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# PERSPECTIVES ON FOOD SECURITY: INCREASING CROP YIELDS BY IMPROVING PHOTOSYNTHESIS

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**Abstract**

The focus on the enhancement of photosynthesis – the process whereby plants turn light energy into chemical energy – is one of the research areas that has great significance for sustainable agriculture and global food security. The main method for converting atmospheric carbon dioxide ($CO_2$) into organic carbon compounds is the Calvin–Benson (CB) cycle, which is very important for the metabolism and the growth of plants. Among the enzymes involved in the process, 8 out of the 11 are dedicated to the regenerative ribulose-1,5-bisphosphate (RuBP), which is the molecule that accepts $CO_2$. There is evidence from research carried out on a variety of plants that the regeneration of RuBP is a key factor in the enhancement of the process of photosynthesis. Also, by using omics technologies and synthetic biology, new pathways for optimizing or improving the process of photosynthesis and yielding more crops are being invented. The present review discusses the significant and effective developments and approaches focused on boosting the photosynthetic capacity and the uptake of $CO_2$ via the CB cycle enzymes, e.g., Rubisco, and genetically modifying such enzymes as sedoheptulose-1,7-bisphosphatase (SBPase) and fructose-1,6-bisphosphate aldolase (FBPA). It recommends integrating emerging technologies such as nanotechnology, synthetic biology, and machine learning to maximize its potential for developing productive and sustainable agri-systems.

**Key words:** Food security, The Calvin-Benson cycle, Photosynthesis, Yields.

## Background

The world's ever-growing population, which is the largest concern, has been a major factor in the food and biofuels hike and that has also come to the forefront of farmers' minds. Hunger is still a serious problem in a world where the majority live below the poverty line and more than 850 million people eat less than they should. Production of Food with the highest quality will be the only way the increased population of 2050, which is expected to be 9.6 billion, will survive. The Anon., (2012) reports that cereal production must increase by 60% to meet food demands. To attain this, cereal crop yield needs to be raised by approximately 50% (Horton, 2000; Uematsu *et al*., 2012).

One of the most promising methods to increase crop production is to optimize photosynthesis, which is the basic biological process that plants use to grow. However, the process of photosynthesis is still considered a less explored target in farming research despite its importance. Genetic engineering, which has recently made significant progress, is still a way to go for enriching photosynthesis that will in turn lead to a considerable increase in crop production through enhancing the fixation rate of carbon (Sharma-Natu & Ghildiyal, 2005; Feng *et al*., 2007).

Photosynthesis is responsible for transforming light energy into ATP and NADPH, which in turn powers the synthesis of different organic substances that are indispensable for the growth and development of plants. Moreover, it produces oxygen and provides carbon skeletons, which are necessary for the metabolic processes. This photonic dilemma consists of two major parts: the light-dependent reactions, which occur in the chloroplast's thylakoid membranes and yield ATP, NADPH, and oxygen, and the CB cycle (or $C_3$ cycle) that takes place in the chloroplast stroma where ATP and NADPH are used to convert $CO_2$ into carbohydrates via carbon fixation (Bassham *et al*., 1950; Stitt *et al*., 2010).

The metabolomics pathway of Carbon encompasses both pathways of the photorespiratory (C2) and CB cycle, working together. This process gets underway with the enzyme Rubisco, which facilitates either the carboxylation or oxygenation of RuBP. The reaction of carboxylation yields 3-phosphoglycerate (3-PGA) while the process of oxygenation gives rise to both 3-PGA formation and 2-phosphoglycolate (2-PG). There is a control over the balance between these two reactions by the relative amounts of $CO_2$ and $O_2$ in leaf tissues (Kebeish *et al*., 2007). This review spotlights and critically assesses a number of promising procedures aimed at boosting the efficiency of photosynthesis as a means of increasing crop yield.

**The CB Cycle: mechanism and regulation:** Photosynthetic carbon dioxide assimilation primarily takes place in the chloroplasts of plants through the CB cycle, a well-defined route functioning in the stroma of the chloroplast. This cycle is the main mechanism for fixing inorganic carbon during photosynthesis and is crucial for plant metabolism and carbon regulation (Geiger & Servaites, 1994). Melvin Calvin and his group first discovered the cycle operational steps during the early 1950s. Later studies not only pointed out the enzymes responsible for these reactions but also investigated their

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characteristics under various controlled conditions. The main output of $CO_2$ assimilation through this cycle is triose phosphates, which are important intermediates that either get directly converted into starch and sucrose or enter into other metabolic pathways as substrates (Bassham *et al.*, 1950; Spreitzer, 1993).

The CB cycle is made up of a total of 13 biochemical reactions that are catalysed by 11 different enzymes and can be generally categorized into three main phases: carboxylation, reduction, and regeneration. In the initial phase, Rubisco, one of the most abundant proteins, facilitates the carboxylation of RuBP by $CO_2$ and produces 3-PGA, a three-carbon compound which is also known as the stable compound; therefore, the cycle is called the $C_3$ pathway as well. The reduction phase consumes ATP and NADPH produced in the light-dependent photosynthetic reactions in the process of reducing 3-PGA to the triose phosphates; glyceraldehyde-3-phosphate (G3P) and dihydroxyacetone phosphate (DHAP). These phosphates are needed by higher plants to support their metabolic activities. In the last phase, RuBP is resynthesized from the triose phosphate pool, which keeps the cycle going. The carbon-rich molecules made by this cycle are essential for plant biomass production and thus, their growth and development (Woodrow & Berry, 1988; Geiger & Servaites, 1994; Lichtenthaler, 1999).

For the CB cycle to keep on functioning, it is very important to have a balance between carbon export and the regeneration of cycle intermediates. Through this process, the enzymes that take part in the cycle get the most precise and careful regulation. The main enzymes, which are SBPase and FBPA, are controlled by redox mechanisms involving the ferredoxin/thioredoxin system that alters enzyme activity according to the presence of light and darkness (Scheibe, 1991; Buchanan, 1991). Moreover, internal factors such as $Mg^{2+}$ concentration in the stroma and pH affect the behaviour of enzymes - particularly SBPase, FBPase, and Rubisco – during dark-light transitions. As the plants move from darkness to light, the chloroplast pH rises from about 7 to approximately 8, which is the most favourable condition for the activity of nearly all CB enzymes (Heldt *et al*., 1973; Werdan *et al*., 1975; Nishizawa & Buchanan, 1981). This kind of regulation allows the plant's metabolic system to alternate between $CO_2$ fixation in the daytime and nighttime NADPH production through oxidative pentose phosphate (OPP) pathway (Schnarrenberger *et al.*, 1995).

Thioredoxins, which are tiny proteins, are weight not more than 12–14 kDa and are of utmost importance in redox regulation along with disulfide bond modification in targeted proteins, which then leads to specific enzymes being activated or deactivated (Meyer *et al*., 1999). These proteins are present in all whether they are prokaryotic or eukaryotic. In the case of plants, different kinds of thioredoxin have been recognized: two in the chloroplast, one in the cytosol, and one in the mitochondrion. The structure of the proteins enables them to selectively interact with different target enzymes. NADPH donates its electrons to thioredoxins in photosynthetic cells, thereby maintaining their reduced state, or these thioredoxins use the system of ferredoxin/thioredoxin to become reduced; the latter, however, is a process exclusive to chloroplasts and is driven by the electron flow during the light reactions of photosynthesis (Faske *et al.*, 1995; Schürmann & Jacquot, 2000).

The light-dependent regulation is an important aspect that connects the light-initiating reactions occurring in the thylakoid membrane and the following biosynthetic processes taking place in the stroma. To give an instance, the hexose phosphates present in the stroma can be directed through the OPP pathway to the plastids, where it would yield NADPH. However, this process opposes the Calvin–Benson cycle, and running both simultaneously would waste energy – specifically, three ATPs per fixed $CO_2$. Therefore, the CB cycle enzymes are generally activated by light, while those involved with the OPP pathway are inactivated by reduced thioredoxin, for example, glucose-6-phosphate dehydrogenase (G6PDH) (Wenderoth *et al*., 1997).

Furthermore, enzymes such as SBPase, FBPase, phosphoribulokinase (PRK), and glyceraldehyde-3-phosphate dehydrogenase (GAPDH) are regulated during the light period via the ferredoxin/thioredoxin system. Moreover, a small precursor protein designated as CP12, which is retained in all photosynthetic organisms, mediates this process in a manner that varies dependent upon the NADPH levels by forming and breaking down a complex with PRK and GAPDH. The complex formation is thought to be one of the modes of regulating CB cycle activity since it could be influenced by the levels of NADPH (Wedel *et al.*, 1997; Wedel & Soll, 1998).

**Rubisco Enzyme: structure and regulation:** Rubisco is an enormous and intricate enzyme that is critical for photosynthesis and is present in the stroma of photosynthetic eukaryotes. It has 16 subunits that coalesce into a hexadecamer consisting of eight large subunits (55 kDa) and eight small subunits (15 kDa). The *rbcL* gene situated in the chloroplast genome codes for the large subunits, where the enzyme's catalytic and binding sites are. Each of these large subunits has an N-terminal domain and a C-terminal that are arranged in an alpha/beta barrel structure. Most of the residues forming the active site of the enzyme are from the loop regions at the opening of this barrel structure, and loops on the N-terminal domain of an adjacent large subunit provide additional contributions (Parry *et al.*, 1987, 2008).

The nuclear rbcS gene encodes for the small subunits, which, though not directly involved in the catalytic process, are believed to play a role in the overall activity of Rubisco. Rubisco catalyses two main reactions: the carboxylation of RuBP to yield two molecules of 3-PGA in the CB cycle, and the oxygenation of RuBP, producing one 2-phosphoglycolate and one 3-PGA in photorespiration (Ellis, 1979).

Rubisco is regarded as a chief control point in the CB cycle, considering that its performance is impacted by environmental conditions (Geiger & Servaites, 1994). The main regulators of this enzyme are carbamylation and inhibitor binding. In carbamylation, a $CO_2$ molecule (different from the one in the carboxylation reaction) binds to a lysine amino acid at Rubisco's active site which leads to the formation of an acidic molecule–$Mg^{2+}$ complex ($E{\cdot}CO_2{\cdot}Mg^{2+}$) that activates the enzyme. Though the particular sugar phosphates can attach to Rubisco and

impede the carbamylation process, thus, Rubisco is not activated. In such situations, the action of Rubisco activase is necessary to get rid of these inhibitors, which allows Rubisco being able to reach the active form (Wang & Portis, 1992; Carmo-Silva *et al.,* 2014).

It appeared that there were two drawbacks in Rubisco that turned out to be a limitation on the optimal exploitation of the resources provided by photosystems. Rubisco is the slowest enzyme operating much slower than all the enzymes in the CB cycle and both photosystems in light phase (Caemmerer *et al*., 2014). Rubisco has a low enough substrate specificity that it cannot be considered a high-precision enzyme. Among its main substrates, which is carbon dioxide, Rubisco also interacts with oxygen and incorporates it into ribulose-1,5-bisphosphate instead of $CO_2$ (Bowes *et al*., 1971; Melnik, 2025).

All the different species of plants have Rubisco activase (Spreitzer & Salvucci, 2002). The significance of the enzyme was brought into the limelight during experiments on an *Arabidopsis* rca mutant, which could not live under normal $CO_2$ conditions because there was no Rubisco activase (Somerville *et al*., 1982; Salvucci *et al*., 1985). Besides that, the enzyme plays the major role in ensuring the activity of Rubisco by driving away the inhibitors like 2-carboxyarabinitol-1-phosphate from the active site of the enzyme (Robinson & Portis, 1988, Portis, 1992).

**Improving the CB cycle to enhance photosynthesis**

**Improving rubisco enzyme activity:** One of the primary objectives in plant biotechnological applications is to modify the different elements and responses in the CB cycle so that the overall crop yield is increased. This includes pinpointing the enzymes that are responsible for the cycle's overall low efficiency and then applying genetic engineering to improve their activity (Raines, 2003). The main gene modification concern has been the C3 photosynthetic pathway, in which the gene of the C3 photosynthetic pathway has been transformed to a higher capacity, and thus plant productivity has been increased. Rubisco has been the most challenging enzyme to alter because of its genetic and biochemical complexity. Nevertheless, there has been a huge amount of research done trying to improve the activity of Rubisco through both direct and indirect ways. Direct approaches furthermore consist of protein engineering, directed evolution, natural variation screening, and gene expression modification in genetically altered plants (Yoon *et al.,* 2020; Gionfriddo *et al.,* 2024). The utilization of $CO_2$-concentrating mechanisms from algae and cyanobacteria, as well as engineered synthetic pathways to bypass photosynthesis, is along with the indirect strategies that are being explored and are indicating success (South *et al*. 2019; Shen *et al*. 2019; Croce *et al*., 2024).

Rubisco, a central enzyme in the $C_3$ cycle, has been a significant target for enhancement as its performance turns out to be the restricting factor under various stresses, especially environmental ones like high temperatures or droughts. The enzyme catalyses the carboxylation of RuBP; however, it is actually quite inefficient because it has a low affinity for $CO_2$ and a slow reaction rate. Furthermore, during the oxygenation of RuBP, Rubisco forms 2-phosphoglycolate, which is then shuttled through the photorespiration pathway that ultimately leads to the release of $CO_2$ and ammonia, thus making this process inefficient and wasteful. In the face of these challenges, scientists have devised several innovative approaches, including the modification of Rubisco, the incorporation of genes from the $C_4$ photosynthetic pathway, and the alteration of photorespiratory pathways to reduce the associated inefficiencies (Raines, 2006; Uematsu *et al.,* 2012).

There are three principal strategies that have been proposed to minimize photorespiration. Of these, two are intended to improve the carboxylation efficiency of Rubisco, either by the enzyme being engineered directly or through the increase of $CO_2$ concentrations to inhibit the activity of the enzyme's oxygenase. The other one centres on perfecting the regeneration of RuBP, which in turn leads to increased overall efficiency of the CB cycle. Yet, these methods have been effective only to a limited extent as RuBP regeneration meets the restriction imposed by the amount of ATP and NADPH that the photosynthetic electron transport chain can provide for this process. Therefore, researchers are slowly moving away from the limitations imposed by Rubisco and towards furthering RuBP regeneration (Rosenthal *et al.,* 2011).

Rubisco is also a key player in nitrogen storage, with the leaf protein content contributing around 50% and the nitrogen content of the leaves about 30% (Mae *et al*., 1993; Parry *et al*., 2003). Nitrogen is an important and expensive nutrient in agriculture; hence, it is necessary to optimize its use. Research with genetically modified plants and growth simulation under high $CO_2$ showed that the present amount of Rubisco is an over-allocation of nitrogen in general. Lowering the Rubisco level might reduce the nitrogen uptake of plants, hence enhancing NUE (Ainsworth & Long, 2005; Parry *et al.,* 2011).

Earlier studies have pointed out that Rubisco is a primary target for genetic manipulation via the antisense RNA method, especially by down-regulating the small subunit to explore its contribution to photosynthesis and plant growth, with the main objective of feed efficiency improvement (Rodermel *et al*., 1988; Hudson *et al*., 1992). The results of these research works showed that in conditions of low light the reduction of Rubisco activity to 50% of its wild type level had only a slight impact on photosynthesis and plant growth (Quick *et al*., 1991). Conversely, at a high light intensity, the tobacco plants with decreased Rubisco activity showed drastic reductions in photosynthetic capacity and biomass gain (Stitt *et al.,* 1991; Hudson *et al.,* 1992).

The conducted experiments on transgenic plants characterized by lowered levels of Rubisco full-grown in an atmosphere with increased $CO_2$ have demonstrated the fact that a reduction of about 15-20% in Rubisco protein can lead to a decrease of approximately 10% in nitrogen needs without affecting photosynthetic productivity (Parry *et al*., 2013). These results indicate the possibility of breeding plant races with less Rubisco that would have higher adaptability to future climates with more $CO_2$ in the air, which, in turn, would result in benefits in nitrogen conservation (Stitt and Schulze, 1994).

In another research, scientists managed to create tobacco plants displaying 50 to more than 80% lower Rubisco activity in comparison to the wild type using antisense technology. The slow growth and the accumulation of higher nitrate levels in these plants under

ambient $CO_2$ conditions (330 μbar) indicated that the nitrogen use efficiency was decreased. Nevertheless, the plants at elevated $CO_2$ had growth comparable to that of wild type plants (Masle *et al*., 1993). In a like manner, the rice experiment employed a similar technique. The gene RbcS was downregulated through the use of antisense RNA in conjunction with the native promoter, resulting in a 35% reduction of Rubisco activity (Makino *et al*., 1997). These rice plants were grown under different nitrogen supplies and $CO_2$ concentrations, and they exhibited photosynthetic NUE improvement at $CO_2$-saturated conditions (Makino *et al.,* 1997; Makino, 2021).

Studies that have utilized the antisense approach have indicated that Rubisco is not the enzyme that controls $CO_2$ assimilation entirely during all conditions. Along with SBPase, other enzymes like FBPA have been proposed as the new targets for the enhancement of photosynthesis (Stitt & Schulze, 1994; Raines, 2003; Croce *et al*., 2024). Following these ideas, the overexpression of transgenic studies has indicated that the increase of SBPase level can lead to an increase in photosynthesis and plant growth in several species, including tobacco (in both greenhouse and field conditions), wheat, and Arabidopsis. Nevertheless, rice did not experience similar benefits (Lefebvre *et al*., 2005; Simkin *et al*., 2015; Driever *et al*., 2017; Suzuki *et al*., 2019). Furthermore, the tomato plants that had increased SBPase activity showed higher cold tolerance and better photosynthetic performance (Ding *et al*., 2017). The tobacco FBPA overexpression led to improved photosynthetic activity and biomass accumulation, while in tomato, it caused increased seed weight both under optimal and stress-induced temperature conditions (Uematsu *et al*., 2012; Simkin *et al*., 2015; Cai *et al.,* 2022).

**Improving RuBP regeneration enzymes (Table 1):** The generation of RuBP has also been enhanced by the integration of new proteins that perform their roles outside the CBB cycle. One of the notable examples of this method is the simultaneous expression of SBPase and FBPA in conjunction with either cyanobacterial ictB (a membrane protein of unknown function that has shown to enhance $CO_2$ assimilation previously) or the glycine decarboxylase (H subunit) (which is believed to increase $CO_2$ fixation possibly by stimulating the photorespiratory cycle and hence lessening the negative impact of the by-products on the CB cycle) in tobacco that has led to a significant rise in photosynthesis and the growth of the plants compared to the single-gene manipulations (Simkin *et al*. 2015; 2017). The overproduction of either the native SBPase enzyme or the dual-type cyanobacterial SBPase/FBPase, together with the algal Cyt C6 protein, not only led to an increase in photosynthesis and crop yield but also improved water use efficiency when the plants were under field conditions (Lopez-Calcagno *et al*., 2020).

The enzyme SBPase catalyses sedoheptulose-1,7-bisphosphate (SBP) dephosphorylation to sedoheptulose-7-phosphate (S7P). The activity of SBPase can increase in the light by more than ten times as a result of the activation by the thioredoxin system, which is responsible for the light perception and response in the plant. Moreover, the SBPase activity is regulated by the levels of $Mg^{2+}$ and pH in the stroma (Ölçer *et al*., 2001). The enzyme SBPase is regarded as a major regulatory enzyme that governs the carbon flow in the CB cycle, as it connects the assimilative phase (starch and sucrose biosynthesis) and the regenerative phase (Raines *et al*., 1999; Rosenthal *et al*., 2011). Understanding the regulatory mechanisms of SBPase and determining how its manipulation affects photosynthesis and crop yield have been gaining traction in metabolic engineering and transgenic methods as important research areas (Raines, 2003; Croce *et al*., 2024).

One research project conducted by Harrison and others involved the generation of transgenic tobacco plants which had their SBPase levels cut down via an antisense approach. The plants having around 80% of the wild-type SBPase exhibited distinct phenotypic alterations. Photosynthetic parameter measurements indicated a drop in carbohydrate and starch content, lower light-saturated photosynthesis rates and $CO_2$ assimilation, implying that the activity of SBPase could be considered as a limiting factor for carbon fixation (Harrison *et al*., 1997).

The study further confirmed that the impact of limiting RuBP regeneration on Rubisco activity was proven by the use of antisense tobacco plants with different degrees of SBPase reduction. The findings indicated a reduction in the maximum RuBP regeneration capacity; however, in vivo Rubisco activity was essentially unchanged. Thus, it seems that even slight SBPase reductions can hold $CO_2$ assimilation back owing to the limitation of RuBP regeneration (Harrison *et al*., 2001). On the other hand, plants that were genetically modified to overexpress SBPase had their photosynthesis rates and leaf areas significantly increased. In the case of young leaves, photosynthetic rates rose by 12%, while in fully expanded leaves, there was only a 6% increase compared to wild-type plants under saturating light. Additionally, biomass accumulation went up by approximately 30%. These results are convincing enough to say that SBPase overexpression can be a key factor in the enhancement of photosynthesis, growth, and yield in the early stages of plant development (Lefebvre *et al*., 2005). In this context, Rosenthal and coworkers pointed out that transgenic tobacco plants with increased Arabidopsis SBPase cDNA expression showed better photosynthesis and yield than the non-transformed control when they were cultivated in the conditions of open-air, elevated $CO_2$. The stably transformed plants showed an increase in $CO_2$ assimilation rates and electron transport activity (Rosenthal *et al*., 2011).

In a similar fashion, Feng and the team utilized the cDNA of SBPase from the indica rice variety, which led to the overexpression of SBPase in the japonica variety. The analysis of the resulting transgenic rice lines demonstrated not only an increase in the levels of SBPase but also improved tolerance to salt stress at the seedling stage, together with a rise in $CO_2$ assimilation and overall stress resistance when compared to wild-type plants (Feng *et al*., 2007a). The same SBPase gene was again overexpressed in rice in a different experiment aimed at increasing heat tolerance during early growth. Higher levels of Rubisco activation and photosynthetic activity were maintained in the transgenic rice under high temperature stress, the reasoning being that the SBPase prevented Rubisco activase from attaching to the thylakoid membranes, thereby allowing carbon assimilation to occur under heat conditions (Feng *et al*., 2007b).

**Table 1. Some example studies of Improved photosynthesis using genetic manipulation approaches.**

| Plants | Targeted genes | Improved traits | References |
|---|---|---|---|
| Rice (*Oryza sativa* L.) | SBPase | Salt tolerance improvement | Feng *et al*., 2007a |
| Tomato (*Solanum lycopersicum*) | FBA1, RCA1, FBP5 and PGK1 through Brassinosteroids | Enhanced CB regulation and photosynthesis | Yin *et al*., 2022 |
| Tobacco (*Nicotiana tabacum*) | SBPase and FBPase | High biomass and more efficient photosynthesis | Li *et al*., 2022 |
| Wheat (*Triticum aestivum*) | SBPase | Improved photosynthesis | Driever *et al*., 2017 |
| Tomato (*Solanum lycopersicum*) | SBPase | Cold tolerance improvement & better photosynthesis | Ding *et al*., 2017 |
| Tobacco (*Nicotiana tabacum*) | FBPaldolase | High biomass and better photosynthesis | Uematsu *et al*., 2012; Simkin *et al*., 2015 |
| Tomato (*Solanum lycopersicum*) | FBPaldolase | Increased seed weight | Cai *et al*., 2022 |
| Rice (*Oryza sativa* L.) | SBPase | Increased heat tolerance | Feng *et al*., 2007b |
| Tobacco (*Nicotiana tabacum*) | FBP/SBPase | Higher biomass and photosynthesis | Tamoi & Shigeoka, 2005 |
| Tobacco (*Nicotiana sylvestris*) | *AaPEPC1* gene from *Agave americana* | Higher rates of photosynthesis & biomass Improvements tolerance to salt & drought | Liu *et al*., 2020 |

FBPA enzyme is commonly perceived as a non-regulated and mainly controlled through changes in gene expression or protein turnover. The enzyme reversibly reacts with G3P and DHAP allowing the synthesis of fructose-1,6-bisphosphate (FBP). In addition, it catalyses the reaction between erythrose-4-phosphate and DHAP leading to the formation of sedoheptulose-1,7-bisphosphate (Haake *et al*., 1999). Nonetheless, through modeling and transgenic studies, the functions of enzymes like TK and FBPA in the regulation of photosynthesis have been suggested as non-regulated. Therefore, these enzymes are currently being considered in overexpression studies to evaluate their effects on plant growth and carbon fixation (Uematsu *et al*., 2012).

The process of genetic engineering was utilized by scientists to insert the FBPA gene, which is expressed in the plastid of Arabidopsis into the transgenic plant of tobacco (*Nicotiana tabacum*). Increased RuBP and its precursor levels were the consequence of this treatment, along with the decrease in 3-phosphoglycerate. Consequently, the elevated photosynthetic rates were mainly caused by a 1.4 to 1.9 times bigger FBPA activity, especially under high $CO_2$ concentrations, which was also a factor in the formation of more biomass (Uematsu *et al*., 2012). Previous research has suggested that one of the determinants in the CB cycle is the RuBP regeneration rate, which can be affected by the activities of certain enzymes, including FBPA and SBPase (Haake *et al*., 1999). When the stomata are completely open, the RuBP regeneration rate limitations can inhibit the assimilation of $CO_2$. On the other hand, the increased availability of RuBP through the overexpression of SBPase has been found to promote photosynthesis and biomass accumulation (Harrison *et al*., 1997; Lefebvre *et al*., 2005; Tamoi *et al*., 2005). Moreover, it has been established that the increased activity of SBPase leads to better photosynthetic performance and higher crop yield even in adverse conditions, such as drought and high temperatures, owing to the support provided to the Rubisco chaperones and activase by the increased SBPase activity (Feng *et al*., 2007).

Recent studies demonstrate that co-overexpression of SBPase and cytosolic FBPase in transgenic tobacco leads to increased biomass (Li *et al*., 2022). As another target for enhanced photosynthetic efficiency, the combination of triose phosphate isomerase (TPI) and other enzymes from the CB cycle could lead to improved carbon assimilation because it solves the triose phosphate restriction (Suzuki *et al*., 2022). The increased expression of CB cycle genes FBA1, RCA1, FBP5 and PGK1 through the Brassinole resistant 1 transcription factor leads to more efficient photosynthesis in Tomato (Yin *et al*., 2022). Moreover, recent studies on the molecular and genetic regulation of photosynthesis have focused on areas such as genetic engineering and transcription factors to improve photosynthetic efficiency. Such advances are vital for enhancing crop yields and addressing food security. Building on this work, the genetic modification of photosynthetic pathways, including the CB cycle, has demonstrated potential increases in crop yields that surpass 40% across different environmental conditions (Simkin *et al*. 2020). In parallel, genetic and biochemical changes occurring through the activation of stress-response genes have been found to support the process of photosynthesis under environmental stress conditions (Angon *et al*., 2022). For example, the thermophilic *Ziziphus spina-christi* species demonstrates improved photosynthetic performance when the temperature reaches its optimal range (Zait *et al*., 2019). In addition, scientists have made genetic advancements that enhance plant resistance to salt and drought through enhanced proline production and improved carbon metabolic pathways (Liu *et al*. 2021). The combination of these findings and modeling advancements creates opportunities to redesign the CB cycle for maximum performance enhancements (Raines, 2022).

**Synthetic biology and omics approaches for optimising photosynthesis:** Synthetic biology is a rapidly advancing interdisciplinary field that bridges biology and engineering, facilitating the reprogramming of cellular systems to improve agricultural productivity. The field of synthetic biology has developed new techniques that enhance photosynthesis and biohybrid systems through improved light harvesting and energy conversion methods. The main approaches combine three strategies: engineering plant carbon fixation systems, developing new RuBisCO enzymes and using C4 metabolic pathways as carbon-concentrating systems to increase biomass output (Kubis & Bar-Even, 2019). In this context, polychromatic solar energy conversion systems have been developed by combining photosynthetic proteins from different organisms to achieve improved light absorption and energy conversion capabilities (Liu *et al*., 2020). Similarly, optogenetics uses light to achieve precise control over gene expression and protein interaction processes (Baumschlager 2022). Building on these advances, artificial photosynthesis uses biohybrid systems to combine biological elements with

synthetic nanomaterials, enabling efficient solar-to-chemical conversions (Brown & King, 2020). In parallel, the development of living photovoltaic systems aim to enhance electron transport and boost solar energy transformation efficiency, linking these innovations to broader goals in sustainable energy and agricultural productivity (Schuergers, 2017; Khan *et al*., 2025).

Research using omics methods—genomics, transcriptomics, proteomics and metabolomics—has been instrumental in improving both crop yields and photosynthetic efficiency. By integrating multi-omics data, researchers can determine how crop genomes connect with their phenotypes, helping them design new crops that produce high yields while withstanding climate change (Yang *et al*., 2021; Mahmood *et al*., 2022). This method supports the development of plant traits that boost photosynthetic efficiency and increase plants' ability to tolerate environmental stress conditions. Current research shows that machine learning, together with integrative omics, successfully enhances genotype-to-phenotype predictions while revealing regulatory networks in wheat and rice. In addition, the combination of omics research with CRISPR technology has led to rapid advancements in modifying the essential genes that control photosynthesis and stress response mechanisms (Chen *et al*. 2024; Bradbury *et al*. 2025). Despite existing obstacles in data handling and verification, future research aims to merge multi-omics with artificial intelligence and remote sensing technologies to advance breeding processes and monitor photosynthetic patterns (Mushtaq *et al*., 2025; Khan *et al*., 2025).

**Future perspectives:** Even though the CB cycle is present in all plant organisms and has been conserved through evolutionary processes, there are still several major gaps in our knowledge (Raines, 2022):

**1.** The natural diversity of separate enzymes, as well as the intricate molecular mechanisms that control the regulation of certain genes, are still not fully revealed (Wang *et al*., 2017; Raines, 2022). If these gaps are bridged, we would get a better understanding of the relationship between the structure and the function of the CB cycle enzymes, especially the roles of amino acids, whether they are conserved or not, in the process of catalysis. The rapid development of whole-genome sequencing, including that of the major agricultural crop species, the advent of omics technologies, eQTL mapping, and bioinformatics, has all combined to make it possible to study these mechanisms in new ways. For instance, researchers studying the tree species *Populus tomentosa* found 40 transcription factors that might be involved in the regulation of the 46 genes of the CB cycle (Wang *et al*., 2019).

**2.** The question of how carbon allocation is regulated and how it interconnects with the local metabolic pathways has not yet been thoroughly answered. A study of the intermediates in the CB cycle of both C3 and C4 plants showed that there is a significant as well as diverse presence of the CB cycle in C3 plants. (Stitt *et al*., 2021). In a comparative study with *Arabidopsis* and rice, it was revealed that although both these C3 species decreased their activity of certain reactions during low light, their priorities were different (Borghi *et al*., 2019). Therefore, such studies indicate that the measures for the improvement of the photosynthetic efficiency of a crop must be according to the crop, and it is very prominent that the systematic analyses at the species and even the cultivar levels are necessary. Though profiling the metabolism may not be a fast, automatic screening process, the data generated through these studies could still be of great help in the formation of predictive models and the management of species-specific interventions under various environmental conditions. (Raines, 2022).

## Conclusion

This review pointed out the main targets and methods to increase the efficiency of photosynthesis, spotlighting their tremendous potential impact on yield increase. The most important and necessary next step is to fuse these different methods together into one comprehensive and coherent framework. A united and single approach that includes betterment of Rubisco activity, speeding up of electron transport, use of new pigments, canopy structure tuning, and stomatal behaviour and environmental response optimisation, could be the ultimate productivity claiming. Yet, seamless merging of all this together demands thorough checking of the possible interplay of positive and negative interactions among these traits, considering the notion of their gaining significant advantage in a field situation. It is not just a matter of stacking the traits one on top of another, but also knowing how they will interact in the complicated agro-ecosystems, for instance: plant development, source-sink dynamics, stress response, and the conditions under which photosynthesis becomes the limiting factor for yield. The need for a comprehensive strategy that does not stop at improving photosynthetic efficiency but also encompasses traits that confer stress tolerance (abiotic as well as biotic) and water and nutrient use efficiency, and helps to reduce the yield gap across different environments. The main thing is, the enhancement of primary productivity opens up new avenues for crop design. The extra carbon dioxide fixing might either bolster production or be rerouted in such a way that no compromise is made on productivity, to increase the vegetative biomass for nutrient and water uptake facilitation and soil health fostering by raising organic carbon levels. The goal in the end is to create new crop varieties that not only yield more but also possess and are capable of adapting to and being resilient in various and changing agricultural environments; thus, the global problem of food security is tackled.

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