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Uphill energy transfer in a chlorophyll *d*-dominating oxygenic photosynthetic prokaryote, *Acaryochloris marina*

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Abstract

The steady-state fluorescence properties and uphill energy transfer were analyzed on intact cells of a chlorophyll (Chl) *d*-dominating photosynthetic prokaryote, *Acaryochloris marina*. Observed spectra revealed clear differences, depending on the cell pigments that had been sensitized; using these properties, it was possible to assign fluorescence components to specific Chl pigments. At 22°C, the main emission at 724 nm came from photosystem (PS) II Chl *d*, which was also the source of one additional band at 704 nm. Chl *a* emissions were observed at 681 nm and 671 nm. This emission pattern essentially matched that observed at −196°C, as the main emission of Chl *d* was located at 735 nm, and three minor bands were observed at 704 nm, 683 nm, and 667 nm, originating from Chl *d*, Chl *a*, and Chl *a*, respectively. These three minor bands, however, had not been sensitized by carotenoids, suggesting specific localization in PS II. At 22°C, excitation of the red edge of the absorption band (which, at 736 nm, was 20 nm longer than the absorption maximum), resulted in fluorescence bands of Chl *d* at 724 nm and of Chl *a* at 682 nm, directly demonstrating an uphill energy transfer in this alga. This transfer is a critical factor for in vivo activity, due to an inversion of energy levels between antenna Chl *d* and the primary electron donor of Chl *a* in PS II.

Keywords: Antenna; Chlorophyll *d*; Fluorescence; Photosynthesis; Uphill energy transfer; *Acaryochloris marina*

1. Introduction

Acaryochloris marina is a newly discovered photosynthetic prokaryote whose major antenna pigment is chlorophyll (Chl) *d* [1]. The absorption maximum of this pigment is located at a wavelength that is 25 nm longer than that of Chl *a* in organic solvents; in intact cells, there are several absorption bands, one with the peak at 714 nm and three minor bands at 694 nm, 726 nm, and 740 nm (revealed by low-temperature spectroscopy) [2]. This alga also contains Chl *a*; however, this is always a minor component, contributing less than 3% of the total Chl [3]. In cells, one absorption band of Chl *a* has been reported at 670 nm [2]. The carotenoid composition of this alga is also unique: its major components are α-carotene and zeaxanthin, whose molar ratio is almost unity [3]. α-Carotene might be associated with several kinds of pigment-protein complexes; however, a lo-

Abbreviations: Chl, chlorophyll; DCMU, 3-(4-dichlorophenyl)-1,1-dimethylurea; DF, delayed fluorescence; HWHM, a half-bandwidth at the half-maximum of the peak; Pheo, pheophytin; PS, photosystem; RC, reaction center

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calization for zeaxanthin has not yet been clearly resolved. These pigment compositions mean that the photosynthetic system for *A. marina* differs from those of other photosynthetic organisms.

The primary electron donor of a photosystem (PS) I reaction center (RC) is reported to be Chl *d* and its antenna consists of Chl *d* [4]. Conversely, we assigned Chl *a* to the primary electron donor for a PS II RC on the basis of delayed fluorescence (DF) observed only in the wavelength region of Chl *a*, i.e., at 681 nm, at −196°C [5]. That the stoichiometry between Chl *a* and pheophytin (Pheo) *a* was 2 to 1, fitting to the case of bacterial RC [6,7], also supported the assignment. Presence of Chl *a* and Pheo *a* was not suggested in PS I [4], thus an antenna pigment of PS II was assigned to Chl *d* [5]. The DF was observed at −196°C with a lifetime of 15 ns, but not at the physiological temperature [5]. There are two kinds of pigment responsible for the DF; one is a pigment directly involved in the charge recombination process in the PS II RC, i.e., the primary electron donor, and the other is a pigment sensitized by the primary electron donor, and Chl *a* should be either of the above two. If Chl *d* is the PS II primary electron donor and Chl *a* is the primary electron acceptor, the observed DF is to be sensitized by Chl *d*. When we assume that the 694 nm Chl *d* band [2] is an energy donor of the 681 nm Chl *a* DF band, the energy difference between these two was approximately six times larger than the thermal energy at −196°C (approx. 50 cm^{-1}), therefore the DF due to uphill energy transfer was scarcely possible. This energy difference can be applied to the relationship between Chl *d* and Chl *a*, irrespective of a function of Chl *a*. Based on the above consideration, the observed DF was explained most reasonably by the assignment that Chl *a* is the primary electron donor of the PS II RC. In the case of green sulfur bacterium *Chlorobium limicola*, the primary electron acceptor is reported to be a Chl *a*-like pigment, whereas the primary electron donor is BChl *a* [8], thus the energy level is far lower in the donor; this is, however, not the case in *A. marina*.

Antenna pigments of the PS II are assigned to Chl *d*. Since the energy level of a primary electron donor is higher than that of its antenna pigment (Chl *d*), uphill energy transfer is a requisite for oxygen evolution. The quantum requirement for oxygen evolution was estimated to be the same for both the 715 nm and 695 nm lights [9]; thus, the uphill energy transfer from Chl *d* to Chl *a* must occur in the in vivo system, even though this has not yet been experimentally confirmed. The steady-state fluorescence properties of this alga were briefly reported by Schiller et al. [2]. We extensively analyzed the time-resolved fluorescence spectra at physiological and cryogenic temperatures [5]; however, a limitation of excitation wavelengths for the time-resolved spectroscopy precluded detailed resolution of the fluorescence properties. Thus, we attempted to measure the fluorescence spectra in the steady state by exciting various pigment species (Chl *a*, Chl *d*, and carotenoids), and successfully detected the occurrence of uphill energy transfer, a requisite for in vivo activity.

2. Materials and methods

A. marina was grown in an Erlenmeyer flask containing 500 ml K+ESM medium [10] under continuous incandescent light (20 μE/(m^2 s)) at 25°C. The medium was stirred with gentle air bubbling. Cells at the stationary-growth phase were harvested and used for measurements without treatment.

Absorption and fluorescence spectra were measured with a Hitachi 2010 spectrophotometer and a Hitachi 850 spectrofluorometer, respectively. For the fluorescence spectrum, cell density was adjusted to less than 3 μg/ml Chl. Measurements were carried out at 22°C and −196°C. For the low-temperature fluorescence spectroscopy, a home-made Dewar bottle and its container were used. Fluorescence was detected from the front surface. Polyethylene glycol (average molecular weight, 3000) was added to a cell suspension (15% final concentration) to obtain homogeneous ice at −196°C. Digitized spectral data were transferred to a microcomputer (HP 216) and processed; that is, the baseline was subtracted, the spectral sensitivity of the fluorometer was corrected for both emission and excitation spectra [11], as well as for the second derivative spectrum, using the method of Savitzky and Golay [12]. Deconvolution of fluorescence spectra was performed based on the least-squares method described earlier [13]. An ambiguity of the location of peaks was ±0.5 nm for absorption and fluorescence spectra.

3. Results

3.1. Steady-state fluorescence at −196°C

3.1.1. Difference in spectra due to difference in the excitation wavelength

An absorption spectrum of *A. marina* cells at 22°C is shown in Fig. 1A. A peak for the Qy transition of Chl *d* was located at 715 nm. This spectrum was significantly longer than any yet located in any other algae. The fluorescence spectra of intact *A. marina* cells at −196°C differed, depending on the pigments that have been sensitized (Fig. 2). Chl *d* excitation at 458 nm (Fig. 2A) caused the emission maximum to reach 736 nm, and a half-bandwidth at the half-maximum (HWHM) was almost the same for both sides of the peak or a little wide on the long-wavelength side. We assigned this component to PS II Chl *d*, based on time-resolved spectroscopy [5]. In addition, a single vibrational band was observed at 772 nm; however, the PS I emission detected at 758 nm by the time-resolved spectra was not observed in this spectrum due to its short lifetime (Mimuro et al., unpublished). Two minor peaks were located at 643 nm and 703 nm in the short-wavelength region of the maximum. The former may originate from phycobiliprotein [14], the latter from either Chl *d* or Chl *a*. After excitation at 435 nm, Chl *a* had absorbed a certain fraction of light but Chl *d* had absorbed the most. Under this condition, the main peak for Chl *d* was located at the same wavelength as that caused by Chl *d* excitation; however, relative intensities of minor peaks differed significantly (Fig. 2B). The 703 nm peak weakened, and a new band was observed at approx. 670 nm. A 643 nm band from phycobiliproteins was also observed. It is of interest to note that the excitation of carotenoids at 495 nm brought about a very different spectrum, especially for minor bands (Fig. 2C). In the wavelength region shorter than 700 nm, there was no apparent peak; the 703 nm band was no longer observed. The intensity of this band was high following Chl *d* excitation, moderate following 435 nm excitation, and apparently non-existent following carotenoid excitation. This suggests that its origin was most probably PS II Chl *d*; energy was not transferred from the carotenoids to this PS II Chl *d* at −196°C, suggesting specific localization in the antenna or reaction center complex(es). This is one of the features in the fluorescence properties of PS II.

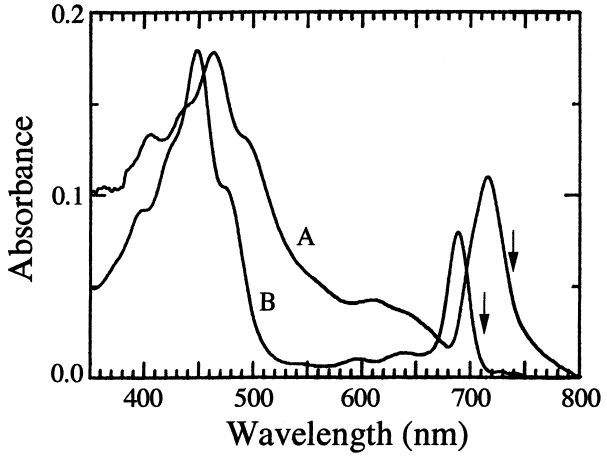

Fig. 1. Absorption spectra of (A) intact cells and (B) acetone extracts of *A. marina* at 22°C. In A, scattering light was partly removed, but not completely. Arrows show the excitation wavelengths for measurements of uphill energy transfer, that is, 710 nm for the cell extracts and 736 nm for intact cells, respectively.

3.1.2. Identification of spectral components by difference spectrum

Observed fluorescence spectra differed by their excitation wavelengths. Therefore, it is possible to use difference spectra to assign an origin of fluorescence. This was done after individual spectra were normalized to the maximum intensity (Fig. 2D). The difference spectrum between Chl *d* excitation and Chl *a* excitation (plus signs) gave one positive band at 704 nm and two negative bands at approx. 668 and 682 nm. The positive band was assigned to Chl *d* and the negative ones to Chl *a*. Parameters for individual curves were obtained by a simulation calculation using a Gaussian band shape. The peaks were resolved at 667.2 nm, 682.8 nm, and 703.9 nm, respectively. The 682.8 nm band was not necessarily clear in the spectrum (Fig. 2A,B); however, its presence was resolved by simulation. This component corresponded to that observed as being the delayed fluorescence at −196°C [5].

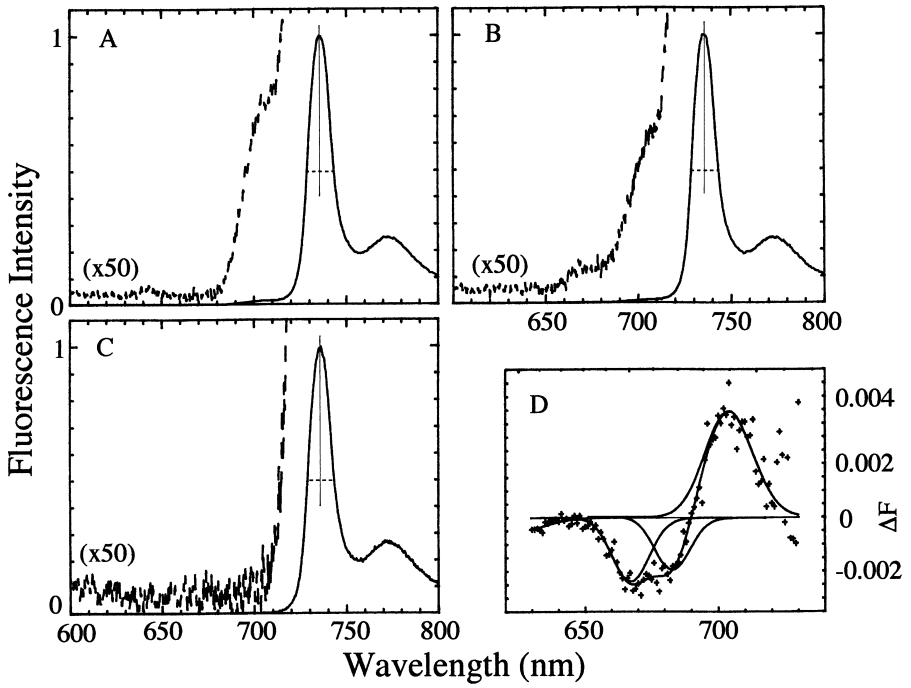

Fig. 2. Steady-state fluorescence spectra of intact cells of *A. marina* at −196°C. Spectrum excited (A) at 458 nm, (B) at 435 nm, and (C) at 495 nm. Dotted lines indicate those magnified up to 50 times. Spectral sensitivity of the apparatus was numerically corrected. Vertical lines indicate the location of the peak, and horizontal broken lines indicate the bandwidth at half the maximum of the peak. (D) Difference spectrum between A and B after normalization to the maximum intensity of individual spectra (plus signs) and simulated curves. A magnitude of difference was shown on the basis of original spectra (A,B).

3.2. Steady-state fluorescence at 22°C

3.2.1. Difference in spectra due to difference in the excitation wavelength

Fluorescence spectra at physiological temperature differed depending on excitation wavelengths (Fig. 3), essentially identical to the case at cryogenic temperature (Fig. 2). When Chl *d* was preferentially excited at 467 nm, the main emission was observed at 724 nm with an asymmetric bandwidth that was wider in the short-wavelength region of the peak (Fig. 3A). This clearly indicates the presence of a minor component(s) in the short-wavelength region of the peak, even though no clear trough or shoulder was resolved. Time-resolved spectroscopy showed that the main peak was assigned to PS II Chl *d*, and that the PS I emission was overlapped at wavelengths longer than 740 nm, even at physiological temperature [5]; however, this PS I band was not resolved by this spectrum. By the second derivative spectrum, three bands had been resolved at 709 nm, 716 nm, and 729 nm, in addition to the 724 nm main peak (data not shown). Upon excitation of Chl *a* at 435 nm (Fig. 3B), the observed spectrum was superimposable to that sensitized by Chl *d*. Difference registered only in the short-wavelength region of the peak; at least two bands registered at approx. 650 nm and 670 nm. The former came from phycobiliproteins, the latter, most probably from Chl *a*. The presence of these components was consistent with the observation at −196°C (Fig. 2A–C). When carotenoids (α-carotene and zeaxanthin) were excited at 500 nm (Fig. 3C), the spectral line shape of the main emission matched that caused by Chl *d* excitation. A minor but clear band was observed at 650 nm, coming from phycobiliproteins.

Upon addition of DCMU (10^{-5} M), fluorescence intensities increased 2.5-fold, on average, for the three excitation conditions (435 nm, 467 nm, and 500 nm); however, spectral patterns showed no difference from those derived without DCMU (data not shown).

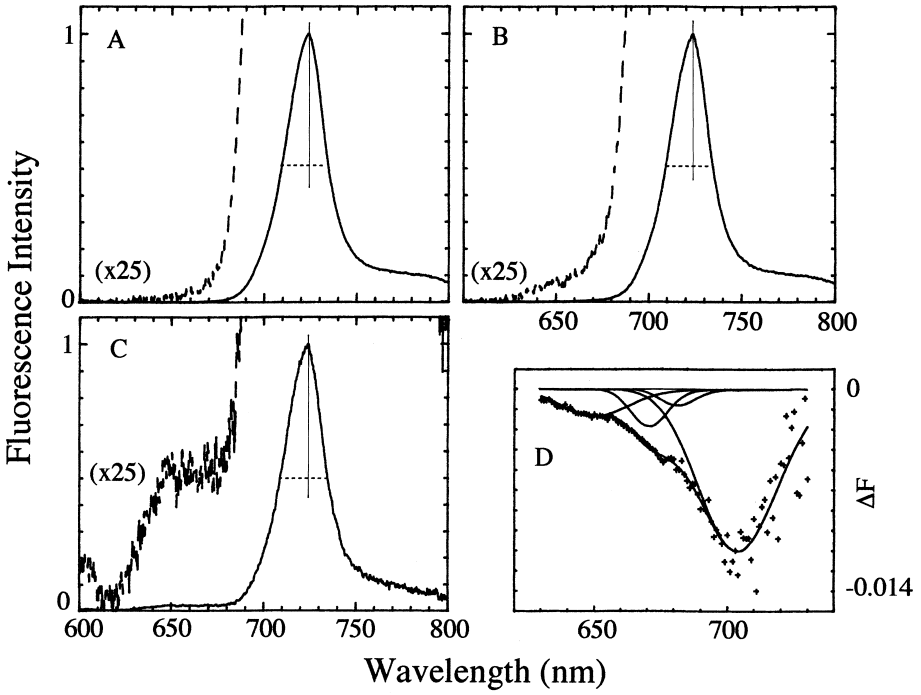

Fig. 3. Steady-state fluorescence spectra of intact cells of *A. marina* at 22°C. Spectra excited at (A) 467 nm, (B) 435 nm, and (C) 500 nm. Dotted lines indicate those magnified up to 25 times. Spectral sensitivity of the apparatus was numerically corrected. Vertical lines indicate a location of the peak, and horizontal broken lines indicate a bandwidth at half the maximum of the peak. (D) Difference spectrum between A and B after normalization to the maximum intensity of individual spectra (plus signs) and simulated curves. A magnitude of difference was shown on the basis of original spectra (A,B).

3.2.2. Identification of spectral components by difference spectrum

A presence of spectral component(s) was analyzed by difference spectra between Chl *d* excitation and Chl *a* excitation after normalization of the spectra (Fig. 3D). Four components were resolved: 650.0 nm, 670.7 nm, 681.2 nm, and 703.8 nm. Except for the emission from phycobiliproteins at 650.0 nm, the remaining three components correspond to those observed at −196°C (Fig. 2D), except that the sign of the 704 nm component was inverted. Thus, at physiological temperature, energy transfer between the 681 and 704 nm components must occur, and sensitization of Chl *d* induces uphill energy transfer, resulting in decreased fluorescence intensity for the 704 nm component. Since the energy difference between these two components at −196°C was larger than the thermal energy, substantial uphill energy transfer did not occur, resulting in a rise in the positive signal of the 704 nm band in the difference spectrum (Fig. 2D).

3.3. Uphill energy transfer at room temperature

An uphill energy transfer process was analyzed by fluorescence spectra sensitized at the red edge of the absorption spectra (see arrows in Fig. 1A). Fig. 4A (broken line) shows a fluorescence spectrum excited at 736 nm and observed in a wavelength region from 650 nm to 730 nm. The difference between this excitation wavelength and the absorption maximum of the cells was approx. 20 nm. It was not reasonable to assume that the 736 nm light was directly absorbed by Chl *a*, because Chl *a* content was only about 3% of the total Chl, and it was exclusively associated with PS II, showing the maximum at shorter than 680 nm [2]. We observed an abrupt increase in the intensity at 730 nm (Fig. 4A, asterisk), indicating scattering light. This was confirmed by measurement with a non-fluorescent, but scattering, material (data not shown). The observed fluorescence maximum was located at 725 nm, and the HWHM for the short-wavelength side of the maximum was 293

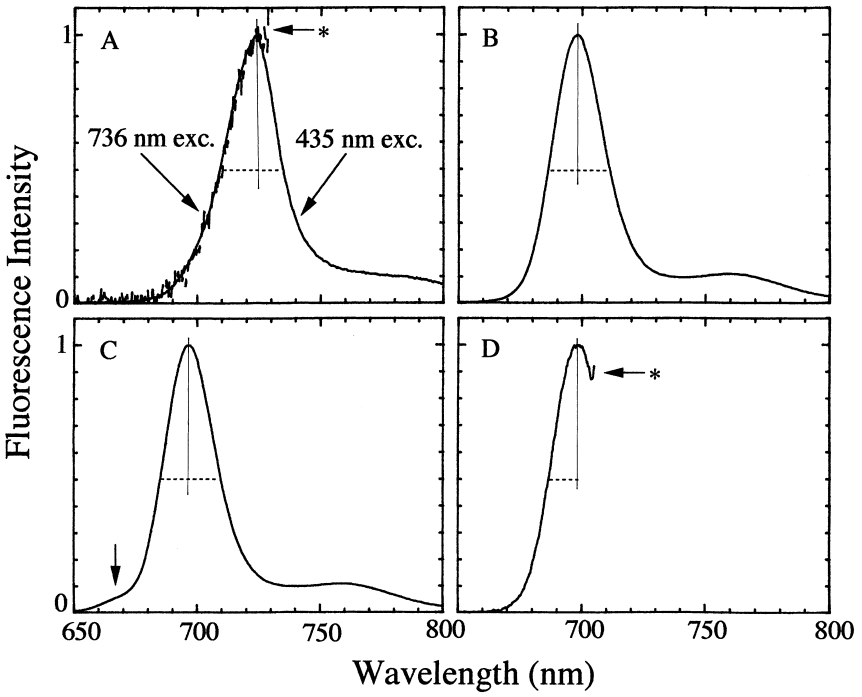

Fig. 4. Uphill energy transfer detected by fluorescence spectra. (A) Fluorescence spectrum of intact cells excited at 435 nm (full line) and at 736 nm (dotted line) at 22°C. (B,C) Spectra of acetone extracts of cells excited at 460 and 435 nm, respectively. An arrow in C shows an emission of Chl *a*. (D) Spectrum of the acetone extracts of cells excited at 710 nm. Asterisks indicate scattering light due to the excitation light, vertical lines indicate the location of the peak, and horizontal broken lines indicate a bandwidth at half the maximum of the peak.

cm^{-1}. The peak location was almost the same as that observed for the downhill energy flow (724 nm) as sensitized by Chl *a* at 435 nm (Fig. 4A, full line), and the HWHM was also identical to that of the downhill energy transfer (292 cm^{-1}). These results indicate the presence of emission band(s) in the short-wavelength region of the peak.

Fig. 4B and C show the fluorescence spectra of an acetone extract of the cells (see Fig. 1B for the absorption spectrum), where the chlorophylls and carotenoids in this solution were assigned a monomer form. Excitation at 465 nm (Fig. 4B) yielded a fluorescence peak at 699 nm, with a symmetric line shape. An HWHM that was almost the same on both sides or a little wider on the long-wavelength side was commonly observed for dyes in a monomer state. A magnitude of the HWHM was 240 cm^{-1} in the short-wavelength region. Following excitation at 435 nm (Fig. 4C), an additional band was observed at 666 nm that originated from either Chl *a* or Pheo *a*. Even under this condition, the main fluorescence band held a symmetric line shape. Upon excitation at 710 nm (a wavelength 20 nm longer than the absorption maximum), the maximum reached 698.5 nm, identical to that observed for Chl *d* and Chl *a* excitation (Fig. 4D). The HWHM in the short-wavelength region of the peak was 244 cm^{-1}, almost identical to that sensitized by the Soret band of Chl *d* (Fig. 4D). A band of Chl *a* was not observed following excitation of the red edge of the absorption spectrum. Thus, the resulting fluorescence spectrum demonstrates that a small fraction of monomer Chl *d* had absorbed the 710 nm light and then fluoresced directly from the first singlet excited state. Energy transfer from monomer Chl *d* to monomer Chl *a* did not occur in an organic solvent or else Chl *a* did not absorb the 710 nm light.

In the case of intact cells, the HWHM in the short-wavelength side of the peak in the spectrum sensitized on the red edge matched that measured in the spectrum sensitized at the Soret band of Chl *a* (Fig. 4A). This clearly indicates the presence of fluorescence component(s) in a wavelength region that is shorter than the maximum; those might be the three

components (671, 681 and 704 nm bands) shown by the deconvolution of the difference spectrum (Fig. 3D), which is the case with a downhill energy flow. It was expected that absorption of the red edge light (at 736 nm) by a specific Chl *d* component and the lack of uphill energy transfer from that same Chl *d* would give rise to a fluorescence band with a symmetry line shape, as indicated in the spectrum of acetone extracts (Fig. 4B). Since the absorption form of Chl *a* is reported only at 670 nm [2], direct absorption of Chl *a* cannot occur. Identical HWHMs of fluorescence spectra for both Soret band and red edge excitations clearly indicate the occurrence of uphill energy transfer from Chl *d* to Chl *a* in this alga, and are essential requisites for in vivo activity.

4. Discussion

4.1. Molecular organization of pigments in an individual PS

A. marina is an oxygenic photosynthetic prokaryote as well as cyanobacteria; thus, its essential machinery for photosynthesis is expected to be the same as that of cyanobacteria. In the PS I RC, the primary electron donor is identified to be Chl *d* [4], and this is the only exception to the oxygenic photosynthetic organisms that have been studied to date. In the PS II RC, the primary electron donor is identified to be Chl *a* [5], with accessory Chl *a* and Pheo *a*; this is essentially identical to other oxygenic photosynthetic organisms. However, because the antenna pigment is Chl *d*, whose energy level is lower than that of Chl *a*, the molecular organization of PS II is not necessarily identical to that of other oxygenic photosynthetic organisms.

The main emission of *A. marina* was observed at 724 nm at physiological temperature (Fig. 3) and at 735 nm at −196°C (Fig. 2), both coming from PS II Chl *d*. In addition, the fluorescence spectra in this study show three components in the PS II emission, resolving at 671 nm, 681 nm, and 704 nm at 22°C (Fig. 3D). The first two are from Chl *a* or Pheo *a*, the third from Chl *d*. These three were not sensitized by carotenoids (α-carotene and zeaxanthin) (Fig. 2C). This might be realized by spatial separation from carotenoid molecules. Since the main PS II antenna, Chl *d*, is sensitized by carotenoids at physiological temperature (Fig. 3C), we assigned the 703 nm Chl *d* emission to a dead end in PS II; the most probable localization is in or near the PS II RC complex. At physiological temperature, an energy exchange is possible between the 704 nm component and the 681 nm component; however, this is interrupted at −196°C, as shown by the difference spectra (Fig. 3D and 2D). It is generally accepted that PS II RC consists of four Chl *a* and two Pheo *a* molecules [15]; however, if PS II RC consists of six Chl *a* and two Pheo *a* molecules [16], the additional two Chl molecules in *A. marina* might be Chl *d*, with an energy level at 703 nm, suggesting a strategy for the evolutionary development of the PS II RC (see [17]). The 695 nm component found in the time-resolved fluorescence spectra at −196°C [5] was not detected in this study. This component was responsible for the DF, thus the fluorescence yield was very low, leading to an undetectable component in the steady-state spectra.

4.2. Uphill energy transfer in the pigment system of A. marina

An uphill energy transfer from Chl *d* to Chl *a* was clearly shown in this study. The energy difference between the components was estimated to be 851 cm^{-1} on the basis of two emission bands at 682 and 724 nm. This magnitude corresponds to that reported for the uphill energy transfer from Chl *a* to phycocyanin (785 cm^{-1}) in two cyanobacteria, *Anacystis nidulans* (*Synechococcus* sp. PCC 7102) [18] and *Anabaena variabilis* [19]. In the case of *Spirulina platensis* [20], an uphill energy transfer was reported also for PS I. In this study, we showed that the fluorescence spectrum sensitized by the red edge of the absorption could be superimposed on that sensitized by the Soret band of Chl *a* (Fig. 4A), a direct indication for an equilibrium of energy migration in the antenna components in PS II. This observation is consistent with the evidence showing that quantum requirements for oxygen evolution of the 695 nm and 715 nm lights are identical [4].

Energy transfer between donors and acceptors is a reversible process whose probability is determined by the matching of energy levels, usually shown by the spectral overlap. In this study, we resolved fluores-

cence components even though we did not know their corresponding absorption spectra. As shown in Fig. 3D, the spectral overlap between the 703 nm and the 670 nm components was significant, the latter of which could be a putative absorption band of the energy acceptor (the 681 nm component) in the uphill energy transfer. The main factor is the wide bandwidth of the 704 nm component. The above information, however, is not necessarily enough to understand the process of uphill energy transfer in the PS II of *A. marina*. Chl *a* was sensitized by Chl *d* at physiological temperature (Fig. 4A); however, DF of the Chl *a* was not transferred to Chl *d* at −196°C (Fig. 5 in [5]), but selectively observed only at 681 and 695 nm. This phenomenon suggests specific locations of respective pigments in PS II. In the case of spinach chloroplasts, DF at −196°C was resolved on the two PS II bands at 685 and 695 nm [21], indicating the similarity of emission properties of PS II core between spinach chloroplasts and *A. marina*. Information regarding the pigment system in the PS II core complex is, however, required in further study.

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