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Review

Dynamics of photosynthetic membrane composition and function

Anastasios Melis

Department of Plant Biology, University of California, Berkeley, CA (U.S.A.)

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Key words: Photosystem stoichiometry; Molecular feedback regulation; Photosystem II heterogeneity; Photosynthetic unit size; Reaction center repair cycle

Contents

Abbreviations: Chl, chlorophyll; PS, photosystem; P680, photochemical reaction center of PS II; Phe, pheophytin primary electron acceptor of PS II; Q_A, primary quinone of PS II; P700, photochemical reaction center of PS I; F_0, non-variable fluorescence yield obtained when all PS II reaction centers are open; F_v, variable fluorescence yield emitted as PS II reaction centers become closed; F_{max}, maximum fluorescence yield emitted when all PS II reaction centers are closed ($F_{max} = F_0 + F_v$); LHC, Chl *a-b* light-harvesting complex; LHC II, LHC of PS II; LHC I, LHC of PS I; PS II_α, PS II centers having $\geq$ 210 Chl ($a + b$) molecules in their light-harvesting antenna; PS II_β, PS II centers with about 130 Chl ($a + b$) molecules; PS II_γ, PS II centers with approx. 50 Chl *a* molecules; DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea; SDS-PAGE, sodium dodecyl sulfate polyacrylamide gel electrophoresis.

Correspondence: A. Melis, Department of Plant Biology, 411 Genetics and Plant Biology Building, University of California, Berkeley, CA 94720, U.S.A.

1. Introduction

In oxygenic photosynthesis, electron transport for the generation of reductant, in the form of reduced ferredoxin and NADPH, and for the formation of ATP takes place in the thylakoid membrane. It requires coordinated interaction between a large number of electron carrier compounds and enzymatic proteins that facilitate the transfer of electrons from H_2O molecules to ferredoxin and $NADP^+$. The electron-transport components are localized in the thylakoid membrane and facilitate the transfer of electrons laterally in the plane of the membrane from the grana regions (appressed thylakoids) to the stroma-exposed regions (unappressed thylakoids) [1–3]. Functionally, electron-transport occurs from intermediate-to-intermediate in a sequential manner formulated as the Z-scheme by Hill and Bendall [4]. The overall process of electron-transport from H_2O to $NADP^+$ is strongly endergonic and is realized through the input and utilization of light energy. The absorption of light and the conversion of excitation energy to chemical energy takes place in Photosystem II (PS II) and Photosystem I (PS I) in the thylakoid membrane [5]. Light energy in PS II facilitates the generation of a strong oxidant capable of oxidizing H_2O molecules. Light energy in PS I facilitates the generation of a strong reductant capable of reducing ferredoxin and $NADP^+$.

The bioenergetics of photosynthesis have been the subject of intense investigation over the last 30–40 years. As a result, significant progress has been achieved, leading to identification of functional intermediates in the thylakoid membrane and to advances on the mechanism of electron-transport and photophosphorylation. As emphasis shifted to structure–function relations in recent years, a number of publications suggested unique dynamic features in photosynthetic membrane composition and function. Included are reports of variable stoichiometry of complexes in the thylakoid membrane and of variable chlorophyll antenna size for the two photosystems. Also included are reports of heterogeneity in Photosystem II, of the apparent inability of a small pool of PS II centers to reduce plastoquinone, of the rapid turnover of the PS II reaction-center protein, and of photoinhibition (damage) in the function of the PS II reaction center under adverse conditions. The goal of this review is to put these features of the thylakoid membrane into perspective, to address cause and effect relationships between the different phenomena, and also to address potential mechanisms for the regulation of these phenomena at the molecular level.

I-A. Photosystem II

I-A.1. Localization

In mature higher plants and green algae, PS II shows a distinct distribution pattern in the thylakoid membrane. Approximately 70–80% of PS II centers are localized in the tightly appressed membranes of the grana regions [1]. The remaining Photosystem II centers are found in the stroma-exposed thylakoids [3,6–8]. Cyanobacteria and red algae lack the differentiation of grana and stroma-exposed lamellae. In these photosynthetic organisms, PS II is associated with the phycobilisome (PBS). The latter is a macromolecular structure, attached peripherally to the stromal side of the thylakoid membrane and is unique to cyanobacteria and red algae. It serves as the auxiliary light-harvesting antenna of PS II [9–12].

I-A.2. Composition

All PS II electron transport intermediates are contained in the so-called D1/D2 32/34 kDa heterodimer protein, coded for by organelle genes *psb*A and *psb*D, respectively [13–17]. Although the precise binding site(s) are not yet known, it is likely that the D1/D2 heterodimer helps stabilize 4 Mn atoms on the lumenal side of the thylakoid membrane. Each protein is known to contain one electron transport intermediate tyrosine residue (denoted as Z and D, respectively). By analogy to the purple bacterial reaction center [18], it is suggested that each protein binds one of the photochemical reaction center chlorophylls (Chl_2) that form P680, one pheophytin, and a quinone-binding site. D1 contains

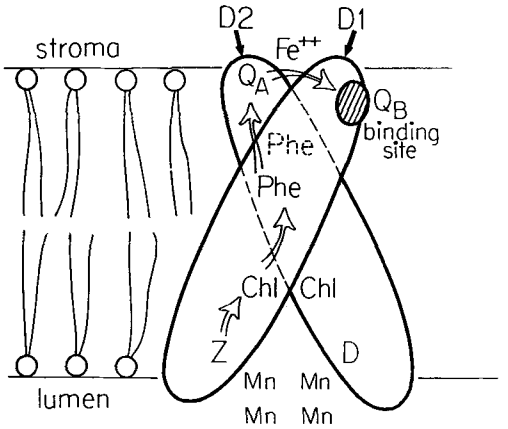

Fig. 1. Schematic representation of the PS II reaction center complex containing the D1/D2 32/34 kDa heterodimer, coded for by organelle genes *psb*A and *psb*D, respectively. Arrows indicate the electron flow pathway from manganese via Z (tyrosine) to the plastoquinone (Q_B) binding site in the PS II-RC.

the plastoquinone (Q_B) or herbicide-binding site, whereas D2 contains a specialized bound plastoquinone molecule (Q_A) that can be reduced to the plastosemiquinone anion form. The PS II reaction center (PS II-RC) may be noted for a structural symmetry (D1 and D2 are homologous proteins) and a functional asymmetry since electron transport is thought to proceed from Mn (D1 and D2) to Z, Chl, Phe (in D1) to Q_A (in D2) to Q_B (in D1) (Fig. 1).

Earlier research revealed a highly unusual property for the D1/32 kDa polypeptide. This reaction-center protein, also known as herbicide-binding or Q_B-binding protein of PS II, accounts for less than 1% of the total thylakoid protein, yet the rate of its synthesis is comparable to that of the abundant large subunit of the RuBP-carboxylase in the chloroplast [19–21]. Since steady-state levels of the D1/32 kDa polypeptide in thylakoids are low, it was inferred that rates of degradation must be high. The fast turnover of the D1/32 kDa polypeptide implicated a need for frequent replacement of the protein. The mechanistic details of this unique phenomenon are rather unclear.

The photochemical apparatus of PS II contains, in addition to the PS II-RC, two 'core antenna' chlorophyll proteins CP47 and CP43 (the organelle *psb*B and *psb*C gene products, respectively) [22,23]. Collectively, PS II-RC, CP47 and CP43 define the PS II-core and they contain about 37 Chl *a* molecules [24]. Light-harvesting by PS II is further aided by the auxiliary chlorophyll *a-b* light-harvesting complex (please see LHC II, below).

Present in PS II are a number of proteins that do not bind chlorophyll. Closely associated with the PS II-RC are two polypeptides (9 kDa and 4 kDa coded for by organelle genes *psb*E and *psb*F) carrying, via two histidine ligands, a *b*-type heme (thus forming a cytochrome *b*-559 molecule) [25]. There is evidence suggesting the presence of two cytochrome *b*-559 molecules per PS II reaction center in situ [26–28]; however, this is still a point of debate in the literature [29]. There are three extrinsic membrane proteins in the lumen (33, 23 and 17 kDa polypeptides are nuclear *psb*O, *psb*P and *psb*Q gene products [30] believed to play a role in Mn stability and in the regulation of Ca^{2+} and Cl^- concentrations near the water-oxidizing complex [31]. A 10 kDa phosphoprotein of unknown function (the organelle *psb*H gene product) is also a component of PS II [32,33]. The phosphorylation/dephosphorylation of this integral thylakoid membrane protein is believed to be subject to the redox control of the plastoquinone pool [34]. There are still other polypeptides of unknown function (the *psb*I-*psb*N and the *psb*R gene products) believed to be associated with PS II [17,30].

I-A.3. Function

Light energy in PS II is trapped by the photochemical reaction center P680, where it causes a direct endergonic charge separation between P680 and the primary electron acceptor pheophytin ($P680^* \cdot Phe \rightarrow P680^+ \cdot Phe^-$) [35,36,112]. The electron from Phe^- is transferred to the primary quinone acceptor, Q_A, thus helping to stabilize the charge separation reaction [37]. Subsequently, the electron is transferred from Q_A^- to the secondary quinone acceptor Q_B [38,39]. The reduction of plastoquinone may not be the only function performed by PS II. The possibilty of cyclic electron-transport involving the cytochrome *b*-559 heme(s) has been discussed in the literature [25,26,40]. Photosystem II is also capable of a direct reduction of ferredoxin without the involvement of PS I, as evidenced from the steady-state photoreduction of ferredoxin-$NADP^+$ by isolated and purified PS II reaction centers [41].

Electron-transport on the oxidizing side of PS II includes electron donation to $P680^+$ from the tyrosine residue (Z) on D1 [42,43], and electron donation from ligand Mn to Z^+. The stepwise accumulation of four positive charges on the oxidizing side of PS II constitutes a necessary and sufficient condition for the oxidation of two H_2O molecules, the release of four electrons, four protons and of molecular O_2 [44]. Recent models emphasized a stepwise light-induced oxidation of each of the four Mn atoms associated with PS II [45–47]. However, results from EPR spectroscopy [48] and X-ray absorption spectroscopy [49] may not be entirely consistent with this interpretation. Rather, the oxidation of a histidine residue in D1 was proposed to occur during the so-called S_2 to S_3 transition [50].

In summary, PS II performs a unique function in nature because it generates a strong oxidant ($P680^+$) capable of extracting electrons and releasing protons from energy-poor but abundant H_2O molecules. This function of PS II sustains virtually all life on earth.

I-A.4. Photoinihibition

The photosynthetic capacity of a plant can be severely lowered following exposure to light intensities in excess of that required to saturate photosynthesis [51]. The threshold intensity for the onset of photoinhibition can be very low, as in shade-adapted species and in plants where environmental stress conditions prevent high rates of CO_2 fixation (e.g., chilling, drought, etc) [52]. It is generally accepted that photoinhibition adversely affects the function of PS II and it is manifested as lowered rates of electron transport and oxygen evolution. Two different hypotheses have been forwarded in order to explain the mechanism of photoinhibition. One suggested damage to the reducing side of PS II, either at the Q_B-binding site [53,54] or at the primary quinone Q_A site [55]. Alternatively, work by other investigators [56–60], suggested that photoinhibition impairs the oxidizing side of PS II and prevents a stable charge separation, indicating damage either to the reaction center (P680) or to tyrosine (Z). A consequence of photoinhibition is the conversion of cytochrome *b*-559 from a high-potential to a low-potential form [55].

I-B. Chlorophyll a-b light-harvesting complex II (LHC II)

I-B.1. Composition

In higher plants and green algae, light absorption in PS II is aided by the auxiliary chlorophyll *a-b* light-harvesting complex (LHC II). The LHC II was discovered more than 20 years ago as a major Chl-containing protein band resolved in SDS-PAGE of non-thermally denatured proteins from higher plant chloroplasts [61]. Since then, considerable information has been gathered on LHC II in terms of its structure and function in the thylakoid membrane [62]. It was demonstrated that LHC II contains about equal numbers of Chl *a* and Chl *b* molecules (Chl *a*/Chl *b* = 1.17). When denatured, polypeptides of the LHC II migrate on SDS-PAGE in the 25–30 kDa region and may contain at least four distinct subunit polypeptides [63,64]. The origin of these polypeptide forms is not known, although evidence suggested that a single precursor LHC protein generated from a single gene can give rise to more than one LHC II polypeptide during in vitro import into chloroplasts [65–69). Collectively, LHC II polypeptides may contain over 200 Chl $(a + b)$ molecules out of the average of about 250 Chl $(a + b)$ molecules in the fully developed antenna of PS II in higher plant chloroplasts [12,70].

Polypeptides of the LHC II are coded for by the nuclear *cab* gene family. Work by Dunsmuir [71], among others, has uncovered the existence of five distinct *cab* gene families. More than 20 genes from ten different species have now been sequenced [72]. On the basis of nucleotide sequencing information, some heterogeneity in both length and polypeptide composition was predicted. *cab* genes code for a transit peptide of about 35 amino acids which is attached to the N-terminus of the mature protein. The physiological significance of the *cab* multigene families is largely unknown [65].

Analysis of the LHC II by SDS-PAGE resolved four distinct subunits in peas and soybean [63,73]. The apparent molecular masses (in soybean) were calculated to be: Polypeptide **a** (29 kDa), polypeptide **b** (28 kDa), polypeptide **c** (27.2 kDa), and polypeptide **d** (26.8 kDa) [63,73]. These polypeptides of the LHC II exhibit a high degree of homology in their primary amino-acid sequence, with the major differences being in their amino termini [65]. Polypeptide **a** is probably the apoprotein of the chlorophyll-protein complex CP29 [73,74–76], or of the chlorophyll-containing complex *LHC IIa* according to the terminology used by Thornber [64,77]. Polypeptide **d** may be the apoprotein of CP27 [78], or of the *LHC IIc* [64,77]. Collectively, polypeptides **b**, **c** and **d** are probably the apoproteins of the major oligomeric form of LHC II isolated from non-denaturing green gels (*LHC IIb* according to the terminology of Thornber [64,77], CPII* according to Green [79] and Staehelin [80], LHCP1 according to Anderson [81]). It is difficult to assign unequivocally a polypeptide stoichiometry to each non-denatured green LHC II because both the non-denatured Chl-proteins and their apoproteins on fully denaturing gels migrate very near each other [77].

I-B.2. Supramolecular organization

The three-dimensional structure of LHC II proposed by Kuhlbrandt [82] infers a radially symmetric complex with three polypeptide subunits per LHC II complex. Patterns of antenna size growth during the development of PS II indicated the existence of two distict subpopulations of LHC II [83,84]. A 'tightly bound' component of the LHC II (LHC II-inner) contained about 80 Chl $(a + b)$ molecules and was postulated to have a $(\mathbf{bcd}) \cdot (\mathbf{b_2c})$ hexameric configuration [73]. The second complement of the LHC II is known as LHC II-peripheral, it may have a $(\mathbf{b_2c})_n$ configuration where $2 \leq n \leq 7$, and it is believed to contain 80 Chl $(a + b)$ molecules when $n = 2$, 120 Chl $(a + b)$ molecules when $n = 3$, and so forth [73]. The two LHC II complements (LHC II-inner and LHC II-peripheral) are probably subpopulations of Anderson's LHCP1 [81], Green's CPII* [79] and Thornber's *LHC IIb* [64,77].

Biochemical support for this supramolecular organization of the LHC II was derived from independent work by other investigators. Larsson et al. [85–87] presented evidence on differential phosphorylation patterns and differential association of two subpopulations of spinach LHC II (inner and peripheral) with PS II. They measured a ratio of (27 kDa)/(25 kDa) = 2/1 for the LHC II-peripheral, in agreement with the proposed $(\mathbf{b_2c})_n$ configuration. However, Larsson et al. [87] re-

ported the presence of a 27 kDa polypeptide only in the LHC II-inner. A non-denaturing preparative isoelectric focusing method yielded two distinct LHC II complexes having a polypeptide ratio (27 kDa)/(25 kDa) = 2/1 and (27 kDa)/(25 kDa) > 10/1. It was suggested these two complexes correspond to the LHC II-peripheral and LHC II-inner, respectively [88–89].

Further evidence for two distinct subpopulations of LHC II was derived from particle size measurements in freeze-fractured thylakoids [80,90,91]. In the latter work, the tightly bound complement of the LHC II was identified with the CP29 and CP24 of green gels whereas the peripheral component was identified with the so-called CPII and CPII*. Thus, there is some agreement in the current literature on the composition and supramolecular organization of the LHC II-peripheral. However, both composition and supramolecular organization of the LHC II-inner remain in the realm of the uncertain.

Further uncertainty exists on the spatial arrangement of LHC II-inner and LHC II-peripheral with respect to the PS II-core complex. One of the models in the current literature postulates an obligatory transfer of excitation from LHC II-peripheral through LHC II-inner to PS II-core. This would require a linear arrangement of the three modular entities in the thylakoid mebrane [73,87,88]. However, other models have presented a parallel rather than linear arrangement in which LHC II-inner and LHC II-peripheral may feed excitation energy independently into CP47 and CP43 of the PS II-core [22,92–95]. It is generally accepted that subunit **a** (CP29) is a linker in excitation energy transfer from LHC II to the PS II-core [96]. Hence, the answer to the above uncertainty may depend upon whether subunit **a** (CP29) is associated only with the LHC II-inner or whether it is associated independently with the two subpopulations of the LHC II.

I-C. Photosystem I

The photochemical apparatus of PS I is composed of the PS I-core and the auxiliary Chl *a-b* light-harvesting antenna (LHC I). The PS I-core contains the 84 kDa heterodimer, coded for by organelle genes *psa*A and *psa*B [97,98] (these PS I subunits migrate on SDS-PAGE in the 62–70 kDa region). Noncovalently bound to this complex is the photochemical reaction center P700 of PS I (a Chl *a* dimer), two electron acceptors including A_0 (a Chl *a* monomer), and A_1 (a phylloquinone molecule). Covalently bound to the complex is the primary 4Fe-4S iron-sulfur cluster X. The *psa*A and *psa*B gene products also bind a total of about 100 Chl *a* molecules [12,99]. Associated with the protein of the *psa*A-*psa*B gene products is a 9 kDa protein (the organelle *psa*C gene product) containing the 4Fe-4S iron-sulfur clusters B and A. Electron transport in PS I originates in P700 (photooxidation of P700 is a strongly endergonic reaction) and proceeds through A_0, A_1, and the iron-sulfur centers X, B and A [100]. Thereafter, electrons are transferred to ferredoxin on the stromal surface of the PS I complex whereas electron donation to $P700^+$ occurs on the lumenal side of the PS I complex by soluble plastocyanin.

The accessory light-harvesting antenna of PS I (LHC I) contains 80–120 Chl *a* and Chl *b* molecules. In contrast to the Chl composition of the LHC II, the LHC I contains more Chl *a* than Chl *b* (Chl *a*/Chl $b \approx 3.5/1$). Polypeptides associated with the LHC I migrate on SDS-PAGE in the 20–25 kDa region [101,102] and are immunologically distinct from those of LHC II [103].

II. Photosystem stoichiometry in oxygenic photosynthesis

Twenty years after the formulation of the Z-scheme, it was widely accepted that PS II and PS I centers existed in a 1:1 ratio in the thylakoid membrane of oxygenic photosynthesis. This assertion was apparently supported by measurements of the electrochromic band-shift at 518 nm [104]. However, thylakoid membrane fractionation experiments showed PS II electron-transport activity in the grana fraction and PS I electron-transport activity both in the grana and in stroma-exposed thylakoids [105,106]. These early fractionation experiments raised questions about the organization and stoichiometry of the photosystems in the thylakoid membrane.

One way to address the question of photosystem stoichiometry is by sensitive absorbance difference spectrophotometry that provides direct quantitation of integral components in the reaction center of PS II and PS I [107]. This method for the quantitative determination of PS II and PS I in thylakoid membranes offers the advantage of 'looking' directly at the reaction center complex of each photosystem. It does not depend on measurements of linear electron flow in the thylakoid membrane where many other electron-transport components must participate. In this approach, thylakoid membranes are poised electrochemically in the dark so that a subsequent illumination will induce primary charge separation in the reaction centers of PS I and PS II. The ensuing oxidation-reduction reactions can be measured spectrophotometrically in a wavelength region specific to the molecule undergoing the redox transition.

The spectrophotometric approach was applied in the quantitation of the specialized quinone acceptor Q_A of PS II (light-induced absorbance change at 320 nm, ΔA_{320}) [70,107–111], in the quantitation of the primary electron acceptor pheophytin (ΔA_{685}) [35,60,108], in the quantitation of the photochemical reaction center P680 of PS II (ΔA_{680}) [112–114], and in the quantitation of

TABLE I

Chlorophyll ratios and photosystem stoichiometry in cyanobacteria, mature vascular plant chloroplasts, Chl b-deficient mutants and developing chloroplasts

Component quantitation (mol:mol) is based on the Chl $(a+b)$ content.

	Chl a / Chl b	Chl / PS I	Chl / PS II	PS II / PS I
Cyanobacteria and red algae	–	160	370	0.4
Green algae	3.7	750	550	1.4
Wild-type chloroplasts [a]	2.8	600	350	1.7
Tobacco *Su/su*	4.7	330	120	2.7
Barley chlorina f2	∞	300	100	3.0
Intermittent-light developing plastids	∞	250	60	4.1

[a] Representative of sun-adapted species like spinach, pea, barley, tobacco.

the photochemical reaction center P700 of PS I (ΔA_{700}) [107,115].

Additional methods for the quantitation of PS II involved the measurement of the Q_B/herbicide binding sites in thylakoid membranes [116–119], the cytochrome *b*-559 content [27,28], and the amounts of Mn and Z [113,120,121]. Repetitive flash illumination of photosynthetic material, in vivo and in vitro, leads to oxidation of water and permits the quantitation of PS II from the oxygen yield per flash [111,122–126].

Quantitation measurements with thylakoids from spinach and from other sun-adapted plants showed the presence of one PS II reaction center per about 350 Chl $(a+b)$ molecules and the presence of one PS I reaction center per about 600 Chl $(a+b)$ molecules. These measurements suggested a photosystem stoichiometry PS II/PS I = 1.7 : 1.0, i.e., more PS II than PS I reaction centers in the thylakoid membrane of higher plant chloroplasts [70,107,127].

Further measurements in different laboratories, and with thylakoid membranes from diverse photosynthetic species, indicated variability in the ratio of PS II and PS I reaction centers. Cyanobacteria and red algae commonly displayed photosystem stoichiometry PS II/PS I ratios between 0.3 and 0.7 (Table I) [107,123,124,128–130]. Green algae have PS II/PS I = 1.4 : 1.0 [131–134]. Higher plant chloroplasts from spinach and from other species grown under direct sunlight have PS II/PS I = 1.8 : 1.0 [127,135]. The chlorophyll deficient tobacco *Su/su* [109,136], the Chl *b*-less chlorina f2 mutant of barley [84] and developing chloroplasts [24,137,138] display PS II/PS I > 2 (Table I).

The experimental evidence that photosystem stoichiometry ratios (PS II/PS I) differed from 'strict unity' (and showed large variations among different photosynthetic membranes) was contrary to the conventional assumption based on the Z-scheme. Moreover, these results raised the question of whether the photosystem stoichiometry in any given thylakoid membrane is fixed or whether it could be variable depending on the prevailing environmental, genetic and developmental conditions. To date, following considerable debate in the literature [107,111,122,125,139–143], it is generally accepted that photosynthetic organisms have the ability to regulate the photosystem stoichiometry in the thylakoid membrane and, thereby, to adjust and optimize the process of light absorption and linear electron transport. Brief summaries of regulation in the PS II/PS I stoichiometry are given below.

II-A. Regulation of photosystem stoichiometry in response to mutations

Virescent (Chl *b*-deficient) mutants played an important role in revealing a cause-and-effect relationship between the balanced utilization of light by the two photoreactions and the photosystem stoichiometry in the thylakoid membrane. Virescent plants are developmental mutants in which the accumulation of Chl and the development of the thylakoid membrane is retarded. Typical among the Chl *b*-deficient mutants are the *Nicotiana tabacum* (tobacco) yellow-green *Su/su* and the yellow *Su/su* var. Aurea [136,144], the soybean Cy_9y_9 and $CY_{11}y_{11}$ [83,145], the No. PBI line LMG mutant of sugar beet [146], and the OY-YG mutant of maize [80], among others (Table II). They have Chl *a*/Chl *b* ratios that are significantly higher than the corresponding wild-type, smaller photosynthetic unit size (lower Chl/P700 and Chl/Q_A ratios, Table II), and they often show altered thylakoid membrane ultrastructure. The lag in Chl *b* accumulation retards or inhibits the assembly/incorporation of the Chl *a-b* LHC of PS II and PS I. It is known that 80% or more of the Chl antenna of PS II consists of the Chl *a-b* LHC II, whereas only about 40% of the Chl antenna of PS I is made up by the LHC I [27,70,102]. It follows that a Chl

TABLE II

Photochemical apparatus organization in Chl b-deficient mutants

Tobacco [109,136,210,212], soybean [83], sugarbeet [146], maize [91].

Chloroplast type	Chl a / Chl b	Chl / P700	Chl / Q_A	*PS II / PS I*
Wild type	2.8	600	350	1.7
Tobacco *Su/su*	4.7	330	120	2.7
Tobacco *Su/su* var. Aurea	5.7	300	75	4.0
Soybean y_9y_9	5.0	500	200	2.5
Soybean $Y_{11}y_{11}$	5.5	480	170	2.8
Sugarbeet No. PBI line LMG	5.2	410	170	2.4
Maize OY-YG	5.6	540	230	2.4

b-deficiency will attenuate the light-harvesting capacity of PS II more than that of PS I and, therefore, PS II units will have an antenna size significantly smaller than that of PS I.

An important common feature in all virescent mutants is the elevated PS II/PS I ratio in the thylakoid membrane (Table II). Since the mutation reduced disproportionately the light-harvesting capacity of PS II, elevated PS II/PS I ratios may be thought of as a response of the plant in restoring the balance of light absorption between PS II and PS I, in essence correcting the effect of the mutation.

II-B. Regulation of photosystem stoichiometry by light-quality

Evidence for the regulation of photosystem stoichiometry by light-quality was provided upon growth of oxygen evolving photosynthetic organisms under light conditions that favored sensitization of one photosystem over the other. For example, in cyanobacteria and red algae, a PS II light would sensitize preferentially the phycobilisome antenna of PS II (550–620 nm region). In higher plant chloroplasts, PS II light would be absorbed more strongly by the Chl *b*-containing antenna of PS II (at 475 and 650 nm) and to a lesser extent by Chl *a* (at 435 and 680 nm). On the other hand, a PS I light source would emit more in the wavelength region where Chl *a* absorbs strongly, and considerably less at wavelengths where the PS II accessory pigments absorb.

Evidence indicated structural adjustments in thylakoid membranes as a plant response to PS II or PS I light conditions during growth. Pea plants grown under PS I light had extensive grana stacks and short intergrana, or stroma-exposed thylakoids. Plants grown under PS II light had small grana stacks and extensive stroma-exposed lamellae [127,137,147]. Similarly, cyanobacteria and red algae under PS I light had high phycobilin-to-Chl ratios, whereas the converse was true under PS II light conditions [123,130,148–150].

The structural changes described above were accompanied by adjustments in photosystem stoichiometry in the thylakoid membrane (Table III). Both in the phycobilisome-containing organisms and in higher plants chloroplasts, the relative PS II/PS I ratio was low under conditions of PS II excitation (PS II light) and substantially higher under conditions of PS I excitation (PS I light) [123,127,130,137,148–153]. Thus, the quality of light during plant growth exerts influence on the thylakoid membrane structure, composition and function. The response of the plant is meaningful since the adjustment of the PS II/PS I ratio restores an optimized (balanced) absorption of light by the two photosystems [149]. This response allows the plant to maintain a high quantum efficiency of photosynthesis under diverse light quality conditions [154–156].

TABLE III

Photosystem stoichiometry under different light qualities

Chloroplast type	Chl *a* / Chl *b*	Chl / P700	Chl / Q_A	PS II / PS I
Pea chloroplast				
PS II-light	3.0	530	430	1.2
Sunlight	2.8	640	360	1.8
PS I-light	2.5	750	330	2.3
Synechococcus 6301				
PS II-light	–	155	580	0.27
Sunlight	–	160	355	0.45
PS I-light	–	170	240	0.70

These findings underscore the dynamic nature of thylakoid membrane composition and function in oxygenic photosynthesis and have important implications for plant growth under different light-quality conditions. For example, there are pronounced gradients in light quality within a single leaf [157–159] and within the canopy of a single tree or within the canopy of a forest [160]. Similarly, strong variations in the light-quality occur within the aquatic environment [161]. Most of these gradients in light-quality result in preferential excitation of one photosystem over the other, thus upsetting the balance of light utilization by the two photoreactions. If left uncorrected, they could lower the efficiency of photosynthesis significantly [154–156], thereby affecting adversely plant growth and productivity.

The adjustment of the photochemical apparatus organization is a long-term but fully reversible response. Fig. 2 shows results of an experiment in which pea plants were grown under PS I light (PS II/PS I = 2.5 : 1). At zero time, they were switched to PS II light conditions (Fig. 2, left panel). The PS II/PS I stoichiometry ratio of nearly expanded leaves was decreased as a function of time until it reached a new steady-state of

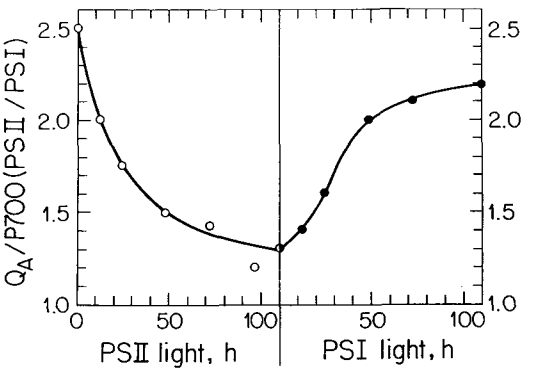

Fig. 2. The response of photosystem stoichiometry (PS II/PS I) to changes in the light-regime during plant growth. Pea plants acclimated to PS I-light were switched (at time zero) to a PS II-light environment. After 110 h, the same plants were switched back to a PS I-light environment.

about 1.3 : 1 with a half-time of about 20 h. Upon transition to PS I light conditions, (Fig. 2, right panel), the PS II/PS I ratio gradually increased to the value typical for PS I-light-grown plants [162]. A similar response was obtained with cyanobacteria [150]. These results suggested the existence of a widely conserved mechanism in photosynthetic organisms designed to sense and correct long-term imbalance in light absorption by the two photosystems through adjustment and optimization of the PS II/PS I stoichiometry ratio. From the evolutionary point of view, it appears that photosynthetic organisms possessing such adaptation mechanism might enjoy a significant selective advantage over others with a fixed photosystem stoichiometry in their thylakoid membranes [154–156].

The response of the photosystem stoichiometry to different light qualities is a long-term adjustment when compared with the so-called 'state transitions' [163] and with the underlying phosphorylation-dephosphorylation of the LHC II through a redox regulated kinase [164,165]. The latter phenomena bring about organizational changes in the thylakoid membrane, they occur on the order of minutes (versus hours for the photosystem stoichiometry adjustment) and they do not involve changes in the composition of the thylakoid membrane. The topic of state transitions and the role of the phosphorylation-dephosphorylation of proteins in thylakoid membranes will not be addressed in this review. The reader is directed to other recent and relevant publications in this area [166–168].

II-C. Partial inhibition of Photosystem II by herbicides

Partial inhibition of PS II by herbicides results in loss of PS II electron-transport capacity. Such deficiency leads to imbalance in electron-transport between PS II and PS I. Higher plants grown in the presence of sublethal concentrations of PS II herbicides respond by enhanced biosynthesis of PS II components, resulting in overall lower Chl *a*/Chl *b* ratios, higher Q_A/P700 content and higher Q_A/PQ ratio in the thylakoid membrane [169,170]. This response is apparently the same with all herbicides acting at the Q_B site. Taken together with the effect of mutations and light quality, the response signals the existence of a mechanism in chloroplasts that senses the balance of electron transport between the two photosystems and, thereby, regulates the rate of biosynthesis/assembly of the various photosystem components.

II-D. Other plant growth conditions that trigger photosystem stoichiometry adjustments

II-D.1. Moderate but chronic photoinhibition

Moderate but chronic photoinhibition is a continuous damage to PS II by excessive light. This phenomenon results in a lower capacity for PS II electron-transport. Recent measurements revealed that, under such conditions, the thylakoid membrane acquires a much greater PS II/PS I ratio. A sizable fraction of PS II, however, is incapable of stable charge separation and it does not participate in electron transport. This photochemically inert pool of PS II appears to be in the process of repair of the reaction center and can be detected only with western (immuno) blot analysis [171].

II-D.2. Low carbon dioxide conditions

Under low carbon dioxide supply conditions, algal cells resort to active uptake of bicarbonate from the surrounding medium. This occurs upon expenditure of cellular ATP [172]. A cause-and-effect relationship has been suggested between the need for a greater ATP/NADPH ratio in the cell and the elevated PS I concentration in the thylakoid membrane (lower PS II/PS I ratio) [173]. In this case, elevated PS I content presumably occurs to enhance cyclic photophosphorylation.

II-E. Regulation of thylakoid membrane composition and function by light intensity

II-E.1. Relative concentration of the cytochrome b_6-f complex

A change in the light intensity during plant growth elicits changes in the stoichiometry of cytochrome b_6-*f* complex and the two photosystems. Under high irradiance conditions (sunlight in the range of 1500–2000 μmol photons m^{-2} s^{-1}), the rate of light absorption by each PS is not limiting, and overall electron-transport in the thylakoid membrane is then limited by the intermediate electron-transport steps. The high content of cytochrome b_6-*f* in such 'high light' plants (cytochrome *f*/PS I = 1.5 : 1.0) is a response of the plant that improves overall electron-transport capacity. The converse is true in plants grown under low solar irradiance (< 100 μmol photons m^{-2} s^{-1}), and in obligate shade species (< 20 μmol photons m^{-2} s^{-1}), in which the rate of light absorption becomes the limiting factor. Under low irradiance conditions, thylakoid membranes contain a relatively low concentration of cytochrome b_6-*f* complex (cytochrome *f*/PS I = 0.8 : 1.0) [174–177]. This observation is consistent with the proposal by Wilhelm and Wild [178] that overall electron-transport capacity, under both light-limiting and light-saturating conditions, could be accurately defined by the relative cytochrome b_6-*f* complex content in the chloroplast.

II-E.2. Relative concentration of the two photosystems

The response of the photosystem stoichiometry to variation in light-intensity appears to depend on the photosynthetic species examined. In *Anacystis nidulans* [124], *Chlamydomonas reinhardtii* [132], and higher plant

chloroplasts from several species [127,179,180], low-light growth conditions result in low PS II/PS I ratios and high-light growth conditions elicit higher PS II/PS I ratios. This response was not observed in *Dunaliella tertiolecta*, which showed invariant PS II/PS I ratios over a broad range of light intensities [181,182]. Similarly, Lee and Whitmarsh [177] reported that only limited variation occurred in the PS II/PS I ratio as a function of light intensity in *Pisum sativum* (pea) cv Progress No. 9. Moreover, in diatoms and brown algae, the response of the cells to the light intensity during growth is opposite to the response of cyanobacteria, green algae and vascular plants [183,184]. Clearly, the cause and effect relationship between light intensity and photosystem stoichiometry is not adequately understood at present.

II.F. Molecular feedback mechanism for the regulation of photosystem stoichiometry

The foregoing suggest the ability of oxygenic photosynthesis to sense imbalance in electron-transport rates between PS II, cytochrome b_6-f and PS I, and the ability to regulate the relative concentration of these complexes in the thylakoid membrane. The molecular mechanism for the adjustment of photosystem stoichiometry must include a 'sensing' and a 'response' component. The similarity of the response of the PS stoichiometry to three independent 'signals' (light quality, Chl *b*-deficiency and partial inhibition by herbicides) seems to eliminate the role of any specialized photoreceptor (i.e., phytochrome) in the signal identification process. Rather, it was proposed that signal perception occurs at the photosynthetic pigment level and that the first step in signal identification occurs in the thylakoid membrane directly, as imbalance in the rate of electron-transport between individual intermediates (Fig. 3, see also Refs. 135, 185, 186).

Likely determinants in signal identification (for example, an imbalance in electron transport between PS II and PS I in the thylakoid membrane) are the steady-state oxidation-reduction level of the plastoquinone pool and/or of the cytochrome b_6-f complex [135,185–188]. The prevailing condition must be 'communicated' further to other metabolic processes in the chloroplast to enable a meaningful response. The nature of the 'signal transduction and transformation' process is unknown, although the *ratio* of chloroplast-generated metabolites, such as ATP/NADPH, might play a role in this process [135].

The 'response' of the plant may involve selective regulation of the biosynthesis/assembly and disassembly/degradation of complexes in the thylakoid membrane. It was proposed that signal transduction and transformation in cyanobacteria may proceed via control of Chl *a* biosynthesis. This hypothesis is based on the observation that partial inhibition of Chl *a* biosynthesis by gabaculine and by 2,2′-dipyridyl in *Synechocystis* PCC 6714, caused a lower PS I to PS II ratio in the thylakoid membrane, even under light quality conditions that normally favor the assembly/accumulation of PS I [189]. Preliminary evidence suggested a strong correlation between the PS I content in the thylakoid membrane and the steady-state level of *psa*A (PS I) gene transcripts in chloroplasts grown under PS II or PS I light [147,190]. Moreover, the process of protein phosphorylation may play a role in the regulation of disassembly/degradation of surplus complexes in the thylakoid membrane (Fig. 3) [12,191].

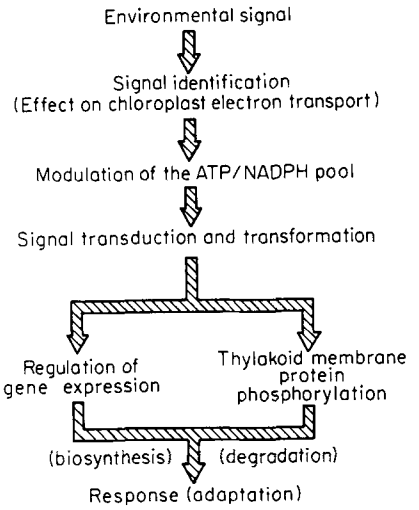

Fig. 3. Schematic of a molecular feedback mechanism for the regulation of photosystem stoichiometry in the thylakoid membrane of oxygenic photosynthesis.

In summary, a variety of environmental, genetic and developmental conditions elicit specific changes in the chloroplast structure, composition and function. The resulting adjustments in photosynthesis ensure efficient utilization of the absorbed light energy, they optimize the electron-transport process in the thylakoid membrane, and they enable enhanced plant growth under a variety of diverse conditions.

III. Photosystem II heterogeneity

III-A. Photosystem II antenna heterogeneity

The concept of PS II heterogeneity was first introduced to explain the biphasic fluorescence induction kinetics observed upon illumination of higher plant thylakoids suspended in the presence of PS II herbicides [192–194]. Fig. 4A shows a typical fluorescence induction kinetic trace with isolated spinach thylakoids suspended in the presence of the herbicide 3-(3,4-dichlorophenyl)-1,1-dimethylurea) (DCMU). Qualitatively, the fast and sigmoidal portion of the fluorescence kinetic

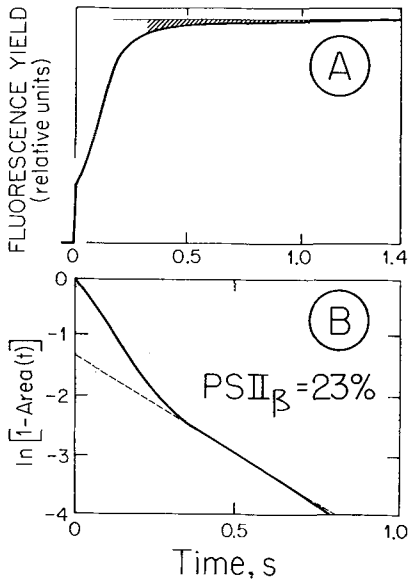

Fig. 4. (A) Fluorescence induction trace with isolated spinach thylakoids suspended in the presence of 20 μM DCMU. The shaded area marks the portion of the fluorescence induction trace where the activity of PS II$_\beta$ is the only component remaining in the kinetics. (B) Semilogarithmic plot (first-order analysis) of the area over fluorescence induction, revealing the biphasic nature of PS II photoconversion. The relative amount of PS II$_\beta$ centers (23% of the total PS II) was determined from the value of the *y*-axis intercept with the slower linear phase (dashed line).

trace is followed by a slower exponential phase (shaded area).

A meaningful analysis of the fluorescence induction kinetics can be obtained only upon consideration of the kinetics of the complementary area growth over the fluorescence induction curve [195]. The complementary area is defined by the ordinate at zero time, the maximal fluorescence yield, F_{max}, and by the boundary of the variable fluorescence induction trace. The precise estimate of this area requires accurate determination of the true value of F_{max} [196–199]. As such, the measurement is sensitive to treatments that may impair the donor side of PS II, or may affect the oxidation state of Fe^{2+} [263]. The kinetics of the complementary area, rather than the kinetics of fluorescence itself, is directly proportional to the amount of Q_A that becomes photoreduced [200–202]. The biphasic nature of the fluorescence induction curve is revealed clearly in a semilogarithmic plot of this area (Fig. 4B) where the fast sigmoidal phase ($0 \leq t \leq 0.27$ s) is followed by a slower linear phase ($0.27 \text{ s} < t$). Analysis of the biphasic data revealed that the slow component accounted for 20–25% of the total phenomenon [139,203]. It was proposed that biphasic fluorescence induction kinetics reflect the function of two distinct populations of PS II centers, termed PS II$_\alpha$ and PS II$_\beta$, respectively [109,193]. Deconvolution of the biphasic kinetics indicated that rates of Q_A^- formation by PS II$_\alpha$ were about 2–3-times faster than those of PS II$_\beta$.

III-A.1. Localization of PS II$_\alpha$ and PS II$_\beta$ in thylakoid membranes

In isolated thylakoid membranes, divalent Mg^{2+} cations, and/or high concentrations of monovalent cations are needed to retain the thylakoid membrane configuration in distinct regions of grana and stroma-exposed lamellae. When divalent cations are omitted from the suspension medium, the thylakoids of the grana regions become unstacked with a concomitant increase in vesicle volume [204].

The selective effect of divalent Mg^{2+} ions on the grana structures and on the fluorescence yield properties of PS II$_\alpha$, and the absence of any Mg^{2+}-induced effect on PS II$_\beta$ [205,206] suggested separate locations for PS II$_\alpha$ and PS II$_\beta$ in the thylakoid membrane. It was proposed that PS II$_\alpha$ units reside in the grana partition regions, while PS II$_\beta$ is localized in stroma-exposed thylakoids [205].

Subsequent fractionation of thylakoid membranes and separation of the grana partition regions from the stroma-exposed regions by the aqueous polymer two-phase method [207] provided direct evidence for the localization of PS II$_\alpha$ in the grana and of PS II$_\beta$ in stroma-exposed lamellae [3,84,208,209].

III-A.2. The absolute light-harvesting chlorophyll antenna size (photosynthetic unit size) of each photosystem

It was recognized that rate differences between the two kinetic components (α and β) reflected different rates of light absorption by the respective photosystem populations (PS II$_\alpha$ and PS II$_\beta$). The different rates of excitation could be caused by different absorption cross-sections of the light-harvesting pigments in PS II$_\alpha$ and PS II$_\beta$. This hypothesis was tested first by the flash saturation profile of PS II fluorescence and by the flash saturation of the α- and β-components in DCMU-poisoned chloroplasts [201]. The results provided evidence that PS II$_\alpha$ has an absorption cross-section about 2–3-times larger than that of PS II$_\beta$. Further support was provided by the findings of Thielen and Van Gorkom [109,210], who showed that primary charge separation in both PS II$_\alpha$ and PS II$_\beta$ operates with a quantum yield of at least 90%, thereby providing independent confirmation that the slower rate of the β-phase is due to a smaller antenna size and not due to a lower quantum yield of photochemistry.

The absolute size of the Chl antenna of PS II$_\alpha$, PS II$_\beta$ and PS I can be determined from the known ratio of total Chl to a reaction center (Chl/PS II I and Chl/PS, Table I) upon partitioning of this total Chl into distinct PS I and PS II components. One method assigned Chl

to each reaction center in direct proportion to the rate of light utilization by each photosystem. The premise of this approach is that, under light-limiting conditions, the rate of light utilization is directly proportional to the light-harvesting antenna size [70,109,210–212]. Applied widely with thylakoid membranes from different photosynthetic organisms, this approach provided estimates of the Chl antenna size of PS I and PS II in different membranes (reviewed recently in Refs. [12,269]).

Results with mature spinach, barley, pea, tobacco and other higher plant chloroplasts revealed that PS II_α contains 250 ± 40 Chl $(a+b)$ molecules in its light-harvesting antenna. By comparison, the antenna size estimate for PS II_β was 120 ± 20 Chl $(a+b)$ molecules. The antenna of PS I contained 210 ± 20 Chl $(a+b)$ molecules [70,109,137]. These antenna size measurements were confirmed independently upon fractionation of thylakoids and isolation of resolved membranes from the grana partition regions (PS II_α) [27,28], and upon isolation of a native PS I complex from spinach [99,102].

III-A.3. Photosystem II heterogeneity in virescent mutants and developing plastids

III-A.3.a. Developing plastids and Chl b-deficient mutants. Developing plastids and chloroplasts from virescent (Chl *b*-deficient) mutants show lower Chl content per leaf area and higher Chl *a*/Chl *b* ratios than mature wild-type chloroplasts. The former have a smaller photosynthetic unit size (Table II) because of the limited availability of chlorophyll [213–216]. Analysis of PS II content in developing plastids and in Chl *b*-deficient mutants from several plant species revealed a substantially enhanced concentration of PS II_β in the thylakoid membrane [83,109,136,137,146]. Unlike the results obtained with mature wild-type chloroplasts, where PS II_α was the dominant form of PS II, it appeared that PS II_β is the dominant form of PS II in developing plastids and Chl *b*-deficient mutants. Quantitation of the amount of PS II_α and PS II_β in Chl *b*-deficient and developing chloroplasts revealed a correlation between the acquisition of Chl *b* in the thylakoid membrane and the relative concentration of the two types of PS II. In the presence of limited quantities of Chl *b* the formation of PS II_β units was favored over that of PS II_α. When sufficient quantities of Chl *b* were present, the formation of PS II_α units was favored over that of PS II_β [73,83,109]. This result suggested a developmental relationship between PS II_β and PS II_α in which PS II_β served as a precursor to PS II_α [139].

III-A.3.b. The Chl b-less chlorina f2 mutant of barley. Results from the research summarized above suggested that, whenever the biosynthesis of Chl *b* is lagging, either because plastids are in the developing stage or because of mutations, PS II_β complexes with an antenna size of 120 ± 20 Chl $(a+b)$ molecules accumulate in the thylakoid lamellae. In the case of the chlorina f2 mutant of barley [217,218], which totally lacks Chl *b*, the phenomenon of PS II antenna heterogeneity is not manifested. Fluorescence induction and ΔA_{320} kinetic measurements, obtained with thylakoid membranes from the Chl *b*-less chlorina f2 mutant, were single exponential functions of time, reflecting the presence of a uniform PS II population of very small photosynthetic unit size [84,219].

Analysis of the PS II Chl antenna size in the chlorina f2 mutant revealed the presence of only 50 Chl *a* molecules [24,84]. A PS II configuration with 50–60 Chl *a* molecules was also encountered in *Dunaliella salina* grown under irradiance stress [171]. These small PS II units will be termed PS II_γ, as they represent the functional PS II form that assembles in the thylakoid membrane in the absence of Chl *b* and of LHC II. Thus, the Chl *b*-less chlorina f2 mutant of barley and irradiance-stressed *Dunaliella salina* provide additional examples of the interplay between Chl *b* availability and the PS II antenna size in the thylakoid membrane.

III-A.4. The modular Photosystem II complex

The combined measurements of PS II antenna size with developing chloroplasts and Chl *b*-deficient mutants [80,83,84,109,137,146,212] corroborate earlier notions of a modular PS II complex [220]. According to this concept, the components of the modular PS II would be PS II_γ (Chl antenna size of about 50 molecules), LHC II-inner and LHC II-peripheral. Evidence in support of this concept is the apparent lack of PS II units with antenna size between 50 Chl *a* (PS II_γ) and 130 Chl $(a+b)$ (PS II_β). Similarly, there is a lack of PS II units with an antenna size between 130 (PS II_β) and 210 Chl molecules (PS II_α). It is postulated that, in the process of photosynthetic unit development, pigment molecules are not inserted continuously, in a linear fashion, to preexisting LHC II polypeptide subunits in the thylakoid lamella. Rather, there is a distinct hierarchy in the assembly of Chl *b*-binding proteins [80,91]. It appears that fully assembled LHC II-inner and LHC II-peripheral complexes, containing the necessary polypeptides and the associated pigment molecules, are involved in a transition from PS II_γ to PS II_β and from PS II_β to PS II_α, respectively [73,83]. Fig. 5 presents a schematic of a step-wise process in the development of the PS II unit in which the addition of LHC II-inner augments the antenna of PS II_γ by about 80 Chl $(a+b)$ molecules to yield PS II_β with an antenna size of 130 Chl $(a+b)$ molecules. In a second step, the addition of LHC II-peripheral increases the antenna size of PS II by at least another 80 Chl $(a+b)$ molecules to yield PS II_α, with an antenna size of 210 (or more) Chl $(a+b)$ molecules. The concept of the mod-

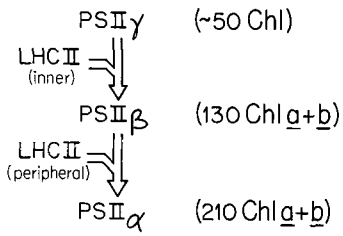

Fig. 5. Schematic defining a step-wise process in the development of the light-harvesting antenna of PS II postulating the addition of two LHC II complements in the developing PS II antenna. The PS II_γ configuration contains about 50 Chl *a* molecules, it lacks LHC II and is present in the Chl *b*-less chlorina f2 mutant of barley. The PS II_β configuration features about 130 Chl ($a + b$) molecules and is obtained upon addition of the LHC II-inner to the PS II_γ complex. The PS II_α configuration features a minimum of 210 Chl ($a + b$) molecules and is obtained upon addition of the LHC II-peripheral to PS II_β units.

ular PS II complex received direct support from the recent isolation and partial characterization of native LHC II-inner and LHC II-peripheral from spinach thylakoids [88,89].

III-A.5. Interconversions between PS II_α and PS II_β

If the formation of the complete PS II unit involves the assembly of modular components (PS II_γ, LHC II-inner, LHC II-peripheral), it would be expected that certain physiological conditions may cause partial or complete disassembly of the modular PS II unit. To date, the dissociation of the LHC II-peripheral from PS II_α, leading to the formation of PS II_β and energetically uncoupled LHC II-peripheral has been documented: phosphorylation/dephosphorylation of the LHC II-peripheral apparently leads to a reversible dissociation of this complex from PS II [87,221–223]. In addition, moderate heat treatment of chloroplast thylakoids [224] and the homogeneous catalytic hydrogenation of thylakoid membrane lipids [225], both lead to a dissociation of the LHC II-peripheral and to the ensuing conversion of PS II_α into PS II_β.

Experimental conditions for the in situ dissociation of LHC II-inner from PS II_β have not been described in the literature. The reversible dissociation of LHC II-peripheral from PS II_α is in contrast to the 'tightly bound' nature of LHC II-inner and suggests different subunit composition between the two LHC II complements and differences in the nature of their association with PS II [73,89,90,212].

III-A.6. Dynamic adjustments in the Chl antenna size of PS II

Long-term light-intensity variations during plant growth elicit changes in the size and composition of the chlorophyll (Chl) antenna of PS I and PS II [135,174]. The amount of the LHC associated with each PS can vary, resulting in variable Chl *a*/Chl *b* ratios in the thylakoid membrane [73,86,153,181,226]. There is evidence in the literature suggesting that variations in the Chl *a*/Chl *b* ratio occur naturally as a plant responds to changes in irradiance [127,175–178,226,227]. This variation in the Chl *a*/Chl *b* ratio implies a variable photosynthetic unit (PSU) size for PS I and PS II in the thylakoid membrane. In general, low irradiance conditions promote larger Chl antenna size for both PS II and PS I (larger photosynthetic unit size). High irradiance promotes a smaller Chl antenna size [132,180–184,226–230]. The adjustment in the Chl antenna size of the photosystems comes about because of light-induced changes in the auxiliary Chl *a-b* LHC II and LHC I of PS II and PS I, respectively [86,231]. This response appears to be well-conserved in all photosynthetic systems examined.

Recent evidence in the literature suggests that individual PS II units possess a constant size and composition for the LHC II-inner but variable polypeptide composition and Chl content for the LHC II-peripheral under different irradiance conditions [73,232]. The LHC II-peripheral may contain as few as 80 Chl molecules and as many as 280 Chl ($a + b$) molecules per complex. Accordingly, the smallest Chl antenna size for PS II_α is 210 Chl ($a + b$) molecules [73] and the largest reported is about 400 Chl ($a + b$) molecules in *Chlorella vulgaris* [227]. The molecular mechanism and the sequence of events at the cellular and membrane levels that lead to the selective regulation of the size of the LHC II-peripheral are not known at present.

III-B. Photosystem II reducing side heterogeneity

III-B.1. Heterogeneity in electron-transport from Q_A to Q_B

Evidence in the literature suggested that a fraction of PS II reaction centers in chloroplasts, although photochemically competent, are unable to transfer electrons efficiently from Q_A^- to Q_B [118,139,233,234]. Following the nomenclature of Lavergne [234], these centers were termed Q_B-nonreducing in order to distinguish them from the plastoquinone reducing centers (Q_B-reducing). Alternatively, they are referred to as PS II centers 'inactive' in PQ reduction [118,235].

A number of different experimental approaches provided quantitation of nonreducing centers. One method is based on the apparent inability of these centers to transfer electrons to plastoquinone (they act like DCMU-poisoned centers). Thus, promptly upon illumination, nonreducing centers undergo a single charge separation and become locked in the Q_A^- state. The stable generation of the semiquinone anion was quantitated by ΔA_{320} and suggested that approx. 25% of all PS II centers in spinach thylakoids were nonreducing [139].

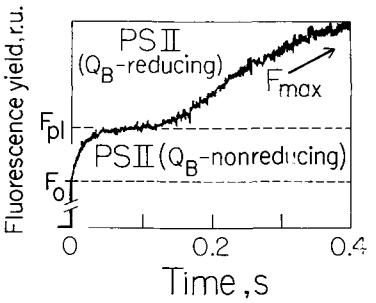

Fig. 6. Fluorescence induction kinetics obtained with a spinach leaf disc under in vivo conditions. The exponential fluorescence yield increase from F_0 to F_{pl} reflects the kinetics of Q_A^- accumulation in 'nonreducing' centers. The fluorescence yield increase from F_{pl} to F_{max} is due to the progressive accumulation of the chemical species Q_A^- in PS II centers with efficient electron transfer to plastoquinone (Q_B-reducing). The lag in the fluorescence transition from F_{pl} to F_{max} reflects the time needed for electrons to accumulate in the plastoquinone pool [267,268].

A different method for the measurement of centers inactive in plastoquinone reduction was based on the electrochromic band-shift (ΔA_{518}) properties of photochemical reaction centers in spinach, studied both under in vitro and in vivo conditions. Whitmarsh and coworkers [235,236] reported that the electrochromic band-shift of about 32% of all PS II centers relaxes with a half-time of 1.5 ± 0.3 s. It is incompatible with the known rate of electron-transport from Q_A^- to PQ in the bulk of PS II centers, which is reportedly faster by about three orders of magnitude [235,237]. Thus, Whitmarsh and co-workers suggested that a significant fraction of PS II centers in the thylakoid membrane are photochemically competent but inactive in the process of plastoquinone reduction.

The photochemical activity of nonreducing centers can be measured with Chl fluorescence induction kinetics. In theory, the accumulation of Q_A^- in these centers should be reflected in the initial fluorescence yield increase from F_0 to the intermediate plateau F_{pl} [238]. A demonstration of this measurement is given in Fig. 6, showing the light-induced fluorescence induction trace of a dark-adapted spinach leaf disc.

It is possible to delineate the fluorescence yield contribution of nonreducing centers upon treating thylakoid membranes with hydroxylamine. Washing of thylakoid membranes with hydroxylamine results in the specific and irreversible inhibition of water oxidation because of the release of Mn from PS II [239,240]. Thus, in hydroxylamine washed thylakoids, the F_{pl} to F_{max} transition is inhibited but the F_0-to-F_{pl} increase continues to be manifested [139]. Under such conditions, the amplitude of the F_0-to-F_{pl} increase is consistent with the estimate of about 25% nonreducing centers in spinach thylakoids [139]. Similar estimates of the nonreducing PS II pool size were given from F_0-to-F_{pl} measurements with untreated samples [203,236].

It should be noted that alternative explanations for the F_0-to-F_{pl} transition exist in the literature. Joliot et al. [241] attributed the F_0-to-F_{pl} increase to the accumulation of the S_2 and S_3 states in the oxygen evolving enzyme of PS II. According to their hypothesis, the fluorescence yield of PS II centers in states S_2 and S_3 (obtained upon illumination) is slightly greater than that in states S_0 and S_1 that prevail in dark adapted thylakoids. Undoubtedly, the origin and the properties of the F_0-to-F_{pl} transition will receive further attention in the literature. Some pertinent information, suggesting that the F_0-to-F_{pl} transition occurs solely due to the accumulation of Q_A^- in nonreducing centers, is given below.

III.B.2. Structural and functional properties of PS II centers inactive in plastoquinone reduction

Studies with photosynthetic material in vivo and in vitro suggested common features between Q_B-nonreducing centers and PS II_β. (a) Both displayed exponential fluorescence induction kinetics of equal rates. (b) The fluorescence yield amplitude controlled by nonreducing centers (F_0 to F_{pl}) was identical to that controlled by PS II_β ($F_{v\beta}$). (c) The fraction of Q_A corresponding to PS II_β was equal to the amount of Q_A photoreduced during the F_0 to F_{pl} transition [139]. (d) The average effective absorption cross-section of nonreducing centers, measured by the flash saturation properties of the electrochromic band shift of PS II, was approx. one-half the average effective absorption cross-section of Q_B-reducing centers [242]. (e) Nonreducing centers were localized in the stroma-exposed region of thylakoid membranes: PS II centers in isolated stroma-exposed lamellae behaved like DCMU-poisoned centers, i.e., they displayed β-type fluorescence kinetics either in the presence or in the absence of added herbicides [84,209,243]. Moreover, isolated vesicles from stroma-exposed thylakoids appeared unable to support PS II electron-transport to hydrophilic electron acceptors. Interestingly, when supplemented with certain lipophilic quinones, such as phenyl-*p*-benzoquinone, they supported considerable rates of oxygen evolution [118,209,244]. (f) Counts of herbicide binding sites revealed that nonreducing centers contain a high-affinity site for herbicide binding with a dissociation constant indistinguishable from that of plastoquinone reducing centers [116–119]. These observations suggest a different configuration for the Q_A-Fe-Q_B complex in nonreducing centers, one that prevents binding/reduction of plastoquinone but retains the capacity for herbicide binding and permits electron-transport from Q_A^- to certain artificially added quinones. (g) Relevant observations and measurements of nonreducing centers were made with soybean [83], maize [91], *Dunaliella salina* [245], and *Chlamydomonas reinhardtii* [243,246]. The results suggested a strong overlap between Q_B-nonreducing centers and PS II_β. A

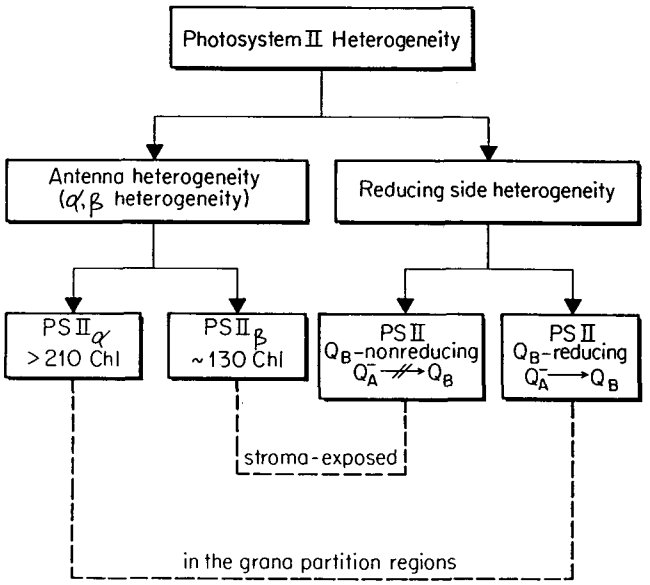

Fig. 7. Schematic delineating the two aspects of Photosystem II heterogeneity discussed in this review. In wild-type mature chloroplasts from higher plants and green algae there is a PS II antenna heterogeneity (α, β heterogeneity). This reflects the presence of a dominant PS II_α, which is localized in the membrane of the grana partition region and contains 210 or more Chl ($a + b$) molecules per reaction center. Photosystem II_β is localized in stroma-exposed lamellae and lacks the LHC II-peripheral, resulting in a smaller antenna size of about 130 ± 20 Chl ($a + b$) molecules. A reducing side heterogeneity reflects the presence of a pool of PS II centers impaired in the Q_A–Q_B electron-transport process (Q_B-nonreducing centers). In wild-type mature chloroplasts, PS II_β and nonreducing centers constitute one and the same pool of PS II centers [139].

summary of the two aspects of PS II heterogeneity is presented in the schematic of Fig. 7 [134].

A strict identity between Q_B-nonreducing centers and PS II_β does not always hold. For example, in Chl *b*-deficient mutants, nonreducing centers with a β-type Chl antenna size constitute 20–25% of all PS II centers. However, total PS II_β centers in these mutants may account for up to 80% of all PS II centers [83,91]. In the chlorina f2 mutant of barley there is a uniform population of PS II centers with a small Chl antenna size (PS II_γ). Only a fraction of these centers (about 20%) qualified as Q_B-nonreducing [84].

III-B.3. Dynamics of PS II heterogeneity

There is a dynamic interplay between the various forms of PS II centers in chloroplasts. Work with *D. salina* provided evidence that the pool size of Q_B-reducing and Q_B-nonreducing centers is not constant but shows transient changes when the light regime is perturbed during cell growth [245]. For example, in cells grown under moderate illumination, nonreducing centers account for about 25% of the total PS II. Dark incubation of the culture induced an increase (half-time of 45 min) in the nonreducing pool size from 25% to 35% of the total PS II. Subsequent illumination of these cells restored the steady-state concentration of nonreducing centers to 25%. In another experiment, transfer of low-light grown cells to moderate light intensity induced a rapid decrease (half-time of 10 min) in the nonreducing pool size and a concomitant increase in the Q_B-reducing pool size [245]. These results suggested accumulation of nonreducing centers in the dark and a light-dependent conversion of nonreducing centers to a Q_B-reducing form.

The requirement of light for the conversion of nonreducing centers to a Q_B-reducing form was addressed further in dark-grown *C. reinhardtii*. This green alga is a facultative heterotroph and, when cultured in the presence of acetate, will synthesize Chl and PS components in the dark [247,248]. Analysis of the thylakoid membrane composition and function in dark-grown *C. reinhardtii* revealed that both complements of the LHC II (LHC II-inner and LHC II-peripheral) as well as photochemically competent PS II reaction centers were synthesized and assembled in the thylakoid membrane. Functionally, the PS II centers were nonreducing with a β-type Chl antenna size [246]. Illumination of dark-grown *C. reinhardtii* caused pronounced changes in the organization and function of PS II. With a half-time of about 30 min, PS II centers were converted from a nonreducing form in the dark, to a Q_B-reducing form in the light. Concomitantly, these centers were coupled energetically with existing LHC II-peripheral antennae and were converted from a PS II_β-type in the dark to a PS II_α-type in the light [246]. This massive light-dependent conversion of PS II_β (Q_B-nonreducing centers) to PS II_α (Q_B-reducing) form suggested the involvement of a light-dependent 'activation' in the Q_A–Q_B electron-transfer reaction in newly assembled PS II units and reinforced the notion of dynamic changes in the PS II heterogeneity phenomenon in green plant chloroplasts.

Further evidence for the dynamic interplay between nonreducing and reducing centers was provided upon investigation of the response of *C. reinhardtii* to adversely strong irradiance [249]. Exposure of low-light (15 μmol photons m^{-2} s^{-1}) grown cells to strong light (2000 μmol photons m^{-2} s^{-1}) caused photodamage (photoinhibition [52]) to the reaction centers of PS II_α [56]. The reaction centers of PS II_β are apparently resistant to such photodamage [56,249,250]. Fluorescence measurements with *C. reinhardtii* indicated that strong irradiance led to a conversion of PS II_β from a nonreducing to a reducing form. Parallel measurements of the rate of oxygen evolution supported the interpretation of 'activation' of nonreducing centers which enables electron-transport to plastoquinone and results in oxygen evolution activity by these centers [249].

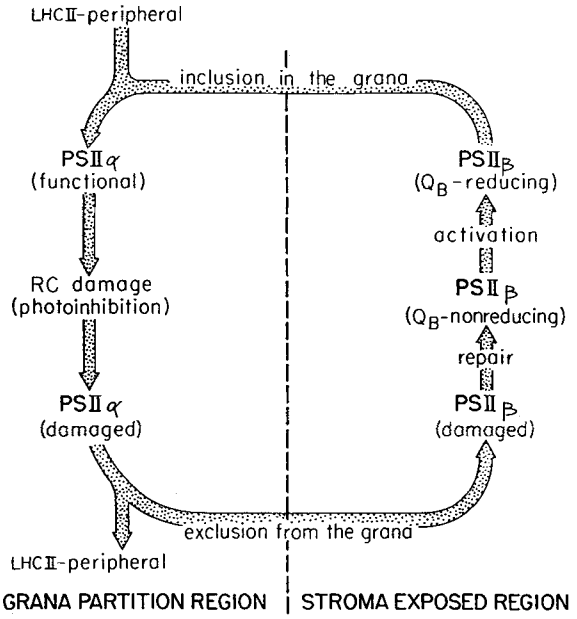

Fig. 8. Schematic of a PS II damage and repair cycle showing two light-dependent steps. It is postulated that a light-dependent reaction center damage in the grana partition region is followed by center translocation from the grana and by inclusion in stroma-exposed lamellae. Following replacement of the D1/32 kDa reaction center polypeptide, the PS II center appears in the Q_B-nonreducing form. A light-dependent activation of the Q_A–Q_B electron transfer reaction is followed by center inclusion in the grana and resumption of PS II activity in terms of water oxidation and plastoquinone reduction.

III-C. The physiological significance of PS II heterogeneity

It was proposed that nonreducing centers are one of the intermediates in a PS II repair cycle responsible for the replacement of the damaged 32 kDa Q_B-binding reaction center protein [251]. This hypothesis is consistent with the observation that nonreducing centers are localized in stroma-exposed regions of the thylakoid lamella, they lack the LHC II-peripheral, and have not yet established a functional interaction between Q_A^- and Q_B. The hypothesis is also consistent with the distribution of the 32 kDa protein in the thylakoid membrane [6,252], with the rapid turnover of the reaction-center 32 kDa protein [253], and with the evidence that newly synthesized 32 kDa polypeptides first 'assemble' in stroma thylakoids and subsequently move to the grana [254,255]. Based on the experimental evidence accumulated until now, the model for the 'PS II repair cycle' (Fig. 8) postulates a sequence of events following damage to the PS II reaction center: (a) Uncoupling of the LHC II-peripheral from the damaged PS II_α unit in the grana partition region. (b) Exclusion of the damaged PS II_β-like center from the grana partition region and inclusion into stroma-exposed thylakoids. (c) Replacement of the damaged 32 kDa reaction-center polypeptide resulting in the formation of a photochemically competent center in which the secondary Q_A^- to Q_B electron transfer interaction has not yet been established (Q_B-nonreducing), (d) Activation of the Q_A^- to Q_B interaction thereby converting the center to a PS II_β Q_B-reducing form. (e) Association of this center with LHC II-peripheral and inclusion in the grana partition region in the form of a newly functional PS II_α unit.

Current evidence indicates that, under physiological growth conditions, thylakoid membranes contain a negligibly small steady-state population of damaged PS II centers. However, after a transient photoinhibitory treatment [53,54] or under chronic photoinhibition conditions [171], the rate-limiting step in the PS II repair cycle is the replacement of the 32 kDa reaction center protein. Under such adverse conditions, damaged PS II units (photochemically inert centers that cannot perform a stable charge separation) accumulate in the thylakoid membrane.

There is a question as to why thylakoids membranes need retain a small but significant pool of PS II centers (about 25% of the total) in the PS II_β or Q_B-nonreducing configuration. The answer is not clear at present, in spite of relevant hypotheses: (a) PS II_β/Q_B-nonreducing centers serve as a *reserve* pool of PS II readily available to augment PS II electron-transport as needed, and to rectify the adverse effect of sudden photoinhibition [249]. According to this hypothesis, the nonreducing pool size is regulated by the light-dependent 'activation' of the Q_A–Q_B electron-transfer reaction. Although the mechanistic details of this 'activation' are not clear, evidence in support of this hypothesis is that the PS II_β/Q_B-nonreducing pool size can be modulated both by the light regime [246,249] and by the prevailing temperature [245,256]. (b) The presence of PS II_β/Q_B-nonreducing centers in stroma-exposed thylakoids may be the consequence of a regulation in the PS II activity in order to prevent photoinhibition [95,209]. Support for this hypothesis is derived from the observation that PS II_β/Q_B-nonreducing centers in stroma-exposed thylakoids are much less sensitive to photoinhibition [56,250]. (c) PS II_β/Q_B-nonreducing centers are converted during illumination to an active form that drives an electron cycle within the reaction center complex and, therefore, quenches the Chl *a* fluorescence [257]. According to this hypothesis, the putative PS II cycle would serve to convert excitation energy to heat under light-saturated conditions, thereby protecting against photoinhibition [258,259].

The hypotheses presented above seek to explain the persistent presence of PS II_β and/or Q_B-nonreducing centers in all mature higher plant chloroplasts and green algae examined. Moreover, they may provide direction(s) for further research in order to completely elucidate the

functional properties of the PS II heterogeneity phenomenon. With respect to the mechanism of the PS II repair cycle, a number of experimental results from different laboratories provide pertinent information: It has been reported that the 32 kDa Q_B-binding reaction center polypeptide of PS II undergoes a light-dependent phosphorylation [33] and that a cleavage of the 32 kDa protein in vivo yields a 23.5 kDa membrane-bound fragment [260]. This primary degradation product has been detected mainly in stroma-exposed lamellae [252]. It is not known whether phosphorylation of the 32 kDa polypeptide might play a role in the primary degradation and whether this primary proteolysis occurs in the grana partition or in the stroma-exposed region of thylakoids. Furthermore, it is not known whether a light-dependent acylation of the 32 kDa polypeptide [254] might play a role in the activation of the Q_A–Q_B electron-transport reaction.

An alternative consideration for the light-dependent activation of the electron-transport reaction between Q_A and Q_B is conformational changes in the D1/D2 32/34 kDa heterodimer. Trebst and co-workers [261,262] reported that plastoquinone, artificial quinones, and even herbicides bound at the Q_B-binding site might have an effect on the conformation of both the D1 and D2 polypeptides. It was suggested that such conformational changes of the D1/D2 heterodimer might be relevant for the events of the rapid turnover of D1, and perhaps in the light-dependent activation following repair of the reaction center complex. Finally, the role of a single atom of Fe, localized between Q_A and Q_B in the PS II reaction center complex [263], cannot be overlooked as the determining factor in the Q_A–Q_B interaction.

Recent evidence from work with isolated spinach thylakoids supports the notion that a strong light treatment and photoinhibition of Photosystem II results in the degradation of the D1 polypeptide, the release of Mn and of the extrinsic 33, 23, and 17 kDa proteins in the lumenal space, followed by the lateral migration of disassembled PS II centers from the appressed to the non-appressed thylakoid regions [264,265]. Conversely, a significant translocation of PS II_β from stroma-exposed thylakoids to the grana partitions was found to occur also upon strong light treatment in *C. reinhardtii* in vivo [243]. The latter did not occur when the strong light treatment was administered at 0 °C [243,245,266], consistent with predictions made on the basis of the above models.

IV. Concluding remarks

In summary, the hypothesis of a PS II antenna heterogeneity (PS II_α, PS II_β) and of a PS II reducing side heterogeneity (Q_B reducing and nonreducing centers) explains sufficiently a score of related observations. It provides an understanding of the supramolecular assembly and organization of PS II in the thylakoid membrane, and it may also provide insight into the mechanism of repair of damaged PS II reaction centers (turnover of the 32 kDa polypeptide).

The PS II heterogeneity has important implications for the PS II/PS I stoichiometry ratio. Estimates of PS II concentration, given in Section II of this review (Tables I–III), made no distinction between reducing and nonreducing centers, or between PS II_α and PS II_β. Rather, all PS II centers capable of a stable charge separation were included. In as much as nonreducing centers do not participate in steady-state electron-transport, they cannot be considered in the definition of the 'operational' photosystem stoichiometry. It should be noted, however, that photosystem stoichiometry adjustments are mainly adjustments in the absolute concentration of PS I in the thylakoid membrane [188,190]. Therefore, the large variability in the PS II/PS I ratio observed in thylakoid membranes from diverse photosynthetic species (Table I), the elevated PS II/PS I ratio in chlorophyll deficient mutants and developing chloroplasts (Tables I and II), and the significantly different PS II/PS I ratio in thylakoids developed under PS II and PS I light conditions (Table III) are not normally accompanied by changes in the relative ratio of Q_B-reducing and Q_B-nonreducing centers (Refs. 84, 91, and unpublished results).

The significance of the proposed PS II repair cycle is the selective replacement of a specific polypeptide in a multi-protein complex (PS II) which is localized in the inaccessible region of the grana partitions in chloroplasts. The underlying reason for the existence of this PS II repair cycle may be found in the function performed by the D1 polypeptide of the PS II reaction center complex. It contains many prosthetic groups including the photochemically active Chl in the reaction center P680, the secondary electron-donor 'tyrosine', and it possibly participates in binding the Mn cluster. These components perform one of the most specialized functions on earth, since photooxidation of P680 generates an oxidant (Chl^+) with a midpoint potential of greater than +1.0 V. Transfer of the oxidizing potential from $P680^+$ via tyrosine to Mn leads to oxidation of water molecules. The highly specialized functions on the donor side of PS II entail damage to functional component(s) and the need for repair. Thus, nature may have devised an elaborate mechanism (the PS II repair cycle) for the selective replacement of a labile protein in a multi protein macrocomplex. The significance of this proposed repair cycle is further manifested upon consideration of the situation that would have prevailed in its absence: grana partition regions would soon be loaded with damaged PS II complexes and the chloroplast would have to undertake the metabolically expensive task of dismantling and replacing entire grana structures.

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