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EDITORIAL

Photosynthesis: diving deep into the process in the era of climate change

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Abstract Photosynthesis provides the building blocks as well as fuels the entire living world around us. Anthropongenic climate change began with the start of the industrial revolution a century and a half ago, but particularly over the past two decades, the planet has experienced unprecedented environmental change that limits the capacity of photosynthesis and, in turn, threatens its ability to adequately sustain the globe. Among the most prominent consequences of climate change are the reduction in plant growth, in crop yield and in the nutritional quality of food and feed. Therefore, it is high time to accelerate our understanding of the effects of climate change on photosynthesis and devise strategies to adapt photosynthesis to achieve optimal yield in the portending future climate. This special issue is intended to serve as a forum for discussing current challenges, reviewing recent relevant research, and developing state-of-the-art practices for adapting and redesigning photosynthesis for its future challenges. The focus of this issue is towards understanding the mechanisms that determine the climate resilience of photosynthetic components, with a few articles also providing insight into another component of global change, the effects of harmful environmental compounds on photosynthesis. At the same time, new tools to study and manipulate the intricacies of the process of photosynthesis are also discussed. This special issue is a timely opportunity to celebrate 90th Birthday of Govindjee, Professor Emeritus of Plant Biology, Biochemistry, and Biophysics at the University of Illinois at Urbana-Champaign, who is popularly known as 'Mr Photosynthesis'.

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Owing to the immense contribution of Govindjee in the area of photosynthesis, this special issue is a sincere effort to honour a person of international repute, a wonderful teacher, a dedicated scientist and a generous human being (Stirbet et al., 2022). Govindjee's scientific contribution to the field are highly significant, ranging from his pioneering study on the mechanics of Photosystem II and chlorophyll fluorescence in plants to his latest work on the history of photosynthesis research. He is renowned for his pioneering work contributing to the discovery of the two-light reactions and two photosystems, leading to the conception of the Z-scheme of the electron transport ws well as for breakthrough advances in oxygen evolution, particulary for the unique role of bicarbonate on the electron acceptor side of PS II. Govindjee continues to be a passionate ambassador for photosynthesis research and education as he collaborates with laboratories around the globe to work on interesting questions on diverse plant species.

CO_2 concentrating mechanism and photosynthetic carbon assimilation

Speciation and diversification acquired through long-term interaction with the various geological factors are associated with adaptations in plants. One such adaptive trait to have evolved in this way was oxygenic photosynthesis, which first appeared in cyanobacteria more that 3 billion years ago. The oxygenation of atmosphere by oxygenic photosynthesis drove the evolution of CO_2 concentrating mechanisms (CCMs) to combat the competition of O_2 and CO_2 for the active site of Rubisco. CCMs evolved independently in multiple lineages of plants in response to the various environmental influences that promoted the oxygenation reaction. *Hydrocharitaceae* is one of the most diverse families of aquatic angiosperms, and it is known to possess numerous CCMs to improve its fitness and thus its survival in the difficult aquatic environment, as discussed in the review of Rangan et al. (2022). Environmental factors such as elevated atmospheric CO_2 levels and soil moisture-deficit can affect photosynthetic ability. Results from experiments conducted on *Conocarpus erectus* L. (Combretaceae) plants grown in a high-CO_2 environment showed that these plants were able to increase their photosynthesis and carbon sequestration rates. This ability to survive under extreme conditions should be explored further possibly paving the way for future crop improvement stratigies. In another study, Sekhar et al. (2022) have studied the effect of rising atmospheric CO_2 on carbon sequestration potential of *Conocarpus erectus* L.–a semi arid tree species. The plants grown under elevated [CO_2] for 180 days, sequestered higher 33.73 kg [CO_2] tree^{-1} while the same in ambient [CO_2] was 12.89 kg [CO_2] tree^{-1} which also resulted in 70% greater biomass yields.

Photosynthesis and bioremediation

Frequent episodes of droughts and floods, and anthropogenic activities (industrialization, urbanization and population growth) pose major threats to crop productivity. Lead (II) ions are extremely dangerous and potentially catastrophic to life on this planet. There is a need to monitor flood events in detail to accurately quantify the contamination dynamics, and to allow resource managers to prioritize the areas for remediation. Maroti and Kis (2022) highlight the role of the photosynthetic purple bacterium *Rubrivivа gelatinosus* and its potential application as accumulator and for biomonitoring of lead pollution in aquatic habitats. Their approach uses both steady-state and flash-induced light absorption measurements along with bacteriochlorophyll fluorescence to detect lead ions in the living microorganism. Pb (II) ions quickly breach the bacterial cell wall and immediately trigger observable physiological changes by detaching and damaging the antenna pigments, which in turn destroy the photosynthetic machinery in bacteria in a step wise manner. Another study presented in this special issue examines how *Spirulina platensis* responds to different toxic levels of Cr (VI) stress on its photosynthetic ability (Sharma et al., 2022). A case study was conducted to assess the negative impact of synthetic dyes on photosynthetic characteristics of this species. Rhodamine is a general-purpose dye usually used for fluorescent staining and acid-fast staining purposes. The authors study the effect of industrial effluents containing such dyes on aquatic plants such as *Eischornia crassipes*. The results shows that rhodamine exposure leads to deterioration of the PSII reaction center. At high rhodamine dosages, the energy transfer from the antenna to the reaction centre was impaired. The toxicity of heavy metal ions and dyes has become a global concern and appropriate steps should be taken to reduce these pollutants as well as improve plant resilence to them. Consequently, it is important to monitor the presence of these pollutants in the environment, especially in aquatic environments.

Photosynthesis and biofortification

Numerous strategies have been used by researchers, breeders, and the food industry to address the issue of undernutrition that confronts nearly 500 million people globally. Composition and presence of key mineral elements in plants affect photosynthesis and plant growth under arid environments. Bio-fortification has proven to be an effective way to improve the nutritional content of wheat, which is globally one of the most important staple crops. In terms of biofortification, the minerals iron (Fe) and nitrogen (N) are especially important because they are required for both plant growth and human health. Singh et al. (2022) set out to understand the combined and individual impacts of nutritional famine in bread wheat. Significant yield loss occurred when N and Fe were deficient. Single and dual deficiencies in Fe and N have a negative influence on crop development and yield potential possibly by lowering the amount of photosynthetic pigments in the leaves, leaf surface area and the rate of photosynthesis. The authors emphasised that the combined effect of N and Fe deficit is more significant than the effect of individual deficiency. Understanding the connection between these nutrients will provide a deeper understanding and will help in developing more efficient coping mechanisms in the face of stress.

Photosynthesis under high temperature

Increasing temperatures and frequent heat stress is evident worldwide as climate change advances. This trend is predicted to increase during the coming years thereby threatening crop productivity and yield. For rice, a crop usually cultivated in water-flooded conditions, grain filling is drastically impacted by drought. Lekshmy et al. (2022) showed significant integration of acquired tolerance traits with water mining traits such as root length to screen promising rice genotypes for semiarid cultivation practices. The study used

21 lines from the 3 K rice IRRI genome panel and reinforced trait mapping with multivariate analysis. The predicted genotype groups with higher acquired tolerance traits (ATTs) and deep root system architecture were correlated with increased spikelet fertility. The increased light exposure that typically accompanies higher temperature makes it difficult for plant species to acclimate to the increased excitation energy. A review by Demming-Adams et al. (2022) emphasises the xanthophyll cycle and related proteins as an indicator of intra-thylakoid pH and excitation energy regulation of illumination because of the direct effect of this exposure on the deposition of metabolites in plants. Moreover, the residual zeaxanthin was highlighted to constitute the leaf's memory of excess light exposure over a short time and assist in subsequent triggering non-photochemical quenching of the excited state of Chl a fluorescence. A thought-provoking artcle by Prince et al. (2022) reviews the possibility of higher light absorption by plants than they require for photosynthesis. The authors contend that the competing behaviour of the trees is to limit the growth of other plants in the vicinity. The study of plant response to different environmental pressures should also pay attention to excess excitation energy since responses to excess light are a common aspect of plant response to a variety of environmental challenges, not only in sun-exposed, open areas but also when plants are subjected to shadowing by over-hanging canopies.

Optimizing photosynthesis using plant breeding techniques

Higher grain yield and biomass output are essential and agronomically-desired outcome for a breeding programme to be successful. Priyadarsini et al. (2022) conducted a field study to look at the differences between different types of basmati rice in terms of growth, photosynthetic characteristics, and yield components. The authors assigned scores to eleven distinct morphological and physiological factors using standard agronomic practises. Variation between rice genotypes was quite substantial for the majority of the growth and photosynthetic indices. Research showed no correlation between photosynthetic rate and shoot biomass or grain yield, but a strong positive correlation between shoot biomass and days to flowering and between gas exchange properties. The study also highlighted that while developing high-yielding basmati rice cultivars, it may be useful to use a variety of morphological and physiological traits diversity and their relationship to grain production as a selection criterion. In an effort to predict the breeding techniques for crop species in humid areas, Alvarez-Iglesis et al. (2022) looked into the variation in photosynthetic properties among multiple crop species. They contend that the genetic diversity for CO_2 assimilation traits in maize and chickpea is low, limiting the opportunity to improve photosynthetic efficiency. However, the higher variance in physiological parameters in pigeonpea, common bean, and pepper provides the scope for photosynthetic improvement in the breeding programme for these latter crops. Another interesting article by Shackira et al. (2022) reviews the green seed photosynthesis and its significance which remains an unexplored area so far. A relatively larger sized antenna of photosystem II (PSII) has been reported to enable the seeds to deal with low light saturation point and operate with low level of plastoquinone than the leaves. These studies contribute towards advancements in understanding the green seed photosynthesis which is a trait yet to be noticed by the plant breeders.

Taken together, this special issue presents a bouquet of research articles and review papers pertaining to climate change describing the fundamental and applied aspects of plant adaptation mechanisms to increased atmospheric CO_2 level, nutrient deficiency, bioremediation, and toxicity stress, as well as biofortification strategies to enhance photosynthesis, nutritional status, and plant growth.

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