Biological Antioxidant Applications: Learning from Photosynthesis

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Abstract: Photosynthesis is the process by which plants use light energy to convert carbon dioxide and water into organic compounds while releasing oxygen. However, the byproducts of this process, such as reactive oxygen species (ROS), can negatively affect plant cells. This paper explores the relationship between photosynthesis and the plant antioxidant system. Research shows that the reducing agents NADPH and ATP generated during photosynthesis are essential energy and material bases for maintaining the antioxidant capacity of plant cells. These substances help eliminate ROS and sustain the normal activity of antioxidant enzymes. Additionally, photosynthetic pigments, besides participating in light absorption and photosynthetic reactions, play a role in the antioxidant process by capturing excess light energy, thereby reducing the likelihood of ROS production. This paper reveals how photosynthesis regulates the plant antioxidant system by providing energy and material foundations and modulating the functions of photosynthetic pigments. It offers theoretical support for plant growth, development, and stress resistance.

Keywords: Photosynthesis, Photoprotection, Biological antioxidants, Singlet quenching, Triplet quenching

1. Introduction

Photosynthesis is a critical biological process as it supplies energy for food, raw materials, and biofuel production, contributing to climate change mitigation. However, light exceeding photosynthetic capacity can cause cellular damage. To counter this, plants have evolved protective mechanisms, including methods to reduce light absorption, detoxify ROS generated by excessive light, and dissipate surplus absorbed light energy as heat. Collectively, these processes constitute photoprotection. These mechanisms occur in the thylakoid membranes of chloroplasts and are pivotal for plants to adapt to light intensity changes and avoid photodamage, a process known as non-photochemical quenching. Throughout their life cycles, plants frequently encounter environmental stressors such as light, drought, salinity, and low temperatures. These stresses often lead to significant ROS accumulation, such as superoxide anions, hydrogen peroxide, and hydroxyl radicals. These ROS can damage cell membranes, proteins, and DNA, affecting plant growth and development. Consequently, plants rely on antioxidant mechanisms to neutralize these harmful ROS and protect themselves from oxidative damage. The activity of the antioxidant enzyme system is influenced by various internal and external factors, including light, temperature, and water availability. These factors regulate the synthesis and activity of antioxidant enzymes through pathways such as gene expression and signal transduction. Different antioxidants work synergistically, complementing each other through redox cycling systems or diverse mechanisms to combat oxidative stress. The plant antioxidant system plays a crucial role in responding to various environmental challenges. For instance:

Under drought conditions, ROS levels in plants significantly increase. By enhancing antioxidant enzyme activity and elevating antioxidant content, plants can effectively neutralize these ROS, mitigating the adverse effects of drought on growth.

Saline-alkaline stress disrupts ionic balance and causes oxidative damage in plants. The antioxidant system aids in combating oxidative stress in saline-alkaline environments by regulating ion channels and boosting antioxidant capacity.

Low temperatures lead to lipid peroxidation and cellular membrane damage. The antioxidant system helps plants maintain normal physiological functions in cold environments by scavenging free radicals and reducing oxidative damage.

This paper specifically elaborates on the relationship between photosynthesis and biological antioxidants.

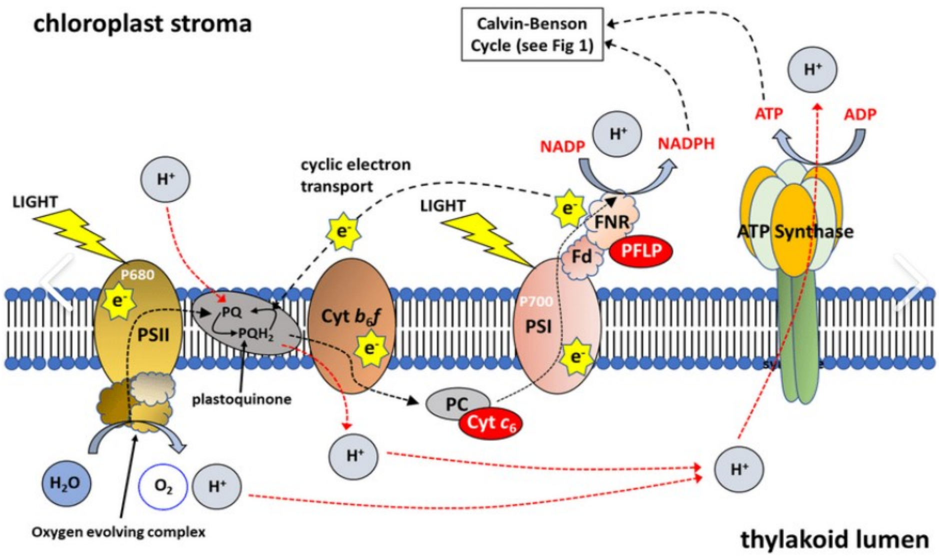

Figure 1: Schematic Diagram of the Electron Transport Chain in the Thylakoid Membranes of Higher Plants [1].

2. Functions of Photosystem I and Photosystem II in Photosynthesis and the Mechanism of Photodamage

Photosynthesis involves Photosystem I (PSI) and Photosystem II (PSII) (see Figure 1). PSI is a complex supramolecular assembly of membrane proteins, primarily comprising the core complex and light-harvesting complex I (LHCI). The core complex consists of approximately 14 protein subunits and houses the primary reaction center at its core, which is the central region for electron transport and energy conversion. LHCI mainly captures light energy and transfers it to the core complex for further conversion. When chlorophyll P700, a key pigment in PSI, is excited by light, it induces an electron transition that triggers a series of electron transport chains. Ultimately, electrons are transferred to ferredoxin, accompanied by ATP synthesis. During this process, light energy is converted into chemical energy, providing the energy and reducing power required for the subsequent dark reaction phase. PSI is prone to photodamage under intense light exposure, a phenomenon closely related to its structure and pigment composition. Studies have shown that deoxygenation treatments

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can mitigate PSI photodamage, potentially involving interactions between chlorophyll and oxygen. Additionally, variations in the light-harvesting complex proteins (e.g., LHCI-680 and LHCI-730) affect their susceptibility to photodamage, possibly due to differences in the type and quantity of carotenoids bound to them. PSII is primarily composed of membrane proteins, pigment molecules, and electron transport components, with a highly complex and refined structure. It includes light-capturing proteins D1 and D2, proteins like Cyt b559 that maintain the stability of the reaction center structure, and receptor pigment complexes that catalyze electron transport reactions. These proteins form a highly ordered electron transport chain through specific structural and molecular interactions. Auxiliary pigment molecules occupy a significant proportion of PSII's structure, functioning mainly to expand the light absorption range and transfer light energy to the reaction center complex. The primary functions of PSII include capturing light energy, splitting water, releasing oxygen, and facilitating electron transport. The working mechanism of PSII involves several complex biochemical reactions, such as light energy absorption and transfer, water photolysis, electron transport and proton accumulation, and ATP synthesis. During the light reaction phase of photosynthesis, PSII is responsible for water splitting and oxygen release, while PSI handles electron transport and the synthesis of ATP and NADPH. These processes supply the necessary energy and reducing power for the subsequent dark reaction phase, maintaining the redox balance within plant cells. Although PSI and PSII do not play a primary role in directly eliminating oxygen molecules, they indirectly influence oxygen production and the intracellular redox state through the photosynthetic process.

3. Mechanism and Role of the Xanthophyll Cycle in Energy Quenching During Photosynthesis

Energy quenching occurs during photosynthesis, and one of its primary mechanisms involves the xanthophyll cycle. The xanthophyll cycle consists mainly of three carotenoids: violaxanthin (V), antheraxanthin (A), and zeaxanthin (Z) [2]. These compounds undergo interconversion within plants through epoxidation and de-epoxidation, forming a dynamic cyclical process (see Figure 2). Under high light conditions, violaxanthin is de-epoxidized by violaxanthin de-epoxidase (VDE), producing antheraxanthin as an intermediate before being further converted into zeaxanthin. Conversely, under low light conditions, zeaxanthin undergoes epoxidation catalyzed by zeaxanthin epoxidase (ZE), regenerating violaxanthin. De-epoxidation is a critical step in the xanthophyll cycle, primarily catalyzed by VDE. Under high light conditions, when excess light energy accumulates in plants, violaxanthin (V) is converted into antheraxanthin (A) through VDE-mediated de-epoxidation, and subsequently into zeaxanthin (Z). This reaction requires the oxidation of ascorbic acid as a cofactor to proceed effectively. In contrast, epoxidation occurs under low light conditions, where zeaxanthin (Z) is converted back into violaxanthin (V) via antheraxanthin (A) under the catalysis of ZE. This process enables plants to adjust their light-harvesting and energy utilization efficiency in response to changes in light conditions [3]. Zeaxanthin plays a direct role in quenching the energy of excited chlorophyll (Chl) molecules, dissipating excess energy as heat. This mechanism is crucial in protecting the photosynthetic system from photodamage [4]. Additionally, zeaxanthin contributes indirectly to photodamage defense by acting as a component of antenna pigments, dissipating surplus light energy.

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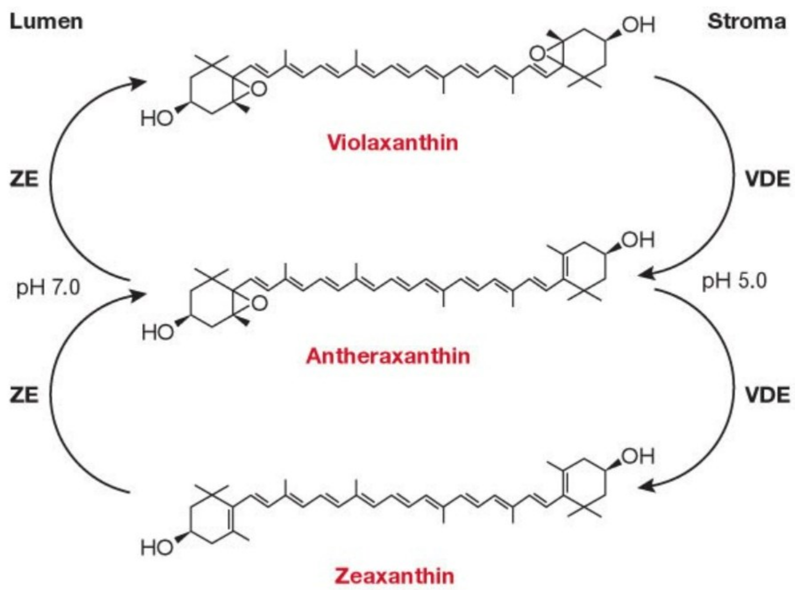

Figure 2: Diagram of the Xanthophyll Cycle [5].

4. Generation, Scavenging, and Physiological Effects of Singlet Oxygen During Photosynthesis

During the light reaction phase of photosynthesis, when chlorophyll absorbs light energy and transfers it to the reaction center, some energy may dissipate as heat or chemical energy. However, excited-state chlorophyll molecules (Chl) can also form. If these molecules fail to transfer energy promptly to the electron transport chain, charge recombination may occur, reacting with ground-state oxygen (O_2) to produce singlet oxygen ($^1O_2$) [6]. Additionally, under environmental stresses such as high light intensity or drought, plants may generate increased levels of $^1O_2$. Singlet oxygen is highly reactive and readily oxidizes unsaturated compounds, such as fatty acids and proteins, leading to oxidative damage. Excess $^1O_2$ in plants can disrupt critical cellular components, including cell membranes, photosynthetic pigments, and proteins, thereby impairing normal physiological functions. In the PSII (photosystem II) reaction center, β-carotene can quench $^1O_2$ produced by interactions between P680 and O_2, although it cannot quench P680 itself. Carotenoids, through direct quenching mechanisms, dissipate the energy of excited Chl as heat, protecting the photosynthetic system from photodamage. During photosynthesis, plants must balance light energy absorption and utilization to prevent photodamage. When light intensity exceeds the processing capacity of the photosynthetic system, a large amount of excited Chl and $^1O_2$ is generated. In such cases, direct quenching mechanisms are activated. Antioxidants such as carotenoids and tocopherols react directly with these harmful molecules, dissipating excess energy [7]. This process not only safeguards the structure and function of the photosynthetic system but also maintains cellular homeostasis and metabolic equilibrium. The plant antioxidant defense system is a complex network comprising enzymatic antioxidants (e.g., superoxide dismutase and catalase) and non-enzymatic antioxidants (e.g., carotenoids, tocopherols, and ascorbic acid). Moreover, $^1O_2$ functions as a signaling molecule, participating in various biological processes, including the regulation of photosynthesis, stomatal movement, and plant defense responses. While antioxidants play a critical role in scavenging $^1O_2$, they may also influence signaling pathways. Thus, during $^1O_2$ scavenging, plants must precisely regulate the levels and distribution of antioxidants to balance oxidative stress management and signal transduction needs.

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5. Triplet-Triplet Annihilation Mechanism and Its Physiological Significance

During photosynthesis, light energy is absorbed by chlorophyll and other photosynthetic pigments and converted into chemical energy. Upon absorbing photons, these pigment molecules transition to an excited state, where some molecules exist in the singlet state (S1), while others undergo intersystem crossing (ISC) to form the triplet state (T1) [8]. Triplet molecules, characterized by their relatively long lifetimes and high energy, participate in various photochemical reactions. However, their high reactivity can lead to oxidative damage to surrounding biomolecules such as proteins and fatty acids. In plants, excess triplet energy can disrupt critical components, including photosynthetic pigments, proteins, and membrane structures, thereby significantly impairing normal physiological functions. When two triplet molecules come into close spatial proximity, they can undergo an annihilation reaction. During this process, the energy of the two triplet molecules is redistributed: one molecule returns to the ground state (S0), releasing energy, while the other is excited to a higher singlet state (e.g., S2 or higher). Due to their high energy and short lifetimes, these singlet molecules quickly dissipate energy through mechanisms such as fluorescence, phosphorescence, or energy transfer. Under high light conditions, plants generate a large number of triplet molecules. If not promptly dissipated, these molecules can cause severe photodamage to the photosynthetic system. Triplet-triplet annihilation (TTA) serves as an effective photoprotective mechanism by rapidly consuming triplet molecular energy and alleviating the stress of photodamage. Carotenoids and other auxiliary pigments play a crucial role in this process. Acting as triplet acceptors, they engage in annihilation reactions with chlorophyll triplet molecules, thereby protecting chlorophyll from photodamage. TTA extends beyond photoprotection and contributes to energy transfer and light signal transduction within plants. Through TTA reactions, triplet molecules transfer energy to other molecules, facilitating efficient energy utilization and transfer. Additionally, TTA may function as part of light signaling pathways, participating in processes such as photomorphogenesis and photoperiod regulation. In photosynthesis, chlorophyll molecules absorb light energy, causing electrons to transition from the ground state to the excited state, forming excited-state chlorophyll molecules. These molecules may undergo further electron transfer and energy dissipation, eventually reaching the triplet state. When two chlorophyll molecules are both in the triplet state, their interactions (e.g., collisions) can result in triplet-triplet annihilation. During this process, one chlorophyll molecule returns to the ground state, while the other transitions to the excited singlet state. Triplet chlorophyll molecules, due to their relatively long lifetimes, readily react with oxygen molecules to produce reactive oxygen species (ROS), such as singlet oxygen and superoxide anions. These ROS can cause oxidative damage to cells. TTA, as a non-radiative energy dissipation pathway, helps reduce ROS formation, thereby protecting the photosynthetic system from photodamage. In addition to carotenoids, other antioxidants in plants, such as tocopherols and ascorbic acid, play indirect roles in photoprotection. Although they do not directly participate in TTA reactions, these substances mitigate photodamage by scavenging free radicals and reactive oxygen species, indirectly supporting the role of TTA in plant photoprotection.

6. Antioxidant Applications in Food, Cosmetics, and Medicine

In the field of food additives and dietary supplements, carotenoids are widely incorporated into foods as excellent antioxidants to enhance their oxidative stability and extend shelf life. For example, carotenoids such as β-carotene and lycopene are frequently added to edible oils, meat products, and dairy products to prevent oxidative spoilage. Additionally, carotenoids are formulated into nutritional supplements for daily use to enhance the body’s antioxidant capacity and prevent diseases. Vitamin C is also commonly used as a food additive to prolong shelf life and preserve the nutritional value of food. Its antioxidant properties help prevent lipid oxidation in foods, thereby maintaining their color and taste. In cosmetics and skincare products, carotenoids are valued for their outstanding antioxidant properties. They scavenge free radicals, protect skin cells from oxidative damage, and thereby delay skin aging, reducing the formation of wrinkles and dark spots. Consequently, many premium cosmetics and skincare products include carotenoids or their derivatives to improve skin quality and enhance antioxidant effects. Similarly, Vitamin C is widely used in cosmetics for skincare and whitening purposes. Its antioxidant action effectively eliminates free radicals, minimizing skin damage. In the medical and health product sectors, carotenoids also play a significant role. Studies have shown that carotenoids can inhibit or downregulate oxidative stress caused by reactive oxygen species (ROS), thereby protecting cells from damage [9]. Moreover, carotenoids enhance the immune system by promoting lymphocyte proliferation and regulating cytokine release. As a result, carotenoids are often used to treat oxidative stress-related diseases, such as cardiovascular diseases and cancer (see Figure 3) [10]. They are also formulated into health products for daily wellness purposes. Vitamin C is employed in the treatment of scurvy, colds, and other conditions and is used as an antioxidant to protect cells from oxidative stress-induced damage.

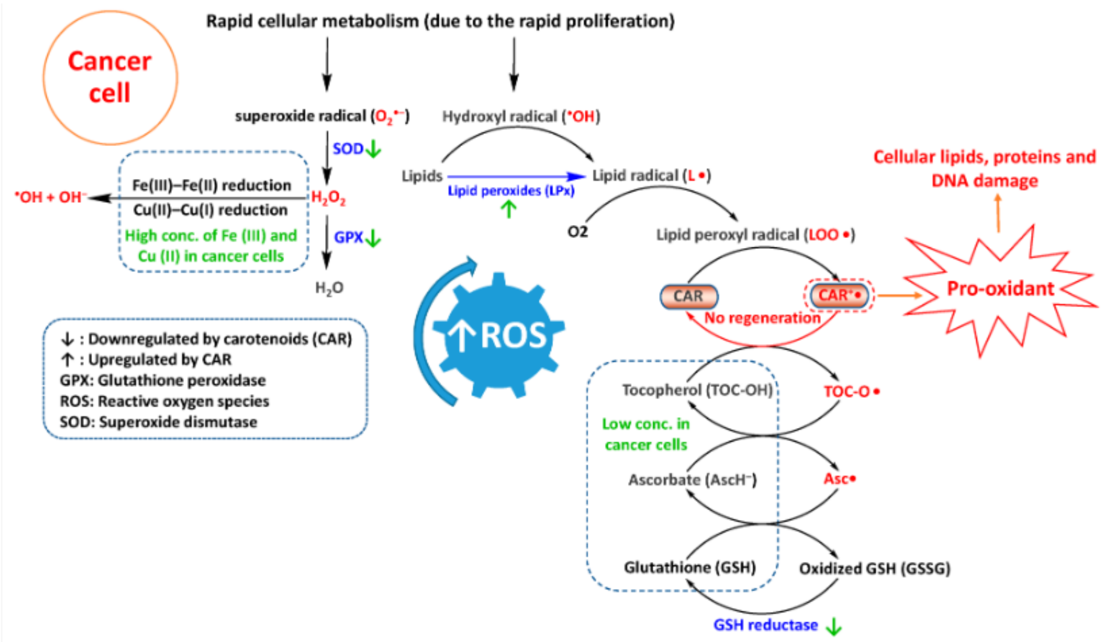

Figure 3: Diagram of Possible Pathways for Carotenoid-Induced ROS Generation in Cancer Cells [11].

7. Conclusion

Photosynthesis is a critical physiological process in plants, closely linked to their antioxidant mechanisms. During photosynthesis, the absorption and conversion of light energy may generate reactive oxygen species (ROS), which can cause oxidative damage to plant cells. However, the plant's antioxidant system can eliminate these ROS, maintaining normal cellular function. The protective mechanisms involving singlet and triplet state reactions play a vital role in this process. In the transition from singlet to triplet states, plants regulate energy transfer through specific molecular structures and pigment molecules, preventing excessive energy accumulation that could lead to ROS generation. Additionally, antioxidants such as carotenoids in plants can quench triplet excited states, thereby preventing oxidative reactions. These protective mechanisms work in concert to ensure the normal progression of photosynthesis, maintain the redox balance within plant cells, and support plant growth, development, and survival. Studying the antioxidant mechanisms in photosynthesis offers new insights and methods for biological antioxidant applications. With further research into the interplay between photosynthesis and antioxidant systems, more details about their mutual regulation will likely be unveiled, providing stronger theoretical foundations and practical guidance for biological antioxidant applications in the future.

References

[1] Simkin AJ. Genetic Engineering for Global Food Security: Photosynthesis and Biofortification. Plants (Basel). (2019). 8(12):586. doi: 10.3390/plants8120586. PMID: 31835394; PMCID: PMC6963231.

[2] Esteban, R., Becerril, J. M., & Garcia-Plazaola, J. I. (2009). Lutein epoxide cycle, more than just a forest tale, Plant Signaling & Behavior, 4:4, 342-344, DOI: 10.4161/psb.4.4.8197.

[3] Garcia-Plazaola, J. I., Matsubara, S., & Osmond, C. B. (2007). The lutein epoxide cycle in higher plants: its relationships to other xanthophyll cycles and possible functions. Functional plant biology : FPB, 34 9, 759-773 . doi: 10.1071/FP07095

[4] Jahns, P., & Holzwarth, A. R. (2012). Jahns, P., & Holzwarth, A.R. (2012). The role of the xanthophyll cycle and of lutein in photoprotection of photosystem II. Biochimica et biophysica acta, 1817 1, 182-93 . doi: 10.1016/j.bbabio.2011.04.012

[5] Lu, D., Zhang, Y., Zhang, A., & Lu, C. (2022). Non-Photochemical Quenching: From Light Perception to Photoprotective Gene Expression. International Journal of Molecular Sciences. 23. 687. doi: 10.3390/ijms23020687.

[6] Szabo, I., Bergantino, E., & Giacometti, G. M. (2005). Light and oxygenic photosynthesis: Energy dissipation as a protection mechanism against photo-oxidation. EMBO Reports, 6, 629-634. doi:10.1038/sj.embor.7400460.

[7] Accomasso, D., Londi, G., Cupellini, L., & Mennucci, B. (2024). The nature of carotenoid S state and its role in the nonphotochemical quenching of plants, 15, 847. doi: 10.26434/chemrxiv-2023-2hk9l.*

[8] Nicol, L., Nawrocki, W. J., & Croce, R. (2019). Disentangling the sites of non-photochemical quenching in vascular plants, 5, 1177–1183. doi: 10.1038/s41477-019-0526-5.

[9] Gall, A., Berera, R., Alexandre, M. T. A., Pascal, A. A., Bordes, L., Mendes-Pinto, M. M., Andrianambinintsoa, S., Stoitchkova, K. V., Marin, A., Valkunas, L., Horton, P., Kennis, J. T. M., van Grondelle, R., Ruban, A., & Robert, B. (2011). Molecular adaptation of photoprotection: triplet states in light-harvesting proteins, 4, 934–942. doi: 10.1016/j.bpj.2011.05.057

[10] Shin, J., Song, M. H., Oh, J. W., Keum, Y. S., & Saini, R. K. (2020). Pro-Oxidant Actions of Carotenoids in Triggering Apoptosis of Cancer Cells: A Review of Emerging Evidence, 9(6):532. doi: 10.3390/antiox9060532.

[11] Pérez-Gálvez, A., Viera, I., & Roca, M. (2020). Green Natural Colorants, 9, 505. doi: 10.3390/molecules24010154.