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Review Article

Light Acclimation in Plants: Photoinhibition and Photoprotection

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ABSTRACT
Plants use light energy as one of the substrate for carrying out the process of photosynthesis, evolving O_2 so sustaining life on the planet. When light energy exceeds limits that plants can use for photosynthesis it results in the production of reactive oxygen species (ROS) which damage biomolecules including photosynthetic apparatus causing light induced photoinhibition. As plants are sessile, they have developed unique mechanisms to adjust with varied light intensities. Light is absorbed by chlorophyll molecules with the help of light harvesting chlorophyll binding proteins (LHCPs) present in pigments-protein complexes of photosysten II and photosysten I. In this review emphasis has given on how plants adjust to changing light conditions by inducing changes in dynamic components of photosystems and dissipation of excess light absorbed as heat known as non-photochemical quenching (NPQ).

Key words: *Non-photochemical quenching; photoinhibition; Photoprotection ; Photosynthesis.*

Abbreviations: LHC: Light harvesting complex; **LHCP:** Light harvesting complex protein; **NPQ:** Non-photochemical quenching; **PSI:** Photosystem I; **PSII:** Photosystem II; **ROS:** Reactive oxygen species.

INTRODUCTION

Photosynthesis is a vital process by which plants make their food with the help of green pigment named chlorophyll in the presence of CO_2 and H_2O releasing O_2 in the environment. Light energy in the chloroplast is utilized by pigment-protein complexes, Photosystem II (PSII) and Photosystem I (PSI). These pigment protein complexes are contained in the membranes of subcellular organelles called chloroplasts which reside inside leaf cells. The pigment-containing membranes inside the chloroplast are referred to as thylakoids and are arranged in stacks called grana connected to each other by stromal membranes [1]. This arrangement of stacked membranes has apparently evolved independently several times as an extremely efficient system for the interception and capture of light energy. The chlorophyll and carotenoids molecules in the thylakoid membranes are not free, but exist in the form of pigment-protein complexes also known as light-harvesting complexes. Initially light energy is absorbed by chlorophyll of light harvesting complex and then to the chlorophyll of the reaction centre of PSII. An excited electron in a PSII reaction center enters this chain of carriers and moves from one to the next until it reaches a PSI reaction center. This transport of electron from PSII to PSI involves formation of proton gradient across thylakoid membrane which is used for ATP formation. Electrons from PSI finally go to $NADP^+$ via several electron carriers including ferredoxin. Reducing equivalents NADPH and ATP produced in light reaction are utilized for the fixation of CO_2 from atmosphere so finally to convert it into sugars [2]. But when light energy is more than utilized for photosynthesis it results in the production of reactive oxygen species (ROS) which damage lipids, DNA and proteins and also results in the inactivation of photosystem known as photoinhibition or photooxidative stress. Proteins are the primary target of ROS, D1 protein of PSII is very susceptible to oxidative stress [3]. Abiotic stresses like salt, drought, temperature and metal stress causing oxidative stress also enhances photooxidative stress. Plants have evolved overtime to protect themselves from photodamage by many ways. The D_1 protein of PSII is continuously synthesized to replace the degraded D_1 protein in stress conditions which is also known as photorepair. Excess light energy can be dissipated in the form of heat which is called non-photochemical quenching [4; 5]. Photodamage in photosystem and light intensity can be sensed by some proteins like pigment bound protein STN7 which by phosphorylation induces the transfer of

LHC between photosystem II and PSI so helping plants in acclimation to low as well as high light according to the situation [6].

SOURCES OF PHOTOOXIDATIVE STRESS IN CHLOROPLAST

Under natural conditions, nearly all photosynthetic organisms have to encounter changing light intensities which may vary from time to time and place to place according to geographical conditions. Plants have developed a number of defense strategies and mechanisms to prevent photo-oxidative damage of the photosynthetic apparatus from reactive oxygen species (ROS) under excess light, allowing either a lowering of ROS formation or the detoxification of already formed ROS. Protein-bound chlorophyll molecules are potent photosensitizers, excess light energy may lengthen the time of chlorophyll singlet state of Chlorophyll ^{1}Chl* increasing the possibility that ^{1}Chl will undergo intersystem crossing to form chlorophyll triplet state ^{3}Chl* that reacts more readily with the ground state oxygen. Physical interaction between ^{3}Chl* and oxygen produces ^{1}O2* which can damage nucleic acid, proteins and lipids. Singlet oxygen produced is very reactive and react with other molecules quickly before travelling apart so ^{1}O2* produced in PSII damage reaction centre of PSII and cause photoinhibition. ^{1}O2* may also inhibit repair of D_1 process this accelerates the cycle of damage in PSII reaction centre. ^{1}O2* on reaction with polyunsaturated fatty acids form lipid peroxides. ^{1}O2* occurrence is more prevalent in PSII due to extended lifetime of ^{1}Chl* in PSII than in PSI. High reduction potential at the acceptor side of PSI is likely to convert oxygen to superoxide under limiting CO_2 concentration [7; 8].

PHOTOPROTECTION MECHANISMS IN PLANTS

Plants possess a variety of mechanisms to maintain the photosynthetic system operational in high-light environment. A precise balance between the use of absorbed light in photosynthesis and the safe dissipation of potentially harmful excess light energy can be critical for plants.

State transitions of Photosystems

Plants acclimate to changing light conditions by adjustment of their photosynthetic apparatus, which consists of the pigment-protein complexes, photosystem II (PSII), cytochrome b_6f complex, and photosystem I (PSI). These multisubunits complexes are located in thylakoid membranes and electrochemically connected in series by the mobile electron carriers including plastoquinone (PQ) and plastocyanin. The property of reaction center chlorophylls of PSII and PSI having absorption maxima at slightly different wavelengths, 680 and 700 nm, respectively gives rise to uneven excitation of the two photosystems at different light intensity. Plants have evolved photosynthetic acclamatory mechanisms that redistribute such unbalanced excitation energy in the short term by state transitions and in the long term by photosystem stoichiometry adjustment [9; 10]. Under light intensity that preferentially excites PSII (PSII light) the PQ pool becomes reduced and the thylakoid associated kinase STN7 is activated [6]. This enzyme is essential for phosphorylation of the light-harvesting complex of PSII (LHCII), the process that initiates subsequent migration of LHCII to PSI (state 1–state 2 transition). Under light intensity that preferentially excite PSI (PSI light), the PQ pool becomes oxidized and STN7 is inactivated. A phosphatase dephosphorylates the LHCII [11] resulting in its backward migration to PSII (state 2–state 1 transition). By this light harvesting capacity of the rate-limiting photosystem is increased and excitation energy is redistributed. In plants, state transitions exhibit kinetics of 15 to 30 min [12]. However, if excitation imbalances persist for hours to days, a long-term response (LTR) readjusts the number of the two photosystems in favor of the rate-limiting one. This readjustment of photosystem stoichiometry has the same but longer-lasting effect on excitation energy redistribution as state transitions [13] and also requires the activity of STN7 [14]. State transitions seem to be not essential for the LTR [15].

Non-photochemical quenching

When light is excessive and excited chlorophyll is unable to drive photochemistry, then the lifetime of the singlet state ^{1}Chl* is extended, resulting in the formation of triplet state of chlorophyll ^{3}Chl*. This is undesirable because energy transfer from triplet chlorophyll to oxygen generates singlet oxygen ^{1}O2*, a highly reactive type of ROS. There is more than one fate for de-excitation of singlet chlorophyll: in addition to driving photochemistry, a singlet state chlorophyll molecule energy can

return to the ground state by the emission of light in the form of chlorophyll fluorescence or by the harmless emission of heat as thermal dissipation. The latter route is a major component of photoprotection, termed nonphotochemical quenching [4; 5]. A number of processes contribute to the induction and relaxation of NPQ over time. One of the components of non-photochemical quenching qE, is turned on and off rapidly (seconds to minutes) and depends on the formation of the proton gradient (ΔpH) across the thylakoid membrane. The second component, recently named qZ [16], is induced and reversed on a slower timescale of approximately tens of minutes and is associated with the synthesis and disappearance of zeaxanthin. Another component, termed qI (phtoinhibitory quenching) has very slow kinetics in the range of hours and has similarities (e.g. lowered Fv/Fm) with more severe types of photoinhibition, and it may also be associated with accumulation of zeaxanthin. In higher plants qE is regulated by two types. First, it has long been known that the development of qE is associated with the xanthophyll cycle (XC) [17]. The XC is a reversible interconversion of zeaxanthin and violaxanthin that is directly linked to the energization of the thylakoid membrane during the induction of photosynthesis in the light. As light saturation is reached, the rise in ΔpH increases the proton concentration within the thylakoid lumen. This has a number of effects, including the activation of the enzyme violaxanthin deepoxidase, which converts violaxanthin to zeaxanthin and increases the depoxidation state of the XC pool. The reverse reaction, converting zeaxanthin to violaxanthin, is catalyzed by zeaxanthin epoxidase. Although there is no doubt that zeaxanthin plays a key role in qE [18], there is still discussion over whether zeaxanthin is a direct quencher of singlet excited chlorophyll or an allosteric effector that alters the sensitivity of qE to the ΔpH: evidence exists for both mechanisms.

The second component which is essential for the qE is the PSII protein PsbS. The role of this protein in qE was confirmed by screening mutant populations of Arabidopsis for altered chlorophyll fluorescence quenching [19]. Mutants lacking PsbS are specifically defective in qE, are more sensitive to photoinhibition [20], and show decreased fitness (measured as seed yield) under fluctuating light conditions in the field or in the laboratory [21]. Although PsbS is a member of the LHC protein family, it does not appear to bind pigments and instead functions as a sensor of lumen pH that is necessary for the rapid induction and relaxation of qE [22]. NPQ with similar characteristics to qE can be induced on a much slower timescale in the absence of PsbS [23]. In green alga (*Chlamydomonas reinhardtii*) a different LHC protein, called LHCSR was found to be necessary for qE [24]. This protein is not present in higher plants, but both the PsbS- and LHCSR-dependent qE systems are present in the moss Physcomitrella patens, where the two types of qE appear to operate independently and additively [25].

Repair of PSII

The PSII is very sensitive to light and other stresses as D1 protein, which is part of the D1/D2 heterodimer within the reaction center of PSII, is readily inactivated by light [26]. This inactivation of PSII is thought to be caused by unavoidable photooxidation and is followed by a repair cycle that includes partial disassembly of the PSII complex, degradation of damaged D_1 protein, and repair of D1 by de novo biosynthesis and reassembly. Although oxidative damage occurs in PSII even at low light intensities, irreversible damage occurs only at high light intensities when the repair of D_1 cannot keeps pace with the constant oxidative damage [27]. This type of damage results in an easily measured and sustained lowering of the quantum yield of PSII (i.e. photoinhibition) and therefore has similar properties to the qI type of NPQ. So the rate of D1 rapeir can limit the recovery from this type of photoinhibition and it depends on environmental conditions and on the species under study.

PSI cyclic electron flow and Water-Water cycle

Cyclic electron flow involves electron flow around PSI that results in ATP synthesis only and does not involve a terminal electron acceptor [28]. Electrons are passed from either NAD(P)H or ferredoxin to plastoquinone, increasing the ΔpH. Instead of capable of adjusting the ATP/NADPH production ratio in the chloroplast to meet the demands of the Calvin-Benson cycle it has a photoprotective role, increasing qE via ΔpH alterations. There may be an increase in cyclic electron flow during transition periods, such as a dark/low light to high light. There are two pathways for cyclic electron flow: the NAD(P)H dehydrogenase complex-dependent pathway and the PGR5-

dependent route [29]. Flowering plants operate both cycles, but the major pathway is thought to be the latter.

The photoreduction of one molecule of O_2 to two molecules of water at the reducing side of PSI via electrons generated from two molecules of water in PSII is known as water-water cycle. The reaction sequence involves superoxide dismutase, ascorbate peroxidase, monodehydroascorbate reductase, dihydroascorbate reductase, glutathione reductase, and ferredoxin-$NADP^+$ reductase [30]. The main function of water-water cycle is the scavenging of superoxide and hydrogen peroxide to prevent damaging reactions in the chloroplast. However, it also dissipates PSII excitation energy and electrons in PSI. Studies of the water-water cycle shows that it is particularly active during stresses such as drought and the transition from darkness to light, before CO_2 induction occurs, and when the electron transport chain has the potential to become highly reduced. In these conditions, the maintenance of PSI in a relatively oxidized state would favor cyclic electron transport and help ΔpH-induced qE activation. The increased ratio of ATP/NADPH production would help activation of the Calvin-Benson cycle [31]. It therefore has similarities in function with cyclic electron transport.

Because of the fundamental biological significance of photosynthesis and its importance in agricultural productivity, a considerable amount of research has been directed toward understanding the effects that environmental factors such as light, temperature, rainfall, salinity, and disease have on the process. So understanding the process of photoinhibition and photoprotection mechanisms will be of immense help in production of better crop varieties through plant breeding or genetic engineering.

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Conflict of Interest

Author declares no conflict of interest.

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