

REVIEW

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Optimization of photosynthesis for sustainable crop production

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Abstract

Crop production will need to increase by about 60% to satisfy the demand of food for the fast-growing population globally. A number of recent studies have provided strong support demonstrating that improving the photosynthetic efficiency via different systems can provide an avenue to improve yield potential of crops. Photosynthesis is a regulated system that drives biological processes including crop yields. Hence, this review focuses on improvement of the efficiency of photosynthesis via different mechanisms; decreasing photorespiration, transforming C3 crops to C4 pathway, optimization of Calvin Benson cycle / Rubisco, and electron transport. Further work should be done on transgenic crops with modified photosynthesis. Optimization of the activity of Rubisco may not be successful in some moisture stress areas, and consideration of photoprotection could offer some advantages. Optimization of source-sink relationship would represent another promising way to improve crop yield. A strong sink can increase crop yield even under stress conditions.

Keyword: Calvin cycle, photorespiration, Rubisco, Yield

Demand and supply of crop production

According to a United Nations estimate released in June 2019, the global population is predicted to reach 9.7 billion by 2050, an increase of 2 billion people from current levels (Arora 2019). Food production will need to increase by about 60% to fulfil this fast-growing demand, requiring 593 million additional hectares of agricultural land (Yu et al., 2016). The "land gap," as defined by the World Resources Institute, is the difference between what is available today and what will be required in the future, and it has significant climate implications. Closing the land gap, by not taking up any additional land to feed the world in 2050, must be a part of a sustainable plan as we approach 2050 (Searchinger et al., 2018).

Agricultural production is a significant contributor to climate change, which means expanding agricultural land to feed the world in 2050 is not really a sustainable

solution (Fróna et al., 2019). According to the World Resources Institute, food production now occupies 37 percent of land on Earth (excluding Antarctica) and accounts for approximately a quarter of global greenhouse gas emissions. More land being used for crops would entail sacrificing vital world ecosystems like forests, which help to moderate our climate and enhance air quality (Searchinger et al., 2014).

To counteract the environmental impacts caused by widespread agriculture and land clearance, it will be important to meet global food demands without expanding the quantity of cultivable land available, highlighting the importance of improving crop yields. Furthermore, any yield enhancements will need to be coordinated with global climate change, considering atmospheric (CO₂) levels anticipated to rise from 409 to 550 ppm by 2050 (Pawlak & Kołodziejczak, 2020).

The aim of this paper is to provide an overview of the current work to improve photosynthetic efficiency. This review explores the different mechanisms by which the efficiency of photosynthesis can be improved to improve crop production and productivity. Decreasing

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photorespiration, transforming C3 crops to C4 pathway, optimization of Calvin Benson cycle / Rubisco and electron transport are some of the mechanisms discussed in this review.

Photosynthesis and crop productivity

Photosynthesis is necessary for all life on Earth; it is required by both plants and animals. It is the only biological activity capable of capturing energy from space (sunlight) and converting it into chemical molecules (carbohydrates) that all organisms utilize to fuel their metabolism. Photosynthesis is a fundamental process that produces oxygen, regulates the climate, and stimulates physiological processes such as crop yields. Yield is the aggregate of the effects of a variety of factors on a number of physiological and morphological processes. Indeed, there has yet to be shown a direct cause–effect relationship between photosynthesis and yield (Liliane & Charles, 2020). Photosynthesis is a well-studied process with models of the limitations in the photosynthetic pathway (Paul, 2021). A substantial effort has been made during the last few years to improve the efficiency of photosynthesis, with the justification that due to the plateauing of main crop yields, crop production gains must be quick and big (Swift et al., 2019). Because the harvest index (HI) has been improved, the next hurdle is photosynthesis. Despite a number of fascinating examples of genetic modification in models (*Arabidopsis* and tobacco) as well as field trials, crop yields have yet to improve from this study (Furbank et al., 2015; Głowacka et al., 2018). Given long-standing evidence and well-reasoned arguments dating back to the 1970s that carbon intake is not a limiting factor for crop growth and production, the focus on photosynthesis has been controversial (Beaupre, 2016; Sinclair et al., 2019).

The failure of photosynthetic research to deliver real improvements in crops so far is drawing increasing criticism with recommendations for a more balanced approach (Araus et al., 2021; Long et al., 2006). However, a recent study found that overexpressing of Rubisco in paddy rice enhances yield in the field by 17–28% when nitrogen is available (Yoon et al., 2020; Zhao et al., 2019). This looks to be the first time photosynthesis has been targeted directly in the field in an important food security cereal crop.

Crop yield is a result of an entire system. So, photosynthesis provides the carbon and energy that the entire system relies on, but this interaction is not linear and is influenced by several factors such as development, leaf and canopy structure and architecture, source-sink relationship, and how photosynthesis is affected within a field crop (Paul, 2021). Furthermore, the outdoor environment, which differs greatly from the laboratory or

greenhouse, has a strong influence on photosynthesis and growth (Flore, 2011). Such interactions and feedbacks really do have a powerful impact on photosynthesis that understanding of individual components as yield limiting factors becomes almost useless in the midst of the system. Long-standing evidence demonstrates that past crop output gains are not connected with enhanced photosynthesis (Sinclair et al., 2019). There has been no increase in carbon exchange rate per unit leaf area for many crops (Richards, 2000; Srinivasan et al., 2017).

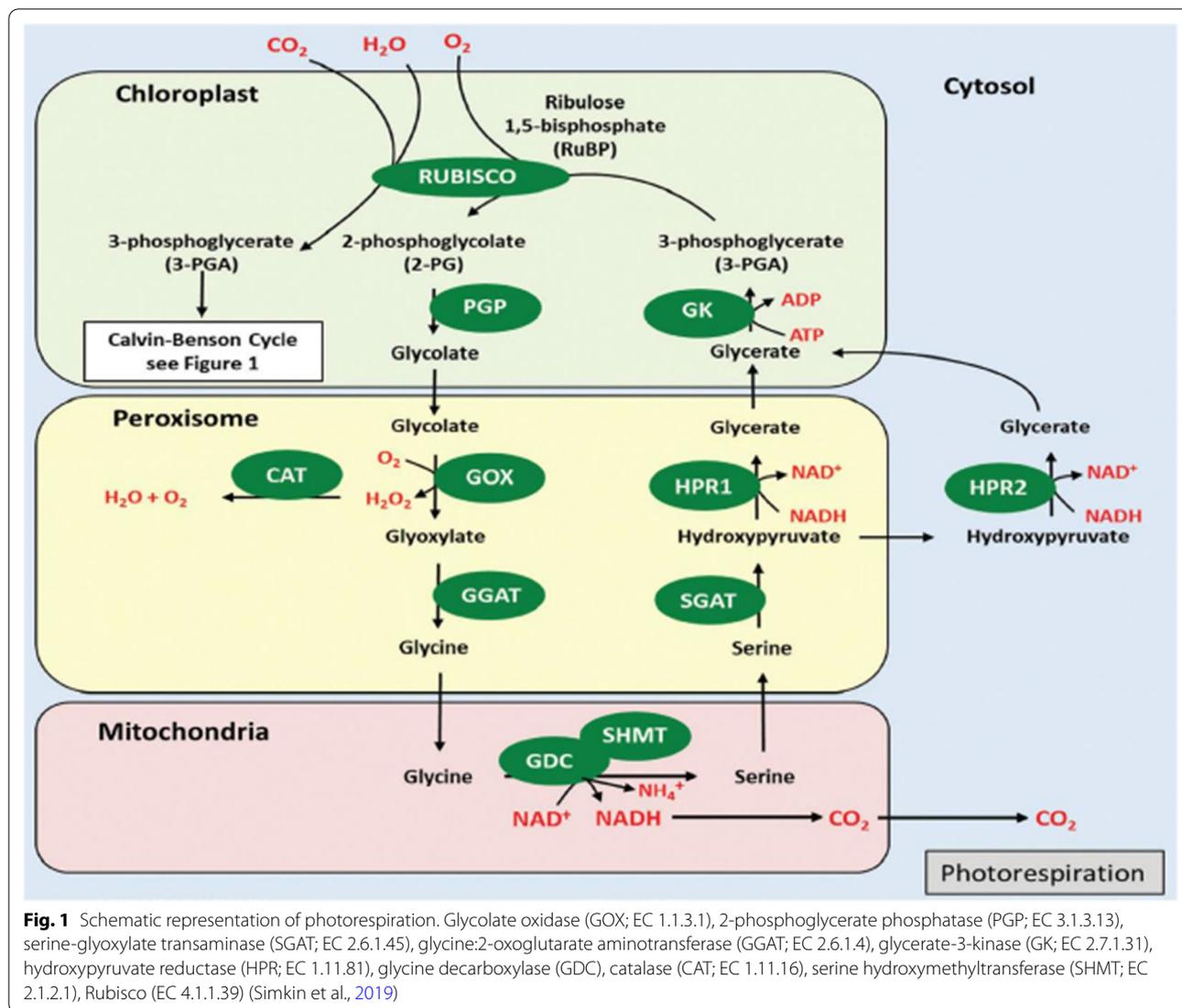
Mechanism to improve efficiency of photosynthesis

Several strategies to improve the efficiency of photosynthesis have been proposed. Decreasing photorespiration, transforming C3 crops into C4, Optimization of Calvin cycle and electron transport are some of the mechanisms which will be discussed in this paper. Reducing light-harvesting antenna size, introducing components of algal CO₂-concentrating mechanisms, engineering of photorespiratory bypasses, and accelerating recovery from photoprotection (NPQ) are strategies which are also recently proposed.

Decreasing photorespiration

In addition to Rubisco's carboxylation process, in which CO₂ is added to RuBP, resulting in carbon flow through the CB cycle, the Rubisco enzyme also performs a competing reaction that results in O₂ fixation (van Lun et al., 2014). Rubisco's oxygenase activity competes with CO₂ fixation at the active site (see Fig. 1), thus oxygen is added to RuBP instead of CO₂, resulting in the synthesis of a molecule of 3-phosphoglycerate (3PGA) and a molecule of 2-phosphoglycolate (2PG) at the cost of one ATP and one NAD(P)H (Paul, 2021). 2PG is recycled into 3PGA in the photorespiratory pathway, which occurs in three organelles (chloroplast, peroxisome, and mitochondria) as well as the cytosol. It was found that this mechanism may recover 75% of the carbon, with the remaining 25% being released as CO₂ in the mitochondria (Peterhansel et al., 2010). Although photorespiration inhibits the build-up of 2PG and the metabolite's subsequent inhibition of CB, it comes at a significant energetic cost.

For all steps leading to glycine formation, this mechanism also generates one molecule each of hydrogen peroxide (H₂O₂) and ammonia (NH₃) for two oxygenation events. H₂O₂ and NH₃ have been shown to function as signaling molecules with important roles in plant fitness, including disease resistance and nitrogen assimilation (Simkin et al., 2019); however, both of these molecules can be toxic if they accumulate to high levels (Peterhansel et al., 2010), and NH₃ re-assimilation via glutamine synthetase (Éva et al., 2019; Huma



et al., 2018; Kromdijk et al., 2016). Photorespiration has long been a target in attempts to increase photosynthesis for these reasons. There have been a variety of ways targeted at engineering photorespiration with the goal of enhancing crop productivity, as discussed previously (Schuler et al., 2016).

Furthermore, even in future climates with higher carbon dioxide levels, photorespiration will have an impact on yield, with models predicting a 12–55 percent increase in gross photosynthesis in the absence of photorespiration, even under climate change scenarios with the highest carbon dioxide levels in the atmosphere. Despite the fact that photorespiration is linked to other vital metabolic functions, the benefit of increasing its efficiency appears to outweigh any potential side effects (Walker et al., 2016).

Photorespiration (also called the oxidative photosynthetic carbon cycle or C₂ cycle) is a plant metabolic process in which the enzyme RuBisCO oxygenates RuBP, losing some of the energy gained by photosynthesis (Timm, 2020). Despite the fact that photorespiration has been ascribed metabolic and defensive tasks, its negative impact on crop productivity has been proved by the fact that doubling CO₂ concentration considerably improves the performance of various crops (Morales et al., 2020). Under ideal conditions, theoretical models suggest that eliminating photorespiration will enhance the yield. However, it has been shown that completely blocking photorespiration metabolism downstream of Rubisco is inefficient (Busch, 2020), and it is unclear what consequences this might have in stressed plants. It's considered that simply restricting photorespiratory flux without

changing oxygenation causes an undesirable build-up of intermediates (Tcherkez et al., 2017). A study by Kebeish et al., (2007) found that diverting part of the chloroplast glycollate straight to glycerate resulted in a partial reduction in photorespiratory metabolite flux and enhanced biomass production. This method preserves any potential protective role for photorespiration while also allowing plants with more efficiency to perform effectively under less favorable conditions (Shim et al., 2020).

Transforming C3 crops into C4

Plants that follow C4 photosynthetic pathway such as maize, sorghum, and sugarcane, approximately have 50% higher photosynthesis efficiency than those of C3 plants such as rice, wheat, and potato (Wang et al., 2012). This is because C4 crops can concentrate CO₂, reducing oxygenase activity and improving photosynthetic efficiency (Lara & Andreo, 2011; Peixoto, 2014). CO₂ concentration is achieved through the C4 pathway, which requires phosphoenolpyruvate carboxylase's first fixation of CO₂ into C4 acids (PEPC) (Paulus et al., 2013). CO₂ is generated from the C4 acids in the following stage of the process, and Rubisco fixes it. It has been questioned if the C4 route can be introduced into C3 crops like rice (Gowik & Westhoff, 2011). This is the only way to achieve a significant increase in biomass output to maintain the necessary yield enhancement. This is an ambitious undertaking but the underlying science is compelling and is attracting more attention (Lappe et al., 2018; Paul, 2021).

Initially, rice genes encoding C4 enzymes such as PEPC, pyruvate orthophosphate dikinase (PPDK), and NADP-malic enzyme (NADP-ME) were used to alter rice (Ermakova et al., 2021). Potato (*Solanum tuberosum*) (Ruan et al., 2012) and tobacco (Yadav & Mishra, 2020) have undergone similar modifications. The underlying processes of these benefits have not been verified, despite reports of higher assimilation rates and some C4 characteristics. Importantly, these techniques overlook the fact that, while C4 and C3 carboxylation can occur in a single cell in some species (Lara & Andreo, 2011), the C4 route in the most prolific species is dependent on Kranz architecture (Covshoff et al., 2014). This results in a spatial separation of ambient CO₂ fixation in mesophyll cells from CO₂ fixation in bundle sheath cells, preventing CO₂ leakage from the mesophyll to the atmosphere and maintaining a suitable CO₂:O₂ ratio at the Rubisco site in the bundle sheath (Cotton et al., 2018; Ducat & Silver, 2012).

Changing cellular differentiation, enzyme partitioning, chloroplast shape, and varied metabolic pathway regulation in each cell type appears immensely complex at first glance. However, evidence that the two metabolic methods coexist in both C3 and C4 plants (Valiela et al., 2018),

that species can switch between C3 and C4 depending on environmental conditions (Chamaillé-Jammes & Bond, 2010), and that C4 evolution has happened independently at least 45 times in angiosperms provide hope (Rowan F Sage et al., 2012). As a result, rather than constructing a single-cell system, much of the present attention is on achieving Kranz anatomy (Luo et al., 2018; Xu et al., 2012).

Even though many attempts have been made in the past to introduce the C4 mechanism into C3 plants, none of them have been successful, owing to a lack of system-level understanding and manipulation of the C3 and C4 pathways. Elucidating not only the processes that control Kranz anatomy and cell-type-specific expression in C3 and C4 plants, but also a thorough understanding of the gene regulatory network underlying C3 and C4 photosynthesis, will be helpful to reengineer C3 crops to C4 pathway (Cui, 2021).

Optimization of calvin cycle / rubisco-related targets

The Calvin-Benson-Bassham (CBB) cycle is responsible for CO₂ assimilation and carbohydrate production in oxyphototrophs. Improving the performance of the CO₂-fixing enzyme ribulose biphosphate carboxylase oxygenase (Rubisco) is among the targets for increasing crop yields. Rubisco has been the focus of several of the proposed ways to improve crop leaf CO₂ absorption rates. Rubisco catalyzes the CO₂ fixation process into a three-carbon molecule (C3 photosynthesis) (Moroney et al., 2013; Spangle, 2016). At ambient concentrations, however, O₂ significantly competes with CO₂, resulting in the creation of phosphoglycollate, which is broken down to release CO₂ in a process known as photorespiration, lowering photosynthetic efficiency (Ghosh & Kiran, 2017). The quantity and in vivo activity of Rubisco are regarded as a rate-limiting factor for carbon fixation under present atmospheric CO₂ and O₂ concentrations and saturating light (Salesse-Smith et al., 2018).

Increasing the Rubisco content in leaves is one straightforward way to get around this constraint.

In theory, increasing the total amount of photosynthetic equipment per unit leaf area can enhance the rate of light-saturated photosynthesis per unit leaf area. In practice, there is an ideal concentration of leaf N, which is governed in part by intra-leaf shading-induced leaf thickness restrictions. The amount of protein that can be stored in the chloroplast and the number of chloroplasts in the mesophyll cell are likewise limited (Morales et al., 2020; Ort et al., 2015).

To counterbalance for its relative inefficiency, plants store substantial amounts of Rubisco in their leaves, which can contribute for 15–30% of total leaf N in C3 plants (R F Sage, 2013). Furthermore, increasing the

plant's N investment, which necessitates an even higher rate of N fertilization, is not sustainable in future crops. High oil costs and crop systems' poor nitrogen use efficiency (NUE), which is around 33% for cereal crops (Lemaire & Ciampitti, 2020), appear to make this alternative unviable, highlighting the urgent need to enhance cereal crops' NUE. The subject of whether N is allocated efficiently across photosynthetic components has gotten a lot of attention recently (Andreiadis et al., 2011).

Increased Rubisco content without additional N input, on the other hand, may drive the plant to relocate its internal N, reducing the amount of other critical enzymes and creating new CO₂ fixation bottlenecks. This could be one of the reasons why altered plants with higher Rubisco levels don't have better photosynthesis (Makino, 2003; Suzuki et al., 2017). It's been debated if such a high Rubisco concentration in leaves is necessary. Excess Rubisco buildup has been discovered in plants with lower Rubisco concentration (Takagi et al., 2020). Similarly, some rice types have been discovered to accumulate Rubisco in excess of what is required to maintain measured photosynthetic rates (Ishikawa et al., 2011). In most crops, light limitation affects a large percentage of the canopy, especially when the maximum LAI is reached, and for such plants, lowering the Rubisco level could enhance the NUE. Moreover, it has been argued that, if atmospheric CO₂ levels rise, a drop in Rubisco levels may be beneficial (Murchie et al., 2009), because photosynthetic NUE is higher in plants cultivated at higher CO₂ levels even at current CO₂ levels.

Rubisco, on the other hand, serves as a huge reservoir of nitrogen that is mobilized for grain N content and new tissue formation (Yoneyama et al., 2016). The total amount of Rubisco and the time of its degradation are both important, but it's unclear how the balance between Rubisco's position as a N store and its photosynthetic function is maintained (Pereira, 2019). By boosting Rubisco activity, it may be able to increase NUE by obtaining the same absorption rate with less protein. The enzyme Rubisco activase determines the fraction of Rubisco active sites that are free of inhibitors and hence capable of catalysis, while a number of inhibitors determine the activity of Rubisco (Hazra et al., 2015). It's been suggested recently that the management of Rubisco activity isn't optimum for maximum crop yield, and that Rubisco activase could be a good target for manipulation (Turumtay, 2015).

An alternate technique for improving Rubisco is to boost its selectivity for CO₂ over O₂ by manipulating the enzyme directly (Bhatia et al., 2019). In terms of specificity, there is evidence of biological variety. Rubisco forms found in plants of the genus *Limonium* that have been adapted to stress have a greater specificity factor than

those found in many crop plants (Galmes et al., 2014). Nevertheless, Rubisco forms with high CO₂ specificity have low maximum catalytic rates of carboxylation per active site, and there is a well-known inverse relationship between these two properties (Studer et al., 2014).

Electron transport

Another strategy for increasing photosynthetic carbon uptake and production is to manipulate the photosynthetic electron transport chain. It was recognized that increased electron transport can lead to increased plant development (Michelet & Krieger-Liszkay, 2012). These researchers discovered that expressing the algal (*Porphyra yezoensis*) cytochrome (Cyt)c6 in Arabidopsis chloroplasts increases chlorophyll and starch content, as well as ATP and NADPH levels (Simkin et al., 2017).

CO₂ assimilation, photosynthetic electron transport efficiency, and biomass all increased as a result of these improvements (Yamori et al., 2016). In response to copper deprivation, Cyt6 has been demonstrated to replace plastocyanin as an electron transporter in cyanobacteria and green algae (Ort et al., 2015). In vivo, (Chida et al., 2007) showed that algal Cyt6 can transfer electrons from the Cytb6f complex to Arabidopsis PSI at a quicker rate than Arabidopsis' native plastocyanin (Simkin et al., 2017). When the Cyt6 gene from *Ulva fasciata* was overexpressed in tobacco, similar consequences were seen (S. K. Yadav et al., 2018). When compared to controls, these researchers noticed a rise in photosynthetic rates, enhanced water use efficiency, and greater growth (Timm et al., 2018). Hence, manipulation of the photosynthetic electron transport chain is another potential option for improving photosynthetic carbon assimilation thereby improving crops yields.

Conclusions and further opportunities

Even though opportunities for enhancing yield through single and multigene manipulation of various photosynthesis processes has been clearly demonstrated, it is unlikely that these alone will provide the large increases in yield required to feed our increasing population in a changing global environment under all conditions and in all crop species.

What new measures will be required in the future to achieve the increase in yield required to support the world's rising population? In addition to the targets addressed in this analysis, it is anticipated that a combination of photosynthesis-related features will be required. This might include, for example, short-circuiting the NPQ relaxing process and minimizing photorespiratory losses by adding novel biosynthetic routes. Although the focus of this review has been on photosynthesis, which increases source capacity, it is likely that it

will also be necessary to address the sink status of plants with enhanced source capacity. The source/sink balance has been the subject of two recent papers, and the potential for combining improvements in both source and sink capacities was highlighted (Paul et al., 2020; Sonnewald & Fernie, 2018).

Improving photosynthesis is one strategy for improving yield potential, but in order to offer resilience, it will be essential to close the yield gap, which will necessitate improvements in water use efficiency (WUE), nitrogen use efficiency (NUE), and biotic and abiotic stress response. In these areas, too, some progress is being made.

Changes in the plastoquinone pool's oxidation state have been proposed as a way to control stomatal movement (Wang et al., 2016) and the PsbS transgenics experiments revealed a linear relationship between stomatal conductance and QA redox values, resulting in decreased stomatal opening in response to light and increased WUE. Furthermore, attempts to boost NUE in a variety of plants, including tobacco, wheat, and rice, have been documented, with higher biomass and grain yield as a result of overexpression of glutamine synthetase (James et al., 2018; Thomsen et al., 2014).

New breeding techniques, such as genome editing approaches for endogenous genes and synthetic biology to manufacture designer promoters and proteins, will be necessary in order to reach the goals required to feed the expanding population (Simkin et al., 2019).

Given the complexity of the processes involved, modeling will be critical in enabling the identification of novel targets. The creation of novel promoters for use in crop plants, which are currently limited, as well as the adoption of new technologies that allow the quick, efficient, and affordable insertion of many transgenes into plants, will be required to realize the full potential of these opportunities. Regulations controlling the use of genetic alteration and genome editing technologies will need to be addressed if these prospects are to be fully realized.

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