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Stabilization and modulation of the phycobilisome by calcium in the calciphilic freshwater red alga *Bangia atropurpurea*

Makio Yokono [a,*], Hiroko Uchida [b], Yuzuru Suzawa [c], Seiji Akiomoto [a,d], Akio Murakami [b]

[a] *Molecular Photoscience Research Center, Kobe University, Kobe, Hyogo 657–8501, Japan*
[b] *Research Center for Inland Seas, Kobe University, Awaji, Hyogo 656–2401, Japan*
[c] *Institute of River Biology Ltd., Munakata, Fukuoka 811–3425, Japan*
[d] *JST, CREST, Kobe, 657–8501, Japan*

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ABSTRACT

The bangiophycean filamentous red alga *Bangia atropurpurea* is distributed in freshwater habitats such as littoral and splash zones of lakes or rapid currents distant from the sea. In these habitats, the distribution and growth of this alga appear to be related to hard water rich in calcium ions. To characterize the eco-physiological properties of this calciphilic red alga, we examined the effects of long-term and short-term Ca^{2+} depletion on photosynthetic growth of the thallus and on the phycobilisome. Long-term culture experiments suggested that higher Ca^{2+} concentrations (>50 mg L^{-1}) were required to sustain thallus growth and pigmentation of cells. In short-term Ca^{2+}-depletion treatments, fluorescence derived from phycoerythrin (PE) fluctuated, although the absorption spectra of the thalli did not change. After 30 min of Ca^{2+} depletion, the fluorescence lifetime of PE became markedly longer, indicating that the energy transfer from PE to phycocyanin (PC) was suppressed. The fluorescence lifetime of PE returned to its original value within a short time after 4 h of Ca^{2+} depletion, however, energy transfer from PE to PC was still suppressed. This suggested that the excitation energy absorbed by PE was quenched during prolonged Ca^{2+} depletion. The efficient energy transfer from PC and allophycocyanin were unchanged during these treatments.

1. Introduction

Aquatic photosynthetic organisms can acclimate to changes in various environmental factors including light (light intensity and quality), nutrients (concentrations of N or P), temperature, pH, etc. through modulation of photosynthetic systems, including reaction centers and antenna complexes [1]. In cyanobacteria, the photosynthetic light-harvesting antenna, the phycobilisome (PBS), responds with high sensitivity to changes in light and nutrients [2,3].

The unicellular red alga *Porphyridium cruentum* has phycoerythrin (PE) — dominating hemiellipsoidal type of PBS and shows state-transition, in which excitation energy harvested by PBS is shared between photosystems I and II [4–6]. It was suggested that state-transition occurs together with quenching of excess excitation energy in the antenna to avoid photodamage [7]. Although red algae may have regulatory mechanisms controlling antenna systems, the mechanism of quenching in the PBS of red algae remains unclear. Spectroscopic analyses can be used to examine the mechanisms that underlie regulation of the photosynthetic antenna complex. Recently, we used such analyses to demonstrate a decrease in energy transfer to the reaction center in evergreen plants and green algae [7,8]

Almost all species of bangiophycean red algae in the genus *Bangia* are epiphytic or epilithic, and are distributed in marine coastal areas worldwide [9]. Only the species *Bangia atropurpurea* is found in freshwater habitats distant from the sea [10]. *B. atropurpurea* is found worldwide, but is restricted to the littoral zone of the Great Lakes (in North America) and in rapid currents in rivers in mountainous areas of Middle Asia and Japan [10,11]. In these habitats, the water has higher electrical conductivity than 'normal' freshwater, and its Ca^{2+} content is higher than the world average for freshwater (15 mg Ca^{2+} L^{-1}) [12]. Molecular phylogenic analyses of *Bangia* suggest that all freshwater species show a distinct lineage from marine species [10], though it is difficult to distinguish between marine and freshwater *Bangia* on the basis of their cytomorphological and spectral properties. The marine species *B. fuscopurpurea* grows in the supralittoral zone and is highly tolerant to extreme drying and large fluctuations in salinity. Similarly, the freshwater species *B. atropurpurea* can adapt (osmoregulate) to a wide range of salinities [13]. Our preliminary culture experiments showed that the Japanese strain of *B. atropurpurea* requires high concentrations of Ca^{2+} in the medium. Thus, this species may be distributed only in areas with extremely hard water containing high concentrations of Ca^{2+}.

To characterize the calciphilic properties of *B. atropurpurea*, we examined the long-term and short-term effects of Ca^{2+} depletion on its

Abbreviations: PBS, phycobilisome; PE, phycoerythrin; PC, phycocyanin; APC, allophycocyanin; TRFS, time-resolved fluorescence spectra

* Corresponding author. Tel.: +81 80 3295 1623; fax: +81 78 803 5705.
E-mail address: filia@mac.com (M. Yokono).

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physiological status. Using a newly established strain, we determined the effects of Ca^{2+} depletion on photosynthetic growth of the thalli, and examined changes in the PE-dominating PBS using picosecond time-resolved fluorescence spectroscopy. The results showed that *B. atropurpurea* requires high concentrations of Ca^{2+} for its photosynthetic growth. The Ca^{2+}-depletion treatment decreased energy transfer from PE to PC, and PE did not accumulate excess energy even though it absorbed light. We discuss energy dissipation mechanisms in the PBS and compare the structural differences between the hemiellipsoidal phycobilisomes and the hemidiscoidal phycobilisomes.

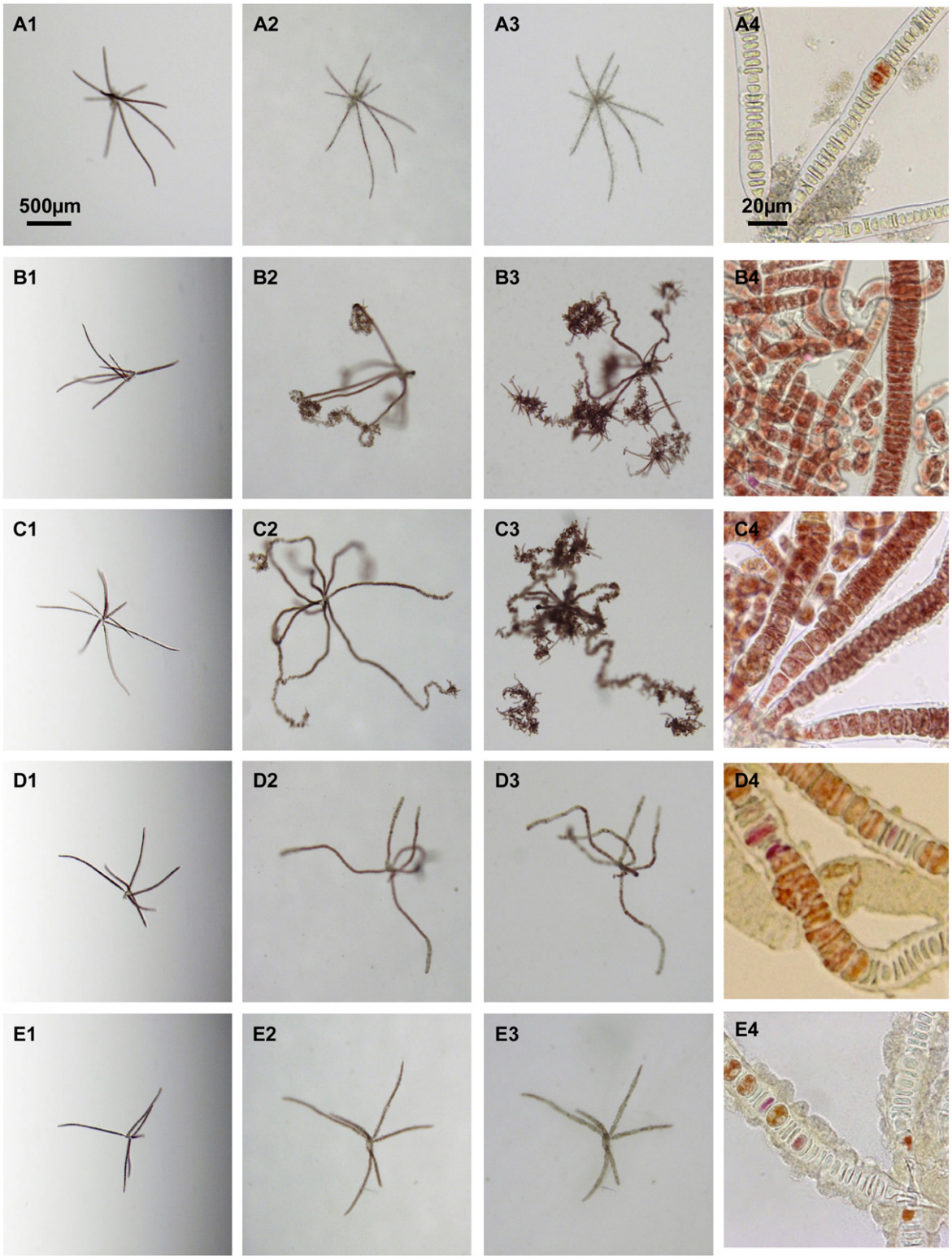

Fig. 1. Growth of *Bangia atropurpurea* in media based on natural seawater. Pre-cultured filamentous thalli were transferred into media containing 0% (A), 25% (B), 50% (C), 75% (D), or 100% (E) natural seawater (salinity of 33‰) enriched with Provasoli's nutrients and cultured for approx. 1 month. Whole thalli at 0, 18, and 36 days culture are shown in columns 1–3. Column 4 shows magnified part of thallus at 36 days of culture.

2. Materials and methods

2.1. Alga and culture

Filamentous thalli of *B. atropurpurea* were collected from the rocky bed of a river with a rapid current in May 2005 and April 2006 in Higashi-kawachisawa (50 km away from the sea and 650 m above sea level), Shizuoka, Japan. The properties of the water in this habitat were as follows: 145–150 μS/cm electrical conductivity, pH 7.6–7.7, and 9.9–11.5 °C. Epiphytic microorganisms were removed by repeatedly dragging the thalli through agar blocks. A uni-algal strain of *B. atropurpurea* was established as the thalli germinated and developed from the isolated spores. The algal thalli were maintained in plastic culture vessels at 10 °C under the following conditions: 10-h light (35 μmol photons m^{-2} s^{-1}) and 14-h dark photoperiod, with light delivered by a 20 W, daylight-type fluorescent tube lamp. The culture media were as follows: 1/4 strength natural seawater, artificial seawater based on ASN-III medium [14], and Ca^{2+}-rich mineral water (Contrex^{R}, Nestlé Waters Marketing & Distribution). The Ca^{2+} concentration of the mineral water was approx. 480 mg L^{-1} [15], which was higher than that of seawater. Enriched nutrients as described by Provasoli were added to all culture media [16].

2.2. Growth measurements

Growth rates of *B. atropurpurea* were determined by measuring elongation of each thallus filament or by counting the number of intact cells in microphotographs. *In vivo* absorption and fluorescence spectra were used as indexes of the intactness of algal thalli during culture.

2.3. Spectroscopic measurements

Steady state absorption spectra at room temperature were measured under a microscope (Olympus BX50) using a light-guided multi-channel photodiode array detector (PMA-11, Hamamatsu Photonics, Japan) [17]. The thalli were returned to the incubator after each absorption measurement. Change of absorption intensity was also monitored using a spectrophotometer with integrated sphere attachment (JASCO V-650 with ISV-722). The thalli were held in the optical cell (1 cm width) using transparent thin filter (Omnipore membrane filters JGWP01300). The optical cell was filled with the medium, and placed in the incubator (10 °C). The optical cell was returned to the incubator after each absorption measurement. Steady-state fluorescence spectra were measured at 10 °C and −196 °C using a spectrofluorometer under temperature control (JASCO FP-6600 with PMU-183 or MCB-100).

Time-resolved fluorescence spectra (TRFS) were measured by the time-correlated single-photon counting method at −196 °C [17]. The excitation wavelength was 400 nm and the time resolution was 6 ps/channel. Samples were replaced after each fluorescence measurement.

3. Results and discussion

Fig. 1 shows the growth of *B. atropurpurea* in natural seawater-based media with different salinities (0–33‰). The thalli cultured in the media containing 25% and 50% natural seawater continued to grow for more than one month (Fig. 1, B1–B3, C1–C3), as reported previously for a strain isolated from Great Lake [13], and almost all cells were alive and in good condition (Fig. 1, B4 and C4). In the 0% or the 100% natural seawater medium, thalli did not grow well (Fig. 1, A1–A3 and E1–E3) and almost all of the cells discolored and died within one month (Fig. 1, A4 and E4). These results showed that freshwater *Bangia* requires appropriate concentrations of some elements (cations) such as Ca^{2+} or Na^{+} that are present in seawater. This is also the case for marine and estuarine red algae [18,19]. Water inhabited by *B. atropurpurea* tends to contain high concentrations of Ca^{2+}. Therefore, we examined whether freshwater *B. atropurpurea* required high Ca^{2+} concentrations for growth. Fig. 2 shows the growth of *B. atropurpurea* under different Ca^{2+} concentrations in artificial seawater and in Ca^{2+}-rich mineral water. Artificial seawater (equivalent to 1/4 strength natural seawater) based on ASN-III medium with different Ca^{2+} concentrations and the Ca^{2+}-rich mineral water after dilution were used as the culture media. In both types of media, higher concentrations of Ca^{2+} fully supported photosynthetic growth (Fig. 2, A and B). The greatest growth was observed in undiluted mineral water (480 mg Ca^{2+} L^{-1}, Fig. 2B, closed circles). Growth was barely maintained in the medium consisting of 1/10 diluted mineral water (48 mg Ca^{2+} L^{-1}, Fig. 2B, semi-closed circles). Thalli did not grow in the 1/30 diluted medium (16 mg Ca^{2+} L^{-1}, Fig. 2B, open circles) after 7 days, and about half of the cells died after 14 days, even though all cells appeared to be alive and in good condition with normal pigmentation in the first 24 h of the experiment (data not shown). These results confirmed that *B. atropurpurea*

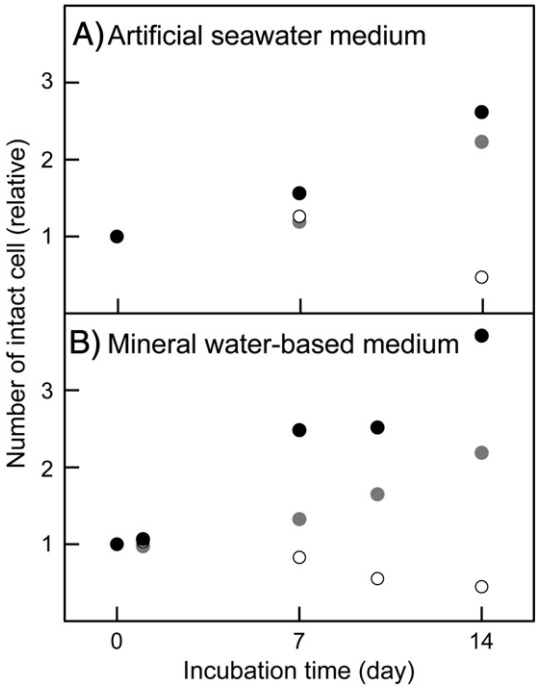

Fig. 2. Effect of Ca^{2+} on growth of *Bangia atropurpurea*. (A) Artificial seawater media (modified ASNIII) containing Ca^{2+} at 450 (closed circles), 45 (semi-closed circle), or 15 mg L^{-1} (open circles). (B) Mineral water-based media containing Ca^{2+} at 480 (closed circles), 48 (semi-closed circles), or 16 mg L^{-1} (open circles) (obtained by diluting Contrex^{R}). Number of intact cells with normal pigmentation was counted for three thalli in each medium.

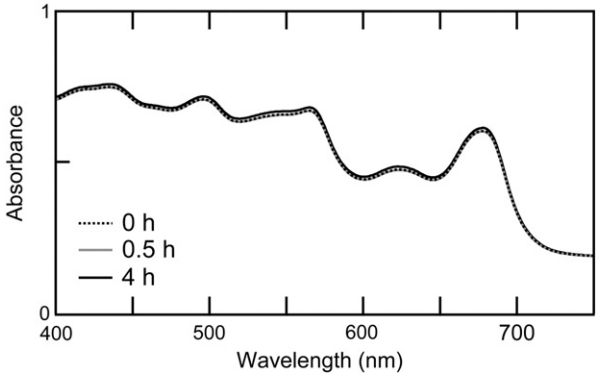

Fig. 3. Absorption spectra of *Bangia atropurpurea* at room temperature. Thalli were incubated in mineral water-based low-Ca^{2+} medium (16 mg Ca^{2+} L^{-1}) at 10 °C. Spectra were measured at 0 (A), 0.5 (B) and 4 h (C) incubation and plotted without normalization.

requires high concentrations of Ca^{2+} to sustain long-term photosynthetic growth and development. This fundamental physiological examination infers that Ca^{2+} depletion could affect photosynthesis of *B. atropurpurea*. In the following experiments, we used the mineral water as the basal medium, and examine the change of energy transfer pathways in PBS under Ca^{2+} depletion condition.

Fig. 3 shows the steady-state absorption spectra of *B. atropurpurea* before and after incubation in medium containing a low concentration of Ca^{2+} (16 mg Ca^{2+} L^{-1}, hereafter, low-Ca^{2+} medium). PE showed two peaks at 498 nm and 566 nm with a shoulder around 545 nm. These peaks originated from phycourobilin (498 nm) and phycoerythrobilin (545 nm and 566 nm) [20]. PC showed a peak around 624 nm. Allophycocyanin (APC) was likely to show a peak around 650 nm, but the peak was difficult to resolve because of overlapping of peaks from PC and chlorophyll *a* (680 nm) [21]. After 4 h incubation in the low-Ca^{2+} medium, the absorption spectra showed no degradation or other changes. However, the time-resolved fluorescence spectra (TRFS) changed markedly under the same incubation treatments. The TRFS of *B. atropurpurea* at −196 °C are represented in contour in Fig. 4. Before incubation in the low-Ca^{2+} medium (Fig. 4A), the TRFS showed a maximum of PE fluorescence at 580 nm (F_{580}) with a shoulder at 560 nm just after excitation. An additional shoulder appeared at 595 nm (F_{595}) within 20 ps after excitation, reflecting energy transfer within PE. Fluorescence from PC, APC, and chlorophyll *a* appeared within 100 ps at 645 nm, 660 nm, and 684 nm, respectively. These reflected efficient energy transfer from the PBS to the reaction centers [21]. After 0.5 h incubation in the low-Ca^{2+} medium (Fig. 4B), the F_{580} showed greater longevity than that before incubation (Fig. 4A), which indicated that energy transfer from PE was partly restricted and that excess energy was accumulated in PE itself. The decreased intensities of PC and APC fluorescence also reflected limited energy transfer from PE. The photosystem II fluorescence at 684 nm disappeared faster than that before incubation. This may indicate a decrease in energy transfer from the PBS to the photosystem II reaction center because of the limited energy transfer from PE. After 4 h incubation in the low-Ca^{2+} medium (Fig. 4C), the fluorescence intensity of PE was lower than that after 0.5 h incubation (Fig. 4B). This indicated that the excess energy accumulated in PE was dissipated. In this case, the fluorescence intensities of PC and APC did not recover (Fig. 4C). Therefore, the energy transfer from PE to PC remained interrupted. These trends were also observed after 15 h incubation (Fig. 4C, inset). These results clearly indicate that excess energy was accumulated in PE after 0.5 h Ca^{2+} depletion, and that the excess energy was dissipated after 4 h Ca^{2+} depletion without recovery of the energy transfer pathway to PC. We note that steady-state fluorescence spectra with PC excitation (610 nm) showed no significant changes in the PC and APC fluorescence region, 630–650 nm (Figs. S1 and S2).

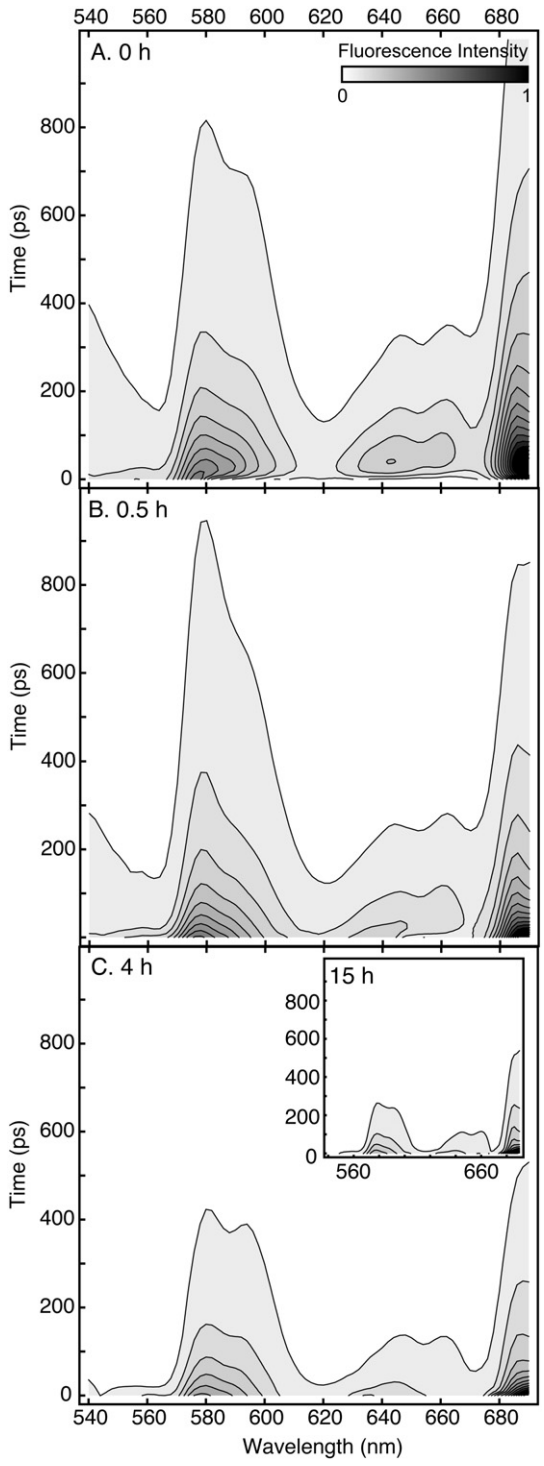

Fig. 4. Time-resolved fluorescence spectra of thalli of *Bangia atropurpurea* at −196 °C. Spectra were measured at 0 (A), 0.5 (B), 4 (C), and 15 h (inset, C) incubation in low-Ca^{2+} medium (16 mg Ca^{2+} L^{-1}). Fluorescence intensity is expressed as a gradation shown at upper side of figure; black indicates high intensity. Vertical axes show delay time after excitation.

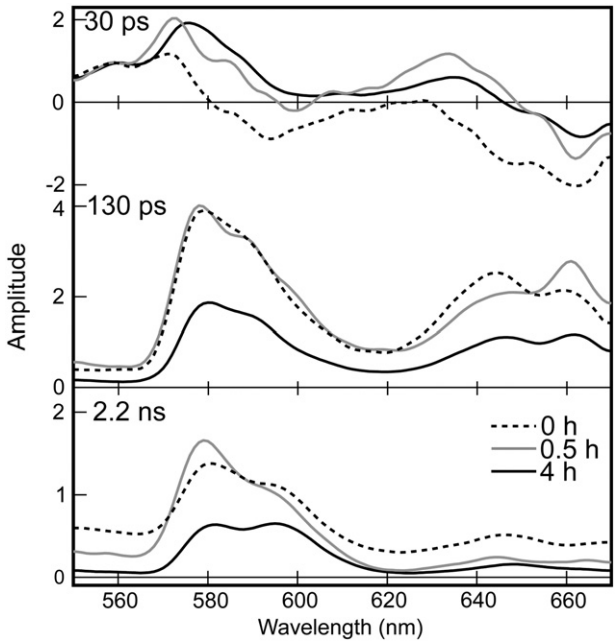

Fig. 5. Fluorescence decay-associated spectra of intact cells of *Bangia atropurpurea* at −196 °C. Analysis was carried out at 2 nm intervals. The intensities were normalized at PE wavelength region (560 nm) in the 30 ps FDAS.

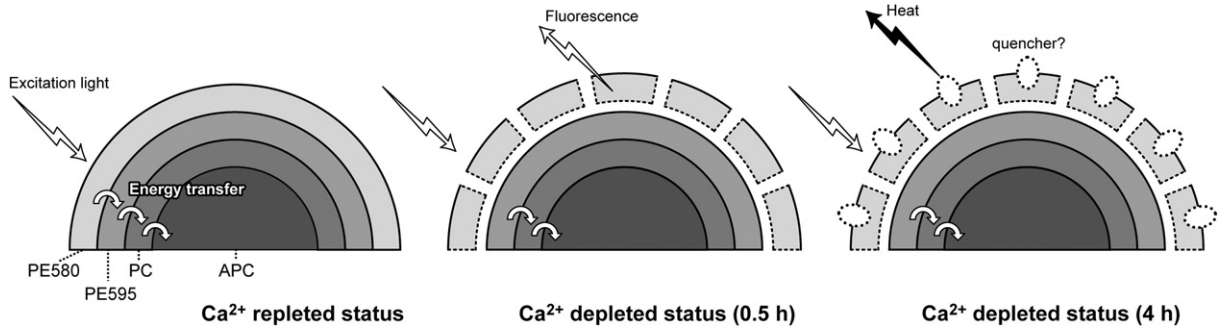

Fig. 6. Schematic model for modulation of the phycobilisome of the red alga *Bangia atropurpurea* during the response to Ca^{2+} depletion. PE580 and PE595 reflect fluorescence maxima of phycoerythrin at 580 and 595 nm, respectively.

These observations may reflect quenching or degradation of decoupled PE. As mentioned above, the absorption spectrum did not changed significantly during incubation in the low-Ca^{2+} medium (Fig. 3), which indicates that degradation of PE was not enhanced at least by 4 h incubation. Therefore, it is likely that some kind of quencher accepted energy from the decoupled PE.

To clarify the changes in energy transfer within PBS, we applied the global analytical method [21]. Fig. 5 shows fluorescence decay-associated spectra (FDAS) of *B. atropurpurea* at −196 °C. Positive and negative peaks in the spectra correspond to the fluorescence decay and rise components, respectively. The TRFS of all samples (0, 0.5, and 4 hours Ca^{2+} depletion treatment) were resolved into three FDAS, where all samples showed common lifetimes (30 ps, 130 ps, and 2.2 ns).

The 30-ps FDAS reflects fast energy transfer between chromophores in PBS. In 0-h treated sample, positive peaks around 580 nm and a negative peak at 595 nm reflects energy transfer from PE580 (shorter-wavelength form of PE) to PE595 (longer-wavelength form of PE). Negative peaks around 640 nm (PC) and 660 nm (APC) reflect successive energy transfer from the peripheral component to the core component of PBS (PE → PC → APC). In 0.5-h treated sample, the negative peak at 595 nm faded, which suggests decrease of energy transfer within PE. A set of positive and negative peak around 640 nm and 660 nm indicates that the energy transfer from PC to APC is sustained.

The 2.2-ns FDAS mainly reflects fluorescence from the chromophores that did not virtually transfer energy to other chromophores. In 0.5-h treated sample, the positive peak at 580 nm was enhanced, indicating accumulated excitation energy in PE580 caused by decreased energy transfer from PE580 to PE595. The amplitude of the 580-nm peak declined in 4-h treated sample, which indicates two following possibilities, (1) recovery of the energy-transfer pathway between PE580 and PE595, or (2) appearance of energy transfer from PE580 to quencher. In the former case, the 30-ps FDAS of 4-h treated sample should show a set of positive and negative peak around 580 nm and 595 nm, respectively, as shown in 0-h treated sample. However, only a large positive peak at 580 nm was observed, and there was no negative peak in the PE and PC fluorescence region. Furthermore, in the 30-ps FDAS, the negative peak in the APC fluorescence region (660 nm) showed the smallest intensity compared to those of 0-h and 0.5-h treated samples. These results indicate that the pathway between PE580 and PE595 did not recover in 4-h treated sample, but PE580 transferred energy quickly to unknown component(s), putative quencher, instead of PC.

The 130-ps FDAS reflects slow energy transfer within PBS. In 4-h treated sample, the intensity decreased compared to 0-h and 0.5-h treated samples. It might indicate that the energy transfer to quencher reduced the contribution of the slow energy transfer pathways in PBS.

In many red algae, the PBS is hemiellipsoidal and contains a large amount of PE at its periphery [22]. Most cyanobacteria have an open-sided hemidiscoidal PBS [23], and therefore, quenchers such as the orange carotenoid protein (OCP) can easily access the APC in the PBS core [24–26]. However, in the hemiellipsoidal PBS packed with a large amount of PE, any quenchers may not be able to access the APC in the PBS core, and OCP was not found in any red algae. Therefore, decoupling of PE followed by attachment of PE-accessible quenchers could be an advantage for the hemiellipsoidal PBS. In Fig. 6, we show a possible scheme for the decoupling and quenching mechanism in the hemiellipsoidal PBS based on our spectrophotometric analyses of *B. atropurpurea*. Previous reports suggested that there is energetic decoupling between PE and its neighbor under stress conditions in cyanobacteria and red algae [27,28]. The details of the quencher that attach to PE are unknown; however, some proteins other than PBS rod linker polypeptides could attach to PE on the peripheral surface of the PBS [29,30]. We suspect that the attachment or replacement of putative protein(s) around PE might affect energy transfer kinetics in the PBS.

Our results suggested that a high concentration of Ca^{2+} is necessary to sustain photosynthetic growth of the freshwater calciphilic species, *B. atropurpurea.* This requirement appears to be specific to the calciphilic *B. atropurpurea*, however, Ca^{2+} at a low concentration acts as signaling agent in photosynthetic eukaryotes including algae, and stabilizes the photosynthetic system in cyanobacteria [31,32]. Our results also suggest that *B. atropurpurea* can adjust the functional connections of PE to reduce the antenna size during exposure to low Ca^{2+} conditions. Although the detailed mechanisms of decoupling and quenching of PE need to be studied further, they could be useful for rapid protection of reaction centers, especially in PE-rich species.

Supplementary materials related to this article can be found online at doi:10.1016/j.bbabio.2011.11.002.

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