Faculty of Agriculture, University of Poonch Rawalakot
Jammu Kashmir Journal of Agriculture
ISSN: 2312-9344 (Online), 2313-1241 (Print)
https://jkjagri.com/index.php/journal
Check for updates

OVERVIEWING SUPERCHARGED FOOD CROPS IN TURKIYE PERSPECTIVES: A WAY FORWARD TO FOOD SECURITY

[a]**Ferhat Kizilgici**, [b]**Muhammad Aamir Iqbal**

[a] *Department of Plant and Animal Production, Kiziltepe Vocational School, Mardin Artuklu University, Mardin, Turkiye.*
[b] *Department of Agronomy, Faculty of Agriculture, University of Agriculture Faisalabad, Pakistan.*

A B S T R A C T

Food and nutritional insecurity, skyrocketing human populace, climate change and stagnate productivity of strategic food crops have emerged as prime challenges of this century. In order to attain UNDP sustainable goal of food security and zero hunger, there is dire need to improve the productivity and nutritional quality of food crops without immense increment in farm input utilization. The supercharged food crops (SFCs) (genetically modified plants entailing potential to grow significantly faster than conventional plants) might contribute produce greater economic yields. Numerous mechanisms such as improvement in photosynthetic efficiency, non-photochemical quenching, imparting C4 life cycle in C3 cereals and enhancing harvest index, are being put into practice for producing SFCs. An amalgamation of genetic engineering and synthetic biology approaches might produce desirable traits. However, future research efforts need to address multiple challenges such as plants traits governed by multiple genes and having little correlation with photosynthesis along with transgenic plants switching back to original physiological pathways.

Keywords: Staple crops; Sustainable development goals; CRISPR/cas9; Photosynthetic efficiency; Genetic engineering

Corresponding Author: Muhammad Aamir Iqbal
Email: aamir1801@yahoo.com

Article history
Received: August 22nd, 2022
Revised: October 7th, 2022
Accepted: October 24th, 2022

INTRODUCTION

Globally, human population is skyrocketing and climate change has been stated to seriously affect the productivity of prevalent farming systems (Chowdhury et al., 2021; Iqbal et al., 2020; Ortiz-Bobea et al., 2021). It has been predicted that by 2050, there is dire need to increase food production by 70% from the same land under cultivation nowadays. Without significant increase in productivity of food crops, neither food security nor UNDP sustainable goals of zero hunger and poverty alleviation can be achieved (Iqbal, 2020; Sabagh et al., 2022). This scenario demands development of new technologies for boosting crops yield because it has been estimated that over 20 years' time might be needed for such inventions to reach out the farmer's fields (Ahmad et al., 2021). The higher rates of crop productivity increment are needed than the current rate and it should be the prime aim in order to trigger reductions in world's hunger (Alghawry et al., 2021; Iqbal et al., 2020). The development of new technologies can provide guard against a variety of unanticipated negative contingencies like climate change, global warming, droughts, floods, shrinking fields under plough etc.

Interestingly, crop yields per unit land area (multiplication of harvest index with mass production on a unit area) has become stagnate especially in countries like Pakistan, India and Turkey. After green revolution, the significant yield enhancement in staple cereals especially wheat was associated to increased harvest index that was achieved by introducing dwarfing genes (Alam et al., 2021). However, further increment in crops yields have not been achieved as per need which require innovative research strives before it becomes the matter of too little too late. One of biologically viable and economically feasible approach might be to develop nutrient-rich crop varieties through the process referred to as bio-fortification. This may assist growers, nutritionists and breeders to reverse the deficiencies of protein and mineral along with imparting resilience to modern farming systems against climate change and emerging threats of biotic and abiotic stresses.

Furthermore, boosting staple crops yield along with enhancement of quality traits might serve as a strategic way to attain the zero hunger goals as envisaged by UN Sustainable Development Goal strategy. Moreover, another sustainable approach for improvement in crop yields can be via increasing the canopy photosynthetic capacity (Long et al., 2006; Long et al., 2015; Murchie and Ruban, 2020; Ort et al., 2015). The experimental uses of transgenics have started which may bring revolution in meeting the supply-demand gap of staple crops in near future.

It is pertinent to mention that for achieving the targeted yield increases and to impart sustainability to modern farming systems, intensified breeding efforts and genetic engineering approaches are direly needed to obtain new crop varieties with higher photosynthetic capacity and improved nitrogen use efficiency. Keeping in view the dire need to improve crop varieties to obtain greater crops yield, this review attempts to highlight the fundamentals of SFCs, their efficiency to produce more food and challenges confronted to producing supercharged crops have been elaborated objectively in Pakistani and Turkish perspectives.

FUNDAMENTALS OF SUPERCHARGED CROPS

In simplest words, supercharged plants are genetically modified plants entailing potential to grow significantly faster than conventional plants. The normal growth rate of presently grown varieties of field crops might be speeded up by modifying and persistently changing the structure of crop plants genes. The genetic modifications enable plants to react quickly to changes in light. In other words, it is actually the photosynthesis (process which turns carbon dioxide and water into food in the presence of sunlight), that is targeted to be modified through genetic engineering. It has been established that increment in photosynthetic efficiency might constitute one on the biologically viable and most potent strategy to attain higher biomass along with boosting the nutrient use efficiency (NUE) as well as water use efficiency (WUE). The supercharged plants tend to grow faster owing to their potential for vigorous responsiveness to changes in light and shade. Recently, Chinese researchers have boosted the rice yield by 40% via tweaking the rice plant's genes.

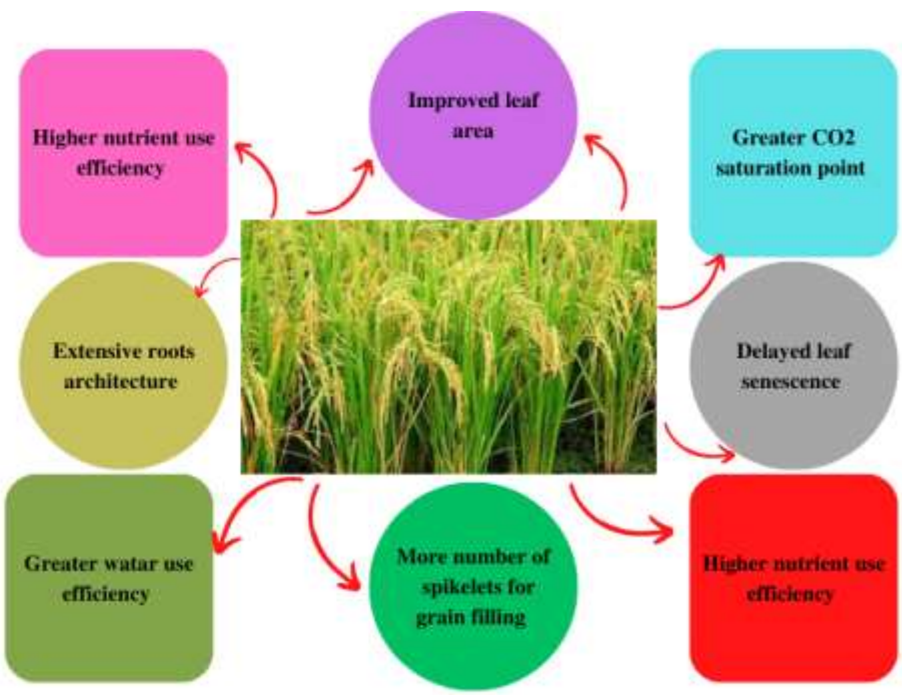

Figure 1. Pronounced characteristics of supercharged rice crop imparted through amalgamation of genetic engineering and synthetic biology approaches.

MECHANISM OF SUPERCHARGING FOOD CROPS

Improvement in photosynthetic rate

Plants can absorb light energy in excess than required for photosynthesis and thus, a greater proportion of molecules of chlorophyll continue to remain in excited state. This situation leads to significant reduction in the electron transport system which causes transfer of energy to the stored oxygen. Ultimately, reactive oxygen species are synthesized (Schmidt et al., 2016) which disrupt numerous vital physiological functions of food crops (Peterhansel et al., 2013). These ROS tend to disturb the functioning of photosynthetic machinery along with cell membranes. It has been reported that ROS are particularly harmful for the photosystem II (PSII) reaction centre which causes temporary loss of photosynthetic efficiency until the plagued reaction centre gets repaired.

Primarily, supercharged crops tend to have higher photosynthetic efficiency which results in greater water use efficiency (WUE) and fertilizer use efficiency (FUE). This higher photosynthetic rate has been using nine different ways such as (1) through improvement in mesophyll conductance, (2) Rubisco specificity enhancement, (3) simultaneous triggering of mesophyll conductance and Rubisco specificity, (4) introduction of C4 biochemistry in C3 crops and (5) inculcation of Kranz anatomy of C4 for effective minimization of CO2 leakage. In addition, other techniques including (6) systematic engineering to achieve full fledge C4 mechanisms, (7) engineering of transporters of cyanobacterial bicarbonates, (8) strengthening of CO2-concentrating with the carboxysome in the chloroplast similar to cyanobacteria and (9) developing an integrated mechanism that combines low ATP cost and the high photosynthetic potential per unit leaf nitrogen (Qu et al., 2021).

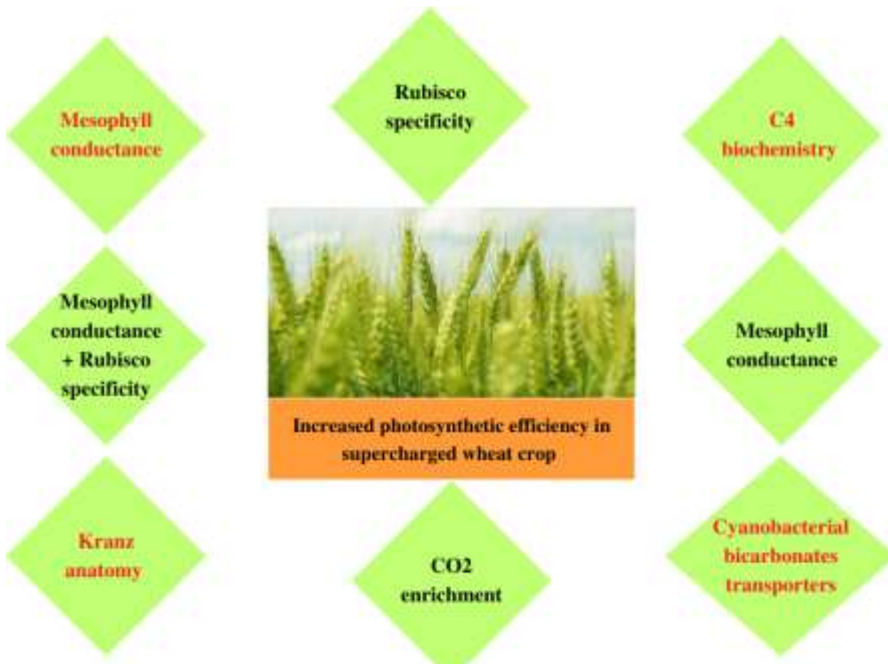

Figure 2. Different possible alterations achieved through genetic engineering for produced supercharged wheat.

Non-photochemical quenching

The fundamental idea behind developing supercharged crops revolves around the fact that plant leaves have the potential to absorb only a fraction of sunlight energy to drive and trigger the photosynthesis process. Thus maximizing the plants leaves potential to absorb more solar radiation can increase photosynthesis by many folds. This research idea was previously supported by the fact that so much solar radiation strikes the leaves that it may crisp and bleach leaf canopy, while plants have evolved mechanisms that get triggered in abundant sunlight in order to dissipate heat as extra energy through a process called non-photochemical quenching (NPQ). One of glitches confronted to NPQ is the time period of half an hour needed for switching off the NPQ in the presence of clouds and different shadows (adjacent tress, plant canopies, weeds etc.) that temporarily restrict the glaring solar rays. Thus instead of gearing up the photosynthetic process and slowing down NPQ, the crop plants tend to waste energy in the form of heat. It has been established that slow NPQ process resulted in the loss of crop productivity in the range of 7-30% (Ahn et al., 2008; Muller et al., 2001; Murchie and Ruban, 2020; Ruban, 2016).

C4 photosynthesis pathway for supercharged crops

The supercharged crops tend to evolve C4 photosynthesis which triggers plants' growth by capturing significantly higher CO_2 from the atmosphere and subsequently concentrating it in leaves specialized cells. That allows the photosynthetic process to operate much more efficiently. Owing to this reason, C4 crops like and sugarcane tend to grow faster and dominant C3 crops in term of productively and same was the case with supercharged rice which overcame traditional rice cultivars by attaining the towering height within a short time span after planting. It has been projected on the basis of preliminary research findings that engineering C4 photosynthesis for staple crops like rice and wheat has the potential to increase crop yields by over 50% (Evans, 2021; Flexas et al., 2004). Alternatively, it has also been forecasted that such supercharged crops would require far meagre irrigation water and plant nutrients for producing the same amount of food as that of their C3 counterparts.

Boosting harvest index

The harvest index is a recognized and empirical technique of relating economical or grain yield to total biomass yield. The economical or grain yield is expressed as a proportion of the above-ground dry matter of economic significance for which a crop is sown. The SFCs such as wheat, rice, oat, sorghum and millets can be prepared by improving the formation of spikelets (florets), the potential for robust pollination and endurable grain filling. The increment in photosynthesis is of little use if greater number of spikelets do not become available for filling. For instance, in rice, number of spikelets develop in greater number on the panicle in certain cultivars which indicates there is unused sink capacity which might be exploited to increase the number of reproductive parts of rice (Evans et al., 2008). Thus, it might be inferred that it is actually the greater photosynthetic efficiency coupled with robust reproductive growth are the actual parameters of SFCs which might be attained through effective breeding to enable crop plants having higher water and nutrient use efficiencies (Yamori et al., 2016).

PERSPECTIVES OF SUPERCHARGED FOOD CROPS

The human population is persistently on rise in Turkiye, while there is a dire need to increase the productivity of food crops for ensuring food security and earning the foreign exchange reserves through exports of food commodities. The SFCs might serve to ensure food security and contribute to the goals of zero hunger and poverty alleviation by producing more yield per unit of land area without utilizing too much farm inputs such as fertilizers and irrigation water (Kizilgeci et al., 2021).

The SFCs hold bright perspectives in the content of low photosynthetic efficiency of C3 pathways. It has been established that crops grain yield and productivity depend on translocation of assimilates towards the harvested portion of the plant. Plants tend to accumulate biomass by intercepting photo-synthetically active radiation (PAR) that has been classified in the range of 400–700 nm. The efficiency of crop plants to utilize PAR is measured in terms of radiation use efficiency (RUE). The RUE is defined as the quantity of dry matter produced by crop plants per unit of intercepted PAR. This radiation is utilized by plants in either C3 mechanism or more efficient one called C4 pathway.

It is interesting to note that most of staple crops such as wheat, rice etc. follow C3 photosynthesis pathway that is lesser efficient than C4 pathway. However in comparison to C4 crops such as maize, C3 pathway tend to have significantly lower photosynthetic efficiency primarily owing to loss of 20–35% of the carbohydrate in the photorespiration (Long et al., 2006; Walker et al., 2016). The photorespiration results from ribulose-1,5-biphosphate oxygenation by Rubisco that constitutes the primary enzyme for fixing CO2. A variety of genetic engineering approached for enhancing efficiency of C3 pathway have been proposed with an ultimate aim to suppress and restrict the photorespiration which might improve crops productivity. Thus, it has been proposed that Rubisco might be replaced with foreign alternatives having higher CO_2:O_2 specificity (Zhu et al., 2004). This might establish a fully functional photorespiratory bypass (Kebeish et al., 2007) leading to transformation CO2-concentrating mechanism as that of C4 crops (Von Caemmerer and Furbank, 2016).

There are serious research efforts in progress for switch off NPQ rapidly especially in rice and tobacco owing to ease of genetic manipulation for supercharging. Interestingly, proteins insertion into tobacco plants has produced encouraging findings by boosting its yield to over 20%. The transgenic tobacco plants were prepared by transferring the genes for three proteins extracted from thale cress plants. The result was amazing as transgenic produced 26% higher yield under same agronomic practices. It was further revealed that genetic divergence existed among tobacco cultivars as different cultivars responded differently to transgenic proteins as evident from yield increment of 13-19%.

Besides tobacco, chickpea is being used for preparing the supercharged crop and it has responded well to transgenic proteins. It is an excellent and cheaper source of numerous dietary elements and fibre and its yield increment can contribute significantly to combat malnutrition and hunger prevalence. It is well known that wild species of chickpea contained much higher tolerance against biotic and abiotic stresses along with having superior nutritional characteristics. Thus, supercharging of chickpea means transferring the superior traits into domesticated crops for imparting the essence of more hardiness and nutritional value in a biological viable way and eco-friendly manner. It has been foreseen that chickpeas biofortification by using supercharging techniques to insert genes from wild species offers bright potential to develop genotypes of staple food crops which might go a long way in improving the diets value. Additionally, SFCs might assist in preventing the incidence and frequency of different diseases and thus increasing the life expectancy for millions of people in developing countries. Moreover, two plant species including Cicer reticulatum and Cicer echinospermum widely present in Turkiye recorded significantly higher protein content along with the concentration of, iron, zinc, and calcium. It is envisaged that these species might be easily crossed with chickpea for developing cultivars having improved agro-botanical traits and economic yield potential under varying agro-ecological conditions.

DOWNSIDES AND LIMITATIONS

One of the themes of SFCs is to increase crops potential to increase utilization of CO_2 due to having higher saturation point. It has been envisaged that by exploiting the natural variation in mesophyll conductance for CO_2 diffusion might result in higher rates of photosynthesis (Chen et al., 2019; Flexas et al., 2004; Gu et al., 2017). However, very non-significant correlation has been found between photosynthesis and crop productivity across germplasm of various food crops and across individual lines of numerous segregating population (Gu et al., 2017). This phenomenon has been reported to be partly owing to relatively smaller natural variation in leaf photosynthesis and various yield related traits especially in cereals. However, to attain the goals of increased crops productivity at a greater speed, an amalgamation of genetic engineering and synthetic biology approaches in an optimized manner might assist to improve leaf photosynthesis (Long et al., 2006; Long et al., 2015; Ort et al., 2015; Singh et al., 2016).

Another pronounced challenge in the way of producing supercharged rice crop is despite numerous genetic alterations, the altered rice plants continued to rely on their usual photosynthesis pathway. It may be suggested that in order to completely switch photosynthetic pathway, genetic engineering efforts need to produce precise arrangement of specialized cells in leaved in order to trigger cells for capturing more CO_2. Likewise, there is also need to produce surrounding storing cells where CO_2 might be stored and concentrated for utilization in photosynthetic process. However, very scant information is available regarding the genes involved in producing these cells and it is suspected that these traits might be controlled by dozens of genes which render genetic engineering tasks more challenging and prone to errors due to mis-targeting.

Although supercharges tobacco has produced significantly higher yield but the fact remains that it a leafy crop and do not produce grains and thus these findings cannot be employed for grain crops like wheat, rice, maize, oat, sorghum, millets etc. Thus, SFCs producing technology packages can only get attraction of researchers and policy-makers when unmatched and verifiable results are reported for different crops.

But there are prominent signs that technology for producing SFCs might position humanity closer to the edges of a Second Green Revolution. This agricultural revolution might be characterized by new types of SFCs which are not only able to withstand biotic stresses (diseases, weeds etc.) but remained little affected by abiotic extremes such as heat, drought, salinity and poor fertility. Thus, SFCs hold potential to bring nutritional and food security to impoverished nations worldwide.

Traditional breeding approaches hold little significance for producing supercharged crops owing to various limitation regarding accuracy, long time span, mis-targeting etc. However, genome editing tools especially CRISPR/cas9 approach might assist to produce desirable botanical traits that allow altering multiple genes governing single traits. Moreover, leaf area might be increased in supercharged crops through genetic engineering but another limitation could be to prevent the leaf senescence so photosynthesis might be persistent over a longer period of time. All these alterations might be induced thorough combined use of breeding and genetic engineering approaches and synthetic biology leading to the development of fortified crops species.

CONCLUSIONS

Under changing climate scenario and rapid urbanization which have reduced agricultural lands available for farming, ensuring food and nutritional security of increasing populace has become a daunting task. Supercharged food crops entailing superior traits to tolerate biotic and abiotic stresses along with greater water, nutrients, CO_2 and photosynthetic efficiencies might bring humanity closer to another green revolution. However, there is need to concentrate research efforts and pool the resources for combining genetic engineering approaches with synthetic biology along with agronomic advancements might result in altering the agro-botanical traits of food crops.

CONFLICTS OF INTEREST

The authors declared no conflict of interest. The funders had no part in the design, collection analyses and interpretation and writing of short communication.

AUTHOR'S CONTRIBUTION

All authors contributed and supported towards writing of this manuscript.

REFERENCES

Ahmad, Z., Waraich, E.A., Tariq, R.M.S., Iqbal, M.A., Ali, S., Soufan, W., Hassan, M.M., Islam, M.S., El Sabagh, A., 2021. Foliar applied salicylic acid ameliorates water and salt stress by improving gas exchange and photosynthetic pigments in wheat. Pakistan Journal of Botany 53, 1553-1560.

Ahn, T.K., Avenson, T.J., Ballottari, M., Cheng, Y.-C., Niyogi, K.K., Bassi, R., Fleming, G.R., 2008. Architecture of a charge-transfer state regulating light harvesting in a plant antenna protein. Science 320, 794-797.

Alam, M.A., Skalicky, M., Kabir, M.R., Hossain, M.M., Hakim, M.A., Mandal, M.S.N., Islam, R., Anwar, M.B., Hossain, A., Hassan, F., 2021. Phenotypic and molecular assessment of wheat genotypes tolerant to leaf blight, rust and blast diseases. Phyton 90, 1301-1320.

Alghawry, A., Unlu, M., Çolak, Y.B., Iqbal, M.A., Barutcular, C., El-Ballat, E.M., Batiha, G.E.-S., Rauf, A., El-Demerdash, F.M., Elshafee, M., 2021. Irrigation rationalization boosts wheat (*Triticum aestivum* L.) yield and reduces rust incidence under arid conditions. BioMed Research International 2021, 1-10.

Chen, Q., Soulay, F., Saudemont, B., Elmayan, T., Marmagne, A., Masclaux-Daubresse, C., 2019. Overexpression of ATG8 in *Arabidopsis* stimulates autophagic activity and increases nitrogen remobilization efficiency and grain filling. Plant and Cell Physiology 60, 343-352.

Chowdhury, M.K., Hasan, M., Bahadur, M., Islam, M.R., Hakim, M.A., Iqbal, M.A., Javed, T., Raza, A., Shabbir, R., Sorour, S., 2021. Evaluation of drought tolerance of some wheat (*Triticum aestivum* L.) genotypes through phenology, growth, and physiological indices. Agronomy 11, 1792.

Evans, J.R., 2021. Mesophyll conductance: Walls, membranes and spatial complexity. New Phytologist 229, 1864-1876.

Evans, K., Frank, E., Gunnell, J., Pace, M., Shao, M., 2008. Coryneum or shot hole blight; Utah pests fact sheet; PLP-008. Utah State University Extension and Utah Plant Pest Diagnostic Laboratory, Logan, UT, USA.

Flexas, J., Bota, J., Loreto, F., Cornic, G., Sharkey, T., 2004. Diffusive and metabolic limitations to photosynthesis under drought and salinity in C3 plants. Plant Biology 6, 269-279.

Gu, J., Zhou, Z., Li, Z., Chen, Y., Wang, Z., Zhang, H., 2017. Rice (*Oryza sativa* L.) with reduced chlorophyll content exhibit higher photosynthetic rate and efficiency, improved canopy light distribution, and greater yields than normally pigmented plants. Field Crops Research 200, 58-70.

Iqbal, M., Hamid, A., Imtiaz, H., Rizwan, M., Imran, M., Sheikh, U., Saira, I., 2020. Cactus pear: a weed of dry-lands for supplementing food security under changing climate. Planta Daninha 38, e02019176.

Iqbal, M.A., 2020. Ensuring food security amid novel coronavirus (COVID-19) pandemic: global food supplies and Pakistan's perspectives. Acta Agric Slov 115, 1-4.

Kebeish, R., Niessen, M., Thiruveedhi, K., Bari, R., Hirsch, H.-J., Rosenkranz, R., Stäbler, N., Schönfeld, B., Kreuzaler, F., Peterhänsel, C., 2007. Chloroplastic photorespiratory bypass increases photosynthesis and biomass production in Arabidopsis thaliana. Nature Biotechnology 25, 593-599.

Kizilgeci, F., Yildirim, M., Islam, M.S., Ratnasekera, D., Iqbal, M.A., Sabagh, A.E., 2021. Normalized difference vegetation index and chlorophyll content for precision nitrogen management in durum wheat cultivars under semi-arid conditions. Sustainability 13, 3725.

Long, S.P., Ainsworth, E.A., Leakey, A.D., Nosberger, J., Ort, D.R., 2006. Food for thought: lower-than-expected crop yield stimulation with rising CO2 concentrations. Science 312, 1918-1921.

Long, S.P., Marshall-Colon, A., Zhu, X.-G., 2015. Meeting the global food demand of the future by engineering crop photosynthesis and yield potential. Cell 161, 56-66.

Muller, P., Li, X.-P., Niyogi, K.K., 2001. Non-photochemical quenching. A response to excess light energy. Plant Physiology 125, 1558-1566.

Murchie, E.H., Ruban, A.V., 2020. Dynamic non-photochemical quenching in plants: From molecular mechanism to productivity. The Plant Journal 101, 885-896.

Ort, D.R., Merchant, S.S., Alric, J., Barkan, A., Blankenship, R.E., Bock, R., Croce, R., Hanson, M.R., Hibberd, J.M., Long, S.P., 2015. Redesigning photosynthesis to sustainably meet global food and bioenergy demand. Proceedings of the National Academy of Sciences 112, 8529-8536.

Ortiz-Bobea, A., Ault, T.R., Carrillo, C.M., Chambers, R.G., Lobell, D.B., 2021. Anthropogenic climate change has slowed global agricultural productivity growth. Nature Climate Change 11, 306-312.

Peterhansel, C., Krause, K., Braun, H.P., Espie, G.S., Fernie, A.R., Hanson, D.T., Keech, O., Maurino, V.G., Mielewczik, M., Sage, R.F., 2013. Engineering photorespiration: current state and future possibilities. Plant Biology 15, 754-758.

Qu, Y., Sakoda, K., Fukayama, H., Kondo, E., Suzuki, Y., Makino, A., Terashima, I., Yamori, W., 2021. Over expression of both Rubisco and Rubisco activase rescues rice photosynthesis and biomass under heat stress. Plant, Cell and Environment 44, 2308-2320.

Ruban, A.V., 2016. Nonphotochemical chlorophyll fluorescence quenching: Mechanism and effectiveness in protecting plants from photodamage. Plant Physiology 170, 1903-1916.

Sabagh, A.E., Barutçular, C., Hossain, A., Çiğ, F., Erman, M., Karademir, E., Islam, M.S., Paul, S.K., Wasaya, A., Iqbal, M.A., 2022. The incidence of heat stress on the quality of food crops in the era of the changing climate: An overview. Improvement of Plant Production in the Era of Climate Change, 71-94.

Schmidt, R., Kunkowska, A.B., Schippers, J.H., 2016. Role of reactive oxygen species during cell expansion in leaves. Plant Physiology 172, 2098-2106.

Singh, R.P., Singh, P.K., Rutkoski, J., Hodson, D.P., He, X., Jørgensen, L.N., Hovmøller, M.S., Huerta-Espino, J., 2016. Disease impact on wheat yield potential and prospects of genetic control. Annual Review of Phytopathology 54, 303-322.

Von Caemmerer, S., Furbank, R.T., 2016. Strategies for improving C4 photosynthesis. Current Opinion in Plant Biology 31, 125-134.

Walker, B.J., VanLoocke, A., Bernacchi, C.J., Ort, D.R., 2016. The costs of photorespiration to food production now and in the future. Annual Review of Plant Biology 67, 107-129.

Yamori, W., Kondo, E., Sugiura, D., Terashima, I., Suzuki, Y., Makino, A., 2016. Enhanced leaf photosynthesis as a target to increase grain yield: Insights from transgenic rice lines with variable Rieske FeS protein content in the cytochrome b6/f complex. Plant, Cell and Environment 39, 80-87.

Zhu, X.G., Ort, D.R., Whitmarsh, J., Long, S.P., 2004. The slow reversibility of photosystem II thermal energy dissipation on transfer from high to low light may cause large losses in carbon gain by crop canopies: A theoretical analysis. Journal of Experimental Botany 55, 1167-1175.