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Light Intensity Adaptation and Phycobilisome Composition of *Microcystis aeruginosa*[1]

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ABSTRACT

Phycobilisomes isolated from *Microcystis aeruginosa* grown to mid-log at high light (270 microeinsteins per square meter per second) or at low light intensities (40 microeinsteins per square meter per second) were found to be identical. Electron micrographs established that they have a triangular central core apparently consisting of three allophycocyanin trimers surrounded by six rods, each composed of two hexameric phycocyanin molecules. The apparent mass of a phycobilisome obtained by gel filtration is 2.96×10^6 daltons. The molar ratio of the phycobiliproteins per phycobilisome is 12 phycocyanin hexamers:9 allophycocyanin trimers. The electron microscopic observations combined with the phycobilisome apparent mass and the phycobiliprotein stoichiometry data indicate that *M. aeruginosa* phycobilisomes are composed of a triangular central core of three stacks of three allophycocyanin trimers and six rods each containing two phycocyanin hexamers. Adaptation of *M. aeruginosa* to high light intensity results in a decrease in the number of phycobilisomes per cell with no alteration in phycobilisome composition or structure.

The light-harvesting systems of cyanobacteria, red algae, and cyanelles are supramolecular aggregates of phycobiliproteins, called phycobilisomes, bound to the external surface of thylakoid membranes (2, 7, 8, 10, 11). Phycobilisomes collect light energy and transfer it with nearly 100% efficiency to the photosynthetic reaction centers, primarily to those of PSII (4, 16, 17, 27). Phycobilisomes can be isolated as intact, functional particles using mild detergents in high ionic strength buffers (1, 22). The major phycobiliproteins comprising the phycobilisome fall into three classes based upon distinctive absorption spectra associated with their covalently-linked tetrapyrrole chromophores. These include phycoerythrin, phycocyanin, and allophycocyanin. All red algae and cyanobacteria contain APC[2] and PC. Many have, in addition, PE or other related phycobiliproteins (2, 8, 11). The PE and PC content is often regulated by chromatic adaptation (24). Light intensity provides an additional control over PC content in some organisms (11, 14, 15, 20, 24, 30).

The ultrastructure of phycobilisomes from different organisms, as observed by transmission EM, is primarily hemidiscoidal, although other structural forms have been reported (1, 2, 8, 10, 11, 24, 28). The central core consists of three discs arranged to form an equilateral triangle in face view. An exception is the two-disc core of *Synechococcus 6301* (9, 11). Each of the core discs is actually cylindrical comprising two to four disc units in depth. The core is surrounded by a hemdiscoidal array of up to six rod-like arms composed of stacks of discs. Biophysical and biochemical evidence suggests that PE hexamers, when present, are equivalent to the outer rod discs and PC hexamers are the rod discs closest to the core which consists of discs of APC trimers (2, 7, 8, 10).

Microcystis aeruginosa is a unicellular cyanobacterium whose phycobilisomes consist of APC and PC. The molecular organization and fine structure of these phycobilisomes are described here. In a previous paper, we showed that *M. aeruginosa* adapted to high light intensity by decreasing the PC and Chl *a* content and the number of photosynthetic units per cell (20). In this paper we report on phycobilisomes characterized from cells grown at low and high light intensities. The objective was to determine if the modulation in PC content per cell is associated with a change in the stoichiometry of PC per phycobilisome, a change in the number of phycobilisomes per cell, or both.

MATERIALS AND METHODS

Culture Conditions. A cloned isolate of *Microcystis aeruginosa* (UV-027), originally collected near Beit Shean, Israel, was kindly provided by Professor J.N. Eloff, Botany Department, University of the Orange Free State, Bloemfontein, South Africa. It was grown at 28°C in 20-L polycarbonate bottles in a modified BG-11 medium (5). High light cells were grown at a light intensity of 270 $\mu E\ m^{-2}\ s^{-1}$ and were aerated with air enriched to 1% CO_2. Low light cells were grown at 40 $\mu E\ m^{-2}\ s^{-1}$ and aerated with air enriched to 0.1% CO_2. Cultures were harvested at mid-log stage of growth (approximately 150 Klett units for low light-grown cells and 200 to 250 Klett units for high light-grown cells). Illumination was provided by white fluorescent lamps (Sylvania, 34W).

Phycobilisome Isolation. Phycobilisomes were prepared as described by Siegelman and Kycia (22). They were purified and their apparent mass (M_r) was estimated by gel filtration chromatography. Approximately 10 mg phycobilisomes suspended in 1 ml 0.7 M K-phosphate (KPi), pH 6.8, were chromatographed on a Sepharose CL-4B column (2.5 × 40 cm) with 0.7 M KPi (pH 6.8). The column was calibrated with phycobilisomes of other cyanobacteria (22), thyroglobulin, and apoferritin.

Phycobilisome Composition. PC and APC were purified, their extinction coefficients and their molar ratios per phycobilisome determined. Purified phycobilisomes were dissociated by dialysis

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[2] Abbreviations: APC, allophycocyanin; PC, phycocyanin; PE, phycoerythrin; KPi and NaPi, K_2HPO_4 or Na_2HPO_4 titrated with KH_2PO_4 or NaH_2PO_4, respectively, to the indicated pH and molarity.

against 0.05 M sodium phosphate buffer (NaPi), 0.5 M NaCl (pH 6.1) for 16 h at 4°C. The phycobiliproteins of the dissociated phycobilisomes were separated by gel filtration chromatography and collected in 2 ml fractions using either Bio-Gel A-0.5 m (10% agarose) (1.6 × 63 cm) or Sephacryl S-300 (2.5 × 70 cm). The elution buffer was identical to the dialysis buffer. The absorbancies of each fraction at 650, 618, and 278 nm were measured and the mg PC and APC calculated using the equations of Bryant *et al.* (1) with the following absorbance coefficients determined for *M. aeruginosa* APC trimers and PC monomers:

$$\text{PC:}\quad E_{650\,nm}^{1\,mg/ml} = 1.91,\ E_{618\,nm}^{1\,mg/ml} = 5.88,\ E_{278\,nm}^{1\,mg/ml} = 1.47$$

$$\text{APC:}\quad E_{650\,nm}^{1\,mg/ml} = 6.34,\ E_{618\,nm}^{1\,mg/ml} = 3.93,\ E_{278\,nm}^{1\,mg/ml} = 1.51$$

PC and APC for amino acid analyses were further purified by hydroxylapatite chromatography (23). Samples for amino acid analyses were dialyzed against water and approximately 0.2 mg aliquots were hydrolyzed for 3 h in 6 N HCl at 120°C in evacuated sealed tubes. The hydrolysates were analyzed on an automated amino acid analyzer.

Phycobiliproteins per g dry wt cells were determined as follows. Low and high light-grown cells were lyophilized. One g samples were stirred with 5 ml 0.05 M NaPi (pH 6.1), 0.2 M NaCl, and then frozen and finely ground in a mortar with liquid N_2 (21). The powder was allowed to thaw and then centrifuged at 27,000*g*. The extraction was repeated three times. A clarified aliquot was diluted 10-fold with the extraction buffer and absorbancies at 650, 618, and 278 nm were measured. The PC and APC content were calculated as described above.

Phycobiliprotein composition and M_r were also determined by SDS-PAGE. Purified phycobilisomes, dissociated against water for 16 h, were suspended in Laemmli's dissociation buffer and electrophoretically separated on SDS-14% polyacrylamide gels using the procedure of Yamanaka and Glazer (29).

Spectroscopic Measurements. Absorption spectra were measured with a Perkin-Elmer 320 spectrophotometer interfaced with a Hewlett-Packard HP-85 computer. Corrected fluorescence emission spectra were obtained with a Perkin-Elmer MPF-4B spectrofluorimeter using samples diluted to $A_{618\,nm} = 0.1$ in 0.7 M KPi (pH 6.8).

Electron Microscopy. The preparative procedure for cells to be examined in thin section by EM was designed to maintain structural integrity while maximizing membrane contrast. The cells were washed in 0.05 M sodium cacodylate buffer (pH 6.8) just prior to fixing for 1 h in 3% glutaraldehyde in the same buffer, rinsed, then fixed for 1 h in freshly prepared 2% aqueous potassium permanganate. The fixed cells were washed, concentrated by gentle centrifugation, and mixed into warm agar which was immediately chilled. The solidified agar containing the cells, was diced into small blocks. The blocks were dehydrated in the cold, embedded in an epoxy resin, sectioned and the sections viewed either unstained, or after staining with uranyl acetate and a concentrated lead citrate solution (3, p. 159).

Purified phycobilisomes were viewed on support grids prepared by evaporating a thin carbon layer on either Formvar or colloidion-coated 400 mesh copper grids. The carbon surface was made hydrophilic by exposing the grids to an oxygen plasma (Plasmod, Tegal Corporation, Richmond, CA) at the minimum power setting for approximately 15 s. The grids were floated on a drop of 0.7 M KPi (pH 6.8), followed by a 0.7 M KPi buffered drop of 1% glutaraldehyde. The purified phycobilisomes were then injected into the glutaraldehyde drop and allowed to attach to the film surface. The grid was then floated on drops containing a graded series of phosphate buffer solutions, then water washes, and a final brief application of 2% uranyl sulfate as a negative stain and immediately blotted. Thin section and negatively stained samples were examined with a Philips 300 electron microscope at 80 kV acceleration.

All chemicals were reagent grade. Sepharose CL-4B and Sephacryl S-300 were obtained from Pharmacia Fine Chemicals, Bio-GelA-0.5 m (10% agarose) from Bio Rad, hydroxylapatite prepared according to the method of Siegelman *et al.* (23), Triton X-100 from Rohm and Haas, Tween-80 from Sigma. Protein calibration standards from Sigma were thyroglobulin (669,000), apoferritin (443,000), aldolase (155,000), BSA (67,000), ovalbumin (44,000) and Cyt *c* (12,500). The protein standard kit for SDS-PAGE was from BioRad.

RESULTS AND DISCUSSION

Previously we reported that *M. aeruginosa* was able to grow at a wide range of light intensities by varying the number of photosynthetic units per cell, fewer being present at high light intensities. The adaptation was accompanied by parallel changes in PC and Chl *a* content per cell, their concentration decreasing as light intensity was increased (20). Here, structural and biochemical characterization of phycobilisomes from high and low light-grown cells are described. A primary objective was to determine if the decrease in PC content in cells grown at high light intensities was associated with a reduction in the number of phycobilisomes per cell or to a decrease in the amount of PC per phycobilisome.

EM was used to examine the distribution of thylakoid membranes and the structure of the phycobilisomes. Micrographs of thin sections of *M. aeruginosa* grown under high light and under low light conditions are presented in Figure 1, a and b, respectively. The cells were fixed with potassium permanganate to enhance membrane visualization (3, 13). The extent of thylakoid membranes in the high light-grown cells is consistently less than in the low light cells. Examination of sections prepared to reveal phycobilisomes (S. Raps and M. Ledbetter, unpublished data) showed little, if any, differences in the density of phycobilisomes on the membranes of high light and low light cells. Although these parameters were not quantified, it seems reasonable to assume, as a first approximation, that the number of phycobilisomes per cell is roughly proportional to the total amount of thylakoid membrane available.

Electron micrographs of negatively stained isolated phycobilisomes from high light and low light-grown cells are shown in Figure 2, a and b, respectively. The fact that clear views showing the core and arms were relatively infrequent may be related to the small size of these phycobilisomes, which approach a spherical form, resulting in a reduced probability that they will attach to the foil in a favorable aspect for analysis. Our interpretation of phycobilisome fine structure from both high light (Fig. 2a) and low light-grown cells (Fig. 2b) is based upon models of hemidiscoidal phycobilisomes in the literature (1, 2, 8, 11, 28). They appear to consist of a central core of three discs with six arms composed, on average, of two discs per arm, borne on the sides of the core discs. Similar observations have been made by numerous other investigators for phycobilisomes isolated from both cyanobacteria and red algae (1, 2, 7, 8, 11, 24, 28). More or fewer than two double discs for each of the six arms are often seen. It is uncertain how much of this variation is due to dissociation and reassociation during sample preparation. The edge-on view of the double discs is usually better defined for the lower arms than the upper, presumably because the lower arms lie within the plane of the core (and carbon support) while the upper arms, which in their native state extend in other directions, are compressed into the plane of the carbon during air drying and are more likely to suffer some distortion.

The M_r of the phycobilisomes was obtained using Sepharose CL-4B gel chromatography. The elution profile of purified phycobilisomes is shown in Figure 3. Identical results were obtained for phycobilisomes from cells grown under high light and low light conditions. The M_r of the phycobilisomes was estimated to

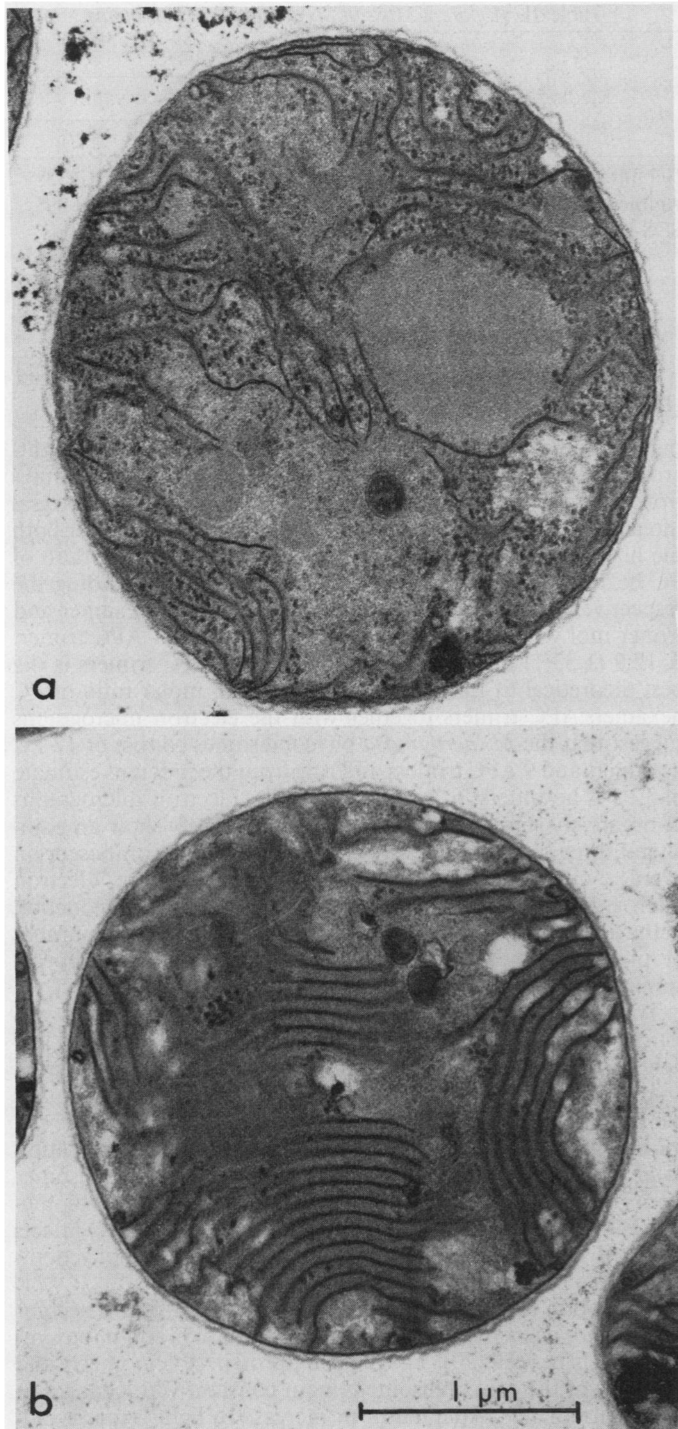

FIG. 1. Electron micrographs of thin sections of *M. aeruginosa* grown under high light (a) and low light (b) conditions. The thylakoid system, seen here as irregular lines within the cytoplasm, is relatively sparse and dispersed in high light cells in comparison to low light cells where it is extensive with a tendency to pack into parallel arrays.

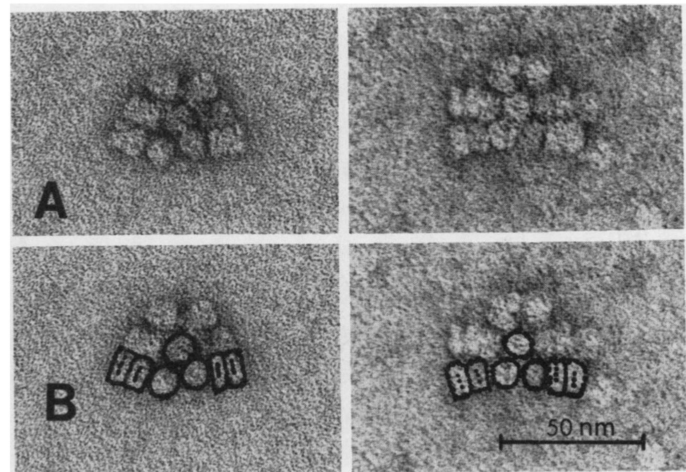

FIG. 2. Electron micrographs of isolated negatively stained *M. aeruginosa* phycobilisomes grown under high light (a) and low light (b) conditions. The lower micrographs duplicate the upper except for inked-in outlines to show the three stacks of APC discs which constitute the core seen face on, and the edge-on view of the double discs which make up the lower two of the six PC arms. The orientation is such that the presumed attachment to the thylakoid would be from the lower two stacks of the core discs to the membrane below. Refer to "Materials and Methods" for preparative procedure.

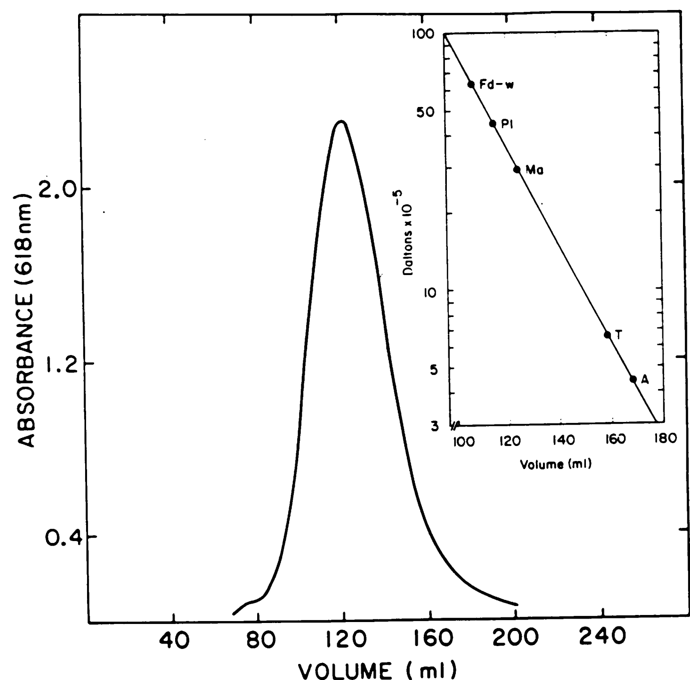

FIG. 3. Elution profile of phycobilisomes from high and low light-grown *M. aeruginosa* (Ma). Phycobilisomes, isolated as described in "Materials and Methods," were chromatographed on Sepharose CL-4B (2.5 × 40 cm) with 0.7 M KPi buffer (pH 6.8). *Phormidium luridum* (Pl) phycobilisomes, white light-grown *Fremyella diplosiphon* (Fd) phycobilisomes, thyroglobulin (T), and apoferritin (A) were used as standards to calibrate the Sepharose CL-4B column as shown in the calibration curve in the inset

be 2.96×10^6 D as determined from prior calibration of the column (inset, Fig. 3).

The PC and APC contents were determined in phycobilisomes from cells grown under the two light regimens. The phycobiliproteins of dissociated phycobilisomes were separated by Sephacryl S-300 or Bio-Gel A-0.5 m (10% agarose) gel chromatography (Fig. 4). The two phycobiliproteins were further purified by hydroxylapatite chromatography (23). The amino acid compositions of APC and PC monomers are shown in Table I. The high acidic and nonpolar amino acid content, as well as the overall amino acid composition of both biliproteins, is very similar to that reported for other cyanobacteria (12, 22, 26) and red algae (6, 18, 19, 25). The monomer, trimer, and hexamer M_r

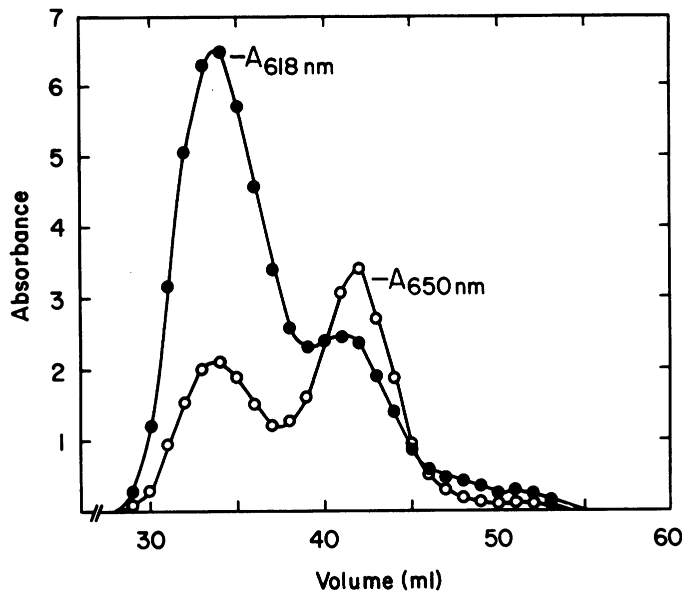

FIG. 4. Elution profile of phycobiliproteins of dissociated phycobilisomes. Phycobilisomes were dissociated by dialysis against 0.05 M NaPi, 0.5 M Nacl (pH 6.1) at 4°C and chromatographed on a Bio-Gel A-0.5 m (10% agarose) column (1.6 × 63 cm) with the dissociation buffer.

Table I. *Amino Acid Composition of M. aeruginosa Phycocyanin and Allophycyanin Monomers*

Amino Acids	Integral Residues	
	PC	APC
Lys	10	16
His	1	1
Arg	15	14
Asp	30	26
Thr	16	13
Ser	24	17
Glu	23	26
Pro	5	9
Gly	21	29
Ala	37	30
½Cys	ND[a] (3)	ND[a] (2)
Val	19	24
Met	7	8
Ileu	14	14
Leu	17	22
Tyr	16	5
Phe	10	7
Total residues	268	263
No. of phycobilin chromophores	3	2
Mol wt with chromophores	30,929	29,162

[a] ND, not determined. The number in parentheses represents the minimal number of cysteines expected and are added into the calculation of the mol wt.

of the phycobiliproteins from amino acid analyses (Table I), gel filtration chromatography (Fig. 4), and SDS-PAGE are shown in Table II. The resultant average M_r is 30.4 kD for APC monomers and 31.6 kD for PC monomers.

The phycobiliprotein stoichiometry of each phycobilisome was determined by combining information from phycobiliprotein composition and M_r (Table II; Fig. 3) using many phycobilisome preparations. The mg quantities of PC and APC were determined from the elution profile of dissociated phycobilisomes (as in Fig. 4) as described in "Materials and Methods." The mg quantities of PC and APC averaged from five different samples were 4.39 mg PC and 1.64 mg APC in phycobilisomes from high light-grown cells and 16.2 mg PC and 6.08 mg APC in phycobilisomes from low light-grown cells. The PC hexamer:APC trimer integral molar ratio was found to be 11.2:9.1 per phycobilisome for both the high light and low light phycobilisomes. The molar ratio of PC hexamers:APC trimers determined directly by dividing the respective mg quantities by the respective average hexamer and trimer mol wt (Table II) gave 1.28 PC hexamers:1 APC trimer. A 12:9 (1.33:1) molar ratio of PC hexamers:APC trimers is the best theoretical fit for this data. The integral molar ratio of PC hexamers:APC trimers together with the electron micrographs suggest that the *M. aeruginosa* phycobilisomes consist of 12 PC hexamers and 9 APC trimers differing from the previous estimate of 12 PC hexamers: 6 APC trimers (22). Electron micrographs of negatively stained phycobilisomes consistently show an equilateral three disc core with from four to six arms composed, on average, of two discs per arm on the sides of the core. Electron micrographs of thin sections of high light cells show a reduction in the density of thylakoid membranes. Qualitatively, the number of phycobilisomes per volume thylakoid membrane appears similar at both light intensities.

Table II. *Apparent Mass of M. aeruginosa Biliproteins*

Method	Apparent Mass			
	Allophycocyanin		Phycocyanin	
	$(APC)_3$	$(APC)_1$	$(PC)_6$	$(PC)_1$
Gel filtration	90,000[a]	30,000[b]	188,000[a]	31,333[b]
Amino acid analysis	87,486[b]	29,162[a]	185,574[b]	30,929[a]
SDS-PAGE		Subunits[c]		Subunits[c]
		α14,700[a]		α15,600[a]
		β17,300[a]		β17,000[a]
	96,000[b]	32,000[b]	195,000[b]	32,600[b]
Mean average	91,162	30,387	189,726	31,621

[a] Experimental data. [b] Calculated from experimental data. [c] Phycobiliprotein α and β subunits.

The concentration of phycobilisomes per g dry wt cells was estimated from several samples of lyophilized high light and low light-grown cells. The data obtained were similar for all samples analyzed. In one such experiment, the weight of phycobilisomes per g dry wt cells was 68 mg for low light-grown cells and 26 mg for high light-grown cells, giving a 2.6-fold greater concentration of phycobilisomes in the low light-grown cells. Phycobilisomes from both cell-types had a similar phycobiliprotein stoichiometry. These data support the conclusion that light intensity affects phycobilisome concentration per cell rather than the phycobiliprotein stoichiometry of the phycobilisome.

Adaptation to high light intensities in this organism is accompanied by a decrease in the number of thylakoids and photosynthetic units per cell (20). The phycobiliprotein stoichiometry and structure of the phycobilisome remain constant with changes in growth irradiance. Adaptation to increase in light intensity apparently results in a decrease in the number of thylakoids per cell accompanied by a change in the number of photosynthetic units and phycobilisomes per cell rather than to a change in the size of the photosynthetic unit or phycobilisome which might result from chromatic adaptation (24). *Mycrocystis* appears to regulate its photosynthetic apparatus at different light intensities by coordinating the amount of thylakoid membrane with the number of light-harvesting phycobilisomes, the number of photosynthetic units, and the total amount of Chl *a* per cell. How this is accomplished, and which of these components may be the primary regulator, are subjects of further investigation.

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