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Review Article

Targeting Photosynthesis under Abiotic Stress

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Abstract

Earth sustains life due to the presence of the photosynthesis process that produced food for other organisms on our planet. But rapidly changing climate of most of the continents results in losses to photosynthetic machinery that ultimately lead to threatening food security worldwide. The major limiting factor in plant growth is abiotic stresses which are thought to become more severe in near future also unabated increase in the world population the future potential yield of commercial crops is under serious threat. The global food demand is expected to double in the coming years. The reduction of photosynthetic capability of various crops due to various abiotic stresses factors like heat, salinity, drought, high light, and heavy metal are gathered to understand the mechanism of stress tolerance and wider adaptability of different crops. We highlight the impact of various abiotic stresses on the performance of the photosynthetic process in crop plants. Further, we reviewed the different new generation solutions for photosynthesis improvements include improving enzyme (Rubisco) kinetic properties, C4 pathway into C3 crops, reducing photorespiration, canopy architecture, light capture, and photosynthetic models approaches also we have reviewed the role of genetic engineering crops with improved photosynthesis process that withstand and provide significant yields under environmental stresses. A better understanding of the photosynthetic process under stress conditions could support the development of new crops with higher yields even under adverse environments.

Key Word: Abiotic stress, Photosynthesis, Photosynthesis Enhancement

1. Introduction

Abiotic stresses are an integral part of climate change and have an unpredictable impact on the environment. The global demand for food is expected to double in 2005 to 2050 years (Tillman *et al.*, 2011), thus a better understanding of the photosynthetic process under stress conditions could support the development of new crops with higher yield even under adverse environments. Photosynthesis is an important process which is presents from crop plants to developing embryos of aquatic and land plants including bacteria. Photosynthesis converts light energy into chemical energy and provides fuel to the various metabolic processes (Chen *et al.*, 2018). Two reactions *i.e* light and dark reactions occur in the chloroplast, and it is very responsive to various abiotic stresses (Mu *et al.*, 2016, Paunov *et al.*, 2018). The abiotic stress is reported to harm photosynthetic components like photosystem I (PSI), Photosystem II(PS II), electron transport chain (ETC) of photosynthesis, and biosynthesis of chlorophyll (Sharma *et al.*, 2016). Along with that stress, induces oxidative damage and reduced stomatal conductance that decreases the activity of the Rubisco enzyme and hampers the process of photosynthesis (Zhang *et al.*, 2014; Kohli*et al.*, 2017).

To develope stress-tolerant crops several genetic engineering approaches are in trend which helps in faster development abiotic stress tolerant crops as compared to conventional methods. One such approach is the manipulation of the photosynthesis process through altering the properties of CO_2 fixation by Rubisco to increase the synthesis of carbohydrates required for plant growth and yield. These approaches also include other aspects of photosynthesis that can be improved such as light capture, CO_2 diffusion into the chloroplast, and flux through the Calvin cycle. Therefore detailed information of the photosynthesis responses due to abiotic stresses is gathered that helps in understanding the internal affected components of photosynthesis. The effect of heat, drought, salinity and heavy metals on the photosynthetic process is discussed here in the current review. Some advanced methods to improve photosynthesis through manipulating enzyme (Rubisco) kinetics, introduction C4 pathway into C3 crops, reducing photorespiration, modification of canopy architecture, light capture, and photosynthetic models approaches under stressful conditions were also summarized. We believe that this information on the photosynthesis process under stress conditions will help in the development of future crops.

2.0 Photosynthesis under Abiotic Stress Condition

Different abiotic stresses like heat, drought, salinity, and heavy metal affect the process of photosynthesis directly and indirectly. The direct and indirect effects include a reduced activity of photosynthesis enzymes, decrease in CO_2 assimilation rate, degradation of chlorophyll content, etc. This effect ultimately results in the overall declined in crop yield (Figure 1 and Table 1).

2.1 Temperature stress

The photosynthetic apparatus is highly susceptible to high temperature and it is the main and first site of inhibition (Mathur *et al.*, 2010). The major components i.e. respiration rates, membrane-bound electron transport processes, and optical conditions are decline under high-temperature stress conditions. Optimal temperature is considered as the main component for the more decline in net photosynthesis under heat stress conditions. High temperatures alter the excitation energy distribution and also by changing the activity of the Calvin cycle, photorespiration, and product synthesis ultimately leading to decreased photosynthesis. This reduced photosynthesis in crop plants is mainly due to protein deactivation of the oxygen-evolving complex (OEC) of PS II (Photosystem II) (Dhir 2018). Similarly, the PQ-pool of photosynthetic ETC is also strongly affected by heat stress (Pshybytko *et al.* 2008). Natural heat tolerances are also reported in various crops and among 100 diverse wheat genotypes, some potential heat-tolerant genotypes were successfully identified(Islam *et al.* 2017). Several studies are also conducted to evaluate germplasm adaptability to a particular growing zone environment (Sareen *et. al.* 2012). Genetic differences for cell membrane stability, triphenyl tetrazolium chloride test, chlorophyll fluorescence, heat response index (HRI), and heat susceptibility index (HSI) among genotypes of bread wheat are reported and several thermotolerance genotypes are identified(Dhanda and Munjal, 2012; 2017). Plants in reaction to higher temperatures produce HSP (Heat shock protein) that is named chaperons and function as proper folding of misfolded proteins under unfavorable conditions. To enhance the stress tolerance through a high expression of HSP genes are reported in Arabidopsis and tobacco (Lee and Schoff, 1996; Park and Hong, 2002). Recently, reported that *Cornuscanadensis* express gene superoxide reductase from the hyperthermophilic archaeon *Pyrococcusfuriosus* shows enhanced heat tolerance. In response to dehydration and heat shock stresses DREB2 transcription factor functions in both stresses. Overexpression of *HsfA1* in tomato plants causes higher thermotolerance encoding the high-temperature transcription factor (Mishra *et. al.* 2002). High-stress tolerance was reported in wheat and rice transgenic overexpressing HSP genes (Xiang *et al.* 2018).

2.2 Photosynthesis under Water Stress

2.2.1 Water logging

Water logging or standing water for long periods results in an anoxia or hypoxia condition in the field soil that also affects the absorption of nutrients (Araki 2006). It has been well reported that uptake of N, P, K and other nutrients in various crops is declined (Mielke and Schaffer 2010). The low oxygen level alters the root growth due to less availability of oxygen, and more soil phytotoxins (Pezeshki 2001). Chlorophyll degradation is observed in leaves when plants face water logging conditions at any stage and grain protein content declines (Pociecha*et al.* 2008; Mishra *et al.* 2008). The absence of oxygen shifts the cell metabolism to the anaerobic mode is not much energy efficient. The other components such as stomatal conductance, carbon exchange rate, internal carbon dioxide, and transpiration are decreased under water logging conditions. In the same experiment, it was reported that photosynthesis was limited by stomatal as well as non-stomatal components along with starch and chlorophyll components, and an increase in membrane injury and alcohol dehydrogenase activity was observed under excess water conditions (Bansal and Srivastava 2015).

2.2.2 Water deficient condition

Water stress negatively affects the process of photosynthesis in C3 plants. Low water availability imposes limited growth due to disturbance in the balance between photosynthesis and respiration. Under stress conditions more than half of the carbon assimilated by the process of photosynthesis is lost in respiration which is needed for growth and maintenance. For example, photosynthesis may completely halt under severe water deficit conditions, whereas respiration rate may either decrease or increase but never come to zero. Water deficiency also hinders the transport of internal carbon dioxide, enzyme activity, and photosynthetic capacity. In the condition of water stress, plants close their stomata to reduce respiratory losses but the closing of stomata also decreases the CO2 concentrations and transportation of non-structural carbohydrates (McDowell and Sevanto 2010; Sevanto 2014) that leads to carbon starvation. Photosynthesis is a universally important physiological process and is the main process that gets altered by drought stress (Sun *et al.* 2013). Photosynthesis is greatly influenced by severe water deficits (Hui *et al.* 2018). Water stress induces non-stomatal mechanisms which ultimately limit photosynthesis by disturbance of membrane, less ATP synthesis, inhibition of RUBISCO activity. It also negatively affects PS II in plants (Tattini et al. 2014), Regeneration of NADP+ (Nishiyama and Murata 2014), therefore, is less available for physiological processes. Two genes AhPORA and AhGLK1 responsible for the chlorophyll biosynthesis are significantly down-regulated under water-deficit conditions. Transcription factor DREB 1A which binds with dehydration-responsive elements (DRE) gets upregulated under drought (Kudo *et al.* 2017). In transgenic maize over expression of the genes for the kinase domain of NPK1 results in a high photosynthetic rate and drought tolerance (Shou *et al.*2004).

2.2.3 Photosynthesis under Saline Conditions

Salinity affects photosynthesis both directly and indirectly. Photosynthetic rate is lowered when plants are exposed to saline conditions especially to sodium chloride. The effect of salinity on photosynthesis is considered under two categories (i) Stomatal closure (ii) Effects on the capacity for CO2 fixation. The rate of photosynthesis under saline conditions depends upon the (i) salinization which is the total amount of salts (in form of osmotic effect) and (ii) ionic compositions of the cells (specific ion effect). Salinity alters the assimilating organs (Glagoleva *et al.* 1992) which includes thylakoid membranes dilation, without grana, and enlarged mesophyll cells ultimately resulting in decreased photosynthesis (Mitsuya *et al.* 2000).

2.2.4 Photosynthesis under Heavy Metal Stress

Stress caused by heavy metals is one of the common abiotic stress leading to losses in productivity of plants and hazardous health concerns (Kumar *et al.* 2019). Heavy metals like cadmium (Cd), lead (Pb), arsenic (As), chromium (Cr), and mercury (Hg) are not necessary for plant growth and development and also they alter physiological and biochemical pathways when entering the plant (Hand*s et al.* 2018; Khanna *et al.* 2019; Kohli *et al.* 2019). It is found that heavy metals also disturb the ultrastructure of chloroplasts. Various experiments carried on different plants suggested excess Cd metal ions leading to reduced number and size of chloroplasts, less accumulation of starch, and degraded chlorophyll but enriched plasto globuli accumulation (Kapoor *et al.* 2019). Different researchers also reported Cd that acts as a potential inhibitor of photosynthesis as it modifies the shape of chloroplast (Najeeb*et* al. 2011). Lipid content of chloroplast and thylakoid membrane lipids like digalactosyldiacyl- glycerol, monogalacto syldiacyl glycerol, and phosphatidyl glycerol get reduced due to heavy metal stress. It is also reported that Cd can alter the photosystem donor site by substituting Ca in the oxygen evolving complex (OEC) chain (Pagliano *et al.* 2006). Cr toxicity reduces photosynthesis as it binds to the heme group of cytochrome and thus alters the electron transport chain (Dixit *et al.* 2002). Some heavy metals also hinders the uptake of other ions for example limiting the uptake of elements like iron (Fe) and Mg (Sharma and Dubey 2005) which increase the activity of enzymes like chlorophyllase fastening the process of chlorophyll degradation (Drazkiewicz 1994). Pb is also identified to adversely affect CO_2 fixation altering the activity of enzyme RuBisCO in the C3 cycle and phosphoenolpyruvate carboxylase in the C4 cycle (Sharma and Dubey 2005). Other heavy metals like Hg, Ni, Cd, Pb, Cu, also can substitute the central Mg of the porphyrin head of the chlorophyll making it inactive during the photosynthesis process (Bertrand and Poirier 2005).

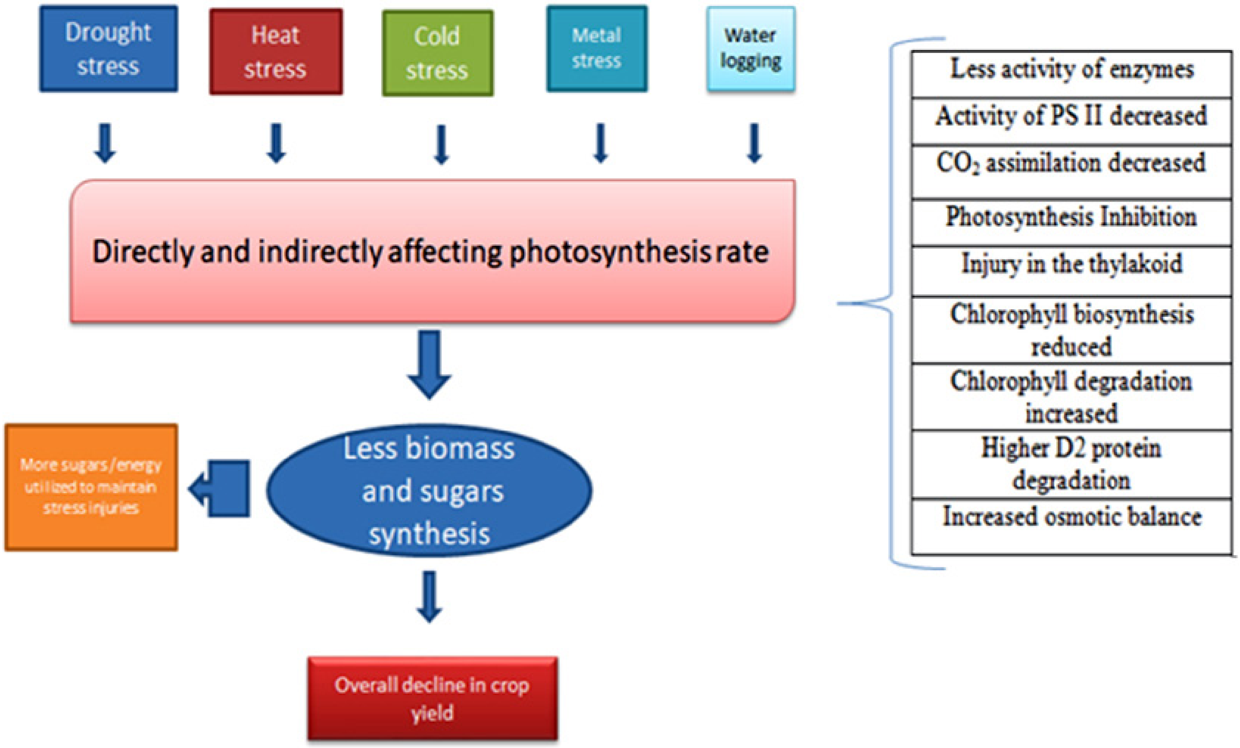

Figure1. Effect of different abiotic stresses on photosynthesis

Table 1. Effect of abiotic stress on photosynthesis in different crops

Crop	**Abiotic stress**	**Photosynthesis effect**	**References**
Wheat	High temperature	Reduction in chlorophyll biosynthesis destroying enzymatic activities	Efeoglu and Terzioglu 2009
Wheat	High temperature	Chlorophyll content and photochemical activity of PS II decreased	Chen *et al.* 2017
Wheat	High temperature	Decreased net photosynthetic rate	Djanaguiraman *et al.* 2018
Wheat	High temperature	Decrease in CO_2 assimilation rate	Hlaváčová *et al.* 2018
Wheat	Low temperature	Photosynthesis Inhibition	Li *et al.* 2014
Wheat	Low temperature	Decline in photosynthesis	Djanaguiraman *et al.* 2018
Wheat	Ni	Decrease in chlorophyll contents	Gajewska and Sklodowska 2007
Wheat	Ni	A decline in chlorophyll contents and net photosynthesis	Yusuf *et al.* 2011
Durum Wheat	Cd	Decrease in the energy transformation efficiency of PS II	Paunov *et al.* 2018

Durum Wheat	Zn	Decrease in the energy transformation efficiency of PS II	Paunov *et al.* 2018
Rice	Low temperature	Reduction in chlorophyll content	Han *et al.* 2017
Rice	Cr	Inhibition of photosynthesis	Hussain *et al.* 2018
Maize	High temperature	Decrease in Rubisco activase activity	Salvucci *et al.* 2001
Maize	High temperature	Inhibition of net photosynthesis rate	Crafts-Brandner and Salvucci 2002
Soybean	High temperature	Rates of photosynthesis increased	Xu *et al.* 2016
Soybean	Low temperature	Down-regulation of photosynthesis	Xu *et al.* 2016
Indian Mustard	Pb	Chlorophyll content decreases	Handa *et al.* 2018
Rapeseed	Cd	Decrease in photosynthetic rate and transpiration rate	Ali *et al.* 2018
Tomato	Low temperature	Net photosynthetic rate reduced	Liu *et al.* 2017
Tomato	Low temperature	Injury in the thylakoid membrane	Yang *et al.* 2018
Tomato	Low temperature	reduced chlorophyll content and proteins involved in photosynthesis	Khan *et al.* 2019
Cotton	High temperature	Less activity of RUBP and declining overall photosynthesis	Wise *et al.* 2004
Pea	High temperature	CO_2 assimilation decreased	Abdulmajeed *et al.* 2017
Sugarcane	Low temperature	chloroplast structure disrupted and overall photosynthetic efficiency reduced	Li *et al.* 2018a
Blackberry	Cd	Photosynthetic pigments content declined	Fidalgo *et al.* 2011

2.2.5 Photosynthesis under elevated CO_2 and O_3

Carbon dioxide (CO_2) and ozone (O_3) are the rich greenhouse gases in the atmosphere, and the concentrations will increase with time in the coming future. There is short-term stimulation of photosynthesis to elevated CO_2 (Drake *et al.*1997) it affects the activity of rubisco. Rubisco activity increases as CO_2 is the limiting factor for rubisco activity and the net CO_2 uptake efficiency will increase as a result of inhibition of the oxygenation reaction. The loss of CO_2during photorespiration will decrease, and a larger part of the energy achieved from the light reactions will be used for assimilation (Long *et al.* 2004). The strong oxidizing nature of O_3it causes decreases in photosynthesis as a consequence of loss of Rubisco activity (Farage *et al.* 1991). It is found that approximately 40 ppb of O_3 present in the environment and it can suppress photosynthesis by an average of 11 % when compared with pre-industrial levels of O_3(10 ppb), whereas stomatal conductance suppresses by an average of 13 % in comparison to pre-industrial ozone levels (Wittig *et al.* 2007).

2.3 Photosynthesis Enhancement

2.3.1 Improving Rubisco kinetic properties

Rubisco is a rich protein as it accounts for about 90 % of the degraded proteins (Miller and Huffaker 1985). It assimilates $CO_2$by carboxylation of ribulose-1, 5-bisphosphate (RuBP) (Ellis 1979). Rubisco has low turnover as compared to other calvin cycle enzymes, low turnover means a relatively large amount of carbon dioxide is needed to sustain sufficient rates and it is called catalytic limitations of Rubisco which compromise the photosynthetic efficiency (Parry *et al.* 2007). Another problem with Rubisco is that it also competes with oxygen catalyzing a wasteful reaction of photorespiration that leads to a loss in fixed carbon and consumes more energy. Under stress conditions, reactive oxygen species produced in chloroplast causes oxidative damage to thylakoid and stromal-bound proteins. Oxidative stress also modifies specific residues on Rubisco and spot the enzyme for degradation (Moreno *et al.* 2008). Due to these three reasons catalytic limitation, the process of photorespiration and rubisco degradation photosynthesis is greatly affected.

Improvement in the catalytic properties of Rubisco has been suggested as one of the most energetically effective approaches for improving photosynthesis efficiency. In nature different forms of Rubisco exist that possess varying catalytic qualities thus there are sufficient scopes to find a better version of Rubisco that is suitable in changing environments. Strategies employed for the improvement of Rubisco are classified into two categories (i) Direct enzyme engineering and (ii) Raising CO_2concentrations within the chloroplast. Attempts to manipulate plant Rubisco by nuclear transformation had limited success whereas modifying its catalysis by targeted changes to its catalytic large subunit via chloroplast transformation has been much more successful. However, the success rate of this is less and the need for development for most major food crops including maize, wheat, and rice. Other bioengineering approaches for improving Rubisco's performance include improving the activity of its ancillary protein, Rubisco activase, in addition to modulating the synthesis and degradation of Rubisco's inhibitory sugar-phosphate ligands (Parry *et al.* 2012). In maize over expressed Rubisco through transgenic approach resulted in a 15% increase in assimilation rate but not yield due to the increased metabolic load. Expression of 2-carboxyd-arabinitol-1-phosphate phosphatase which removes Rubisco inhibitor, 2-carboxy-d-arabinitol-1-phosphate in wheat resulted in high yield (Lobo *et al.* 2019). It is documented that manipulation of Rubisco is not a straightforward approach to enhance photosynthesis and yield as many complexities associated with it are not fully analyzed.

2.3.2 Introduction of the C4 pathway into C3 crops

The plant adopts three types of biochemical mechanisms to fix carbon dioxide. C4 photosynthesis is one of three other than C3 and CAM pathways. More than 66 times independently at least in 19 families have evolved C4 photosynthesis. C4 photosynthesis evolution entails alteration in cellular structure and biochemistry. The introduction of the C4 pathway into C3 crops is suggested because a specialized form of photosynthesis has developed a carbon concentration mechanism around the Rubisco enzyme thus eliminating photorespiration. Other benefits associated with C4 plants are higher water use efficiency because of higher concentration gradient for CO_2 diffusion that can be maintained through partly closed stomata, higher radiation use efficiency as it does not get saturated at a high light intensity, and higher nitrogen use efficiency as it requires less Rubisco and hence less nitrogen, Plants having C4 photosynthesis are more productive at high temperature. To take all these advantages there are efforts toward inserting the C4 mechanism from C4 plants like maize to C3 plants like wheat or rice. C4 genes such as PEPC, CA, NADP-ME, and NADP-MDH are cloned from maize and transformed into rice. Also, transporters like 2- oxoglutarate/malate transporter, dicarboxylate transporter1 and 2, mesophyll envelope protein, and triosephosphatetranslocators which are overexpressed in C4 plants are also expressed in C3 plants like rice. Promising genes which control Kranz anatomy were also introduced in rice that has been engineered with C4 biochemical pathway genes. Another enzyme of the Calvin cycle that could be targeted is sedoheptulose 1,7-bisphosphatase (SBPase). The introduction of novel pigment synthesis pathways is also an interesting proposal consisting of engineered crops to express a complete red-shifted cyanobacterial PSII complex with a PSII-like an oxygenic reaction center using bacteriochlorophyll b (ort et al. 2015).

2.3.3 Reduction in photorespiration

In C3 plants during carbon fixation, ribulose 1,5bisphosphate(RuBP) bind with Rubisco and CO_2 to form phosphoglycerate, but under low CO_2concentration and high temperature, it also has an affinity to bind with oxygen greater than carbon dioxide catalyzing a reaction between RuBP and oxygen results in the formation of 2-phosphoglycolate and phosphoglycerate. The 2 phosphoglycerates converted back to phosphoglycerate by a process called photorespiration which uses previously fixed carbon dioxide and extra energy is used thus it is a wasteful process limiting the photosynthetic efficiency. Scientists are trying to minimize this wasteful process to increase photosynthetic efficiency. There are different ways to reduce photorespiration. One way is to reduce glycine decarboxylase protein in mesophyll cells and restrict its accumulation in bundle sheath cells so that decarboxylation of glycine occurs in bundle sheath only and thus generates high carbon dioxide concentration in bundle sheath cell. Another approach is to capture photorespirationCO_2 by transferring the (*E. coli I*) glycolate catabolic pathway to the chloroplast, in which glycolate in the chloroplast is directly converted to glycerate with reduced photorespiration and enhanced photosynthesis.

2.3.4 Relaxation from photoprotection

Relaxation from photoprotectionis a broad term that covers all the mechanisms which prevent damage caused by reactive oxygen species (ROS) which might have harmful effects on photosynthetic efficiency and other processes in the leaf ultimately reducing plant growth and fitness. Manipulation of photoprotective pathways can enhance both photosynthetic productivity and stress tolerance in plants. There should be a need to balance between photoprotection that limits damage from higher lighting a way to enhance productivity. Photoprotection can be accomplished by avoidance of excess light absorption by altering the orientation of leaves to optimize light absorption and reduce leaf temperature. Chloroplast adjusts themselves in the periclinal walls perpendicular to the light under low light conditions, however, in high light conditions, chloroplast shifts towards the anticlinal walls that decrease excitation and saturation of the photosystem.

These days progress has been made to identify genes that confer the movement of stomata away and toward the source of light sources. Another way for photoprotection includes changes in amounts of soluble enzymes of photosynthesis and modifies pigment-protein complexes of the photosystem. Enhancement of non-photochemical quenching is also a possible way to attain optimum photosynthesis. non-photochemical quenching involves the conversion of ROS like singlet oxygen produced due to excess light into less reactive species with the help of biomolecules like xanthophylls and carotenoids. This inactivation of PSII is thought to be caused by unavoidable photooxidation and is followed by a repair cycle thus more rapid and efficient repair system can lead to enhanced photosynthetic efficiency. Flavodi iron proteins were naturally lost in the ancestor to all flowering plants but ubiquitous found in all cyanobacteria and are found in many plants (Ilik*et al.* 2017). Flv reintroduced in Arabidopsis by (Yamamoto *et al.* 2016) and in tobacco (Gomez *et al.* 2017) speed up recovery under fluctuating light. A high level of photoprotection is found in the green alga and diatoms. Green algae (*Chlorella ohadii*) can grow in high light conditions with minimum photodamage (Ananyev*et al.* 2017; Treves *et al.* 2016). Similar to that diatom has resistance to photodamage around PSII and it can also activate NPQ (Feikema *et al.* 2006). Plants can also be introduced with foreign photosystems and antennae components as foreign photosystems have distinct subunits which are considered to be more stress-tolerant. Cardona *et al.* (2015) found that *Chroococcidiopsisthermalis* PCC 7203 which encode six subunits of D1 can be expressed differentially expressed as par the suitability to the environment One divergent type of D1 subunit (ChlF) that permit growth in far-red light (Ho *et al.* 2016), another copy of D1 might be expressed under low or high-light conditions to enhance the function of the PSII complex as reported in other cyanobacteria (Mulo*et al.* 2009; Vinyard*et al.* 2013). Transformed tobacco plants having synthetic glycolate metabolic pathways to inhibit glycolate export increased photosynthetic quantum yield by 20% and enhanced biomass productivity by >40% field trials.

These can be used as a model to improve photoprotection in plants to improve photosynthesis and yield.

2.3.5 Improve canopy architecture

Manipulating photosynthesis at the chloroplast or leaf level will only be beneficial if it confers an improvement at the level of the plant canopy. Cultivars with more erect leaves, especially at the top of the canopy, have led to improved light environments inside a canopy and hence, improved canopy photosynthetic CO_2 uptake rate (Long *et al.* 2006). The challenge is to identify the ideal canopy architectural and leaf metabolic features to breed or engineer for increased canopy photosynthesis for current, and more importantly, for future conditions. This is a challenge, partially due to the lack of efficient methods to measure canopy photosynthesis although many efforts have been devoted to developing canopy photosynthesis chambers (Steduto *et al.* 2002) many canopy photosynthesis models with different levels of detail have been developed to date. Depending on the level of complexity, these models can be roughly divided into three categories: (*i*) The big-leaf model (Lloyd *et al.* 1995); (*ii*) The sunlit–shaded model (Dai *et al.* 2004); (*iii*) and the multi-layer model.

2.3.6 Improving light capture

One of the potential approaches to enhance photosynthesis is to improve light capturing and converting this energy to yield. Both photosystem I and II are made up of chlorophylls and carotenoids (Su *et al.* 2017; Mazor*et al.*

2017). It is believed that reduced antenna systems allow uniform and better light capture resulting in enhanced photosynthesis (Kirst *et al.* 2017). It is reported that mutation which results in reduced antenna accumulate more biomass compare to wild type. Another way to improve light capture is to use a light-harvesting system from other plants. It is believed that extending photosynthetically active radiation toward far-red light could cause an increase in available photons by 19% (Chen and Blankenship 2011). This can be achieved by the introduction of cyanobacterial genes responsible for chlorophyll d or chlorophyll f synthesis into plants (Ho *et al.* 2016). These approaches will help to convert solar energy into more valuable yield terms.

2.3.7 Photosynthetic models approach

Models associated with photosynthesis are the better way to identify the limiting step in enhancing photosynthesis. Wu *et al.* (2019) developed a model of diurnal photosynthesis stomatal conductance. It connects photosynthesis of leaf to yield of crop associated with Australian cropping region for limited and non-limited water condition for crops like wheat and sorghum. The model is mainly based on the wheat and sorghum biomass and stimulated by canopy response for diverse field data set. The data subset includes parameters like Maximum carboxylation rate of Rubisco electron transport capacity, and mesophyll conductance for $CO_2$for enhancing C3 and C4 photosynthesis to improve crop yields. By increasing the entire three components under irrigated conditions yield improvements at 9.2% and 12.2% for sorghum and wheat, respectively.

2.3.8 High through approach to improve photosynthesis

High through put approach for measuring Chlorophyll fluorescence (ChlF) a powerful non-invasive technique for probing photosynthesis allowed assessment of the native genetic diversity in ChlF traits while considering the diurnal dynamics of photosynthesis (Zendonadi *et al.* 2021). The light-induced fluorescence transient (LIFT) sensor provides active ChlF data for rapid and remote characterization of plant photosynthetic performance. The LIFT fluorometer (Kolber *et al.* 2005) has emerged as an alternative high-throughput approach for continuous remote measurement of the photosynthetic status of terrestrial vegetation. LIFT-measured ChlF empirically provides not only PAM-analogous photosynthetic parameters but also measures the downstream electron transport rates (ETR) from the primary quinone acceptor (QA) to the plastoquinone (PQ) pool, and ultimately, towards PSI (Osmond *et al.* 2019). Using the LIFT method for automated plant phenotyping under semi-field conditions Keller *et al.* (2019) demonstrated that the ChlF-based parameters not only facilitated the understanding of photosynthetic interactions with varying environmental factors but also identified differences between and within crop species. A link between remote sensing and photosynthetic physiology can be applied to agricultural species for studying phenotypic variation in photosynthetic capacity among hundreds of thousands of plants representing genotypic variation within a reasonable time. This can be done by utilizing agricultural models and to identify variation in photosynthetic physiology for breeding efforts. Partial least squares regression (PLSR) model is used to predict photosynthetic capacity from leaf hyperspectral reflectance. PLSR based spectral models predict photosynthetic capacity in genetically modified plants, across growing seasons, and can predict Vc,max and Jmax independent of leaf nitrogen. Tobacco was chosen as a model crop species to test the effectiveness of modifications to the photosynthetic pathway based on the ease of genetic transformation, short growing seasons, and large number of seeds produced (Kromdijk *et al.* 2016). In recent years, due to the continual innovation of molecular breeding methods, many excellent genes have been applied for increasing yields. The hexokinase gene OsHXK1 was knocked out via the CRISPR/Cas9 gene-editing method in the indica rice varieties increased light saturation points, stomatal conductance, light tolerance, photosynthetic products, and rice yields. Moreover, transcriptome analysis showed that the expression of photosynthesis-related genes significantly increased. Thus knocking out OsHXK1 via the CRISPR/Cas9 gene-editing method could effectively lead to the cultivation of high-photosynthetic efficiency and high-yielding rice varieties (Zheng *et al.* 2021).

3. Conclusion and Future Perspective

Abiotic stresses are the main reason for crop yield losses all over the globe. These stresses reduced the average yields of the major crop by more than 50%. Plants being sessile are constantly exposed to abiotic stresses like high and low temperatures, water logging and deficits, salinity, and carbon dioxide (CO2), and ozone (O3) concentrations.

The best strategy to increase crop production is through improving photosynthetic potential to support yield. High photosynthetic efficiency is achieved by improving rubisco kinetic properties, the introduction of the C4 pathway into C3 crops, reduced photorespiration, and relaxation from photoprotection, increased activity of sedoheptulosebisphosphatase, including improved canopy architecture. In the future, the reduction of the Rubisco oxygenase reaction will be a target for future improvement of photosynthesis. As the improvement of the C_3 cycle is not just about increasing CO_2 fixation but should also aim to increase both nitrogen use efficiency and water use efficiency while maintaining high productivity, therefore, manipulation of the C3 cycle to improve these parameters is an important goal in the future also the discovery of genes related to Kranz anatomy. There is a timely need to accelerate understanding of the photosynthetic process in crops to allow informed and guided improvements.

Conflict of interest

There is no Conflict of interest among authors

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