We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

6,300

Open access books available

172,000

International authors and editors

190M

Downloads

Our authors are among the

154

Countries delivered to

TOP 1%

most cited scientists

12.2%

Contributors from top 500 universities

WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.
For more information visit www.intechopen.com

Chapter

Photosynthetic Antenna Size Regulation as an Essential Mechanism of Higher Plants Acclimation to Biotic and Abiotic Factors: The Role of the Chloroplast Plastoquinone Pool and Hydrogen Peroxide

*Maria M. Borisova-Mubarakshina, Ilya A. Naydov,
Daria V. Vetoshkina, Marina A. Kozuleva, Daria V. Vilyanen,
Natalia N. Rudenko and Boris N. Ivanov*

Abstract

The present chapter describes the mechanisms of reactive oxygen species formation in photosynthetic reactions and the functional significance of reactive oxygen species as signal messengers in photosynthetic cells of plants. Attention is given to the acclimation mechanisms of higher plants to abiotic and biotic factors such as increased light, drought, soil salinity and colonization of plants by rhizosphere microorganisms. Special attention is paid to the reactions of reactive oxygen species with the components of the chloroplasts plastoquinone pool leading to production of hydrogen peroxide as a signal molecule, which is involved in acclimation of plants to these stress conditions. The chapter also presents the data demonstrating that regulation of the size of the light-harvesting antenna of photosystem II is one of the universal mechanisms of the structural and functional reorganization of the photosynthetic apparatus of higher plants exposed to the abiotic and biotic factors. These data were obtained for both model *Arabidopsis* (*Arabidopsis thaliana*) plants as well as for agricultural barley (*Hordeum vulgare*) plants. It is hypothesized that hydrogen peroxide, produced with involvement of the plastoquinone pool components, plays the role of a signaling molecule for regulation of the photosystem II antenna size in higher plants when environmental conditions change.

Keywords: photosynthesis, photosynthetic antenna, higher plants, acclimation, hydrogen peroxide

1. Introduction

Studies of such a global biological process as photosynthesis are always relevant. This is confirmed by a huge number of laboratories around the world studying different aspects of this process. Over the history of photosynthesis studies, various changes in photosynthetic parameters were constantly observed under the influence of external conditions, environmental factors, such as light intensity, temperature, the content of carbon dioxide in the air, drought, and soil salinity. For practical human needs, investigation of the mechanisms of these changes may give some clues that can help to maintain high productivity of food crops and other economically important photosynthesizing organisms.

Currently, one of the hot spots in this field is the problem of signal transmission from the photosynthetic apparatus to other systems of the photosynthetic cell, primarily to the systems responsible for the composition and structure of photosynthetic apparatus. It turns out that all signaling mechanisms are interconnected and in many cases represent a network of signals transferred from one signal messenger to another. An important milestone in the early 1990s was the discovery that nuclear systems react on the redox state of the chloroplast plastoquinone (PQ) pool and that the PQ pool plays an important role in protection of the photosynthetic apparatus of plant cells under various environmental conditions [1]. For instance, it was shown that PQ pool is involved in regulation of the size of photosynthetic light-harvesting antenna of photosystem II (PS II) in plants. Photochemically active PQ pool is situated within thylakoid membranes of chloroplasts. This fact raises a question: how exactly can it affect the expression of nuclear-encoded antenna genes in leaf cells when the environmental conditions change [2]?

Apart from that, for over 40 years, scientists have been studying the signaling functions of reactive oxygen species (ROS). One of the ROS, hydrogen peroxide (H_2O_2), was shown to play a major role in many signaling pathways in plants [3]. In the present chapter, we summarize the evidence that the PQ pool components are involved in H_2O_2 formation in chloroplast and that the hydrogen peroxide plays the essential role in regulation of photosynthetic antenna size of PS II under biotic and abiotic factors.

2. General structure of photosynthetic electron-transport chain

In the photosynthetic electron-transport chain (PETC) of thylakoid membranes, the absorption of energy of photons and the subsequent photochemical transformation of energy is performed by pigment-protein membrane complexes: photosystem II (PS II) and photosystem I (PS I). When plants are illuminated, the electrons originating from water decomposition are transported from PS II via the plastoquinone pool (PQ pool) to the cytochrome b_6/f complex and subsequently, via plastocyanin, to PS I for reduction of ferredoxin (Fd), which serves as an electron donor for NADP^+ reduction catalyzed by ferredoxin- NADP^+ reductase (FNR). Electron transport is accompanied by protons pumping into the thylakoid lumen, a slit-shaped intrathylakoid space, resulting in the creation of a transmembrane electrochemical proton gradient required for ATP synthesis.

Each photosystem consists of a reaction center (RC) and a light harvesting complex (LHC), or “antenna”. The energy of photons is captured by the antenna complexes of both photosystems, with LHC I capturing excitation energy for PS I, and LHC II capturing excitation energy for PS II, however LHC II can function as antenna for both photosystems (see further) [4]. The PS II core complex of higher plants is surrounded by complexes that include polypeptides encoded by the *lhcb*

(light-harvesting complex b) gene family and contain chlorophylls *a* and *b* as well as carotenoids in different proportions [5]. The inner antenna is comprised of three small monomeric proteins CP29, CP26, and CP24 (encoded by the *lhcb4*, *lhcb5*, and *lhcb6* genes, respectively). The outer peripheral LHC II antenna is mainly formed by three types of heterotrimers of proteins encoded by genes *lhcb1*, *lhcb2*, and *lhcb3*: strongly bound heterotrimers of two Lhcb1 and one Lhcb2 proteins (S-type), moderately bound heterotrimers of two Lhcb1 and one Lhcb3 proteins (M-type), and loosely bound heterotrimers of two Lhcb1 and one Lhcb2 proteins (L-type) [6–8]. CP29, CP26, and CP24 proteins bind directly to the core complex of PS II; the M-trimers bind to PS II via the CP29 and CP24 proteins, and the S-trimers bind via CP26 [7, 9]. The resulting PS II-LHC II complex can additionally associate with L trimers.

LHC I consists of four separate polypeptides (Lhca1–4, which are encoded by the *lhca* (light-harvesting complex a) gene family, combined into two heterodimers: Lhca1-Lhca4 and Lhca2-Lhca3. PS I has a docking site for LHC II consisted of PsaH, PsaL, and PsaI subunits [10, 11].

3. Superoxide anion radical and hydrogen peroxide formation in chloroplasts

Photosynthetic apparatus does not only evolve molecular oxygen (O_2) via water oxidation in PS II in the light, but also reacts with O_2 molecules that leads to O_2 consumption and formation of reactive oxygen species (ROS). In the ground state, O_2 molecule has two unpaired electrons localized on different anti-bonding orbitals (triplet state). Most organic molecules exist in a singlet state that limits their spontaneous reactions with O_2 , and this is a favorable factor for biological life. When O_2 is reduced by the PETC components or other cell components, such ROS as superoxide anion radical ($O_2^{\bullet-}$) and hydrogen peroxide (H_2O_2) are initially formed. $O_2^{\bullet-}$ has been found to be the primary product of O_2 reduction in PETC [12]. *In vivo*, O_2 reduction and CO_2 assimilation occur simultaneously, with oxygen accounting for 5 to 50% of the electrons from the PETC in various plants under various conditions [13]. Another ROS, singlet oxygen (1O_2), emerges because of spin inversion of one electron on the outer orbital of O_2 molecules. In the PETC, 1O_2 is formed in PS II, and $O_2^{\bullet-}$ is formed predominantly by the components of PS I. In chloroplasts, other ROS are also formed: perhydroxyl radical ($HO_2^{\bullet}$), hydroxyl radical ($HO^{\bullet}$), as well as hydroperoxides ($ROOH$) and radicals of organic molecules: peroxide radical ($ROO^{\bullet}$) and alkoxyl radical ($RO^{\bullet}$).

A stromal protein Fd, which is an electron carrier from the terminal cofactors of PS I to FNR, has long been considered a major O_2 reducing agent in chloroplasts. A number of studies have shown that addition of Fd to isolated thylakoid membranes devoid of stroma components significantly increased oxygen reduction [14, 15]. However, Kozi Asada, a pioneer researcher in the field of ROS formation in chloroplasts, observing a very low stimulation of $O_2^{\bullet-}$ production following the addition of Fd to the thylakoid suspension, concluded that Fd is not involved in O_2 reduction *in vivo* [16]. Indeed, the rate constant of Fd oxidation by O_2 is as low as $10^3 \text{ M}^{-1} \text{ s}^{-1}$ [17] meaning that a significant O_2 reduction with Fd can only be achieved with a significant increase in the amount of Fd itself [18]. In the presence of $NADP^+$, *i.e.*, under optimal conditions preventing the accumulation of the reduced Fd in large amounts, the Fd-dependent reduction of oxygen was limited to 5–7% of the total oxygen reduction rate [19]. The fraction of Fd-dependent oxygen reduction can increase when $NADP^+$ is deficient, for example when CO_2 is limited or Calvin-Benson cycle enzymes are inhibited. Low rates of O_2 reduction by Fd has a great

physiological meaning since *in vivo* reduced Fd is used as an electron donor not only for NADP⁺ reduction but for numerous reactions in the chloroplasts stroma.

Based on direct [20, 21] and indirect [21] evidence it has been shown that PS I is the main site of O₂ reduction to O₂^{•-}. It has long been accepted that O₂ is reduced by the terminal cofactors of PS I, [4Fe-4S] clusters F_A/F_B, located in the protein subunit PsaC exposed to stroma. However, the rapid electron flow from F_A/F_B to O₂ *in vivo* may prevent efficient reduction of Fd. The contribution of another [4Fe-4S] cluster of PS I, F_X, to O₂ reduction was suggested in the study showed that light-induced H₂O₂-dependent iodination of thylakoid proteins occurred primarily in PS I subunits harboring F_X cluster [20]. However, no direct experimental confirmation of F_X involvement has been presented. It has recently been shown that removal of the F_A/F_B cofactors by chemical treatments, making F_X the terminal cofactor in the treated PS I complexes, results in a decreased rate of oxygen reduction [22], which argues against the assumption of a key role of F_X in oxygen reduction.

The involvement of another PS I cofactor, phylloquinone (PhQ) in the quinone-binding sites (A₁-sites), in O₂ reduction was suggested based on the stimulation of flash-induced O₂ uptake when PhQ was added to thylakoid membranes devoid of quinones [23]. O₂ reduction in PS I under steady-state illumination was investigated in isolated PS I complexes from the cyanobacterium *Synechocystis* sp. PCC 6803 of wild-type and a mutant strain with blocked PhQ biosynthesis (the mutant *menB*), in which PQ is incorporated into the A₁-sites [24]. It was shown that O₂ reduction rate in high light was lower in the PQ-containing PS I than in PhQ-containing, while the steady-state electron transport from quinone to F_A/F_B and then to O₂ was barely changed under studied conditions. This effect was attributed to the greater ability of phyllosemiquinone, PhQ^{•-}, to reduce O₂ due to the lower redox potentials of PhQs at the A₁-sites compared to PQ. Moreover, unlike PhQ^{•-}, plastosemiquinone, PQ^{•-}, molecules at the A₁-sites are easily protonated [25] that also reduces the probability of their reaction with oxygen, while increases the probability of PQ^{•-} double reduction to PQH₂. In work with isolated PS I complexes from green alga *Chlamydomonas reinhardtii*, the involvement of PhQ in oxygen reduction has been also shown [22]. It was found that PhQ is the main site of oxygen reduction under increasing illumination, even under conditions of concurrent NADP⁺ reduction, i.e., when Fd, FNR, and NADP⁺ are present. Moreover, the principal role of PhQ^{•-} of one of the asymmetric branches of PS I (A-branch) was suggested based on the results with PS I complexes, in which the lifetime of PhQ^{•-} in the A-branch is ~2 orders of magnitude longer.

When considering the possible components involved in the reduction of O₂ in the membrane, the shift in the redox potential of the O₂/O₂^{•-} pair from -160 mV at 1 M O₂ in water to approximately -550 mV in a hydrophobic environment must be considered. The E_m values of PhQ/PhQ^{•-} pairs in the A- and B-branches of cyanobacterial PS I are -671 and -844 mV, respectively [26] that makes their reaction with oxygen thermodynamically favorable even in such a hydrophobic environment as that of PhQ in its binding sites in PS I. One consequence of this reaction can be the appearance of O₂^{•-} within the thylakoid membrane. Indeed, this appearance has been shown in a number of studies [18, 27, 28]. Addition of Fd and NADP⁺ did not suppress formation of O₂^{•-} within thylakoid membranes [18] emphasizing the physiological significance of the observed process.

O₂^{•-}, formed in the chloroplast stroma, are disproportionated there with the formation of H₂O₂ (reaction 1).

In chloroplasts, disproportionation reaction is catalyzed by superoxide dismutase (SOD) with the rate constant $\sim 10^7 \text{ M}^{-1} \text{ s}^{-1}$. The SOD content in the stroma is high, and it is concentrated mostly at the stromal surface of the thylakoids [29]. In the stroma, ascorbate and glutathione also can reduce $\text{O}_2^{\bullet-}$ to H_2O_2 .

However, using isolated thylakoids it was shown that H_2O_2 is produced not only outside the thylakoid membrane (implying the stroma phase *in vivo*) but also within the membrane; this H_2O_2 was called the “membrane” H_2O_2 [30]. Using various approaches [30–32], it was shown that the rate of the “membrane” H_2O_2 production correlated with increasing illumination and reached 60% of the total H_2O_2 produced in the light. We suggest that the “membrane” H_2O_2 is formed not due to the disproportionation reaction (since this reaction is hampered in aprotic membrane phase) but due to the reaction between reduced plastoquinone PQH_2 and the $\text{PhQ}^{\bullet-}$ -generated $\text{O}_2^{\bullet-}$ (reaction 2):

This reaction is thermodynamically favorable in aqueous solutions because of the high difference between the Em_7 values of the redox pairs $\text{PQ}^{\bullet-}/\text{PQH}_2$ (370 mV) and $\text{O}_2^{\bullet-}/\text{H}_2\text{O}_2$ (940 mV). This reaction can occur predominantly at the membrane/stroma interfaces since PQH_2 molecules and water molecules tends to form hydrogen bonds. The first indirect evidence in favor for the reaction of PQH_2 with $\text{O}_2^{\bullet-}$ was obtained by studying the oxidation of the PQ pool after swithing off the light cessation [33]. The PQ pool in thylakoids, which was reduced during illumination and consisted of PQH_2 molecules, was not oxidized in the dark in the absence of oxygen [33, 34]. Under aerobic conditions, the PQ pool oxidation exhibited two-phase kinetics [33, 35], with the fast component being attributed to oxidation of PQH_2 molecules by $\text{O}_2^{\bullet-}$ that accumulated in the membrane in the light. Further, the occurrence of reaction 2 was confirmed by evaluating the redox state of the PQ pool when $\text{O}_2^{\bullet-}$ was artificially supplied to the thylakoid membrane from a xanthine-xanthine oxidase system [36]. The higher apparent electron capacity of the PQ pool in the presence of external $\text{O}_2^{\bullet-}$ showed the additional electron leakage from the PQ pool during $\text{O}_2^{\bullet-}$ generation and confirmed the occurrence of reaction 2.

4. Mechanisms of acclimation of higher plants to light conditions and the regulatory role of the redox state of the plastoquinone pool

Effective adaptation to changing environmental conditions is a prerequisite for plant survival and competitiveness. Plant acclimation to different light conditions has been a subject of interest of many scientists for a long time [37, 38]. Plants are divided into shade-tolerant and light-demanding plants, although there is also an intermediate category. Studies show that shade-tolerant plants are generally less adaptable to changing light conditions than light-demanding plants [39].

Under varying light conditions, plants require different amounts of photosynthetic products such as ATP and NADPH for normal metabolism. The synthesis of ATP and NADPH is regulated by changes in the functioning of the photosynthetic electron-transport chain. Light intensity is the most rapidly and frequently changing abiotic factor, but it is also one of the most important, given that it is the energy of photons that is required to activate photosynthesis. “Proper” adaptation of plants to light conditions is essential to ensure efficient use of light under low light conditions and to prevent photo-oxidative damage under high light conditions.

The following typical characteristics of plants adapted to high light intensity compared to plants growing at low light intensity are recognized:

1. leaves are thicker with higher amount of cell layers, larger cells [40–42];
2. higher ratio of Chl *a* to Chl *b* [42, 43];
3. increase in the number of chloroplasts in the cell [38];
4. decrease in granular structure [43, 44];
5. high content of β -carotene and xanthophyll cycle pigments [38];
6. higher PS II/PS I ratio [45];
7. higher electron transfer rates, higher CO₂ assimilation rates, and higher starch content; transition of the photosynthetic electron transfer chain to a reduced state [40, 42, 46];
8. higher energy dissipation capacity [47–49];
9. changes in the activity of carbonic anhydrases, enzymes that catalyze the reversible reaction of carbonic acid formation from carbon dioxide and water [50];
10. changes in the ratio of alternative electron transport pathways, accumulation of ROS and induction of corresponding signaling pathways influencing the gene expression [46].

It was found that during changes in plant illumination, the optimization of photosynthetic activity at the level of light energy absorption occurs due to activation of mechanisms leading to changes in the size of photosynthetic antenna complexes. When the spectral composition of light changes, the photosynthetic antenna complexes of thylakoids can be reorganized by reversible migration of the outer part of LHC II between PS II and PS I that leads to changes in the antenna sizes of both photosystems. This process is called state transitions and represents the reorganization of light-harvesting pigment-protein complexes of thylakoid membranes by the action of light through phosphorylation/dephosphorylation of LHC II proteins [51, 52]. Only weakly bound LHC II trimers, which consist of products of the *lhcb1* and *lhcb2* genes, have been shown to migrate between photosystems, whereas strongly and moderately bound trimers remain bound to PS II [53]. Phosphorylation of LHC II proteins by the enzyme STN7 kinase [54] leads to LHC II migration from PS II to PS I under red light illumination that excites predominantly the reaction centers of PS II. Dephosphorylation by the phosphatase enzyme TAP38/PPH1 [55] enables LHC II to return from PS I to PS II when illuminated with far-red light that excites predominantly PS I reaction centers, or in the dark. The STN7 kinase is a transmembrane protein [56, 57]. The involvement of the PQ pool in state transitions is not disputed; however, this does not appear to be directly related to the redox state of the pool, but rather to the appearance of PQH₂ molecules in the light. Interaction of STN7 kinase with the stromal loop subunit of the complex results in the kinase activation, while binding of PQH₂ molecules to the oxidation site of the cyt b₆/f complex leads to dissociation of the kinase from the cyt b₆/f complex [58, 59].

It is generally accepted that state transitions occur at low light intensities ($100\text{--}200\ \mu\text{mol photons m}^{-2}\text{ s}^{-1}$) [60, 61]. There is evidence that state transitions do not occur at high light intensity [62, 63] because of the inhibition of STN7 kinase by reduced thioredoxin [64]. We found that state transitions proceed in barley at higher light intensities than in *Arabidopsis* [65].

Not only LHC II proteins but also PS II core proteins can exhibit reversible phosphorylation [66, 67]. Phosphorylation of core proteins occurs by STN8 kinase activity, whereas dephosphorylation occurs by PBCP phosphatase. In high light, as previously described, STN7 kinase activity is inhibited, whereas STN8 kinase becomes active, resulting in phosphorylation of PS II core proteins only [60, 68]. Apparently, the described reversible phosphorylation of PS II and LHC II proteins plays a major role in the distribution of energy between the photosystems when the light intensity changes [60]. Phosphorylation of the PS II core proteins in high light facilitates the “unpacking” of PS II-LHC II complexes that is necessary to repair damaged PS II centers [69, 70]. Reversible phosphorylation of PS II RC proteins affects the ultrastructure of the thylakoid membrane and regulates the PS II repair cycle [71–73].

A change in the expression of chloroplast genes such as *psbA*, *psaA*, and *psaB*, which encode PS II and PS I reaction center proteins, is also a mechanism of plant acclimation to light conditions [74]. This process has been shown to be slower than state transitions, but faster than the long-term response (see further) [75]. This response is necessary for rapid changes in the biosynthesis of photosynthetic electron transport chain proteins that are encoded by chloroplast genome, in particular, as described above, the RC subunits that allows the regulation of the stoichiometry of the photosystems to be adjusted [74]. This stoichiometry can be different depending on environmental conditions, ensuring optimal equilibrium in the photosynthetic electron transport chain. The chloroplast sensor kinase, CSK, has been shown to play an important role in adjusting the PS II to PS I stoichiometry and the PQ pool was considered to be the main site of the photosynthetic redox control of chloroplast gene expression [76]. However, the signal that affects the chloroplast sensor kinase is still unknown.

Another mechanism of plant acclimation to light is the regulation of the PS II antenna size. Higher plants can increase the size of LHC II in shade and, conversely, decrease the size of LHC II in high light [38], thus optimizing photosynthetic activity and protecting the photosynthetic electron transport chain from photoinhibition. Since PS II is unstable in high light, the change in the PS II antenna size is one of the important mechanisms of plants to adapt to high light intensities. When irradiance is increased for a prolonged period (days), the PS II antenna size is reduced by suppressing the biosynthesis of the peripheral LHC II proteins, disassembling of the PS II pigment-protein complexes, which include these proteins, and subsequently by proteolysis the proteins. Such changes are necessary to reduce the amount of absorbed light energy and, as a consequence, to adapt to long-term high light. The “adaptive” antenna size reduction is seen as the decrease in the levels of Lhcb1, Lhcb2, Lhcb3, and Lhcb6 proteins [37, 77]. The minimal antenna unit in high-light-adapted higher plants contains Lhcb4, Lhcb5, and S-type LHC II trimers in addition to the PS II core complex [77, 78]. It has been shown that proteolysis of Lhcb proteins is triggered after the first 24 hours in high light [79, 80].

PS II antenna size has been found to be regulated by the redox state of the PQ pool [81–83]. A detailed analysis of the mechanism of this regulation was performed using *viridis zb63*, a barley mutant devoid of PS I, but with an actively functioning PS II [84]. It was found that even at low light intensities, the PQ pool was reduced as much as possible, and the PS II antenna size was reduced in the mutant but not in wild type.

It can be concluded that the chloroplast PQ pool is involved not only in the regulation of state transitions, but also in the regulation of gene expression of both chloroplast- and nuclear-encoded genes [85].

5. Establishing the signaling role of H_2O_2 in the regulation of the size of the photosystem II light harvesting antenna in higher plants

As presented above, the redox state of the PQ pool plays an important role in triggering signaling pathways, which are necessary for regulating plastid and nuclear gene expression [86]. It is generally accepted that a high level of PQ pool reduction is the chloroplast signal to reduce the antenna size of PS II under high light conditions. Since the 1960s and 1970s, scientists have been involved in understanding the molecular signal about the redox state of the plastoquinone pool. However, the question about the nature of the signal indicating the redox state of the PQ pool remained open for a long time.

In Section 2.2 the data showing the involvement of the PQ pool in production of the membrane H_2O_2 in thylakoids were presented, therefore it was proposed that this H_2O_2 can be a candidate by which the redox state of the PQ pool imposes its regulatory effect in acclimation of higher plants to light conditions. In [86], using barley plants (*Hordeum vulgare*), several approaches were developed to change the H_2O_2 content in leaves at both low and high light intensities without affecting the redox state of the PQ pool allowing the correlation between the level of hydrogen peroxide, the PQ pool redox state, and the PS II antenna size to be assessed. The effect of hydrogen peroxide on composition of the thylakoid pigment-protein complexes, in particular on the PS II antenna composition, was revealed. The downsizing of the PS II antenna was suppressed in high light in leaves possessing high reduction level of the PQ pool, but low hydrogen peroxide content; at the same time, a decrease in the antenna size was observed in low light in the presence of elevated amount of hydrogen peroxide in leaves in spite of low reduction level of the PQ pool. The data obtained in that work indicate that it is the H_2O_2 content that determines the size of the PS II antenna, *i.e.*, the amount of pigment-protein complexes of the PS II antenna in leaves. This work was the first direct evidence, confirming the involvement of H_2O_2 in the signaling pathway leading to adjustment of the PS II antenna size in higher plants.

6. Acclimation mechanisms of plants to drought and soil salinity conditions and the discovery of the PS II antenna size regulation under these conditions

Abiotic and biotic stress factors affect many physiological processes, especially photosynthetic activity. Drought conditions are one of the major factors limiting plant growth and productivity, leading to significant changes in plant cell metabolism [87, 88]. Under drought conditions, photosynthesis is slowed down due to both a reduction in leaf area and a decrease in rate of photosynthesis per unit of leaf surface. The decrease in metabolism results from closure of stomata, reduced CO_2 availability and carbon metabolism that was shown for model *Arabidopsis thaliana* plants as well for agricultural plants such as *Vitis vinifera*, *Oryza sativa* and others [89].

In arid regions plants have developed xeromorphic traits to reduce transpiration. To do this, plants may shed leaves, reduce the number and the size of new leaves [90]. Another adaptive response is sclerophyllia (stiff-leafliness): stiff leaves are less affected by drought and easily regain functionality under normal conditions [91].

To reduce the negative effects of drought on photosynthesis, the photosynthetic apparatus increases thermal dissipation of absorbed energy and changes the activity of the xanthophyll cycle and ROS production/detoxification. Biochemical efficiency of photosynthesis under drought conditions depends on ribulose-1,5-bisphosphate regeneration and ribulose bisphosphate carboxylase/oxygenase activity [88, 92]. C4-photosynthesis is considered as a major adaptation, necessary to limit water loss, to reduce photorespiration, and to increase photosynthetic efficiency under drought conditions [93]. However, many crop plants, including rice, buckwheat, soybeans, and potatoes, use C3-photosynthesis. Drought is known to affect electron transport along the PETC [94, 95], to lead to decreased activity of the PS II oxygen-evolving complex, as well as PS II and PS I RCs [96–98], and to lead to lipid peroxidation of thylakoid membranes and hence to membrane damage [99–101].

C3-plant adaptation to drought involves multiple interactions of hormones, ROS, sugars, and many metabolic pathways. Computational models integrating data on gene expression, physiological and metabolic processes, as well as modern transgenic crossbreeding techniques, allow to improve photosynthesis as well as crop yield. Key phytohormones such as abscisic acid (ABA), cytokinins, gibberellic acid (GA), auxin, and ethylene control drought adaptation processes [102]. If plants are exposed to drought, ABA is synthesized in the roots and transported to the leaves to increase plant tolerance to this stress through stomatal closure and slower growth [103].

In many plants, drought primarily affects the root system [104]. The growth of tap roots is usually unaffected by drought, but lateral roots grow much slower due to suppression of lateral root meristem activity [105]. Small lateral roots provide an absorptive surface for water that also represents an adaptive strategy. Special tissues, such as rhizoderma, with thickened walls or corked exoderm, or reduced cortical layers are also considered to play role in acclimation to drought [90]. Hydrotropism also helps plants to adapt to drought stress [106, 107]. The interaction of auxin, cytokinins, GA, and ABA could be a potential way for changes in root architecture [108].

Under drought conditions, osmotic regulation is responsible for stomatal conductance, photosynthesis, leaf water capacity, turgor, and plant growth [109, 110]; at the same time both salt content and mechanical resistance change [111]. Sugars (sucrose, glucose, fructose, trehalose) are osmolytics affecting osmotic regulation [112, 113]. Substances such as proline, glycine, and betaine help protecting the plants from the damaging effects of drought [114].

Soil salinity is another major issue that negatively affects crop productivity of agricultural plants. The physiological response of plants to soil salinity includes many aspects that have not yet been fully characterized [115]. Under salinity conditions, plant growth and development are impaired due to water deficit, cytotoxicity is increased due to excessive ion uptake that consequences in an imbalance in plant metabolism. In addition, salinity is accompanied by oxidative stress due to increased ROS formation in plant cells [116, 117]. It was shown that in *Romaine lettuce*, a low salt-tolerant plant, long-term salt treatment led to enhancement of total carotenoid content [118].

Plant responses to salinity have been divided into two main stages [119, 120]. The first stage is ion-independent and occurs within minutes and first days, causing closure of the stomata and inhibition of cell expansion, primarily in the shoots, and results in limitation of plant growth [121–123]. The second stage occurs over several days or even weeks and is associated with an increase in the levels of cytotoxic ions, which slows down metabolic processes, causes premature senescence and eventually cell death [120, 124]. Salt stress causes outflow of water through aquaporins, which increases intracellular ion concentration, inactivating the photosynthetic apparatus [125]. Tolerance to both types of salt stress is regulated by multiple physiological and molecular mechanisms such as osmotic tolerance, ion tolerance, tissue tolerance, etc. [120, 123].

Salinity has been shown to change the ultrastructure of chloroplasts in higher plants: thylakoids swell [126], chloroplast structure changes [127], the number and size of plastoglobules increase [128]. The interaction of organelles, especially chloroplasts, mitochondria, and peroxisomes, is important for plant adaptation to stress conditions, particularly salinity [129]. Mitochondria, peroxisomes, and other organelles localize near chloroplasts for more efficient metabolite exchange [127].

For a large number of species [130, 131], it was shown that effects of drought and salinity lead to a more efficient conversion of starch into sucrose, which functions as an osmoprotector to reduce negative effects of environmental factors.

In Section 5 the data demonstrating that the amount of hydrogen peroxide determines the size of the PS II light-harvesting antenna were presented [86, 132]. Since the increase in hydrogen peroxide production also occurs in response to other stress conditions, *e.g.*, to drought and salinity, we hypothesized that the reduction of PS II antenna size may be one of the universal mechanisms of changing the structural and functional organization of photosynthetic apparatus during plant adaptation to various stress conditions. Acclimatory responses of *Arabidopsis thaliana* and barley (*Hordeum vulgare*) plants to drought and salinity conditions and the variations in the PS II antenna size were studied in detail recently [133, 134]. The main objective of these studies was to investigate the course of acclimatory changes before the manifestation of the negative effects of the selected stressors. The changes indicating an increase in the reduction level of the PQ pool were detected several days after introduction of these stress factors. After 7–14 days (depending on plant species), a decrease in the size of PS II light harvesting antenna was observed in plants under conditions of drought and salinity that was confirmed by a decrease in content of PS II antenna proteins and by downregulation of gene expression of these proteins under the stress conditions. Drought and salinity resulted in almost two-fold increase in the content of hydrogen peroxide in leaves compared to control leaves. Therefore, these data demonstrated that the reduction of the size of PS II antenna represents one of the universal mechanisms acclimation of higher plants to mild stress conditions. The PQ pool reduction state along with the hydrogen peroxide content were proposed to be the important factors needed for the observed structural rearrangement [133, 134].

7. Changes in the functioning of higher plants and in the PS II antenna size in response to colonization by rhizosphere microorganisms

Environmental fluctuations and low soil fertility determine low yields and, consequently, low profitability of the agricultural sector of the economy. It is possible to avoid dependence of agricultural production on external conditions by increasing the resistance of plants to adverse environmental factors. The problem of low photosynthetic efficiency of agricultural crops (*e.g.*, of corn) when growing in the field is associated with the fact that most of the plant biomass is in shade [135]. Therefore, approaches to improve the acclimation of agricultural plants to suboptimal light conditions are being actively developed to improve their yield [136–138]. To increase crop yields a complex of approaches is required, including methods of biological protection of plants under stress conditions, under both biotic and abiotic environmental factors. At the moment, biotechnological development of methods to increase plant resistance is being actively pursued. One of such approaches is the use of rhizosphere microorganisms that are non-pathogenic for plants and should be non-pathogenic for animals and humans.

The plant rhizosphere is a narrow region of soil that is closest to the root system of plant, where the roots secrete large amounts of metabolites from the root hairs.

These metabolites act as chemical signals for motile bacteria, some of which can stimulate plant growth, increase plant productivity, and resistance to phytopathogens and abiotic factors. The plant microbiome has been proposed as a new area of interest for the next green revolution [139], and it has been shown that plants can adapt to changing environmental conditions not only by changing their own metabolism, but also by regulating the composition of the rhizosphere microbiota. This phenomenon was called “Cry for Help” [140–142].

Plant growth-promoting rhizobacteria (PGPR) [143] can activate a mechanism of plant resistance called “Induced Systemic Resistance” (ISR). Induced resistance is activated by various biotic and abiotic factors [144]. ISR activation by rhizosphere bacteria is similar to pathogen induced Systemic Acquired Resistance (SAR) in the sense that both of them lead to the development of resistance even in non-stressed plant parts. Strains with plant growth promoting activity have been identified from various genera, of which *Pseudomonas* and *Bacillus* have been studied most extensively and are capable of triggering ISR [145, 146].

The application of PGPR has been studied using a variety of agricultural plants such as canola, radicchio, soy, potato, maize, oat, peas, tomato, lentil, barley, wheat, and cucumber [147]. However the details of the direct and indirect mechanisms by which PGPRs promote plant growth and development are still widely discussed, but they are known to differ between bacteria [148]. Some PGPRs are able to produce plant hormones such as auxins, cytokinins, gibberellins, ABA, and ethylene [149, 150] and thus directly affect plant physiology. For example, cytokinins, which are produced by PGPR, stimulated cell division and led to an increase in the surface area of roots of agricultural plants through the enhanced formation of lateral and adventitious roots. There is evidence of the effect of PGPR-produced cytokinins on growth, development and productivity of wheat [151], soybeans [152], rape and lettuce [153]. Other strains increase mineral and nitrogen availability in the soil, thus improving plant growth. PGPRs have also been shown to inhibit the development of pathogenic soil microorganisms, thereby also promoting plant growth [154]. It has been shown that PGPR strains, individually or in a consortium, increase yields and growth of Chinese cabbage, even under conditions of infection with black rot caused by *Xanthomonas campestris* pv. *Campestris* [155] due to activation of ISR (see above). Other PGPR strains are capable of producing antibiotics, which leads to protection against phytopathogens [156]. The literature data show positive effects of plant PGPR colonization on various photosynthetic parameters, particularly chlorophyll content, transpiration rate, internal CO₂ concentration, and stomatal conductance [157].

The positive effect of PGPR colonization on plant tolerance to drought [158], soil salinity [159], high temperatures, changes in atmospheric carbon dioxide content, etc. is well presented in the literature [for a review see 148]. However, an equally important factor affecting plant growth and development is light conditions. The influence of colonization of barley plants by soil nonpathogenic *Pseudomonas* bacteria on the structure of the photosynthetic apparatus of leaves and the effect of light intensity of the parameters studied was made in [61]. Rhizosphere bacteria *Pseudomonas putida* (*P. putida*) BS3701 which are a part of a consortium that effectively degrades petroleum products, were used for the colonization of barley plants in that work. It was shown that colonized plants at low light intensity were characterized by higher activity of antioxidant systems, reduced hydrogen peroxide content and larger PS II antenna size compared to control plants, allowing colonized plants to capture more light, resulting in higher values of photosynthetic efficiency parameters. Thus, it was shown that the change in the size of the light harvesting antenna of PS II, and hence the regulation of light energy absorption, occurs not only under the action of abiotic environmental factors (Sections 5 and 6), but also during colonization of plants by PGPR, i.e. under the action of biotic factors.

In the same study [61], the effect of plant PGPR colonization on the course of barley plant adaptation to increased light was investigated as well. To reveal differences in the course of adaptation responses in control plants and plants colonized with *P. putida* BS3701, the plants were grown at moderate light intensity ($100 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$), and then transferred to conditions of high light intensity ($1000 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$) without night period. It was found that the adaptive reduction in PS II antenna size occurred in both control and colonized plants and had the same molecular mechanisms. However, the barley plants colonized by *P. putida* BS3701 adapted more rapidly and were more resistant to increased illumination. Taking into account the fact that before the plants were transferred to the conditions of increased illumination, the colonized plants had a significantly larger PS II antenna size compared to control plants. The decrease in PS II antenna size was more pronounced in the colonized plants, which, apparently, was the reason for more effective and faster adaptation of the photosynthetic apparatus of *P. putida* BS3701 colonized plants to new light conditions. Thus, PGPR colonization of plants leads to the optimization of the photosynthetic apparatus structure and an increase in the efficiency of adaptation mechanisms of higher plants.

8. Conclusion and assumptions

The most significant function of chloroplasts is oxygenic photosynthesis. However, chloroplasts perform many other functions essential for proper plant growth and development, including synthesis of amino acids, nucleotides, fatty acids, phytohormones, some vitamins and secondary metabolites, as well as nitrogen and sulfur assimilation. Acclimation processes occurring in chloroplasts under both abiotic and biotic stresses are important for plant–environment interaction, which promotes plant adaptation to stress factors, including drought, salinity, increased light, colonization by microorganisms, and many others.

The chapter presents data showing that the change in the size of the PS II antenna pigment-protein complex occurs in plants not only under changes in light intensity, but also under other abiotic factors (drought, soil salinity), as well as under the action of a biotic factor – colonization by the rhizosphere bacteria *P. putida* BS3701. Thus, we hypothesized that the regulation of PS II antenna size is one of the universal mechanisms of regulation of the structural and functional organization of photosynthetic apparatus necessary for the adaptation of higher plants to stress conditions. It is suggested that the reaction of $\text{O}_2^{\bullet-}$ with PQH_2 , leading to the formation of “membrane” H_2O_2 in thylakoids, plays a determining role in this process [132].

The Lhcb proteins of the PS II light-harvesting antenna complex are encoded in the nuclear genome [160], therefore, the regulation of the expression of these genes under stress conditions appears to occur through the retrograde chloroplast-nucleus signal transduction pathway. The question arises, how exactly the expression of genes of PS II antenna proteins is regulated with the involvement of hydrogen peroxide? It is assumed that transcription factors are one of the main participants in retrograde signaling [161]. For example, the transcription factor ABSCISIC ACID INSENSITIVE 4 (ABI4) is a key factor in multiple retrograde signaling pathways generated by GUN1 (genome uncoupled; tetrapyrrole-dependent signal transduction from plastid to nucleus) [162]. GUN1 is known to transmit a signal that induces ABI4 binding to the promoter sequences of *lhcb* genes in the nucleus that blocks *lhcb* gene expression [161], leading then to a reduction in PS II antenna size. Another transcription factor, PTM, a chloroplast envelope-associated homeodomain (PHD) factor, also functions in multiple retrograde signaling pathways. PTM connects the GUN1 pathway in plastids to the ABI4 pathway in the nucleus [162, 163]; for this

Figure 1. Hypothetical mechanism of the involvement of “thylakoid membrane” H_2O_2 in the PS II (LHC II) antenna size regulation in the cells of higher plants. PS II, photosystem II; PS I, photosystem I; PQ, oxidized plastoquinone; $PQ^{\bullet-}$, plastosemiquinone; PQH_2 , plastoquinone; PC, plastocyanine; Fd, ferredoxin; FNR, ferredoxin-NADP⁺ reductase; SOD, superoxide dismutase; APX, ascorbate peroxidase; PTM, chloroplast envelope-associated homeodomain transcription factor; ABI4, nuclear transcription factor. According to our hypothesis, H_2O_2 , which is formed in chloroplasts in the light as a result of the reaction of $O_2^{\bullet-}$ With PQH_2 , diffuses through the chloroplast membrane, changes the activity of the serine protease, which, in turn, converts PTM into its soluble form and, thus, affects the expression of lhcb genes that encode LHC II proteins.

purpose, a soluble shortened form of PTM is released from the chloroplast envelope into the cytoplasm, moves into the nucleus, and activates ABI4 expression. The soluble form of PTM is formed as a result of proteolysis of this transcription factor by a serine protease, leading to its detachment from the transmembrane domains [164]. What exactly affects the activity of the serine protease is still unclear. SBcas3.3 serine protease activity in *Escherichia coli*, which belongs to the S8A subfamily of serine proteases, has been shown to increase when H_2O_2 is added at concentrations up to 10 g L^{-1} , but decreases when H_2O_2 is added at a higher concentration of 50 g L^{-1} [165]. It can be assumed that H_2O_2 formed in chloroplasts, when diffuses across the chloroplast membrane, changes the protease activity, affecting the transformation of PTM into the soluble form. At low concentrations, H_2O_2 , enhances serine protease activity, leading to suppression of lhcb gene expression and to decreasing the PS II

antenna size. Conversely, at high concentrations of H_2O_2 , inactivation of the serine protease may occur and, as a consequence, no acclimatory change in the size of the PS II antenna complex should be observed. A hypothetical mechanism for the involvement of the “membrane” H_2O_2 in the PS II antenna size changes is presented in the **Figure 1**.

The possibility of regulating the antenna size in plants by changing the amount of H_2O_2 can be used for practical purposes in the future, for example, in order to grow plants in higher latitudes. Increasing the size of the light harvesting antenna of PS II can be achieved by hyperexpression of genes of antioxidant system proteins, which will result in a decrease in the amount of H_2O_2 . This will lead to a more efficient use of light energy for photochemical processes and, in the long term, to a productive increase in biomass. The effect of plant colonization by rhizobacteria on changes in the size of PS II antenna reveals the potential of application of such microorganisms in agriculture without the need for plant genetic modifications.

Funding information

The preparation of the manuscript was supported by the Russian Science Foundation (project no. 17-14-01371).

Author details

Maria M. Borisova-Mubarakshina*, Ilya A. Naydov, Daria V. Vetoshkina, Marina A. Kozuleva, Daria V. Vilyanen, Natalia N. Rudenko and Boris N. Ivanov
Institute of Basic Biological Problems of the Russian Academy of Sciences, Federal Research Center, Pushchino Scientific Center for Biological Research of the Russian Academy of Sciences, Pushchino, Russia

*Address all correspondence to: mubarakshinamm@gmail.com

IntechOpen

© 2021 The Author(s). Licensee IntechOpen. This chapter is distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/3.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

References

- [1] Allen JF. Control of gene expression by redox potential and the requirement for chloroplast and mitochondrial genomes. *J Theor Biol.* 1993 Dec 21;165(4):609-631. doi: 10.1006/jtbi.1993.1210
- [2] Karpinski S, Reynolds H, Karpinska B, Wingsle G, Creissen G, Mullineaux P. Systemic signaling and acclimation in response to excess excitation energy in *Arabidopsis*. *Science.* 1999 Apr 23; 284(5414):654-657. doi: 10.1126/science.284.5414.654
- [3] Foyer CH, Noctor G. Redox regulation in photosynthetic organisms: signaling, acclimation, and practical implications. *Antioxid Redox Signal.* 2009 Apr;11(4):861-905. doi: 10.1089/ars.2008.2177
- [4] Wientjes E, van Amerongen H, Croce R. LHCII is an antenna of both photosystems after long-term acclimation. *Biochim Biophys Acta.* 2013 Mar;1827(3):420-426. doi: 10.1016/j.bbabi.2012.12.009
- [5] Jansson S. The light-harvesting chlorophyll a/b-binding proteins. *Biochim Biophys Acta.* 1994 Feb 8;1184(1):1-19. doi: 10.1016/0005-2728(94)90148-1
- [6] Damkjaer JT, Kereiche S, Johnson MP, Kovacs L, Kiss AZ, Boekema EJ, et al. The photosystem II light-harvesting protein Lhcb3 affects the macrostructure of photosystem II and the rate of state transitions in *Arabidopsis*. *Plant Cell.* 2009 Oct;21(10):3245-3256. doi: 10.1105/tpc.108.064006
- [7] Boekema EJ, van Roon H, Calkoen F, Bassi R, Dekker JP. Multiple types of association of photosystem II and its light-harvesting antenna in partially solubilized photosystem II membranes. *Biochemistry.* 1999 Feb 23;38(8):2233-2239. doi: 10.1021/bi9827161
- [8] Minagawa J. Dynamic reorganization of photosynthetic supercomplexes during environmental acclimation of photosynthesis. *Front Plant Sci.* 2013 Dec 17;4:513. doi: 10.3389/fpls.2013.00513
- [9] Kouřil R, Dekker JP, Boekema EJ. Supramolecular organization of photosystem II in green plants. *Biochim Biophys Acta.* 2012 Jan;1817(1):2-12. doi: 10.1016/j.bbabi.2011.05.024
- [10] Lunde C, Jensen PE, Haldrup A, Knoetzel J, Scheller HV. The PSI-H subunit of photosystem I is essential for state transitions in plant photosynthesis. *Nature.* 2000 Nov 30;408(6812):613-615. doi: 10.1038/35046121
- [11] Zhang S, Scheller HV. Light-harvesting complex II binds to several small subunits of photosystem I. *J Biol Chem.* 2004 Jan 30;279(5):3180-3187. doi: 10.1074/jbc.M311640200
- [12] Allen JF, Hall DO. Superoxide reduction as a mechanism of ascorbate-stimulated oxygen uptake by isolated chloroplasts. *Biochemical and Biophysical Research Communications.* 1973 Jun 8;52(3):856-862. doi: 10.1016/0006-291X(73)91016-4
- [13] Badger MR. Photosynthetic Oxygen Exchange. *Annual Review of Plant Physiology.* 1985;36(1):27-53. doi: 10.1146/annurev.pp.36.060185.000331
- [14] Allen JF. Oxygen reduction and optimum production of ATP in photosynthesis. *Nature.* 1975 Aug; 256(5518):599-600. doi: 10.1038/256599a0
- [15] Ivanov BN, Red'ko TP, Shmeleva VL, Mukhin EN. Role of ferredoxin in pseudo-cyclic electron transport in isolated pea chloroplasts. *Biochemistry Moscow.* 1980 Aug 1;45(8):1425-1432.
- [16] Asada K, Kiso K, Yoshikawa K. Univalent reduction of molecular

oxygen by spinach chloroplasts on illumination. *Journal of Biological Chemistry*. 1974;249(7):2175-2181.

[17] Golbeck J, Radmer R. Is the rate of oxygen uptake by reduced ferredoxin sufficient to account for photosystem I-mediated O₂ reduction. *Advances in photosynthesis research*. 1984;1:561-561.

[18] Kozuleva M, Goss T, Twachtmann M, Rudi K, Trapka J, Selinski J, et al. Ferredoxin:NADP(H) Oxidoreductase Abundance and Location Influences Redox Poise and Stress Tolerance. *Plant Physiology*. 2016 Nov 1;172(3):1480-1493. doi: 10.1104/pp.16.01084

[19] Kozuleva MA, Ivanov BN. Evaluation of the participation of ferredoxin in oxygen reduction in the photosynthetic electron transport chain of isolated pea thylakoids. *Photosynthesis research*. 2010;105(1):51-61.

[20] Takahashi M, Asada K. Superoxide production in aprotic interior of chloroplast thylakoids. *Archives of Biochemistry and Biophysics*. 1988 Dec 1;267(2):714-722. doi: 10.1016/0003-9861(88)90080-X

[21] Hormann H, Neubauer C, Asada K, Schreiber U. Intact chloroplasts display pH 5 optimum of O₂-reduction in the absence of methyl viologen: Indirect evidence for a regulatory role of superoxide protonation. *Photosynth Res*. 1993 Jul 1;37(1):69-80. doi: 10.1007/BF02185440

[22] Kozuleva M, Petrova A, Milrad Y, Semenov A, Ivanov B, Redding KE, et al. Phylloquinone is the principal Mehler reaction site within photosystem I in high light. *Plant Physiology* 2021, accepted

[23] Kruk J, Jemioła-Rzemińska M, Burda K, Schmid GH, Strzałka K. Scavenging of Superoxide Generated in Photosystem I by Plastoquinol and Other Prenylipids in Thylakoid

Membranes. *Biochemistry*. 2003 Jul 1;42(28):8501-8505. doi: 10.1021/bi034036q

[24] Kozuleva MA, Petrova AA, Mamedov MD, Semenov AY, Ivanov BN. O₂ reduction by photosystem I involves phylloquinone under steady-state illumination. *FEBS letters*. 2014;588(23):4364-4368.

[25] McConnell MD, Cowgill JB, Baker PL, Rappaport F, Redding KE. Double Reduction of Plastoquinone to Plastoquinol in Photosystem 1. *Biochemistry*. 2011 Dec 27;50(51):11034-11046. doi: 10.1021/bi201131r

[26] Ptushenko VV, Cherepanov DA, Krishtalik LI, Semenov AY. Semi-continuum electrostatic calculations of redox potentials in photosystem I. *Photosynth Res*. 2008 May 16;97(1):55. doi: 10.1007/s11120-008-9309-y

[27] Kozuleva M, Klenina I, Proskuryakov I, Kirilyuk I, Ivanov B. Production of superoxide in chloroplast thylakoid membranes: ESR study with cyclic hydroxylamines of different lipophilicity. *FEBS Letters*. 2011 Apr 6;585(7):1067-1071. doi: 10.1016/j.febslet.2011.03.004

[28] Kozuleva M, Klenina I, Myslin I, Kirilyuk I, Opanasenko V, Proskuryakov I, et al. Quantification of superoxide radical production in thylakoid membrane using cyclic hydroxylamines. *Free Radical Biology and Medicine*. 2015 Dec 1;89:1014-1023. doi: 10.1016/j.freeradbiomed.2015.08.016

[29] Ogawa K, Kanematsu S, Takabe K, Asada K. Attachment of CuZn-Superoxide Dismutase to Thylakoid Membranes at the Site of Superoxide Generation (PSI) in Spinach Chloroplasts: Detection by Immuno-Gold Labeling After Rapid Freezing and Substitution Method. *Plant and Cell Physiology*. 1995 Jun 1;36(4):565-573. doi: 10.1093/oxfordjournals.pcp.a078795

- [30] Mubarakshina M, Khorobrykh S, Ivanov B. Oxygen reduction in chloroplast thylakoids results in production of hydrogen peroxide inside the membrane. *Biochimica et Biophysica Acta (BBA) - Bioenergetics*. 2006 Nov 1;1757(11):1496-1503. doi: 10.1016/j.bbabi.2006.09.004
- [31] Mubarakshina MM, Khorobrykh SA, Kozuleva MA, Ivanov BN. Intra-membrane formation of hydrogen peroxide during oxygen reduction in thylakoids of higher plants. *Dokl Biochem Biophys*. 2006 Jun;408(1):113-116. doi: 10.1134/S160767290603001X
- [32] (Mubarakshina) Borisova MM, Kozuleva MA, Rudenko NN, Naydov IA, Klenina IB, Ivanov BN. Photosynthetic electron flow to oxygen and diffusion of hydrogen peroxide through the chloroplast envelope via aquaporins. *Biochimica et Biophysica Acta (BBA) - Bioenergetics*. 2012 Aug 1;1817(8):1314-1321. doi: 10.1016/j.bbabi.2012.02.036
- [33] Ivanov B, Mubarakshina M, Khorobrykh S. Kinetics of the plastoquinone pool oxidation following illumination: Oxygen incorporation into photosynthetic electron transport chain. *FEBS Letters*. 2007 Apr 3;581(7):1342-1346. doi: 10.1016/j.febslet.2007.02.044
- [34] Kruk J, Strzałka K. Dark reoxidation of the plastoquinone-pool is mediated by the low-potential form of cytochrome b-559 in spinach thylakoids. *Photosynthesis Research*. 1999 Dec 1;62(2):273-279. doi: 10.1023/A:1006374319191
- [35] McCauley SW, Melis A. Quantitation of plastoquinone photoreduction in spinach chloroplasts. *Photosynth Res*. 1986 Jan;8(1):3-16. doi: 10.1007/BF00028472
- [36] Borisova-Mubarakshina MM, Naydov IA, Ivanov BN. Oxidation of the plastoquinone pool in chloroplast thylakoid membranes by superoxide anion radicals. *FEBS Letters*. 2018 Oct 1;592(19):3221-3228. doi: 10.1002/1873-3468.13237
- [37] Bailey S, Walters RG, Jansson S, Horton P. Acclimation of *Arabidopsis thaliana* to the light environment: the existence of separate low light and high light responses. *Planta*. 2001 Sep;213(5):794-801. doi: 10.1007/s004250100556
- [38] Anderson JM. Photoregulation of the Composition, Function, and Structure of Thylakoid Membranes. *Annual Review of Plant Physiology*. 1986;37(1):93-136. doi: 10.1146/annurev.pp.37.060186.000521
- [39] Poorter H, Niinemets Ü, Ntagkas N, Siebenkäs A, Mäenpää M, Matsubara S, et al. A meta-analysis of plant responses to light intensity for 70 traits ranging from molecules to whole plant performance. *New Phytologist*. 2019;223(3):1073-105. doi: <https://doi.org/10.1111/nph.15754>
- [40] Ludlow MM, Wilson GL. Photosynthesis of Tropical Pasture Plants III. Leaf Age. *Aust Jnl Of Bio Sci*. 1971; 24(4):1077-1088. doi: 10.1071/bi9711077
- [41] Wild A, Wolf G. The Effect of Different Light Intensities on the Frequency and Size of Stomata, the Size of Cells, the Number, Size and Chlorophyll Content of Chloroplasts in the Mesophyll and the Guard Cells during the Ontogeny of Primary Leaves of *Sinapis alba*. *Zeitschrift für Pflanzenphysiologie*. 1980 May 1;97(4):325-342. doi: 10.1016/S0044-328X(80)80006-7
- [42] Boardman NK. Development of Chloroplast Structure and Function. In: Trebst A, Avron M, editors. *Photosynthesis I: Photosynthetic Electron Transport and Photophosphorylation* [Internet]. Berlin, Heidelberg: Springer; 1977 [cited 2021 Mar 26]. p. 583-600. (Encyclopedia of Plant Physiology). doi: 10.1007/978-3-642-66505-9_42

- [43] Lichtenthaler HK, Buschmann C, Döll M, Fietz H-J, Bach T, Kozel U, et al. Photosynthetic activity, chloroplast ultrastructure, and leaf characteristics of high-light and low-light plants and of sun and shade leaves. *Photosynth Res.* 1981 Jun 1;2(2):115-141. doi: 10.1007/BF00028752
- [44] Anderson JM, Goodchild DJ, Boardman NK. Composition of the photosystems and chloroplast structure in extreme shade plants. *Biochimica et Biophysica Acta (BBA) - Bioenergetics.* 1973 Dec 14;325(3):573-585. doi: 10.1016/0005-2728(73)90217-X
- [45] Albanese P, Manfredi M, Meneghesso A, Marengo E, Saracco G, Barber J, et al. Dynamic reorganization of photosystem II supercomplexes in response to variations in light intensities. *Biochimica et Biophysica Acta (BBA) - Bioenergetics.* 2016 Oct 1;1857(10):1651-1660. doi: 10.1016/j.bbabi.2016.06.011
- [46] Antal T, Mattila H, Hakala-Yatkin M, Tyystjärvi T, Tyystjärvi E. Acclimation of photosynthesis to nitrogen deficiency in *Phaseolus vulgaris*. *Planta.* 2010 Sep 1;232(4):887-898. doi: 10.1007/s00425-010-1227-5
- [47] Brugnoli E, Cona A, Lauteri M. Xanthophyll cycle components and capacity for non-radiative energy dissipation in sun and shade leaves of *Ligustrum ovalifolium* exposed to conditions limiting photosynthesis. *Photosynth Res.* 1994 Sep 1;41(3):451-463. doi: 10.1007/BF02183047
- [48] Demmig-Adams B, Adams WW. Xanthophyll cycle and light stress in nature: uniform response to excess direct sunlight among higher plant species. *Planta.* 1996 Sep 1;198(3):460-470. doi: 10.1007/BF00620064
- [49] Park YI, Chow WS, Anderson JM. Chloroplast Movement in the Shade Plant *Tradescantia albiflora* Helps Protect Photosystem II against Light Stress. *Plant Physiology.* 1996 Jul 1;111(3):867-875. doi: 10.1104/pp.111.3.867
- [50] Rudenko NN, Fedorchuk TP, Terentyev VV, Dymova OV, Naydov IA, Golovko TK, et al. The role of carbonic anhydrase α -CA4 in the adaptive reactions of photosynthetic apparatus: the study with α -CA4 knockout plants. *Protoplasma.* 2020;257(2):489-499.
- [51] Dall'Osto L, Caffarri S, Bassi R. A Mechanism of Nonphotochemical Energy Dissipation, Independent from PsbS, Revealed by a Conformational Change in the Antenna Protein CP26. *The Plant Cell.* 2005 Apr 1;17(4):1217-1232. doi: 10.1105/tpc.104.030601
- [52] Demmig-Adams B, Adams WW. Photoprotection in an ecological context: the remarkable complexity of thermal energy dissipation. *New Phytologist.* 2006;172(1):11-21. doi: <https://doi.org/10.1111/j.1469-8137.2006.01835.x>
- [53] Galka P, Santabarbara S, Khuong TTH, Degand H, Morsomme P, Jennings RC, et al. Functional Analyses of the Plant Photosystem I–Light-Harvesting Complex II Supercomplex Reveal That Light-Harvesting Complex II Loosely Bound to Photosystem II Is a Very Efficient Antenna for Photosystem I in State II. *The Plant Cell.* 2012 Jul 1;24(7):2963-2978. doi: 10.1105/tpc.112.100339
- [54] Rochaix J-D, Lemeille S, Shapiguzov A, Samol I, Fucile G, Willig A, et al. Protein kinases and phosphatases involved in the acclimation of the photosynthetic apparatus to a changing light environment. *Philosophical Transactions of the Royal Society B: Biological Sciences.* 2012 Dec 19;367(1608):3466-3474. doi: 10.1098/rstb.2012.0064
- [55] Shapiguzov A, Ingelsson B, Samol I, Andres C, Kessler F, Rochaix J-D, et al. The PPH1 phosphatase is specifically involved in LHCII dephosphorylation

and state transitions in Arabidopsis. PNAS. 2010 Mar 9;107(10):4782-4787. doi: 10.1073/pnas.0913810107

[56] Depège N, Bellafiore S, Rochaix J-D. Role of Chloroplast Protein Kinase Stt7 in LHCII Phosphorylation and State Transition in Chlamydomonas. Science. 2003 Mar 7;299(5612):1572-1575. doi: 10.1126/science.1081397

[57] Lemeille S, Willig A, Depège-Fargeix N, Delessert C, Bassi R, Rochaix J-D. Analysis of the Chloroplast Protein Kinase Stt7 during State Transitions. PLOS Biology. 2009 Mar 3;7(3):e1000045. doi: 10.1371/journal.pbio.1000045

[58] Shapiguzov A, Chai X, Fucile G, Longoni P, Zhang L, Rochaix J-D. Activation of the Stt7/STN7 Kinase through Dynamic Interactions with the Cytochrome b6f Complex. Plant Physiology. 2016 May 1;171(1):82-92. doi: 10.1104/pp.15.01893

[59] Dumas L, Zito F, Blangy S, Auroy P, Johnson X, Peltier G, et al. A stromal region of cytochrome b6f subunit IV is involved in the activation of the Stt7 kinase in Chlamydomonas. PNAS. 2017 Nov 7;114(45):12063-12068. doi: 10.1073/pnas.1713343114

[60] Mekala NR, Suorsa M, Rantala M, Aro E-M, Tikkanen M. Plants Actively Avoid State Transitions upon Changes in Light Intensity: Role of Light-Harvesting Complex II Protein Dephosphorylation in High Light. Plant Physiology. 2015 Jun 1;168(2):721-734. doi: 10.1104/pp.15.00488

[61] Vetoshkina DV, Pozdnyakova-Filatova IY, Zhurikova EM, Frolova AA, Naydov IA, Ivanov BN, et al. The increase in adaptive capacity to high illumination of barley plants colonized by rhizobacteria P. putida BS3701. Applied Biochemistry and Microbiology. 2019; 55(2):173-181.

[62] Rintamäki E, Martinsuo P, Pursiheimo S, Aro E-M. Cooperative regulation of light-harvesting complex II phosphorylation via the plastoquinol and ferredoxin-thioredoxin system in chloroplasts. PNAS. 2000 Oct 10; 97(21):11644-11649. doi: 10.1073/pnas.180054297

[63] Trotta A, Suorsa M, Rantala M, Lundin B, Aro E-M. Serine and threonine residues of plant STN7 kinase are differentially phosphorylated upon changing light conditions and specifically influence the activity and stability of the kinase. The Plant Journal. 2016;87(5):484-94. doi: <https://doi.org/10.1111/tpj.13213>

[64] Lemeille S, Rochaix J-D. State transitions at the crossroad of thylakoid signalling pathways. Photosynth Res. 2010 Nov 1;106(1):33-46. doi: 10.1007/s11120-010-9538-8

[65] Vetoshkina DV, Kozuleva MA, Terentyev VV, Zhurikova EM, Borisova-Mubarakshina MM, Ivanov BN. Comparison of state transitions of the photosynthetic antennae in Arabidopsis and barley plants upon illumination with light of various intensity. Biochemistry (Moscow). 2019;84(9):1065-1073.

[66] Tikkanen M, Grieco M, Kangasjärvi S, Aro E-M. Thylakoid Protein Phosphorylation in Higher Plant Chloroplasts Optimizes Electron Transfer under Fluctuating Light. Plant Physiology. 2010 Feb 1;152(2):723-735. doi: 10.1104/pp.109.150250

[67] Bonardi V, Pesaresi P, Becker T, Schleiff E, Wagner R, Pfannschmidt T, et al. Photosystem II core phosphorylation and photosynthetic acclimation require two different protein kinases. Nature. 2005 Oct;437(7062):1179-1182. doi: 10.1038/nature04016

[68] Pursiheimo S, Rintamäki E, Aro E-M. Reversible phosphorylation of LHCII proteins in rye leaves — redox

- control and physiological significance. In: Garab G, editor. *Photosynthesis: Mechanisms and Effects: Volume I–V: Proceedings of the XIth International Congress on Photosynthesis, Budapest, Hungary, August 17–22, 1998* [Internet]. Dordrecht: Springer Netherlands; 1998 [cited 2021 Mar 26]. p. 1903–6. doi: 10.1007/978-94-011-3953-3_443
- [69] Tikkanen M, Nurmi M, Kangasjärvi S, Aro E-M. Core protein phosphorylation facilitates the repair of photodamaged photosystem II at high light. *Biochimica et Biophysica Acta (BBA) - Bioenergetics*. 2008 Nov 1;1777(11):1432–1437. doi: 10.1016/j.bbabi.2008.08.004
- [70] Kirchhoff H, Hall C, Wood M, Herbstová M, Tsabari O, Nevo R, et al. Dynamic control of protein diffusion within the granal thylakoid lumen. *PNAS*. 2011 Dec 13;108(50):20248–20253. doi: 10.1073/pnas.1104141109
- [71] Herbstová M, Tietz S, Kinzel C, Turkina MV, Kirchhoff H. Architectural switch in plant photosynthetic membranes induced by light stress. *PNAS*. 2012 Dec 4;109(49):20130–20135. doi: 10.1073/pnas.1214265109
- [72] Baena-González E, Barbato R, Aro E-M. Role of phosphorylation in the repair cycle and oligomeric structure of photosystem II. *Planta*. 1999 Apr 1;208(2):196–204. doi: 10.1007/s004250050550
- [73] Barber J, Anderson JM, Baena-González E, Aro E. Biogenesis, assembly and turnover of photosystem II units. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*. 2002 Oct 29;357(1426):1451–1460. doi: 10.1098/rstb.2002.1141
- [74] Allen JF. Why chloroplasts and mitochondria retain their own genomes and genetic systems: Colocation for redox regulation of gene expression. *PNAS*. 2015 Aug 18;112(33):10231–10238. doi: 10.1073/pnas.1500012112
- [75] Allen JF, Pfannschmidt T. Balancing the two photosystems: photosynthetic electron transfer governs transcription of reaction centre genes in chloroplasts. Osmond CB, Foyer CH, Bock G, editors. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*. 2000 Oct 29;355(1402):1351–1359. doi: 10.1098/rstb.2000.0697
- [76] Puthiyaveetil S, Allen JF. Transients in chloroplast gene transcription. *Biochemical and Biophysical Research Communications*. 2008 Apr 18;368(4):871–874. doi: 10.1016/j.bbrc.2008.01.167
- [77] Ballottari M, Dall'Osto L, Morosinotto T, Bassi R. Contrasting Behavior of Higher Plant Photosystem I and II Antenna Systems during Acclimation*. *Journal of Biological Chemistry*. 2007 Mar 23;282(12):8947–8958. doi: 10.1074/jbc.M606417200
- [78] Morosinotto T, Bassi R, Frigerio S, Finazzi G, Morris E, Barber J. Biochemical and structural analyses of a higher plant photosystem II supercomplex of a photosystem I-less mutant of barley. *The FEBS Journal*. 2006;273(20):4616–30. doi: https://doi.org/10.1111/j.1742-4658.2006.05465.x
- [79] Želisko A, García-Lorenzo M, Jackowski G, Jansson S, Funk C. AtFtsH6 is involved in the degradation of the light-harvesting complex II during high-light acclimation and senescence. *PNAS*. 2005 Sep 20;102(38):13699–13704. doi: 10.1073/pnas.0503472102
- [80] Wagner R, Aigner H, Pružinská A, Jänkänpää HJ, Jansson S, Funk C. Fitness analyses of *Arabidopsis thaliana* mutants depleted of FtsH metalloproteases and characterization of three FtsH6 deletion mutants exposed to high light stress, senescence and chilling. *New Phytologist*. 2011;191(2):449–58. doi: https://doi.org/10.1111/j.1469-8137.2011.03684.x

- [81] Lindahl M, Yang D-H, Andersson B. Regulatory Proteolysis of the Major Light-Harvesting Chlorophyll a/b Protein of Photosystem II by a Light-Induced Membrane-Associated Enzymic System. *European Journal of Biochemistry*. 1995;231(2):503-9. doi: <https://doi.org/10.1111/j.1432-1033.1995.0503e.x>
- [82] Pfannschmidt T, Nilsson A, Allen JF. Photosynthetic control of chloroplast gene expression. *Nature*. 1999 Feb;397(6720):625-628. doi: 10.1038/17624
- [83] Escoubas JM, Lomas M, LaRoche J, Falkowski PG. Light intensity regulation of cab gene transcription is signaled by the redox state of the plastoquinone pool. *PNAS*. 1995 Oct 24;92(22):10237-10241. doi: 10.1073/pnas.92.22.10237
- [84] Frigerio S, Campoli C, Zorzan S, Fantoni LI, Crosatti C, Drepper F, et al. Photosynthetic Antenna Size in Higher Plants Is Controlled by the Plastoquinone Redox State at the Post-transcriptional Rather than Transcriptional Level*. *Journal of Biological Chemistry*. 2007 Oct 5;282(40):29457-29469. doi: 10.1074/jbc.M705132200
- [85] Dietzel L, Gläßer C, Liebers M, Hiekel S, Courtois F, Czarnecki O, et al. Identification of Early Nuclear Target Genes of Plastidial Redox Signals that Trigger the Long-Term Response of Arabidopsis to Light Quality Shifts. *Molecular Plant*. 2015 Aug 3;8(8):1237-1252. doi: 10.1016/j.molp.2015.03.004
- [86] Borisova-Mubarakshina MM, Ivanov BN, Vetoshkina DV, Lubimov VY, Fedorchuk TP, Naydov IA, et al. Long-term acclimatory response to excess excitation energy: evidence for a role of hydrogen peroxide in the regulation of photosystem II antenna size. *J Exp Bot*. 2015 Dec 1;66(22):7151-7164. doi: 10.1093/jxb/erv410
- [87] Zandalinas SI, Mittler R. ROS-induced ROS release in plant and animal cells. *Free Radical Biology and Medicine*. 2018 Jul 1;122:21-27. doi: 10.1016/j.freeradbiomed.2017.11.028
- [88] Lawlor DW. Limitation to Photosynthesis in Water-stressed Leaves: Stomata vs. Metabolism and the Role of ATP. *Ann Bot*. 2002 Jun 15;89(7):871-885. doi: 10.1093/aob/mcf110
- [89] Chaves MM, Flexas J, Pinheiro C. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. *Annals of Botany*. 2009 Feb 1;103(4):551-560. doi: 10.1093/aob/mcn125
- [90] Basu S, Ramegowda V, Kumar A, Pereira A. Plant adaptation to drought stress. *F1000Res*. 2016 Jun 30;5:1554. doi: 10.12688/f1000research.7678.1
- [91] De Micco V, Aronne G. Morpho-Anatomical Traits for Plant Adaptation to Drought. In: Aroca R, editor. *Plant Responses to Drought Stress: From Morphological to Molecular Features* [Internet]. Berlin, Heidelberg: Springer; 2012 [cited 2021 Apr 11]. p. 37-61. doi: 10.1007/978-3-642-32653-0_2
- [92] Medrano H, Parry MAJ, Socias X, Lawlor DW. Long term water stress inactivates Rubisco in subterranean clover. *Annals of Applied Biology*. 1997;131(3):491-501.
- [93] Edwards G, Walker D. C Three C Four: Mechanisms, Cellular and Environmental Regulation of Photosynthesis. University of California Press; 1983. 558 p.
- [94] Dalal VK, Tripathy BC. Water-stress induced downsizing of light-harvesting antenna complex protects developing rice seedlings from photo-oxidative damage. *Scientific Reports*. 2018 Apr 13;8(1):5955. doi: 10.1038/s41598-017-14419-4
- [95] Zhou Y, Lam HM, Zhang J. Inhibition of photosynthesis and energy dissipation induced by water and high light stresses

in rice. *Journal of Experimental Botany*. 2007 Mar 1;58(5):1207-1217. doi: 10.1093/jxb/erl291

[96] Alberte RS, Fiscus EL, Naylor AW. The Effects of Water Stress on the Development of the Photosynthetic Apparatus in Greening Leaves. *Plant Physiology*. 1975 Feb 1;55(2):317-321. doi: 10.1104/pp.55.2.317

[97] Giardi MT, Cona A, Geiken B, Kučera T, Masojídek J, Mattoo AK. Long-term drought stress induces structural and functional reorganization of photosystem II. *Planta*. 1996 May 1;199(1):118-125. doi: 10.1007/BF00196888

[98] He JX, Wang J, Liang HG. Effects of water stress on photochemical function and protein metabolism of photosystem II in wheat leaves. *Physiologia Plantarum*. 1995;93(4):771-7. doi: <https://doi.org/10.1111/j.1399-3054.1995.tb05130.x>

[99] Chakraborty N, Tripathy BC. Involvement of Singlet Oxygen in 5-Aminolevulinic Acid-Induced Photodynamic Damage of Cucumber (*Cucumis sativus* L.) Chloroplasts. *Plant Physiology*. 1992 Jan 1;98(1):7-11. doi: 10.1104/pp.98.1.7

[100] Murata N, Allakhverdiev SI, Nishiyama Y. The mechanism of photoinhibition in vivo: Re-evaluation of the roles of catalase, α -tocopherol, non-photochemical quenching, and electron transport. *Biochimica et Biophysica Acta (BBA) - Bioenergetics*. 2012 Aug 1;1817(8):1127-1133. doi: 10.1016/j.bbabo.2012.02.020

[101] Schmitt F-J, Renger G, Friedrich T, Kreslavski VD, Zharmukhamedov SK, Los DA, et al. Reactive oxygen species: Re-evaluation of generation, monitoring and role in stress-signaling in phototrophic organisms. *Biochimica et Biophysica Acta (BBA) - Bioenergetics*. 2014 Jun 1;1837(6):835-848. doi: 10.1016/j.bbabo.2014.02.005

[102] Wilkinson S, Kudoyarova GR, Veselov DS, Arkhipova TN, Davies WJ. Plant hormone interactions: innovative targets for crop breeding and management. *J Exp Bot*. 2012 May;63(9):3499-3509. doi: 10.1093/jxb/ers148

[103] Wilkinson S, Davies WJ. Drought, ozone, ABA and ethylene: new insights from cell to plant to community. *Plant Cell Environ*. 2010 Apr;33(4):510-525. doi: 10.1111/j.1365-3040.2009.02052.x

[104] Spollen WG, Sharp RE. Spatial distribution of turgor and root growth at low water potentials. *Plant Physiology*. 1991;96(2):438-443.

[105] Deak KI, Malamy J. Osmotic regulation of root system architecture. *The Plant Journal*. 2005;43(1):17-28.

[106] Chen H, Li Z, Xiong L. A plant microRNA regulates the adaptation of roots to drought stress. *FEBS Letters*. 2012;586(12):1742-7. doi: <https://doi.org/10.1016/j.febslet.2012.05.013>

[107] Jaffe MJ, Takahashi H, Biro RL. A Pea Mutant for the Study of Hydrotropism in Roots. *Science*. 1985 Oct 25;230(4724):445-447. doi: 10.1126/science.230.4724.445

[108] Blilou I, Xu J, Wildwater M, Willemsen V, Paponov I, Friml J, et al. The PIN auxin efflux facilitator network controls growth and patterning in Arabidopsis roots. *Nature*. 2005;433(7021):39-44.

[109] Chaves MM, Oliveira MM. Mechanisms underlying plant resilience to water deficits: prospects for water-saving agriculture. *Journal of Experimental Botany*. 2004 Nov 1;55(407):2365-2384. doi: 10.1093/jxb/erh269

[110] Oosterhuis DM, Wulschleger SD. Osmotic Adjustment in Cotton (*Gossypium hirsutum* L.) Leaves and Roots in Response to Water Stress. *Plant Physiol*. 1987 Aug;84(4):1154-1157. doi: 10.1104/pp.84.4.1154

- [111] Sauter A, Davies WJ, Hartung W. The long-distance abscisic acid signal in the droughted plant: the fate of the hormone on its way from root to shoot. *J Exp Bot.* 2001 Oct;52(363):1991-1997. doi: 10.1093/jexbot/52.363.1991
- [112] He X, Chen Z, Wang J, Li W, Zhao J, Wu J, et al. A sucrose:fructan-6-fructosyltransferase (6-SFT) gene from *Psathyrostachys huashanica* confers abiotic stress tolerance in tobacco. *Gene.* 2015 Oct 10;570(2):239-247. doi: 10.1016/j.gene.2015.06.023
- [113] Ge L-F, Chao D-Y, Shi M, Zhu M-Z, Gao J-P, Lin H-X. Overexpression of the trehalose-6-phosphate phosphatase gene *OsTPP1* confers stress tolerance in rice and results in the activation of stress responsive genes. *Planta.* 2008 Jun;228(1):191-201. doi: 10.1007/s00425-008-0729-x
- [114] Ashraf M, Foolad MR. Roles of glycine betaine and proline in improving plant abiotic stress resistance. *Environmental and Experimental Botany.* 2007 Mar 1;59(2):206-216. doi: 10.1016/j.envexpbot.2005.12.006
- [115] Isayenkov SV, Maathuis FJM. Plant Salinity Stress: Many Unanswered Questions Remain. *Front Plant Sci* [Internet]. 2019 [cited 2021 Mar 26];10. doi: 10.3389/fpls.2019.00080
- [116] Isayenkov SV. Physiological and molecular aspects of salt stress in plants. *Cytol Genet.* 2012 Sep 1;46(5):302-318. doi: 10.3103/S0095452712050040
- [117] Tsugane K, Kobayashi K, Niwa Y, Ohba Y, Wada K, Kobayashi H. A Recessive Arabidopsis Mutant That Grows Photoautotrophically under Salt Stress Shows Enhanced Active Oxygen Detoxification. *The Plant Cell.* 1999 Jul 1;11(7):1195-1206. doi: 10.1105/tpc.11.7.1195
- [118] Kim H-J, Fonseca JM, Choi J-H, Kubota C, Kwon DY. Salt in irrigation water affects the nutritional and visual properties of romaine lettuce (*Lactuca sativa* L.). *J Agric Food Chem.* 2008 May 28;56(10):3772-3776. doi: 10.1021/jf0733719
- [119] Gilroy S, Swanson SJ. Gravitropic Signaling in Plants. In: eLS [Internet]. American Cancer Society; 2014 [cited 2021 Mar 26]. doi: 10.1002/9780470015902.a0025267
- [120] Roy SJ, Negrão S, Tester M. Salt resistant crop plants. *Current Opinion in Biotechnology.* 2014 Apr 1;26:115-124. doi: 10.1016/j.copbio.2013.12.004
- [121] Munns R, Passioura JB. Hydraulic Resistance of Plants. III. Effects of NaCl in Barley and Lupin. *Functional Plant Biol.* 1984;11(5):351-359. doi: 10.1071/pp9840351
- [122] Munns R, Termaat A. Whole-Plant Responses to Salinity. *Functional Plant Biol.* 1986;13(1):143-160. doi: 10.1071/pp9860143
- [123] Rajendran K, Tester M, Roy SJ. Quantifying the three main components of salinity tolerance in cereals. *Plant, Cell & Environment.* 2009;32(3):237-49. doi: <https://doi.org/10.1111/j.1365-3040.2008.01916.x>
- [124] Munns R, Tester M. Mechanisms of salinity tolerance. *Annu Rev Plant Biol.* 2008;59:651-681. doi: 10.1146/annurev.arplant.59.032607.092911
- [125] Allakhverdiev SI, Sakamoto A, Nishiyama Y, Inaba M, Murata N. Ionic and Osmotic Effects of NaCl-Induced Inactivation of Photosystems I and II in *Synechococcus* sp. *Plant Physiology.* 2000 Jul 1;123(3):1047-1056. doi: 10.1104/pp.123.3.1047
- [126] Yamane K, Kawasaki M, Taniguchi M, Miyake H. Differential effect of NaCl and polyethylene glycol on the ultrastructure of chloroplasts in rice seedlings. *Journal of Plant Physiology.* 2003;160(5):573-575.

- [127] Yamane K, Oi T, Enomoto S, Nakao T, Arai S, Miyake H, et al. Three-dimensional ultrastructure of chloroplast pockets formed under salinity stress. *Plant Cell Environ.* 2018 Mar;41(3):563-575. doi: 10.1111/pce.13115
- [128] Locy RD, Chang CC, Nielsen BL, Singh NK. Photosynthesis in Salt-Adapted Heterotrophic Tobacco Cells and Regenerated Plants. *Plant Physiology.* 1996 Jan 1;110(1):321-328. doi: 10.1104/pp.110.1.321
- [129] Foyer CH, Allen JF. Lessons from redox signaling in plants. *Antioxidants and Redox Signaling.* 2003;5(1):3-5.
- [130] Monroe JD, Storm AR, Badley EM, Lehman MD, Platt SM, Saunders LK, et al. β -Amylase1 and β -Amylase3 Are Plastidic Starch Hydrolases in Arabidopsis That Seem to Be Adapted for Different Thermal, pH, and Stress Conditions. *Plant Physiology.* 2014 Dec 1;166(4):1748-1763. doi: 10.1104/pp.114.246421
- [131] Thalmann M, Santelia D. Starch as a determinant of plant fitness under abiotic stress. *New Phytol.* 2017 May;214(3):943-951. doi: 10.1111/nph.14491
- [132] Borisova-Mubarakshina MM, Vetoshkina DV, Ivanov BN. Antioxidant and signaling functions of the plastoquinone pool in higher plants. *Physiologia Plantarum.* 2019;166(1):181-198. doi: 10.1111/pp.12936
- [133] Borisova-Mubarakshina MM, Vetoshkina DV, Naydov IA, Rudenko NN, Zhurikova EM, Balashov NV, et al. Regulation of the size of photosystem II light harvesting antenna represents a universal mechanism of higher plant acclimation to stress conditions. *Functional Plant Biology.* 2020;47(11):959-969.
- [134] Balashov NV, Zhurikova EM, Naydov IA, Rudenko NN, Vetoshkina DV, Ivanov BN, et al. Regulation of PSII antenna size under drought and salt stress. In: *Proceedings of the 2nd Russia-Japan Joint Forum for Education and Research.* Moscow, Russia: Moscow State University; 2018.
- [135] Hirth M, Dietzel L, Steiner S, Ludwig R, Weidenbach H, and JP, et al. Photosynthetic acclimation responses of maize seedlings grown under artificial laboratory light gradients mimicking natural canopy conditions. *Front Plant Sci [Internet].* 2013 Sep 12 [cited 2021 Apr 11];4. doi: 10.3389/fpls.2013.00334
- [136] Meacham K, Sirault X, Quick WP, von Caemmerer S, Furbank R. Diurnal Solar Energy Conversion and Photo-protection in Rice Canopies. *Plant Physiol.* 2017 Jan;173(1):495-508. doi: 10.1104/pp.16.01585
- [137] Cammarisano L, Donnison IS, Robson PRH. Producing Enhanced Yield and Nutritional Pigmentation in Lollo Rosso Through Manipulating the Irradiance, Duration, and Periodicity of LEDs in the Visible Region of Light. *Front Plant Sci.* 2020;11:598082. doi: 10.3389/fpls.2020.598082
- [138] Horton P, Murchie EH, Ruban AV, Walters RG. Increasing Rice Photosynthesis by Manipulation of the Acclimation and Adaptation to Light. In: *Novartis Foundation Symposium 236 - Rice Biotechnology: Improving Yield, Stress Tolerance and Grain Quality [Internet].* John Wiley & Sons, Ltd; [cited 2021 Apr 11]. p. 117-34. doi: 10.1002/9780470515778.ch9
- [139] Rodriguez R, Durán P. Natural holobiome engineering by using native extreme microbiome to counteract the climate change effects. *Frontiers in Bioengineering and Biotechnology.* 2020;8.
- [140] Carrión VJ, Perez-Jaramillo J, Cordovez V, Tracanna V, De Hollander M, Ruiz-Buck D, et al. Pathogen-induced activation of disease-suppressive functions in the endophytic

root microbiome. *Science*. 2019; 366(6465):606-612.

J Microbiol. 1996 Mar;42(3):207-220.
 doi: 10.1139/m96-032

[141] Li X, Jousset A, de Boer W, Carrión VJ, Zhang T, Wang X, et al. Legacy of land use history determines reprogramming of plant physiology by soil microbiome. *The ISME journal*. 2019;13(3):738-751.

[150] Arkhipova TN, Prinsen E, Veselov SU, Martinenko EV, Melentiev AI, Kudoyarova GR. Cytokinin producing bacteria enhance plant growth in drying soil. *Plant Soil*. 2007 Mar 1;292(1):305-315. doi: 10.1007/s11104-007-9233-5

[142] Rolfe SA, Griffiths J, Ton J. Crying out for help with root exudates: adaptive mechanisms by which stressed plants assemble health-promoting soil microbiomes. *Current opinion in microbiology*. 2019;49:73-82.

[151] Timmusk S, Nicander B, Granhall U, Tillberg E. Cytokinin production by *Paenibacillus polymyxa*. *Soil Biology and Biochemistry*. 1999;31(13):1847-1852.

[143] Schroth MN, Kloepper JW. Plant growth promoting rhizobacteria on radish. In: *Proceedings of the fourth conference plant pathogenic bacteria* Ed Station de Pathogenic Vegetable ET (Phytobacteriologic) INRA Angers. 1978. p. 876-82.

[152] García de Salamone IE, Hynes RK, Nelson LM. Cytokinin production by plant growth promoting rhizobacteria and selected mutants. *Canadian Journal of microbiology*. 2001;47(5):404-411.

[144] Van Loon LC, Bakker P, Pieterse CMJ. Systemic resistance induced by rhizosphere bacteria. *Annual review of phytopathology*. 1998;36(1):453-483.

[153] Noel TC, Sheng C, Yost CK, Pharis RP, Hynes MF. Rhizobium leguminosarum as a plant growth-promoting rhizobacterium: direct growth promotion of canola and lettuce. *Canadian Journal of Microbiology*. 1996;42(3):279-283.

[145] Kumar A, Prakash A, Johri BN. *Bacillus* as PGPR in crop ecosystem. In: *Bacteria in agrobiolgy: crop ecosystems*. Springer; 2011. p. 37-59.

[154] Glick RE, Schlagnhauer CD, Arteca RN, Pell EJ. Ozone-Induced Ethylene Emission Accelerates the Loss of Ribulose-1,5-Bisphosphate Carboxylase/Oxygenase and Nuclear-Encoded mRNAs in Senescing Potato Leaves. *Plant Physiology*. 1995 Nov 1;109(3):891-898. doi: 10.1104/pp.109.3.891

[146] Van Wees SC, Van der Ent S, Pieterse CM. Plant immune responses triggered by beneficial microbes. *Current opinion in plant biology*. 2008;11(4):443-448.

[155] Liu K, Garrett C, Fadamiro H, Kloepper JW. Induction of systemic resistance in Chinese cabbage against black rot by plant growth-promoting rhizobacteria. *Biological Control*. 2016;99:8-13.

[147] Gray EJ, Smith DL. Intracellular and extracellular PGPR: commonalities and distinctions in the plant-bacterium signaling processes. *Soil biology and biochemistry*. 2005;37(3):395-412.

[156] Haas D, Défago G. Biological control of soil-borne pathogens by fluorescent pseudomonads. *Nature reviews microbiology*. 2005;3(4):307-319.

[148] Dimkpa C, Weinand T, Asch F. Plant-rhizobacteria interactions alleviate abiotic stress conditions. *Plant, cell & environment*. 2009;32(12):1682-1694.

[157] Ansari WA, Atri N, Ahmad J, Qureshi MI, Singh B, Kumar R, et al. Drought mediated physiological and

[149] Patten CL, Glick BR. Bacterial biosynthesis of indole-3-acetic acid. *Can*

molecular changes in muskmelon (*Cucumis melo* L.). PLOS ONE. 2019 Sep 24;14(9):e0222647. doi: 10.1371/journal.pone.0222647

[158] Naveed M, Mitter B, Reichenauer TG, Wieczorek K, Sessitsch A. Increased drought stress resilience of maize through endophytic colonization by Burkholderia phytofirmans PsJN and Enterobacter sp. FD17. Environmental and Experimental Botany. 2014;97:30-39.

[159] Jha Y, Subramanian RB. PGPR regulate caspase-like activity, programmed cell death, and antioxidant enzyme activity in paddy under salinity. Physiology and Molecular Biology of Plants. 2014;20(2):201-207.

[160] Jansson S. A guide to the Lhc genes and their relatives in Arabidopsis. Trends in Plant Science. 1999 Jun 1;4(6):236-240. doi: 10.1016/S1360-1385(99)01419-3

[161] Yurina NP, Odintsova MS. Chloroplast Retrograde Signaling System. Russ J Plant Physiol. 2019 Jul 1;66(4):509-520. doi: 10.1134/S1021443719040149

[162] Sun X, Feng P, Xu X, Guo H, Ma J, Chi W, et al. A chloroplast envelope-bound PHD transcription factor mediates chloroplast signals to the nucleus. Nature communications. 2011;2(1):1-10.

[163] Zhang Z-W, Zhang G-C, Zhu F, Zhang D-W, Yuan S. The roles of tetrapyrroles in plastid retrograde signaling and tolerance to environmental stresses. Planta. 2015;242(6):1263-1276.

[164] Adam Z. Plastid intramembrane proteolysis. Biochimica et Biophysica Acta (BBA)-Bioenergetics. 2015;1847(9):910-4.

[165] Biver S, Portetelle D, Vandenbol M. Characterization of a new oxidant-stable serine protease isolated by functional metagenomics. Springerplus. 2013;2(1):1-10.