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 M^{-1} 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 O_2 reduction to $O_2^{\bullet-}$. It has long been accepted that O_2 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 O_2 *in vivo* may prevent efficient reduction of Fd. The contribution of another [4Fe-4S] cluster of PS I, F_X, to O_2 reduction was suggested in the study showed that light-induced H_2O_2-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 (A_1-sites), in O_2 reduction was suggested based on the stimulation of flash-induced O_2 uptake when PhQ was added to thylakoid membranes devoid of quinones [23]. O_2 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 A_1-sites [24]. It was shown that O_2 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 O_2 was barely changed under studied conditions. This effect was attributed to the greater ability of phyllosemiquinone, $PhQ^{\bullet-}$, to reduce O_2 due to the lower redox potentials of PhQs at the A_1-sites compared to PQ. Moreover, unlike $PhQ^{\bullet-}$, plastosemiquinone, $PQ^{\bullet-}$, molecules at the A_1- sites are easily protonated [25] that also reduces the probability of their reaction with oxygen, while increases the probability of $PQ^{\bullet-}$ double reduction to PQH_2. 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 $PhQ^{\bullet-}$ 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 $PhQ^{\bullet-}$ in the A-branch is ~2 orders of magnitude longer.

When considering the possible components involved in the reduction of O_2 in the membrane, the shift in the redox potential of the $O_2/O_2^{\bullet-}$ pair from −160 mV at 1 M O_2 in water to approximately −550 mV in a hydrophobic environment must be considered. The E_m values of $PhQ/PhQ^{\bullet-}$ 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 $O_2^{\bullet-}$ 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 $O_2^{\bullet-}$ within thylakoid membranes [18] emphasizing the physiological significance of the observed process.

$O_2^{\bullet-}$, formed in the chloroplast stroma, are disproportionated there with the formation of H_2O_2 (reaction 1).

$$O_2^{\bullet-} + O_2^{\bullet-} + 2H^+ \rightarrow H_2O_2 + O_2 \quad (1)$$

In chloroplasts, disproportionation reaction is catalyzed by superoxide dismutase (SOD) with the rate constant ~10^7 M^{-1} 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 $O_2^{\bullet-}$ 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 aprotonic membrane phase) but due to the reaction between reduced plastoquinone PQH_2 and the $PhQ^{\bullet-}$ -generated $O_2^{\bullet-}$ (reaction 2):

$$PQH_2 + O_2^{\bullet-} \rightarrow PQ^{\bullet-} + H_2O_2 \qquad (2)$$

This reaction is thermodynamically favorable in aqueous solutions because of the high difference between the Em_7 values of the redox pairs $PQ^{\bullet-}/PQH_2$ (370 mV) and $O_2^{\bullet-}/H_2O_2$ (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 $O_2^{\bullet-}$ 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 $O_2^{\bullet-}$ 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 $O_2^{\bullet-}$ 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 $O_2^{\bullet-}$ showed the additional electron leakage from the PQ pool during $O_2^{\bullet-}$ 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 CO_2 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 PQH_2 molecules in the light. Interaction of STN7 kinase with the stromal loop subunit of the complex results in the kinase activation, while binding of PQH_2 molecules to the oxidation site of the cyt b_6/f complex leads to dissociation of the kinase from the cyt b_6/f complex [58, 59].

It is generally accepted that state transitions occur at low light intensities (100–200 μmol photons m^{-2} 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-leafiness): 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, theses 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 μmol quanta m^{-2} s^{-1}), and then transferred to conditions of high light intensity (1000 μmol quanta m^{-2} 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 $O_2^{\bullet -}$ 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 ABSCISCIC 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

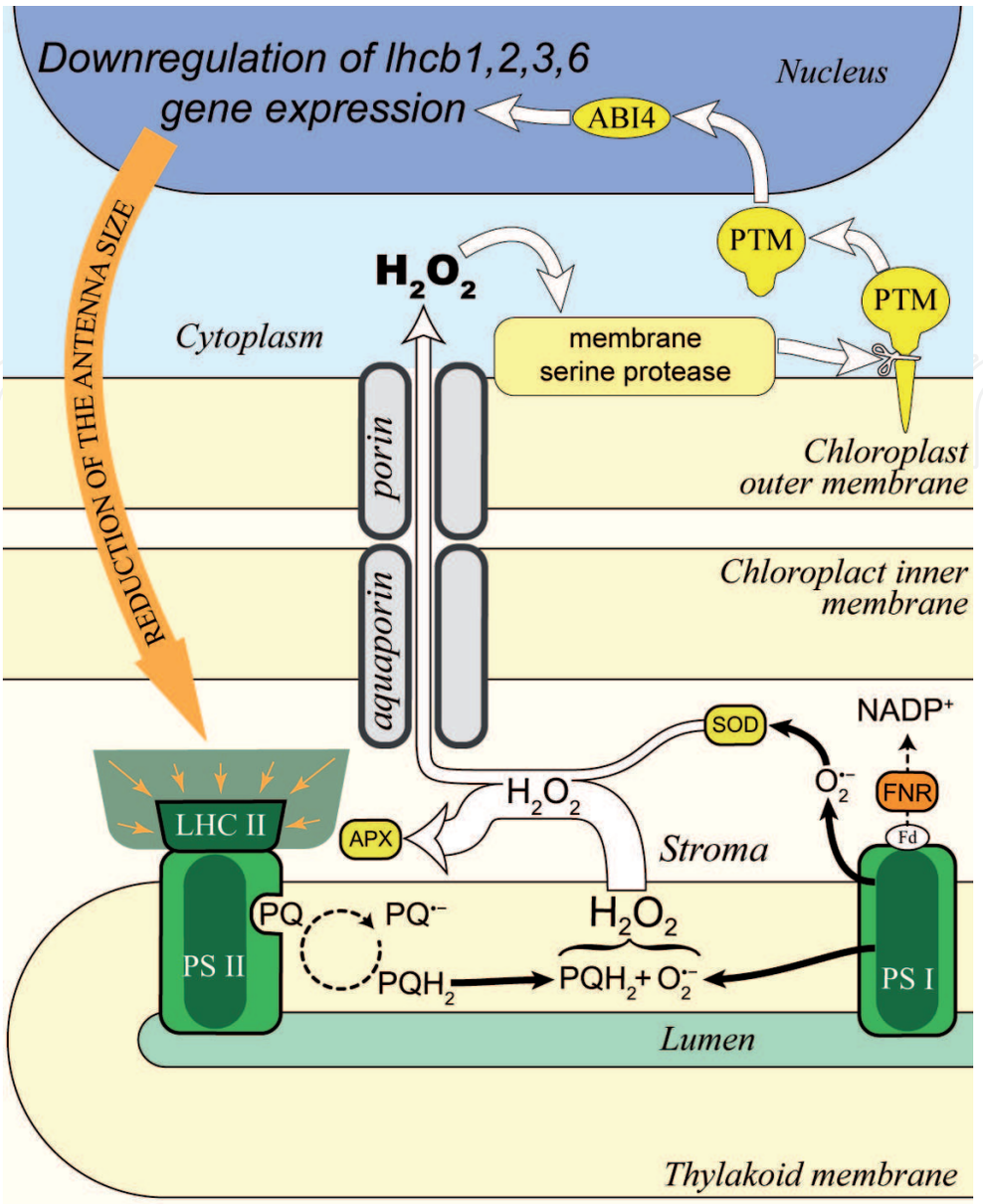

Figure 1.
Hypothetical mechanism of the involvement of "thylakoid membrane" H_2O_2 in the PS II (LHC II) antenna size regulation in the cells of higher plants. PS II, photosystem II; PS I, photosystem I; PQ, oxidized plastoquinone; $PQ^{\bullet-}$, plastosemiquinone; PQH_2, plastohydroquinone; PC, plastocyanine; 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.

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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

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