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Yield Improvement by Manipulation of Photosynthesis

(*Himani P. Vadodariya, Dhairya Makwana and Bhagyasri Majhi)
Department of Genetics and Plant Breeding, Navsari Agricultural University, Navsari
*Corresponding Author's email: himanivadodariya@gmail.com

Photosynthesis is the fundamental process by which plants convert light energy into chemical energy, forming the basis of life on Earth. It is the primary mechanism by which energy enters the biosphere, and it plays a crucial role in the productivity of crops. However, the efficiency of photosynthesis in most plants is suboptimal, and enhancing this process has been recognized as a key strategy for increasing crop yields to meet the demands of a growing global population. Since the harvest index for many crops, such as rice, is approaching a ceiling value, an increase in yield potential will have to involve an increase in crop biomass, i.e. there will have to be more net photosynthesis.

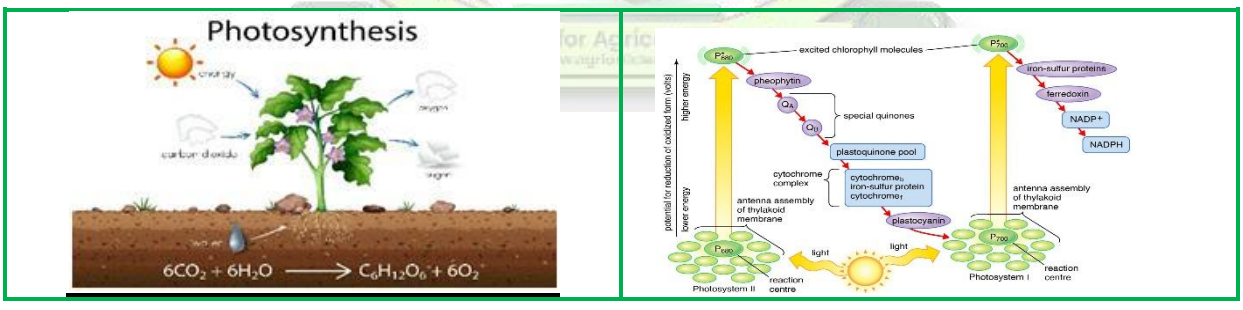
This may be achieved by an increase in Leaf Area Index (LAI) or an increase in net photosynthesis per unit leaf area. Since LAI is generally already high in most crops, the increased assimilate production must come from improved photosynthesis.

The approach to achieving this goal is to bring about an increase in photosynthesis at the leaf level. With appropriate crop management, this increase could then be integrated into an increase in carbon gain at the canopy level and an increase in yield.

The Basics of Photosynthesis and Its Efficiency

Photosynthesis occurs in the chloroplasts of plant cells, where light energy is captured by chlorophyll and used to convert carbon dioxide (CO_2) and water (H_2O) into glucose and oxygen. This process can be divided into two main stages: the light-dependent reactions and the light-independent reactions (Calvin cycle).

1. **Light-dependent reactions**: These occur in the thylakoid membranes and involve the conversion of light energy into chemical energy in the form of ATP and NADPH.
2. **Calvin cycle**: This occurs in the stroma of the chloroplasts, where ATP and NADPH are used to fix CO_2 into organic molecules like glucose.

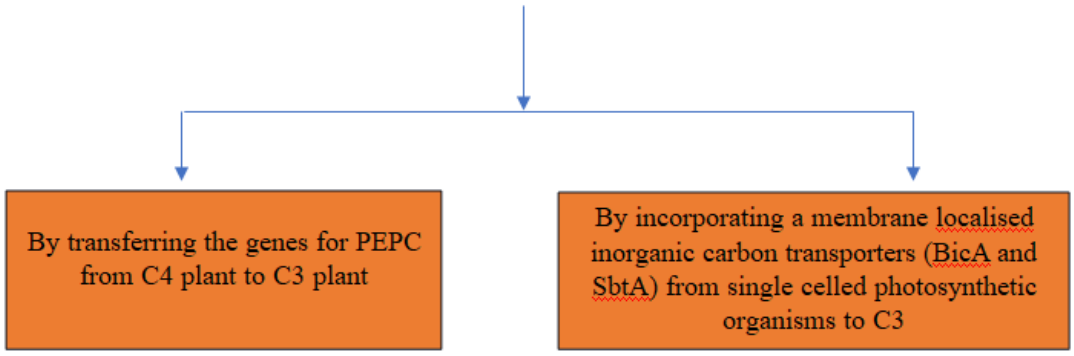


What Parts of the Photosynthetic Process Could be Modified to Enhance the Amount of Carbon Gained?

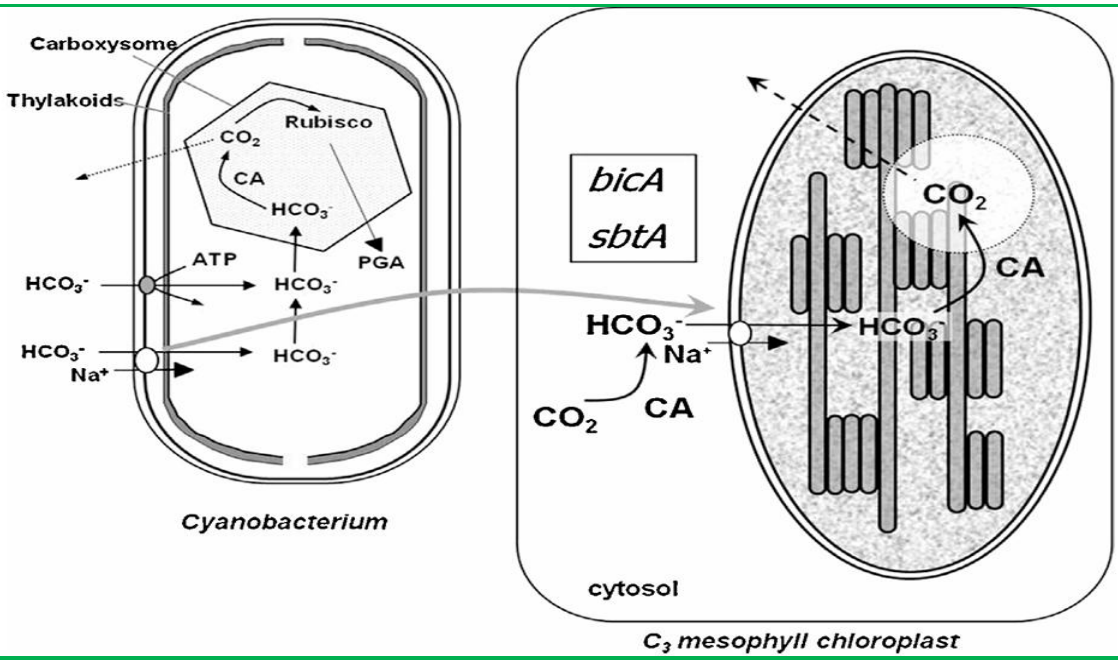
1. **Concentrating CO_2 in the vicinity of RuBisCO:** At low concentrations of RuBisCO fixes more O_2 relative to CO_2, which leads to loss of energy and carbon. In the current climatic conditions at 30 °C, about 25% of the assimilated CO_2 was released in the

photorespiration process. However, this problem is not faced by the C4 and CAM plants, because they have a carbon concentrating mechanism around RuBisCO. The C4 plants have the PEP carboxylase and other enzymes that shuttle the CO2 into the bundle sheath cell concentrating around the RuBisCO leads to higher photosynthesis. Although the C3 plants also have all the key enzymes of the C4 cycle but their expres-sion is very low and are thought to perform housekeeping functions. Increasing CO_2 around Rubisco can have a dual effect in reducing wasteful photorespiration and increasing the rate of catalysis of Rubisco as it operates closer to substrate saturation.

There are two possible ways to install CO_2 concentrating mechanism in C3 plants.



Second approach might be less technically challenging than engineering a C4 photosynthetic pathway due to the smaller number of genes required and also, the energy costs of a CCM may be inherently lower than that of the C4 pathway.



Candidate bicarbonate transporters from cyanobacteria which could be suitable for Installation into the mesophyll chloroplast of C3 cereals are the single subunit bicA and sbtA genes encoding HCO3−/Na+ symporters.

2. **Antenna engineering:** An optimum quantum flux of sunlight is necessary to maintain light-induced photosynthesis; otherwise, excess photons result in decreased photosynthetic rate. To avoid photosystem II from the damage to the extra light, LHC utilizes the excess quantum flux for thermal dissipation and fluorescence. At the molecular level, it is reported that minimizing the chlorophyll antenna size of the

photosystem resulted in improved photosynthetic solar energy conversion efficiency and productivity. The enhancement in plant productivity was observed by different researchers by the reduction of antenna size of the photosystems and expansion of the light absorption spectrum to absorb more of the available light. Kirst *et al.* (2018) also demonstrated that downregulation of the signal recognition particle 43 (SRP43) gene expression in tobacco resulted in truncated photosynthetic light-harvesting antenna and which in turn leads to greater leaf to stem ratio, enhanced photosynthetic productivity and canopy biomass accumulation under high density cultivation conditions. the increased biosynthesis of Chl b could increase the abundance of light-harvesting chlorophyll proteins and proteins of the electron transport chain leading to increased capture of light as well as enhanced (40–80%) electron transport rates of photosystems I and II at both limiting Sand saturating light intensities.

3. **Improving Rubisco Efficiency:** Rubisco (Ribulose-1,5-bisphosphate carboxylase/ oxygenase) is the key enzyme in the Calvin cycle responsible for fixing CO_2. However, it is also inefficient because it can catalyze a wasteful reaction with oxygen, leading to photorespiration, which reduces photosynthetic efficiency.

- **Genetic modifications**: Traditional breeding methods aimed at selecting naturally occurring variants with more efficient Rubisco enzymes have shown limited success. However, with advances in genetic engineering, it is now possible to introduce Rubisco from other species with higher catalytic rates or lower oxygen affinity into crop plants. For example, some algae have Rubisco variants that are more efficient than those in higher plants.
- **Regulation of Rubisco activase**: Rubisco activase is a protein that regulates Rubisco's activity. Enhancing the expression or activity of Rubisco activase can improve the overall efficiency of Rubisco, particularly under stress conditions.

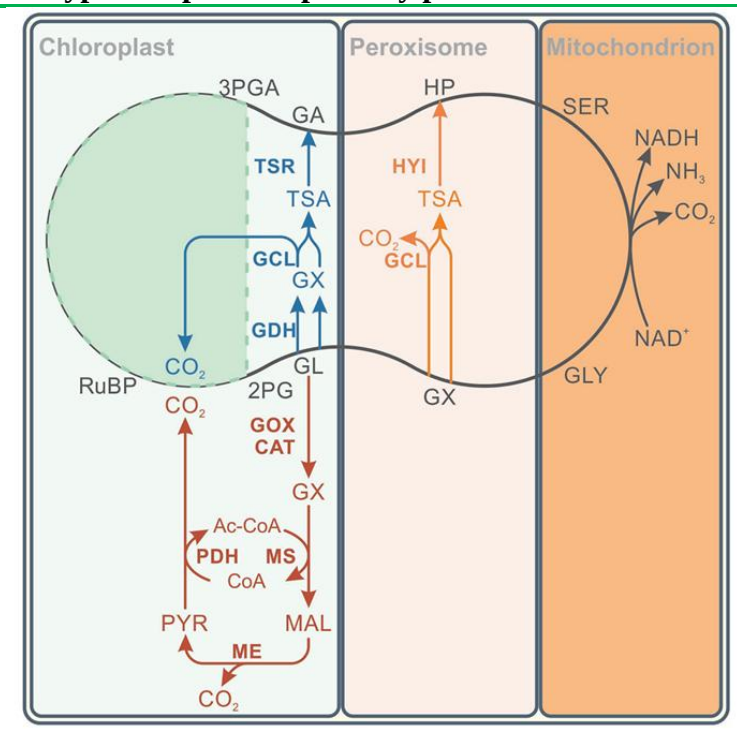
Limitation: RuBisCO is a multimeric enzyme, and its large subunit is encoded by the plastid genome, and the small subunit is encoded by the nuclear genome. Hence its manipulation is very challenging. RuBisCO of red algae having specificity factor is reported to have high specificity along with high catalytic rates, but when expressed in the higher plants, the subunits do not assemble correctly.

Solution: The RuBisCO activase (RCA) enzyme is very much unstable at a higher temperature above 30 °C and it regulates the activation of the RuBisCO by removing the inhibitory sugar phosphates from its catalytic sites. The thermostable form of the RCA can be another alternative option to enhance the photosynthetic efficiency even in the case of heat stress conditions.

4. **Manipulating the electron transport chain:** Manipulating the electron transport chain (ETC) increases photosynthesis efficiency by optimizing the flow and utilization of electrons during the light-dependent reactions of photosynthesis. By enhancing the efficiency of this chain, more light energy can be converted into chemical energy in the form of ATP and NADPH, which are essential for driving the Calvin cycle and carbon fixation. This optimization reduces energy losses as heat or through non-photochemical quenching (NPQ) and can improve the stability and function of photosystem II, the starting point of the ETC. Additionally, by incorporating or enhancing alternative electron pathways, plants can better manage excess light energy and maintain high photosynthetic efficiency even under stress conditions like high light intensity. These adjustments lead to more efficient energy conversion and ultimately result in increased plant growth and productivity. The variations in the plastocyanin content are also reported to alter the ETC efficiency. Therefore, plastocyanin is found to be a better candidate for enhancing plant productivity.

NAD kinase (NADK) catalyzes the conversion of NAD to NADPH through the phosphorylation process; overexpression of the NADK of the *A. thaliana* in rice resulted in enhanced electron transport and CO_2 assimilation rates. Apart from the various studies on the ETC modification, it is observed that Cyt b6 and plastocyanin provide excellent opportunities for enhancing its efficiency, but still more focused research is required to improve the conversion rate of solar energy to biomass and to develop the photosystem with less sensitivity to photodamage or should produce lesser reactive oxygen species.

5. Bypass of photorespiratory process



Black Lines: photorespiratory cycle
Dotted line:
the Calvin–Benson cycle
Blue line:
Kebeish bypass
(E.coli glycolate catabolic pathway)
Orange line:Carvalho bypass
Red line: Maier bypass
(glycolate catabolic cycle)

First approach, glycolate was converted to glycerate directly in the chloroplast by introducing the Escherichia coli glycolate catabolic pathway, thus avoiding or at least competing with the peroxisomal and mitochondrial reactions of photorespiration.

The second approach was to introduce a complete glycolate catabolic cycle that oxidized 2PG to CO2 in the chloroplast. Both bypasses were reported to enhance biomass production by up to 30% although only under short-day conditions.

Third bypass to photorespiration has been engineered by introducing the E. coli enzymes glyoxylate carboligase and hydroxy pyruvate isomerase into tobacco for the conversion of glyoxylate into hydroxypyruvate directly in the peroxisome. While this alternative pathway may potentially reduce the cost of 2PG recycling.

6. **Engineering of calvin benson cycle (C3 cycle):** In this reaction, about 11 different enzymes catalyze the 13 reactions, and the carbon fixation is initiated by the RuBisCO. The enzyme sedoheptulose-1,7-biphosphatase (SBPase), fructose-1,6-biphosphatase (FBPase), aldolase, and transketolase are predicted to enhance productivity and could generate extra thermodynamic push and leads to better flux control. Moreover, in earlier studies, overexpression of the cyanobacterial FBPase and SBPase in tobacco resulted in enhanced photosynthetic rate and biomass yield, but in later studies, independent overexpression of both enzymes shows SBPase to be more potent for enhancing the plant productivity.

Other enzymes of the Calvin Benson cycle such as FBPase, FBPA and photorespiratory glycine decarboxylase-H (GDH-H), were also targeted to enhance the photo synthesis and biomass yield. The photorespiratory GDH-H overexpression in tobacco was

reported to enhance photosynthesis and biomass. Co-overexpression of the different enzymes has also been tested in various crops. Likewise, co-overexpression of the SBPase and FBPA in tobacco enhanced photosynthesis. Moreover, co-overexpression of the three enzymes GDC H, SBPase, and FBPA in Arabidopsis resulted in enhanced leaf area, photosynthetic rate and biomass.

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