Plasticity of Biological System for Light-Energy Conversion in Oxygenic Photosynthesis

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Light-energy conversion in oxygenic photosynthesis is driven by two photochemical reactions in PS I and PS II complexes. Thus, the efficiency of energy conversion is primarily determined by the balance between the two photoreactions. The balance is always monitored and is adjusted by a regulatory mechanism when imbalance occurs. Two types of regulation occur. The one is regulation of excitation-energy distribution between PS I and PS II complexes, and the other, regulation of quantitative composition of functional components in the system such as molar ratio between two PS complexes. The former, called "short term" regulation, occurs rapidly but in a limited range, and the latter, "long term" regulation, is slow but adjusts in a wide range. Some details of the regulation of two types are explained.

1. Introduction

1.1 Oxygenic photosynthesis, its past and present importance (cf. 1)

Oxygenic photosynthesis was born on the earth at a very early stage of the earth history. It has been estimated that it was almost 3.0 Gyr ago. The living way based on the oxygenic photosynthesis is strictly autotrophic. The organisms which can perform oxygenic photosynthesis do not require any organic materials produced by other organisms for maintaining their life. They require, except for solar energy, only inorganic materials such as CO_2, NO_3^- or NH_3, PO_4^{3-}, SO_4^{2-} and some other minerals. Some of organims performing anoxygenic photosynthesis and chemosynthesis are also strict autotrophs. However, they need reduced inorganic compounds such as H_2S and Fe^{2+} to drive their energy-yielding metabolism, anoxygenic photosynthesis and respiration. However, oxygenic photosynthesis can use H_2O, which is generally present on the earth, as the electron source to drive photosynthetic energy conversion, instead of special reduced compounds.

Probably due to this advantage, the prokaryotic organisms performing oxygenic photosynthesis like cyanophytes and prochlorophytes on the present earth, were rap-

idly developed to form a great population in the ocean area. O_2 evolution by oxygenic photosynthesis occurred in a quite large scale in aquatic environment, and the earth-environment, first in the oceanic then in the terrestrial area, became oxidative. Thus, the chemical nature of the present earth-environment was produced and has been maintained by the biological action, oxygenic photosynthesis. The effect of molecular oxygen produced in the earth-environment not only caused a dramatic change of the earth-environment but also brought about an evolutional epoch in the life history on the earth, the birth of O_2-respiration. O_2-respiration is the most efficient energy-yielding metabolism for the life of heterotrophic organisms and maintains the life of most organisms, including human beings, in the biosphere on the present earth. A high efficiency of energy conversion in O_2-respiration may be a main biological basis of the phylogenic progress which has brought about a marked variety of organisms on the present earth. Thus, oxygenic photosynthesis can be recognized as a very important biological action which has determined and maintained both the earth-environment and the organisms on the present earth. Oxygenic photosynthesis, first born in the prokaryotic organism, was settled in the eukaryotic organisms about 1.5 Gyr ago. Since then, the life based on oxygenic photosynthesis has brought about first the world of algae, and later, rather recently, the world of higher plants. Extensive development of such a plant kingdom has enabled to bring about the present prosperity of living things on the earth.

When the oxygenic photosynthesis was born on the earth, this photosynthesis was not a sole biological system, which can convert the solar energy into the energy form to support the life of organisms. It has been recognized that before the birth of oxygenic photosynthesis, the systems, which produce organic materials with consumption of the solar energy and reduced substances such as H_2S and organic acids, had already existed. These must be similar to the anoxygenic photosynthesis, which occurs in the present photosynthetic purple and green bacteria. Thus, the system for oxygenic photosynthesis may be created being based on the existed systems for anoxygenic photosynthesis. As described above, the oxygenic photosynthesis is more advantageous than the anoxygenic type in that the former does not need any special reduced materials to drive the system.

1.2 System of energy conversion in oxygenic photosynthesis

In all types of photosynthesis, the light-energy is converted and stabilized as the electrochemical form in the photochemical protein complex. The reaction is a charge separation, with expense of excitation-energy, between two

molecules of chlorophylls or between chlorophyll and pheophytin specially installed in the protein complex. The charge separation drives electron transport in the complex and in the photosynthetic membranes. The electron transport in the membranes produces biochemical energy and reducing power, ATP and NAD(P)H, for CO_2-fixation, on one hand, and requires electron supply from the outside of the system, on the other hand. In oxygenic photosynthesis, the source of electrons for the electron transport is not a special compound but H_2O, which is available infinitely and everywhere on the earth, differently from the special source required by anoxygenic photosynthesis. This advantage, however, depends on a more complexed system than that for anoxygenic type. In the latter, the electron transport is driven by a single photochemical system. However, the electron transport in oxygenic photosynthesis is driven by two photochemical systems. H_2O is a very stable molecule in oxidation-reduction reaction. Oxidation of H_2O needs a very strong oxidant, which is hardly produced in an ordinary biological reaction. H_2O oxidation in oxygenic photosynthesis is coupled with photochemical reaction. The photochemical charge separation in one of the photochemical protein complexes can cause Chl a cation of a very high redox potential, which can drive H_2O oxidation. Due to necessity for H_2O oxidation, two types of photo-

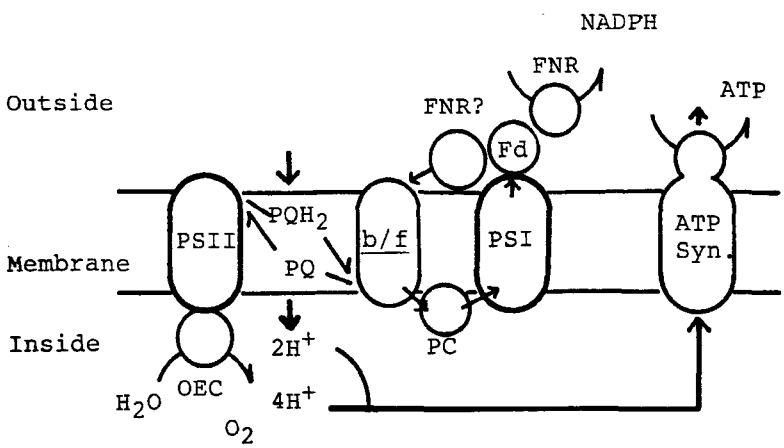

Fig. 1. Schematic presentation of thylakoid system for light-energy conversion. Thin arrows in the membrane indicate direction of electron flow, and thick ones, direction of proton movement. ATP syn., ATP synthase; b/f, Cyt b_6-f complex; Fd, ferredoxin,; FNR, Fd-$NADP^+$ oxidoreductase; OEC, oxygen evolving center; PC, plastocyanin; PQ, PQH_2, plastoquinone, plastohydroquinone.

chemical reactions are involved in the energy conversion process of oxygenic photosynthesis; the one (PSII) functions at the electron input to the electron transport system, and the other (PSI), at the electron output to $NADP^+$.

Figure 1 is a schematic presentation of the system for light-energy conversion in oxygenic photosynthesis occurring in thylakoids in chloroplasts or cells. Conversion of light energy into biochemical form occurs in the thylakoid, a membrane system of a flat-bag type, in chloroplasts of eukaryotic cells or in cytoplasmic area of prokaryotic cells (cf. Fig. 3). Four huge protein complexes are arrayed in this membrane system. Two of them are the complexes for photochemical reactions, and each consists of more than 10 peptides, which form the molecular field for the charge separation and for the electron transport to stabilize the electrons.

PS II complex causes H_2O oxidation and transfers electrons to plastoquinone (PQ) in the membranes. Cyt $\underline{b}_6$ - $\underline{f}$ complex, the third protein complex, mediates the electron transport from PQ to plastocyanin, a Cu redox-protein located at the inner surface of the membranes. This Cu protein donates electrons to Chl $\underline{a}$ cation in PS I complex, which is formed by the photochemical charge separation. PS I complex donates electrons to $NADP^+$ reduction system consisting of ferredoxin (Fd) and Fd-$NADP^+$ oxidoreductase (FNR).

Reduction of PQ occurs at the outer side of membranes, and its oxidation, at the inner side. Thus, 2 protons, per mol PQ, at the outside of thylakoids are consumed by the reduction, and 2 protons are released to the inside of thylakoids by the oxidation. This causes proton-gradient across the thylakoid membranes. Since H_2O oxidation occurs at the inside of thylakoids, and $NADP^+$ reduction, at the outside, proton-gradient becomes more marked. Protons thus accumulated at the inside of thylakoids move to the outside through a proton channel formed by the fourth protein complex, ATP synthase. ATP formation by the complex occurs at the outer surface of the membranes coupling with proton movement through the proton channel.

Besides the straightforward electron transport driven by the two photoreactions, occurrence of a cyclic electron transport around PS I has been known. An electron backflow from FNR to cyt $\underline{b}_6$ - $\underline{f}$ has been assumed to form a cyclic electron transport driven by PS I action. This electron transport causes only the proton-gradient, and so ATP formation. Details of the mechanism in thyalkoid system can be obtained from the references cited (2,3).

2. Regulation of system-function in the thylakoid system

Although the mechanism of the light-energy conversion in thylakoids is complicated, the conversion efficiency is

high. Quantum yield of O_2 evolution is a little greater than 0.1. The value is very close to the theoretical one expected by the model of two-light reaction. The reason of such a high efficiency is primarily attributed to the elaborate structure of each functional protein molecule or protein complex. Geometrical assembly of functional molecules in the membrane is also one of the essential conditions for high efficiency. However, the efficiency can not necessarily be maintained only by the nature of functional molecules and system assembly but is also supported by a regulatory mechanism for balancing the actions of respective functional molecules in the system.

Since the energy conversion in oxygenic photosynthesis is achieved by the actions of two PS complexes, balance between the two actions is an important determinant of the efficiency. However, the light regime for photosynthesis does not always fit for a balanced state of two photoreactions. When PS II action exceeds the action of PS I due to light regime for photosynthesis, the electron transport system (ETS) including the two photosystems, becomes electron flood, and so, most of PS II cannot react even though photons are transferred to PS II. In contrast, electron transport system becomes electron poor under the light exciting preferentially PS I, and so, most of PS I cannot react. Increase in the number of inactive photosystem lowers the efficiency of energy conversion.

Besides light regime for photosynthesis, other environmental factors also affect the balance of the two photoreactions. CO_2 stress is one of such examples. In most algae, HCO_3^- is incorporated into cells when CO_2 is not available in the environment for photosynthesis. This HCO_3^- incorporation requires ATP, and so, the balance between ATP and NADPH required by CO_2 fixation has to be changed. This causes changes in proportion of straightforward to cyclic electron flow, and so balance between two photoreactions.

Under such conditions, the thylakoid system adjusts its system-function so as to recover from low efficiency in two ways. The one is a "short term" regulation which occurs fast but within a limited range, and the other, a "long term" regulation, which is slow but occurs in a wide range. The following is a brief explanation of the regulatory ability of thylakoid system. In this article, the regulation of system-function in response to the light regime is mainly introduced because it has been studied well.

2.1 A "short term" regulation of thylakoid system: Regulation of excitation distribution to two photosystems

Since PS complexes contain many Chl a molecules, PS complexes themselves can capture the light-energy for driving photochemical reactions. However, most of light-energy is

collected by a pigment system, which is specially designed pigment protein complex to collect the light-energy. The size of this light-harvesting system (LH system) is far greater than those of PS complexes in the number of pigment molecules, and the light-energy captured by LH system is transferred to the two photosystems (Fig. 2). However,

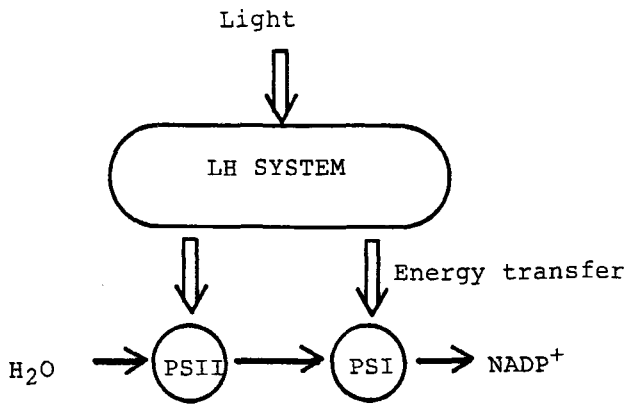

Fig. 2. Relationship between LH system and two photosystems.

distribution of the excitation-energy from LH system to the two photosystems is not even. Distribution to PS II is generally greater than that to PS I. The former has been estimated 2 times greater than the latter in green plants which have the LH system of Chl a and b (4). In an extreme case which is found in cyanophytes and red algae, almost all energy is transferred to PS II (5). Thus, as far as the photosynthesis depends on the light energy captured by LH system, a marked imbalance between actions of the two photosystems appears to occur.

However, this defect of LH system is compensated by the two types of regulatory mechanism in energy distribution between the two photosystems. The one occurs in the excitation-energy transfer from LH system to the two photosystems. The proportion of the energy flow to the two photosystems described above is not fixed, but is variable depending on the state of ETS. The value described above is obtained for the system kept in the dark before determination. Extensive study of this regulation has been made for the LH system of green plants (cf. 6). The structure of thylakoids in chloroplasts of green plants is not simple. As shown in Figure 3, a dense folding of thylakoids occurs locally, and the thylakoid membranes in

this area are attatched to each other. PS II complex is mainly located in the thylakoid membranes of this area while PS I is located in the non-folding thylakoids (7). Most of LH system, Chl a - b protein complex (LHC II) is also located in the folding thylakoids in the dark and associated with PS II complex. Some part of LH system (LHC I) is associated with PS I complex in the non-folding thylakoids. Thus, most of light-energy captured by LHC is transferred to PS II in the dark-adapted system.

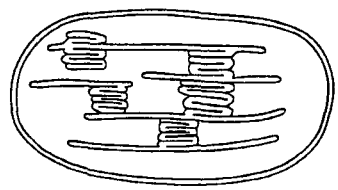

Fig. 3. Schematic presentation of thylakoid structure in chloroplasts of higher plants.

However, it has long been observed that the proportion of energy transfer from LHC to PS I becomes greater when the plants or chloroplasts are illuminated with the light absorbed by LHC, i.e., by Chl b. At the same time, the proportion to PSII decreases so as to balance the actions of the two photosystems (this has been called state 2 of pigment system). This indicates that the energy transfer from LHC II to PS I is induced. In contrast, this energy transfer is decreased under the light exciting mainly PS I (the light at wavelengths longer than 680 nm) or in the dark, and the transfer to PS II is increased (this is called state 1 of pigment system). As this variation of the energy transfer from LHC II compensates the imbalance between excitations of two photosystems, this regulation functions in maintaining the efficiency of system-function of thylakoids. Then, three questions arise; the first, what is the signal for regulation, the second, what is the signal transduction, and the third, how is the transfer regulated. At present, the answers to these questions are not very conclusive.

For the first question, correlation between the state of ETS and the regulation has been extensively investigated. The intermediate electron pool between the two photosystems, PQ and Cyt b_6 - f, has to be electron flood when the action of PS I limits the overall reaction, and when PS II

limits, the electron pool has to be very poor in electrons. Such a biassed redox state of the intermediate components can be a probable candidate for the signal of the regulation. Indeed, the reduced state of PQ pool correlates to the increase of energy transfer to PS I (8). This correlation has led us to assume that the reduced PQ, PQH_2, is the signal and transformed in some way to regulate the energy transfer. However, the analyses with use of a mutant for Cyt $\underline{b}_6$ - $\underline{f}$ complex (9 - 12) and inhibition of Cyt $\underline{b}_6$ - $\underline{f}$ reaction (9) have indicated that Cyt $\underline{b}_6$ - $\underline{f}$ is the molecule to elicit the signal for the regulation. The question which is the signal elicitor has not been resolved yet, but the latter, Cyt $\underline{b}_6$ - $\underline{f}$ complex, is probably the molecule in ETS associating to the signal.

For the second question, an evidence has been known that phosphorylation of LHC II protein occurs when the energy transfer becomes the state 2 (8,13). Correlation between LHC II phosphorylation and regulation of energy transfer has been documented well (14), and a current concept for the signal transduction involves protein kinase which is bound to thylakoid membranes (cf. 14). It has been reported that the kinase is present in thylakoid membranes closely associated with Cyt $\underline{b}_6$ - $\underline{f}$ complex (15), suggesting a close relationship between the signal and Cyt $\underline{b}_6$ - $\underline{f}$ complex.

These features provide an answer to the third question also. Phosphorylated LHC II is modified in its electric nature at the surface of molecular complex. The modification may occur to release from the folding area, and so LHC II can move rather freely into non-folding area. At the same time, the modification may increase the affinity to PS I complex. Thus, modified LHC II become associated with PS I complex and acts as the light-harvesting antenna for PS I. On the other hand, dephosphrylation may occur always, so that deactivation of the kinase under the state 1 causes non-phosphorylated LHC II which is associated with PS II in the folding thylakoids. The regulation between state 1 and state 2 of pigment system in red algae and cyanophytes, in which phycobilisome (PBS), a very different pigment protein complex, acts as LH system, seems not to include protein phosphorylation (16).

Besides the regulation of the excitation-energy transfer from LH system to photosystems, it has been known that an excitation-energy transfer from Chl $\underline{a}$ of PS II to that of PS I also occurs (4). The mechanism has not been determined yet, but the transfer seems to be regulated in response to the state of PS II. It seems to occur from inactive PS II to PS I, and so adjust the energy distribution between the two photosystems so as to balance the two photoreactions. The state shift of the pigment system in cyanophytes and red algae may not depend preferentially on the excitation-energy transfer from LH system, PBS, to

the two photosystems, but mainly on the transfer from PS II to PS I, the third energy transfer path as described above.

In summary, a "short term" regulation in response to light regime occurs at the level of excitation-energy transfer among LH system and two photosystems so as to balance of two photoreactions (Fig. 4). The one is regulation of energy distribution from LH system to two photosystems, and the other, the energy transfer from PS II to PS I. This regulatory net work in the excitation-energy transfer among LH system and two photosystems responds rapidly to changes in the light regime. The time range of response is at most several minutes. However, the range of adjustment is rather limited as explained below.

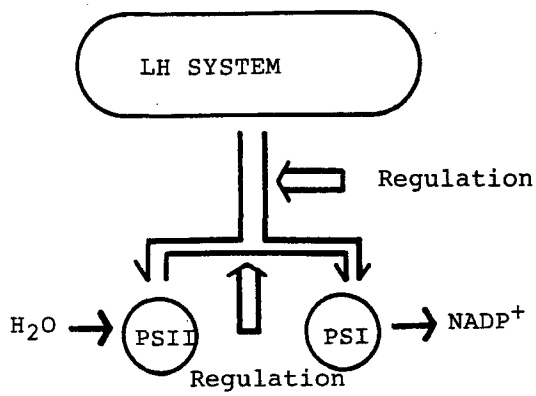

Fig. 4. Two sites of excitation-energy transfer controlled in "short term" regulation.

2.2 A "long term" regulation: The regulation of stoichiometry among the thylakoid components

Thirty years ago, Yocum and Blinks (17), and Brody and Emerson (18) independently reported for red algae that quantum yield of photosynthesis at the wavelength region for Chl a absorption is enhanced, when the algal cells have been grown under the light for Chl a absorption. These are the first reports about occurrence of a "long term" regulation of thylakoid system in response to light regime. As described above, LH system of red algae, as well as cyanophytes, is PBS, a supramolecular structure of phycobilin proteins, chromoproteins containing tetrapyrrole pigments

as their chromophores (19), which transfer its excitation-energy preferentially to PS II. Thus, the phenomenon indicates that the number of Chl a, which transfers its excitation-energy to PS II, is increased relatively to that of Chl a for PS I under the light for Chl a absorption. Changes in the number of Chl a for PS II may occur in two possible ways. The one is that the number of PS II complex is increased relatively to that of PS I, and the other, that the number of Chl a in PS I and/or PS II complexes is changed; decrease in Chl a of PS I and/or increase in Chl a of PS II. PS I and PS II complexes have a definite molecular structure, and so, number of Chl a installed in the complex must be constant; around 120 molecules Chl a has been counted for one PS I complex, and 60 molecules, PS II complex (20). Thus, the first possibility is more feasible; stoichiometry between two photosystems is adjustable in response to the light regime for photosynthesis. Indeed, the stoichiometry has been found to vary in response to the light-quality (21, 22) and to the light-intensity (23, 24).

Another adjustment has been known to occur in the size of LH system in response to the light-intensity. As explained below, both adjustment are achieved by regulation of synthesis of photosystem complexes or pigment-protein complexes of LH system during the growth of cells or chloroplasts. Thus, the adjustment occurs more slowly in this case than that for the excitation-energy transfer, and so it is called "long term" regulation (25).

2.2.1 Regulation of size of LH system in response to the light-intensity

In green plants, the LH system is composed by Chl a - b proteins. Chl b is present only in LHC, and so the ratio of Chl b to a indicates the size of LH system, relative to the abundance of the two photosystems. Table 1 indicates the relationship between this ratio and the light intensity for growth of the green alga Chlorella pyrenoidosa. The ratio, i.e., the size of LHC, is distinctly greater in cells grown under weak light than in cells grown under strong light, indicating that the size is regulated. A similar variation of the size of LH system occurs in cyanophytes, in which LH system is PBS (27). Table 2 shows an example of the evidence indicating that decrease in the size of LHC under strong light is not due to degradation of LHC. When cells of Chlorella grown under weak light are illuminated with a strong light, Chl b level decreases during cell growth. However, this decrease is suppressed when protein synthesis depending on either nuclear or chloroplast genome is suppressed. If the decrease in LHC size would be due to degradation of LHC, decrease should be observed even under suppression of protein synthesis. Analysis of Chl b

Table 1. Size of LHC indicated by Chl b/a in the green alga Chlorella pyrenoidosa grown under various light intensities (from Ref. 26).

Light intensity*	Abundance** of Chl a	Chl b	Chl b/a
1.00	0.96	0.18	0.19
0.75	1.24	0.29	0.23
0.54	3.10	0.82	0.26
0.15	4.00	1.19	0.30

* Relative to that for light-saturation of cell proliferation under photosynthetic growth.
** Percentages of dry weight.

Table 2. Effect of chloramphenicol (CAP) and cycloheximide (CHX) on the decrease in LHC size in Chlorella pyrenoidosa grown under strong white light (calculated from Ref. 28).

Incubation under strong white light	Chl b/a	Cell density (10^7 cells/ml)
0 hr	0.32	0.8
30 hr	0.17	3.7
30 hr, with CAP	0.30	1.6
30 hr, with CHX	0.31	0.9

Cells grown under weak white light (7.5 W/m^2) were incubated under strong white light (300 W/m^2) with or without CAP (1.2×10^{-3} M) or CHX (0.03 μg/ml).

deficient mutant of higher plant (29) and of greening of etiolated seedlings under limited light illumination (30) has indicated that Chl synthesis and supply to the assembling of LHC and two photosystems determines the stoichiometry among these Chl protein complexes. Priority of Chl supply is the highest to PS II, and the lowest to LHC (cf. 28). Further, Chl a synthesis is suppressed under strong light (28). Thus, the LHC formation is reduced by limited supply of Chl a under strong light. Although a detailed mechanism has not been available, the regulation of the size of LHC must occur under the mechanism outlined in Figure 5. Prophyrin synthesis at the early step, which must be common to Chl and heme synthesis, is in some way

regulated in response to the light-intensity for photosynthesis. This regulation causes great variation in the size of light-harvesting antenna, and so, provides adjustment of collection of light-energy in response to the amount of light in the environment.

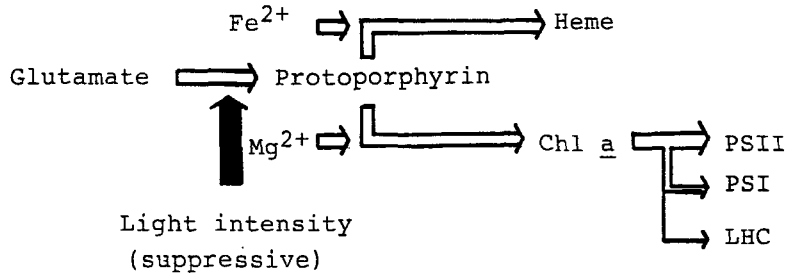

Fig. 5. Path of Chl a synthesis. Dark arrow indicates regulation by light intensity. Thickness of arrows from Chl a to photosystem and LHC complexes indicates affinity of Chl a supply to each assembling.

2.2.2 Regulation of stoichiometry between PS I and PS II complexes in thylakoids

Except for the thylakoids in chloroplasts in matured leaves of higher plants, the stoichiometry between the two photosystems in thylakoids is variable depending on the light regime for photosynthesis. A general feature is that (i) the level of PS I is greater than that of PS II under the light to excite PS II more strongly than PS I, or under a weak white light, and (ii) the PS I level becomes lower than that under the conditions for (i), when light excites mainly PS I or causes a light-saturation of photosynthesis (cf. 31).

Table 3 shows stoichiometric characteristics of thylakoid system of the cyanophyte Synechcystis PCC 6714 grown under various light regimes. A common feature is that abundance of PS I varies in response to the light regime, indicating that PS I level is regulated. PS I level is high under the light absorbed by PBS, and so, exciting mainly PS II or weak white light, and the level is low under the light absorbed by Chl a, and so, exciting preferentially PS I, or under strong white light. Changes in

PS I level induced by the shift of light regime occurs slowly depending on the cell growth (32), indicating that thylakoid formation during cell growth is essential for the

Table 3. Abundance, per cell, of PSI, PSII and Cyt $\underline{b}_6$-$\underline{f}$ complexes and PBS in cells of Synechocystis PCC 6714 grown under various light regimes (from Ref. 20, 24).

Light regime	Abundance* of PSI	PSII	Cyt $\underline{b}_6$-$\underline{f}$	PBS
PSII light**	6.3	2.1	1.8	1.7
PSI light***	3.0	2.4	2.1	2.2
Weak white light (3 W/m^2)	6.5	2.2	2.0	--
Strong white light (40 W/m^2)	2.4	1.8	1.5	--

* 10^4 molecules per cell.
** A weak orange light absorbed by PBS, and so, exciting mainly PSII.
*** A weak red light absorbed by Chl $\underline{a}$, and so, exciting mainly PSI.

Table 4. Photosynthetic efficiency and reactive state of PSI and PSII in Synechocystis PCC 6714 before and after regulation of PSI/PSII stoichiometry in response to light regime (from Ref. 33 and 34).

Cell type	Light regime	Photosynthetic efficiency*	Active form** of PSI	PSII
Low PSI/PSII				
Before	PSII light	0.38	1.00	0.39
After		1.00	1.00	1.00
High PSI/PSII				
Before	PSI light	0.37	0.35	1.00
After		0.90	0.85	1.00

* O_2 evolution per absorbed quantum, and expressed as relative to the maximum.
**Ratio of active form to the total.

Cells of low (grown under PSI light) and high PSI/PSII (grown under PSII light) were determined under PSII and PSI light before and after regulation of PSI/PSII stoichiometry, respectively.

change of PS I/PS II stoichiometry. Synthesis or degradation of PS I complex probably is regulated during thylakoid formation. This regulation brings about a high efficiency of photosynthesis under respective light regimes as shown in Table 4. Thus, it is a regulation to maintain a high photosynthetic efficiency, together with the regulation of excitation-transfer. The same regulation of PS I/PS II stoichiometry in response to the light-quality (35) and the light-intensity (36) has been observed for thylakoid system in young seedlings of higher plants. It has also been reported that in the former case, the regulation maintains a high efficiency of photosynthesis under respective light regimes (35). Besides cyanophytes and higher plants, the regulation of PS I/PS II stoichiometry has been observed with red algae (21, 37). Occurrence of this regulation in organisms of very different phyla indicates that this regulation is a common ability of the system in oxygenic photosynthesis.

The range of adjustment in this regulation is much greater than the "short term" regulation. As shown in Table 4, more than half of PS II has to be inactive in cells grown under PS I light when they have been illuminated with PS II light. This is due to a strict limitation of overall reaction at PS I action. Thus, "short term" regulation of the excitation-energy transfer cannot balance the two photoreactions in this case. Then, "long term" regulation of PS I/PS II stoichiometry occurs, and the balance again recovers. In a reverse case, inactive PS I can become active after the regulation of PS I/PS II stoichiometry to smaller value. This feature indicates the relationship between two types of regulation. "Long term" regulation occurs rather slowly but can adjust the system-function in a wide range; "short term" regulation functions as a fine tuning to the light regime quickly but in a limited range.

Then, question arises as to whether synthesis or degradation of PS I complex is controlled in this "long term" regulation. Table 5 shows the relationship between protein synthesis and changes in PS I level. Again, changes in PS I level is suppressed by the translation inhibitor even when decrease in PS I level is induced by PS I light or strong white light. Analysis of changes in abundance of peptides constructing PS I complex has indicated that synthesis of PS I complex, but not degradation is regulated (Aizawa et al., submitted to Photosyn. Res.). Preliminary experiments for determining the rate of PS I synthesis at the level of peptide synthesis have indicated that a short illumination with PS II light enhances twice as much the rate of PS I synthesis in cells grown under PS I light (Table 6). Thus, changes in PS I/PS II stoichiometry can be recognized as that PS I synthesis is regulated in response to light regime so as to maintain a PS I/PS II stoichiometry to balance two photoreactions.

Table 5. Effect of CAP on the decrease in PSI abundance induced by PSI light (Exp.1) and by strong white light (Exp.2) in cells of Synechocystis PCC 6714 grown under PSII light (from Ref. 24 and 38).

Incubation	Abundance* of PS I	PSII	Cyt b_6-f
Exp.1 (PS I light)			
0 hr	5.2	2.2	2.5
10 hr	3.5	2.1	2.7
10 hr, with CAP	5.3	2.0	2.4
Exp.2 (strong white light)			
0 hr	8.7	2.8	2.6
22 hr	4.9	2.3	2.3
22 hr, with CAP	6.7	2.1	2.5

* 10^4 molecules per cell.

Cells grown under PSII light were incubated under PSI light (Exp.1) and under strong white light (40 W/m^2, Exp.2) without and with CAP (2×10^{-4}M), resepctively.

Table 6. Enhancement of synthesis of PSI core peptides in cells of Synechocystis PCC 6714 grown under PSI light by illumination with PSII light (Aizawa and Fujita, unpublished data).

	^{35}S incorporation into PSI core peptides*
Before	5.6±1.8
After	10.3±3.4

* Values are % of total incorporation into membrane fractions.

Cells grown under PSI light were pulse-labelled (2 min) with ^{35}S-methionine before and after illumination with PSII light for 3 hr. Labelling was done under PSI light for Before, and under PSII light for After.

As described above, the "short term" regulation at the level of the energy transfer from LH system to two photosystems occurs in response to the redox state of Cyt $\underline{b}_6$ - $\underline{f}$. Then, what is the signal for the "long term" regulation of PS I/PS II stoichiometry? A conclusive answer to this question is not available at present. However, the study of the relationship between the state of ETS and the regulation of PS I level has indicated that the redox state of Cyt $\underline{b}_6$ - $\underline{f}$ is again closely related to the regulation; a highly reduced state of the cytochrome seems to cause the increase in PS I level (24, 34). If this correlation really reflects the nature of the signal, it is very probable that two regulations, "short term" and "long term", occur in response to a common signal.

Molecular mechanism of the regulation of PS I synthesis has not been clear yet and has been under investigation. However, the study of the relationship between Chl $\underline{a}$ synthesis and the regulation has suggested a possibility that the regulation occurs at the level of Chl $\underline{a}$ supply to PS I assembling (39). This is consistent with the evidence that the synthesis of PS I apoproteins is initiated by Chl $\underline{a}$ supply in the greening process in etiolated seedlings of higher plants (40, 41). If it is correct, the regulatory mechanism may be, at least in part, common to the regulation of the size of LH system, another type of "long term" regulation. Figure 6 shows a work model for mechanism of the regulation of PS I level. A highly reduced state of Cyt $\underline{b}_6$ - $\underline{f}$, probably the state of Cyt $\underline{b}_6$, is monitored and transduced to the form to control PS I assembly through the signal transducing system. The PS I assembly is controlled at the step of Chl $\underline{a}$ synthesis and/or synthesis of PS I apoproteins. Therefore, both "long term" and "short term" regulations appear to occur monitoring the state of ETS between the two photosystems.

Because the state of ETS is, or is closely related to, the signal for the regulation, the regulation occurs in response to not only light regime but also other environmental factors for photosynthesis. An example is CO_2 concentration in the environment. PS I/PS II stoichiometry becomes greater when cells of cyanophytes have been grown under low CO_2 conditions (42). Low CO_2 conditions induce development of HCO_3^- incorporation system, which requires ATP. Thus, the photosynthetic ETS has to produce more ATP through an enhancement of cyclic electron transport driven by PS I action. The extra ATP requirement must break a balance between levels of NADPH and ATP for CO_2 fixation, and cause a temporary accumulation of NADPH, which, in turn, may donate electrons to Cyt $\underline{b}_6$ - $\underline{f}$ through FNR and stimulate temporarily cyclic electron transport. If this assumption is correct, the state of Cyt $\underline{b}_6$ - $\underline{f}$ may be shifted to more reduced state due to the enhanced electron inflow from PS I. In response to such a state,

PS I formation may be stimulated. As far as ATP is required by HCO_3^- incorporation, such a state of Cyt $\underline{b}_6$ - $\underline{f}$ may remain, and stimulation of PS I synthesis may be maintained. A similar feature is expectable when the

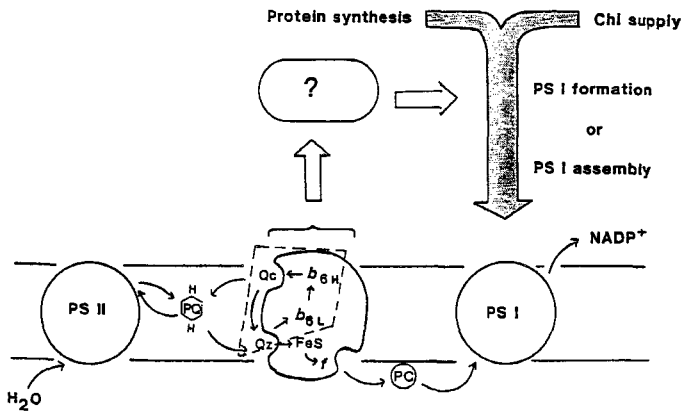

Fig. 6. A work model for regulation of PS I formation in response to the state of ETS. Questionmark indicates unknown system for signal transduction.

ratio of ATP and NADPH required for photosynthesis is changed due to changes in nutritional and physicochemical environments.

3. Concluding remarks

In summary, the thylakoid system for photosynthetic energy conversion has the ability for adjustment of the system-function to maintain a high efficiency of energy conversion at least in two ways (Fig. 7). When changes in photosynthetic environment occur, the balance between two photoreactions has to be broken. If the imbalance is rather moderate, the adjustment by the "short term" regulation of the excitation-energy trnasfer can recover the system from biassed state. If it is not, the signal indicating the biassed state must be still greater. Then, the regulation of PS I synthesis is induced as far as cells or chloroplasts are still growing. The range of the adjustment by this "long term" regulation is great enough for responding to a drastic environmental change. Thus, the growing thylakoid system in algal cells and in young seedlings of higher plants can show a much more marked plasticity to the photosynthetic environment than the system in chloroplasts of matured leaves, in which the "long term" regulation no longer occurs.

A great advantage of oxygenic photosynthesis is its ability for H_2O oxidation. However, the reaction depends

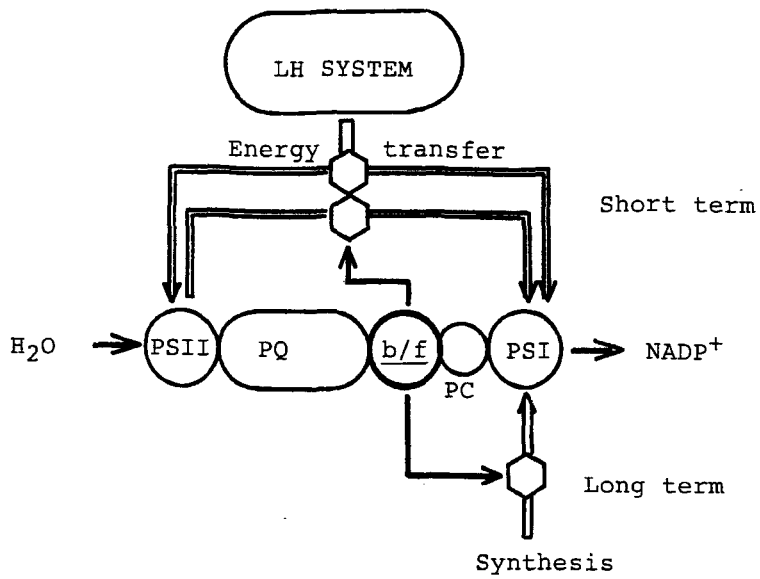

Fig. 7. Schematic presentation of "short term" and "long term" regulations.

on the photochemical reaction of PS II, and so the overall reaction for the energy conversion has to be driven by two photoreactions. This feature is more complexed than the system for anoxygenic photosynthesis which is driven by a single photoreaction. Complexity of the system is liable to lower the efficiency of the system-function. However, a net work of the system-regulation introduced here can maintain the efficiency at high level.

As noted above, the mechanism of these regulatory processes has not been clear in molecular level. Most of studies on this problem have still remained at physiological level. However, development of molecular biology for the thylakoid system has been very rapid. This current must be extended to the problem introduced here, and will provide detailed information about the molecular mechanism of the homoeostatic ability of thylakoid system, the characteristic as a biological system.

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