

Editorial

Plant Photochemistry, Reactive Oxygen Species, and Photoprotection

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Light energy, absorbed as photons by chlorophylls and other pigment molecules consisting of light-harvesting complexes (LHCs), is transferred to the reaction centres (RCs), where, through charge separation, electrons flow from photosystem II (PSII) through cytochrome b6f and diffusible electron carriers to photosystem I (PSI) [1–3]. This is a highly regulated process in which PSII and PSI work coordinately for an efficient electron transfer and are located in the photosynthetic membranes of chloroplasts (i.e., the thylakoids) [1,3–5]. The outcomes of light reactions are the formation of ATP and reducing power (reduced ferredoxin and NADPH) requiring coordination with the activity of metabolic processes for the synthesis of carbohydrates and other essential organic molecules [1–4]. Still, in the light reactions of photosynthesis, at both photosystems (PSII and PSI), reactive oxygen species (ROS), such as superoxide anion radical ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), and singlet oxygen (1O_2), are continuously produced at basal levels but are scavenged by different antioxidant mechanisms [6–9].

Under excess light conditions or other abiotic or biotic stresses, the overexcitation of PSII increases the probability of the formation of the triplet chlorophyll state ($^3Chl^*$) from the singlet excited states ($^1Chl^*$) through the intersystem crossing, producing single oxygen (1O_2) [9–14]. Photoprotection mechanisms preventing ROS formation by downregulating $^1Chl^*$ through the process of non-photochemical quenching (NPQ), by quenching $^3Chl^*$, or by scavenging ROS are activated to prevent damage and improve fitness [6,7,15,16]. Constant overexcitation is neutralised by the long-term reduction in the PSII antenna's size [17]. Thus, if the absorbed light energy exceeds that which can be used, this excess excitation energy must be quenched by the photoprotective mechanism of NPQ, so as to not damage the photosynthetic apparatus by the increased ROS production that can lead to oxidative stress [6,7,18–21].

ROS (e.g., $O_2^{\bullet-}$, H_2O_2 , OH^{\bullet} , 1O_2) are partially reduced or activated forms of atmospheric oxygen (O_2) and, in plant cells, are constantly formed by the unavoidable leakage of electrons onto O_2 from energy metabolism activities in chloroplasts, mitochondria, and peroxisomes, in plasma membranes, or as by-products in the various metabolic pathways located in diverse cellular parts [22–25], with chloroplasts and peroxisomes rather than mitochondria being considered as the main ROS birthplaces in irradiated photosynthetic cells [26].

The hydroxyl radical (OH^{\bullet}) reacts with almost all molecules, as it is the most reactive of all ROS and yet the shortest lived (half-life of 1 ns) [27]. Electron leakage to O_2 at PSI results in O_2^{\bullet} formation, which is shorter lived than H_2O_2 , into which it rapidly converts [28]. The superoxide anion radical ($O_2^{\bullet-}$) is also shorter lived than 1O_2 but longer lived than OH^{\bullet} , while H_2O_2 is the most stable and least reactive ROS with the longest lifetime, as it is able to easily diffuse through the membranes [28]. The global ROS levels in cells must be controlled and balanced, allowing only a basal ROS level to employ its beneficial function [24,29]. The efficient utilisation of sunlight photons for the production of energy-rich carbohydrates and other essential organic molecules must be accompanied by the harmless removal of unused photons that would otherwise transfer excitation energy to potentially toxic ROS [30].



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Abiotic or biotic stress-induced ROS accumulation is scavenged by enzymatic antioxidants, such as superoxide dismutase (SOD), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), glutathione peroxidase (GPX), guaiacol peroxidase (GOPX), glutathione-S-transferase (GST), and catalase (CAT), and non-enzymatic metabolites such as ascorbic acid, glutathione, α -tocopherol, carotenoids, phenolic compounds, flavonoids, and proline [11,31,32].

ROS produced in chloroplasts generate oxidative stress, but also confer an important biological function (e.g., plant growth, development, and redox signalling) [23,25,28]. As the ROS formed by energy transfer ($^1\text{O}_2$) and electron transport ($\text{O}_2^{\bullet-}$, H_2O_2) are produced simultaneously, it seems likely that the signalling pathways of one occasionally interfere with the signalling pathways of the other, therefore sometimes it may antagonize each other [5,9,11,25,33]. The role of chloroplast antioxidants, often having covering or interdependent functions, does not totally remove ROS but rather accomplishes a suitable balance between creation and deletion, so as to match the process of photosynthesis, allowing an effective scattering of signals to the nucleus [33–35]. Accordingly, ROS provide cells with tools to monitor electron transport and, thus, avoid over-reduction or over-oxidation and also create redox regulatory networks that enable plants to sense and react to biotic and abiotic stress conditions [34,36–38]. ROS activate the plant's defence mechanisms in order to cope with oxidative stress, and are important signalling molecules for the regulation of a plethora of metabolic functions, accomplishing plant function and development [20,21,37–40]. Consequently, at the same time, as cells maintain high enough energy reserves to scavenge ROS, ROS are beneficial to both biotic and abiotic stresses, permitting them to regulate their metabolism and support a proper acclimation response [41–44]. There are more than 150 genes able to encode ROS-producing and ROS-detoxifying proteins in Arabidopsis cells consisting of the ROS gene network [29].

Environmental stresses such as drought, salinity, chilling, metal toxicity, and UV-B radiation, as well as pathogen attacks, lead to an enhanced generation of ROS in plants due to the disruption of cellular homeostasis [39,45]. During the last few decades, fluctuations in weather conditions have enormously affected rainfall patterns, influencing plant growth and development, eventually affecting crop yield and quality, as well as plant survival [39]. As a consequence of global climate change, the frequency, intensity, and duration of drought and high-temperature scenarios are increasing, resulting in reduced worldwide productivity [39]. Water deficit, among all environmental factors, has been characterised as one of the key hazards for the future of agriculture [39]. Under drought stress, as well as other environmental stresses, the absorbed light energy exceeds what can be used for photochemistry and, thus, an excess accumulation of ROS occurs able to damage the chloroplast, with photosystem II (PSII) being particularly exposed to damage [2,18,39,46].

Though ROS were initially believed to be toxic by-products of aerobic metabolism having to be scavenged to avoid the oxidative damage of cells, now it is widely accepted that ROS are used by most organisms as crucial signal transduction molecules [29]. It is well documented that a basal level of ROS is essential to sustain life [24,25]. Hence, the amount of ROS in cells needs to be retained [16].

The scenarios of global climate change demand a better understanding of the relationship between plant photochemistry and the role of ROS as signalling molecules for photoprotection, but also for generating oxidative stress under different environmental conditions. The elucidation of the mechanism in this interaction could help to enhance agricultural sustainability under global climate change.

In this Special Issue of *Photochem*, we expect to publish a collection of papers regarding recent advances in plant photochemistry, reactive oxygen species, and photoprotection.

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