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Review

Bioengineering of Canopy Photosynthesis in Rice for Securing Global Food Security: A Critical Review

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Abstract: The emerging threat of climate change is posing a scientific conundrum for global food and nutritional security. As a primary staple food, half of the global human population is supported by rice crop. Thus, enhancing rice yield is highly critical to ensure food security. Photosynthesis is the defining physiological process of plants that determines maximum attainable yield. Efficiently capturing solar radiation and converting the carbon assimilates into rice grain is critical to achieve high yield. Genetic interventions to modify the plant architecture for enhanced light capture can improve rice yield significantly. Enhancement of cellular photosynthesis by synthetic biology approaches targeting important nodes of the light harvesting and carbon assimilation pathways are critical for breaking yield ceiling. The possible targets for improving photosynthesis include the light capture, chloroplast electron transport, Calvin cycle enzymes, sugar transport mechanisms, minimization of photorespiration, and improving source–sink relations. Conversion of C_3 rice into a C_4 type plant is also an option being vigorously pursued. Here, we review the determinants of canopy photosynthesis in rice with special reference to genetic factors and cellular photosynthetic capacity.

Keywords: chloroplast; CO_2-concentrating mechanisms; crop modeling; productivity; radiation use efficiency; QTL

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1. Introduction

As an outcome of the green revolution, rice (*Oryza sativa* L.) became the staple food for nearly half of the global population. In 2020, the global rice production was 756.7 million tons from a cultivated area of 164.2 million ha [1]. Rice is mostly cultivated in hot and humid climates, with a global average yield of only 4.6 t ha^{-1} [2]. Rice belongs to the genus *Oryza*, tribe Oryzeae, subfamily *Bambusoideae*, family Poaceae. Out of total 24 species under the genus, only two species, *Oryza sativa* and *Oryza glaberrima*, are cultivated. *Oryza sativa* constitutes three subspecies, namely, indica, japonica, and javanica. Indica rice is long/short-grained with nonsticky texture after cooking, predominantly cultivated in tropical regions. Japonica is short-grained and glutinous (hence, sticky), and is widely cultivated in the subtropical and temperate regions of East Asia [3]. Adoption of high-input responsive dwarf rice cultivars since the green revolution, along with the investment in irrigation facilities, has played a crucial role in increasing the global production of rice, and it is estimated that global production of rice will reach 550 million tons by 2030 [4]. Rice uses 34–43% of the global irrigation water and is responsible for the withdrawal of 24–30% of the world's total freshwater [5]. Thus, an increase in per-unit resource is critical to meet Sustainable Development Goals (SDG) 1 (No poverty), SDG 2 (Zero hunger), and SDG 13 (Climate action) [1].

In light of the great importance of rice crop in sustaining a huge population amid the challenges of climate change and resource degradation, a strong research boost is required to break yield barriers and boost rice productivity [6]. A major goal of rice researchers worldwide is to develop a new plant type (NTP) of rice with enhanced canopy photosynthetic efficiency. Varieties based on such plant type are expected to have a productivity of 12.5–13 t ha^{-1}. These newly defined plant types could also be used to develop hybrid rice varieties with a yield advantage of about 25% over any of the parents. Such hybrids with yield potential of 15 t ha^{-1} are expected in the near future [7,8]. Thus, genetic improvement of photosynthesis in rice can greatly contribute to boosting yield potential.

Photosynthesis is the major driver of life on Earth. Modulation of photosynthesis can provide novel solutions for increasing yields [9]. More than 90% of the biomass and yield of crops is derived from photosynthesis, and the remaining is from the absorbed and assimilated minerals. Escalating photosynthetic efficiency and capacity would better utilize the solar energy and atmospheric carbon dioxide (CO_2) that can be translated into yield [10,11]. Various genetic and physiological traits have been identified and targeted for enhancing photosynthesis. This would subsequently help in increasing grain yield potential to secure a new "green revolution" [12,13]. Modern breeding techniques assisted by genomics as well as functional biology approaches enabled the identification and utilization of candidate genes for photosynthetic enhancement [14,15]. There is a need to redesign plant systems at a systems biology level to target enhancing crop yield through improved photosynthetic efficiency [16,17]. In this review, we examine the potential constraints in rice photosynthesis and the strategies to overcome them.

2. Approaches for Improving Rice Productivity

2.1. Improving Radiation Use Efficiency

Out of the total solar energy reaching the Earth's crust, nearly 48% is photosynthetically active radiation (PAR) [18]. The highest energy conversion efficiency of the PAR received from the Sun is about 2.4 and 3.7%, respectively, for C3 and C4 crops [19]. The intercepted PAR (IPAR) is the total solar radiation intercepted by the crop canopy, which depends upon canopy architecture, size, and duration of leaf area. For estimating crop growth, researchers have been widely utilizing the concept of RUE [20]. The IPAR is measured using probe PAR sensors, where PAR from the top of canopy as well as below the canopy is measured. Radiation use efficiency (RUE) is the quantity of biomass accumulated per unit of photosynthetically active radiation (PAR) intercepted by the crop canopy. Hence, grain yield is a function of IPAR × RUE × Harvest index [21].

For enhancing RUE, traits such as high chlorophyll content, photosynthetic metabolism, source–sink relations, and harvest index have been attempted in different crops [22,23]. Under optimal growing conditions, plants with extended leaf area duration trap more radiation. The length of the grain filling period is the prominent factor that contributes to grain yield in rice [24]. In addition, yield is determined by light capture efficiency, biomass conversion efficiency from light, and partitioning coefficient to grain [25]. The protein editing on Rubisco for doubling its specificity for CO_2 has the potential to increase Pn (net photosynthetic rate) at saturating light intensities by 20% [26,27]. Thus, both enhancing the canopy photosynthesis and photosynthetic efficiency and rate at unit leaf levels give great potential for enhancing RUE in crop plants [28].

Studies on yield improvement in rice suggest that increase in yield potential can be achieved predominantly through IPAR [29] or higher RUE [30], depending upon the genotypes studied. Comparison of a super hybrid rice cultivar Yliangyou 3218 (YLY) and an inbred super rice cultivar Zhendao 11 (ZD) revealed that yield advantage of YLY is due to its faster green leaf area index (GLAI) formation, greater maximum GLAI (GLAImax), and 54.7% higher radiation use efficiency (RUE) than that of ZD before heading [31]. In crop canopy, actively photosynthesizing cells can experience rapid changes from high to low light and vice versa as a cloud masks or crosses the path of the sun. In another daily situation, the continuous change in solar angle can mask one leaf from another. This

shifts the mesophyll cell from light-saturated to light-limited condition, together with dissipation of incident radiation, as heat can lower the efficiency of photosynthesis [32,33]. Among the sunlit and shaded leaves in rice, the lower leaves exhibited stronger absorbance and lower reflectance [34]. During senescence or under certain conditions by proteolysis, Rubisco is degraded and the resultant amino acids will be accumulated in protein bodies for storage. These proteins could be reutilized for the synthesis of certain vacuolar proteins in paraveinal mesophyll that assist nutrient remobilization in plants towards sinks [35].

Improving RUE of canopy for photosynthesis in place of extrapolating from the leaf data for photosynthesis holds great potential. Crop modeling using dynamic systems of canopy photosynthesis could be used to design the optimal canopy architecture that promotes physiological parameters aiming to maximize CO_2 uptake. Modern crop geneticists can inculcate such canopy models by germplasm survey, followed by breeding programs. Such models are promising in genomics-assisted breeding and phenotype modification of crops to enhance RUE [36].

2.2. Improving Canopy Photosynthesis

Plant architecture is the three-dimensional organization of the aboveground part of the plant in space in the field. It is determined by tillering pattern, plant height, surface characters, specific leaf weight, number and arrangement of leaves, inflorescence structure, number of panicles, and their architecture. These traits determine effectiveness of light interception, the degree of competition between neighboring plants, adaptability of plant to cultivation, and, ultimately, grain yield [37,38]. Considering the canopy, the leaves at the top are light-saturated, thicker, with higher chl a/b ratio and Rubisco levels, while bottom leaves are usually light-limited [36]. Leaf photosynthetic efficiency is correlated to increased leaf thickness, decreased leaf area index, increased leaf chlorophyll concentrations, and higher biomass accumulation. Comparative analysis of rice genotypes differing in chlorophyll content indicated that the pigment content is not correlated with CO_2 fixation capacity [39,40]. In a "smart canopy", the upper leaves should be more vertical, with shorter antenna left outside thylakoid membrane, having a higher enzymatic specificity of Rubisco, as compared to lower canopy layers [16].

Accurate quantification of processes that determine photosynthetic rates of all leaves in the canopy are impractical. Instead, physiological attributes, namely, maximal carboxylation rate of Rubisco under the saturating concentration of RuBP and CO_2 (Vcmax) and maximal electron transfer rate of light reaction machinery (Jmax), can be determined. The leaf-level photosynthetic rate is influenced by additional traits such as stomatal response, leaf chlorophyll and crude protein content, rate of recovery from the photoprotective state, and engagement of cyclic electron transfer for ATP production [36,41]. Stomatal response is affected by external environmental conditions such as light, CO_2, temperature, and humidity, that determines the photosynthetic induction (transient increase in CO_2 uptake with proportionate light intensity) in rice. Moreover, Rubisco activity becomes the determining factor, in addition to stomatal conductance [42,43]. Erectophile leaves allow higher light penetration and enhanced light distribution in a canopy, and, thus, enhanced canopy photosynthesis under current and elevated CO_2. Development of semi-dwarf genotypes contributed to reduce lodging, and the additional maintenance respiratory cost for stem was also reduced. However, internode length below a minimum threshold leads to mutual shading in crop stands. It will attenuate the total absorbed solar energy and decrease canopy CO_2 uptake rate (Ac) [44].

Canopy microclimatic parameters such as photosynthetic photon flux density (PPFD), canopy temperature, vapor pressure deficit, and CO_2 concentration are additional determining factors. These unpredictable environmental situations can influence the estimation of Ac and place a bearing on optimal parameter values to maximize photosynthetic output [45]. The effect of canopy features such as length of culm, leaf length, width, angle, and curvature need to be independently evaluated to examine their optimal values. Parameters such as tiller number can influence planting density, which in turn can influence the ratio of

red/far-red among lower leaves, leading to adaptive modification in the length and width of leaf [44].

2.3. Improving Light Distribution and Reducing Shading Losses

Light interception and distribution are equal contributors for RUE and yield [46]. Diffused light is scattered by the atmosphere, and hence the effect of shading from top is partially bypassed [47]. The 3D modeling studies in rice suggested that reducing mutual-shading is important for light use efficiency at the higher leaf area index, and combination of 3D digitizing and 3D light modeling can be applied to evaluate IPAR and canopy photosynthesis in rice. In one instance, the 3D canopy model of two rice lines differing in the expression of tiller and leaf–angle increasing gene *PROSTRATE GROWTH 1* was reconstructed. The erect growing type (Teqing) exhibited a higher spike grain number and test weight over the prostrate growing (YIL18) line owing to the efficient solar interception [48]. The IPAR is a nonlinear function of the light extinction coefficient (k) and LAI [49]. Large variation in extinction coefficient (k) of rice crop is reported in various studies, ranging from 0.38 to 0.69. The *sd1* allele in rice genotype Takanari led to an erect phenotype withlower leaf inclination that resulted in low k value, as compared to SD1 allele in Koshihikari having a higher leaf inclination [50,51].

Shading effects happen when a plant part obstructs light flow to the leaves beneath, and under cloudy environments. Shading negatively affects plant growth as it significantly reduces the incident light on canopy [52]. In rice, low light intensity reduces the number of productive tillers, grain filling rate, grain weight, and grain yield [53,54]. In rice, the phenotyping of *slac1* (*slow anion channel-associated 1*) mutants gave insights into a regulatory pathway involving stomata for fluctuating light conditions. These mutants exhibited constitutive open stomata phenotype, and are useful for the maintenance of higher intercellular CO_2 concentration with higher photosynthetic rate under all irradiance levels, ranging from low to high. Thus, shade-tolerant plants exhibit a slow stomatal closure mechanism and high stomatal conductance to tap the benefits of irradiance reaching the canopy during sunflecks [34]. Fine-mapping of a QTL for photosynthetic rate and biomass led to the identification of qPn8.1 from *O. longistaminata*. This region also contains ARE1, which encodes a chloroplastic protein and has positive effects on Pn and BM. The ARE1 was also found to increase NUE and yield under stress, and hence is useful to improve photosynthesis, NUE, and yield in rice [55].

Shade causes a low red/far-red (R/FR) ratio and blue light. Phenotyping large number of rice genotypes led to the identification of Swarnaprabha as a shade-tolerant genotype. Transcriptome comparison of shade-tolerant Swarnaprabha and susceptible Nagina 22 showed that panicle emergence under low light and higher expression of ETHYLENE RESPONSE ELEMENT BINDING PROTEIN-2, MOTHER OF FLOWERING TIME 1, SHORT PANICLE 1, and novel microRNA genes are associated with sustainability of higher yield in Swarnaprabha under shade [56] (Table 1). About 513 new miRNAs in rice were identified, whose targets were mostly regulated by the genes involved in photosynthesis and metabolic pathways [57].

Table 1. Genes associated with rice canopy and panicle architecture and their impact on biomass/yield.

Sl. No	Gene	Encoded Protein	Functions and Impact on Biomass/Yield	Reference
1.	SP1	Peptide transporter family protein.	Positive regulator of panicle elongation. Mutants exhibited a short panicle phenotype in rice.	[56]
2.	*TAD1*	Co-activator of APC/C.	Targets MOC1 for degradation. Negatively regulates tillering and panicle number.	[58]
3.	*TE*	Substrate-recognition and binding factor of APC/C.	Degradation of MOC1. Negatively regulates tillering and branching.	[59]

Table 1. *Cont.*

Sl. No	Gene	Encoded Protein	Functions and Impact on Biomass/Yield	Reference
4.	*LAX1*	bHLH transcription factors.	Required for initiation of lateral meristem.	[60]
5.	*LAX2/GNP4*	Nuclear protein.	Regulates formation of axillary meristem. Positively regulates number of branches and spikelet.	[61]
6.	*DLT*	GRAS family transcription factor.	Positively regulates tiller number, panicle length, and seed set.	[62]
7.	*SD1*	Gibberellin biosynthesis gene.	Positively regulates plant height. Negatively regulates yield.	[63]
8.	*SUB1A*	Ethylene response factor.	Limits shoot elongation by modulating GA signaling.	[64]
9.	*D1/LW5*	G protein α subunit.	Source–sink balance, plant architecture, grain size.	[65]
10.	*D2, D11*	BR biosynthesis, members of cytochrome P450 family.	Promotes plant height, leaf, panicle grain morphology.	[66]
11.	*D61*	BR receptor kinase.	Promotes internodes and panicle elongation.	[67]
12.	*D3*	F box LRR protein.	Promotes bud dormancy and reduces bud activity. Regulates culm length, grain size.	[68]
13.	*D17, IHTD1, D10*	Strigolactone biosynthesis.	Negatively regulates axillary buds, tillering, and panicle size.	[69]
14.	*D27*	F-box, leucine-rich repeat (LRR).	Tiller bud outgrowth.	[70]
15.	*D14/D88/ HTD2*	Iron-containing, esterase/lipase/thioesterase.	Negatively regulates tiller bud outgrowth.	[71]
16.	*D53*	Repressor protein.	Strigolactone signaling.	[72]
17.	*EUI*	Cytochrome P450.	Deactivates the bioactive gibberellin, GA4, to control plant height.	[73]
18.	*MOC1*	GRAS TF (GAI, RGA and SCR).	Positively regulates tillering, panicle number, and yield.	[74]
19.	*MOC2*	GRAS TF (GAI, RGA and SCR).	Tiller bud outgrowth.	[75]
20.	*MOC3*	GRAS TF (GAI, RGA and SCR).	Axillary bud formation.	[76]
21.	*OsCKX2*	Cytokinin oxidase/dehydrogenase.	Promotes root growth. Reduces yield.	[77]
22.	*OsAAP3*	Amino acid transporter.	Negatively regulates tiller number.	[78]
23.	*OsHAP2E*	Heme activator protein.	Increases photosynthesis and tillering.	[79]

2.4. Improving Canopy and Panicle Architecture

Phytohormones, namely, auxin, gibberellins, cytokinins, brassinosteroids, and strigolactones, play key roles in regulating the growth, development, and architecture of shoot [34]. Numerous genes involved in shoot and panicle architecture have been functionally characterized (Table 1). These genes were identified by fine-mapping of yield related QTLs, correlated with transcriptome profiling, and validated to improve grain yield [80,81]. Genetic regulation of plant architecture in paddy is determined under different developmental modules and can be manipulated through genomics-based crop improvement strategies. IDEAL PLANT ARCHITECTURE (IPA1) encodes Squamosa promoter binding protein-like14 (SPL14), which acts as a transcription factor controlling the inflorescence structure. Panicle branching is promoted by the expression of *O. sativa TEOSINTE BRANCHED1* (*OsTB1*) and *O. sativa DENSE AND ERECT PANICLE1* (*OsDEP1*) [82].

The rice mutant *shi1* exhibited a lower number of tillers, together with stronger culm and increase in panicle branching. The SHORT INTERNODES1 (OsSHI1) is localized

in nucleus and encodes a transcription factor regulating plant architecture. *OsSHI1* is exclusively expressed in auxiliary bud and young panicle. OsSHI1 acts as a master regulator in the signaling module, which represses the activity of IPA1 by attenuating its DNA binding activity. Native IPA1 act as a transcriptional activator by binding to the promoters of both *OsTB1* and *OsDEP1*. Thus, SHI1 promotes increased tillering and panicle size in rice [83]. Similarly, miR156f and RCN2 promote panicle branching, while OsRAMOSA2 (OsRA2) regulates pedicel length [61]. OsRA2 was found to act downstream of RCN2 (Rice TERMINAL FLOWER 1/CENTRORADIALIS 2) for the pedicel and branch length traits, while it acts upstream for the length of secondary branches [84]. A particular shoot architecture is attained by organization of axillary, apical, intercalary, inflorescence meristems, and subsequent development of leaves and shoot branches with inflorescence. The genetic and hormonal control via auxins, strigolactone, and genes, including IPA1 and TB1, control shoot architecture. These architectural features help in the improvement of productivity and performance of rice [34].

2.5. Increasing Calvin Cycle Efficiency in Rice Leaf

The Calvin–Benson cycle is the basic carbon fixation pathway in C3, C4, and Crassulacean acid metabolism (CAM) plants. This pathway occurs in stroma of chloroplasts and includes three major steps: (1) carboxylation of ribulose-1,5-biphosphate (RuBP), (2) reduction of 3-phosphoglycerate, and (3) regeneration of the CO_2 acceptor RuBP; providing intermediates required for starch and sucrose biosynthesis [85]. Increasing Rubisco activity, higher affinity (low Km) for CO_2, and/or lower affinity (high Km) for O_2 are the promising strategies to enhance yield and biomass in rice [30]. Rubisco has low catalysis rate (Kcat), a major factor explaining its high concentration in rice plant leaves. Photosynthetic capacity is also closely related to leaf nitrogen content. The carboxylation could be increased by upregulating the content of Rubisco protein in chloroplast [86,87]. High levels of Rubisco protein are correlated with high photosynthetic rate in rice. If Rubisco activity can be improved, less protein will be required by the cell. The nitrogen invested for the enzyme biosynthesis could be reallocated to the proteins involved in various metabolic processes and structural integrity. Such interventions by genetic manipulation have been attempted in rice and various model systems with varying degrees of success [12,88]. The enzyme sedoheptulose-1,7-bisphosphatase (SBPase) is the key enzyme for partitioning assimilated carbon towards regeneration of RuBP, the acceptor of CO_2, and for sucrose or starch biosynthesis. Overexpression of *Brachypodium distachyon* SBPase enhanced photosynthesis, biomass, and grain yield in wheat [89] and tobacco [90]. In rice, lines having a mutant allele of SBPase resulted in severe reduction of growth, tillering, and grain yield. The iodine staining of mutant leaf exhibited the absence of starch accumulation till booting stage [91].

Rubisco activase (RCA) serves as an activator of Rubisco, which in turn is activated by the ferredoxin–thioredoxin system [92]. RCA exhibits a temperature-dependent moonlighting function. At optimum temperature, it releases inhibitory sugar phosphate from the Rubisco active site; and at heat-stress condition, it functions as a chaperone by associating with thylakoid bound 70S ribosome. In rice, the role of RCA was studied by overexpression, where steady-state and non-steady-state photosynthesis were recorded. Overexpression of *RCA* in rice showed its a critical role for Rubisco activation and steady-state photosynthesis at high-temperature conditions, along with contribution to non-steady-state photosynthesis at all leaf temperatures [93]. It was also reported that rice RCA greatly limits the light-dependent induction of photosynthesis, but not so for steady state [94]. Co-overexpression of RCA and Rubisco enhances photosynthesis at optimum temperatures [95].

Some genes which play a role in stomatal regulation and nitrogen metabolism, when overexpressed, showed tremendous increase in yield in rice. Overexpression of PM H^+-ATPase gene *OSA1* resulted in enhanced NH_4^+ uptake and assimilation in roots, better stomatal opening, and thus higher photosynthesis and 36% increase in grain yield [96]. Similarly, overexpression of *Dehydration-Responsive Element-Binding Protein 1C* (*OsDREB1C*) regulated both photosynthesis and NUE. About 9735 putative targets of OsDREB1C, in-

cluding *Rubisco Small Subunit 3* (*OsRBCS3*), *Nitrate Reductase 2* (*OsNR2*), *Nitrate transporter 2.4* (*OsNRT2.4*), and *Nitrate transporter 1.1B* (*OsNRT1.1B*), were identified by using chromatin immunoprecipitation sequencing (ChIP-seq) and transcriptomic analyses, and thus overexpression of *DREB1C* improved the yield by 41–68% in rice. Similar yield increment was also observed in wheat and Arabidopsis [97].

2.6. Introduction of Cyanobacterial CO_2-Concentrating Mechanisms into Chloroplasts

Cyanobacteria has an avoidance mechanism against oxygenation of Rubisco through a unique CO_2-concentrating mechanism (CCM) by means of carboxysome. The β-carboxysome is an integrated complex of assembled Rubisco subunits in the vicinity of carbonic anhydrase, thereby concentrating high CO_2 near the microcompartment. This mechanism that indirectly improves the carboxylation of Rubisco can be incorporated into plant chloroplasts [98]. Even though the cyanobacterial enzyme has a low affinity for CO_2 compared to plant type Rubisco, the photosynthetic mechanism is efficient under the present atmospheric oxygen levels. The striking benefit is that the total protein requirement for Rubisco to fix a unit amount of CO_2 will be less. The assimilated nitrogen can be relocated to other metabolic and synthesis pathways, improving nitrogen use efficiency [99]. Using the crop model GECROS, analysis of nine routes of photosynthetic upregulation in rice involving CCM under various weather conditions was recorded across 31 years. The mechanism involving low ATP requiring cyanobacterial CCM along with the high photosynthetic capacity in a given level of leaf nitrogen gave >50% yield increment [100]. Even though the mechanism was not attempted in rice, it was shown to be possible in *Nicotiana benthamiana,* where the shell proteins of the β-carboxysome were functionally assembled [26,101]. Another mechanism was also picked from cyanobacteria, where the bicarbonate transporter was introduced into tobacco chloroplasts and was found to be functional [102].

2.7. Pathway Editing for Minimization of Photorespiration

Rubisco is not completely capable of discriminating between CO_2 and O_2, and it poses a disadvantage to C3 plants under current atmospheric O_2 (21%) and CO_2 (0.04%) levels. It was estimated that at 25 °C, nearly 35% of all reactions of Rubisco are oxygenation of RuBP, i.e., photorespiratory reaction. In rice, the Rubisco oxygenation/carboxylation ratio at low CO_2 levels was estimated to be 0.569, which is more than 10 times that of maize [103]. Oxygenation of RuBP by Rubisco produces 3PGA and 2-phosphoglycolate (2PG) (Figure 1). The 2PG release during RuBP oxygenation is considered toxic, as it will not contribute to anaplerotic reactions and directly inhibits the C3 cycle enzymes. The natural variants or mutants with reduced photorespiration rates together with higher yields were screened over a large population. Preliminary experiments on tobacco showed low photorespiring lines, though their correlation with yield was meagre [104]. Another study from an experiment spanning 40 years of field trials in wheat and soybean concluded that genotypes with high photosynthesis only had a high photorespiration [105]. Certain rice varieties exhibited high photosynthetic rate, photorespiration, and dark respiration. Several cultivars, such as IR 8, Ratna, Pankaj, Vijaya, ADT 27, B 76, and TKM 6, exhibited good yield and low photorespiration [106]. Thus, donors for this trait are available in germplasm for future applications.

Studies on T-DNA insertion mutant corresponding to the chloroplast membrane localized gene *OsPLGG1* (*Plastidic Glycolate/Glycerate Translocator 1*) showed a reduction in photosynthetic rate and activity of PSI and PSII. The mutant lines showed a stunted phenotype with pale green leaves and reduced tiller number and grain weight. The ill effects were rescued by elevated CO_2 conditions only [107]. The remaining steps of photorespiration downstream to 2PG are involved in the conversion of toxic 2PG to 3PGA. This pathway requires additional energy costs and is hence suggested as a target of crop improvement [108,109]. The targeted knockdown of glycine decarboxylase (GDC), the mitochondrial enzyme that provides substrate for decarboxylation, by amiRNA was attempted in rice. Several phenotypic defects, such as poor regeneration of RuBP under photorespira-

tory conditions, size of mesophyll cells, chloroplast, mitochondria, and peroxisomes, were observed [110].

Reduction of Rubisco oxygenase activity appears to be a straightforward approach for future improvement of photosynthesis. In order to analyze natural variation of rice crop in different environments, several physiological growth parameters, such as specific leaf area, relative growth rate, crop growth rate, net assimilation rate, biomass, and grain yield, should be examined [111]. In addition, it is now understood that eradicating photorespiration from rice will lead to hazardous outcomes [112]. Therefore, the primary focus to improve photosynthesis will be maximizing net carbon gain, rather than abolishing C2 cycle. The CO_2-concentrating mechanisms will be a promising strategy to improve the source capacity of rice [113]. Metabolic pathway editing by converting glycolate to glycerate is also a pursued strategy. These synthetic biology approaches to channelize glycolate to metabolic pathway intermediates will lead to net photosynthetic carbon gain with less ATP consumption [114]. The combined approaches of editing the metabolic pathway as well as Rubisco efficiency will bring several options for carbon assimilation and yield. The preliminary efforts in this field will be carried out by in silico approaches, namely, 3D structure prediction and docking studies. Synthetic biology will help in delivering superior rice varieties to farmers' fields [115].

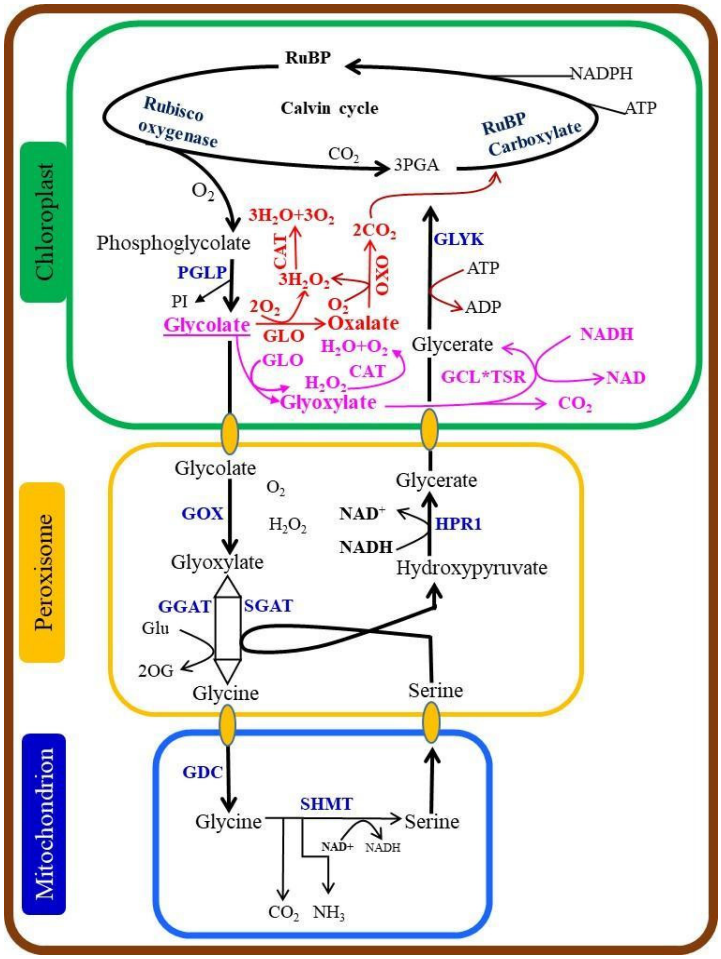

Figure 1. Photorespiratory pathway involving three organelles, i.e., chloroplast, peroxisome, and mitochondrion, for refixation of CO_2. Enzymes involved in the pathway are provided in blue color. The photorespiratory bypasses are provided in red/pink. NAD: Nicotinamide adenine dinucleotide; NADPH: Nicotinamide adenine dinucleotide phosphate; PGLP: 2-phosphoglycolate phosphatase; GLYK: Glycerate-3-kinase; GOX: Glucose oxidase; HPR1: Hydroxypyruvate reductase 1; GGAT: Gamma-glutamyltransferase; GDC: Glycine decarboxylase complex; SHMT: Serine hydroxymethyltransferase. GCL: Glyoxylate carboligase; TSR: Tartronic semialdehyde reductase.

2.8. Scavenging of Photorespiratory CO_2

The CO_2 released as a byproduct of photorespiration can accumulate in inter/intracellular space and is refixed in photosynthesis [116]. The accurate estimation method of photorespiratory CO_2 being reassimilated was devised [117]. They employed ^{13}C-labeled CO_2 and measured its exchange rate by infrared gas analyzer (IRGA), in various herbaceous crops (cabbage, chicory, tomato, spinach, cowpea) and tree species (*Prunus*, *Quercus* sp.). The results indicated that photorespiratory CO_2 is scavenged to the level of about 80%, where the losses accounted for only 20%. Using an advanced radiogasometry technique, dissection of decarboxylation from respiration and photorespiration revealed that in light, primary photosynthates, and not stored starch, are decarboxylated. This study, carried out in C3 crops such as wheat, can be extrapolated to rice. At 320 ppm CO_2, the refixation coefficient of CO_2 in rye was 21.8% [118]. The scavenging/recycling aspect of photorespiratory CO_2 is unexplored in rice.

Even though gasometric studies for scavenging are absent in rice, the lobbing of mesophyll cells and appression of chloroplasts near cell walls is hypothesized to act as a scavenging mechanism for CO_2 [119]. In mesophyll cells of rice, the chloroplasts also extend their hands in the form of stromules over mitochondria so that the CO_2 cannot escape to the cell wall region. This mechanism acts as a major means of passive reassimilation of CO_2 lost by respiration or photorespiration [118]. Studies on three species of Oryza for the subcellular positioning of mitochondria and chloroplasts revealed the adaptation to promote CO_2 scavenging. About 65–75% of mitochondria, the decarboxylating organelles, were positioned towards the center of the cell. For chloroplasts, about 60–75% were localized towards the cell wall. This increases the diffusional distance for CO_2 through cytoplasm and a higher probability of its refixation in chloroplasts. In addition, the plastids were positioned near the intercellular space for efficient CO_2 uptake [119]. Similar observations were also made [120] in rice genotype IR64, where reassimilation accounts for more than 50% at 350 ppm CO_2.

2.9. Optimization of the Photorespiratory Enzymes and Photorespiratory Bypasses

Being a protective mechanism, photorespiration should not be prevented in C3 plants. Pleiotropic negative effects were observed in C3 plants where photorespiration was prevented by genetic approaches. Several bypasses have been devised in plants for the optimization or bypassing of photorespiratory processes. Three bypasses were reviewed by [109] (Figure 1). The common factor among all these pathways is avoiding the decarboxylation step involving Glycine decarboxylase (GDC) and Serine hydroxymethyl transferase (SHMT) in mitochondria. By means of a hypothetical model, it was shown that the feedback negative regulation of GDC by NADH and CO_2 is mediated by malate dehydrogenase and carbonic anhydrase [121]. In addition, the cyclic electron flow of chloroplasts and alternate oxidase of mitochondria are found to complement the photorespiratory activity in several plants, including rice [122]. The glyoxylate that is possibly leaked from the peroxisome is immediately detoxified by two Glyoxylate Reductase (GR) homologs in rice. The OsGR1 is localized in cytosol, while OsGR2 is chloroplastic. CRISPR/Cas-mediated silencing of either or both of these homologs resulted in growth retardation under photorespiratory conditions in rice [123]. The *CHLOROPLAST VESICULATION* (*OsCV*) gene is expressed during senescence and abiotic stresses that encode a protein mediating the degradation of chloroplastic proteins in rice. RNAi-mediated downregulation of *OsCV* gene in rice maintained a higher Rubisco oxygenation, photorespiration (even under high CO_2 conditions), and increased grain yield with a high protein content [124].

Studies on the quality traits of two bypass systems in cultivar Zhonghua11 were carried out by [96]. The bypass systems studied were Glycolate oxidase 3, Oxalate oxidase 3, and Catalase (GOC) [125]; and Glycolate oxidase 1, Catalase, Glyoxylate carboligase, and Tartronic semialdehyde reductase (GCGT) [126]. The calculated ATP requirement for GOC and GCGT pathways is 20 and 11.75% less than native photorespiration [109]. In transgenic rice plants engineered with GOC bypass, Glycolate oxidase 3 catalyzes conversion of

photorespiratory glycolate into oxalate, which is then converted into $2CO_2$ and $3H_2O_2$ by Oxalate oxidase 3. The H_2O_2 is detoxified by catalase, and the CO_2 is prefixed by Rubisco. The GOC-engineered rice plants exhibited a decrease in photorespiration rate by 18–31%, and ammonia emission from leaf decreased by 11–19%. Several pleiotropic effects, such as increased net photosynthetic rate, light saturation point, light-saturated photosynthetic rate, and decreased CO_2 saturation point, were observed. Agronomic traits, namely, productive tillers, width of flag leaf, dry biomass, panicle length, number of spikelets per panicle, and single plant yield, under photorespiratory conditions were increased in rice lines [127]. In rice plants engineered with GCGT pathway, Glycolate oxidase catalyzes conversion of photorespiratory glycolate into glyoxalate, which is then converted to glycerate by Glyoxylate carboligase and Tartronic semialdehyde reductase enzymes within chloroplasts. The GCGT plants exhibited 6–16% increase in photosynthetic rate, 14–19% reduction in photorespiration, and a recovery of 75% CO_2. The engineered plants produced 16–28% higher biomass and 13–27% higher grain yield over the WT plants [109]. Overexpression of chloroplastic pyruvate dehydrogenase is also suggested as a strategy to promote photorespiratory bypass and increase biomass and yield in rice [128].

2.10. Conversion of C3 Photosynthetic Pathway into C4 in Rice

Rice genome encodes orthologs of enzymes essential for C4 pathway. Their expression and activities are tightly regulated under various environmental conditions [129]. The presence of native genes also provides scope for single cell C4 pathway in near future [130]. With the current progress of genome-editing techniques, these native genes can be over-expressed by CRISPR-Act2.0 systems designed for rice, and promoter cis-element editing to regulate the gene expression is also possible [131]. Towards the conversion of C3 to C4 rice, two schools of thought are targeted: the first one being the complete replacement of C3 cycle form mesophyll cells and their restriction to bundle sheath cells. The alternate one being the combined pathway where both C4 and C3 cycles are spatially separated, parallelly running in all mesophyll cells. These two possibilities were modeled in a 3D reaction diffusion model which revealed that the parallel pathways will prove beneficial for rice [132]. Considering the advancements attained to date, the methods to convert C3 to C4 rice in general have not led to increment in photosynthesis. Various groups have attempted to address this limitation [133]. Considering this objective, the *PEPCase* (*Phosphoenolpyruvate Carboxylase*) from *Setaria italica* was incorporated into rice. The lines exhibited increased photosynthetic rate, stomatal conductance, transpiration rate, water use efficiency, and yield [134].

In an attempt to introduce C4 pathway in rice, four key genes of the pathway were introduced in rice, and their effects on CO_2-concentrating mechanisms were studied. The quadruple gene cassette contained the maize NADP malic enzyme type genes, namely, *ZmPEPC*, *ZmNADP-MDH*, *ZmPPDK,* and *ZmNADP-ME*. The lines exhibited a significant accumulation of ^{13}C-labeled malate, with no incorporation into 3PGA. Hybridization of this line with a rice line weakly expressing *OsGDCH* (Glycine Decarboxylase H-protein; having poor photorespiration) led to higher accumulation of ^{13}C-labeled malate, aspartate, and citrate. It was suggested that the incorporation of anatomical changes in rice will complement the effect of genes in yield improvement [135]. In another study, quintuple gene construct was employed to overexpress *ZmCA*, *ZmPEPC*, *ZmNADP-MDH*, *ZmPPDK,* and *ZmNADP-ME*. In comparison to wild type, the resultant lines had no alteration in Rubisco activity, total chlorophyll content, or leaf weight per unit area. Experiments using C13 under light exposed for 10 min showed labeling in C4 intermediates, primarily malate, and aspartate. These lines accumulated more PGA and Rubisco, but the relative increase in radiolabeling was not recorded with respect to wild type. The C4 sugar intermediates were found to be channeled to citric acid cycle [136]. Thus, generating a successful photorespiratory bypass or developing C4 rice needs to address these limitations in rice.

2.11. Balancing Source and Sink

The source consists of the photosynthesizing tissues that synthesizes sugars and metabolites, and accumulate minerals. The sink constitutes the organs such as stem, root, flower and seed that utilize or stores the carbohydrate, protein and mineral reserves in nonstructural forms. During remobilization, some sink tissues such as stem and sheath in rice will act as source and contribute to grain filling. Thus, source strength is the total of current and stored assimilates for grain development. Source strength is determined by the crop growth before and after heading in rice. The sink size is synonymous to potential yield. The sink strength is determined by grain number and grain weight in rice. In rice, about 60% of grain filling ingredients are accumulated after heading [137,138]. Thus, active photosynthesis from the source becomes significant for yield and quality. Analysis of inter-sub-specific hybrid super rice cultivars showed that they have a leaf area index of 8, with approximately 60,000 spikelets per square meter. This balance between a strong source and sink led to about 13.98–16.42% yield increment over inbred japonica super rice cultivars [139]. The relative significance of source and sink on rice using six genotypes each of indica and japonica showed that dry mass of grain is primarily correlated with source size over sink size. The source size was found to be limiting in rice for yield. In addition, dry matter partitioning and nonstructural carbohydrates contribute to grain filling and productivity [140].

A wider exploration of QTLs related to source and sink traits by genome-wide association studies (GWAS) in 272 Xian rice accessions (indica) revealed several promising genetic loci. Among the 70 QTLs identified for 11 source–sink traits, 5 QTLs were consistent in different environments. From the QTLs, 24 candidate genes also were identified for their role in yield improvement [127]. Environment has prime effects on the source–sink relations. High temperature during the early developmental stages led to poor build-up of source, for instance, tillers per hill, which afflicts yield [141]. The transport of assimilates between source to sink via phloem is the determining factor in grain filling. The *LW5* (*LEAF WIDTH 5*) gene encodes a G protein α subunit involved in signaling related to transport and grain filling. The *lw5* mutants exhibited shorter grain size and poor grain filling rate. Thus, LW5 is involved in the promotion of sink strength and, thereby, rice yield [65]. Thus, a proper balance between source and sink contributes proportionately to rice yield.

2.12. QTL-Based Targeting of Genetic Loci and Genes

The fine-mapping of QTL from Indonesian land race Daringan was carried out with an NIL developed in IR64 background. The QTL studied was qTSN (total spikelet number per panicle), where the underlying gene, namely, *SPIKE/NAL1* (*SPIKELET NUMBER/NARROW LEAF 1*), was identified and validated to increase yield when introgressed in indica cultivars [142,143]. The stay-green trait in rice was explored in a cross between the *indica* cultivar IR72 and the *japonica* cultivar JN. The corresponding gene was fine-mapped to chromosome 9, and the map-based introgression of the allele led to delayed senescence with improved yield [144]. The GNP1 (Grain Number per Plant 1) QTL was successfully identified from a RIL population developed from a cross between Lemont (*japonica*) and Teqing (*indica*) genotypes. Identification of corresponding gene revealed that grain number was increased in the RILs owing to the overexpression of gibberellin biosynthesis gene *GA20 oxidase* [145]. With the objective of developing heavy-panicle type rice, the PND1 (Panicle Neck Diameter 1) QTL was identified. The cloning of the underlying gene indicated a loss of function mutation in *GRAIN NUMBER 1A/CYTOKININ OXIDASE 2 (Gn1A/OsCKX2)* gene [146]. The expression of *CKX2* was further positively regulated by a zinc finger transcription factor DST. This gene was identified and named after the QTL Drought and Salt Tolerant, which showed multiple abiotic stress tolerance and increased grain number [147]. The detailed investigation on the regulation of *DST* gene showed that a coactivator DST-interacting protein 1 (DIP1)/Mediator subunit 25 (OsMED25) promotes the activity by direct interaction [148] (Table 2). Thus, it can be inferred that the various genes present in yield contributing QTLs work in collaboration for optimizing grain yield.

Table 2. Genes/QTLs mapped for source strength, sink strength, and partitioning efficiency in rice.

Gene	Complete Name & Function	Remarks	Reference
		Leaf Area	
NAL1/SPIKE	NARROW LEAF1/SPIKELET NUMBER. Involved in polar Auxin Transport (Os04g52479).	Loss of function leads to narrow leaf; the functional japonica NAL1 allele confers larger panicles, leaves, and seed yield; LSCHL4 allele enhances photosynthesis; partially functional NAL1/GREEN FOR PHOTOSYNTHESIS (GPS) balances leaf photosynthesis.	[149,150]
TDD1	TRYPOTOHAN DEFICIENT DWARF 1. Anthranilate synthase beta-subunit, which catalyzes the first step of the Trp biosynthesis pathway.	Loss-of function mutation led to reduced leaf width, increase in leaf angle.	[151]
lm7	Leaf Mutant 7. OsHSP40 (heat shock protein).	Loss of function mutation led to reduced leaf size.	[152]
OsCHR4	A CHD3 family chromatin remodeler.	Loss of function causes narrow and rolled leaves with increased cuticular wax.	[153]
		Leaf Angle	
OsARF4	Auxin Response Factor.	*OsARF4*-overexpressing lines showed erect leaves.	[154]
OsARF19	Auxin response factor binds to the promoter of OsGH3-5 and brassinosteroid insensitive 1 (OsBRI1) directing their expression.	Loss of function causes erect leaves.	[155]
OsmiR167a	It targets OsARF12, OsARF17 and OsARF25.	Control rice tiller angle.	[156]
		Leaf Area Duration	
OsSGR	STAY-GREEN. Chlorophyll-degrading Mg++-dechelatase.	Promoter variation in japonica OsSGR alleles associated with less expression. Indica genotypes introgressed with japonica OsSGR allele led to delayed senescence, enhanced photosynthesis, and, thus, higher grain yield.	[157]
NYC1	NON-YELLOW COLORING 1. Short-chain dehydrogenase/reductase (SDR).	nyc1and nol (nyc1-like) mutant is stay-green and shows delayed leaf senescence.	[157]

Table 2. *Cont.*

Gene	Complete Name & Function	Remarks	Reference
		Photosynthate Partitioning and Assimilation	
OsQUA2	Pectin methyltransferase.	*Osqua2* mutant showed decrease in the methylesterification of Homogalacturonan in the culm-sieve element cell wall, sucrose overaccumulation in the culm, and lower yield.	[158]
OsSUT1, *OsSUT5*	Sucrose–proton symporter SUT family members.	Mutants are impaired in seed filling and reduced yield.	[159–161]
OsDOF11	DNA BINDING WITH ONE FINGER 11. OsDOF11 directly binds the promoter of sugar transporters.	Positive regulator of SUT (OsSUT1, OsSUT3, OsSUT4, and OsSUT5) and SWEET (OsSWEET11 and OsSWEET14) sugar transporter genes.	[162]
OsRRM	RNA-Binding Protein.	OsRRM binds directly to messenger RNAs encoded by sugar transporter genes and thus helps stabilize and enhance expression of sugar transporter genes; *osrrm* mutant is impaired in sugar partitioning, seed filling, and reduced yield.	[163]
OsNAC129	NAM, ATAF1/2, and CUC2 (NAC) TF.	Negative regulator of grain size and starch biosynthesis.	[164]
		Sink Strength (Grain Number and Size)	
OsMKKK10	Signaling cascade OsMKKK10-OsMKK4-OsMAPK6.	Loss of function *osmkk10* results in small and light grains and short panicles, while constitutively active OsMKKK10 results in large and heavy grains and long panicles. OsMKK4 gain-of-function mutant (large11-1D) produces large and heavy grains.	[165]
GSN1	GRAIN SIZE AND NUMBER 1. Mitogen-activated protein kinase phosphatase OsMKP1, a dual-specificity phosphatase inactivates OsMPK6 via dephosphorylation.	GSN1 is a negative regulator of the OsMKKK10-OsMKK4-OsMPK6 cascade; GSN1 negatively regulates grain size but positively regulates grain number.	[166]
OsER1	OsERECTA1. Negatively regulates spikelet number per panicle	OsER1 acts upstream of the OsMKKK10-OsMKK4-OsMPK6. In *er1* mutant, *CKX2* was significantly downregulated; OsMPK6 phosphorylates *DST* which in turn activates the expression of CKX2.	[167]
OsDIP1	DST-interacting protein 1 (DIP1), a Mediator subunit OsMED25, acts as an interacting coactivator of DST.	Similar to *dst* mutant, *osmed25* mutant also exhibited enlarged panicles, with enhanced branching and spikelet number.	[148]
OsHKX1-10	Rice genome encodes 10 hexokinases, which act as sugar sensor except HKX3; regulate photosynthetic gene expression.	hkx1 mutants exhibited enhanced photosynthesis and grain yield; hkx3 exhibited lower grain size, and overexpression increased grain yield in rice.	[168,169]

3. Conclusions

Rice is a crop which can contribute to the first three components of the Sustainability Development Goals of the United Nations. The genetic potential of the crop is continuously being explored for novel traits and its QTLs and regulatory genes for yield improvement. Being a field crop, the primary trait being targeted is the radiation use efficiency for photosynthesis. For this, the light distribution above and below the canopy will be optimized by altering the shoot architecture. The canopy photosynthesis can be enhanced by improving Rubisco carboxylation efficiency, regulation of stomatal responses, crop modeling, and developing ideotypes. The canopy and panicle architecture are regulated by auxin-, cytokinin-, ethylene-, gibberellin-, brassinosteroid-, and strigolactone-dependent signaling pathways. Several biochemical interventions can be followed in rice, such as activation of Rubisco by Rubisco activase and improving the level of Calvin cycle pathway enzymes. Metabolome editing for increased photosynthesis has been carried out by mutagenized population-based studies, improving Rubisco specificity to CO_2 and introducing CO_2-concentrating mechanisms from cyanobacteria. The photorespiration was also optimized by incorporating photorespiratory bypasses by multigene transformation and attempting to convert rice to C4 photosynthetic type. The various attempts to develop rice expressing C4 pathway genes were not met with the desired success. In addition to improving the source strength, the capacity of sink can also be targeted for improving grain yield. The various targeted traits are demarcated to QTLs and the underlying genes have been progressively unraveled from rice. These novel genes were shown to exhibit promising results when introgressed to popular cultivars. The present review thus provides a platter of various research progress and prioritizable arenas for improving rice productivity and food security.

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