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Improving Photosynthesis to Increase Food and Fuel Production by Biotechnological Strategies in Crops

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Global food production will need to increase more than 50% before 2050 to satisfy the food and fuel demands of an increasing population. Despite the fact that more than 90% of crop biomass is derived from photosynthetic products, increasing photosynthetic capacity and/or efficiency has not yet been addressed by breeding. Thus, photosynthetic improvements are being considered as a way to increase crop yields. We now need to identify the specific targets that will directly improve leaf photosynthesis to realize a new "green revolution". In this mini-review article, current proposals to improve photosynthesis are summarized (Table 1).

Improving the Rubisco Performance via Quality Control and/or Quantity Control

Ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) is the most abundant protein on Earth and is an essential component of the photosynthetic process of fixing CO_2 into organic carbon. Rubisco is known to have a low catalytic rate, a primary factor explaining its high concentration in C_3 plant leaves. Therefore, improving the Rubisco performance via quality control and/or quantity control is an obvious target for both increasing photosynthetic performance and nitrogen use efficiency. Recently, the introduction of a C_4-Rubisco small subunit *(RbcS)* gene from sorghum into rice successfully produced chimeric Rubisco with a greater catalytic turnover rate of Rubisco (k_{cat}) in the transgenic rice [1]. Also, single residues controlling enzymatic properties of Rubisco have been identified and successfully engineered to produce greater Rubisco proteins in *Flaveria* species from C_3 to C_4 catalysis [2]. Moreover, it has been reported that antisense reductions of Rubisco improved the photosynthetic rate at high CO_2 concentrations in rice [3], as it may be possible to reallocate a large amount of nitrogen from Rubisco to the other photosynthetic components (e.g., Calvin cycle enzymes, electron transport systems). Thus, many attempts have been made to improve Rubisco function by genetic manipulation.

1.	Improving the Rubisco function
	i. Improving Rubisco catalytic activity
	ii. Altering Rubisco amount per leaf area
2.	Increasing the thermostability of Rubisco activase to sustain Rubisco activity at high temperature
3.	Enhancing CO_2 concentration around Rubisco to maximize catalytic rate and minimize photorespiration
	i. Turning C_3 plants into C_4 plants
	ii. Installing algal or cyanobacterial carbon-concentrating mechanisms CCM) into C_3 plants
	iii. Redesigning photorespiratory metabolism
	iv. Improving CO_2 transfer pathways via stomata and/or mesophyll cells
4.	Enhancing chloroplast electron transport rate
	i. Improving whole chain electron transport
	ii. Modifying light-harvesting systems
5.	Enhancing enzyme activity of Calvin cycle (e.g., SBPase)
6.	Enhancing the capacity of metabolite transport processes and carbon utilization
7.	Others
	i. QTL analyses
	ii. Manipulation of mitochondrial respiration
	iii. Improving photosynthesis under fluctuating light conditions

Table 1: Potential targets for improving plant photosynthesis.

Increasing the Thermotolerance of Rubisco Activase to Sustain Rubisco Activity under High Temperatures

The activation state of Rubisco is dependent on the heat sensitive enzyme, Rubisco activase. The introduction of a thermostable Rubisco activase into *Arabidopsis* resulted in increases in plant tolerance to heat stress and photosynthetic performance at high temperature [4,5]. In addition, the thermal stability of photosynthesis was increased slightly when maize Rubisco activase was overexpressed in rice [6]. Thus, manipulating Rubisco activase could be a potential target for stimulation of photosynthesis and especially growth at high temperature.

Enhancing CO_2 Levels Around Rubisco to Maximize Catalytic Rate and Minimize Photorespiration

It has been shown that increases in photosynthesis via CO_2 enrichment can improve crop yield [7,8]. CO_2 enters the intercellular air spaces through the stomata from the atmosphere and diffuses through air spaces, cell walls, cytosol, and chloroplast envelopes and finally reaches the chloroplast stroma where it is fixed by Rubisco. The primary resistances for CO_2 diffusion are considered to be at the stomata and at mesophyll cells. Thus, improving mesophyll CO_2 conductance via overexpressing aquaporin [9,10] as well as stomatal CO_2 conductance via manipulating stomatal characteristics [11,12] could be a great target for enhancing CO_2 levels around Rubisco. On the other hand, a variety of strategies for introducing CO_2-concentrating approaches into C_3 plants are also under way. These approaches aim to improve productivity by introducing C_4-like features into rice (C_4 rice) [13], by introducing cyanobacterial bicarbonate transporters (CO_2/HCO_3^- transporter) into the C_3 chloroplast membranes in higher plants [14], or by engineering new pathways into the chloroplast that bypass photorespiration and release CO_2 directly into the chloroplast stroma [15,16].

Enhancing Rate of Chloroplast Electron Transport

Plants capture light energy with their light-harvesting systems, including chlorophylls and carotenoids, and drive photosynthetic

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electron transport through the thylakoid membranes of the chloroplasts. ATP and NADPH produced by the chloroplast electron transport are utilized in the later photosynthesis processes (e.g., Calvin cycle). It has been reported that overexpression of plastocyanin or its algal substitute cytochrome c_6 improved the plant biomass in *Arabidopsis thaliana* [17,18] and that increased phosphorylation of thylakoid proteins improved the photosynthetic electron flow under certain light conditions [19]. Thus, photosynthetic efficiency under certain conditions can be improved by enhancing chloroplast electron transport. Recently, possible improvements for the reactions of photosynthetic electron transport by modifying the light-harvesting system have been suggested [20]. They proposed that the introduction of prokaryotic pigments or entire prokaryotic light-harvesting systems into plants may make it possible to expand the absorption spectrum of photosynthesis and thus increase photosynthetic efficiency at low light intensity. Moreover, optimization of chlorophyll antenna size could be a strategy to maximize photosynthetic efficiency at the canopy level, since light distribution via light penetration and light absorption is very important within the canopy.

Enhancing Enzyme Activity of Calvin Cycle

The Calvin cycle is an important process for the reduction of fixed carbon to begin the synthesis of hexose sugars, as well as for the regeneration of the starting compound, ribulose 1,5-bisphosphate (RuBP). Bottleneck processes of the Calvin cycle have been studied. Several transgenic antisense works suggested that sedoheptulose 1,7-bisphosphatase (SBPase), plastid aldolase, and transketolase might be targets for improving C_3 cycle flux [21]. Indeed, overexpression of either a bifunctional SBPase/FBPase or plant SBPase in tobacco plants resulted in increased photosynthetic rates and plant growth [22,23].

Enhancing the Capacity of Metabolite Transport Processes and Carbon Utilization

Sink strength is a major determinant of photosynthetic capacity because it could avoid photosynthetic suppression by accumulating sugars and/or starch [24,25]. Photoassimilates are exported via the pholem; from the source tissues to the sink tissues. It has been shown the triose-phosphate/phosphate translocator (TPT) strongly limits photosynthesis under high CO_2 conditions [26]. The TPT provides a regulatory link between CO_2 assimilation and cytosolic carbon metabolism. Moreover, there is an approach for increasing plant yield by overexpressing sucrose transporters in sink cells, thereby enhancing sink demand and inducing an increase in photosynthesis and assimilate export. When overexpresssing a potato sucrose symporter (*StSUT1*) in storage parenchyma cells of pea seeds, there was enhanced sucrose influx into cotyledons and greater cotyledon growth rates [27]. In addition, it has been shown that enhancement of sucrose synthase activity represents a useful strategy for increasing starch accumulation and yield in potato tubers [28]. In a future world of higher CO_2 concentration, enhancing the capacity for sucrose export and carbon utilization would be an important component for maximizing photosynthesis and yield. While altering transport capacity alone is unlikely to change photosynthetic capacity, enhancing photosynthetic capacity as well as transport capacity could lead to improve plant growth and yield.

Others

Application of the next generation sequencing, QTL analysis and innovative phenomic screening, can provide important information for breeding plants with great photosynthesis and plant growth. A comparison with a study of QTL for intra- and interspecific variation has enormous and unexplored potential for future exploitation to improve yield through manipulation of photosynthesis [29,30].

The manipulation of mitochondrial metabolism has been proposed as a potential way to enhance photosynthesis. Antisense inhibition of the mitochondrial malate dehydrogenase enhanced the photosynthetic rate in transgenic tomato [31], although the exact details concerning how photosynthesis is up-regulated in these plants are still unclear. Thus, genetic manipulation of certain steps of the tricarboxylic acid (TCA) cycle could prove to enhance photosynthesis and crop yield.

So far, research into finding new ways to increase crop yields has focused on improving steady-state photosynthesis. However, leaves in natural plant canopies experience a highly variable light environment over the course of a day (*i.e.*, cloud cover and overshadowing canopy cover). Therefore, it is also important to study how we can improve photosynthesis in natural environments where irradiance often fluctuates. Recently, overexpression of Rubisco activase from a maize transgene improved photosynthetic rate following an increase in light intensity in the transgenic rice plants [6,32]. Also, it would be important to consider the photosynthetic performance at the canopy level as well as the leaf level.

Recent technology for nucleus or chloroplast genome transformation has been advancing and it would enable easier and more precise manipulation of the photosynthesis process. It is expected that such plants could exhibit more efficient photosynthesis under controlled conditions: the plant factory in which plants are produced in an optimized growth environment would have potential advantages of high productivity. In the future, the combined uses of several strategies (Table 1) would greatly help to improve photosynthetic capacity and thus plant growth.

References

1. Ishikawa C, Hatanaka T, Misoo S, Miyake C, Fukayama H (2011) Functional incorporation of sorghum small subunit increases the catalytic turnover rate of Rubisco in transgenic rice. Plant Physiol 156: 1603-1611.
2. Whitney SM, Sharwood RE, Orr D, White SJ, Alonso H, et al. (2011) Isoleucine 309 acts as a C_4 catalytic switch that increases ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) carboxylation rate in Flaveria. Proc Natl Acad Sci USA 108: 14688-14693.
3. Makino A, Shimada T, Takumi S, Kaneko K, Matsuoka M, et al. (1997) Does decrease in ribulose-1,5-bisphosphate carboxylase by antisense rbcS lead to a higher N-use efficiency of photosynthesis under conditions of saturating CO_2 and light in rice plants?. Plant Physiol 114: 483-491.
4. Kurek I, Chang TK, Bertain SM, Madrigal A, Liu L, et al. (2007) Enhanced thermostability of Arabidopsis rubisco activase improves photosynthesis and growth rates under moderate heat stress. Plant Cell 19: 3230-3241.
5. Kumar A, Li C, Portis Jr AR (2009) Arabidopsis thaliana expressing a thermostable chimeric Rubisco activase exhibts enhanced growth and higher rates of photosynthesis at moderately high temperatures. Photosynth. Res 100: 143-153.
6. Yamori W, Masumoto C, Fukayama H, Makino A (2012) Rubisco activase is a key regulator of non-steady-state photosynthesis at any leaf temperature and, to a lesser extent, of steady-state photosynthesis at high temperature. Plant J 71: 871-880.
7. Long SP, Zhu XG, Naidu SL, Ort DR (2006) Can improvement in photosynthesis increase crop yields? Plant Cell Environ 29: 315-330.
8. Zhu XG, de Sturler E, Long SP (2007) Optimizing the distribution of resources between enzymes of carbon metabolism can dramatically increase photosynthetic rate: a numerical simulation using an evolutionary algorithm. Plant Physiol 145: 513-526.
9. Hanba YT, Shibasaka M, Hayashi Y, Hayakawa T, Kasamo K, et al. (2004)

Overexpression of the barleyaquaporin HvPIP2;1 increases internal CO_2 conductance and CO_2 assimilation in the leaves of transgenic rice plants. Plant Cell Physiol 45: 521-529.

10. Tsuchihira A, Hanba YT, Kato N, Doi T, Kawazu T, et al. (2010) Effect of overexpression of radish plasma membrane aquaporins on water-use efficiency, photosynthesis and growth of Eucalyptus trees. Tree Physiol 30: 417-430.

11. Tanaka Y, Sugano SS, Shimada T, Hara-Nishimura I (2013) Enhancement of leaf photosynthetic capacity through increased stomatal density in Arabidopsis. New Phytol 198: 757-764.

12. Kusumi K, Hirotsuka S, Kumamaru T, Iba K (2012) Increased leaf photosynthesis caused by elevated stomatal conductance in a rice mutant deficient in SLAC1, a guard cell anion channel protein. J Exp Bot 63: 5635-5644.

13. Covshoff S, Hibberd JM (2012) Integrating C_4 photosynthesis into C_3 crops to increase yield potential. Curr Opin Biotechnol 23: 209-214.

14. Price GD, Badger MR, von Caemmerer S (2011) The prospect of using cyanobacterial bicarbonate transporters to improve leaf photosynthesis in C_3 crop plants. Plant Physiol 155: 20-26.

15. Kebeish R, Niessen M, Thiruveedhi K, Bari R, Hirsch HJ, et al. (2007) Chloroplastic photorespiratory bypass increases photosynthesis and biomass production in Arabidopsis thaliana. Nature Biotech 25: 593-599.

16. Maier A, Fahnenstich H, Von Caemmerer S, Engqvist MK, Weber APM, et al. (2012) Transgenic introduction of a glycolate oxidative cycle into *A. thaliana* chloroplasts leads to growth improvement. Front Plant Sci 3: 38.

17. Chida H, Nakazawa A, Akazaki H, Hirano T, Suruga K, et al. (2007) Expression of the algal cytochrome *c6* gene in Arabidopsis enhances photosynthesis and growth. Plant Cell Physiol 48: 948-957.

18. Pesaresi P, Scharfenberg M, Weigel M, Granlund I, Schroder WP, et al. (2009) Mutants, overexpressors, and interactors of Arabidopsis plas-tocyanin isoforms: revised roles of plastocyanin in photosynthetic electron flow and thylakoid redox state. Mol Plant 2: 236-248.

19. Pribil M, Pesaresi P, Hertle A, Barbato R, Leister D (2010) Role of plastid protein phosphatase TAP38 in LHCII dephosphorylation and thylakoid electron flow. PLoS Biol 8:1-12.

20. Blankenship RE, Tiede DM, Barber J, Brudvig GW, Fleming G, et al. (2011) Comparing photosynthetic and photovoltaic efficiencies and recognizing the potential for improvement. Science 332: 805-809.

21. Raines CA (2011) Increasing photosynthetic carbon assimilation in C_3 plants to improve crop yield: current and future strategies. Plant Physiology 155: 36-42.

22. Miyagawa Y, Tamoi M, Shigeoka S (2001) Overexpression of a cyanobacterial fructose-1,6-/sedoheptulose-1,7-bisphosphatase in tobacco enhances photosynthesis and growth. Nat Biotechnol 19: 965-969.

23. Lefebvre S, Lawson T, Zakhleniuk OV, Lloyd JC, Raines CA (2005) Increased sedoheptulose-1,7-bisphosphatase activity in transgenic tobacco plants stimulates photosynthesis and growth from an early stage in development. Plant Physiol 138: 451-460.

24. Graf A and Smith AM (2011) Starch and the clock: the dark side of plant productivity. Trends Plant Sci 16: 169-175.

25. Weise SE, van Wijk KJ, Sharkey TD (2011) The role of transitory starch in C_3, CAM, and C_4 metabolism and opportunities for engineering leaf starch accumulation. J Exp Bot 62: 3109-3118.

26. Häusler RE, Schlieben NH, Nicolay P, Fischer K, Fischer KL, et al. (2000) Control of carbon partitioning and photosynthesis by the triose phosphate/phosphate translocator in transgenic tobacco plants *(Nicotiana tabacum L.)*. I. Comparative physiological analysis of tobacco plants with antisense repression and overexpression of the triose phosphate/phosphate translocator. Planta 210: 371-382.

27. Rosche E, Blackmore D, Tegeder M, Richardson T, Schroeder H, et al. (2002) Seed-specific overexpression of a potato sucrose transporter increases sucrose uptake and growth rates of developing pea cotyledons. Plant J 30: 165-175.

28. Baroja-Fernández E, Munoz FJ, Montero M, Etxeberria E, Sesma MT, et al. (2009) Enhancing sucrose synthase activity in transgenic potato (Solanum tuberosum L.) tubers results in increased levels of starch, ADPglucose and UDPglucose and total yield. Plant Cell Physiol 50: 1651-1662.

29. Fukuoka S, Ebana K, Yamamoto T, Yano M (2010) Integration of genomics into rice breeding. Rice 3: 131-137.

30. Takai T, Arai-Sanoh Y, Iwasawa N, Hayashi T, Yoshinaga S, et al. (2012) Comparative Mapping Suggests Repeated Selection of the Same Quantitative Trait Locus for High Leaf Photosynthesis Rate in Rice High-Yield Breeding Programs. Crop Sci 52: 2649-2658.

31. Nunes-Nesi A, Carrari F, Lytovchenko A, Smith AM, Loureiro ME, et al. (2005) Enhanced photosynthetic performance and growth as a consequence of decreasing mitochondrial malate dehydrogenase activity in transgenic tomato plants. Plant Physiol 137: 611-622.

32. Fukayama H, Ueguchi C, Nishikawa K, Katoh N, Ishikawa C, et al. (2012) Overexpression of Rubisco activase decreases the photosynthetic CO_2 assimilation rate by reducing Rubisco content in rice leaves. Plant Cell Physiol 53: 976-986.