Biochimica et Biophysica Acta 892 (1987) 48–55
Elsevier

BBA 42541

Excitation-energy redistribution in the cryptomonad alga *Cryptomonas ovata*

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(Received 29 October 1986)
(Revised manuscript received 18 February 1987)

Key words: Photosynthesis; Fluorescence; Energy redistribution; P-700 oxidation; Light-state transition; Electron transport; (*C. ovata*)

We have studied the redistribution of excitation energy in the cryptomonad alga *Cryptomonas ovata*. Low-temperature fluorescence emission spectra from cells preilluminated with light 1 and light 2 show that preferential excitation of Photosystem II (PS II) leads to decreased fluorescence emission from chlorophyll (Chl) *a* associated with PS II relative to the emission following the preferential excitation of Photosystem I (PS I). The fluorescence change is indicative of a light-state transition by the cells. However, comparision of measurements of the kinetics of P-700 photooxidation by cells fixed with glutaraldehyde following illumination with light 1 or light 2 shows that the relative activity of PS I is lower in cells fixed in light 2. This is in contrast to the expectation for cells in State 2. Excitation spectra for the fluorescence emission from PS II Chl *a* show that preferential excitation of PS II leads to a decreased probability for energy transfer from phycoerythrin and Chl c_2 to PS II when compared to cells in which PS I is preferentially excited. This result is in accordance with recent picosecond time-resolved fluorescence studies (Bruce, D., Biggins, J., Charbonneau, S. and Thewalt, M. (1987) in Progress in Photosynthesis Research (Biggins, J., ed.), Vol. II, pp. 777-780, Martinus Nijhoff, Dordrecht) and we, therefore, suggest that *C. ovata* does not undergo a classical light-state transition. However, preferential excitation of PS II or PS I appears to cause pigment-protein conformational changes which change the probability for energy transfer from phycoerythrin to PS II, and we suggest that this may be a mechanism for photoprotection of PS II. Studies of the kinetics of excitation-energy redistribution, and of the effects of electron-transport inhibitors and uncouplers of photophosphorylation indicate that the mechanism for excitation-energy redistribution in *C. ovata* and phycobilisome-containing organisms may be similar.

Introduction

An optimal rate of photosynthetic electron transport requires a balanced rate of turnover of the two photosystems. An imbalance in the amount of excitation energy delivered to PS I or PS II can be compensated by redistribution of the energy between the photosystems. This phenomenon discovered by Murata [1] in the red alga *Porphyridium cruentum* and by Bonaventura and Myers [2] in the green alga *Chlorella pyrenoidosa* is known as the light-state transition. The mechanism of the light-state transition appears to depend on the kind of pigment-protein antenna complex associated with PS II. In green algae and higher plants, a reversible phosphorylation of a thylakoid pig-

Abbreviations: PS, Photosystem; Chl, chlorophyll; PE, phycoerythrin; DCMU, 2-(3,4-dichlorophenyl)-1,1-dimenthylurea; DCIP, 2,6-dichlorophenolindophenol; DBMIB, 2.5-dibromo-3-methyl-6-isopropyl-*p*-benzoquinone; CCCP, carbonylcanide *m*-chlorophenylhydrazone; LHC, light-harvesting chlorophyll; PQ, plastoquinone.

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ment protein complex, the Chl-*a*/Chl-*b* LHC, and antenna relocation is a key event in the mechanism [3]. In red algae and cyanobacteria, which contain phycobilisomes, we have suggested that in contrast to the LHC-containing organisms the antenna remains associated with PS II in both states, and that cyclic electron transport and an accompanying electrochemical gradient play a critical role in driving an intramembrane conformational change. Our model has recently been challenged by Allen et al. [7] who proposed an alternative model for state transitions in phycobilisome-containing organisms. A refutation of their view has been recently presented [8].

Other photosynthetic organisms exist which have pigment-protein antenna complexes associated with PS II that are neither Chl-*a*/Chl-*b* complexes nor phycobilisomes. The cryptomonads are a unique group of algae that have both an integral thylakoid membrane Chl-*a*/Chl-c_2 carotenoid complex, and phycobilin antennas. Unlike the phycobilisome-containing organisms, the cryptomonads contain only one type of phycobilin (phycoerythrin or phycocyanin), which is found densely packed within the thylakoid lumen [9,10], rather than as phycobilisomes. Also cryptomonads do not have allophycocyanin [11], which makes up the core of the phycobilisome in red algae and cyanobacteria and transfers energy to high molecular mass terminal pigments and PS II chlorophyll [12]. Cryptomonad phycobiliproteins do not aggregate above dimeric states and do not form phycobilisomes [13,14]. The detailed structure of the organization of the phycobiliproteins with respect to energy transfer to PS II and PS I in vivo is not known, but it has been suggested that in the cryptomonad *C. rufescens*, phycoerythrin is linked to PS II centers via a phycobilin-Chl antenna complex [15].

In this report we present data which show that selective excitation of pigments associated with PS I or PS II in *C. ovata* lead to changes in the distribution of excitation energy. Although there are similarities in the phycobilisome-containing organisms with respect to regulation of excitation-energy distribution, our data on changes on electron-transport rates following preillumination protocols suggest that *C. ovata* does not undergo a light state transition. Redistribution of excitation energy in this alga appears to be a mechanism for photoprotection of PS II and may be related to the phenomena in diatoms described by Owens [16].

Materials and Methods

C. ovata (UTEX 358) was grown autotrophically on Bristol's medium with vitamins at 25 $\mu E \cdot m^{-2} \cdot s^{-1}$, 20 °C. Exponential phase cells were harvested and suspended in Bristol's medium at a concentration of 0.7–1.0 μg Chl *a* per ml. Cells were preilluminated with monochromatic light of 700 nm or 566 nm light (bandwidth, 1.3 nm at half height) at intensities indicated in the figure legends using a SPEX Industries Multimate duochrometer and 450 W 2e arc source. Corrected fluorescence excitation and emission spectra were determined with a SPEX Industries spectrofluorimeter for 100 μl samples suspended in 1 mm diameter capillaries as described previously [4]. The samples were preilluminated in the capillaries and rapidly frozen in liquid nitrogen.

Studies on the effects of electron-transport inhibitors and uncouplers of photophosphorylation on excitation energy redistribution were carried out as follows. A 2.4 ml aliquot of cells was placed in the spectrofluorimeter sample chamber for a 3 min dark adaptation. The sample was stirred continuously throughout the experiment. After the 3 min, two 100 μl samples were withdrawn and quick-frozen in liquid nitrogen. Next the inhibitor or uncoupler was added and incubated with the cells for 30 s. Two 100 μl samples were withdrawn and frozen. The remaining 2 ml of cells were then illuminated for 2 min with either light 1 (700 nm) or light 2 (566 nm) as indicated before further 100 μl samples were withdrawn. 77 K fluorescence emission spectra were then determined for all the frozen samples. Spectra from samples subject to the same treatment were averaged.

For PS I electron-transport turnover, the photo-induced absorption change of P-700 was measured on cells chemically fixed with glutaraldehyde (grade 1, Sigma Chemical Co., St. Louis, MO) as described previously [17,18]. The activation PS2 flashes were subsaturating (230 $\mu E \cdot m^{-2} \cdot s^{-1}$) and of wavelengths absorbed primarily by phycoerythrin (500–600 nm). The PS I electron trans-

port induced as the result of the PS II activation flashes included cyclic and linear reactions.

Absorption spectra of intact *C. ovata* were measured using a Varian-Cary model 219 spectrophotometer according to the method of Beale and Chen [19].

Results

Preillumination effects

The low-temperature (77 K) fluorescence emission of intact cells preilluminated with light absorbed preferentially by PS I (light 1) or by PS II (light 2) are shown in Fig. 1. The four fluorescence maxima are attributed to PE (620 nm), PS II Chl *a* (687–690 nm, 695–700 nm) and PS I Chl *a* (720 nm). The change in the yield of fluorescence emission is reversible and the difference in excitation energy distribution between the photosystems is characteristic of a light-state transition. The inset of Fig. 1 shows the excitation spectra for the 77 K fluorescence emission from Chl *a* associated with PS II (688 nm) and PS 1 (725 nm). Chl c_2 (465 nm) and PE (566 nm) transfer excitation energy preferentially to PS II. State 2, which is obtained by preillumination of cells with light 2, is characterized by a low ratio of fluorescence from PS II relative to PS I (F_{695}/F_{720}). Far red preillumination is required to bring *C. ovata* to the condition that yields a fluorescence spectrum characteristic of cells in State 1.

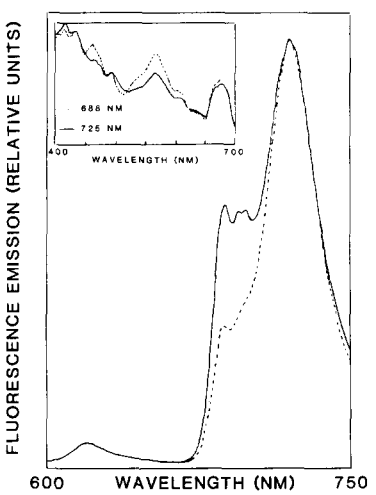

Fig. 1. 77 K fluorescence emission spectra of *C. ovata*. Light 1:700 nm (30 $\mu E \cdot m^{-2} \cdot s^{-1}$) 2.6 nm bandwidth (———); light 2: 566 nm (100 $\mu E \cdot m^{-2} \cdot s^{-1}$) 2.6 nm bandwidth (- - - - -). Cells were dark adapted for 2 min and preilluminated with light 1 for 2 min or light 2 for 30 s and frozen in liquid N_2. Excitation wavelength for fluorescence emission was 566 nm. Spectra were normalized to maximum emission. Inset: 77 K fluorescence excitation spectra of PS II Chl *a* and PS I Chl *a*. Excitation spectra were normalized to 435 nm.

As was previously demonstrated in *P. cruentum* and in *A. nidulans* [4,20], the conformational state of the thylakoid membrane accompanying the high and low fluorescence ratios can be stabilized using the bifunctional cross-linking reagent, glutaraldehyde. The 77 K fluorescence emission spectra from fixed *C. ovata* are similar to those obtained from untreated cells (data not shown).

Action spectrum

An action spectrum for the low-temperature fluorescence emission change (Fig. 2) shows that the ratio of F_{695}/F_{720} changes as a function of preillumination wavelength. Wavelengths absorbed by pigments associated with PS II (465, 566, 670 and 680 nm) yield the lowest values for the ratio F_{695}/F_{720}. Preillumination with wavelengths absorbed by carotenoid (495–510 nm) lead to higher ratios and preillumination of long-wavelength Chl *a* yields the highest value for F_{695}/F_{720}. The intermediate value of F_{695}/F_{720} at 500 nm may be due to simultaneous excitation of carotenoid associated with both PS II and PS I.

The excitation spectra for 77 K fluorescence

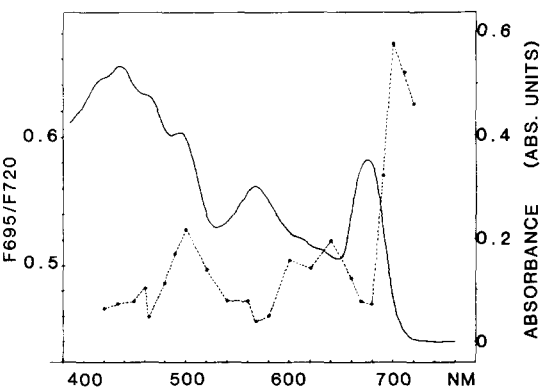

Fig. 2. Absorbance spectrum (———) of intact *C. ovata* and action spectrum (- - - - -) for the change in excitation energy distribution in *C. ovata*. Cells were dark adapted for 2 min and illuminated at subsaturating intensity (50 $\mu E \cdot m^{-2} \cdot s^{-1}$) for 2 min prior to freezing.

emission (not shown) show an increase in the contribution of PE and Chl c_2 to PS II fluorescence for cells preilluminated with light 1 compared to those preilluminated with light 2 indicating that energy transfer from PE and Chl-c_2 to PS II is more efficient in cells preilluminated with light 1.

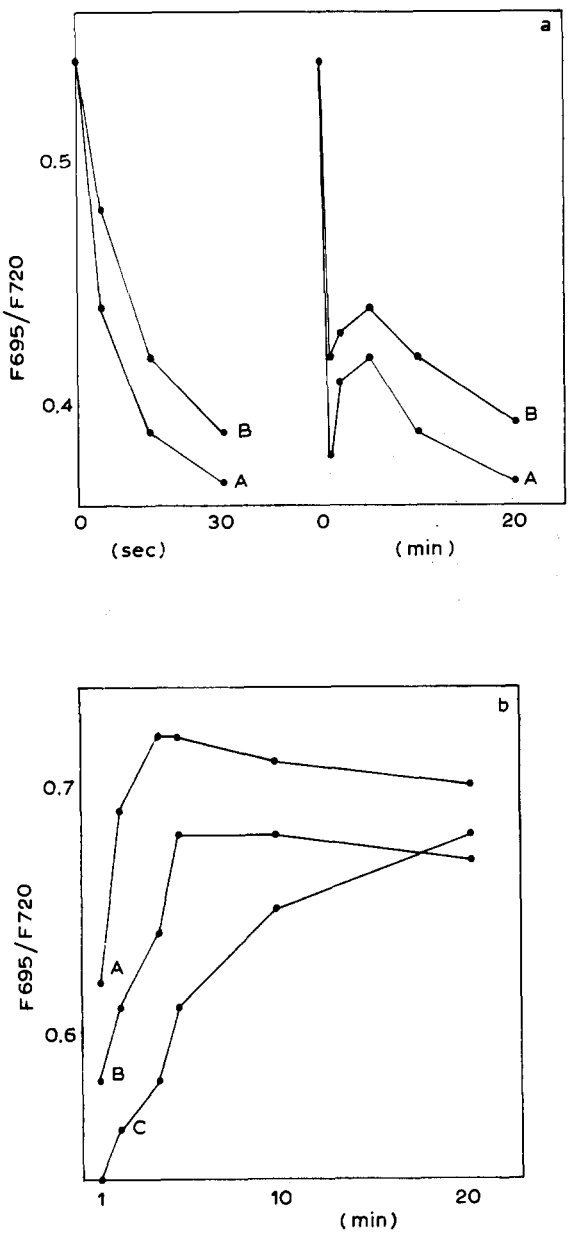

Fig. 3. Kinetics of the change in excitation-energy distribution in *C. ovata* (a) Cells preilluminated with light 2 following 2 min dark adaptation. Light intensities were 120 $\mu E \cdot m^{-2} \cdot s^{-1}$ (A) and 55 $\mu E \cdot m^{-2} \cdot s^{-1}$ (B). (b) Cells preilluminated with light 1. Light intensities were 30 $\mu E \cdot m^{-2} \cdot s^{-1}$ (A) and 5 $\mu E \cdot m^{-2} \cdot s^{-1}$ (B). Kinetics of dark adaptation (C).

Kinetics of the fluorescence changes

The kinetics of the transition to the low fluorescent state at two light intensities are shown in Fig. 3a. Both the initial rate of attaining the minimum F_{695}/F_{720} (left panel) and the extent of the relative decrease in emission from PS II (right panel) are intensity dependent. From the 2 min dark-adapted state, the transition to a minimum ratio F_{695}/F_{720} occurs within 30 s. Over a period of 5 min the ratio increases slightly, but by 20 min the ratio decreases to the minimum value. The transient increase probably reflects an induction phenomenon that occurs upon bringing the cells from the dark to relatively high-intensity light absorbed preferentially by PS II. Induction effects were also observed in the transition from State 1 to State 2 in *P. cruentum* [21].

The kinetics of the transition to the high fluorescent state are shown in Fig. 3b. The ratio of conversion to the maximal F_{695}/F_{720} and the extent of the maximum depend on the intensity of the 700 nm light. Fig. 3b also shows the change in the low-temperature emission as a function of the time of dark adaptation. Cells left in the dark 20 min prior to freezing exhibit fluorescence emission spectra characteristic of cells in the high fluorescent state.

Effect of electron-transport inhibitors and ionophores

To elucidate the mechanism of the light induced 77 K fluorescence changes we studied the effects of electron transport inhibitors and proton ionophores. DCMU inhibits electron transfer from the primary acceptor of PS II (Q) to the intersystem electron-transport chain. The addition of DCMU to *C. ovata* and subsequent preillumination with light 2 resulted in the inhibition of the transition to the minimum F_{695}/F_{720} ratio. The 77 K fluorescence emission from DCMU-poisoned cells is characteristic of untreated cells preilluminated with light 1 (Fig. 4a).

DBMIB inhibits oxidation of the intersystem electron carrier plastoquinone (PQ) at a high af-

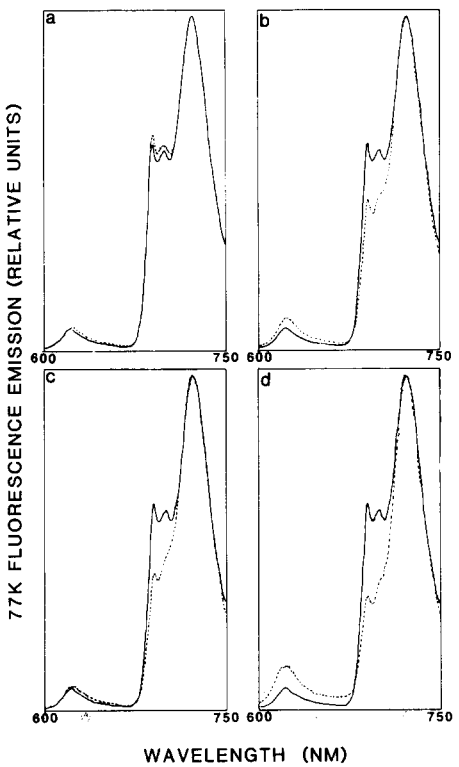

Fig. 4. The effect of electron-transport inhibitors and uncouplers on the change in excitation energy distribution in *C. ovata*. Cells were dark adapted for 3 min and then illuminated with light 1 for 2 min. (see Materials and Methods). Fluorescence emission of withdrawn samples for excitation at 566 nm (———). (a) 1 μM DCMU (------), cells illuminated with light 2; (b) 5 μM DBMIB (------), cells illuminated with light 1; (c) 1 μM CCCP (------), cells illuminated with light 1; (d) 1.2 μM gramicidin (------), cells illuminated with light 1. Chlorophyll concentration: [Chl *a*] = 0.68 μg/ml.

finity binding site [22]. The transition to the high fluorescence ratio with preillumination by light 1 was inhibited in DBMIB-poisoned cells (Fig. 4b). The fluorescence spectrum of these cells is characteristic of untreated cells preilluminated with light 2. That PE is more energetically uncoupled from PS I and PS II is indicated by the increase in the relative amplitude of fluorescence at 620 nm (Fig. 4b).

CCCP and gramicidin both act as uncouplers of photophosphorylation via dissipation of the proton electrochemical potential across the thylakoid membrane. CCCP is a weak lipophilic acid and gramicidin is a channel-forming ionophore. Both were found to inhibit the transition to the high fluorescent state (Fig. 4c and d).

The contribution of PE to the 77 K fluorescence emission spectra was very sensitive to the concentration of DBMIB or ionophore incubated with the cells. Concentrations greater than 5 μM led to extensive uncoupling of the phycobilin from the thylakoid membrane with respect to excitation energy transfer to PS II and PS I, and produced emission spectra with very high PE fluorescence at 620 nm. However, the transition to a minimum F_{695}/F_{720} still occurred in the presence of these high concentrations.

Changes in PS I electron transport

In order to conclude that changes in excitation energy distribution as measured by fluorescence are indicative of cells which have undergone a light state transition, it is essential to show that there are differences in electron transport rates following the preillumination protocols. Bonaventura and Myers [2] were the first to correlate such measurements in *Chlorella*, thus lending credence to the use of fluorescence changes as an assay for the state transition. Biggins [4] and Biggins et al. [5] have also correlated changes in the rate of cytochrome *f* oxidation with 77 K fluores-

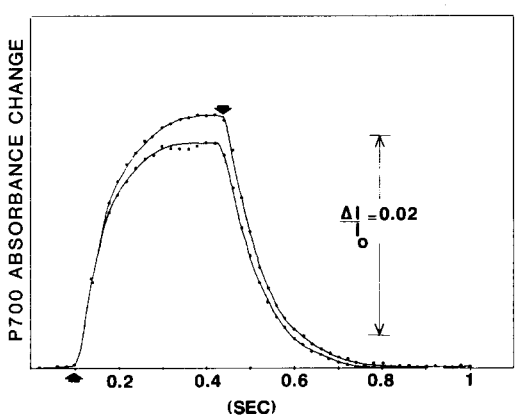

Fig. 5. Photoinduced absorption changes due to P-700 of *C. ovata*. Cells were fixed with glutaldehyde during illumination with light 1 (upper curve) or light 2 (lower curve) and subjected to broad band green activation flashes (500–600 nm) at an intensity of 230 $\mu E \cdot m^{-2} \cdot s^{-1}$. The curves shown were derived by averaging four spectra each composed of the sum of 128 flashes. The fixed cells were suspended in 4 μM DCMU, 10 mM DPIP, 4 mM ascorbate and 200 μM methyl viologen.

cence emission spectra *P. cruentum* in State 1 and State 2.

Fig. 5 shows photoinduced absorption changes of P-700 in *C. ovata* in response to subsaturating activation by light 2. The kinetics of dark reduction following the flash were identical in cells preilluminated with light 1 or light 2, therefore the observed difference in steady state amplitude of $P\text{-}700^+$ was a result of a difference in rate of P-700 photooxidation. The data indicate that, contrary to expectation for cells that have undergone a state transition, the turnover of PS I is greater for cells preilluminated with light 1.

Discussion

The data presented here show that the cryptomonad alga *C. ovata* undergoes reversible changes in excitation-energy distribution in response to selective excitation of PS I or PS II. The 77 K fluorescence emission spectra of cells preilluminated with light 1 and light 2 are qualitatively similar to those spectra for Chl-*b*- and phycobilisome-containing organisms in light state 1 or State 2. The low fluorescent state in *C. ovata*, which is analogous to State 2, can be achieved by preferential excitation of the accessory light-harvesting pigments of PS II (PE, Chl c_2, carotenoid and short wavelength Chl *a*). Preferential excitation of PS I in *C. ovata* is most efficiently achieved as in higher plants with 700 nm light absorbed by long-wavelength Chl *a*.

The excitation spectra for 77 K fluorescence emission at 688 nm indicate that in the case of preillumination with light 1, PE is more tightly coupled to the photosystems. Excitation energy transfer from Chl c_2 to PS II is also more efficient and is confirmed by picosecond-time-resolved spectroscopy. Bruce et al. [23] found that the fluorescence decay kinetics of PE, Chl c_2, and Chl *a* 684 depend upon preillumination wavelength, while those of PS II Chl *a* 695 and PS I Chl *a* 720 do not. The relative contribution of the fast decay component of PE, Chl c_2, and Chl *a* 684 was greater in cells preilluminated with 710 nm light than in cells preilluminated with 566 nm light. These results are in contrast to those found for the phycobilisome-containing alga *P. cruentum* and the cyanobacterium *A. nidulans* where the largest state transition induced change was shown to be the decay kinetics of Chl *a* 695 [24].

The results obtained from the excitation spectra for emission at 688 nm of cells preilluminated with light 1 and light 2, from time-resolved picosecond spectroscopy [23], and from measurements of the P-700 absorbance changes reported above, suggest that selective preillumination of PS II or PS I in *C. ovata* leads to a conformational change between PE, the Chl *a*/Chl c_2 LHC and the PS II core complex. The ability to cross-link the cells chemically during illumination with light 1 or light 2 such that they are fixed into the high or low fluorescent state is highly suggestive of a membrane-conformational change occurring during the transition. For excitation-energy transfer to occur via radiationless resonance energy transfer, the distance and orientation between participating chromophores is critical [25]. Selective excitation of PS II antenna leads to a decreased probability for energy transfer to Chl *a* associated with the PS II core complex and may be the result of an energetic uncoupling of PE from the pigments on the lumenal side of the thylakoid membrane.

The effects of electron-transport inhibitors and uncouplers of photophosphorylation suggest that the mechanism of excitation energy redistribution in *C. ovata* is more closely related to that of phycobilisome-containing organisms than that of higher plants. In higher plants, regulation of the light state transition occurs via a thylakoid membrane bound protein kinase. The kinase is activated when the PQ pool is reduced and phosphorylation of the Chl-*a*/Chl-*b* LHC by kinase leads to State 2. DCMU inhibits the transition to State 2 by blocking electron transfer from the primary acceptor of PS II (Q) to PQ [3]. Murata [1] originally had found that DCMU inhibits the low-temperature fluorescence changes induced by preillumination of PE (State 2) in *P. cruentum*. DCMU also inhibits the transition to the low fluorescent state in *C. ovata*. Thus it appears that linear electron flow from PS II is required to produce the condition characteristic of thylakoids in State 2. This is corroborated by the result obtained in higher plants, phycobilisome-containing organisms and in *C. ovata* that the presence of DBMIB keeps the thylakoids in the low fluorescent state (or State 2). DBMIB also prevents the transition to the high

fluorescent state (or State 1). This inhibitory aspect of DBMIB suggests that cyclic electron flow around PS I may be required to attain the high fluorescent state [5,26]. That a phosphorylation event is not involved in the regulation of excitation energy redistribution in *C. ovata* is indicated by the effect of the uncouplers CCCP and gramicidin. The transition to the low fluorescent state is not inhibited in their presence as would be expected if ATP were required for a protein kinase activity. But these uncouplers did inhibit the transition to the high fluorescent state as they do in *P. cruentum* [5]. Accordingly, we suggest that the transition to the high fluorescent state (analagous to State 1) also requires coupled PS-I-driven cyclic electron transport. Since the cryptomonad phycobilins are located within the thylakoid lumen they would most likely be inaccessible to a membrane-bound protein kinase particularly if it were located on the stromal side of the thylakoid membrane where ATP is produced.

While certain aspects of the regulation of excitation energy distribution in *C. ovata* are similar to phycobilisome-containing organisms, *C. ovata* does not appear to undergo a classical light-state transition in a manner analogous to Chl-*b*- or phycobilisome-containing organisms. For the latter, preillumination with light 1 leads to a conformational change of the photosynthetic apparatus such that more energy is transferred to PS II at the expense of PS I leading to changes in electron transport [4,5,27,28]. Preillumination of *C. ovata* with light 2 leads to an apparent uncoupling of PE from the Chl-*a*/Chl-c_2 and PS II core complexes and a decrease in PS I activity. We suggest that this could be a protective process. It is known that over excitation of PS II can lead to photoinhibition, and that plants and algae have evolved mechanisms to protect against the damaging effects of high light [29,30]. We suggest that in *C. ovata* regulation of excitation energy distribution might contribute to the photoprotection of PS II.

Acknowledgements

We wish to thank Dr. A. Coleman for the generous gift of *Cryptomonas ovata* and Dr. D.H. Bruce for valuable advice throughout the project and for criticism on the manuscript. The research was supported by the Science of Educational Administration of the United States Department of Agriculture under grant number 85-CRCR11575 from the Competitive Research Grants Office (J.B.).

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