tiller angle 1 resulted in erectness phenotype [91]. These genes are likely related to polar auxin transport and regulate the tiller erectness ideotypes [92].

3.3. Extending the duration of canopy photosynthesis

The duration of canopy photosynthesis can be improved by early field coverage, delayed senescence and improved nutrition use efficiency. Delaying senescence is highly sought out by breeders and is an important agricultural practice for enhancing crop yield. It has been shown that the slower decline in leaf photosynthesis at the late growth stage is associated with the higher biomass accumulation in hybrids compared with the inbred corn [93].

The use of nutrients has been an important agricultural practice for high-yielding cultivation of crops. Nitrogen is quantitatively the most essential nutrient for plant growth and development. Nitrogen is used to increase leaf area index and sink size at early growth stages, delays senescence at later growth stages and adjusts source-sink balance. NO₃⁻, a signal molecule, stimulates cytokinin synthesis which promotes cell division and expansion and delays leaf senescence [94]. There are strong interactions between C and N metabolism [95]. The elevated [CO₂] stimulation of biomass was low under limited N, but increased significantly when N is sufficient in *Arabidopsis* [96], in rice [20] and in wheat [40], indicating sufficient N input is needed for plants grown under elevated [CO₂]. Legumes appear to have the potential to maximize the benefit of elevated [CO₂] by matching stimulated photosynthesis with increased N₂ fixation [97]. Maintaining a desirable C/N balance is critical for photosynthesis and carbon partitioning and

crop yield. When N is applied, sugar flux will be directed toward more N assimilation, synthesis of chlorophyll and protein, and less starch accumulation because N induces nitrate reductase, genes involved in ammonia assimilation and enzymes of carbon metabolism such as phosphoenolpyruvate carboxylase, isocitrate dehydrogenase, mitochondrial citrate synthase, etc., and down-regulates ADP-glucose pyrophosphorylase [98].

Nutrient absorption is an excellent target for crop improvement via better photosynthesis. Transgenic canola and rice plants over-expressing a barley alanine aminotransferase (AlaAT) cDNA driven by a tissue-specific promoter caused a significantly increased N uptake influx and the plant biomass and 30–40% increase in seed yield in comparison with control plants [99,100]. The ectopic expression of nitrate transporters (NRT1/Chl1, NRT2) increases nitrate influx [72]. Enhancement of crop production requires a significant investment in many other essential nutrients including iron (Fe), phosphate (P), potassium (K), magnesium (Mg) and others. For example, transgenic lettuce plants over-expressing soybean ferritin, an iron-binding protein, had higher iron levels in the leaves, higher photosynthesis and grew faster and larger than the untransformed control lettuce plants [101]. Transgenic sweet potato plants over-expressing an *E. coli* *appA* gene (a bifunctional enzyme exhibiting both phytase and acid phosphatase activities) enhanced phosphate acquisition from soil where phytate, the organic phosphate, is usually high and enhanced the levels of leaf pigments and tuber yield [102]. Recent discoveries of transporters for nitrate, phosphate and potassium uptake [103] and others offer new opportunities for genetic modifications for crop improvement for better nutrient use efficiency and photosynthesis.

Extending the growth season may have a profound effect on crop production. Information concerning the manipulation of current growth and productivity pattern of crop plants (typically 3–6-month growth season) to one that is continuous is currently lacking. However, this change may become possible when the genes that control this trait are discovered. A wide range in maturity exists among varieties. Elevated [CO₂] and rising temperature as projected in the future would make plants such as wheat and rice mature earlier [19,40], thus late maturity varieties can be applied in the future to the area in which the late varieties are unable to grow today to extend the duration of photosynthesis. Alternately, the current varieties can be expanded in the future to the “colder” area where the current varieties are unable to grow today due to lower temperature.

3.4. Increasing carbon partitioning to sinks to alleviate feedback inhibition of photosynthesis

Crop productivity of current cultivars may tend to become sink-limited in future high [CO₂] atmospheres. Less stimulation of seed yield than biomass, Rubisco down-regulation, high glucose accumulation and higher respiration than necessary for plant growth under elevated [CO₂] (Table 1) may indicate a substantial sink limitation with rising [CO₂]. Maximum photosynthesis would be maintained only when sink capacity is not limiting. Therefore, increase in carbon partitioning into sink should maintain high photosynthesis for a longer period, reduce excessive respiration loss, and further enhance net photosynthesis and productivity.

Heterosis has been and will remain one of the most effective approaches for improvement of photosynthesis and crop yield. Heterosis was once thought applicable only for open-pollinated plants such as corn and sorghum, but has proven applicable also for self-pollinated plants. Hybrid rice is the best known example, which generally has a yield advantage of 20% or more over conventional open pollinated varieties and now accounts more than 50% of the total rice planting area in China [104]. Elevated [CO₂] stimulation of the seed yield is much higher in hybrid rice

(32%) than the conventional open pollinated varieties (13%) [33,34] and many other C₃ crops (Table 2). Hybrid rice plants have larger sinks with larger panicles allowing more effective carbon partitioning, which effectively increases the sink size without adding too many tillers and leaves under elevated [CO₂]. Elevated [CO₂] stimulated each of the yield components in the two hybrid rice cultivars, indicating a better balanced sink-source compared to the conventional open pollinated varieties.

Manipulation of photosynthate translocation is another approach to enhancing sink strength and crop yield. Well developed vascular bundles have positive effects on photosynthate translocation. There is a positive correlation between the area of the cross section of the vascular bundles in the stem (product of the number of vascular bundles and the area of the cross section of vascular bundles) and the number of spikelets of the panicle in rice [105]. Many sugar transporters have been discovered [106,107] and can be used to manipulate sink strength. For example, transgenic potato plants over-expressing both glucose-6-phosphate/phosphate translocator (GPT) and adenylate translocator (NTT1) under the control of a patatin promoter increased tuber starch content by up to 28% and tuber yield by up to 19%, compared with control plants [108]. Single over-expression of either one of the two genes had no effect on tuber starch content or tuber yield [108], suggesting that starch synthesis within amyloplasts is co-limited by the supply of carbon source and the import of energy.

Many genes enhance sink strength. Target of rapamycin (TOR), a kinase that promotes cell growth in response to favorable conditions in yeast, animal and plants, was positively linked with *Arabidopsis* seed yield as well as plant growth [109]. Reduced expression of cytokinin oxidase 2, a gene for an enzyme that degrades cytokinin, causes cytokinin accumulation in inflorescence meristems and increases the number of seeds and grain yield in rice [110]. Manipulation of numerous other hormone responses has also led to an increase in the number of seeds and seed yield in addition to morphological change and biomass change (see Section 3.2).

Over-expressing sucrose phosphate synthase and ADP-glucose pyrophosphorylase would potentially increase sink strength and crop yield in addition to photosynthetic capacity (see Section 3.1). Over-expression of deregulated ADP-glucose pyrophosphorylase driven by maize endosperm-specific sh2 (shrunken 2) promoter substantially increased ADP-glucose pyrophosphorylase activity, biomass and seed mass in growth chambers in rice [111] and in wheat [112]. The field trials for the transgenic wheat plants showed that significantly higher yields were more likely to occur in space-planted, irrigated environments than densely planted, non-irrigated environments [113]. Cassava transgenic plants over-expressing a modified bacterial glgc gene encoding an ADP-glucose pyrophosphorylase under the control of a patatin promoter had 52–166% increased tuber yield and 27–56% increased shoot biomass [114]. The large increase in tuber yield and biomass in the transgenic cassava plants is probably due to the combination of the enhanced sink strength through elevated ADP-glucose pyrophosphorylase with the novel characteristics such as high photosynthesis, high sucrose content, drought tolerance and less limited root growth [115]. Genetically modified cassava provides a new opportunity for crop production in the future. Under elevated [CO₂] ADP-glucose pyrophosphorylase would likely play even more important roles in photosynthesis and crop yield.

4. Concluding remarks

FACE studies show that the crop yields at [CO₂] projected for 2050 are enhanced by an average 18% with the current cultivars tested and ~30% with the most responsive hybrid rice cultivars. In

order to achieve 50% increase in crop yield by the middle of 21st century, photosynthetic radiation use efficiency need to be substantially improved. Both the source activity and the sink strength will need to be coordinately enhanced to maximize net photosynthesis and yield. Crop improvement will continue by plant breeding. The advances in genomic sequencing, functional genomic studies, new biotechnology methods and systems biology allow one to be optimistic that better photosynthetic radiation use efficiency can be achieved. Indeed, many demonstrations of beneficial manipulations and proofs of concept for improving photosynthetic radiation use efficiency have already been made as reviewed above. The scientific community remains enthusiastic about the power of biotechnology to create genetically modified (GM) plants and consequently fight world hunger; yet the public still harbors concerns of health risks and environmental hazards that may be caused by GM plants. Just as those plants created by conventional breeding and mutation, the safety of GM plants needs to be studied on a case-by-case basis to validate their utility, safety, and appropriateness [116,117].

More FACE studies for interactions of CO₂, O₃, drought, temperature and nitrogen levels on more crops in more geographical locations are needed to accurately understand the impacts of global warming, reduced soil moisture, changes in nitrogen use efficiency and other factors of impending global change. Soil moisture can be controlled in FACE to study the effects of drought stress on crop yield [37]. Awnings have been developed in SoyFACE to reduce soil moisture, which can be deployed during the rain and retracted if it's not raining. Temperature can be increased in FACE as well. Artificial infra-red lights have been installed in SoyFACE which can increase air temperature above crop canopy by 2–5 °C compared with the ambient. Humidity control in FACE is a challenge but is possible. For example, "dry air" from a compressed source can be released constantly above crop canopy to reduced air humidity. More studies utilizing a variety of the cultivars with different source/sink ratios and responses to elevated [CO₂] are needed. Plant density and the distribution of nitrogen fertilizer across the entire growing duration may also affect crop responses to elevated [CO₂]. Other global change interactions including plants-insects, plants-pathogens, plants-weeds and plants-microorganisms are so far larger uninvestigated. Additionally we need to understand how climate change will affect the structures and activities of crop root systems, food and grain quality and on farm sustainability. For example, seed yield increased whereas seed crude protein decreased by 9–14% in wheat [118] and rice [119] crops grown under elevated [CO₂] in FACE. The system studies of many factors related to the global change offer a promising move towards reliable projections of future crop yield and impacts for future crop improvements.

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