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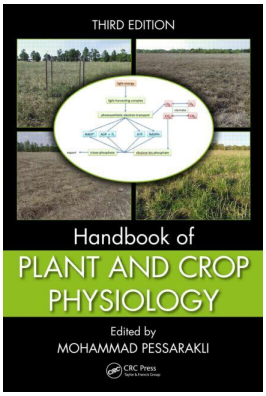

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Pessarakli Mohammad

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3 Alterations in Structural Organization Affect the Functional Ability of Photosynthetic Apparatus

Emilia L. Apostolova and A.N. Misra

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3.1 INTRODUCTION

Photosynthesis in oxygenic organisms such as higher plants, green algae, and cyanobacteria is driven by cooperation of two photosystems, photosystem I (PSI) and photosystem II (PSII), which are embedded in thylakoid membranes and are responsible for converting the light energy into chemical energy [1–4]. These membranes of higher plants and some green algae consist of two main domains: (1) the grana lamellae, which are stacked or the appressed regions of thylakoid membranes, and (2) the stroma (exposed) lamellae, which are unstacked or the unappressed regions of thylakoid membranes [5–8]. Both these domains are well connected. Mem-brane models, derived through freeze fracture, immune-localization, and electron micrographs, show a spatial distribution of PSII and its antenna pigment–protein complexes, the light-harvesting complex of PSII (LHCII), reside mainly in the appressed regions of the stacked grana thylakoid membranes [9], while that of PSI reside predominantly in the unstacked and unappressed stroma (exposed) thylakoid membranes [9,10]. This heterogeneous distribution of PSII, PSI, and the LHCs plays a vital role in the maintenance of structural integrity and functional ability of the photosynthetic apparatus of higher plants and algae under varying environmental stress conditions [3,10–16].

In contrast, the cyanobacterial photosynthetic membranes do not form grana stacking regions [7,17,18]. Cyanobacterial strains display differences in intracellular organization, in particular having various arrangements of the thylakoid within the cell. In addition, it was found that the distances between thylakoid membranes are correlated with the size of the phycobilisome (PBS) antenna and that they change reversibly and rapidly upon illumination [19].

Light harvesting occurs in the pigment bed of the pigment–protein complexes that are organized as antenna complexes and reaction center complexes of PSII and PSI, with their characteristic absorption and emission characteristics [1–4,10].

The structure of the thylakoid membrane is not rigid, akin to other biological membranes, it is fluidic in nature due to the presence of the lipid bilayer and is composed of lipoprotein complexes dispersed in it. The organization of the thylakoid membranes undergoes dynamic changes as per the environmental cues [16,20–22]. On the other hand, the structure of the thylakoid membranes depends on the species of the photosynthetic organisms. The relationship between the organization of pigment–protein complexes and the function of photosynthetic apparatus as well as the role of the different oligomeric structure in the photosynthetic apparatus is particularly important. Taking these facts into consideration, the relationship between the structural organization of the photosynthetic apparatus and its functional activity is described in this review.

3.2 MOLECULAR ORGANIZATION AND COMPOSITION OF THYLAKOID MEMBRANES

Thylakoid membranes are highly specialized and vectorially oriented membranes, which provide an ideal system for studying the relationship between the structure and the function of these membranes. Functional characteristics of these membranes include the light-driven reactions that are defined by a highly ordered structural arrangement [23].

3.2.1 Organization and Function of Photosystem II

PSII is a multisubunit chlorophyll–protein complex, embedded in the lipid environment of the thylakoid membrane of plants, green algae, and cyanobacteria [10,24,25]. The light-driven reaction carried out in this complex leads to the photolysis of water, which releases oxygen, electrons, and protons. The function of PSII is associated with charge separation across the thylakoid membranes [26]. The charge separation between the excited chlorophyll in the reaction center ($P680^{\bullet}$) and pheophytin (Phe) molecule produces the primary charge-separated state ($P680^{+\bullet}Phe^{-\bullet}$), which is followed by rapid charge stabilization by secondary electron transport reactions [27]. The electron from the reduced Phe is transferred to the quinine acceptors (Q_A and Q_B) and subsequently to the mobile pool of plastoquinone (PQ). $P680^{+\bullet}$ is reduced by the redox-active tyrosine of the D1 protein (Tyr-Z), which received electrons from the oxygen-evolving complex (OEC) [see Ref. 27]. It can be assumed that the modification of PSII, which influenced the charge stabilization processes in this complex, leads to increasing the lifetime of $P680^{+\bullet}Phe^{-\bullet}$ [27].

PSII complex is composed of a PSII core and a light-harvesting antenna complex system. The LHCII in the thylakoid membrane of the higher plants binds more than 40% of the total chlorophyll and is the most abundant pigment–protein complex [28,29]. LHCII comprises six polypeptides (Lhcb 1–6) [30]. Lhcb 1–3 form the major antenna complex, which are present as trimers [31], while Lhcb 4–6 (CP29, CP26, and CP24) are present as monomers in the thylakoid membranes [32,33]. The amino acid sequence studies of the isoforms of Lhcb 4 led Klimmek et al. [34] to suggest the extension of LHCII into eight (Lhcb 1–8) groups.

The function of LHCII is to absorb light and transfer the excitation energy to the reaction center of PSII. As such, this complex plays a vital role in efficient light harvesting or photoprotection. LHCII in the granal thylakoid membranes forms large chiral-aggregated structures [35,36]. This higher-order oligomeric structural organization of the major LHCII stabilizes the membrane ultrastructure

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and is important for the dynamics and efficient functioning of the photosynthetic apparatus [37–40]. This process is regulated by the changes in lumen acidification and redox regulation of the protein phosphorylation in the photosystems, leading to the dynamic rearrangement of antenna pigment–protein complexes in the appressed grana lamellae, contributing exciton transfer to PSII, or move away to unappressed stroma lamellae donating photon to PSI [41,42]. The antenna system regulates the quantum efficiency of PSII and prepares the photosystems to avoid the deleterious effects of high light or photoinhibition and other stress conditions. The photochemical efficiency is higher in nonstressed photosynthetic systems growing under ambient climatic conditions [43]. However, under stress conditions, the excitation pressure yields ^{3}Chl* and subsequently by intersystem crossing yields $^1O_2$ [44]. These conditions are overcome by transferring LHCII complexes between PSII and PSI, thereby balancing the exciton transfer through the change in antenna size [6] or by the process of nonphotochemical quenching (NPQ) that dissipates excess energy into heat [45]. A recent hypothesis propounded by Grieco et al. [46] postulates that the LHCII phosphorylation, NPQ, electron transfer via cyt b_6f, and turnover of PSII in the maintenance of the photosynthetic machinery in the thylakoid membrane occur in order to prevent oxidative damage of PSI, also.

The role of light-harvesting antenna in cyanobacteria is performed by PBSs, which are attached to the outer surface of the thylakoid membranes [47,48]. PBSs are large multisubunit assemblies of phycobiliproteins. The molecular mass of PBS depends on the species and light quality of the environment [49]. PBS can interact with PSI as well as PSII, and the lipids play a role in controlling PBS–reaction center interaction [50].

The core complex of PSII also contains LHCs, CP43 and CP47, which transfer excitation to pigments in the reaction center. CP43 and CP47 are located nearer to the D1/D2 heterodimer, and two chlorophyll molecules from these complexes are probably involved in excitation energy transfer [51].

The precise structure of the PSII core complex from higher plants is not available at present, but it is supposed to be very similar to that of cyanobacteria. The main difference in the protein composition is related to the extrinsic protein(s) involved in the stabilization of the OEC [51]. The PSII core polypeptides are complemented by three tightly bound polypeptides, PsbO, PsbP, and PsbQ (in eukaryotes) or PsbO, PsbV, and PsbU (in cyanobacteria) [52]. The catalytic center of OEC is located in the luminal side of PSII. This complex contains inorganic cofactors, Mn, Ca, and Cl atoms. The rate of the oxygen evolution, corresponding to an electron flow from the OEC to the PQ pool, and the kinetics of P680 reduction depend on the S_i state transitions [53,54]. It is well known that the OEC accumulates successively four positive charges in the Mn-binding site. These states are denoted as S_0–S_4 states, which reflect different oxidation states of the Mn atoms. These state transitions take place before the evolution of a molecule of oxygen [55–57]. The operation of two parallel mechanisms (noncooperative and cooperative) is suggested to be involved in the oxygen evolution process [58–60]. The oxygen evolution by noncooperative Kok's mechanism [55] is faster, whereas the cooperative mechanism is slower because it involves recombination between various oxygen-evolving centers. Our investigation revealed that organization of the PSII complex (in particular, the peripheral antenna of this complex) strongly influenced the ratio of the PSII centers evolving oxygen by cooperative and noncooperative mechanisms [61–63].

3.2.2 Organization and Function of Photosystem I

PSI is a large macromolecular pigment–protein complex embedded in thylakoid membranes, which catalize the transfer of electrons from plastocyanin to ferredoxin [64,65]. This complex is composed of 15 core subunits, with the associated LHCI consisting of four subunits, Lhca1 to Lhca4 in higher plants [65–68], while in cyanobacteria, PBS acts as peripheral antenna systems under normal growth conditions. The proteins of LHCI are organized in dimers [69]. The core complex of PSI binds to about 100 molecules of chlorophyll *a* and 30 molecules of β-carotene as well to a large number of cofactors, which act as inner antenna, but not involved in electron transfer reactions [64]. Some of the antenna chlorophyll molecules absorb at wavelengths longer than the reaction center

itself and are often referred as the "red forms" [64]. The main part of antenna chlorophylls in cyanobacteria is located in PSI [70]. Cyanobacterial PSI is assembled as a trimer with a molecular weight of more than 1 million Da [71]. PSI antenna among the cyanobacteria differs in content and spectral characteristics of long-wavelength chlorophylls. In some species, the amount of these chlorophylls in monomers and trimers of PSI differs [72 and ref. therein].

The light absorbed by antenna pigments is transferred to the reaction center, P700, which is located in the heterodimeric protein PsaA/B in the central part of the complex [72]. It has been shown that P700 is tightly bound to the core antenna chlorophylls, and so the PSI reaction center cannot be isolated without the antenna chlorophylls [72]. The primary charge separation occurs, and the electron transfer is initiated by P700 in PSI. Electrons are transferred from P700 to the primary electron acceptors, A_0 (chlorophyll *a* molecule). The charge separation is stabilized by series of electron transfer steps involving the acceptor, A_1 (phylloquinone molecule) and from there to the three [4Fe4S] clusters, F_X, F_A, and F_B [71,73]. The electron transport carriers can carry out both cyclic and linear electron flows. The cyclic electron flow creates a proton gradient across the photosynthetic membrane and allows ATP synthesis independent of PSII activity. During linear electron flow, reduced Fd provides the electron necessary for NADP reduction in a reaction catalyzed by ferredoxin:NADP-oxidoreductase [74].

3.2.3 Lipid Composition of Thylakoid Membranes

Thylakoid membranes of photosynthetic organisms are composed of monogalactosyldiacylglycerol (MGDG), digalactosyldiacylglycerol (DGDG), sulfoquinovosyldiacylglycerol (SQDG), and phosphatidylglycerol (PG) [75]. The lipids are important not only for the formation of the lipid bilayer but also for the structure and function of the complexes of the photosynthetic apparatus. Duchêne and Siegenthaler [76] proposed that the current model of thylakoid membrane lipid composition is one that consists simultaneously of bulk and specific lipids. PG and SQDG possess negatively charged head groups, whereas MGDG and DGDG are noncharged lipids. Depending on the nature of its head group, each lipid is expected to have a specific role in the photosynthetic process [75].

Various studies have indicated the influence of lipids in the assembly and function of PSII. Loll et al. [77] found that 14 different lipids are integrally bound to isolated PSII complex. There are four DGDG, six MGDG, three SQDG, and one PG associated with PSII complex [77]. The specific role of different classes of lipids has been studied by biochemical and molecular genetic approaches. Using mutants of *Arabidopsis*, it has been concluded that the total content of anionic lipids is limiting for chloroplast structure and function, and is critical for overall photoautotrophic growth and plant development [78]. It was established in cyanobacteria *Synechocystis* and *Synechococcus* that the anionic lipids SQDG and PG could be functionally complement each other, as their total content is compensated by the synthesis of each other [79].

PG, which is the only and the indispensable anionic phospholipid component of thylakoid membranes [80], plays an important role both in the structure and in the function of the photosynthetic apparatus [81–87]. PG is essential for cell growth and is required for the maintenance of chlorophyll–protein complexes and of normal conformation and activity of both PSII as well as PSI complex [88]. It has been shown that three PG molecules are strongly bound the PSI reaction centers [89] and one to the PSII reaction center between CP43 and D1 [77]. PG is needed for the binding of CP43 to the reaction center core [90]. PG is also essential for the PSII dimer formation and for the electron transfer between the primary and secondary PQ electron acceptors, Q_A and Q_B [81,83,84,91,92]. It plays a pivotal role in the structural stability and function of the donor side of PSII, mainly at the OEC [87]. Besides this, PG is associated with the formation of the oligomeric form of LHCII [93] and with the binding of LHCII to the reaction center of PSII [94]. In addition, this lipid is involved in the stacking of thylakoid membranes forming grana [95].

MGDG and DGDG are major components of thylakoid membranes, amounting to about 50% and 30% of total lipids, respectively [96]. These lipids not only take part in the formation of the lipid

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bilayer, but are also very important for the structure and function of the photosynthetic complexes. Mutant analysis showed that DGDG plays an important role in the structural organization of the photosynthetic apparatus [97]. Only a small fraction of DGDG and MGDG is essential for a fully active PSII [75]. In addition, it has been shown that this small fraction of DGDG is very important for the proper structure and function of PSII, mainly at the donor side [87,98,99]. These studies revealed that a part of the total violaxanthin pool is located in an MGDG phase surrounding the LHCII, whereas another part was bound to the LHCII apoproteins.

The lipids of thylakoid membranes are characterized by high levels of unsaturation of their fatty acids, which determined their physical and biochemical characteristics and play an important role in the function of the photosynthetic apparatus [100,101]. The level of unsaturation is mediated by the activity of fatty acid desaturase. The expression of lipid desaturase genes is light regulated and thereby modulates the thylakoid membrane assembly [102].

3.3 ROLE OF OLIGOMERIZATION OF PIGMENT–PROTEIN COMPLEXES IN THYLAKOID MEMBRANES

Pigment–protein complexes in thylakoid membranes exist mainly as oligomers that are functionally active as monomers but more stable due to their ability to dissipate excess energy [72]. Aggregates of LHCII are the structures characterized by a relatively high rate of excitation quenching, and these structures defend the photosynthetic apparatus against oxidative damage [103,104]. It is suggested that dissipation of excess absorbed energy of aggregates of LHCII takes place with a contribution of peripherally located chlorophylls and carotenoids [72]. The high-light-grown plants show the formation of a dimeric (C2S2) PSII supercomplex [105,106], through the binding of monomeric CP29 and CP26, located near the core of PSII, which mediate a tight or strong (S) binding of trimeric LHCII antenna complex [107]. This supercomplex, however, becomes enlarged (C2S2M2) in low- or moderate-light-grown plants, in order to increase the absorption cross section of PSII, by binding to two more LHCII trimers (M: moderately and L: loosely bound) and one more monomer CP24 [108,109]. The conserved sequence of the antenna polypeptides gives an insight into their specific role in photosynthetic function during evolution [110–114]. In cyanobacteria and green algae, it has been reported that several small subunits are involved in the stabilization of the dimeric form of the PSII complex [115–118].

The PSI complex in the thylakoid membranes of cyanobacteria is organized as a trimer [119–121], while in the higher plant exists as monomer [67]. Earlier experiments reveal that the PSI trimers contain the most "red chlorophylls," and it is suggested that long-wavelength chlorophylls contribute to the dissipation of the excess energy in PSI complex [72]. The physiological relevance of the trimers in cyanobacteria has not yet been fully elucidated.

3.4 INFLUENCE OF MODIFICATION OF PIGMENT COMPOSITION ON FUNCTION AND ORGANIZATION OF PHOTOSYNTHETIC APPARATUS

3.4.1 Influence of Decreased Chlorophyll Content

In higher plants, chlorophyll *b* is specifically required for the assembly, stability, and function of light-harvesting proteins. Chlorophyll-deficient mutants have often been used to investigate the role of chlorophyll proteins for photosynthetic efficiency and organization of the photosynthetic apparatus.

The chlorophyll molecules per antenna pigment complexes associated with PSII vary up to 350 chlorophyll *a* and chlorophyll *b* molecules, but that in the antenna of PSI vary up to 300 chlorophyll *a* molecules only [108,122]. Most of these pigment molecules are organized into LHCs (Lhcb1–6 or 8 in

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PSII and Lhca1–4 in PSI). The amount of these LHCs determines the size of the functional antenna of the photosystems. So the antenna size shows dynamism in every photosynthetic organism varying substantially as per the genetic, physiological, and environmental conditions thereby regulating the developmental aspect of these antenna supercomplexes and their stability. Usually, the size of the antenna matters in the photo-adaptation of plants. Plants growing under low-light intensities show a large chlorophyll antenna size and that under high light have a smaller antenna size [122]. The antenna size in response to light intensity is a mechanism of the chloroplasts to prevent overexcitation of the pigment systems in PSII and PSI, and thereby preventing the possible photooxidative damage [108,122].

Earlier studies in *Hordeum vulgare*, pea, and soybean mutants revealed that a decrease in the synthesis of chlorophyll *b* leads to (1) a smaller functional antenna size for both photosystems, (2) a higher PSII/PSI ratio, and (3) an enhanced PSIIβ content [61,123–125]. Further studies on chlorophyll *b*–less mutants of higher plants reaffirmed that the mutants either lack or have significantly lower amounts of LHCII and LHCI in their thylakoid membranes [126–132]. The relative increase in PSII/PSI ratio is interpreted as a response of the plants to the lowered light-harvesting capacity of PSII in the photosynthetic apparatus of these mutants [123].

In contrast to higher plants, the chlorophyll *b*–less mutant of the green algae—*Chlamydomonas reinhardtii*—showed a decrease in the functional antenna size of PSII, but that of PSI remained fairly constant [133,134]. In addition, Polle et al. [134] suggested the presence of the inner subunits of LHCII and the entire complement of LHCI in these mutants. However, the decreased antenna size of PSII in *C. reinhardtii* leads to a decrease in the quantum yield, saturated rate of photosynthesis, and the photochemical efficiency of PSII [134].

It is well known that PSII complexes exist in two different populations, known as PSIIα and PSIIβ centers [135]. PSIIα centers display a lower chlorophyll *a/b* ratio, larger antenna size, and are located in the appressed region of grana stacks forming a cluster of three to four PSIIα centers. But PSIIβ centers have smaller chlorophyll antenna size and form isolated units in unappressed stroma-exposed region of chloroplast thylakoid membranes [135]. Under certain conditions, interconversion between the two types of PSII centers can be carried out. Accumulation of PSIIβ in the chlorophyll *b*–less thylakoid membranes is correlated with the degree of chlorophyll *b* deficiency [124]. PSIIβ centers are supposed to be an intermediated state in the development of the mature PSII complex [123,124]. *Chlorina f2* chlorophyll *b*–less mutant thylakoid membranes, in which main LHCII (Lhcb 4–6) is absent, lack the differentiation of PSII into PSIIα and PSIIβ centres [123].

The photosynthetic oxygen evolution is altered with the modifications in the organization in PSII complex. The size and degree of the oligomerization of LHCII influence the rate of the oxygen evolution and on the S_0–S_1 state distribution, which suggest the structural changes in the Mn clusters. The enhanced population of centers in the S_0, observed in the membranes with a higher degree of LHCII oligomerization, indicates a reduction of Mn^{3+} to Mn^{2+} [61]. Nugent et al. [136] also have shown that the oxygen evolution process is particularly sensitive to structural changes, which may alter the redox potentials of the S_i state intermediates, hydrogen bonding, and pKa values of amino acids surrounding the complex. Moreover, thylakoid membranes from *Chlorina f2* mutant of barley, with strongly reduced antenna size and lack of the trimeric structure of LHCII [137,138], do not register flash oxygen yields [61]. The earlier facts clearly show the role of the structural organization of the PSII complex for oxygen-evolving activity. On the other hand, the decreased light-harvesting efficiency in mutant cells of *Synechocystis* sp. PCC6803 with partial and complete elimination of PBS decreases the amount of the functionally active PSII centers and the rate of the oxygen evolution [63].

The changes in the chlorophyll *a/b* ratios were observed in plants grown at different light irradiations [139]. Anderson and Aro [140] revealed that the ratio of chlorophyll *a/b* is a sensitive index of membrane staking, that is, the relative proportion of stacked versus unstacked membrane domains, as measured by the cross-sectional area of stacked membranes per chloroplast. Recently we have shown that changes in the ratio of chlorophyll *a/b* correlate with the ratio of the oligomeric (heterotrimers) to monomeric forms of the LHCII [61]. This is also correlated with the negative surface charge density of the thylakoid membranes, which influence the energy redistribution between the

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two photosystems. Our data suggest that higher degree of oligomerization of LHCII, which correlates with lower values of the membrane electric moments, causes a decrease in the energy spillover between PSII and PSI. The degree of LHCII oligomerization (high ratio of the trimeric to monomeric forms of LHCII) has also a determining role in the energy transfer within the LHCII–PSII complex when the chlorophyll *b* is excited, which reveals a significant role of the LHCII oligomerization in the energy transfer between the molecules of chlorophyll *b* and chlorophyll *a*. Therefore, the protein conformational changes in the LHCII complex, related to the oligomerization of the major LHCII and the variation of the electric properties, might regulate the energy transfer between chlorophyll–protein complexes [61]. The influence of the electric properties of the membrane on the energy transfer between the pigment–protein complexes was also shown in the thylakoid membranes from mutants of *Synechocystis* sp. PCC6803 with the modification of the pigment–protein complexes of the photosynthetic apparatus [63].

The variation in the chlorophyll *b* content, which influenced the structure of the PSII complex, also influenced its functional activity. The decreased content of chlorophyll *b* leads to a decreased photochemical activity of both photosystems as well as the electron transport activity of whole-chain electron transport from water to NADP in the pea thylakoid membranes [141,142].

3.4.2 Influence of Decreased Carotenoid Content

Carotenoids are light-harvesting accessory pigments, and they are very important for the function and the stability of pigment–protein complexes in the photosynthetic apparatus [143–145]. There are two main classes of carotenoids: the carotenes that are cyclized or uncyclized hydrocarbons (e.g., β-carotene), and the xanthophylls that are oxygenated derivatives of carotenes (e.g., lutein, violaxanthin, antheraxanthin, zeaxanthin, and neoxanthin) [146]. These pigments are located in the antenna and core complexes of both photosystems and have a special role in the thermal dissipation of excess light energy [147,148].

The most important function of carotenoids is the photoprotection of the photosynthetic apparatus by quenching triplet chlorophyll, singlet oxygen, and other reactive oxygen species [149]. β-Carotene performs the critical role of photoprotection in the reaction centers by quenching triplet chlorophyll and singlet oxygen [150]. Carotenoids are structural components of PSII and PSI, and they are involved in the stabilization of the LHCII trimers as well as in the assembly of LHCII monomers and PSII core complex [151–154]. Ruban et al. [155] found that violaxanthin and zeaxanthin induce disaggregation and aggregation of the major LHCII, respectively. The monomeric forms of LHCII undergo conformational changes upon lumen acidification [156], preferentially the xanthophyll binding site in L2 subunits of these polypeptides, and facilitate the exchange of violaxanthin to zeaxanthin for the enzymatic de-epoxidation [157] under high-light or photo-inhibitory conditions and is correlated to NPQ [158]. This process is essential for the photoprotection of plants [159,160].

The amount and composition of the carotenoids depend on the environment conditions [161–166]. Demmis-Adams et al. [167] showed that the ratio of the carotenoid molecules per chlorophyll molecule is typically greater in the sun compared with shade leaves of higher plants. There is a strong increase in the fraction of xanthophyll cycle pigment in sun leaves, which play an important role in the photoprotection of photosynthetic apparatus under environmental stress [168]. On the other hand, carotenoids are indispensable constituents of the photosynthetic apparatus, being essential not only for antioxidative protection but also for an efficient synthesis and accumulation of photosynthetic proteins, especially that of PSII antenna subunits [169].

Moreover, it has been ascertained that carotenoids can also operate in thylakoid membranes as a stabilizer of the lipid phase [169]. Recently, it was shown that the fluidity of photosynthetic membranes in cyanobacteria is influenced by the ratio of polar to nonpolar carotenoid pools under different environmental conditions [166]. The elimination of both xanthophylls and/or polyunsaturated fatty acids caused remarkable alterations of the molecular architecture mainly in the inner side of lipid bilayer.

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Rakhimberdieva et al. [170] proposed that the quenching induced by carotenoids could be a new regulatory mechanism protecting photosynthetic apparatus of cyanobacteria against photodamage. The authors presented spectral and kinetic evidence that cyanobacterial carotenoids activated by absorbing blue light induce reversible quenching of PBS emission.

A decrease in the carotenoid content is accompanied by changes in the amount of chlorophylls [62,171]. It was suggested that the decrease in the amount of chlorophylls could be the result of a carotenoid deficiency–induced photooxidation of the chlorophylls. Recently, we have shown the structural changes in the photosynthetic apparatus and a decrease in functionally active PSII centers as a result of decreased carotenoid content [62]. In addition, it has been shown that the core antenna complex of PSII is more damaged under illumination than the peripheral complexes, which is a result of higher sensitivity of these complexes to high light [62,172]. Carotenoid depletion leads to the inhibition of the photochemistry of both photosystems, a decrease in the ratio of the functionally active PSIIα to PSIIβ centers, as well as the rate constant of the oxygen evolution [62]. In addition, it has been shown that the changes in the carotenoid composition, after treatment with bleaching herbicide (fluridone), influence the lipid-to-protein ratio, membrane fluidity, the structural organization of the chloroplasts and antenna complex of PSII, as well as the stability of the membrane complexes [173,174]. All these changes influence the function of both photosystems, with relatively more influence on PSII than on PSI [62]. Also it was shown that these effects have stronger influence on the structural organization and function of PSI in the grana margins than in the stroma lamellae [62].

3.5 INFLUENCE OF MODIFICATION OF LIPID COMPOSITION ON FUNCTION OF PHOTOSYNTHETIC APPARATUS

Studies of a *Synechocystis* PCC6803 mutant, in which a gene encoding PG phosphate synthase (pgsA) has been disrupted, revealed that long-term deprivation of PG resulted in a decrease in the activities of both photosystems and in the degradation of PSI trimers and monomerization of PSII [85,86]. In the PG-depleted thylakoid membranes, there is a strong decrease in the energy transfer from PSII to PSI antenna pigments as well as the changes in the surface charge density of the thylakoid membranes [175].

The depletion of the second anionic lipid (SQDG) in thylakoid membranes of *C. reinhardtii* leads to a decrease in the PSII activity [176]. This observation could be due to impairment in PSII reaction center or a decrease in the efficiency of the energy transfer from LHC to the reaction center. A diminished PSII activity due to a decreased amount of SQDG is probably brought about either by a conformational change in PSII complex caused by the lack of specific binding of SQDG of the PSII complex in the thylakoid membrane or by the changes in the lipophilic surrounding at the Q_B binding site of the PSII complex even without the conformational changes in the protein complex [177].

Investigation with the mutants of *Arabidopsis thaliana* reveals that the total content of the anionic lipids is limiting for chloroplast structure and is critical for the photoautotrophic growth and development of plants [78,178]. The DGDG-deficient mutant of *A. thaliana* showed a decreased ratio of PSII to PSI, which is a result of a decrease in the amount of PSII and a concomitant increase in the amount of PSI [179]. This decrease in the amount of PSII is compensated with an increase in the amount of peripheral (main) LHCII relative to the inner antenna complex of PSII [179].

The role of polyunsaturated lipids is established by the studies on fatty acid desaturation-deficient mutants [180,181]. The enzyme brings about different saturation levels of membrane lipids. The modifications in the membrane lipids bring about a change in the energy redistribution between PSII and PSI, and changes in the surface electric charge distribution as a consequence of modification of the lipids and/or changes in the organization of the supramolecular complexes in the thylakoid membranes [182]. On the other hand, the changes in the membrane as a result of a decrease in lipid unsaturation do not inhibit cation-induced changes in the excitation energy distribution between chlorophyll–protein complexes of thylakoid membranes as well as their lateral

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rearrangement [180,183]. It has been shown also that a decrease in the proportion of the polyunsaturated fatty acids of the thylakoid lipids increases the stability of protein–protein interaction between and within PSII complex [184]. The replacement of all polyunsaturated fatty acids by monounsaturated fatty acids suppressed the growth of the cyanobacterium *Synechocystis PCC* 6803 [185] due to severe impairment of photosynthetic function.

3.6 CONCLUSIONS

In conclusion, the influence of the modification of the structural organization of the photosynthetic apparatus, in particular the pigment and lipid composition, can be summarized as follows (Figure 3.1):

1. The variation of the chlorophyll and carotenoid content affect the organization of the LHC and subsequently modify the PSII supercomplex. The earlier alterations influence the stability of the complex, its light-harvesting ability and photoprotection functions, as well as the primary photochemistry and oxygen-evolving activity.
2. The changes in the pigment composition also infuence the lipid phase of the membrane.
3. The amount of the PG affects the oligomerization of the thylakoid membrane pigment–protein complexes and the functional activity of both the photosystems, PSII and PSI.
4. A decrease in the amount of SQDG leads to an impairment of PSII reaction center and/or a decrease in the efficiency of the energy transfer from light-harvesting complex to the reaction center.

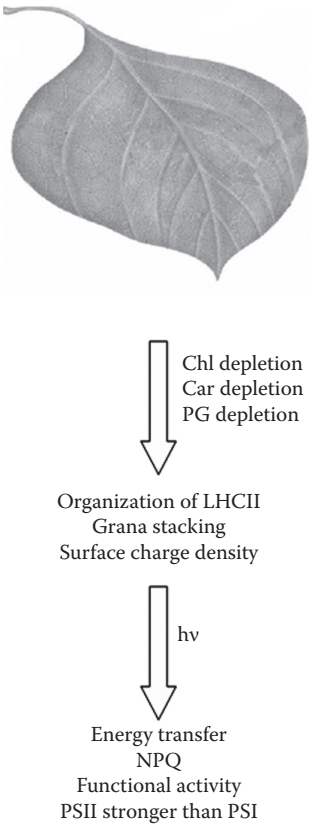

FIGURE 3.1 Effect of decreased amount of carotenoids, chlorophylls, and lipids on the structure and function of the thylakoid membranes.

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The present review illustrates that changes in the pigment and lipid composition strongly influence the organization and function of the photosynthetic antenna complexes. Extensive studies on the role of the antenna complex on the structural and functional stability of photosystems (PSII and PSI) so far emphasize its regulatory role on energy distribution, dissipation, and reorganization of the pigment–protein complexes in the thylakoid membranes leading to their functional stability. There is a myriad of information available on the role of these complexes preferably for the stability of PSII. However, antenna chlorophyll–protein complexes, through their redistribution and mobility in the thylakoid membranes, also play a vital role in the stability of PSI. With the advent of membrane proteomics, x-ray crystallographic data, and single-cell imaging systems, studies on the role of antenna pigment protein systems are certainly going to change, in the changing environment of the future.

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