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Review

Perspectives of improving rice photosynthesis for higher grain yield

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ABSTRACT

Many efforts have been made to enhance rice photosynthesis for higher grain yields, although such knowledge has seldom been integrated into rice breeding programs. In this review, I first address the limitations and challenges of the theory that yield is controlled by photosynthesis, a concept rooted in the fact that carbon forms a significant part of plant mass, with photosynthesis acting as the fundamental pathway for carbon assimilation. Subsequently, the discussion covers photosynthesis indices, their measurement techniques, and the challenges in establishing correlations between photosynthesis indices and yields. The review then delves into recent advancements, including leveraging natural variations, enhancing the electron transport chain, augmenting the efficiency of ribulose bisphosphate carboxylase/oxygenase (Rubisco), increasing CO_2 concentration around Rubisco, initiatives like the C_4 rice project, strategies for photorespiration bypass, and non-leaf photosynthesis contributions. The conclusion emphasizes future research directions such as advocating for the incorporation of photosynthesis within broader organismic processes, unraveling the complex link between photosynthesis and grain yield, developing efficient and direct methods for photosynthesis phenotyping, and assessing photosynthetic performance under actual field conditions.

1. Introduction

Rice stands as a vital staple food on a global scale, with a rapidly increasing demand. It has been projected that for every increment of one billion people in the global population, an extra 100 million tons of rice must be produced annually (Seck et al., 2012). Given the unlikelihood of further expansion in agricultural land, the rice grain yield per unit farmland will need to accelerate beyond recent rates to satisfy the increasing rice consumption demands of the growing global population. When examining physiological factors, rice yield emerges from the interaction between the volume of resources that the crop absorbs and how efficiently these resources are utilized. Given that biomass accumulation predominantly stems from light through photosynthesis, enhancing photosynthetic processes is deemed a crucial route for augmenting yields in crops, including rice. In recent decades, researchers have proposed various strategies and targets aimed at enhancing rice photosynthesis. However, the broader scientific community recognizes that these endeavors to amplify yield have largely been unsuccessful (Araus et al., 2021; Flexas, 2016; Sinclair et al., 2019). In this review, I summarize the current efforts in enhancing photosynthesis to boost rice yield and discuss the challenges and directions for future research.

2. The link between photosynthesis and grain yield

As plants use energy from the sun to drive primary production through photosynthesis, photosynthetic light use efficiency is widely suggested to determine crop yields (Burgess et al., 2023; Garcia et al., 2023; Wu et al., 2019a; Zhu et al., 2010). In the context of the light use efficiency by canopies, the crop yield is, in theory, the product of four components, namely, the total incident solar radiation across the growing season, the light interception efficiency (LIE) by crop canopy, the light conversion efficiency (LCE), and the amount of total biomass energy partitioned into the harvested portion of the crop, also termed the harvest index (HI). Apparently, the total annual solar radiation at a particular location, despite being notably impacted by air pollution and cloudy conditions (Musiolková et al., 2021), tends to remain consistent over extended periods. Nonetheless, for cereal crops such as rice, it is possible to modify the total incident solar radiation during their growth phase by altering the planting date and/or the onset of critical growth stages (Minoli et al., 2022).

The HI of rice is a pivotal agronomic trait that has garnered significant attention from agronomists. During the Green Revolution, rice yield surges was resulted from the integration of a dwarfing gene, boosting the HI by approximately 0.30 to 0.50 (Hay, 1995). Research indicates that

there might be a very constrained scope for further amplification of this index in rice (Long et al., 2006, 2015). This perspective arises from observations that enhancements in grain yield for new rice cultivars primarily originate from biomass accumulation. Intriguingly, the rice HI has consistently hovered at approximately 0.50 in recent decades (Yang and Zhang, 2023), while an analytical theory posits a 0.65 ceiling for rice (Hay, 1995), and recent discoveries have identified a few QTLs capable of elevating the index to 0.62 under experimental setups (Saito et al., 2021; Zhang et al., 2017). It is also well recognized that the HI is strongly influenced by environmental variables, making it a central factor in determining rice yield stability across multiple environmental conditions (Muehe et al., 2019; Saito et al., 2021).

Early studies, exemplified by Monteith (1977), demonstrated a consistent positive correlation between biomass production and the quantity of intercepted light over prolonged periods, highlighting the pivotal role of improving canopy LIE as a fundamental high-yield trait in crop production. In practical terms, canopy light interception, as assessed through the canopy light extinction coefficient (K), indicates the extent to which light can penetrate and reach the lower part of the canopy (Wolf et al., 1972). Inherent genetic limitations, which include traits such as leaf area, leaf distribution, biomass allocation, and maximum plant height, along with environmental elements such as light quality and crop row orientation, collectively influence LIE (Liu et al., 2021; Murchie and Burgess, 2022). These characteristics shape the plant architecture, specifically the canopy. As a result, plant architecture is deemed central to determining crop LIE. In addition, early and rapid growth to quickly cover the land, manifested as increased early vigor, along with the retention of greenness during the later reproductive stages, are pivotal traits for improving crop LIE. However, the strategy of enhancing early vigor has been somewhat overlooked in efforts to optimize canopy light interception (Liu et al., 2021).

The conversion efficiency is defined as the ratio of canopy intercepted radiation energy converted to biomass energy over a growth period (Slattery and Ort, 2015). In theory, the LCE is determined by the photosynthesis and respiration rates of plants. A reduced respiration rate is suggested to be an important pathway for improving crop yield, as respiration loss is significant, especially under high-temperature conditions (Joshi et al., 2023; Li et al., 2021). However, the energy and products from respiration are necessary for life activities, and the impact of significantly reducing respiration on plant development and defense is still unclear (Amthor et al., 2019; Reynolds et al., 2021). Major efforts are therefore on identifying the limitations to, and opportunities for, improving photosynthesis in crops.

In 1968, Donald pioneered the ideotype concept for high-yield crop breeding. He described a "crop ideotype" as an idealized plant form, integrating characteristics optimal for photosynthesis, growth, and grain production, derived from insights into plant and crop physiology and morphology. Following this, there was accelerated engagement in both model simulations and ideotype-based breeding for major crops, as noted by Trethowan (2014). Within the realm of rice, the International Rice Research Institute (IRRI) initiated the "New Plant Type" breeding project. Moreover, during the 1990s and 2000s, China launched an extensive "Super Rice" breeding initiative targeting a significant increase in rice yield through deliberate plant architectural selection (Peng et al., 2008). Both projects prioritized large panicle size and high total aboveground biomass production. These concerted efforts have notably enhanced rice grain yield, with the success of the "Super Rice" program considerably increasing rice production in China.

Long et al. (2006) initially proposed that the selection of ideotypes during the Green Revolution in crops resulted in increased grain yields through improved LIE. Although direct evidence is scarce, this concept is frequently referenced in the literature to underscore the untapped potential of the LCE as a pathway for future yield enhancements (Araus et al., 2021; Faralli and Lawson, 2020; Leister, 2023; Slattery and Ort, 2021; Zhu et al., 2010). Although LIE and LCE are conceptually distinct parameters, they are intrinsically linked, and both have strong ties to

plant architecture. The daily average light flux can vary drastically, often by a factor of up to 100, from the top to the bottom of a canopy based on its architecture (Slattery and Ort, 2021). Leaves situated at the top of the canopy shade those below, which may lead to an oversaturation of light at the top and a scarcity of light deeper within the canopy. It is evident that any alterations to the light distribution inside the canopy caused by changes in plant architecture could directly impact LCE. As observed in many studies (Buckley et al., 2014; Niinemets, 2023; Niinemets et al., 2015), leaf functional traits within the canopy adapt to specific light conditions, which subsequently has a profound impact on the LCE.

3. Various photosynthesis indices and their relationship with grain yield

Photosynthesis is the biological process by which light energy is seized and conserved through a sequence of events that transform this raw energy into the essential free energy required to fuel life. In experimental research, the photosynthetic rate serves as a prevalent metric for quantifying photosynthesis (Hunt, 2003). There are various definitions of the photosynthetic rate, each with its unique role and significance. While there are notable reviews that aggregate common photosynthetic rate measures and their association with grain yield (Adachi et al., 2020; Araus et al., 2021; Murchie et al., 2009; Murchie and Ruban, 2020; Zhu et al., 2022), a unified, comprehensive source detailing all photosynthetic rate indices remains elusive. Such a source, offering a systematic evaluation of the advantages and drawbacks of each photosynthetic rate index in the context of the relationship between the photosynthetic rate and grain yield, would be invaluable. It would equip both researchers and students with the means to scrutinize photosynthesis more effectively and select the most appropriate indices based on their specific research objectives or situations. In this review, I have classified the multitude of photosynthetic rate entities into groups based on the following boundaries: optical method-based, gas exchange method-based, and carbohydrate production method-based, as detailed in Table 1. It is essential to note that this review does not cover the photosynthetic rate indices for non-terrestrial life forms, such as aquatic plants, algae, and bacteria. Consequently, some well-known measurements from manometric techniques, Hill's reaction, and O_2 probe methods are excluded.

The complex photochemical and biochemical processes of photosynthesis occur in chloroplasts and are generally split into two stages: the light reaction and the dark reaction. The rate of the dark reaction is typically measured using the radioactive isotope ^{14}C method, which has historically been used to map photosynthetic pathways (Benson et al., 1950). The light reaction, also known as the "photosynthetic electron transport reaction", transforms light energy into chemical energy at the thylakoid membrane. Here, photosystem II (PSII) absorbs photon energy, initiating the photo-oxidation of water and providing electrons and hydrogen ions to the electron transport chain and the thylakoid membrane's luminal side, respectively (Barber, 2003; Nelson and Yocum, 2006). The electron transport rate (ETR) through PSII is often assessed as the quantum yield of PSII ($\varphi_{PSII}\varphi_{PSII}$) using chlorophyll fluorescence techniques (Murchie and Lawson, 2013), although there are some uncertainties (Baker, 2008). Likewise, the ETR through photosystem I (PSI), referred to as the quantum yield at PSI, is assessed using saturated-pulse illumination methods (Shimakawa and Miyake, 2019). While these indices are commonly utilized to delve into the molecular aspects of the light reaction process, chlorophyll fluorescence-based parameters are also employed to explore the connection between photosynthesis and grain yield (see bibliometrics analysis by Zavafer et al., 2020), especially under stress conditions (Kimm et al., 2021; Pinto et al., 2020). Research by Camino et al. (2019) also explored photosynthetic variation in crops. However, as Porcar-Castell et al. (2014) critically analyzed, the correlation between chlorophyll fluorescence measurements and actual leaf photosynthesis is not straightforward.

Most modern measurements of crop photosynthetic rates, from the organ to canopy levels, are based on the common principle of CO_2 uptake

Table 1
Commonly used photosynthetic rate indices and definitions in crop science.

Photosynthetic rate indicator	Definition	Key reference
1. Optical method		
1.1. Chlorophyll fluorescence		Murchie and Lawson (2013)
φ_{PSII}	PSII operating efficiency which is estimated from chlorophyll fluorescence signals as the ratio of variable to maximal fluorescence	
ETR	Rate of electron transport through PSII at a given light intensity	
F_v/F_m	Maximum quantum efficiency of PSII photochemistry	
F_v'/F_m'	Maximum efficiency of PSII photochemistry in the light, if all centers were open	
NPQ	Non-photochemical quenching which estimates the rate constant for heat loss from PSII	
1.2. Absorption		
P700	Absorption of P700 which is the main absorption in the leaf at 820 nm, reflecting redox kinetics of the PSI center	Klughammer and Schreiber (1994)
2. Gas exchange		
2.1. Organ to individual scales		Busch et al. (2024)
A or P_n	Net CO_2 Assimilation which is the gross photosynthesis minus photorespiration and respiration	
A_{max}	Maximum CO_2 assimilation rate at light and CO_2 saturated conditions	
A_{sat}	Light saturated CO_2 assimilation rate at the ambient CO_2 conditions	
V_{cmax}	Maximum rate of carboxylation by Rubisco	
J_{max}	Maximum rate of electron transport	
g_s	Stomatal conductance	
2.2. Ecosystem and canopy scales		
NEE	Ecosystem net exchange of CO_2 between an ecosystem and the atmosphere over a given time which can be from hours to years. Typically measured using eddy covariance method	Papale et al. (2006)
3. Carbohydrate production		
^{14}C uptake rate	Like the gas exchange, it involves using a gas scintillation counter to monitor the isotope in a gas stream flowing over the enclosed leaf	Benson et al. (1950)

rate. Since respiration is essentially a reverse process of photosynthesis, these methods often measure the balance between photosynthesis and respiration, rather than solely measuring photosynthesis. Consequently, the term, net photosynthetic rate, is commonly used. While there are numerous physical and chemical techniques, such as conductimetric and opto-acoustic techniques, that can potentially determine the mole fraction of CO_2, non-dispersive infrared gas analysis (IRGA) is the only method currently extensively employed for quantifying photosynthetic CO_2 uptake. Heteroatomic molecules, both CO_2 and H_2O, absorb infrared radiation in specific submillimeter infrared wavebands, while gas molecules with two identical atoms do not. The Beer–Lambert Law can be used to measure CO_2 and H_2O concentrations by measuring the decline in the infrared signal from a detector as the CO_2 and H_2O concentrations or waveguide length increase. To meet the needs of plant science applications, a variety of commercially available IRGAs and chambers are available for measuring CO_2 assimilation rates ranging from organs (i.e. Licor-6800, LI-COR, Inc., NE, USA; GFS-3000, Heinz Walz, Effeltrich, Germany; and CIRAS-4, PP Systems Inc., MA, USA) to plants (CAPTS, Millet Hill, Ltd., Shanghai, China). By combining IRGA devices with other technologies, we can measure a myriad of photosynthetic traits beyond the plant CO_2 assimilation rate, including the maximum photosynthetic rate under saturated CO_2 concentration (A_{max}), photosynthetic rate under saturated light intensity (A_{sat}), stomatal conductance (g_s), mesophyll conductance (g_m), maximum carboxylation rate (V_{cmax}), and maximum ETR (J_{max}). Gas exchange technology, while promising, is not without its potential pitfalls, and it necessitates meticulous experimental design and precise measurement operations to be effective (Busch et al., 2024). Regional-scale CO_2 exchange can be assessed by monitoring CO_2 movement between the external atmosphere and within the canopy, which is influenced by factors such as wind speed and direction, and temperature. A specialized open-path IRGA, the LI-7500 (LI-COR, Inc., NE, USA), has been developed for such measurements.

Measuring the rate of photosynthesis through the quantification of photosynthetic product production represents an alternative quantitative approach. However, practical quantification of these products is hindered by several challenges. First, photosynthetic products are swiftly relocated from chloroplasts and utilized in various cellular processes, making it difficult to measure their concentrations at specific time points. For instance, photorespiration has been confirmed using recent photoassimilate (Tregunna et al., 1964). Second, these products are extensively involved in a wide range of biochemical reactions, both within and outside of chloroplasts. This complexity makes it challenging to isolate and measure individual components accurately (Heise et al., 2014). Last, the separation of photosynthetic products from one another and from other cellular compounds poses an additional set of difficulties.

The current methods for analyzing photosynthesis, spanning from the molecular level to the canopy scale, are primarily aimed at assessing the instantaneous photosynthetic rate, and they do not facilitate continuous tracking of the photosynthetic rate. This limitation makes it challenging to establish causal relationships between photosynthetic indices and grain yields, as they differ in scale. Although a new canopy photosynthesis and transpiration measurement system (CAPTS) for continuous gas exchange measurements at the canopy level was introduced (Song et al., 2016), there were significant differences in the agricultural traits between plants grown inside CAPTS chambers and those grown in open fields within the same plot, the latter being crucial for grain yield estimations. The environmental conditions within the CAPTS chambers, such as air temperature, humidity, wind, and light, were substantially different from those in the open fields (unpublished data).

As mentioned above, current methods for estimating photosynthesis primarily focus on the leaf level, detailing the physical and chemical steps that convert light into chemical energy. However, this intricate process, unfolding discretely within cells, is profoundly influenced by a multitude of factors when examined at the broader plant scale (Baslam et al., 2020; Wu et al., 2019a; Yin et al., 2022). Within the context of resource acquisition, which encompasses nutrients, water, light, and CO_2 from both the soil and the atmosphere, plants must orchestrate their carbon allocation strategies to different organs, adapting to a spectrum of growth conditions rather than singularly prioritizing the enhancement of photosynthesis (Furbank et al., 2020; Sinclair et al., 2019; Yin et al., 2022). Furthermore, plants engage in complex ecological interactions with a diverse array of organisms, including competitors, symbiotic partners, and potential herbivores, profoundly influencing their photosynthetic performance. Adding to this complexity, plants must function

within an ever-fluctuating environment, a departure from the typically ideal conditions often prescribed for practical photosynthesis measurements (Kaiser et al., 2018; Long et al., 2022). Physiological and biochemical processes during photosynthesis rapidly respond to environmental changes, and the ability of plants to adapt to chronic and acute abiotic stresses is a pivotal determinant of their photosynthetic capabilities within this intricate interplay (Johnson and Lawson, 2015). Consequently, the existing leaf-level photosynthetic indices are inadequate for capturing the temporal and spatial variations in photosynthetic rates across crop canopies, leading to unreliable correlations between estimated photosynthetic rates and grain yields. This inconsistency presents a challenge in forming a reliable link between photosynthesis and crop yields. Indeed, research has shown varying correlations between leaf photosynthetic rates and grain yields in rice and other crops, from negative to positive or even no correlation at all. There is a clear need for future research to develop reliable methods for tracking canopy photosynthesis.

4. Current major efforts to improve photosynthesis in rice

Photosynthesis in plants involves intricate reactions. To streamline understanding, a widely accepted steady-state biochemical model for C_3 photosynthesis, the Farquhar model (Farquhar et al., 1980), is often used to depict this process. Based on the Farquhar model, this review organizes steady-state photosynthetic characteristics into three principal categories: electron transport-related traits, ribulose bisphosphate carboxylase/oxygenase-associated (Rubisco) traits, and CO_2 diffusion conductance. It should be emphasized that while a considerable number of studies have explored the constraints on photosynthesis under stress conditions (Johnson and Lawson, 2015; Moore et al., 2021), the present study does not delve into these aspects, as they are beyond the scope of this paper. Moreover, photosynthesis, which is essential for plant survival, demonstrates a biochemical mechanism that is remarkably consistent across higher plants. The steps and biochemical reactions involved are well defined, with approximately one hundred genes recognized as crucial to its fundamental machinery. These genes encode enzymes and complexes essential for the processes involved in the light and dark reactions of photosynthesis (Theeuwen et al., 2022). Despite this knowledge, the distinct roles and impacts of these enzymes and complexes on the photosynthetic efficiency of various plants have not been fully determined, although researchers have attempted to model these dynamics. It is suggested that enhancing the quantity of key elements in the core photosynthetic machinery via a transgenic approach could improve crop photosynthetic rates. This section summarizes the endeavors to modify rice photosynthesis. It is important to acknowledge that many transgenic plants (Li et al., 2020; Wei et al., 2022; Zhang et al., 2021), particularly those with genes associated with high yields, show improved photosynthetic phenotypes without directly targeting the core photosynthetic components. As such, they fall outside the scope of this paper.

4.1. Exploiting natural variations in rice photosynthetic traits

Genetic variation is key for improving crop performance through selective breeding. However, the extent to which photosynthesis traits are selected during modern crop breeding processes remains a topic of debate. Contrary to the belief held by numerous researchers that photosynthesis traits are not directly targeted in breeding programs (Furbank et al., 2015; Long et al., 2015), a handful of studies on historical rice cultivars indicate that these traits might be inadvertently selected to increase yields. For instance, Ju et al. (2016) reported a strong correlation between the increase in yield of Chinese rice varieties over the past 70 years and the increase in A_{sat} in flag leaves after heading. Similarly, Zhang and Kokubun (2004) linked the 20th century increase in Japanese rice grain yield to increased A_{sat} in flag leaves during ripening. Conversely, Hubbart et al. (2007) observed a contrasting trend in IRRI varieties between 1966 and

1995, characterized by a reduction in A_{sat} for those released from 1966 to 1980 and then an increase thereafter. This fluctuation is attributed to shifts in yield improvement strategies, specifically the transition from prioritizing a higher HI before 1980 to a focus on increased biomass after 1980, which significantly influenced the approaches to enhancing yield in IRRI varieties. More recently, Honda et al. (2023) also found no correlation between leaf photosynthetic rate and release years across temperate *japonica* cultivars, although the grain yields of those cultivars were not measured. It is important to note that gas exchange measurements in the study of Hubbart et al. (2007) were taken on the ninth leaf, not the flag leaves, which are believed to be more closely related to grain yield.

Crop wild relatives exhibit substantial genetic diversity, which is thought to provide genetic material to cultivated crops. The *Oryza* genus, comprising 18–24 species and taxa (Kellogg, 2009), includes two major cultivated species: Asian rice (*O. sativa*) and African rice (*O. glaberrima*). Despite ongoing discussions regarding their phylogenetic relationships, many studies in recent decades have focused on the photosynthetic characteristics of both wild and cultivated rice species (Acevedo-Siaca et al., 2021b; Giuliani et al., 2013; Kiran et al., 2013; Mathan et al., 2021; Phillips et al., 2022; Xiong et al., 2017; Yeo et al., 1994). Yeo et al. (1994) analyzed these characteristics in 22 wild rice species and a cultivated genotype and found notable variations in A_{sat} among the species. In their study, *O. sativa* was found to have a high A_{sat} value, although not the highest, which is consistent with findings from other studies. Additionally, there is significant variation in photosynthetic traits within genotypes of the same *Oryza* species. Kiran et al. (2013) noted a 2.06-fold difference in A_{sat} between genotypes of *O. nivara*, and Giuliani et al. (2013) identified a 2-fold difference in *O. latifolia*. This genotype-based variation within a single species may explain the discrepancies in the photosynthetic rate rankings of wild species reported in various studies, which often include only a limited number of genotypes per species. For example, *O. latifolia* was regarded as a species with high photosynthetic efficiency in studies by Xiong et al. (2017) and Giuliani et al. (2013), but it was considered to have low photosynthetic efficiency in research by Yeo et al. (1994). Therefore, future research could benefit from focusing on variations at the genotype level rather than exclusively at the species level.

Unlike the use of genetic resources from different species, which often requires advanced biotechnologies, the use of genetic diversity within a single species can be effectively achieved through crossbreeding (Labroo et al., 2021). The foundation for enhancing crop photosynthesis through crossbreeding lies in the natural variation in photosynthetic traits among different varieties (Flood, 2019; Flood et al., 2011; Lawson et al., 2012). Extensive research has been conducted on the variation in photosynthetic traits such as A_{sat}, A_{max}, g_s, g_m, V_{cmax}, and J_{max} across rice genotypes, confirming significant differences (Xiong and Flexas, 2018). However, the heritability of these photosynthetic traits has been less studied due mainly to the low efficiency of photosynthesis measurement methods. Studies that do exist suggest low heritability for photosynthetic traits, with results varying based on the developmental stage and species (Flood et al., 2016; Prado et al., 2018). For rice, Acevedo-Siaca et al. (2021a) recently assessed the broad-sense heritability of photosynthetic traits in thirty accessions. They found high heritability for A_{max} (65%), V_{cmax} (63%), and J_{max} (68%), but low heritability for A_{sat} (22%) and g_s (30%), indicating that photosynthetic traits, particularly A_{sat} and g_s, are heavily influenced by the growth environment. Ecophysiological research has investigated how biochemical, morphological, and anatomical traits affect leaf photosynthesis among different genotypes and under varying environmental conditions. This area was comprehensively reviewed by Xiong and Flexas (2018), and as such, it will not be elaborated extensively here. Briefly, across rice genotypes, A_{sat} is strongly correlated with V_{cmax} and leaf CO_2 diffusion conductance. The V_{cmax} is intimately linked to leaf nitrogen content, while the conductance of CO_2 diffusion is mainly determined by morpho-anatomical features such as stomatal density and size, the spatial distribution of stomata, the shape of mesophyll cells, and the thickness of cell walls. Furthermore, research indicates that the

hydraulic conductance of rice plants plays a role in the variation in photosynthesis across genotypes by influencing the water status of leaves (Xiong et al., 2017).

Advances in molecular plant breeding technologies have made genetic mapping an indispensable tool for identifying QTLs that influence phenotypic variations in specific traits. This has significantly changed breeding strategies by enabling marker-assisted selection, which allows breeders to improve traits without comprehensive gene information (Tanksley and Nelson, 1996). While QTL analysis traditionally depends on linkage mapping, a method slowed by the need to develop inbred lines, the last decade has introduced genome-wide association studies (GWAS) as a quicker alternative, propelled by rapid advancements in whole-genome sequencing (Uffelmann et al., 2021). However, research on QTLs related to photosynthetic traits such as A_{sat}, V_{cmax}, and J_{max} in rice is still scarce (Furbank et al., 2020; Sharwood et al., 2022). It is particularly concerned that QTLs have rarely been consistently verified across different studies and experimental years. For instance, Gu et al. (2012) found a significant QTL for A_{sat} and related traits in 94 rice chromosome introgression lines under varying soil moisture conditions, suggesting that photosynthetic traits might cluster together. Recent studies identified a major QTL affecting A_{sat} and g_s on chromosome 8 in three distinct populations, indicating a linkage between these traits (Adachi et al., 2011; Honda et al., 2023). Additionally, Adachi et al. (2019) identified 10 more QTLs for A_{sat} using two different rice cross populations.

Several factors contribute to the variation in results when identifying QTLs associated with photosynthesis. First, the core biochemical mechanisms of photosynthesis are remarkably consistent across different species and are governed by approximately one hundred genes (Berry et al., 2013). Although some variations in photosynthesis, especially under stress conditions, might be linked to changes in the concentrations of key photosynthetic components, it is essential to recognize that variations within a population could also arise from thousands of genes not directly related to the core photosynthetic process, as detailed by Theeuwen et al. (2022). The impact of these genes on photosynthesis may be minor but is heavily influenced by the genetic backgrounds of the genotypes. Second, the environmental conditions where plants are cultivated can differ among studies, which may influence their photosynthetic performance. For example, a study by Qu et al. (2017) revealed a weak correlation between the photosynthetic efficiency of identical rice varieties grown in Beijing and Shanghai, underscoring the significance of environmental factors on photosynthesis. Third, perhaps the most significant barrier to identifying photosynthetic QTLs is the limitations and uncertainties inherent in measurement techniques (Furbank et al., 2019). In contrast to traits such as grain yield, there are no direct high-throughput methods available for accurately measuring photosynthesis, adding another layer of complexity to research in this area. Photosynthetic reactions are significantly affected by constantly changing ambient environments, leading to the general practice of estimating the photosynthetic rate under stable conditions for genetic comparisons. Measuring the stable state of gas exchange in rice leaves with a commercial system usually requires more than 10 min per measurement (Barbour et al., 2016). Further complicating matters, photosynthesis follows a distinct daily cycle, causing significant fluctuations in photosynthetic rates throughout the day (Busch et al., 2024). To address these challenges, researchers have turned to various indirect high-throughput techniques, such as thermal imagery, hyperspectral reflectance, chlorophyll fluorescence, leaf color analysis, and infrared thermography, for photosynthetic phenotyping (Fu et al., 2022; Furbank et al., 2020; Keller et al., 2024). However, the relationships between these indirect photosynthetic indices and direct gas exchange measurements remain unclear. With the immediate feasibility of high-throughput measurements for stable gas exchange in doubt, forging a reliable link between these measurements and high-throughput methods is increasingly vital. Nonetheless, this does not diminish the importance of developing innovative steady-state gas exchange techniques. Recent efforts, such as those by Salter et al. (2018), who reduced measurement times by using multiple leaves in multiple chambers simultaneously, and Du et al. (2020), who

enhanced efficiency by pre-accommodating in vitro rice tillers under controlled conditions, have highlighted ongoing advancements in this area.

4.2. Modifying the electron transport chain

The light reactions in oxygenic photosynthesis involve two key photochemical complexes, PSI and PSII. These complexes operate in harmony with their corresponding light-absorbing antenna complexes, light-harvesting complex I (LHCI) and light-harvesting complex II (LHCII), which are interconnected by the electron transport chain (ETC). In this context, potential strategies to enhance the efficiency of energy processing by the photosynthetic apparatus have been extensively reviewed (Batista-Silva et al., 2020; Cardona et al., 2018; Gu, 2023; Leister, 2019, 2023), leading to the proposal of various approaches. Initially proposed strategies for enhancing photosynthetic efficiency focused on increasing the number of ETC components, including reaction centers and cytochrome b_6f complexes, and extending the lifespan of the photosynthetic apparatus (Walter and Kromdijk, 2022). Additionally, optimizing the redox kinetics of these components and reducing the proportion of secondary quinone-nonreducing PSII reaction centers are identified as key tactics (Gu, 2023). Experiments to overexpress the genes of reaction centers and cytochrome b_6f complexes in *Arabidopsis* and tobacco plants have demonstrated increased assimilation rates (Simkin et al., 2017; Yadav et al., 2018). However, similar research has rarely been conducted on rice, possibly because rice usually thrives in natural open fields where light intensity is sufficient for carbon assimilation. In rice, Yamori et al. (2016) reported that reductions in the cytochrome b_6f complex led to decreased electron transport through PSII, adversely affecting A_{sat}. Interestingly, another study (Gu et al., 2017) showed that rice mutants with reduced chlorophyll content and smaller antenna sizes can improve PSII efficiency, increase ETR, and minimize the risk of light over saturation.

A reduction in chlorophyll content could also alter the spectral light distribution within the canopy, allowing deeper penetration of certain light wavelengths and thereby enhancing photosynthesis in lower leaves (Leister, 2023). At the canopy level, the decrease in chlorophyll could mitigate the reduction in light intensity, especially in the far-red spectrum. However, considering the role of minor antennae proteins, especially Lhcb (an LHCII subunit), in non-photochemical quenching (NPQ), this approach may have drawbacks, potentially affecting NPQ optimization efforts (Murchie and Ruban, 2020). Therefore, adopting a whole-plant "low-chlorophyll" strategy may involve compromises, particularly for upper canopy leaves exposed to significant light variation.

Enhancing the dissipation of excess excitation energy in field crops under high-light conditions such as NPQ is one of the important strategies to improve light utilization efficiency (Murchie and Ruban, 2020), as confirmed in tobacco (Kromdijk et al., 2016) and soybean (de Souza et al., 2022). This is particularly true during rapid increases in sunlight and for leaves at the top of the canopy. In rice, a targeted genetic strategy involved overexpressing the *PsbS* gene, which encodes an antenna-related protein, to boost NPQ capacity and its dynamic response (Hubbart et al., 2018). Observations under constant light conditions revealed that plants with *PsbS* overexpression exhibited normal or slightly reduced growth rates, and their heightened NPQ levels interfered with the light activation of photosynthesis, particularly when Rubisco and stomatal activities were not major limiting factors. Conversely, when these genetically modified plants were cultivated to full maturity in a glasshouse designed to simulate varying field conditions, they displayed increased productivity. This improvement was attributed to a decrease in photoinhibition, particularly in the middle to upper layers of the canopy, leading to better overall plant growth and yield.

4.3. Improving Calvin cycle enzymes

In contrast to the limited research on the ETC, extensive studies have aimed at improving the Calvin cycle and associated biochemical enzymes

in rice. Previous investigations have consistently demonstrated that the constraints on rice photosynthesis stem from biochemical factors and the diffusion of CO_2. Typically, these biochemical constraints are categorized into limitations related to Rubisco and the regeneration of ribulose 1,5-bisphosphate (RuBP), with the potential for triose phosphate export limitations under specific circumstances. The regeneration of RuBP is linked to the electron transport capacity and involves 12 reactions catalyzed by 10 distinct enzymes starting from 3-phosphoglyceric acid. Among these reactions, the enzyme sedoheptulose-bisphosphatase (SBPase) plays a critical role. Enhancing the expression of the *SBPase* gene has been proven to increase photosynthesis, although such studies have yet to be conducted on rice.

Rubisco plays a vital role in photosynthesis by facilitating CO_2 fixation and makes up approximately a quarter of the total leaf protein in rice. Its relatively slow catalytic rate (k_{cat}) has been the focus of engineering efforts to increase photosynthesis efficiency in agricultural practices for many years, as detailed in a recent review by Prywes et al. (2023). Researchers have aimed to improve photosynthesis by either increasing Rubisco levels or enhancing Rubisco activation through higher concentrations of Rubisco activase (RCA). In a notable study, Suzuki et al. (2007) genetically modified rice plants to overproduce Rubisco by about 30% by transforming the complementary DNA of Rubisco small subunit 2 (*OsRBCS2*) in the sense direction. This modification led to increased photosynthetic capacity in flag leaves, higher rice yields, and improved nitrogen use efficiency when the transgenic plants were cultivated in paddy fields, as reported by Yoon et al. (2020). However, a subsequent in-depth analysis revealed that the contribution of increased photosynthetic rate to grain yield might have been over-emphasized, given that the genetically modified rice plants develop larger flag leaves that remain functional for extended periods during the ripening phase (Tanaka et al., 2022). Additionally, excess Rubisco might divert leaf nitrogen from other enzymes, potentially introducing new photosynthetic limitations. Moreover, Kanno et al. (2017) found that reducing Rubisco slightly through RNA interference in Rubisco small subunit (*rbcS*) genes under high CO_2 conditions could increase A_{sat} and biomass.

For Rubisco to achieve catalytic functionality, it requires activation by RCA, which aids in the ATP-dependent removal of inhibitory sugar phosphates and supports carbamylation (Bracher et al., 2017). Notably, only a substantial decrease in the RCA content (over 60%) impacts Rubisco activation (Masumoto et al., 2012; Yamori et al., 2012), suggesting that the RCA is sufficient for maintaining Rubisco activation and photosynthesis under natural conditions. Nonetheless, the effectiveness of RCA in Rubisco activation may be compromised under fluctuating light and high temperatures, potentially limiting photosynthesis. Transgenic rice with elevated RCA levels exhibited enhanced Rubisco activation and accelerated photosynthesis under changing light conditions (Yamori et al., 2012). However, an increase in RCA can paradoxically lead to lower Rubisco levels and thus diminish photosynthesis rates (Fukayama et al., 2012). The correlation between RCA levels and Rubisco content appears inconsistent across various studies, with some reporting increased Rubisco in plants with suppressed RCA and others observing no significant change (Fukayama et al., 2012, 2018; Masumoto et al., 2012), underscoring the uncertainty surrounding RCA manipulation's impact on Rubisco content. Suganami et al. (2021) demonstrated that transgenic rice plants engineered to overproduce both Rubisco and RCA significantly enhanced photosynthesis rates at moderately high temperatures, suggesting that the simultaneous overproduction of these components could be a viable approach to boost photosynthesis and yield in rice.

Another proposed strategy is to transfer Rubisco from high-efficiency organisms to different species. Often, it is crucial to co-express supportive factors for the proper folding and assembly of foreign Rubisco within transgenic chloroplasts. This necessity arises because the large (RbcL) and small (RbcS) subunits of plant Rubisco are encoded in different locations—the RbcL in the chloroplast genome and the RbcS in the nuclear genome—with the latter significantly influencing Rubisco contents.

A notable achievement was the introduction of cyanobacterial Rubisco into tobacco plants, as documented by Lin et al. (2014). However, the Rubisco levels in these modified plants were approximately 10% of those in the wild types, necessitating elevated CO_2 for growth. Despite the increased CO_2, the growth of these plants still lagged behind that of the wild types. To date, there have been no reports of successful transfer of cyanobacterial Rubisco to rice, and research has instead focused on transferring Rubisco from C4 plants to rice. For instance, integrating RbcS from *Sorghum bicolor* into rice led to containing hybrid Rubisco with enhanced C4-like properties, including a higher k_{cat} (Ishikawa et al., 2011). Later, researchers eliminated the rice RbcS multigene family and completely replaced it with sorghum RbcS, creating a hybrid Rubisco with nearly C4 plant-like catalytic properties (Matsumura et al., 2020). Similar to the tobacco plants with cyanobacterial Rubisco, the transgenic rice lines had lower Rubisco levels. Nevertheless, they showed a slightly higher photosynthetic capacity and maintained comparable biomass production under high CO_2 conditions to wild-type rice.

4.4. Elevating the CO_2 concentration inside chloroplasts

Rubisco is a bifunctional enzyme capable of fixing both CO_2 and O_2 with RuBP as its primary substrate (Prywes et al., 2023). Elevating the CO_2 concentration near Rubisco suppresses its oxygenase activity, thus reducing photorespiration and enhancing photosynthetic efficiency. One approach to achieve this involves increasing the CO_2 levels around Rubisco by facilitating CO_2 diffusion from the surrounding air into the chloroplast stroma (Flexas et al., 2016). The CO_2 diffusion process involves boundary conductance, g_s, and g_m, with the latter describing the transfer of CO_2 from substomatal cavities to carboxylation sites. Although much of the current research has focused on g_s and g_m, the role of boundary layer conductance has been less explored, yet it could significantly influence leaf gas exchange, particularly in high humidity environments (Buckley et al., 2017).

The g_s depends on stomatal density, aperture, and size, with a proven correlation between stomatal density and size. Most knowledge on stomatal density regulation comes from studies on the model plant *Arabidopsis*, which is now being extended to grass species such as rice (Cheng and Raissig, 2023; McKown and Bergmann, 2020). Various molecular factors regulate rice stomatal development, including transcription factors, plasma membrane proteins, and signalling molecules (Wu et al., 2019b). A group of signalling peptides called epidermal patterning factors (EPFs and EPF-like peptides, or EPFLs), also referred to as STOMAGEN in some studies, plays a crucial role in determining stomatal density. Rice has two *EPF* genes, *OsEPF1* and *OsEPF2*, due to grass-specific gene duplication. Overexpressing *OsEPF1* and *OsEPF2* leads to lower stomatal density in rice (Caine et al., 2019; Lu et al., 2019), resulting in increased water use efficiency and drought resistance without affecting yield (Caine et al., 2019). Manipulating stomatal density in grasses is currently in its infancy, necessitating extensive further research. The increasing focus of scientists on the regulation of stomata in grass species is promising, paving the way for new research paths into altering stomatal density to achieve high productivity in rice.

Rapid adjustments in the behavior of stomata in response to environmental changes are crucial for improving g_s under fluctuating conditions. The regulation of stomatal movement encompasses a sophisticated control mechanism that oversees the transport of key osmotic solutes, including potassium, chloride, and malate, together with water, across both the plasma membrane and the tonoplast (Lawson and Matthews, 2020). According to the widely accepted model, the opening of stomata begins with hyperpolarization of the plasma membrane due to H^+-ATPase activity, which creates an inward pH gradient and electrochemical gradients that facilitate ion movement. Conversely, stomatal closure is initiated by the release of anions through anion channels, leading to depolarization. This in turn activates potassium channels, enabling the synchronized release of potassium and anions. Over the past few decades, many studies have focused on genetically modifying the

rate of stomatal opening in dicotyledons, particularly in *Arabidopsis* (Nguyen et al., 2023b). Conversely, rice has been the subject of only one such study, where the overexpression of the plasma membrane H^+-ATPase 1 (*OSA1*) gene accelerated stomatal opening in response to light, resulting in higher photosynthesis rates than in the wild type (Zhang et al., 2021).

The *SLAC1* gene, first discovered in *Arabidopsis*, is crucial for stomatal closure, encoding an anion channel protein in the plasma membrane of guard cells that responds to environmental cues. Kusumi et al. (2012) introduced a *SLAC1*-deficient mutant in rice, named *slac1*, and determined that *SLAC1* plays a role in regulating stomatal closure speed in rice. More recently, Qu et al. (2020) discovered that enhancing the expression of a rice Na^+/H^+ antiporter gene in the tonoplast, *OsNHX1*, significantly shortened the stomatal closure time during drought. Recent investigations have also highlighted the significance of non-chemical factors, such as the formation of cuticular ledges around stomata and changes in cell wall thickness and pectin composition, especially in the polar regions of stomatal complexes, in facilitating efficient stomatal movement in *Arabidopsis* (Carroll et al., 2022; Hunt et al., 2017). However, the impact of these structural elements on rice g_s has yet to be examined. Moreover, despite frequent mentions of the crucial role that subsidiary cells play in stomatal movements, empirical data remain scarce. For instance, Raissig et al. (2017) observed that removing subsidiary cells in Brachypodium significantly slowed stomatal opening and closing. Similarly, Franks and Farquhar (2007) noted that in species with dumbbell-shaped guard cells such as *Triticum aestivum*, achieving observed g_s necessitates a considerable reduction in subsidiary cell turgor pressure and a diminished mechanical advantage.

The g_m refers to the efficiency with which CO_2 molecules diffuse from intercellular air spaces to chloroplasts, where photosynthesis occurs. This process involves the movement of CO_2 through various cellular components such as cell walls, membranes, and cytoplasm before it reaches chloroplasts (Evans, 2021). Each component presents a barrier to CO_2 diffusion, with the degree of resistance varying among different species (Xiong, 2023). The role of cell walls in determining g_m has been extensively researched (Flexas et al., 2021). In rice, a study by Ellsworth et al. (2018) revealed that a mutant (*cslf6*) with defects in cell wall mixed-linkage glucan production exhibited a notable decrease in g_m, emphasizing the impact of cell wall porosity and the path length of the liquid phase on g_m. Furthermore, enhancing the expression of the *OsAT10* gene in rice, which changes the composition of cell wall hydroxycinnamic acids, leads to thinner mesophyll cell walls and, consequently, higher g_m (Pathare et al., 2023).

Biological membranes consist of numerous proteins and have a limited lipid surface area available for CO_2 free diffusion (Groszmann et al., 2017). It is understood that the transit of CO_2 through these membranes is facilitated by specialized protein channels known as aquaporins (AQPs), which are divided into seven families (Maurel et al., 2015): plasma membrane intrinsic proteins (PIPs), tonoplast intrinsic proteins (TIPs), nodulin 26-like intrinsic proteins (NIPs), small basic intrinsic proteins (SIPs), uncategorized intrinsic proteins (XIPs), hybrid intrinsic proteins (HIPs), and GlpF-like intrinsic proteins (GIPs). Studies indicate that specific members of the PIP family act as CO_2 transporters. In the context of rice, 11 *OsPIP* genes have been discovered, with *OsPIP1;1*, *OsPIP1;2*, and *OsPIP2;1* being implicated in playing a role in g_m. Nonetheless, the extent of their contribution to g_m has varied across different studies, and there are serious doubts (Ding et al., 2016, 2019; Huang et al., 2021; Xu et al., 2019). Huang et al. (2021) recently elucidated that the impact of *OsPIP* genes on g_m is influenced by the growth conditions and developmental stages of rice plants, yet the underlying mechanisms remain to be clarified. The considerable homology among rice AQP isoforms has led to speculation about potential compensation effects among different AQP isoforms, which could obscure the impacts of individual gene alterations (Groszmann et al., 2017).

Carbonic anhydrase (CA) enzymes are thought to be crucial for CO_2 transport within plant leaves, which exist in multiple isoforms within

three distinct families: α, β, and γ (DiMario et al., 2017). The specific cellular locations and varying gene expression levels during different developmental stages are believed to play a significant role in each family's contribution to g_m. Despite this, our understanding of the precise impact of various CA isoforms on g_m, especially across different cellular locations, is still in the preliminary stages (Momayyezi et al., 2020). A review of the literature revealed that, to date, no studies have specifically explored the role of CAs in regulating g_m in rice plants. This is despite evidence indicating that the elimination of the β-carbonic anhydrase (*βCA*) gene in rice can lead to decreased photosynthetic efficiency (Chen et al., 2017).

4.5. Photorespiration bypass

Rubisco acts as an enzyme with dual functions, and under current atmospheric conditions, it frequently reacts with O_2. This reaction leads to the production of 3-phosphoglyceric acid (3PGA) and 2-phosphoglycolic acid (2PG). 2PG inhibits essential enzymes in the Calvin cycle, notably triose phosphate isomerase and sedoheptulose 1,7-bisphosphate phosphatase (Bauwe, 2023; Busch, 2020; Smith et al., 2023). Plants convert 2PG back to 3PGA through photorespiration, a less efficient process in C_3 plants characterized by significant carbon loss as CO_2 and high energy consumption. This inefficiency, due to both carbon loss and the energy-intensive nature of the conversion process, has spurred extensive research into alternative metabolic pathways to improve photosynthetic efficiency (Busch, 2020). Recent successes include synthetic pathways that metabolize glycolate in the chloroplast stroma, enhancing photosynthesis (Eisenhut et al., 2019). However, altering the peroxisomal stages of the traditional photorespiration pathway did not improve photosynthetic performance as expected (Smith et al., 2023). The subject of photorespiration bypass in plants has been thoroughly reviewed (Eisenhut et al., 2019; Jin et al., 2023; Smith et al., 2023; Xin et al., 2015), and here, I will focus on advancements made in rice.

Two synthetic pathways have been engineered into rice to bypass photorespiration: (1) the GOC bypass (Shen et al., 2019), which integrates glycolate oxidase 3 (*OsGLO3*), oxalate oxidase 3 (*OsOXO3*), and catalase (*OsCATC*) genes; and (2) the GMA bypass (Xu et al., 2023), which incorporates glycolate oxidase 1 (*OsGLO1*), *Cucurbita maxima* malate synthase (*CmMS*), and ascorbate peroxidase 7 (*OsAPX7*) genes. For the GOC bypass to function, three enzymes—glycolate oxidase, oxalate oxidase, and catalase—must be present in the chloroplast stroma, as opposed to their native location in the peroxisomes, facilitating the complete conversion of glycolate to CO_2. The GOC-modified rice exhibited superior biomass yield compared to the wild type in field trials, although the grain yield was inconsistent, showing up to a 16% reduction in the fall due to lower seed-setting rates (Shen et al., 2019). In contrast, GMA bypass, activated by a light-inducible Rubisco small subunit promoter (*pRbcS*), led to a notable increase in photosynthetic rates and a significant increase in grain yield under both greenhouse and field conditions. The GMA-modified rice did not experience a decrease in seed-setting rates, marking an improvement over GOC bypass in grain yield (Xu et al., 2023). Despite these advancements, critical questions remain unanswered, particularly concerning the specific mechanisms that lead to yield enhancements and the impact of photorespiratory bypasses on seed-setting rates.

4.6. C₄ rice project

The increased CO_2 concentration around Rubisco in C_4 pathway species offsets Rubisco's catalytic inefficiency and reduces assimilate loss from photorespiration (Hibberd et al., 2008; von Caemmerer et al., 2012). This advantage led to the launch of the "C_4 rice project" aimed at incorporating the C_4 pathway into rice. As stated on the project's website (www.c4rice.com), the endeavor originated at the IRRI and has received funding from the Bill & Melinda Gates Foundation since 2008. Initially,

the project set a 15-year timeline to develop C$_4$ rice for plant breeders, with a phased approach: 3 years for gene discovery and tool development, another 3 years to engineer rice with Kranz anatomy and C$_4$ metabolic enzymes, 5 years to refine C$_4$ functionality in transgenic rice, and the final 4 years to integrate C$_4$ traits into local rice varieties (Sheehy et al., 2008). Despite exceeding the intended timeline, the project has not met the anticipated outcomes, as noted in recent reviews (Bin Rahman and Zhang, 2023; Ermakova et al., 2020). The project has since refrained from setting further time expectations. Notably, the Bill & Melinda Gates Foundation's Phase IV has redirected its goal toward developing a prototype for C$_4$ metabolism.

In the C$_4$ pathway, the process begins with (1) the initial capture of CO$_2$ by phosphoenolpyruvate carboxylase (PEPC), which leads to the production of a C$_4$ acid; followed by (2) the breakdown of this C$_4$ acid to liberate CO$_2$ close to where the Calvin cycle occurs; and (3) the reformation of the primary CO$_2$ acceptor, phosphoenolpyruvate (PEP), facilitated by pyruvate phosphate dikinase (PPDK). The release of CO$_2$ from C$_4$ acids, which increases cellular CO$_2$ levels, occurs away from the initial CO$_2$ capture site. This spatial separation is managed through bundle sheath cells (BSCs) and mesophyll cells in traditional C$_4$ plants, or across two distinct subcellular compartments in single-cell C$_4$ plants. The chloroplasts at these two sites are characterized by unique structural and biochemical features. Based on this understanding, the "C$_4$ rice project" aims to integrate C$_4$ photosynthetic mechanisms into rice through a three-pronged approach: modifying leaf anatomy, altering biochemical pathways, and fine-tuning the entire system. The final step of system optimization relies on the successful reconfiguration of both leaf anatomic and biochemical routes. Consequently, current researches and efforts related to C$_4$ rice have focused on the modification of leaf structure and biochemical processes. Given that the effort to engineer C$_4$ pathways into C$_3$ plants has been extensively reviewed (Ermakova et al., 2020; Furbank et al., 2023; Schuler et al., 2016; Sedelnikova et al., 2018; Wang et al., 2016), here, I will only briefly address these aspects.

The Kranz anatomy characteristic of C$_4$ plants is notably distinct from the traditional C$_3$ anatomy, particularly in terms of vein spacing within the leaf, the differentiation of cell types surrounding the veins, and the specialized functions of organelles within these cells. To successfully incorporate Kranz anatomy into rice, it is necessary to adjust the patterns of vein spacing to bring veins closer together within the leaf. Additionally, BSCs must be adapted to enhance their photosynthetic capacity, which includes augmenting their chloroplast content. Although there are known gene candidates and transcription factors that may influence vein spacing, the overarching transcriptional network that governs this trait is yet to be fully understood. For instance, recent attempts to induce C$_4$-like leaf anatomy in rice through the constitutive expression of maize Kranz anatomy regulators have not been successful (Wang et al., 2017a). However, a different study showed that organelle development in rice vascular sheath cells can be stimulated using maize *GOLDEN2-LIKE* (*GLK*) genes (Wang et al., 2017b). The advancements in research and prospective pathways for modifying Kranz anatomy in rice were comprehensively reviewed by Sedelnikova et al. (2018).

The current C$_4$ rice project seeks to engineer rice to have the complete two-cell type Kranz mechanism. This endeavor necessitates not only the genetic sequences of the relevant photosynthetic proteins but also the appropriate promoters within the specific cell types of rice. When the C$_4$ rice project was proposed, the genes encoding C$_4$ pathway enzymes were well identified (Ermakova et al., 2020); however, a significant challenge has been the scarcity of promoters that can effectively drive bundle sheath expression in C$_3$ rice plants. Currently, promoters from C$_4$ species for phosphoenolpyruvate carboxykinase (PEPCK) and glycine decarboxylase (GDCP) have been used to drive the expression of these genes in rice BSCs, although the efficacy of these promoters remains a concern for the project's engineering aspects. Ermakova et al. (2020) summarized that five essential C$_4$ cycle enzymes—CA, PEPC, PPDK, malate dehydrogenase (MDH), and NADP-malic enzyme (NADP-ME)—have been successfully expressed in rice via a single construct. Despite these genetic advancements, the engineered rice did not exhibit enhanced photosynthesis. The shortfall could stem from multiple factors. First, the absence of Kranz anatomy, which is crucial for C$_4$ photosynthesis, may limit the efficiency of C$_4$ enzymes in transgenic rice. Second, the efficiency of the C$_4$ pathway depends on a complex network of membrane transporters for swift metabolite exchange between cells, a system that is not yet fully understood (Schuler et al., 2016). Third, the complexity of the C$_4$ photosynthetic pathway means that altering a single gene might have a minimal impact on the overall performance of the whole system. However, rapid advancements in synthetic biology offer promising prospects for integrating the complete C$_4$ photosynthetic pathway into rice (Schuler et al., 2016). Obviously, the development of C$_4$ rice currently faces significant technological, regulatory, and effectiveness challenges, which are difficult to accomplish in the near term.

4.7. Panicle photosynthesis

Although leaves are widely recognized for their role in photosynthesis, it is becoming evident that other green parts of plants also play a crucial role in absorbing CO$_2$ through photosynthesis. With the growing emphasis on enhancing photosynthesis to boost crop yields, the importance and contribution of these non-leaf green tissues to a plant's overall carbon assimilation are receiving increased attention (Brazel and Ó'Maoiléidigh, 2019; Hu et al., 2019; Lawson and Milliken, 2023; Sanchez-Bragado et al., 2020; Simkin et al., 2020). Research on nonfoliar photosynthesis in rice predominantly centers around the panicle, specifically targeting components such as spikelets, rachises, and branches. However, the photosynthetic processes occurring in the sheath and ligule have been comparatively overlooked and warrant further attention. The focus on panicle-related nonfoliar photosynthesis might stem from several factors: (1) panicles are usually positioned at the top of the canopy where light exposure is more abundant than in lower regions; (2) the carbon fixed in panicles is proximal to the developing grains, which reduces the distance for assimilate transport to these grains; and (3) panicles typically senesce later than leaves, particularly under challenging conditions such as drought, potentially offering a prolonged period for photosynthesis (Chang et al., 2020).

The extent to which panicle photosynthesis contributes to grain filling remains a contentious topic. Certain research indicates that the photosynthetic capacity of panicles is minimal, contributing to less than 8% of the photosynthetic rate observed in flag leaves (Takeda and Maruta, 1956; Tsuno et al., 1975). Conversely, other studies argue that panicles can assimilate CO$_2$ at rates exceeding 30% of that in flag leaves, suggesting a significant role in the process (Chang et al., 2020; Imaizumi et al., 1990). A key challenge in accurately determining the contribution of nonfoliar photosynthesis to overall carbon assimilation is the limitations inherent in current methodologies. Complicating factors include the complex three-dimensional panicle structure, the variability of CO$_2$ sources, and the existence of diverse photosynthetic pathways. Research methods for studying panicle photosynthesis, such as removing or shading panicles, applying herbicides, tracing isotopes, measuring gas exchange in spikelets, and assessing chlorophyll fluorescence, all have inherent drawbacks. These include the potential negative effects of shading and herbicides on the function of organs, possible compensatory responses, the impact of environmental and physiological factors on the precision of stable isotope analysis, and biases in gas exchange measurements caused by inconsistent lighting, temperature variations, and diverse CO$_2$ sources (Tambussi et al., 2021). Despite the evidence pointing to high photosynthetic potential in panicles, underscored by their enzyme activity and stomatal behavior (Bertolino et al., 2022; Imaizumi et al., 1990), I am inclined to think that meaningful progress in understanding rice panicle photosynthesis will be difficult to achieve without the establishment of a reliable method for its measurement.

5. Future directions

Theoretical calculations have suggested that enhancing photosynthesis is the sole viable strategy for further high-yield breeding (Long et al., 2015; Zhu et al., 2010). Consequently, a variety of strategies have been explored (Araus et al., 2021; Furbank et al., 2020; Zhu et al., 2022), and most of those efforts were also made in rice, as outlined in earlier sections. Over the past decade, the application of synthetic biology, rooted in a comprehensive molecular understanding, has significantly refined photosynthesis, yielding notable progress. For example, more than seven photorespiration bypass pathways have been successfully integrated into plants (Smith et al., 2023). Additionally, recent work by Chen et al. (2023) has advanced the reconstruction of bacterial carboxysomes in plants, resulting in the formation of almost complete carboxysomes within the chloroplasts of tabacum. With the rapid progress in synthetic biology, it is expected that utilizing these techniques for engineering photosynthesis will emerge as a key area of focus in photosynthetic research. In my opinion, the success of diverse engineering strategies to boost photosynthesis is influenced not only by breakthroughs in scientific research but also by governmental decrees and public attitudes. Embracing a variety of techniques may offer substantial benefits in improving photosynthesis. Given the extensive reviews on future directions for engineering photosynthesis with modern biotechnologies (Johnson, 2022; Nguyen et al., 2023a; Zhu et al., 2022), here, I propose some strategies that breeders and agronomists should play attention (Fig. 1).

5.1. Integrating photosynthesis into organismic processes

Adopting a whole-plant perspective on photosynthesis illuminates the complexity and variability inherent in this process, which is often overshadowed by a narrow focus on individual leaves in many research endeavors. This oversight can lead to a fragmented understanding of photosynthesis, neglecting its integration within the entire plant system. It is crucial to recognize that photosynthesis is not merely a leaf-level phenomenon but rather a critical process that underpins the growth, development, and reproductive success of plants by supplying the necessary energy and organic compounds. Although photosynthesis occurs at the cellular level within chloroplasts, it is significantly affected by numerous factors at the whole-plant level (Calzadilla et al., 2022). Here, I will delve into two specific examples: the interactions between shoots and roots and the regulation of source-sink dynamics.

Roots and shoots play a pivotal role in the optimal capture and use of essential resources such as light, CO_2, water, and nutrients, which are vital for photosynthesis. By focusing solely on photosynthesis, it would be ideal to allocate the primary products to the leaves to maximize light use. However, an increase in leaf area necessitates a more extensive root system not only for sufficient water and mineral absorption, which are vital for photosynthesis and transpiration, but also to provide stability to the plant canopy. This balance in resource allocation highlights the intricate decision-making plants undergo, adapting to environmental changes. In this scenario, the optimization of carbon and other source distributions becomes a pivotal aspect, affecting photosynthetic efficiency at the individual plant and canopy levels. Whole-plant models have shown that the strategic allocation of resources between roots and shoots is fundamental for boosting canopy photosynthesis (Buckley, 2021; Yin et al., 2022).

The roles of sink-source regulation in the relationship between photosynthesis and crop yield have sparked considerable debate among crop physiologists (Chang et al., 2017; Fabre et al., 2019; Furbank et al., 2020; Paul et al., 2020). It is essential to differentiate between source-limited scenarios, where the capacity for photosynthesis is the limiting factor, and sink-limited scenarios, where the bottleneck is the ability to use or store photosynthesis products. Studies involving the enrichment of air with CO_2 have demonstrated that while boosting photosynthesis with increased CO_2 can sometimes improve yield, its impact is often limited by the plant's 'sink strength' (Dingkuhn et al., 2020; Furbank et al., 2020; White et al., 2016). Such constraints are primarily due to the role of sugar signalling in regulating key photosynthetic genes and nutrient levels, underlining the intricate relationship between the activities of the source and the demands of the sink (Furbank et al., 2020; Paul, 2021; Paul et al., 2018). Moreover, some studies have shown that a feed-forward approach – where enhancing photosynthesis boosts the plant's ability to form 'sinks' – could overcome traditional limitations in the source-sink relationship (Chang et al., 2017; Furbank et al., 2020). This indicates that sink strength also regulates
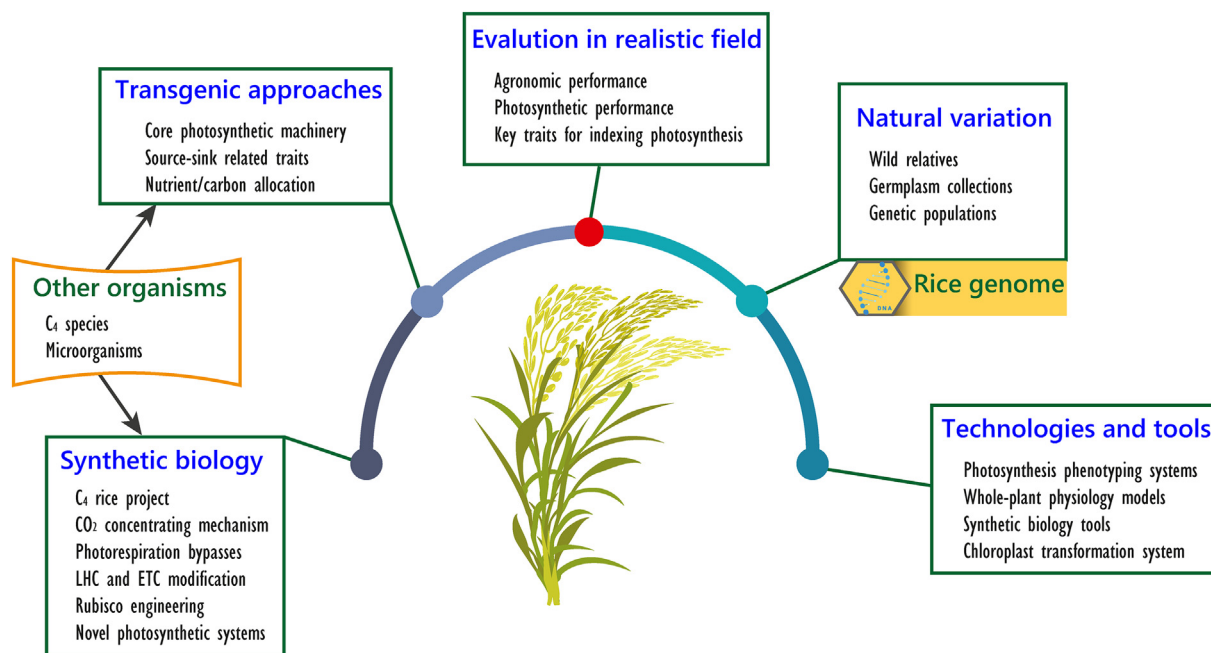

Fig. 1. Summary of the main areas of scientific activity required to improve rice photosynthesis for high yield. LHC and ETC are Light-harvesting complexes and electron transport chain, respectively.

photosynthetic capacity, underscoring the importance of integrating photosynthesis into whole-plant processes.

5.2. Identifying key photosynthetic trait dimensions linked to grain yield

As mentioned earlier, a wide array of photosynthetic indices has been recognized. However, a thorough understanding of the correlation between these widely used photosynthetic rate indices and crop yields remains elusive. This lack of comprehensive insight has resulted in dispersed research efforts in photosynthesis aimed at boosting crop yields. Simultaneously measuring all existing photosynthetic indices is not only challenging but also often redundant due to their considerable overlap. Therefore, reducing the dimensions of photosynthetic traits and elucidating the relationships between pivotal photosynthetic traits and grain yield are essential for advancing photosynthesis research. Indeed, dimensionality reduction has a long tradition in plant ecology, exemplified by the effective deployment of the leaf economic spectrum framework (Wright et al., 2004). Leaves display a broad spectrum of variations, including a range of morphological, physiological, and biochemical features that have been thoroughly investigated and documented (refer to the TRY plant trait database: www.try-db.org). Among these features, leaf dry mass per area (LMA) was identified as a central trait. LMA shows a strong correlation with photosynthetic traits, elemental contents, respiration rates, and lifespan across different species worldwide. These correlations have led to the generalization of the leaf economic spectrum, which posits that fast-growing, resource-acquisitive species typically have lower LMA, higher mass-based photosynthetic rates, and higher nitrogen content and respiration rates, but a shorter leaf lifespan compared to slow-growing, resource-conservative species. Apparently, it is imperative for future research to formulate theories akin to the leaf economic spectrum framework. Such theories should concentrate on a selected number of critical photosynthetic traits to deepen our understanding of the intricate relationship between photosynthesis and grain yield.

5.3. Developing photosynthesis phenotyping methods

The rice genome was released more than 20 years ago, leading to the development of a diverse sequenced panel known as the 3K population, which includes *indica* and *japonica* rice genotypes from various pedigrees and geographic origins. This panel is currently expanding to encompass 10,000 entries (Wang et al., 2018). Despite these advancements, allelic variations in key genes/proteins that regulate photosynthetic flux have seldom been assessed. The challenge lies in the low throughput of estimating photosynthetic traits. Recent innovations have introduced phenotyping platforms equipped with commercial sensors such as hyperspectral and fluorescence meters in both indoor and outdoor settings (Fu et al., 2022; Furbank et al., 2019). These platforms offer a non-invasive and efficient means to monitor plant growth over time, significantly enhancing our understanding of growth physiology across different scales, from leaves to canopies. Such advancements may also contribute to reducing the dimensions of photosynthetic traits. Nonetheless, as noted earlier, the connection between photosynthetic efficiency and the metrics derived from these techniques is indirect and frequently inconsistent across diverse studies. There is a pressing need for high-throughput and direct methodologies to address this issue, as breakthroughs in this area are critical for overcoming the obstacles in breeding programs.

5.4. Evaluating photosynthetic performance under field conditions

Current research focused on improving photosynthesis predominantly takes place in growth chambers and laboratories, with only a minor fraction undergoing validation under actual field conditions. Recognizing the significant disparities in plant growth between controlled settings and outdoor field environments is crucial (Poorter et al., 2016). To effectively apply these scientific insights to real-world

agricultural issues, comprehensive field evaluations of both existing and newly developed plant materials are essential. This necessitates well-maintained experimental fields to facilitate extensive field trials. Given that the traits influencing source capacity are likely subject to significant interactions between genotype and environment, conducting evaluations across multiple experimental sites becomes imperative. Such a holistic approach to research will ensure that improvements in photosynthesis can be effectively harnessed to increase agricultural productivity and sustainability.

6. Conclusions

In this review, I have synthesized current research on enhancing photosynthesis to improve rice grain yield, highlighting both the advances and the remaining challenges. The discussion begins by addressing the limitations and challenges in linking photosynthesis to yield. Subsequently, I summarized various photosynthesis indices, their measurement techniques, and the difficulties in directly correlating these indices with grain yield. Moreover, the review delves into recent advancements that show promise for improving photosynthetic efficiency in rice such as exploiting natural genetic variations enhancing the electron transport chain, and increasing the efficiency of Rubisco. It also discusses strategies like elevating the CO_2 concentration around Rubisco and innovative projects such as the C_4 rice. The review further considers the contributions of non-leaf photosynthesis and strategies to circumvent photorespiration, both of which could enhance the photosynthetic efficiency of rice. Lastly, I suggested that future research should focus on refining photosynthesis phenotyping tools and broadening our understanding of the genetic basis of photosynthetic efficiency. I also highlighted that these laboratory findings are effectively translated into field conditions, necessitating rigorous field evaluations to confirm that enhancements in photosynthetic performance led to tangible increases in crop productivity under diverse environmental scenarios.

Abbreviations

Not applicable.

Availability of data and materials

Not applicable.

Authors' contributions

D.X.: conceptualization, draft writing, editing, and revision.

Declaration of competing interest

I declare that I have no competing interests. As an Editor-in-Chief, I was not involved in the peer review of this article and did not have access to any information regarding its peer-review process. Full responsibility for the editorial process of this article was delegated to Prof. Shaobing Peng.

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