Biochimica et Biophysica Acta, 546 (1979) 383—393

BBA 47675

PHOTOSYNTHETIC VESICLES WITH BOUND PHYCOBILISOMES FROM *ANABAENA VARIABILIS*

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(Received September 18th, 1978)

Key words: Phycobilisome; Phycocyanin; Photosystem II; Photosynthetic vesicle; (Anabaena variabilis)

Summary

Photosynthetically active vesicles with attached phycobilisomes from *Anabaena variabilis*, were isolated and shown to transfer excitation energy from phycobiliproteins to F696 chlorophyll (Photosystem II). The best results were obtained when cells were disrupted in a sucrose/phosphate/citrate mixture (0.3 : 0.5 : 0.3 M, respectively) containing 1.5% serum albumin. The vesicles showed a phycocyanin/chlorophyll ratio essentially identical to that of whole cells, and oxygen evolution rates of 250 μmol O_2/h per mg chlorophyll (with 4 mM ferricyanide added as oxidant), whereas whole cells had rates of up to 450. Excitation of the vesicles by 600 nm light produced fluorescence peaks (−196°C) at 644, 662, 685, 695, and 730 nm. On aging of the vesicles, or upon dilution, the fluorescence yield of the 695 nm emission peak gradually decreased with an accompanying increase and final predominant peak at 685 nm. This shift was accompanied by a decrease in the quantum efficiency of Photosystem II activity from an initial 0.05 to as low as 0.01 mol O_2/einstein (605 nm), with a lesser change in the V_{max} values. The decrease in the quantum efficiency is mainly attributed to excitation uncoupling between phycobilisomes and Photosystem II. It is concluded that the F685 nm emission peak, often exclusively attributed to Photosystem II chlorophyll, arises from more than one component with phycobilisome emission being a major contributor. Vesicles from which phycobilisomes had been removed, as verified by electron microscopy and spectroscopy, had an almost negligible emission at 685 nm.

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Abbreviations: DCIP, 2,6-dichlorophenol indophenol; PS I, PS II, Photosystem I and II, respectively; Chl, chlorophyll.

Introduction

The photosynthetic apparatus of blue-green algae is characteristically different from those of higher plants in that the former is much more fragile than the latter when isolated in aqueous media. Suspension of the thylakoids of blue-green algae in conventional sucrose media, such as applied for isolating chloroplasts, has generally resulted in a release of phycobiliproteins and a loss of photosystem II (PS II) activity. In past studies on the photosynthetic apparatus of blue-green algae, efforts were focused on isolating photochemically active membrane preparations [1—9] and little attention was paid to the integrity of phycobiliproteins even though these pigments are the major light harvesters in these algae [10,11].

Recent work from this laboratory has revealed that the phycobilisomes of various blue-green and red algae can be isolated in their intact form using high concentration of phosphate buffer [12,13]. These conditions, however, were not suitable for preparation of active phycobilisome vesicles, and this necessitated our attempts in finding conditions whereby active preparations could be obtained. Here we describe the isolation of active vesicles and the correlation between efficient transfer of excitation energy absorbed by phycobiliproteins to chlorophyll (Chl), and high electron transfer rates in these preparations.

Materials and Methods

Anabaena variabilis, strain M3, IAM Collection, University of Tokyo, were grown in an inorganic medium (medium I) [14] at 30°C supplied with 5% CO_2 and air. Continuous illumination was provided by fluorescent lamps at a light intensity of 13.5 nE $\cdot$ $cm^{-2} \cdot min^{-1}$.

For preparation of phycobilisome-containing vesicles, cells were collected in the early stationary phase, washed twice with distilled water and resuspended in a sucrose/phosphate mixture (0.5 : 0.1 M, respectively, pH 7.2). Lysozyme was added to this suspension (to 1 mg/20 ml) and allowed to react for 90 min (at 20°C) with gentle stirring. After this incubation the cells were collected by centrifugation and suspended in a mixture consisting of: sucrose/phosphate/citrate (0.5 : 0.5 : 0.3 M, respectively) and 1.5% bovine serum albumin at a cell density of 0.2—0.3 g (wet weight)/ml. The suspension was passed through a chilled French press at 8000 lb/inch^2, and the disrupted cells were vigorously stirred at 0°C to disperse the clot which normally formed. Although DNAase was effective in dissolving the clot, it was not routinely applied since it resulted in vesicle preparations with lower efficiencies of excitation transfer. Unbroken cells and wall layers were removed by sedimentation at 2000 $\times g$ for 10 min. The vesicle fraction was subsequently collected from the supernatant by centrifugation at 10 000 $\times g$ for 20 min. The vesicle pellet was stored in the cold until needed, and just before use it was rinsed and resuspended in the sucrose/phosphate/citrate/albumin medium at room temperature.

For dissolving the phycobilisomes from the vesicles, freshly prepared vesicles, as above, were rinsed in a mixture of 0.3 M sucrose and 0.05 M phosphate buffer (pH 6.8) and stored for 2 h at 0°C. The phycocyanin and allophycocyanin content was significantly reduced by three rinses in the same

mixture and centrifugation at 10 000 X *g* for 20 min.

Oxygen evolution was measured with a Clark-type O_2 electrode, which was kept at 25°C by a circulating water-bath. The reaction mixture for Hill activity was composed of the sucrose/phosphate/citrate/albumin mixture plus potassium ferricyanide (2 mM) and potassium ferrocyanide (2 mM). For the Mehler reaction, it was composed of the sucrose/phosphate/citrate/albumin mixture plus methylviologen (67 mM). For PS I activity, it consisted of the sucrose/phosphate/citrate/albumin mixture plus methylviologen (67 mM), 2,6-dichlorophenol indophenol (DCIP) (50 μM), and sodium ascorbate (10 mM).

Illumination was provided by a 1 kW xenon lamp, equipped with an 8 cm long (circulating) water filter. Intensity was controlled by the arc current and calibrated with wire screens. Irradiance was measured by a calibrated photometric sensor (Lambda Instruments Co.).

To determine the quantum efficiency of photosynthesis of phycobiliprotein absorption in the vesicles, the light intensity dependence of O_2 evolution rates (V) with ferricyanide as electron acceptor was measured under a range of intensities (from 1.2 to 63 nE/cm^2) at three different wavelengths: 605, 670 and 690 nm. Measurements were completed within a 10 min time period. The interference filters used had the following half-bandwidths: 3 nm for the 605 nm filter, and 10 nm for the 670- and 690-nm filters. By a modification of the conventional saturation curve

$$\frac{I_{abs}}{V} = \frac{K_M + I_{abs}}{V_{max}}$$

the inverse of quantum yield (I_{abs}/V) should be a linear function of absorbed quanta (I_{abs}). When the values of I_{abs}/V observed at different light intensities of a given wavelength were plotted against I_{abs}, the points generally fit a linear relationship giving coefficient of determination (r^2) values greater than 0.96. We estimated the quantum efficiency at zero light intensity from the inverse of the y-intercept, K_m from the x-intercept and V_{max} from the inverse of the tangent of the curve. The fraction of absorbed quanta was approximated from the difference between the transmission at the wavelength to be measured and at 750 nm, where vesicle preparations have only negligible absorbance.

Chlorophyll and phycobiliprotein contents in the vesicles were estimated as in Arnon et al. [15]. Fluorescence spectra were made in an NMR tube (4 mm inner diameter) and recorded on an Aminco-Bowman spectrofluorimeter in the standard mode, or in the quantum emission correction mode (corrected up to 700 nm). Bandwidths of the excitation and emission monochromators were 11 nm and 2.7 nm, respectively. In the standard mode corrections were not made because of the even photomultiplier response in the spectral range used. Fluorescence measurements were made at a final concentration 48 μg Chl/ml, and never above 80 μg Chl/ml.

For electron microscopy, vesicles were fixed with 4—8% buffered glutaraldehyde (pH 6.8) before or after applying them to the electron microscope grids. Fixation (5—30 min) was followed by three rinses in distilled water and staining with 1% aqueous ammonium molybdate, or 2% phosphotungstic acid (both adjusted to pH 6.8).

Results

Isolation conditions

The absorption spectra of the vesicle preparations are similar to those of the whole cells from which they were derived (Fig. 1). When the vesicles, suspended in sucrose/phosphate/citrate/albumin medium, were excited by 600 nm light the emission spectra at room temperature exhibited a peak at 655 nm with a shoulder at 680 nm, while at liquid nitrogen temperature peaks were resolved at 644, 662, 685, 698, and 730 nm (Fig. 2). The peaks at 644 and 662 nm are attributable to phycocyanin and allophycocyanin, respectively. The 698 and 730 nm have generally been assumed to originate from Photosystem II and I, respectively, with the 685 nm peak probably arising from phycobilisomes. On excitation of chlorophyll by 435 nm light at liquid nitrogen temperature, the fluorescence was predominant at 730 nm with small peaks at 685 nm and 695 nm. Both these patterns are very close to the corresponding fluorescence emission of whole cells, but for a minor modification of the 695 nm peak (F696) which appeared at 695 nm in whole cells and at 698 nm in vesicle preparations (but also considered to be F696). In addition, the 730 nm fluorescence yield in vesicle preparations (−196°C) was higher than in whole cells. When these vesicles were suspended in a mixture of low salt content, such as buffer B of Binder et al. [6] or the conventional sorbitol/

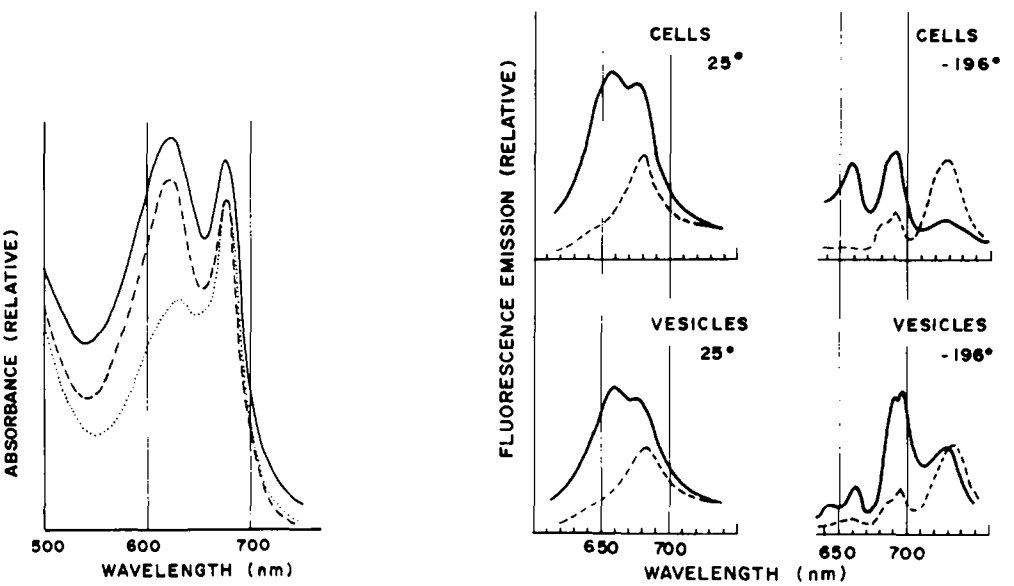

Fig. 1. Absorption spectra (25°C) at equal Chl concentration of whole cells (———), and phycobilisome vesicles (- - - - -), isolated and suspended in the sucrose/phosphate/citrate/albumin medium (details in Materials and Methods). Vesicles (· · · · ·) isolated in the buffer according to Binder et al. [6] show reduced phycobiliprotein absorption.

Fig. 2. Fluorescence emission spectra at 25°C (left) and −196°C (right) of whole cells (top) and vesicles (bottom) excited at 435 nm (- - - - -) and 600 nm (———). Whole cells were resuspended in 0.05 M phosphate (pH 7.2) and vesicles were suspended in sucrose/phosphate/citrate/albumin medium; in either case A_{670} was below 0.2.

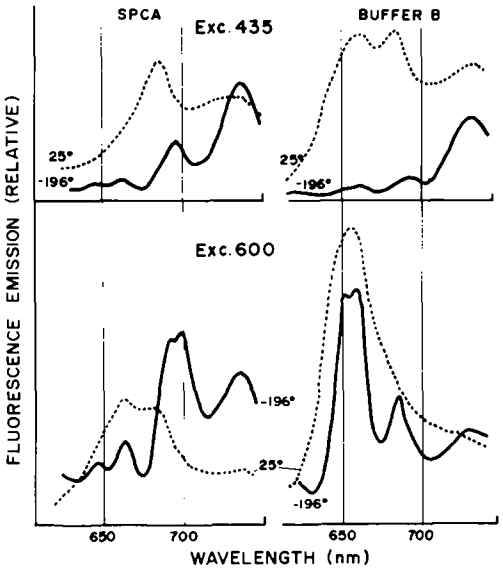

Fig. 3. Effect of suspending media on fluorescence emission at 25°C (- - - - - -) and at −196°C (———) excited at 435 nm (top) and 600 nm (bottom). Vesicles were suspended in sucrose/phosphate/citrate/albumin medium (left) or in buffer B [3] containing 10 mM Tricine/NaOH, 10 mM $MgCl_2$ and 5 mM sodium and potassium phosphate, pH 7.8 (right).

pyrophosphate solution used for chloroplast isolation [16], the fluorescence emission spectra changed instantaneously (Fig. 3). The fluorescence peak at 655 nm, originating from uncoupled phycocyanin and allophycocyanin became overwhelming, a change which was not reversible when these treated vesicles were subsequently placed in sucrose/phosphate/citrate/albumin medium, reflecting the disintegration of phycobilisome structure. However, when they were suspended in higher concentrations of phosphate (0.75 M) or citrate (0.5 M), both with added sucrose (0.5 M), the vesicles exhibited a broader peak around 685—695 nm. When they were subsequently placed in sucrose/phosphate/water/albumin medium, the F696 nm peak was restored with a minor shoulder at 685 nm, providing the time interval was brief (i.e. within 15 min).

Photochemical activity

In the presence of ferricyanide as electron donor, the vesicle preparations evolved oxygen at rates of 250 μmol O_2/h per mg Chl (Table I), while the photo-

TABLE I

PHOTOCHEMICAL ACTIVITY OF VESICLE PREPARATIONS WITH BOUND PHYCOBILIPROTEINS

Details of isolation in Materials and Methods. The activities were tested immediately after 5 μl of vesicles (1.8—2.3 mg Chl/ml) were suspended in 1.0 ml sucrose/phosphate/citrate/albumin medium.

Activity in:	μmol O_2/h per mg Chl
H_2O—ferricyanide	247 ± 22
Methylviologen—H_2O	72 ± 13
Methylviologen—DPIPH_2	276 ± 14

TABLE II

COMPARISON OF PHOTOSYNTHESIS IN WHOLE CELLS AND HILL REACTION IN VESICLE PREPARATIONS V_{max}, K_m AND QUANTUM YIELD OF OXYGEN EVOLUTION

O_2 evolution of whole cells was measured in 0.05 M phosphate, and that of the vesicles in sucrose/phosphate/citrate/albumin medium containing potassium ferricyanide and potassium ferrocyanide (2 mM each). Measurements were completed within 10 min after dilution with sucrose/phosphate/citrate/albumin medium to minimize decay of the quantum efficiency during the measurement. Fresh vesicles were stored undiluted, but aged vesicles were stored for 4 h at 0.48 mg Chl/ml (I), or at 0.19 mg Chl/ml (II) prior to making the measurements.

	Actinic light (nm)	V_{max} (μmol O_2/h per mg Chl)	K_m (nE_{abs}/s per cm^2)	Quantum yield (mol/E_{abs})
Whole cells	605	407	2.55	0.07
	670	412	2.64	0.07
	690	382	7.00	0.02
Vesicles, fresh	605	190	2.89	0.05
	670	192	2.61	0.06
	690	182	7.22	0.02
Vesicles, aged I	605	156	8.71	0.02
	670	155	3.87	0.04
	690	—	—	0.02
Vesicles, aged II	605	83	7.60	0.01
	670	86	3.43	0.02
	690	76	6.00	0.01

synthetic rates of the whole cells from which they were derived showed 330—450 μmol O_2/h per mg Chl.

Such preparations were also capable of catalyzing methylviologen-mediated oxygen uptake both in the presence and absence of ascorbate-reduced DCIP. The activity without added $DCIPH_2$ was stable only in sucrose/phosphate/citrate/albumin medium and decayed rapidly in a low phosphate (0.1 M) medium, while the reaction with $DCIPH_2$ showed higher stability. The activity without $DCIPH_2$ would correspond to electron transport from the O_2-evolving site to the reducing site of Photosystem I.

To estimate the contribution of phycobilisomes in these vesicles to Photosystem II activity, the quantum efficiency of O_2 evolution rates was measured with ferricyanide as electron acceptor either under the light absorbed by phycocyanin and allophycocyanin (605 nm) or by chlorophyll (670 and 690 nm). As seen from Table II, the quantum efficiency of freshly suspended vesicles is about 80% as high as of photosynthesis in whole cells, and the ratio of the quantum efficiency with 605 nm light to that with 690 nm light in the fresh vesicles (2.50) is close to the corresponding ratio in the whole cells (2.76). These data indicate good integrity of the isolated vesicles, both in their photosynthetic transport chain and in their excitation energy coupling between phycobilisomes and PS II chlorophyll.

Degeneration of photochemical integrity in isolated vesicles

The photochemical activity of the isolated vesicles does not decrease appreciably if they are stored in the cold as a tightly packed pellet free from supernatant. However, if they are rinsed with any kind of suspending media, the

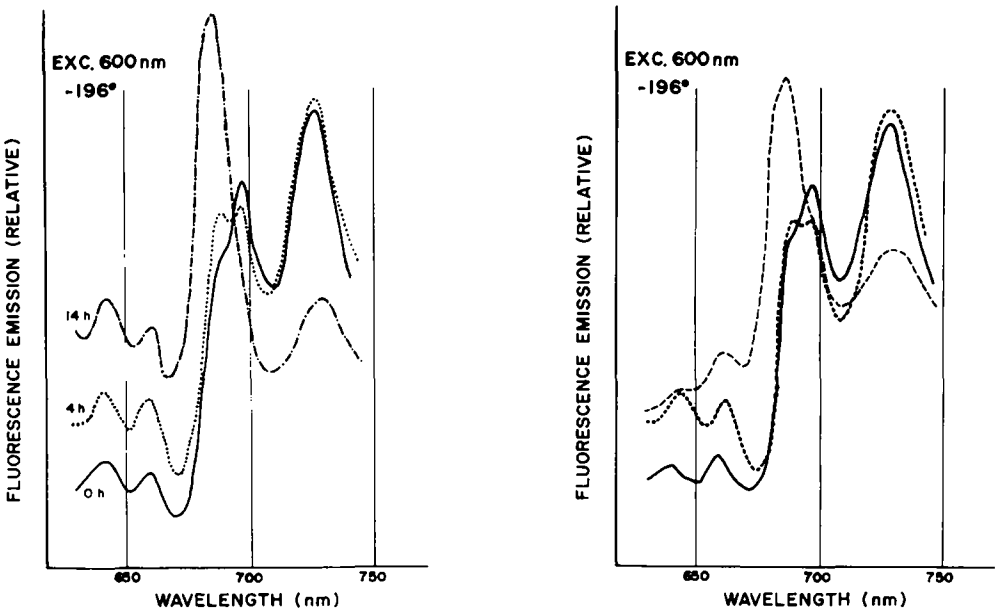

Fig. 4. Effect of time of incubation on fluorescence emission spectra (—196°C) of phycobilisome vesicles with excitation at 600 nm. The vesicles (0.48 mg Chl/ml) were incubated in sucrose/phosphate/citrate/albumin medium for 0, 4, and 14 h in the dark at 25°C, and diluted (10 fold) in the same mixture just prior to being recorded.

Fig. 5. Effect of dilution on phycobilisome vesicles incubated in the sucrose/phosphate/citrate/albumin medium for 4 h at 25°C in the dark. Concentrations in mg Chl/ml: ———, 0.96; · · · · · ·, 0.48, and - - - - - -, 0.048 mg. Final concentration of all preparations at which emission (excitation at 600 nm) was recorded at 0.048 mg.

photochemical activity of the vesicles begins to decay. Of the various suspending media tested, the rate of the decay was slowest in the sucrose/phosphate/citrate/albumin medium. The activity also greatly decreased with time (Fig. 4) and was affected by the density of the suspension (Fig. 5 and Table II). Lowered transfer activity was indicated by a shift in the fluorescence emission. The F696 nm peak, which was predominant in freshly suspended vesicles, decreased with time of incubation and a gradual shift occurred with the increase of a major peak at 685 nm. The rate of change was also affected by the density of the suspension (Fig. 5) and exhibited a similar change in emission pattern, as with the aging vesicles. With freshly suspended vesicles, at a density of 0.96 mg Chl/ml, the fluorescence pattern remained essentially unchanged for 4 h, whereas at 0.048 mg Chl/ml the 685 nm peak became predominant during that period. The vesicles incubated for 4 h at 0.48 mg Chl/ml showed a V_{max} value of 156 μmol O_2/h per mg Chl and quantum yield of 0.02 mol/E with 605 nm light, while those incubated at 0.19 mg Chl/ml showed a V_{max} of 82.8 μmol O_2/h per mg Chl and a quantum yield of 0.01, suggesting that the changes in fluorescence emission pattern is correlated with the lowered efficiency of excitation transfer from phycocyanin to PS II chlorophyll.

Fluorescence emission of vesicles with and without phycobilisomes

Photochemically active vesicles rich in phycobiliproteins can be seen to be

densely covered with phycobilisomes (Fig. 6A). Upon rinsing of the vesicles in low phosphate buffer (0.05 M, and 0.3 M sucrose), the phycobilisomes disappeared (Fig. 6B). Three rinses resulted in the removal of 98% of the phycocyanin. Removal of the phycobilisomes was correlated with a radical change in the fluorescence emission pattern. Excitation at 600 nm (−196°C) in phycobilisome-deficient vesicles showed only minor emission at 685 and

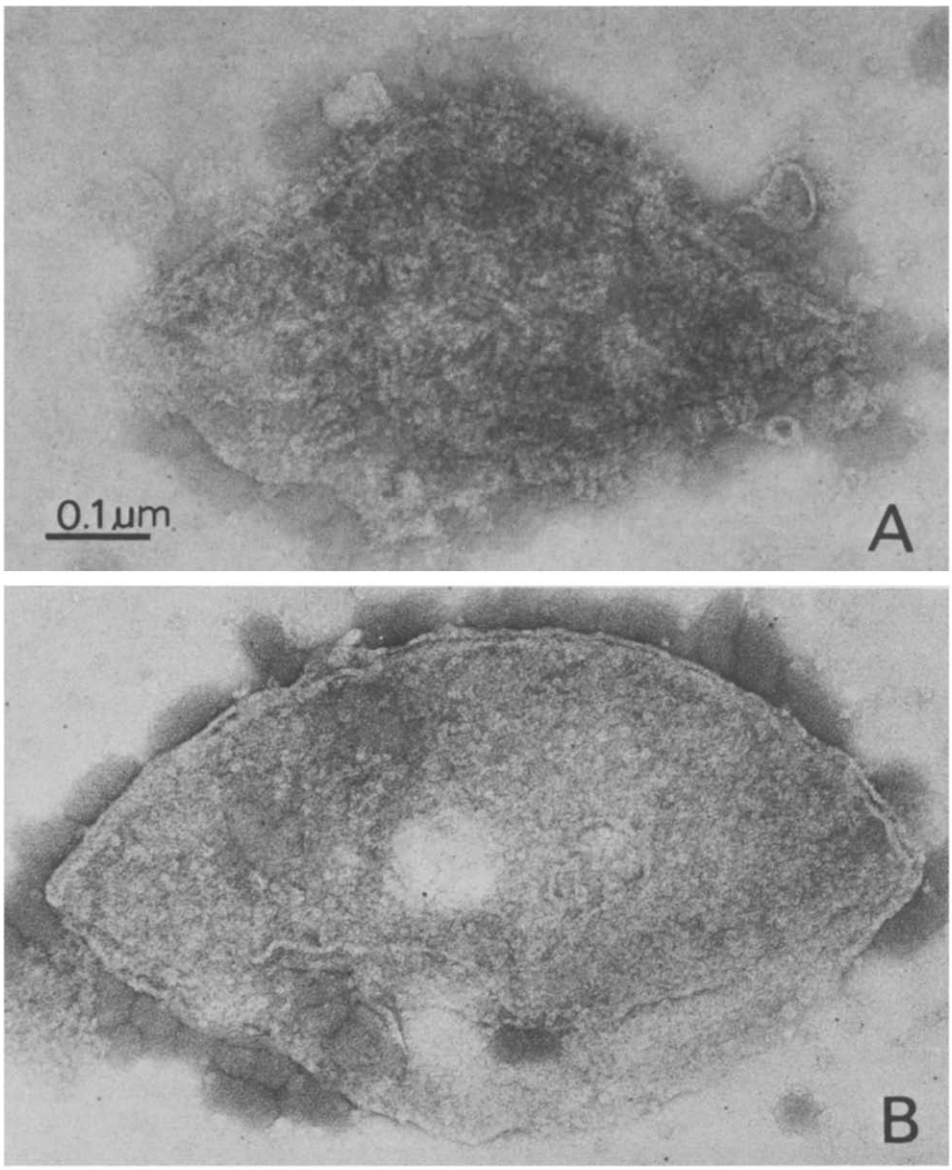

Fig. 6. Electron micrographs of thylakoid vesicles. (A) Photosynthetically active phycobilisome vesicles covered with phycobilisomes. (B) Vesicles after removal of phicobiliproteins by rinsing in 0.05 M phosphate in 0.3 M sucrose. (Stained grayish bodies around vesicle are glycogen-type storage products). (A) and (B) were fixed in glutaraldehyde prior to being stained with 1% ammonium molybdate. Magnification 138 000×.

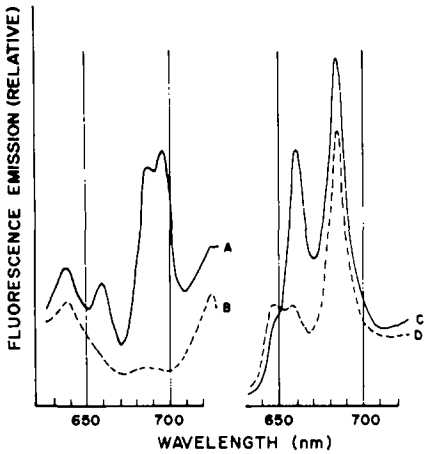

Fig. 7. Comparison of emission spectra (—196°C, excitation at 600 nm) of vesicles and phycobilisomes. (A) Photochemically active phycobilisome vesicle preparation. Sample is equivalent to Fig. 6A. (B) Rinsed vesicles with phycobilisomes removed. Sample is equivalent to Fig. 6B. (C) Isolated phycobilisomes after exhaustive extraction in acetone. (D) Acetone-extracted phycobilisome vesicles. (Specific extraction protocols in Materials and Methods and Results).

698 nm when compared to photochemically active vesicles (Fig. 7, lines A and B). Only the peaks of chlorophyll at 730 nm and of uncoupled phycocyanin at 640 nm, were prominent.

To assess the contributions of the 685 nm fluorescence emission further, phycobilisome vesicle preparations were exhaustively extracted with acetone to remove chlorophyll. When the vesicle suspension was poured dropwise into 90% aqueous acetone (cooled with solid CO_2 to —25°C, with vigorous stirring) more than 99% of constituent chlorophyll and more than 97% of the carotenoids was extracted in the first supernatant, leaving a blue-colored pellet. Upon suspending such a preparation in 0.75 M phosphate and excitation by 600 nm light at —196°C, it showed fluorescence emission peaks at 685 nm and 660 nm (Fig. 7, line C). Separately isolated phycobilisomes of this alga gave a similar emission pattern with a sharp peak at 685 nm (not shown) as was also the case for phycobilisomes of other algae [17]. The 660 nm emission peak in the phycobilisome preparation represents a partial uncoupling due to the treatment, and can also be observed under dissociating conditions in phycobilisomes from several blue-green algae. Furthermore, acetone-extracted phycobilisome vesicles (Fig. 7, line D) similarly had a major peak at 685 nm and lesser peaks at 645 and 660 nm. The cause of the lower 660 nm peak of the acetone-extracted preparation vs. that of the unextracted phycobilisomes (Fig. 7, line C) is not known.

Discussion

The photosynthetic vesicles obtained here are distinct from other preparations of blue-green algae thus far reported [1—9] in that they have functionally bound phycobilisomes, and exhibit efficient transfer of excitation energy from phycocyanin to PS II chlorophyll and also have high rates of electron transport

activity from the O_2-evolving site to the reducing site of PS I. The quantum yield of 0.05/molar oxygen observed with 605 nm light is about twice as high as the values observed in digitonin-treated vesicles of *Nostoc*, free from phycobilin pigments, with 670 nm light [18].

The quantum efficiency with 605 and 670 nm light in whole cells and fresh vesicles are very close. The slightly lower value at 605 nm vs. 670 nm of fresh vesicles, if significant, can probably by accounted for by a redistribution of quanta to PS I where it would serve in ferricyanide reduction as in the case of chloroplast electron transport [19].

The sucrose/phosphate/citrate/albumin medium was devised for the stabilization of photosynthetic vesicles and has not yet been fully characterized. Further improvements for greater phycobilisome vesicle stability will be required. For the present, it is noteable for its high concentrations of phosphate and citrate. Since lower salt concentrations, when applied to cell-free vesicles, caused a release of phycobilin pigments from the thylakoids [6,8], as well as inactivation of PS II [3—5], the high concentration of salts in the sucrose/phosphate/citrate/albumin medium is considered to act protectively on the vesicles by stabilizing the phycobilisomes structure, and by preserving the thylakoid structure.

The stability of phycobilisome structure in a high concentration of phosphate has been well investigated with the phycobilisomes of various algae [12,13,20]. But when the algal cells were disrupted in 0.75 M phosphate, a concentration generally applied in phycobilisome isolation, vesicle preparations did not show any excitation tranfer from phycocyanin to PS II chlorophyll, even though more than 75% of the phycobilisomes remained in the vesicle-bound form (unpublished data). Although bovine serum albumin and citrate were found essential for good excitation coupling between phycobilisomes and PS II chlorophyll, we do not know their function. As the isolated membranes of blue-green algae exhibit high activity of PS II even in media with low salt concentration [6,8,18], a high concentration of phosphate and citrate, as applied in sucrose/phosphate/citrate/albumin medium in the present study, is considered essential only for the phycobilisome binding at the specific acceptor sites on the thylakoid membranes.

A fluorescence peak at 685 nm (at −196°C), in blue-green algae as well as in green plants has normally been attributed to arise from chlorophyll. Our results suggest that this peak arises primarily from phycobilisomes, and that the contribution from chlorophyll may be considerably lower than had been previously assumed [21,22]. It is now well established that phycobilisomes contain allophycocyanin forms [23,24] which emit at 685 nm and are responsible for the final emission of isolated phycobilisomes [17].

The reasons for assuming that the 685 nm emission (at −196°C) arises primarily from phycobilisomes are based on observations which show that: (a) membrane vesicles from which phycobilisomes have been removed have only a low fluorescence emission at 685 nm (Fig. 7, line B). (b) Phycobilisomes whether or not [17] extracted with acetone (Fig. 7, line C) have a predominant peak at 685 nm. (c) Phycobilisome vesicles exhaustively extracted to remove chlorophyll (Fig. 7, line D) exhibit a high 685 nm emission. (d) A decline of the 695 nm emission occurs when the 685 nm emission rises and is correlated

with a decrease in the photoactivity and quantum efficiency (Figs. 4 and 5, Table II). It is of further interest to note that when phycobilisome vesicles were analyzed on a sucrose density gradient (0.25—1.5 M, in sucrose/phosphate/citrate/albumin medium) greater amounts of free but not dissociated phycobilisomes were separable from the aged vesicles than from fresh vesicles. Whereas physical separation of the phycobilisomes and thylakoids results in energetic uncoupling, it is not the only indication of uncoupling. For example, *Porphyridium cruentum*, phycobilisome vesicles [12,27] isolated in 0.75 M phosphate buffers have been shown to be physically bound but energetically totally uncoupled.

Although our data are consistent with the above interpretation, and are actually closer to what might be expected from the reports which have shown that the chlorophyll component of PS II is rather small and rather invariant [22,25—27] in blue-green algae, certain other possibilities need to be considered. Phycobilisomes, attached to the vesicles, even if uncoupled from F696 chlorophyll, could transfer to another form such as F685 nm [21]. It is further possible, that separate chlorophyll and phycobilisome emission peaks exist, as yet unresolved, in the relatively broad 685 nm emission peak.

Acknowledgements

This work was supported in part by Department of Energy Contract No. EY-76-5-05-4310.

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