Improving the Photosynthetic Efficiency and Productivity of Cowpea in Sub Saharan Africa: A Review

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Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

Review Article

ABSTRACT

Recent studies have found compelling evidence that enhancing photosynthetic mechanisms through genetic engineering can increase crop yield potential. This paper focuses on cowpea productivity in Sub-Saharan Africa, its importance, factors limiting photosynthetic potential, and techniques towards boosting cowpea photosynthetic efficiency. High light intensity, low temperature, low CO_2 environment, and water scarcity have all been identified as key limiting factors for crop photosynthetic efficiency. Deactivation of Rubisco functioning in shade has also been noted to reduce cowpea photosynthetic potential. However, recent successes have been observed through genetic manipulation of photosynthesis traits so as to improve photosynthetic efficiency and yield under control conditions with considerable increase in yield from 14 to 40%. Thus, improving photosynthesis has the potential to increase crop productivity.

Keywords: Cowpea; productivity; photosynthetic efficiency; photosynthetic potential.

1. INTRODUCTION

"The efficiency with which a crop collects light and turns it into biomass over the growing season is a crucial driver of eventual output, be it biomass or grain" [1,2]. "Yield potential is the highest yield possible from a crop, and it is defined as the maximum yield feasible when the

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best-adapted crop variety is grown under perfect conditions with no biotic or abiotic stress" [3]. Light availability, light collection, energy conversion, and the shape of the plant canopy are the factors that influence yield potential. Energy conversion, which is dictated by photosynthetic efficiency, is a major limiting factor affecting carbohydrate partitioning crops including rice, wheat, and maize, as well as cowpeas, that contributes to yields below their potential maximum [4,5]. Because photorespiration might lose up to 50% of fixed carbon under some conditions, Carbondioxide (CO_2) enrichment experiment has continuously provided compelling evidence towards enhanced yields. It might be obtained by greater CO_2 uptake, indicating that improved photosynthetic CO_2 assimilation can result in higher yields [6,7]. "Despite the fact that some studies have indicated a negative relationship between leaf area, photosynthesis and yield, Makino [8] discovered a positive relationship between photosynthetic rates, biomass, and wheat production".

"Cowpea (*Vigna unguiculata* L Walp), also called black-eyed pea, is an annual leguminous crop widely produced in sub-Saharan Africa (SSA). Cowpeas are grown for both their grains and their veggies" [9]. "The cowpea plant is a warm-season herbaceous annual that requires temperatures of at least 18°C at all stages of development, with an optimal growing temperature of around 28°C" [10]. "Cowpea is generally a day-shortening or, in some cases, day-neutral plant. In many cowpea accessions, floral bud initiation and development are photoperiods sensitive, and the degree of photoperiod sensitivity (the amount of blooming delay) is controlled by temperature in some genotypes" [11,12,13]. "It grows well in a wide range of soils and conditions, although it thrives in well-drained sandy loams or sandy soils with pH values between 5.5 and 6.5" [14,15]. "The crop performs well even when produced in poor nutrient soils due to its ability to (BNF) fix nitrogen in the soil" [16]. Cowpea is a multipurpose crop that nourishes both humans and animals while also delivering a lucrative and constant income flow to farmers and grain traders [17] (Ngum et al., 2022). It is vital to the livelihoods of millions of people in Sub-Saharan Africa [18,19] and comes in a variety of forms, including young leaves, green pods, and green seeds that are eaten as vegetables, as well as dry seeds that are used in a variety of food preparations. Cowpea is an important source of protein, minerals, and vitamins in daily diets across Sub-Saharan Africa, with 25 percent protein (on a dry-weight basis) in its seeds and young leaves [20,21]. Owade et al. [9] and Philipo et al. [22] noted cowpea leaves as a vegetable are rich in micronutrients including iron and vitamin A whose deficiencies are prevalent in Sub Saharan Africa. By combining the synergistic effects of high protein and high lysine from cowpea with high methionine and high energy from starchy foods like yam, maize, and cassava, even a small quantity of cowpea ensures nutritional balance and improves protein quality.

The purpose of this paper is to provide an overview of current research on increasing cowpea crop photosynthetic efficiency. It explores the production of cowpea in sub–Saharan African, importance of cowpea, factors that limit photosynthetic potential in cowpea and strategies towards improving photosynthetic efficiency in cowpea productivity

2. COWPEA PRODUCTION IN SUB SAHARAN AFRICA

Cowpea is widely grown in the tropics, with widespread cultivation in Africa. Due to the non-existent of data on cowpea production since the late 1970s by the Food and Agriculture Organisation (FAO), current production data for most nations has been extremely difficult to come across. However, it was able to estimate cowpea production by subtracting production statistics for dry beans (*Phaseolus vulgaris*), broad beans, peas, chickpeas, and lentils from FAO production data for total pulses.

Around 11 million hectares of cowpea were cultivated in Africa in 2017, with the majority of output concentrated in West Africa (10.6 million hectares), especially in Niger, Nigeria, Burkina Faso, and Mali. According to FAOSTAT (2017), Africa produces approximately 87% of cowpeas. Brazil, on the other hand, increased cowpea farming in South America, and the country is currently the world's third-largest producer. Cowpeas are mostly grown in West Africa Taylor et al. [23], which accounts for 60% of global production in Sub-Saharan Africa. In 2017, the globe produced more than 7.4 million tons of dried cowpeas, with Africa generating about 7.1 million. Nigeria, Africa's greatest producer and consumer, is responsible for 48% of African production and 46% of global production. Africa only exports and buys a little

Table 1. Top 12 cowpea producing countries in Africa (2020)

NO	Countries	Harvested area (ha)	Yield (Kg/ha)
1	Burkina Faso	1376717	483.8
2	Cameroon	225086	789.6
3	Kenya	239131	1104.7
4	Mali	406698	491.2
5	Mozambique	349589	264.4
6	Niger	5723820	460.8
7	Nigeria	4695849	776.7
8	Sudan	853088	173.7
9	DR Congo	159681	444.5
10	Senegal	289895	875.8
11	Tanzania	126987	1099.0
12	Ghana	150126	1362.9

Source: FOASTAT, 2020

number of goods. According to Olayiwola and Soremi, [24], 52% of Africa's cowpea crop is used for food, 13% for animal feed, 10% for seeds, 9% for other uses, and 16% is wasted due to inability of famers to understand the cultivation and agronomic practices to avert losses right from planting until value addition for storage and use.

3. IMPORTANCE OF COWPEA

"Cowpeas are often consumed as a dry grain or raw vegetable. Mathiot [25] and Carmo-Silva (2022) reported that cowpeas are grown throughout Africa because of their high protein content, but especially important in West Africa, where they are the most important source of vegetable protein". "Cowpea grain contains high protein, carbs, vitamins, and fibre. It also contains minimal fat, which is beneficial in the prevention of a variety of metabolic and cardiovascular illnesses" (Bettino et al., 2019). Horn et al. [18,93] explained that cowpea is the cheapest source of protein in most farming areas in sub-Saharan Africa. It has multiple benefits as animal feed, food, and source of income [26] (Simons, 2019). "It is one of the nutrient-dense African indigenous vegetables with the potential to improve food and nutrition security in Sub-Saharan Africa In certain situations, full-sized pods are plucked right before they dry up, and the grains are cooked and consumed like a vegetable. Its popularity as a fresh leafy vegetable has grown rapidly in Sub-Saharan Africa" [27]. "Cowpea varieties that mature early are essential in providing food during the ravenous time before other crops such as maize, rice, pearl millet, sorghum, and other landraces of cowpeas and peanuts are harvested" [27]. Phares et al. [28], also reveals

that cowpeas play enormous role in improving soil fertility. Cowpea cultivars when inter seeding as a living mulch crop such as maize, reduce weed biomass and biodiversity, which consequently improve soil physical properties (Mustapha et al. 2021). "Intercropping with cowpea has been reported to reduce and smother weeds in dryland farming systems in the smallholder farming sector, according to" [29,27]. Other cowpea varieties have been shown to control the nematode (*Scutellonema cavenessi*), a serious pest of various crops in Sub-Saharan Africa [30] because of cowpea's ability to fix nitrogen and improving soil fertility there by inhibiting nematodes attack which is quite commonly associated with poor soil fertility regions or areas. Using cowpeas as cover crops can suppress pests, prevent erosion, and increase carbon sequestration [31,32,33].

4. FACTORS THAT LIMIT PHOTOSYNTHETIC POTENTIAL IN COWPEA

Photosynthesis efficiency of crops is limited when subjected to stress conditions such as high light intensity, low temperature, low CO_2 environment, and water limitation. Keys [34] and Fernie and Bauwe, [35] regarded photosynthesis as a wasteful process in their studies. Taylor et al. (2022) indicated that deactivation of Rubisco functioning in shade reduce cowpea photosynthetic potential. Although studies have been done on the biochemical processes that determine chlorophyll content chloroplast photosynthetic efficiency or the ability to convert light energy into carbon [36], there is the need to carry out more detail research to understand the whole process to improve photosynthestic efficiency in

cowpea. Thus, photosynthesis efficiency is a balance between energy provided for plant growth and energy used to preserve the photosynthetic equipment from light damage (Pralon, 2020; Gao et al., 2022). Because of an evolutionary adaptive carbon-concentrating process that enriches RuBisCO with CO_2 to maximum saturation limits, C3 and C4 crops are photosynthetically more effective than the former (Gurbachan et al., 2020). CO_2 leakage was reduced by concentrating CO_2 in the bundle sheath cells, allowing Rubisco's carboxylase activities to be maximized (Hussain et al., 2020). Other research explains that lowering the Rubisco concentration in crops reduces photosynthetic efficiency. Water stress has been found to stand out amongst various abiotic stress that limits photosynthesis efficiency for its large area occurrence [37] (Nunes, 2022). Some other factors such as photorespiration, structure of the plant leaf, CO_2 concentration and temperature have been well studied and are discussed below

4.1 Structure of the Plant Leaf

Three or more layers of leaves are typical of a mature, healthy plant. At midday, the uppermost layer of leaves in plants with leaves that are about horizontal covers the majority of the light, while the second layer receives 10% of the light and the layer below that receives a mere 1%. As a result, at least two-thirds of the energy that is blocked by the highest leaves goes unused. Plant architecture should be changed to allow the highest leaves to capture a smaller fraction of the light, allowing lighter to reach the leaves in the lower layers [38,39,40]. This is possible when the highest leaves are vertical and the lowermost leaves are horizontal [38,39,40]. An erect leaf at a 75° angle to the horizontal leaf would catch just enough light energy per unit area to saturate photosynthesis. The remaining direct light would reach the canopy's lowest tiers' leaves [41,42,43,44]. With an optimal distribution of leaves on the main stem, models have anticipated an increase in light energy-use efficiency. According to the model proposed by Miglani et al. [42], replacing plants with roughly horizontal leaves with upright upper leaves would result in a more than twofold gain in light energy-use efficiency at midday in full sunlight. Earlier kinds of rice with more horizontal leaves have been replaced by newly bred types with more vertical leaves in the top layer, based on predictions from such models [45]. The effect of this change in canopy design is significant. The increase in yield is greatest when the Sun is directly overhead but as the Sun angle decreases, this benefit gradually diminishes. Kumagai et al. [46] and studies by other authors Gitelson et al. [47] investigated whether a drop in chlorophyll content would result in an increase in canopy photosynthesis in soybeans using several canopy photosynthesises models [92,95]. Correlation between leaf Chlorophyll content, leaf optical characteristics, and biochemical capacity in several soybean accessions, as well as a wild type and a Chlorophyll content -deficient mutant, using a variety of criteria was tested. It was concluded that canopy photosynthesis could be conserved by lowering leaf chlorophyll content and increasing light interception by lower canopy leaves [47]. This will result in a reduction in extra photon load on upper canopy leaves and enrichment of lower canopy leaves with sufficient light to contribute to photosynthetic yield. The key limiting factor for canopy photosynthesis is lower canopies leaf area, according to Digrado et al. (2022); while, the major limiting factor in greater biomass canopies was the light environment. According to Digrado et al. [95]; canopy architecture has a considerable impact on canopy photosynthetic efficiency and water consumption efficiency, implying that enhancing canopy structures can help increase agricultural yields.

4.2 Temperature

Study by Hall and Rao, [48] have shown that at low light intensities the rate of photosynthesis is the same at 15^0C and 25^0C. The reaction in the light limiting region, like true photochemical reaction are not sensitive to temperature. At higher light intensities, however, the rate of photosynthesis is much higher at 25^0C than 15^0C. Temperature, both at low and higher levels, reduces photosynthetic efficiency, productivity, and yield of crops around the world. Temperature is an important abiotic factor that affects plant growth and development [49]. Abiotic stress, such as high temperatures, reduces the plant's photosynthetic rate [50]. The plant's vegetative development characteristics and metabolic activities are also negatively impacted. Aside from it, emergence, maturity/ ripening, harvesting time (duration/ stage), and plant production are all influenced (Prasad et al., 2008; Shah et al., 2011). Low temperatures (chilling stress) have also been shown to affect plant metabolism and severely effect plant growth and development [13,14]. Low

temperatures (chilling stress) also have an adverse effect on germination, seedling emergence, and plant vigor, resulting in a reduction in plant productivity [51].

4.3 Photorespiration

"Photorespiration (also called the oxidative photosynthetic carbon cycle or C2 cycle) is a plant metabolic process in which the enzyme RuBisCO oxygenates RuBP, losing some of the energy gained by photosynthesis. In crop plants such as tobacco plants growing in full sunshine, photorespiration plays a significant role in the regulation of photosynthetic electron transport under fluctuating light and under natural conditions where plants are subjected to dynamic changes in light intensities" [52]. "However, plant carbon fixation is limited by photorespiration, which releases CO_2 and uses cellular energy to recycle the RuBisCO oxygenation product, 2-phosphoglycolate, back into the Calvin cycle [100]. This process reduces agricultural output by emitting CO_2 and dissipating energy" (Trudeau et al., 2018). Around one-third of the carbohydrate in C3 plants is lost due to photorespiration (Monteith, 1977). This physiological process can be viewed as a necessary evil because the cyclic mechanism (also known as the C2 cycle) is capable of recovering 75% of the carbon lost during RuBP oxidation [95]. It also plays a role in N-metabolism and keeps levels of the hazardous metabolite 2-phosphoglycolate generated by the RuBisCO oxygenation reaction to a minimum. In warm environments, the rate of photorespiration increases as the temperature rises. The photorespiratory C2 metabolism downstream of RuBisCO can be delayed by removing or downregulating an enzyme in the C2 pathway.

4.4 Carbondioxied (CO_2) Concentration

Hall and Rao [48], reported that in the light-limiting zone, lowering CO_2 content has no effect on photosynthesis rate, which implies that CO_2 does not participate directly in the photochemical activity. Photosynthesis is significantly increased by raising CO_2 concentration at light intensity above the light limitation area. As indicated by the constantly declining leaf net photosynthetic rate with higher CO_2 concentrations, CO_2 causes down-regulation of leaf photosynthesis [53]. The maximum carboxylation rate and the maximum electron transport rate were both drastically reduced at higher CO_2 concentrations,

exceeding their ideal values of roughly 600 ppm and 400 ppm, respectively [53]. Reduced stomatal conductance was partly related to photosynthesis at high CO_2 concentrations, as evidenced by decreases in stomatal density and area, as well as alterations in the spatial distribution pattern of stomata [54]. Reduced photorespiration and dark respiration, as well as increased carboxylation efficiency, may contribute to increased net photosynthesis rate under high CO_2 concentrations. In response to rising carbon dioxide levels, specific leaf area shrank considerably [55]. Baligar et al. (2021) found that increasing carbon dioxide and photosynthetic photon flux density (PPFD) levels greatly boosted net photosynthesis and water-use efficiency attributes but dramatically reduced stomatal conductance and transpiration in cacao genotypes. The stomatal conductance of water is reduced by an average of 22% when CO_2 levels are increased [56]. Because photosynthesis and stomatal activity are so important to plant carbon and water metabolism, plant development in high CO_2 environments has a wide range of downstream consequences on plant physiology [96,97,102]. The CO_2 concentration outside continues to rise, now reaching 400 parts per million (ppm) – and significantly higher in urban areas. While this rise has severe environmental consequences, it is a key component of photosynthesis, which boosts plant growth in a subtle way. The CO_2 concentration inside a greenhouse, on the other hand, is rarely at 400 ppm. When greenhouses are closed for the winter and loaded with crops, for example, CO_2 is utilized by the plants, and the concentration drops to as low as 200 ppm. Low CO_2 concentration has two repercussions, according to Hudson et al. [57]: photosynthesis is reduced and the light saturation point is reduced (The light saturation point is the point at which further increases in light have no effect on photosynthesis). At low CO_2 concentrations, the value of additional lighting is diminished. Photosynthesis increases as CO_2 levels rise until it reaches a saturation point usually around 1,000 ppm [100].

5. STRATEGIES FOR IMPROVING PHOTOSYNTHETIC EFFICIENCY IN COWPEA

The previously achieved extraordinary improvement in agricultural yields has now come to a halt, as the limits of selection and optimization of cultivation processes have

reached a halt (Kubis and Bar-Even 2019). Novel techniques to improve the proficiency with which plants can transform additional light energy into biomass are needed to attain the photosynthetic efficiency and sustain crop productivity (yield) needed to feed the growing global population. In the past, improvements in the harvest index, rather than an increase in biomass, have accounted for the majority of gains in wheat yield potential. Because of the limitations given by low biomass to translocate reserve assimilates to grain sinks, further extraordinary progress in the harvest index is unlikely in the current context. The potential for increasing productive biomass and harvestable grain exists, but photosynthetic limitations create constraints such as chlorophyll retention, radiation utilization, and RuBisCO efficiency that must be overcome to boost crop yield. Even a minor increase in net photosynthetic rate can result in significant increases in biomass and thus yield [58].

5.1 Stay Green

The heritable delayed foliar senescence trait in model and agricultural plant species is known as Stay-Green. It's an important trait for improving the genetics of numerous crops because it helps plants to maintain their leaves active photosynthetically even when they're stressed [59] (Wu et al., 2022). Chlorophyll degradation during leaf senescence, on the other hand, is required for the mobilization of mineral nutrients, particularly nitrogen, to newly formed sinks. When mutations in genes producing enzymes such as Mg-dechelatase and chl b reductase occur, the catabolic pathway is disrupted, resulting in tissue greenness [60]. Stay greens were divided into two categories in studies by Miglani et al. [42]:

i.   cosmetic stay-green, in which a lesion prevents chlorophyll degradation at an early stage.
ii. functional stay-greens, in which the transition from the carbon-capture to the nitrogen-mobilization (senescence) phase of canopy development is delayed and/or the senescence syndrome is sluggish.

5.2 Enhancing Photosynthetic Processes by Modifying Photorespiration Metabolism

The successful creation of this pathway, as well as the improved growth of plants overexpressing the functional pathway, provide independent proof that diverting glycolate metabolism from the photorespiratory pathway in the chloroplast can really boost photosynthesis. Recycling the 2-phosphoglycolate produced by Rubisco's oxygenase process necessitates a complex and energy-intensive series of events known as the photorespiratory cycle. Several ways (optimizing flux through the native photorespiratory pathway, installing non-native alternative photorespiratory pathways, and lowering or even eliminating Rubisco-catalyzed oxygenation of RuBP to reduce substrate entrance into the photorespiratory cycle), have been proposed to reduce rates of photorespiratory energy or carbon loss, based on either natural variation screening or genetic engineering. Recent research suggests that altering photorespiratory fluxes or creating artificial by passes to photorespiration can significantly boost plant production. Photorespiration is the principal physiological process that detoxifies 2-phosphoglycolate (2-PG) and is responsible for 20–50% yield loss, depending on the environmental circumstances and the kind of photosynthesis used by the plant species [61]. A "bin" is a genetic map location with a distinct segregation pattern that is separated from neighboring bins by a single recombination event [62]. Between two fixed Core Markers, the genetic maps are partitioned into 100 segments, called bins, of 20 cM each according to [63]. A bin is the interval between the leftmost or top Core Marker and the following Core Marker that includes all loci. The accuracy with which a locus is assigned to a bin is determined on the precision of mapping data, which improves as the number of markers or populations grows. Bin 1 refers to the beginning of a range, while bin 2 refers to the end of the range, whenever the placement is statistically ambiguous. For one gene, two or more chromosomal numbers or bins may exist. Many gene families and proteins are formed as a result of gene duplication. Duplication may have happened at an evolutionary time point, causing gene sequences to diverge over time, resulting in genes being present in many chromosomal positions. RuBisCO, for example, is made up of eight small subunits coded by the nuclear multigene family rbcS and eight large subunits coded by the chloroplast genome's single gene rbcL [64]. OsRBCS1, OsRBCS2, OsRBCS3, OsRBCS4, and OsRBCS5 are the eight rbcS cDNA clones produced from five separate rbcS genes. While OsRBCS1 is found on chromosome 2, the rest are found on

chromosome 12 [42]. This process involves an energy-intensive metabolic route that recycles RuBisCO oxygenation reactions' harmful by products. The energy used in this inefficient process (equal to 12.25 ATP per cycle) lowers assimilate production and raises agricultural yield costs. As a result, research into alternate pathways (which metabolize 2-PG in the same production compartment, i.e., chloroplast, oxidation of 2-PG at a lower energy cost) is predicted to improve the photorespiratory mechanism.

In this era of synthetic biology, these pathways will provide significant yield advances by providing new chances for enhancing photosynthetic efficiency [65]. Moore et al. [66] also highlighted a variety of ways for decreasing substrate entrance in the photorespiratory pathway to boost crop yield, such as optimizing metabolite flow and reducing RuBP oxygenation. Optimizing the flux of the toxic metabolite 2-PG to speed up 3-phosphoglycerate recovery could be a potential method for increasing production. However, anatomical changes should be made to ensure that inter-organellar metabolic flux is not restricted by spatial constraints, such as the conversion of glycolate into glycine in the peroxisome and further decarboxylation in the mitochondrial compartment in the photorespiration salvage pathway. Transgenics overexpressing mitochondrial glycine decarboxylase also showed better photosynthesis as a result of increased metabolic flux via photorespiration [67]. As indicated by Eisenhut et al. [68], genetic interventions that construct new synthetic bypasses of photorespiration in a single chloroplast compartment will be very useful in enhancing photosynthetic efficiency. Alternative photorespiratory pathways have the potential to boost C3 crop output significantly. Alternative photorespiratory methods have been tried in tobacco, including the E. coli glyoxylate oxidation pathway, glycolate oxidase, and malate dehydrogenase pathways. Without the involvement of mitochondria or peroxisomes, Arabidopsis and potato convert 2-glycolate to glycerate completely in chloroplasts [69].

In tobacco chloroplasts, Naseem et al. [70] assessed the outcomes of these three different photorespiratory (AP) routes. Plant development and carbon fixation were likewise slowed in mutant rice lines with defective Os PLGG1. This was due to the function of PLGG1 in regulating glycolate/glycerate concentrations in chloroplasts to safe levels [71]. These researches on creating photorespiratory bypass channels by membrane transporter alterations pave the way for greater photosynthetic efficiency and agricultural yield potential [72,73]. However, so far, genetic-engineering technology has had only little success in enhancing photosynthetic efficiency [68]. Modification of genes regulatory sequences could be another way to improve photosynthetic efficiency. Fine-tuning gene expression, modifying substrate affinities to improve enzyme catalytic performance, and inducible systems are all innovative ways to manipulate photorespiration in agricultural plants. A promising method for increasing photosynthetic productivity is to reduce photorespiratory loss.

5.3 Carbon Concentration Mechanism

The Carbon Concentration Mechanism is a biological response to low carbon dioxide levels in the atmosphere. It is a technique that boosts photosynthetic output in algal cells by elevating inorganic carbon levels several times higher than the carbon dioxide concentration in the environment. Price et al. [74] regard carbon concentration mechanism (CCM) as a unique adaptation that many photosynthetic organisms have acquired to increase photosynthetic efficiency in low-CO_2 aquatic environments. Synthetic biology, on the other hand, offers fresh techniques to manipulating C3 metabolism downstream of the oxygenation phase. Changes in RuBisCO's catalytic capabilities or an increase in CO_2 concentration at the RuBisCO site could be an effective way to boost photosynthesis. Because of the sluggish diffusion of CO_2 in apoplastic space and RuBP oxygenation by RuBisCO, C3 plants' photosynthetic efficiency declines under hot, dry circumstances. The RuBisCO catalysis fixes oxygen instead of carbon when the CO_2 concentration in the chloroplasts falls below 50 ppm (mg/L). This is a huge waste of energy, and the RuBisCO only runs at about a fifth of its maximum speed as a result. Plants with a CCM surrounding the RuBisCO site are able to overcome the problem of photorespiration (C4 and CAM plants). Under current atmospheric CO_2 concentrations, C4 photosynthesis has a significantly higher conversion efficiency than C3 photosynthesis [75]. PEPC levels increased with reduced sensitivity of photosynthetic absorption to O_2 in transgenic rice and Arabidopsis overexpressing C4-specific PEP carboxylase (PEPC) [76]. Overexpression of PEPC in transgenics results in the generation of

extra amino acids and proteins due to its anaplerotic role in replenishing organic acids in C3 plants [77]. Thus, simply overexpressing C4 enzymes like PEPC to achieve photosynthetic enhancement would put a strain on plant roots for N nutrition, resulting in the production of extra proteins with lower requirements, which should be taken into account during C3 to C4 interconversion for a specific crop species.

For decades, a significant number of worldwide consortia have been attempting to increase photosynthesis and the transition of C3 rice into C4 rice. C4 rice that is transgenic has yet to be developed. The C4 rice consortium's research sheds light on the constraints imposed by compartmentalization of a two-celled C4 mechanism in a single-celled C3 rice biological system. Another feasible technique for C4 rice engineering is to introduce a single-celled C4 mechanism similar to that found in Hydrilla (which lacks normal kranz anatomy, i.e., no compartmentalization of initial and final fixation of CO_2 in mesophyll and bundle sheath cell; famously known as non-Kranz C4). In constructing C4 crops like rice, these investigations demonstrated the importance of aspects including diurnal regulation of enzyme activity, enzyme manufacturing site, and phosphorylation status inside chloroplasts [78]. However, incorporating the increasingly efficient C4 photosynthetic pathway into staple grains will be a major accomplishment. The C4 photosynthetic pathway is more efficient than the C3 pathway in terms of light, nitrogen, and water usage. However, if anthropogenic activities under the banner of "progress" continue to increase atmospheric CO_2, this efficiency advantage is projected to fade in the near future.

5.4 Manipulation of Rubisco Biogenesis

When ribulose 1, 5- bisP (RuBP) regeneration is limited, modifying Rubisco to increase selectivity for CO_2 compared to oxygen would reduce photorespiration and increase photosynthesis [79]. The amount of CO_2 fixed per Rubisco protein would increase if the catalytic turnover rate was increased. However, manipulating is huge challenge especially in higher plant as a result of it multi nature and regulation by nuclear and chloroplast endcoded genes [58]. Rubiscos with higher specificity have been discovered naturally in red algae, and Rubiscos from C4 species have higher catalytic turnover rates. Crop models suggest that integrating a "better Rubisco" into C3 crop

species will result in significant increases in canopy photosynthesis [58]. Rubisco is a hexadecamer made up of eight chloroplast-encoded large subunits and eight nucleus-encoded tiny subunits found in higher plants. Rubisco structure-function investigations of higher plant Rubisco have been impeded by the inability to build Rubisco from any photosynthetic eukaryote within Escherichia coli. Understanding chaperoning action in the folding and assembly of hexadecameric Rubisco is progressing (Liu et al., 2010). Despite the availability of Rubisco crystal structures, the idea of increasing Rubisco's kinetic characteristics through rational design remains a goal for the future. Meanwhile, novel Rubiscos are being created through directed evolution in E. coli that is dependent on Rubisco activity [80]. Chloroplast transformation mechanisms must be created in additional species to modulate Rubisco inside higher plants. The development of a tobacco (*Nicotiana tabacum*) master line that expresses Rubisco from Rhodosprillum rubrum allows for the quick transformation of tobacco with changed Rubisco [81].

More efficient RuBisCO with catalytic ability is another technique for increasing photosynthetic carbon uptake. The catalytic effectiveness of RuBisCO is determined by two key factors: stronger CO_2 specificity and a faster carboxylation turnover rate. Specificity and RuBP carboxylation turnover rate have been found to be inversely related in studies [82]. So, in order to improve RuBisCO catalysis, these two aspects must be prioritized. Higher plants have also been found to have a wide range of RuBisCO catalysis. According to a study on such RuBisCO variants in the Triticeae tribe to increase wheat photosynthesis, such variation in RuBisCO turnover rate and specificity factor can be used for a CO_2-enriched crop [82]. Furthermore, changes in carboxylation efficiency are due to the L-subunit, which contributes directly to catalytic action. Genetic modification of the chloroplast-encoded L-subunit is another viable method for enhancing RuBisCO catalysis and thus photosynthetic efficiency.

5.5 Accelerating Recovery from Photoprotection (NPQ)

The dissipation of surplus energy in the form of heat, known as non-photochemical quenching (NPQ), is a key technique for photoprotection. Non-photochemical quenching (NPQ) is a

technique used by plants and algae to protect themselves from the harmful effects of too much light [83,84,85]. Exposure to light in the lack of appropriate photoprotection reduces photosynthetic light usage efficiency, according to [86]. Under low light conditions, the maximum efficiency with which light may be used to drive electron transport (PSIImax) or CO_2 fixation (CO_2,max) and photosynthesis can be determined [86]. When the amount of light absorbed by a leaf exceeds the leaf's assimilatory capacity, the proton conductance of the chloroplast ATPase decreases, resulting in a fast drop in the thylakoid lumen pH [87,88]. By dispersing the surplus absorbed light energy as heat, a change in pH activates and protects the photosynthetic equipment against short-term changes in light intensity [89,23]. A major stage in the NPQ process is the activation of the xanthophyll cycle, which is dependent on the activities of the enzymes violaxanthin de-epoxidase (VDE) and zeaxanthin epoxidase (ZEP), as well as the detection of changes in lumen pH by proteins such as PsbS, and PSII.. This induction mechanism occurs on a second-to-season time frame and is unaffected by changes in gene expression. Although NPQ changes occur quickly, they are not instantaneous. Down-regulation of PSII occurs long after light levels have restored to non-stress levels, which can lead to loss of potential photosynthetic capacity [73]. Both components of the NPQ system were adjusted by Kromdijk and Walter [86], who increased the amount of PsbS for pH sensing and the amount of ZEP and VDE for faster xanthophyll cycle kinetics. These plants had a faster NPQ relaxation and CO_2 fixation rate recovery, as well as potentially improved photoprotection under high light circumstances. The overall CO_2 fixation of plants subjected to varying light conditions could be enhanced without directly affecting photosynthetic capacity, maximal carboxylation capacity (Vcmax), or ribulose bisphosphate regeneration capacity (Jmax). Under both controlled and field situations, crops evaluated exhibited a 14–20% increase in biomass [22]. Accelerating NPQ responses increased photosynthetic efficiency and biomass productivity by 15% in both greenhouse and field environments [22]. The effects of overexpression of PsbS and VPZ on photosynthetic efficiency and productivity appear to be species and growth situation specific. Walter and Kromdijk [22] increased plant density in many staple crops, which resulted in an increased proportion of leaves

being exposed to strong light intensity variations, potentially making output more dependent on photosynthetic efficiency. Adapting photosynthetic and photoprotective responses to changing production conditions could improve photosynthetic efficiency and productivity of crops like cassava, cowpea and soybean, among other important crops.

6. ENHANCING COWPEA YIELD BY IMPROVING PHOTOSYNTHETIC EFFICIENCY

Crop photosynthetic systems haven't made much progress in recent years, and photosynthetic efficiency remains considerably below its biological limit. Interactions with crop growth, development dynamics, and temperature changes may limit the yield outcome of manipulating photosynthetic machinery. Wu et al. [90] developed a reliable model in wheat and sorghum that predicts which photosynthetic changes in plants can increase yield in these crops.

In real-world agricultural situations, this model can estimate yield gains due to photosynthesis. Increasing photosynthesis alone will not always result in increased crop production. In water-limited cropping circumstances, enhanced photosynthesis, for example, resulted in a yield drop in sorghum [90]. Keeping the rate of CO_2 entering or water vapor exiting the stomata consistent can help to prevent yield loss [94,98]. Excessive investments in photosynthesis to fulfill demand for mineral components required in the maintenance of chlorophyll, the electron transport chain, and enzyme activities during CO_2 fixation will result in a nutritional load on the plant system [99,101]. As a result, in cowpea yield-improvement initiatives targeted at increasing photosynthetic efficiency, optimizing crops to improve light absorption and CO_2 assimilation throughout the canopy has been proposed by Digrado et al. (2019) as a strategy to increase yield and meet the needs of a growing population by 2050, and root and canopy design must be taken into account. RIPE team have proposed about nine research strategies to increase crop yield. They have, however, looked into a few major photosynthesis manipulation targets to boost crop yield: (I) increasing the activity of RuBisCO, a key photosynthetic enzyme; (ii) increasing the capacity of plant leaves to transport electrons; and (ii) increasing CO2

movement via the internal layers of the leaf involved in yield formation [90]. Under non-irrigated conditions, the researchers reported yield variations ranging from 1% reduction to 12% increase depending on the combination of photosynthetic targets, crop, and climatic factors such as water availability [90]. (iv) Improving genes involved in relaxation of photoprotection and up-regulate the genes that speed up this relaxation, the researcher reported an increase in yield by 14 to 20% after replicated in field conditions [91].

7. CONCLUSION

Limitation of photosynthetic potential in cowpea have been uncovered and effort have taken to increase its efficiency to improve cowpea productivity. Improving photosynthetic conversion efficiency will necessitate a systems approach informed by coupled models capable of correlating a change in the chloroplast to yield in the field, as well as a full suite of tools such as genome editing approaches for endogenous gene modification, gene transfer, and synthetic biology in bringing about the desired photosynthesis alteration. Improving cowpea productivity in SSA should be possible since factors such as high light intensity, low temperature, low CO_2 environment, water limitation and deactivation of Rubisco functioning in shade have been noted to limit photosynthetic potential in cowpea productivity.

Improving photosynthesis is one technique for increasing yield potential, but in order to provide resilience, improvements in water use efficiency (WUE), nitrogen use efficiency (NUE), and biotic and abiotic stress response will be required.

Modification of gene(s) regulatory sequences could be another way to improve photosynthetic efficiency. Fine-tuning gene expression, modifying substrate affinities to improve enzyme catalytic performance, and inducible systems are all innovative ways to manipulate photorespiration in agricultural plants. A promising method for increasing photosynthetic productivity is to reduce photorespiratory loss. The potential for improving photosynthetic efficiency and cowpea productivity exists, but photosynthetic limitations create constraints such as chlorophyll retention, radiation utilization, and RuBisCO efficiency that must be overcome to boost crop yield.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

REFERENCES

1. Furbank RT, Jimenez-Berni JA, George-Jaeggli B, Potgieter AB, Deery DM. Field crop phenomics: Enabling breeding for radiation use efficiency and biomass in cereal crops. New Phytol. 2019;223(4):1714-27.
DOI: 10.1111/nph.15817, PMID 30937909.
2. Zhang C, Liu J, Shang J, Dong T, Tang M, Feng S et al. Improving winter wheat biomass and evapotranspiration simulation by assimilating leaf area index from spectral information into a crop growth model. Agric Water Manag. 2021;255: 107057.
DOI: 10.1016/j.agwat.2021.107057.
3. Langridge P, Braun H, Hulke B, Ober E, Prasanna BM. Breeding crops for climate resilience. Theor Appl Genet. 2021;134(6): 1607-11.
DOI: 10.1007/s00122-021-03854-7, PMID 34046700.
4. Bhattacharya A. Dry matter production, partitioning, and seed yield under soil water deficit: A review. Soil Water Deficit Physiol Issues Plants. 2021; 585-702.
5. Srivastava R, Kobayashi Y, Koyama H, Sahoo L. Overexpression of cowpea NAC transcription factors promoted growth and stress tolerance by boosting photosynthetic activity in Arabidopsis. Plant Sci. 2022; 319:111251.
DOI: 10.1016/j.plantsci.2022.111251, PMID 35487661.
6. Curtis PS, Vogel CS, Wang X, Pregitzer KS, Zak DR, Lussenhop J, et al. Gas exchange, leaf nitrogen, and growth efficiency of Populus tremuloides in a CO_2-enriched atmosphere. Ecol Appl. 2000;10(1):3-17.
7. Tang C, Gao X, Shao Y, Wang L, Liu K, Gao R, et al. Investigation on the rotary regenerative adsorption wheel in a new strategy for CO_2 enrichment in greenhouse. Appl Therm Eng. 2022; 205:118043.
DOI:10.1016/j.applthermaleng.2022.118043
8. Makino A. Photosynthesis, grain yield, and nitrogen utilization in rice and wheat. Plant Physiol. 2011;155(1):125-9.

DOI: 10.1104/pp.110.165076, PMID 20959423.

9. Owade JO, Abong' G, Okoth M, Mwang'ombe AW. A review of the contribution of cowpea leaves to food and nutrition security in East Africa. Food Sci Nutr. 2020;8(1):36-47.
DOI: 10.1002/fsn3.1337, PMID 31993130.

10. Dhanasekar P, Souframanien J, Suprasanna P. Breeding cowpea for quality traits: A genetic biofortification perspective. In: Breeding for enhanced nutrition and bio-active compounds in food legumes. Cham: Springer. 2021;157-79.

11. Hussain ST. Role of crop management in mitigation of heat stress in different agro-climate regions. Appl New Technol Agric Avoid Environ Contam. 2018;59.

12. Bhattacharya A. Effect of low-temperature stress on germination, growth and phenology of plants: a review. Physiol Processes Plants Low Temp Stress. 2022;1-106.

13. Bhattacharya A. Physiological processes in plants under low temperature stress. Springer verlag, Singapor; 2022.

14. Aina FB. Evaluation of insecticide spraying times and weeding regime on cowpea insect pests and grain yield in the Southern Guinea savanna of Nigeria ([doctoral dissertation]. Kwara State University (Nigeria)); 2022.

15. Burger J. Quantifying the role of soil microbial activity in cover crops on newly established fruit trees in the Western Cape; 2022.

16. Ayalew T, Yoseph T. Cowpea (*Vigna unguiculata* L. Walp.): A choice crop for sustainability during the climate change periods. J Appl Biol Biotechnol. 2022; 10(3):154-62.
DOI: 10.7324/JABB.2022.100320

17. Jackson J, Kinabo J, Lekalake R, Mogotsi K. Processing and utilization of dry beans and pulses in Africa. Dry Beans Pulses Prod Process Nutr. 2022;409-30.

18. Horn LN, Nghituwamata SN, Isabella U. Cowpea production challenges and contribution to livelihood in sub-Saharan region. Agric Sci. 2022;13(1):25-32.
DOI: 10.4236/as.2022.131003

19. Kondwakwenda A, Mutari B, Simango K, Nchanji EB, Chirwa R, Rubyogo JC, et al. Decades of cultivar development: A reconciliation of maize and bean breeding projects and their impacts on food, nutrition security, and income of smallholder farmers in sub-Saharan Africa. In: Food security for African smallholder farmers. Singapore: Springer. 2022;3-26.
DOI: 10.1007/978-981-16-6771-8_1

20. Simion T. Breeding cowpea *Vigna unguiculata* l. Walp for quality traits. Annals Rev Res. 2018;3(2):555609.

21. Uebersax MA, Urrea C, Siddiq M. Physical and physiological characteristics and market classes of common beans. Dry Beans Pulses Prod Process Nutr. 2022;57-80.

22. Philipo M, Ndakidemi PA, Mbega ER. Importance of common bean genetic zinc biofortification in alleviating human zinc deficiency in sub-Saharan Africa. Cogent Food Agric. 2021;7(1):1907954.
DOI: 10.1080/23311932.2021.1907954.

23. Long SP, Taylor SH, Burgess SJ, Carmo-Silva E, Lawson T, De Souza AP, et al. Into the shadows and back into sunlight: photosynthesis in fluctuating light. Annu Rev Plant Biol. 2022; 73:617-48.
DOI: 10.1146/annurev-arplant-070221-024745, PMID 35595290.

24. Olayiwola MO, Soremi PAS. Variability for dry fodder yield and component traits in cowpea [*Vigna unguiculata* (L.) Walp.]. Electron J Plant Breed. 2014;5(1):58-62.

25. Mathiot C. Measurement of photosynthetic linear and cyclic electron flows, CO_2 capture in green microalgae ([doctoral dissertation]. Aix, Marseille); 2020.

26. Kebede E, Bekeko Z. Expounding the production and importance of cowpea (*Vigna unguiculata* (L.) Walp.) in Ethiopia. Cogent Food Agric. 2020;6(1):1769805.
DOI: 10.1080/23311932.2020.1769805

27. Nkomo GV, Sedibe MM, Mofokeng MA. Production constraints and improvement strategies of cowpea (*Vigna unguiculata* L. Walp.) genotypes for drought tolerance. Int J Agron. 2021; 2021:1-9.
DOI: 10.1155/2021/5536417

28. Phares CA, Atiah K, Frimpong KA, Danquah A, Asare AT, Aggor-Woananu S. Application of biochar and inorganic phosphorus fertilizer influenced rhizosphere soil characteristics, nodule formation and phytoconstituents of cowpea grown on tropical soil. Heliyon. 2020; 6(10):e05255.
DOI: 10.1016/j.heliyon.2020.e05255, PMID 33088981.

29. Mlango DB. Effects of sonchus (*S. oleraceous*) in maize and cowpea cropping

systems ([doctoral dissertation]. Pwani University); 2018.

30. Nderi LM. Effect of different spacing intervals on growth and yield of cowpea varieties in Kilifi County, Kenya (Doctoral dissertation, KeMU); 2020.

31. Adetunji AT, Ncube B, Mulidzi R, Lewu FB. Management impact and benefit of cover crops on soil quality: A review. Soil Till Res. 2020; 204:104717.
DOI: 10.1016/j.still.2020.104717

32. Grabau ZJ, Rios E. Management of nematodes with cowpea cover crops: ENY712/IN516.
2021;12/2021. EDIS. 2021(6).

33. Ndiritu JM, Kinama JM, Muthama JN. Assessment of ecosystem services knowledge, attitudes and practices of coffee farmers using legume cover crops. Ecosphere. 2022;13(4): e4046.
DOI: 10.1002/ecs2.4046

34. Keys AJ. RuBisCO: its role in photorespiration. Phil Trans R Soc Lond B. 1986;313(1162):325-36.
DOI: 10.1098/rstb.1986.0040

35. Fernie AR, Bauwe H. Wasteful, essential, evolutionary stepping stone? The multiple personalities of the photorespiratory pathway. Plant J. 2020;102(4):666-77.
DOI: 10.1111/tpj.14669, PMID 31904886.

36. Ahmad S, Wang GY, Muhammad I, Farooq S, Kamran M, Ahmad I, et al. Application of melatonin-mediated modulation of drought tolerance by regulating photosynthetic efficiency, chloroplast ultrastructure, and endogenous hormones in maize. Chem Biol Technol Agric. 2022;9(1):1-14.

37. Bhardwaj S, Sharma D, Singh S, Ramamurthy PC, Verma T, Pujari M, et al. Physiological and molecular insights into the role of silicon in improving plant performance under abiotic stresses. Plant Soil. 2022;1-19.
DOI: 10.1007/s11104-022-05395-4

38. Arthur Sampson DA, Smith FW. Influence of canopy architecture on light penetration in lodgepole pine (*Pinus contorta* var. latifolia) forests. Agric Forest Meteorol. 1993;64(1-2):63-79.
DOI: 10.1016/0168-1923(93)90094-X

39. Niinemets Ü. A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. Ecol Res. 2010;25(4):693-714.
DOI: 10.1007/s11284-010-0712-4

40. Mubarak ANM, Mufeeth M, Roshana MR, Kumara ADNT. Influence of canopy architecture on the light interception, photosynthetic and biomass productivity in irrigated elite Sri Lankan rice varieties. J Agric Sciences. 2022;17(1).
DOI: 10.4038/jas.v17i1.9616

41. Hatfield JL, Dold C. Photosynthesis in the solar corridor system. In: The solar corridor crop system. Academic Press. 2019;1-33.

42. Miglani GS, Kaur R, Sharma P, Gupta N. Leveraging photosynthetic efficiency toward improving crop yields. J Crop Improv. 2021;35(3):361-402.
DOI: 10.1080/15427528.2020.1824168

43. Tooley EG. The unique canopy structure, leaf morphology, and physiology of Cornus drummondii [doctoral dissertation]; 2022.

44. Zhi X. Hyperspectral sensing methods and genome-wide association studies to improve photosynthetic capacity in sorghum; 2022.

45. Murchie EH, Burgess AJ. Casting light on the architecture of crop yield. Crop and environment; 2022.

46. Kumagai E, Burroughs CH, Pederson TL, Montes CM, Peng B, Kimm H, et al. Predicting biochemical acclimation of leaf photosynthesis in soybean under in-field canopy warming using hyperspectral reflectance. Plant Cell Environ. 2022;45(1):80-94.
DOI: 10.1111/pce.14204, PMID 34664281.

47. Gitelson AA, Peng Y, Arkebauer TJ, Schepers J. Relationships between gross primary production, green LAI, and canopy chlorophyll content in maize: Implications for remote sensing of primary production. Remote Sens Environ. 2014; 144:65-72.
DOI: 10.1016/j.rse.2014.01.004

48. Hall DO, Rao K. Photosynthesis. Cambridge University Press; 1999.

49. Muhammad I, Shalmani A, Ali M, Yang QH, Ahmad H, Li FB. Mechanisms regulating the dynamics of photosynthesis under abiotic stresses. Front Plant Sci. 2021; 11:2310.

50. Sharma A, Kumar V, Shahzad B, Ramakrishnan M, Singh Sidhu GP, Bali AS, et al. Photosynthetic response of plants under different abiotic stresses: A review. J Plant Growth Regul. 2020; 39(2):509-31.
DOI: 10.1007/s00344-019-10018-x

51. Sabagh AE, Hossain A, Islam MS, Iqbal MA, Fahad S, Ratnasekera D, et al. Consequences and mitigation strategies of

heat stress for sustainability of soybean (*Glycine max* L. Merr.) production under the changing climate. Plant stress physiology; 2020.

52. Wang H, Wang XQ, Zeng ZL, Yu H, Huang W. Photosynthesis under fluctuating light in the CAM plant Vanilla planifolia. Plant Sci. 2022; 317:111207.
DOI: 10.1016/j.plantsci.2022.111207, PMID 35193751.

53. Zheng J, Zhuang Y, Mao H, Jang I. Elevated CO_2 concentration induces photosynthetic down-regulation with changes in leaf structure, nonstructural carbohydrates and nitrogen content of soybean. BMC Plant Biol. 2019;19(1):1-18.
DOI: 10.1186/s12870-018-1600-2

54. Xiong D, Flexas J. From one side to two sides: the effects of stomatal distribution on photosynthesis. New Phytol. 2020; 228(6):1754-66.
DOI: 10.1111/nph.16801, PMID 32652573.

55. Gamage D, Thompson M, Sutherland M, Hirotsu N, Makino A, Seneweera S. New insights into the cellular mechanisms of plant growth at elevated atmospheric carbon dioxide concentrations. Plant Cell Environ. 2018;41(6):1233-46.
DOI: 10.1111/pce.13206, PMID 29611206.

56. Baca Cabrera JC, Hirl RT, Schäufele R, Macdonald A, Schnyder H. Stomatal conductance limited the CO2 response of grassland in the last century. BMC Biol. 2021;19(1):50.
DOI: 10.1186/s12915-021-00988-4, PMID 33757496.

57. Hudson GS, Evans JR, von Caemmerer S, Arvidsson YB, Andrews TJ. Reduction of ribulose-1,5-bisphosphate carboxylase/oxygenase content by antisense RNA reduces photosynthesis in transgenic tobacco plants. Plant Physiol. 1992;98(1):294-302.
DOI: 10.1104/pp.98.1.294, PMID 16668627.

58. Parry MA, Reynolds M, Salvucci ME, Raines C, Andralojc PJ, Zhu XG, et al. Raising yield potential of wheat. II. Increasing photosynthetic capacity and efficiency. J Exp Bot. 2011;62(2): 453-67.
DOI: 10.1093/jxb/erq304, PMID 21030385.

59. Kamal NM, Alnor Gorafi YSA, Abdelrahman M, Abdellatef E, Tsujimoto H. Stay-green trait: A prospective approach for yield potential, and drought and heat stress adaptation in globally important cereals. Int J Mol Sci. 2019; 20(23):5837.
DOI: 10.3390/ijms20235837, PMID 31757070.

60. Zhang J, Li H, Huang X, Xing J, Yao J, Yin T, et al. Staygreen-mediated chlorophyll a catabolism is critical for photosystem stability during heat-induced leaf senescence in perennial ryegrass. Plant Cell Environ. 2022;45(5):1412-27.
DOI: 10.1111/pce.14296, PMID 35192197.

61. Hernandez JS, Nägele T. The trade-off function of photorespiration in a changing environment. bioRxiv; 2022.

62. Abed A, Badea A, Beattie A, Khanal R, Tucker J, Belzile F. A high-resolution consensus linkage map for barley based on GBS-derived genotypes. Genome. 2022;65(2):83-94.
DOI: 10.1139/gen-2021-0055, PMID 34870479.

63. Thakur S, Kumar R, Vikal Y, Vyas P, Sheikh I, Dhaliwal HS. Molecular mapping of popping volume QTL in popcorn (*Zea maize* L.). J Plant Biochem Biotechnol. 2021;30(3):496-503.
DOI: 10.1007/s13562-020-00636-y

64. Martin-Avila E, Lim YL, Birch R, Dirk LMA, Buck S, Rhodes T, et al. Modifying plant photosynthesis and growth via simultaneous chloroplast transformation of RuBisCO large and small subunits. Plant Cell. 2020;32(9):2898-916.
DOI: 10.1105/tpc.20.00288, PMID 32647068.

65. Batista-Silva W, da Fonseca-Pereira P, Martins AO, Zsögön A, Nunes-Nesi A, Araújo WL. Engineering improved photosynthesis in the era of synthetic biology. Plant Commun. 2020;1(2):100032.
doi: 10.1016/j.xplc.2020.100032, PMID 33367233.

66. Moore CE, Meacham-Hensold K, Lemonnier P, Slattery RA, Benjamin C, Bernacchi CJ, et al. The effect of increasing temperature on crop photosynthesis: From enzymes to ecosystems. J Exp Bot. 2021;72(8): 2822-44.
DOI: 10.1093/jxb/erab090, PMID 33619527.

67. Timm S, Hagemann M. Photorespiration—how is it regulated and how does it regulate overall plant metabolism? J Exp Bot. 2020;71(14):3955-65.
DOI: 10.1093/jxb/eraa183, PMID 32274517.

68. Eisenhut M, Roell MS, Weber APM. Mechanistic understanding of photorespiration paves the way to a new green revolution. New Phytol. 2019; 223(4):1762-9.
DOI: 10.1111/nph.15872, PMID 31032928.

69. Bauwe H, Fernie AR. With a little help from my friends: the central role of photorespiration and related metabolic processes in the acclimation and adaptation of plants to oxygen and to low-CO2 stress. In: Photosynthesis, respiration, and climate change. Cham: Springer. 2021;355-85.
DOI: 10.1007/978-3-030-64926-5_12.

70. Naseem M, Osmanoglu Ö, Dandekar T. Synthetic rewiring of plant CO_2 sequestration galvanizes plant biomass production. Trends Biotechnol. 2020; 38(4):354-9.
DOI: 10.1016/j.tibtech.2019.12.019, PMID 31959363.

71. South PF, Walker BJ, Cavanagh AP, Rolland V, Badger M, Ort DR. Bile acid sodium symporter BASS6 can transport glycolate and is involved in photorespiratory metabolism in Arabidopsis thaliana. Plant Cell. 2017; 29(4):808-23.
DOI: 10.1105/tpc.16.00775, PMID 28351992.

72. Long SP, Marshall-Colon A, Zhu XG. Meeting the global food demand of the future by engineering crop photosynthesis and yield potential. Cell. 2015;161(1):56-66.
DOI: 10.1016/j.cell.2015.03.019, PMID 25815985.

73. Simkin AJ, López-Calcagno PE, Raines CA. Feeding the world: Improving photosynthetic efficiency for sustainable crop production. J Exp Bot. 2019; 70(4):1119-40.
DOI: 10.1093/jxb/ery445, PMID 30772919.

74. Price GD, Badger MR, Woodger FJ, Long BM. Advances in understanding the cyanobacterial CO2-concentrating-mechanism (CCM): Functional components, Ci transporters, diversity, genetic regulation and prospects for engineering into plants. J Exp Bot. 2008;59(7):1441-61.
DOI: 10.1093/jxb/erm112, PMID 17578868.

75. Spangle D. May 5, 2016 photosynthesis can be optimized to feed and fuel the world: evolutionary challenges and engineering possibilities; 2016.

76. Miyao M. Molecular evolution and genetic engineering of C4 photosynthetic enzymes. J Exp Bot. 2003;54(381):179-89.
DOI: 10.1093/jxb/erg026, PMID 12493846.

77. Doubnerová V, Ryšlavá H. What can enzymes of C4 photosynthesis do for C3 plants under stress? Plant Sci. 2011; 180(4):575-83.
DOI: 10.1016/j.plantsci.2010.12.005, PMID 21421406.

78. Daniell H, Jin S, Zhu XG, Gitzendanner MA, Soltis DE, Soltis PS. Green giant— A tiny chloroplast genome with mighty power to produce high-value proteins: history and phylogeny. Plant Biotechnol J. 2021; 19(3):430-47.
DOI: 10.1111/pbi.13556, PMID 33484606.

79. Zhang A, Carroll AL, Atsumi S. Carbon recycling by cyanobacteria: Improving CO_2 fixation through chemical production. FEMS Microbiol Lett. 2017;364(16).
DOI: 10.1093/femsle/fnx165, PMID 28873946.

80. Hauser T, Popilka L, Hartl FU, Hayer-Hartl M. Role of auxiliary proteins in RuBisCO biogenesis and function. Nat Plants. 2015;1(6):15065.
DOI: 10.1038/nplants.2015.65, PMID 27250005.

81. Li S, Chang L, Zhang J. Advancing organelle genome transformation and editing for crop improvement. Plant Commun. 2021;2(2):100141.
DOI: 10.1016/j.xplc.2021.100141, PMID 33898977.

82. Parry MAJ, Andralojc PJ, Mitchell RA, Madgwick PJ, Keys AJ. Manipulation of RuBisCO: the amount, activity, function and regulation. J Exp Bot. 2003;54(386):1321-33.
DOI: 10.1093/jxb/erg141, PMID 12709478.

83. Müller P, Li XP, Niyogi KK. Non-photochemical quenching. A response to excess light energy. Plant Physiol. 2001; 125(4):1558-66.
DOI: 10.1104/pp.125.4.1558, PMID 11299337.

84. Wu H, Jiang H, Liu C, Deng Y. Growth, pigment composition, chlorophyll fluorescence and antioxidant defenses in the red alga Gracilaria lemaneiformis (Gracilariales, Rhodophyta) under light stress. S Afr J Bot. 2015; 100:27-32.
DOI: 10.1016/j.sajb.2015.05.017

85. van Amerongen H, Chmeliov J. Instantaneous switching between different modes of non-photochemical quenching in plants. Consequences for increasing biomass production. Biochim Biophys Acta Bioenerg. 2020;1861(4):148119.
DOI: 10.1016/j.bbabio.2019.148119, PMID 31734196.

86. Kromdijk J, Walter J. Relaxing non-photochemical quenching (NPQ) to improve photosynthesis in crops. Burleigh Dodds Science Publishing; 2022.

87. Zivcak M, Brestic M, Kunderlikova K, Sytar O, Allakhverdiev SI. Repetitive light pulse-induced photoinhibition of photosystem I severely affects CO_2 assimilation and photoprotection in wheat leaves. Photosynth Res. 2015;126(2-3):449-63.
DOI: 10.1007/s11120-015-0121-1, PMID 25829027.

88. Kanazawa A, Ostendorf E, Kohzuma K, Hoh D, Strand DD, Sato-Cruz M, et al. Chloroplast ATP synthase modulation of the thylakoid proton motive force: implications for photosystem I and photosystem II photoprotection. Front Plant Sci. 2017; 8:719.
DOI: 10.3389/fpls.2017.00719, PMID 28515738.

89. Kono M, Terashima I. Long-term and short-term responses of the photosynthetic electron transport to fluctuating light. J Photochem Photobiol B. 2014; 137:89-99.
DOI: 10.1016/j.jphotobiol.2014.02.016, PMID 24776379.

90. Wu A, Hammer GL, Doherty A, von Caemmerer S, Farquhar GD. Quantifying impacts of enhancing photosynthesis on crop yield. Nat Plants. 2019;5(4):380-8.
DOI: 10.1038/s41477-019-0398-8, PMID 30962528.

91. Kromdijk J, Głowacka K, Leonelli L, Gabilly ST, Iwai M, Niyogi KK, et al. Improving photosynthesis and crop productivity by accelerating recovery from photoprotection. Science. 2016;354(6314): 857-61.
DOI: 10.1126/science.aai8878, PMID 27856901.

92. Bailey-Serres J, Parker JE, Ainsworth EA, Oldroyd GED, Schroeder JI. Genetic strategies for improving crop yields. Nature. 2019;575(7781):109-18.
DOI: 10.1038/s41586-019-1679-0, PMID 31695205.

93. Battino M, Forbes-Hernández TY, Gasparrini M, Afrin S, Cianciosi D, Zhang J et al. Relevance of functional foods in the Mediterranean diet: The role of olive oil, berries and honey in the prevention of cancer and cardiovascular diseases. Crit Rev Food Sci Nutr. 2019;59(6): 893-920.
DOI: 10.1080/10408398.2018.1526165, PMID 30421983.

94. Blommaert L, Chafai L, Bailleul B. The fine-tuning of NPQ in diatoms relies on the regulation of both xanthophyll cycle enzymes. Sci Rep. 2021;11(1):1-16.

95. Digrado A, Mitchell NG, Montes CM, Dirvanskyte P, Ainsworth EA. Assessing diversity in canopy architecture, photosynthesis, and water-use efficiency in a cowpea magic population. Food Energy Secur. 2020;9(4):e236.
DOI: 10.1002/fes3.236, PMID 33381299.

96. Kalaji HM, Govindjee, Bosa K, Kościelniak J, Żuk-Gołaszewska K. Effects of salt stress on photosystem II efficiency and CO2 assimilation of two Syrian barley landraces. Environ Exp Bot. 2011;73: 64-72.
DOI: 10.1016/j.envexpbot.2010.10.009

97. Khan MIR, Jalil SU, Chopra P, Chhillar H, Ferrante A, Khan NA, et al. Role of GABA in plant growth, development and senescence. Plant Gene. 2021; 26:100283.
DOI: 10.1016/j.plgene.2021.100283

98. Nji QN, Babalola OO, Ekwomadu TI, Nleya N, Mwanza M. Six main contributing factors to high levels of mycotoxin contamination in African foods. Toxins. 2022;14(5):318.
DOI: 10.3390/toxins14050318, PMID 35622564.

99. Sales CRG, Wang Y, Evers JB, Kromdijk J. Improving C4 photosynthesis to increase productivity under optimal and suboptimal conditions. J Exp Bot. 2021;72(17): 5942-60.
DOI: 10.1093/jxb/erab327, PMID 34268575.

100. Short AH, Fay TP, Crisanto T, Hall J, Steen CJ, Niyogi KK, et al. Xanthophyll-cycle based model of the rapid photoprotection of Nannochloropsis in response to regular and irregular light/dark sequences. J Chem Phys. 2022;156(20): 205102.
DOI: 10.1063/5.0089335, PMID 35649869.

101. Thomas H, Ougham H. The stay-green trait. J Exp Bot. 2014;65(14):3889-900.
DOI: 10.1093/jxb/eru037. PMID 24600017.

102. Wu N, Yao Y, Xiang D, Du H, Geng Z, Yang W, et al. A MITE variation-associated heat-inducible isoform of a heat-shock factor confers heat tolerance through regulation of jasmonate ZIM-DOMAIN genes in rice. New Phytol. 2022;234(4): 1315-31.

DOI: 10.1111/nph.18068, PMID 35244216.

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