Plant Physiol. (1986) 82, 185–189
0032-0889/86/82/0185/05/$01.00/0

Cyanobacterial Acclimation to Photosystem I or Photosystem II Light[1]

Received for publication February 26, 1986 and in revised form May 15, 1986

ANNAMARIA MANODORI AND ANASTASIOS MELIS*
Division of Molecular Plant Biology, 313 Hilgard Hall, University of California, Berkeley, California 94720

ABSTRACT

The organization and function of the photochemical apparatus of *Synechococcus* 6301 was investigated in cells grown under yellow and red light regimes. Broadband yellow illumination is absorbed preferentially by the phycobilisome (PBS) whereas red light is absorbed primarily by the chlorophyll (Chl) pigment beds. Since PBSs are associated exclusively with photosystem II (PSII) and most of the Chl with photosystem I (PSI), it follows that yellow and red light regimes will create an imbalance of light absorption by the two photosystems. The cause and effect relationship between light quality and photosystem stoichiometry in *Synechococcus* was investigated. Cells grown under red light compensated for the excitation imbalance by synthesis/assembly of more PBS-PSII complexes resulting in high PSII/PSI = 0.71 and high bilin/Chl = 1.30. The adjustment of the photosystem stoichiometry in red light-grown cells was necessary and sufficient to establish an overall balanced absorption of red light by PSII and PSI. Cells grown under yellow light compensated for this excitation imbalance by assembly of more PSI complexes, resulting in low PSII/PSI = 0.27 and low bilin/Chl = 0.42. This adjustment of the photosystem stoichiometry in yellow light-grown cells was necessary but not quite sufficient to balance the absorption of yellow light by the PBS and the Chl pigment beds. A novel excitation quenching process was identified in yellow light-grown cells which dissipated approximately 40% of the PBS excitation, thus preventing overexcitation of PSII under yellow light conditions. It is hypothesized that State transitions in O_2 evolving photosynthetic organisms may serve as the signal for change in the stoichiometry of photochemical complexes in response to light quality conditions.

When photosynthetic organisms are grown under different light regimes, the stoichiometry of electron-tranport complexes in the thylakoid membrane and the relative amounts of the light-harvesting pigments are adjusted and optimized in response to the prevailing light conditions (13). Acclimation of cyanobacteria to different light qualities can take two forms. Complementary chromatic adaptation describes changes in the ratio of pigments within the light-harvesting PBS.[2] This type of adaptation has been the subject of intense investigation and is reviewed by Tandeau de Marsac (17). In inverse chromatic control, described by Jones and Myers (4), there is little change in the PBS pigment content with light quality. Instead, the amount of Chl relative to PC varies. Yellow light, absorbed primarily by the PBS, results in lower PC/Chl ratios, with the reverse being true for cells grown under red (Chl) light. Moreover, Myers *et al.* (14) recognized that the successful long-term adaptation of spontaneous PC mutants of *Synechococcus* 6301 to red light (>650 nm) strongly depended on alteration of the PSII/PSI reaction center ratio.

In this work we determined the structural and functional organization of the photosynthetic apparatus of *Synechococcus* 6301 after a 70 h acclimation to red or yellow light. We determined the pigment content and reaction center stoichiometry under the yellow and red light growth conditions. We found a 3-fold variation in the bilin/Chl ratio between red light and yellow light-grown cells. This was paralleled by similar amplitude variation in the PSII/PSI complex ratio. Thus, the response of the cyanobacterial cells to changes in the light-quality is an adjustment in the stoichiometry of PSII and PSI complexes. The acclimation of red light-grown cells was sufficient to balance the absorption of light and electron-transport between PSII and PSI. The acclimation of cyanobacteria to yellow light, however, was not fully sufficient to compensate for PBS overexcitation. We identified a novel excitation quenching mechanism operating under yellow light growth conditions which dissipated approximately 40% of the PBS excitation before such excitation reached the reaction center of PSII.

MATERIALS AND METHODS

Cell Culture. *Synechococcus* 6301, Pasteur culture collection strain 6301 (16), was grown autotrophically under the conditions and in the medium described by Arnon *et al.* (1). The cultures were bubbled with 3% CO_2 in N_2 and stirred continuously. This allowed for uniform growth conditions within each culture. Illumination was provided either by a combination of 100-W tungsten incandescent lamps and a red Plexiglas cutoff filter (No. 2423 from Rohm and Haas), or by a combination of warm white Sylvania fluorescent lamps and a yellow cutoff filter (No. 2208). Control cells (white light) were illuminated with tungsten incandescent lamps. The spectral distribution of the light used for cell growth is shown in Figure 1. The photon flux density of the PAR was 43, 37, 34 μmol m^{-2} s^{-1} and the cell doubling time was 12, 14, and 17 h for *Synechococcus* 6301 grown in white, yellow, and red light, respectively.

The RL and YL grown cultures were always inoculated with cells from the WL culture at a density of 1×10^7 cells/ml and allowed to adapt to the new light regime for 70 h before harvest. It was determined that cell pigment content reached a steady state within 60 h. Samples were either harvested by centrifugation or used directly in their growth medium for the various measurements.

Pigment Content and Reaction Center Concentrations. Chl concentrations were calculated from the absorbance spectra of the cells, using the system of equations derived by Myers *et al.* (14). Phycocyanobilins were measured by the method described

[1] Supported by a United States Department of Agriculture Competitive Research Grant.

[2] Abbreviations: PBS, phycobilisome; PC, phycocyanin; RL, red light; YL, yellow light, WL, white light.

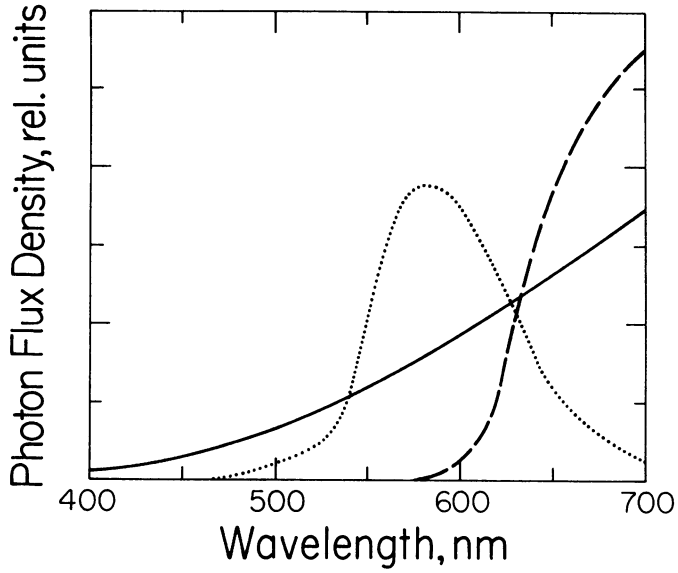

FIG. 1. Emission spectra of the photosynthetically active radiation of the YL (·····), WL (——), and RL (– – –) used for *Synechococcus* 6301 cell growth.

in Manodori *et al.* (8). Cells were counted with a Neubauer hemacytometer. Each count consisted of four loadings with a minimum of 200 cells counted per loading.

Photosynthetic membranes were isolated following the procedure described by Manodori and Melis (9). In isolated thylakoid membranes, Chl concentrations were determined in 80% acetone using MacKinney's extinction coefficient of 82 mM^{-1} cm^{-1} for absorption at 663 nm (7). The concentration of Q (PSII) and P700 (PSI) were measured by sensitive absorbance difference spectrophotometry in the UV (ΔA_{320}) and red (ΔA_{700}) regions of the spectrum as described by Melis and Anderson (12).

Phycobilisome Isolation. Phycobilisomes were isolated by the procedure of Yamanaka *et al.* (20) in 0.65 M NaK-phosphate buffer at pH 8.0. Aliquots of PBS containing supernatant were layered onto continuous sucrose gradients (0.5–1.0 M sucrose in 0.75 M NaK-phosphate [pH 8.0]), then centrifuged at 104,000*g* for 12 h at 18°C. The PC to allophycocyanin (AP) ratios were calculated from the absorbance peaks at 624 and 654 nm of the isolated PBSs (19).

Integrated Absorbance of Light by PSII and PSI. The relative rate of light absorption by PSII and PSI in YL, WL, and RL-grown cells was determined from the integrated effective absorbance spectra of PSII and PSI. The effective absorbance spectra of PSII and PSI were determined according to Ghirardi and Melis (3) from the product of the absorbance spectrum of a PBS-PSII or PSI complex, times the emission spectrum of the light source used during cell growth. We derived the absorbance spectra of PBS-PSII and PSI complexes by deconvolution of the absorbance spectra of the three cell cultures. This was accomplished by using the known PSII/PSI reaction center ratio (Table I) and by assuming that about 140 Chl *a* molecules are specifically associated with each PSI, whereas about 35 Chl *a* molecules are associated with each PSII complex (8).

Kinetic Measurements. The rate of light absorption by PSII reaction centers was determined from the kinetics of fluorescence induction under weak PBS excitation of DCMU-poisoned cells. The kinetics of Chl *a* fluorescence emission was measured at 700 nm. Actinic illumination was provided by a combination of a broadband Baird atomic 600 nm interference filter and a Corning CS 2-62 cutoff filter (5% transmittance at 593 and 654 nm, maximum of 43% transmittance at 620 nm) at an intensity of 10 μmol m^{-2} s^{-1}. The rate of light absorption by PSI was measured from the kinetics of P700 photooxidation also under PBS excitation conditions with RL (λmax = 620 nm as for the fluorescence kinetic measurements). The actinic intensity was set at 20 μmol m^{-2} s^{-1} and the reaction mixture contained 25 μg Chl/ml, 20 μM DCMU, 200 μM methyl viologen, and 1 μM diphenylphenanthroline.

Fluorescence Emission Spectra. Corrected fluorescence emission spectra of intact cells at room temperature were scanned with a SLM 8000 photon-counting spectrofluorometer. Excitation of PBSs in intact cells was provided at 580 nm. Excitation at 540, 580, and at 620 nm resulted in invariant fluorescence emission peak ratios (655/680 nm). In intact cells, the PC to Chl ratio was estimated from the *A* at 625 and 678 nm using the equations of Myers *et al.* (14). Isolated photosynthetic membranes were added to the red-cell suspension to bring the PC/Chl ratio equal to that estimated for the yellow cells. The final reaction mixture contained cells at a PC concentration of 1 μM, 40 μM DCMU, and 2 mM NH_2OH.

RESULTS

Reaction Center Concentrations. Absorbance spectra of *Synechococcus* 6301 cells grown under YL, WL, and RL cells are presented in Figure 2. Qualitatively, cells grown with RL (Fig. 2, dashed line) have a much higher PC/Chl ratio than cells grown under YL (Fig. 2, dotted line). The cells grown under RL apparently compensated for the lower PC excitation by synthesizing more PC relative to Chl. Similarly, the cells grown under YL compensated for the lower excitation of Chl by synthesizing more Chl relative to PC. The relative pigment content in the three cultures at the time of harvest is presented in Table I. We

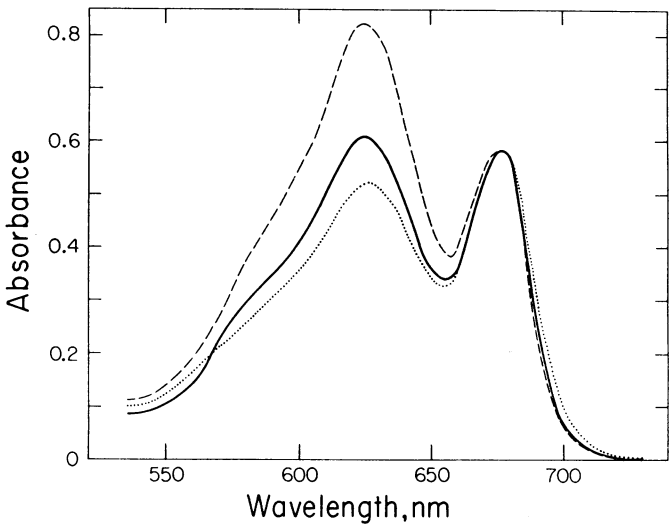

FIG. 2. Absorbance spectra of *Synechococcus* 6301 cells grown under YL (·····), WL (——), and RL (– – –). The spectra were arbitrarily normalized at the Chl absorbance maximum of 678 nm.

Table I. *Pigment Content and Reaction Center Stoichiometries in Synechococcus 6301 Cells Grown under Different Light Qualities*

The concentration of Chl, total bilin, P700 (RCI), and Q(RCII) in YL and RL cells was determined 60 to 90 h following cell inoculation from a WL culture. All values represent the average of at least 6 measurements ± SE.

Light Conditions	Bilin/Chl	Chl/Q	Chl/P700	RCII/RCI
Yellow	0.42 ± 0.04	575 ± 40	156 ± 5	0.27 ± 0.02
White	0.53 ± 0.06	370 ± 43	160 ± 1	0.43 ± 0.02
Red	1.30 ± 0.08	230 ± 18	163 ± 5	0.71 ± 0.06

estimated that the chromophore molar ratio of bilin/Chl is low (= 0.42) in the YL-grown cells and over 3-fold greater in the RL-grown cells (bilin/Chl = 1.3).

To determine the stoichiometry of the photosystems we measured the absolute concentration of the reaction centers from the amplitude of the light-induced absorbance change at 320 nm (Q) and at 700 nm (P700) (12). The result of such quantitation is also presented in Table I. We determined Chl/Q values equal to 575, 370, and 230 in the thylakoid membrane of YL, WL, and RL cells, respectively. The Chl/P700 ratios were 156, 160, and 163, respectively. Therefore, the stoichiometry of the reaction centers (RCII/RCI) is 0.27, 0.43, and 0.71 for YL, WL, and RL cells, respectively. Since the antenna size of individual PSI and PBS pigment beds remained constant under the various light quality conditions (5, 11), it is implied that elevated bilin/Chl ratios in RL cells is the direct consequence of elevated PSII/PSI complex ratios.

Integrated Absorbance of Light by PSII and PSI. We tested to see whether the photosystem stoichiometry adjustment in YL, WL, and RL-grown cells is necessary and sufficient to ensure balanced absorption of light between the two photosystems. To this end, we compared the integrated absorbance of light by PSII and by PSI in YL and RL-grown cells. This was implemented from the solution of the following integral equation:

$$\sigma = \int_{450}^{750} A(\lambda) \cdot T(\lambda) \cdot d\lambda \qquad (1)$$

where σ is the integrated effective absorbance of light by a photosystem in a cell, $A(\lambda)$ is the absorbance spectrum of a photosystem in the cell, and $T(\lambda)$ is the emission spectrum of the light source during cell growth. Table II shows that in RL-grown cells light absorption by the two photosystems is fairly well balanced (σ_{II}/σ_I ratio approximately equal to 1), suggesting that a photosystem stoichiometry adjustment in these cells was fully sufficient to compensate for the light quality effect and thus to ensure an overall equal distribution of absorbed light between the two photosystems. Cells grown under YL conditions (which favors excitation of the PBS, hence of PSII) had the lowest PSII/PSI reaction center ratio equal to 0.27 (Table I). However, and in spite of this adjustment, the overall absorbance of light by PSII exceeded that of PSI by a factor of 2.4 in YL cells (σ_{II}/σ_I = 2.4, see Table II). Thus, the stoichiometry adjustment of YL-grown cells was necessary but not sufficient to balance light absorption between the two photosystems.

Excitation Energy Transfer from PBS to RCII. To test for the efficiency of excitation energy transfer from PBS to RCII in intact YL and RL grown cells, we determined the rate of light absorption by the PSII reaction centers under PBS excitation. We illuminated DCMU-poisoned cells with 620 nm light, absorbed primarily by the PBS, and monitored the kinetics of Chl *a* fluorescence induction. The variable fluorescence kinetics are shown in Figure 3. The kinetic traces are monophasic functions of time, suggesting a uniform PBS antenna size for the absorption

Table II. *Integrated Absorbance of Light and Rates of Light Trapping in Synechococcus 6301 Cells Grown under Different Light Qualities*

The parameter σ reflects the total absorbance of light by a photosystem in the cell taking into account the relative concentration of that PS in the cell. The rate of light absorption by RCII (K_{II}) was estimated from the analysis of fluorescence induction kinetics of DCMU-poisoned cells. The rate of light absorption by RCI (K_I) was determined from the kinetics of P700 photooxidation in intact cells under PBS excitation.

Light Conditions	σ_{II}/σ_I	K_{II620}	K_{I620}
		s^{-1}	
Yellow	2.4	29 ± 1	2.0
White	1.1	34 ± 1	1.7
Red	1.1	52 ± 2	1.5

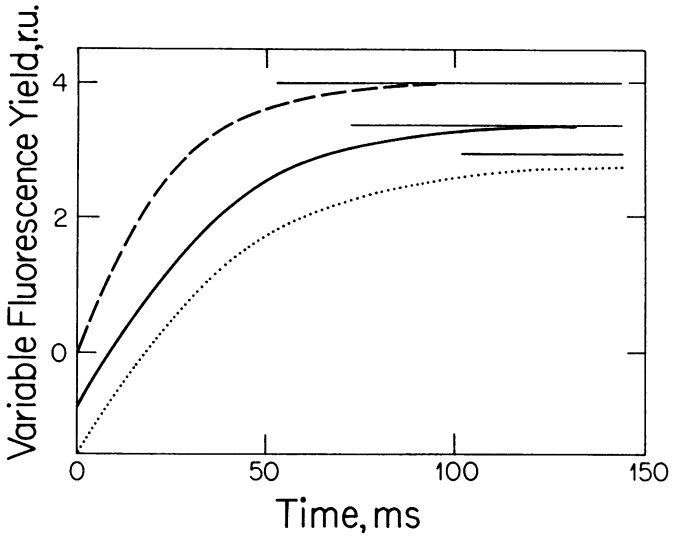

FIG. 3. Variable Chl *a* fluorescence kinetics of *Synechococcus* 6301 cells grown under YL (·····), WL (——), and RL (– – –). Cells were suspended in the presence of 20 μM DCMU. Actinic excitation was provided at 620 nm at an intensity of 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

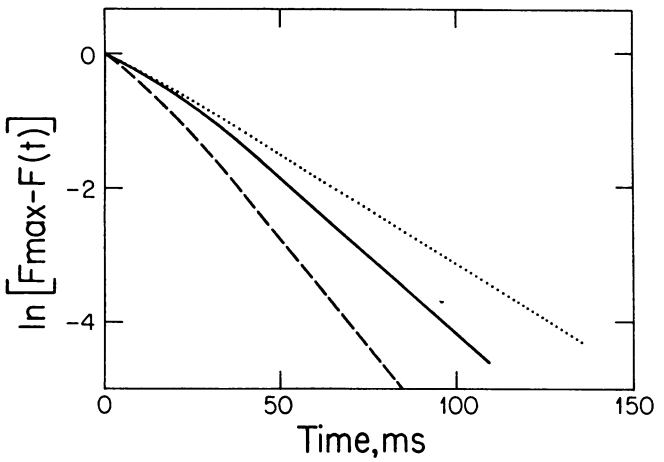

FIG. 4. Semilogarithmic plot of the variable fluorescence kinetics of *Synechococcus* 6301 cells grown under YL (·····), WL (——), and RL (– – –). The slope of each line defined the rate of photon trapping (K_{II620}, see Table II) by PSII reaction centers.

of light and the transfer of excitation to the photochemical centers of PSII in these cells. The slope of the semilogarithmic plots of these curves (Fig. 4) defined K_{II620}, which is a direct measure of the rate of light trapping by the PSII reaction centers.

Table II shows that K_{II620} is substantially different for the YL and RL cells. We estimated a rate K_{II620} = 29 photons s^{-1} arriving at the reaction centers of PSII in the YL cells. The corresponding value for the RL cells was equal to 52 photons s^{-1}, *i.e.* almost twice as large. Cells grown under white (incandescent) light showed intermediate rates of photon trapping (K_{II620} = 34 s^{-1}, Table II).

Based on the absorbance ratio of PC/AP (A_{624}/A_{654}) in isolated PBSs, we determined that individual PBSs in YL-grown cells have a smaller optical cross section (by about 10%) than PBSs in RL-grown cells (11). Hence, the rate of light absorption by individual PBSs is approximately the same in YL and RL cells. The substantially different rates of photon arrival at RCII between YL and RL-grown cells implies substantially different efficiencies of excitation energy transfer from PBS to RCII in the two cell types. Our measurement indicated that when compared

with RL cells the energy absorbed by the PBS in YL cells is transferred with only about 60% relative efficiency to the PSII reaction centers. We attempted to identify the cause of this lower efficiency of excitation transfer from PBS to RCII in the YL cells. First we tested whether the large difference between the rate of photon trapping by the RCII of RL and YL-grown cells (52 s^{-1} *versus* 29 s^{-1}) is the direct consequence of excitation transfer from PBS to PSI in YL cells. We reasoned that if ~40% of the light energy absorbed by the PBS in YL cells was transferred to PSI, this would account for the lower rate of excitation energy transfer to RCII. In this case, there would be a large difference in the rate of P700 photoactivity between YL and RL cells upon excitation of the PBS. We tested this hypothesis by measuring the rate of P700 photooxidation under 620 nm illumination *in vivo*. Figure 5 shows the kinetic traces of P700 photooxidation in YL and RL cells. The respective semilogarithmic plots are shown in Figure 5 (inset). The slope of the semilogarithmic lines defined K_{1620}, the rate of light absorption by PSI under PBS excitation. We determined K_{1620} = ~2.0 s^{-1} in the YL cells and K_{1620} = 1.5 s^{-1} in the RL cells (Table II). If ~40% of PBS excitation in YL cells were delivered to PSI, one would have expected $K_{1620} > 18$ s^{-1} which clearly is not the case. The low K_{1620} values in both YL and RL cells is attributed to the weak absorption of 620 nm light by the Chl pigment bed of PSI. The small difference between the rate constants K_{1620} of YL and RL cells may be due to the greater relative PC content of the RL cells than in the YL cells (Table I). Phycocyanin in RL cells absorbs a greater fraction of the 620 nm light leaving a lower intensity for direct absorption by Chl. The results of this experiment confirm previous findings that PBSs are associated exclusively with PSII reaction center complexes and that PBS excitation is not transferred to PSI (8, 9).

In view of the results presented above, we are faced with the YL cells where the PBS absorbs 620 nm excitation at a rate comparable to that of RL cells. However, only about 60% of the PBS excitation in YL cells is delivered to RCII. The remaining 40% of the PBS excitation is not delivered to PSI and cannot be directly accounted for. We tested for possible quenching of excitation in the PBS-PSII complex of YL cells under *in vivo* conditions. We reasoned that cyanobacterial cells may possess a mechanism of excitation quenching to prevent overexcitation of RCII. In an attempt to identify a site in the photochemical apparatus of YL cells where excitation quenching might occur, we compared the fluorescence emission spectra of intact RL and YL cells in their growth media. To decrease any scattering and self-absorption effects, the cells were diluted with Tris buffer to give a PC concentration of 1 μM. To correct for the different optical properties of the two type cells, we mixed isolated thylakoid membranes with the RL cells to yield the same PC/Chl ratio as in the YL cells. The resulting fluorescence emission spectra are presented in Figure 6. The emission peak at 655 nm most likely originates from free PC, the shoulder at 660 nm is due to free AP, and the emission peak at 680 nm is due to both the 75 kD terminal exciton acceptor polypeptide and the Chl *a* from the light-harvesting antenna of PSII (2, 10). The YL cells showed a considerably lower fluorescence yield at 680 nm suggesting excitation energy quenching at the AP terminal exciton acceptor of the PBS and/or in the Chl pigment bed of PSII in the YL cells. We estimated a fluorescence yield ratio at 680 nm $F(YL)/F(RL)$ = 0.50. Thus, the existence of this excitation quenching mechanism in YL-grown cells will account for the substantially different rates of PSII photoactivity in RL and YL cells.

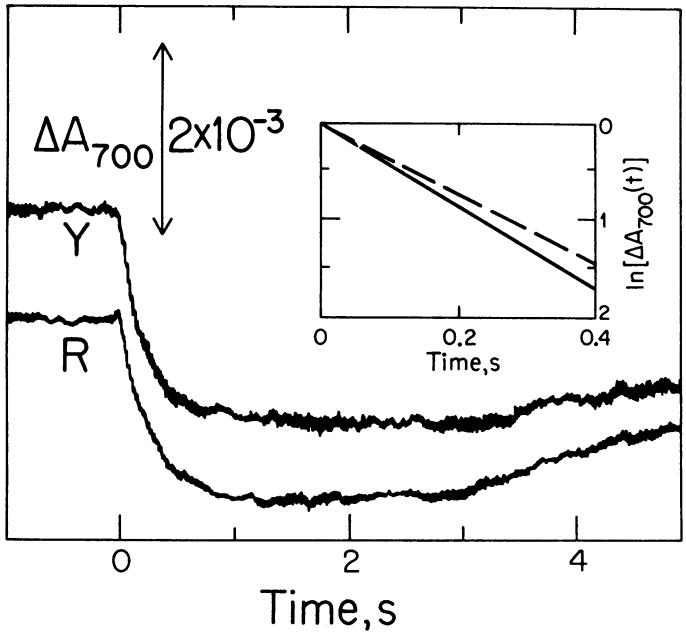

FIG. 5. Absorbance change kinetics at 700 nm of *Synechococcus* 6301 cells grown under YL and RL. Actinic excitation was provided at 620 nm at an intensity of 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Actinic light came ON at 0 s, and it went OFF at 3 s. Inset, Semilogarithmic plot of the light-induced absorbance decrease in YL-cells (——) and RL-cells (– – –). The slope of each line defined the rate of photon trapping (K_{1620}, see Table II) by PSI reaction centers, respectively.

DISCUSSION

Growth of *Synechococcus* 6301 in YL and RL causes distinct differences in the organization of the photochemical apparatus of photosynthesis. When cells growing under WL are transferred to RL conditions, they are faced with an imbalance in light absorption by the two photosystems since RL sensitizes predominantly the Chl antenna of PSI. The response of the cells to the RL environment was enhanced PBS-PSII concentration in the thylakoid membrane. This compensation was necessary and sufficient to balance electron flow between the two photosystems. On the other hand, when cells growing under WL are transferred to YL, they are faced with overexcitation of PSII since YL

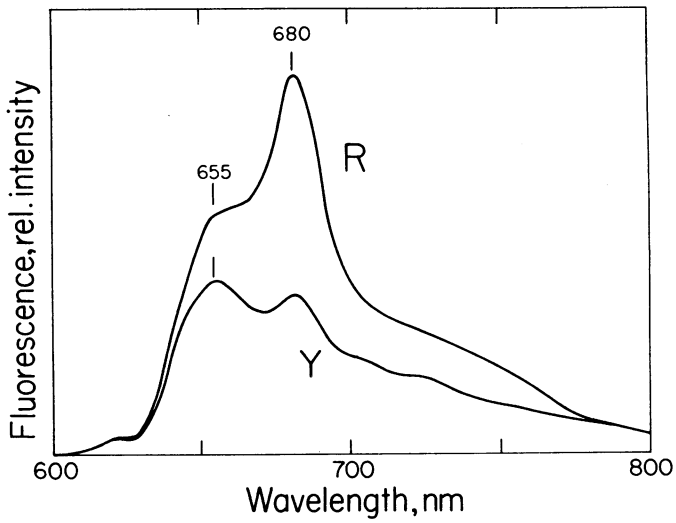

FIG. 6. Room temperature fluorescence emission spectra of intact *Synechococcus* 6301 cells suspended in the presence of DCMU and hydroxylamine. Cells were grown under YL or RL conditions. Excitation was provided at 580 nm. Note that the PC concentration was 1 μM in both samples.

sensitizes predominantly the PBS antenna of PSII. To adjust for this excitation imbalance in favor of PSII, *Synechococcus* cells synthesized and assembled more PSI complexes in the thylakoid membrane. However, this response was not sufficient to compensate fully for the excitation imbalance. Thus, under YL, and in spite of the very low PSII/PSI stoichiometry (= 0.27), the PBS-PSII complexes collectively absorbed 2.4 times more YL than PSI did. The extra excitation energy was not delivered to the PSII reaction center (low K_{II620}) nor was it transferred to PSI. Rather, it was dissipated via an unknown excitation quenching process, possibly at the Chl pigment bed of PSII. Such quenching attenuated the rate of photon-trapping by PSII in YL-grown cells and resulted in balanced electron turnover by the two photosystems. The overall effect of the acclimation response in both cell cultures, in the cells illuminated with PSII-light (YL) or PSI-light (RL), was equal growth rates and therefore equal rates of photosynthesis.

A clue to the location of the excitation quenching in YL-cells was provided by the kinetics of PSII photoactivity. The results of Figures 3 and 4 demonstrate that the sigmoidicity in the fluorescence induction curve is mostly lost in the YL-grown cells (dotted line in Fig. 4). The sigmoidicity is a manifestation of the presence of two PSII complexes per PBS (10). Each PSII complex is connected to a 75 kD terminal exciton acceptor protein of the PBS (10). The lack of sigmoidicity in the YL-grown cells suggests that a sizable population of the PBSs is associated with only one PSII complex. It is conceivable that the quenching of absorbed energy in these cells occurs at the 75 kD polypeptide terminal acceptor which is not connected to a PSII complex.

It is worth noting that transfer of cell cultures from WL to YL is the equivalent of a state 2 transition, whereas transfer of cell cultures from WL to RL constitutes a state 1 transition (18). Our work raises the question whether the long-term effect of state transitions is the adjustment of photosystem stoichiometry in the thylakoid membrane in order to optimize the electron transport process. If this were the case, changes in the steady state course of fluorescence emission and rate of O_2 evolution that normally accompany state transitions (18) may reflect the initial events of the impending change in the stoichiometry of photosystems (13).

An interesting question to address in this light-quality related acclimation of *Synechococcus* 6301 is why do YL cells retain a large PBS size when excitation conditions decisively favor PSII. The answer to this question is presently unclear. Lonneborg *et al.* (6) reported reversible changes both in the stoichiometry of PSII/PSI and in the PBS size upon transferring *Synechococcus* 6301 from high-intensity WL to low-intensity RL. On the other hand, Raps *et al.* (15) reported a constant PBS size in *Microcystis aeruginosa* cultures independent of light intensity during cell growth. Clearly, more work is needed to delineate the interplay between light-intensity and light-quality in the acclimation of cyanobacteria.

LITERATURE CITED

1. ARNON DI, BD MCSWAIN, HY TSUJIMOTO, K WADA 1974 Photochemical activity and components of membrane preparations from blue-green algae. I. Coexistence of two photosystems in relation to chlorophyll *a* and removal of phycocyanin. Biochim Biophys Acta 357: 231–245
2. GANTT E 1981 Phycobilisomes. Annu Rev Plant Physiol 32: 327–347
3. GHIRARDI ML, A MELIS 1984 Photosystem electron-transport capacity and light-harvesting antenna size in maize chloroplasts. Plant Physiol 74: 993–998
4. JONES LM, J MYERS 1965 Pigment variations in *Anacystis nidulans* induced by light of selected wavelengths. J Phycol 1: 6–13
5. KHANNA R, JR GRAHAM, J MYERS, E GANTT 1983 Phycobilisome composition and possible relationship to reaction centers. Arch Biochem Biophys 224: 534–542
6. LONNEBORG A, LK LIND, SR KALLE, P, GUSTAFSSON, G ÖQUIST 1985 Acclimation processes in the light-harvesting system of the cyanobacterium *Anacystis nidulans* following a light shift from white to red light. Plant Physiol 78: 110–114
7. MACKINNEY G 1941 Absorption of light by chlorophyll solutions. J Biol Chem 140: 315–322
8. MANODORI A, M ALHADEFF, A GLAZER, A MELIS 1984 Photochemical apparatus organization in *Synechococcus* 6301 (*Anacystis nidulans*). Effect of phycobilisome mutation. Arch Microbiol 139: 117–123
9. MANODORI A, A MELIS 1984 Photochemical apparatus organization in *Anacystis nidulans* (cyanophyceae). Effect of CO_2 concentration during cell growth. Plant Physiol 74: 67–71
10. MANODORI A, A MELIS 1985 Phycobilisome—photosystem II association in *Synechococcus* 6301 (Cyanophyceae). FEBS Lett 181: 79–82
11. MANODORI A, A MELIS 1986 Light quality regulates photosystem stoichiometry in cyanobacteria. *In* G Akoyunoglou, H Senger, eds, Regulation of Chloroplast Differentiation. Plant Biology Series, Alan R Liss Inc, New York, pp 653–662
12. MELIS A, ANDERSON JM 1983 Structural and functional organization of the photosystems in spinach chloroplasts. Biochim Biophys Acta 724: 473–484
13. MELIS A, A MANODORI, RE GLICK, ML GHIRARDI, SW MCCAULEY, PJ NEALE 1985 The mechanism of photosynthetic membrane adaptation to environmental stress conditions: a hypothesis. Physiol Veg 23: 757–765
14. MYERS J, JR GRAHAM, RTK WANG 1980 Light harvesting in *Anacystis nidulans* studied in pigment mutants. Plant Physiol 66: 1144–1149
15. RAPS S, JH KYCIA, MC LEDBETTER, HW SIEGELMAN 1985 Light intensity adaptation and phycobilisome composition of *Microcystis aeruginosa*. Plant Physiol 79: 983–987
16. RIPPKA R, J DEREULLES, JB WATERBURY, M HERDMAN, RY STANIER 1979 Generic assignments, strain histories and properties of pure cultures of cyanobacteria. J Gen Microbiol 111: 1–61
17. TANDEAU DE MARSAC N 1983 Phycobilisomes and complementary chromatic adaptation in cyanobacteria. Bull Inst Pasteur 81: 201–254
18. WANG RT, J MYERS 1974 On the State 1-State 2 phenomenon in photosynthesis. Biochim Biophys Acta 347: 134–140
19. YAMANAKA G, AN GLAZER 1981 Dynamic aspects of phycobilisome structure: modulation of phycocyanin content of *Synechococcus* phycobilisomes. Arch Microbiol 130: 23–30
20. YAMANAKA G, AM GLAZER, RC WILLIAMS 1978 Cyanobacterial phycobilisomes. Characterization of the phycobilisomes of *Synechococcus* sp 6301. J Biol Chem 253: 8303–8310