

Review Article

IMPROVING THE PHOTOSYNTHETIC EFFICIENCY AND PRODUCTIVITY OF COWPEA IN SUB SAHARAN AFRICA: A REVIEW PAPER

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 CO₂ 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

1.0 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” (Furbank *et al.*, 2019; Zhang *et al.*, 2021). “Yield potential is the highest yield possible from a crop, and it is defined as the maximum yield feasible when the best-adapted crop variety is grown under perfect conditions with no biotic or abiotic stress” (Langridge *et al.*, 2021). 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 (Bhattacharya, 2021; Srivastava *et al.*, 2022). Because photorespiration might lose up to 50% of fixed carbon under some conditions, Carbondioxide (CO₂) enrichment experiment has continuously provided compelling evidence towards enhanced yields. It might be obtained by

greater CO₂ uptake, indicating that improved photosynthetic CO₂ assimilation can result in higher yields (Curtis *et al.*, 2000; Tang *et al.*, 2022). “Despite the fact that some studies have indicated a negative relationship between leaf area, photosynthesis and yield, Makino (2011) 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” (Owade *et al.*, 2020). “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” (Dhanasekar *et al.*, 2021). “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” (Hussain, 2018; Bhattacharya, 2022). “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” (Aina, 2022; Burger, 2022). “The crop performs well even when produced in poor nutrient soils due to its ability to (BNF) fix nitrogen in the soil” (Ayalew and Yoseph, 2022). 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 (Ngum *et al.*, 2022; Jackson *et al.*, 2022). It is vital to the livelihoods of millions of people in Sub-Saharan Africa (Horn *et al.*, 2022; Kondwakwenda *et al.*, 2022) 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 (Simon, 2018; Uebersax *et al.*, 2022). Owade *et al.* (2020) and Philipo *et al.* (2021) 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

2.0 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.* (2022), 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 number of goods. According to Olayiwola and Soremi, (2014), 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.

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

3.0 Importance of Cowpea

“Cowpeas are often consumed as a dry grain or raw vegetable. Mathiot (2020) 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.* (2022) 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 (Simons, 2019; Kebede and Bekeko, 2020). “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” (Nkomo *et al.*, 2021). “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” (Nkomo *et al.*, 2021). Phares *et al.* (2020), 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” (Mlango 2018; Nkomo *et al.*, 2021). Other cowpea varieties have been shown to control the nematode (*Scutellonema cavenessi*), a serious pest of various crops in Sub-Saharan Africa (Nderi, 2020) 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 (Adetunji *et al.*, 2020; Grabau and Rios, 2021; Ndiritu *et al.*, 2022).

4.0 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 CO₂ environment, and water limitation. Keys (1986) and Fernie and Bauwe, (2020) 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 gain (Ahmad *et al.*, 2022), there is the need to carry out more detail research to understand the whole process to improve photosynthetic 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 CO₂ to maximum saturation limits, C₃ and C₄ crops are photosynthetically more effective than the former (Gurbachan *et al.*, 2020). CO₂ leakage was reduced by concentrating CO₂ 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 (Bhardwaj *et al.*, 2022; Nunes, 2022). Some other factors such as photorespiration, structure of the plant leaf, CO₂ 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 (Sampson

and Smith, 1993; Niinemets, 2010; Mubarak *et al.*, 2022). This is possible when the highest leaves are vertical and the lowermost leaves are horizontal (Sampson and Smith, 1993; Niinemets, 2010; Mubarak *et al.*, 2022). 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 (Hatfield and Dold, 2019; Miglani *et al.*, 2021; Tooley, 2022; Zhi, 2022). 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.* (2021), 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 (Murchie, and Burgess, 2022). 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.* (2022) and studies by other authors Gitelson *et al.* (2014) investigated whether a drop in chlorophyll content would result in an increase in canopy photosynthesis in soybeans using several canopy photosynthesis models. 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 (Gitelson *et al.*, 2014) . 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.* (2022); 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, (1999) have shown that at low light intensities the rate of photosynthesis is the same at 15 °C and 25°C. 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°C than 15°C.. 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 (Muhammed *et al.*, 2021). Abiotic stress, such as high temperatures, reduces the plant's photosynthetic rate (Sharma *et al.*, 2020). 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 (Bhattacharya, 2022). Low temperatures (chilling stress) also have an adverse effect on germination, seedling emergence, and plant vigor, resulting in a reduction in plant productivity (Sabagh *et al.*, 2020).

4.4 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” (Wang *et al.*, 2022). “However, plant carbon fixation is limited by photorespiration, which releases CO₂ and uses cellular energy to recycle the RuBisCO oxygenation product, 2-phosphoglycolate, back into the Calvin cycle. This process reduces agricultural output by emitting CO₂ 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. 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

risers. The photorespiratory C₂ metabolism downstream of RuBisCO can be delayed by removing or downregulating an enzyme in the C₂ pathway.

4.5 Carbondioxied (CO₂) concentration

Hall and Rao (1999), reported that in the light-limiting zone, lowering CO₂ content has no effect on photosynthesis rate, which implies that CO₂ does not participate directly in the photochemical activity. Photosynthesis is significantly increased by raising CO₂ concentration at light intensity above the light limitation area. As indicated by the constantly declining leaf net photosynthetic rate with higher CO₂ concentrations, CO₂ causes down-regulation of leaf photosynthesis (Zheng *et al.*, 2019). The maximum carboxylation rate and the maximum electron transport rate were both drastically reduced at higher CO₂ concentrations, exceeding their ideal values of roughly 600 ppm and 400 ppm, respectively (Zheng *et al.*, 2019). Reduced stomatal conductance was partly related to photosynthesis at high CO₂ concentrations, as evidenced by decreases in stomatal density and area, as well as alterations in the spatial distribution pattern of stomata (Xiong and Flexas, 2020). Reduced photorespiration and dark respiration, as well as increased carboxylation efficiency, may contribute to increased net photosynthesis rate under high CO₂ concentrations. In response to rising carbon dioxide levels, specific leaf area shrank considerably (Gamage *et al.*, 2018). 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 CO₂ levels are increased (Baca Cabrera *et al.*, 2021). Because photosynthesis and stomatal activity are so important to plant carbon and water metabolism, plant development in high CO₂ environments has a wide range of downstream consequences on plant physiology. The CO₂ 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 CO₂ 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, CO₂ is utilized by the plants, and the concentration drops to as low as 200 ppm. Low CO₂ concentration has two repercussions, according to Hudson *et al.* (1992): 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 CO₂ concentrations, the value of additional

lighting is diminished. Photosynthesis increases as CO₂ levels rise until it reaches a saturation point usually around 1,000 ppm.

5.0 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 (Parry *et al.* 2011).

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 (Kamal *et al.*, 2019; 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-dechelataase and chl b reductase occur, the catabolic pathway is disrupted, resulting in tissue greenness (Zhang *et al.*, 2022). Stay greens were divided into two categories in studies by Miglani *et al.* (2021):

- 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 (Hernandez and Nägele, 2022). A "bin" is a genetic map location with a distinct segregation pattern that is separated from neighboring bins by a single recombination event (Abed *et al.*, 2022). Between two fixed Core Markers, the genetic maps are partitioned into 100 segments, called bins, of 20 cM each according to (Thakur *et al.*, 2021). 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* (Martin-Avila *et al.*, 2020). *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. (Miglani *et al.*, 2021). 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 (Batista-Silva *et al.*, 2020). Moore *et al.* (2021) 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 (Timm and Hagemann, 2020). As indicated by Eisenhut *et al.* (2019), 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 (Bauwe and Fernie, 2021).

In tobacco chloroplasts, Naseem *et al.* (2020) 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 (South *et al.*, 2017). These researches on creating photorespiratory bypass channels by membrane transporter alterations pave the way for greater photosynthetic efficiency and agricultural yield potential (long et al., 2015; Simkin et al., 2019). However, so far, genetic-engineering technology has had only little success in enhancing photosynthetic efficiency (Eisenhut and Weber, 2019). 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.

UNDER PEER REVIEW

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.* (2008) regard carbon concentration mechanism (CCM) as a unique adaptation that many photosynthetic organisms have acquired to increase photosynthetic efficiency in low-CO₂ 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 CO₂ concentration at the RuBisCO site could be an effective way to boost photosynthesis. Because of the sluggish diffusion of CO₂ 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 CO₂ 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 CO₂ concentrations, C₄ photosynthesis has a significantly higher conversion efficiency than C₃ photosynthesis (Spangle, 2016). PEPC levels increased with reduced sensitivity of photosynthetic absorption to O₂ in transgenic rice and Arabidopsis overexpressing C₄-specific PEP carboxylase (PEPC) (Miyao, 2003). 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 (Doubnerová and Rylavá, 2011). 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 CO₂ 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 (Daniell *et al.*, 2021). 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 CO₂, 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 CO₂ compared to oxygen would reduce photorespiration and increase photosynthesis (Zhang *et al.*, 2017). The amount of CO₂ 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 encoded genes (Parry *et al.*, 2011). 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 (Parry *et al.*, 2011). 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 (Hauser *et al.*, 2015). 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 *Rhodospirillum rubrum* allows for the quick transformation of tobacco with changed Rubisco (Li *et al.*, 2021).

. 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 CO₂ specificity and a faster carboxylation turnover rate. Specificity and RuBP carboxylation turnover rate have been found to be inversely related in studies (Parry *et al.*, 2003). 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 CO₂-enriched crop (Parry *et al.*, 2003). 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 (Muller *et al.*, 2001; Wu *et al.*, 2015; Van Amerongen and Chmeliov, 2020). Exposure to light in the lack of appropriate photoprotection reduces photosynthetic light usage efficiency, according to (Kromdijk and Walter 2022). Under low light conditions, the maximum efficiency with which light may be used to drive electron transport (PSII_{max}) or CO₂ fixation (CO_{2,max}) and photosynthesis can be determined (Kromdijk and Walter (2022). 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. (Zivcak *et al.*, 2015; Kanazawa *et al.*, 2017). 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 (Kono and Terashima, 2014; Long *et al.*, 2022). 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 (Simkin *et al.*, 2019). Both components of the NPQ system were adjusted by Kromdijk and Walter (2022), 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 CO₂ fixation rate recovery, as well as potentially improved photoprotection under high light circumstances. The overall CO₂ fixation of plants subjected to varying light conditions could be enhanced without directly affecting photosynthetic capacity, maximal carboxylation capacity (V_{cmax}), or ribulose biphosphate regeneration capacity (J_{max}). Under both controlled and field situations, crops evaluated exhibited a 14–20% increase in biomass (Kromdijk and Walter, 2022). Accelerating NPQ responses increased photosynthetic efficiency and biomass productivity by 15% in both greenhouse and field environments (Kromdijk and Walter, 2022). The effects of overexpression of PsbS and VPZ on photosynthetic efficiency and productivity appear to be species and growth situation specific. Walter and Kromdijk (2022) 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.

6.0 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.* (2019) 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 (Wu *et al.* 2019). Keeping the rate of CO₂ entering or water vapor exiting the stomata consistent can help to prevent yield loss. Excessive investments in photosynthesis to fulfill demand for mineral components required in the maintenance of chlorophyll, the electron transport chain, and enzyme activities during CO₂ fixation will result in a nutritional load on the plant system. As a result, in cowpea yield-improvement initiatives targeted at increasing photosynthetic efficiency, optimizing crops to improve light absorption and CO₂ 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 (Wu *et al.* 2019). 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 (Wu *et al.* 2019). (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 (Kromdijk *et al.*, 2016).

7.0 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 CO₂ 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.

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