Biochimica et Biophysica Acta, 767 (1984) 335–344
Elsevier

BBA 41629

LOW-TEMPERATURE OPTICAL PROPERTIES AND PIGMENT ORGANIZATION OF THE B875 LIGHT-HARVESTING BACTERIOCHLOROPHYLL-PROTEIN COMPLEX OF PURPLE PHOTOSYNTHETIC BACTERIA

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(Received June 7th, 1984)

Key words: Bacterial photosynthesis; Chlorophyll-protein complex; Light-harvesting complex; Circular dichroism; Fluorescence polarization; (Rps. sphaeroides)

Optical and structural properties of the B875 light-harvesting complex of purple bacteria were examined by measurements of low-temperature circular dichroism (CD) and excitation spectra of fluorescence polarization. In the B875 complex isolated from wild-type *Rhodopseudomonas sphaeroides*, fluorescence polarization increased steeply across the long-wavelength Q_y bacteriochlorophyll *a* (BChl) absorption band at both 4 and approx. 300 K. With the native complex in the photosynthetic membranes of *Rhodospirillum rubrum* and *Rps. sphaeroides* wild-type and R26-carotenoidless strains, this significant increase in polarization from 0.12 to 0.40 was only observed at low temperature. A polarization of -0.2 was observed upon excitation in the Q_x BChl band. The results indicate that about 15% of the BChl molecules in the complex absorb at wavelengths about 12 nm longer than the other BChls. All BChls have approximately the same orientation with their Q_y transition dipoles essentially parallel and their Q_x transitions perpendicular to the plane of the membrane. At low temperature, energy transfer to the long-wavelength BChls is irreversible, yielding a high degree of polarization upon direct excitation, whereas at room temperature a partial depolarization of fluorescence by energy transfer between different subunits occurs in the membrane, but not in the isolated complex. CD spectra appear to reflect the two spectral forms of B875 BChl in *Rps. sphaeroides* membranes. They also reveal structural differences between the complexes of *Rps. sphaeroides* and *Rhs. rubrum*, in both BChl and carotenoid regions. The CD spectrum of isolated B875 indicates that the interactions between the BChls but not the carotenoids are altered upon isolation.

Introduction

Two different types of pigment-protein complexes can be isolated from the photosynthetic membranes (chromatophores) of purple bacteria; these consist of light-harvesting complexes and reaction centers. *Rhodopseudomonas sphaeroides* and related species contain two different antenna complexes designated B800-850 and B875 [1,2]. B800-850 is usually present in larger amounts than B875 and is thought to form large 'lakes' in which smaller assemblies of B875, each containing one or several reaction center complexes, are embedded

Abbreviations: BChl, bacteriochlorophyll *a*, B800-850, B855, B870, B875, B880, antenna complexes identified by their near-infrared absorption maxima; BPh, bacteriopheophytin *a*; CD, circular dichroism.

[3,4]. Of the two antenna complexes, the B800-850 complex can be most easily isolated and it has been characterized extensively [5–7], whereas much less is known about B875. Only recently an isolation procedure has been described [8], yielding a complex which appeared to have retained most of its spectral properties [9]. The fluorescence polarization of the isolated B875 complex, which showed a sharp increase across the absorption band at 875 nm and the form of the near-infrared band in the CD spectrum, did not make clear whether the isolated complex had remained structurally intact [9]. Data on the fluorescence polarization and the CD of the native B875 complex (i.e., in the intact membrane of *Rps. sphaeroides* wild-type) have not been reported and the relation to the 'B870' complexes in the R26 mutant and the B880 complex of other purple bacteria is still not clear [1,10–12].

The protein moiety of B875 consists of two different subunits, the α- and β-apoproteins, with molecular weights of about 5000–7000 each [12–15]. Recently, the primary structures of these polypeptides have been determined [13–15]. These appeared to be homologous to those of the polypeptides of the B800-850 complex, both containing a central hydrophobic, presumably α-helical stretch and N- and C-terminal polar regions. As in B800–850, the α-helices are thought to traverse the membrane and each contain the conserved histidine residues believed to be involved in binding the BChl molecules. In the *Rps. sphaeroides* complex, each polypeptide probably binds a carotenoid molecule, yielding a BChl/carotenoid ratio of 1 [8]. In the B880 complex of *Rhodospirillum rubrum*, only one carotenoid per two BChl 880 is found [11,12].

In order to investigate further the spectral properties of the B875 complex, we studied the absorption, fluorescence polarization and CD properties of the isolated complex at low temperature and compared these to spectra of the native complex in the chromatophore membrane and homologous complexes from different strains and species of purple bacteria.

Materials and Methods

Cells of *Rps. sphaeroides* wild-type (NCIB 8253) and of the carotenoidless mutant R26 (kindly provided by R.J. Cogdell) were grown as described in Ref. 8. The B875 pigment-protein complex and the LM reaction center particle were isolated using lithium dodecyl sulfate/polyacrylamide gel electrophoresis [8]. Intracytoplasmic membrane and nascent invaginations of the cytoplasmic membrane of *Rps. sphaeroides* were isolated as chromatophores and 'upper pigmented band', respectively, by sucrose density gradient centrifugation as described by Niederman et al. [16]. *Rhs. rubrum* chromatophores were isolated by differential centrifugation.

Absorption, fluorescence and fluorescence polarization spectra were recorded on a single-beam spectrophotometer described in Ref. 17. CD spectra were measured as in Ref. 18. The absorbance of the samples was approx. 1.0 at the near-infrared maximum. For low-temperature experiments, 55% glycerol was added to prevent crystallization.

Results

Fluorescence polarization

The low-temperature absorption spectrum of the B875 complex isolated from *Rps. sphaeroides* 8253 is shown in Fig. 1. Apart from the sharpening of the 875-nm band and the shift of this band from 875 to 889 nm, the spectrum is similar to the room-temperature spectrum published before [8].

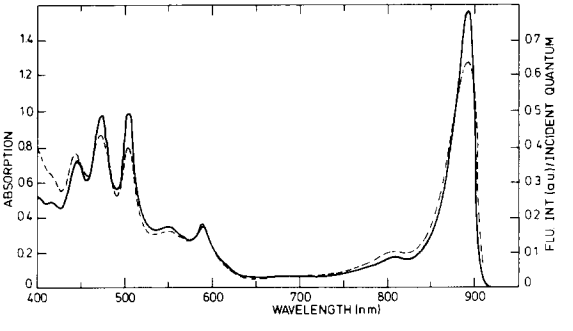

Fig. 1. Low-temperature (4 K) absorption (———, left-hand scale) and fluorescence excitation (— — —, right-hand scale) spectra of the isolated B875 antenna complex of *Rps. sphaeroides*. Detection at 915 nm. The bandwidth of the monochromator was 0.5 and 4.0 nm for the absorption and excitation spectrum, respectively, which may account for the difference in near-infrared bandwidth in the excitation spectrum.

In the visible region, the Q_x band is at 589 nm and the carotenoid bands appear at 444, 472 and 504 nm. The excitation spectrum of the fluorescence, detected at 915 nm, is also shown in Fig. 1 (dashed curve). The efficiency of energy transfer from carotenoid to BChl was determined by comparing the ratio of either the 505 and 589 nm bands or of the 505 and the 889 nm bands. For the intensity of the near-infrared band, the area under the band was taken. Both methods yielded an efficiency of 70% in agreement with the results of Hunter et al. [19].

Fig. 2 shows the polarized excitation spectra (detection wavelength 920 nm) of the B875 complex. In agreement with earlier results at room temperature [9], the component polarized parallel to the polarization of the excitation beam peaks at longer wavelength than the perpendicular component. As a consequence, the polarization increases steeply across the band (Fig. 2, dotted line) from a value of 0.11 at 870 to 0.35 at 900 nm, indicating that the B875 band is not homogeneous. The polarization of the Q_x band was -0.17, which is somewhat higher than the value reported at 300 K [9].

To compare the optical properties of isolated B875 with those of native complexes, membranes were isolated from B875-enriched *Rps. sphaeroides* 8253 and from the R26 mutant and *Rhs. rubrum* which contain only a 'B875-type' antenna complex. Growth of *Rps. sphaeroides* 8253 at very high light intensity yielded chromatophores and an upper pigmented band with a strongly enhanced B875 to B800-850 ratio (Fig. 3) but with constant B875 per reaction center [20]. The latter membrane fraction forms a band near the top of sucrose gradients after centrifugation of disrupted cells and is thought to arise from membranes which are in an early phase of photosynthetic membrane development [16,21]. The 4 K absorption spectrum, given in Fig. 3, clearly shows the increased amounts of B875; the B875/B800-850 molar ratios, calculated from 300 K spectra with the extinction coefficients given by Clayton and Clayton [22], were 2.2 for the chromatophores and 4.1 for the upper pigmented fraction. Thus, the latter was enriched 1.8-fold in B875 in comparison to chromatophores, in agreement with the possibility that the B800-850 complex is incorporated into the membrane at a later phase of photosynthetic membrane development [21].

Fig. 4 gives the low-temperature absorption spectrum of the R26 carotenoidless mutant of *Rps. sphaeroides*. This strain contains only a 'B870' antenna in contrast to the strain of R26 that is most often used which also contains a 'B855' antenna complex; the latter is probably a revertant of the original R26 strain and has been designated R26.1 (Ref. 23). The near-infrared absorption maximum is near 884 nm and contributions by reaction center BChl at 805 and BPh at 760, 545 and 530 nm are also detectable. The 4 K absorption spectrum of *Rhs. rubrum* is also presented in Fig. 4. It shows a band in the near-infrared at 895 nm, due

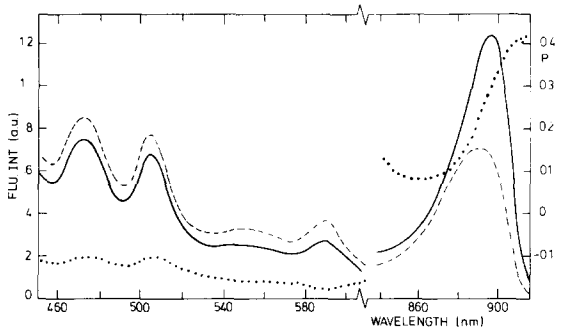

Fig. 2. Excitation spectra (4 K) of fluorescence polarized either parallel (———) or perpendicular (– – –) to the polarization of the excitation beam of the isolated B875 complex of *Rps. sphaeroides*, detected at 920 nm. The spectrum of the degree of polarization, $p = (I_{\parallel} - I_{\perp})/(I_{\parallel} + I_{\perp})$, is also shown (dots, right hand scale).

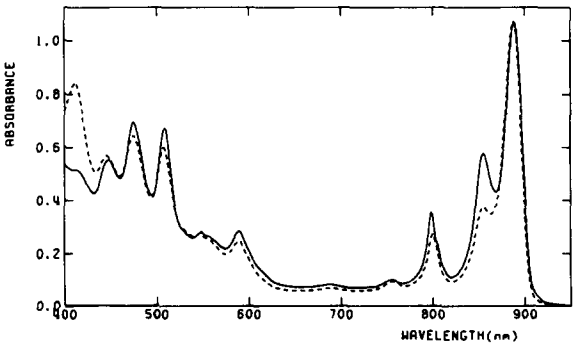

Fig. 3. Absorption spectra, recorded at 4 K of chromatophores (———) and upper pigmented band (— — —) from *Rps. sphaeroides* 8253 grown at high light intensity (32000 lx).

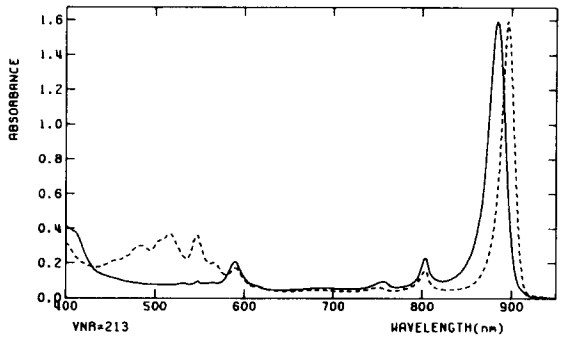

Fig. 4. Low-temperature absorption spectra (4 K) of chromatophores of *Rps. sphaeroides* R26 (———) and *Rhs. rubrum* (— — —).

to the B880 complex and bands of the reaction center pigments at 804 and 752 nm.

Fluorescence polarization spectra of chromatophores and the upper pigmented band are given in Fig. 5. As in the isolated complex, the component polarized parallel to the polarization of the excitation beam peaks at a longer wavelength than the perpendicular component. The degree of polarization, p, increases from 0.11 at 880 nm to 0.33 at 900 nm in chromatophores and from 0.12 (880 nm) to 0.42 (910 nm) in the upper pigmented band (Fig. 5). Apparently, the proposed heterogeneity of the B875 absorption band is a property of the native complex and is not caused by the isolation procedure. The polarization of the BChl 850 band was about 0.11, both upon detection of the B850 emission at 880 nm (not shown) and upon detection of the B875 emission at 915 nm (Fig. 5). This value is about the same as the value found for the isolated B800-850 complex which has been shown to be the intrinsic value for the basic unit of this complex [7]. Apparently, the polarization of the isolated B800-850 complex is the same as of the native complex in chromatophores, and energy transfer from the B800-850 complex to B875 does not induce a further depolarization of the fluorescence. The polarization of the Q_x band was -0.20, both in the chromatophores and the upper pigmented band. At the short-wave side of the Q_x band, the polarization tended to a more positive value due to the Q_x band of BChl 800, which peaks at somewhat shorter wavelength and has a positive polarization [7]. The carotenoid bands show a small negative polarization.

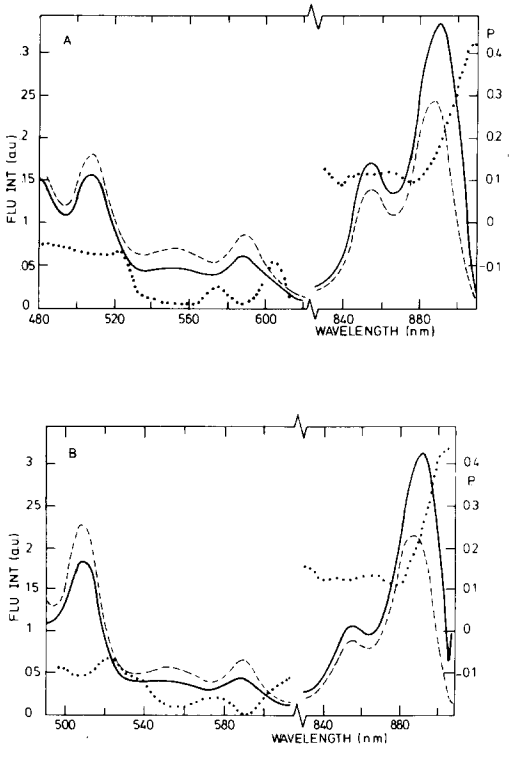

Fig. 5. Polarized excitation and polarization spectra recorded at 4 K for chromatophores (A) and upper pigmented band (B) of *Rps. sphaeroides* 8253. For details see Fig. 2.

The polarization spectra of chromatophores of *Rps. sphaeroides* R26 and of *Rhs. rubrum* are given in Fig. 6A. Both spectra show the same strong increase across the B875 absorption band as do the isolated B875 and the B875 complex in chromatophores and upper pigmented band of *Rps. sphaeroides* 8253. The value of the polarization increased from about 0.10 to 0.4 in all chromatophores studied. The polarization of the Q_x band was -0.21 for both preparations (not shown).

Fig. 6B shows the polarization spectrum of chromatophores of *Rps. sphaeroides* (8253 and R26) and of *Rhs. rubrum,* recorded at room temperature. In contrast to the results obtained with the isolated complex [9], the polarization was almost constant over the long-wavelength band, indicating that energy transfer between different BChl molecules tends to smooth out differences in polarization between pigments absorbing at different wavelengths.

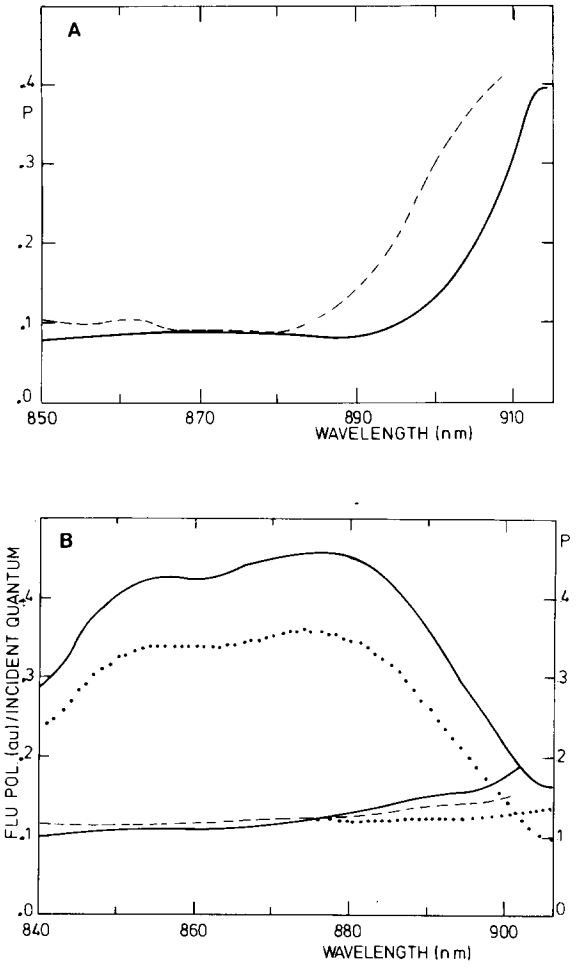

Fig. 6. (A) Polarization spectra of the fluorescence, recorded at 4 K of chromatophores of *Rhs. rubrum* (———) and *Rps. sphaeroides* R26 (– – —). (B) Excitation spectra (left-hand scale) of the room-temperature emission polarized parallel (———) or perpendicular (·····) to the polarization of the excitation beam of chromatophores of *Rps. sphaeroides* 8253. Right-hand scale: polarization spectra of chromatophores of *Rps. sphaeroides* (———), R26 (— — —) and *Rhs. rubrum* (·····).

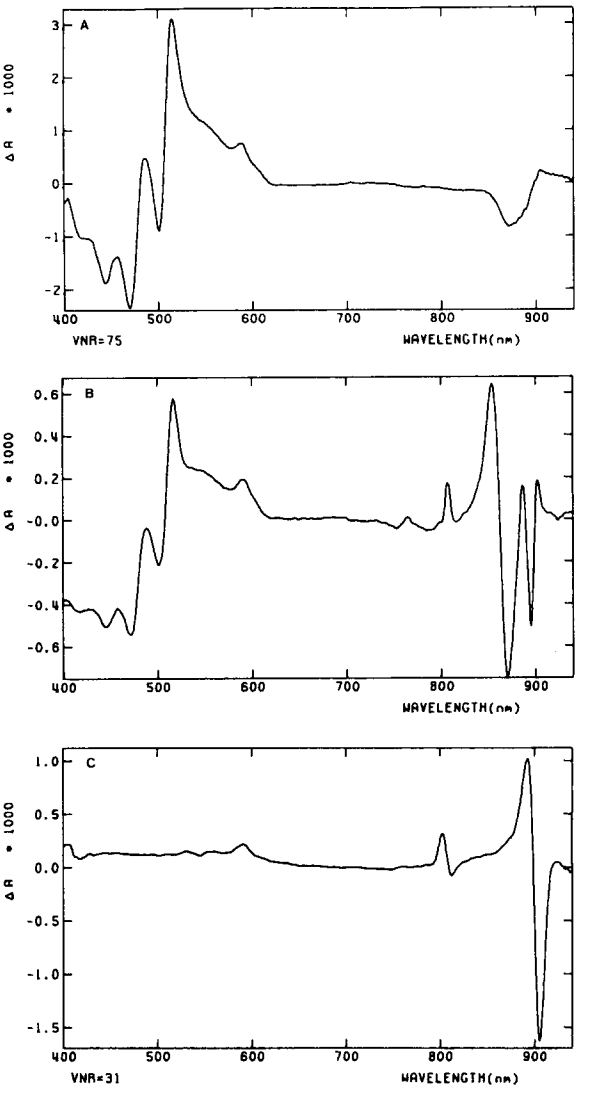

Fig. 7. CD spectra ($A_L - A_R$) of (A), isolated B875 complex of *Rps. sphaeroides* 8253 recorded at 77 K; (B), chromatophores of *Rps. sphaeroides* 8253 recorded at 4 K; (C) chromatophores of *Rhs. rubrum* recorded at 77 K.

CD spectra

The CD spectrum of the B875 complex isolated from *Rps. sphaeroides* 8253 recorded at 77 K is shown in Fig. 7. The spectrum is in general agreement with the room-temperature spectrum published before [9], with a rather broad negative band at 878 nm and a small positive one at 905 nm. In addition, a weak shoulder on the long-wave side of the 878 nm band is present in the low-temperature spectrum. In the visible region, the spectrum shows the characteristic carotenoid bands observed earlier at room temperature [9].

The low-temperature (4 K) CD spectrum of chromatophores obtained from *Rps. sphaeroides* grown at high light intensity is also given in Fig. 7. In the near-infrared, the spectrum is rather complicated and contains contributions from the reaction center, visible as the positive band at 805 nm, from the B800-850 complex centered around 864

nm, and from the B875 complex, at longer wavelengths. The CD signal that can be attributed to B875 does not resemble that of the isolated complex and displays a sharp negative signal at 896 nm and two smaller positive bands at 887 and 904 nm. The negative band lies 7 nm more to the red and is much narrower than the absorption band.

In order to examine the contributions of the reaction center to the spectrum, we also measured the CD spectrum of the LM reaction center particle, obtained by lithium dodecyl sulfate/polyacrylamide gel electrophoresis [8]. The spectrum is given in Fig. 8 and is generally similar to the spectrum of reaction center preparations of *Rps. sphaeroides* at room temperature [24]. It shows bands at 760 nm (negative) due to BPh, at 805 nm (positive), 815 nm (negative) and a broad positive band at 895 nm due to P870. From the spectrum it can be seen that above 830 nm, the contribution of the reaction center to the CD signal of chromatophores must be very small (see Fig. 7). Therefore, the fact that the CD signal around 864 nm in *Rps. sphaeroides* chromatophores is nonconservative (Fig. 7), in contrast to that of chromatophores with a low ratio of B875 to B800-850 (not shown), must be explained by interaction between BChl 850 and BChl 875 giving rise to a negative band at about 870 nm. It is also clear that the isolated B875 complex (Fig. 7) did not contain any significant amount of reaction center. The CD spectrum of the upper pigmented band fraction was similar to that of the chromatophores, except for a somewhat higher contribution of the reaction center bands and a somewhat more intense band at 904 nm (not shown).

Fig. 8 also shows the 77 K CD spectrum of chromatophores of the R26 mutant of *Rps. sphaeroides*. The spectrum of the B870 is very similar to that of B875 of the wild-type, with a central negative band at 889 nm and two positive bands of variable intensity. These bands peak at somewhat shorter wavelengths than those of the wild-type. The position of the central band, however, was again clearly at a longer wavelength than that of the absorption band, which peaks at 884 nm at this temperature (not shown). Note the strong contribution of the reaction center at 804–816 nm. The CD spectrum of the chromatophores of *Rhs. rubrum* is also given in Fig. 7. The

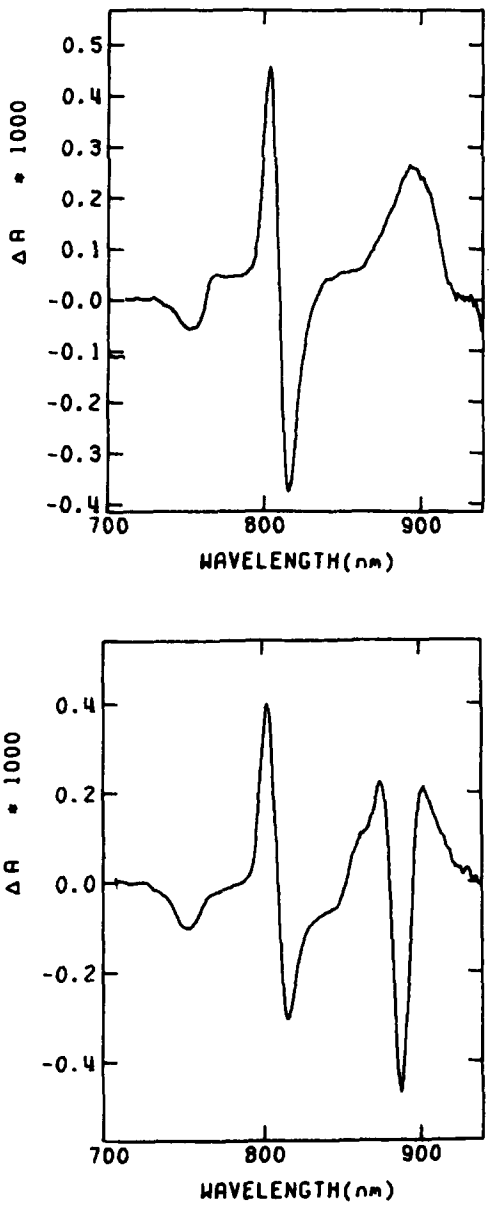

Fig. 8. CD spectrum of (A) LM reaction center particle recorded at 4 K; and (B) chromatophores of *Rps. sphaeroides* R26 recorded at 77 K.

CD spectrum of the B880 complex of this species differs from that of *Rps. sphaeroides* and shows a positive band at 894 nm and a negative one at 906 nm. In the visible region, the carotenoid bands are almost absent in the CD spectrum.

Discussion

One of the aims of the present study was to compare the low-temperature optical properties of the isolated B875 complex with those of native B875 from *Rps. sphaeroides* with B880 of *Rhs. rubrum*. The most striking property of the complexes in all these cases is the heterogeneity which is apparent across the near-infrared absorption band in the low-temperature fluorescence polarization spectrum.

To explain the observed data, we assume the presence of a small component in the B875 and B880 complexes absorbing at lower wavelengths than the remaining BChls. We designate this pigment BChl 896 according to its estimated maximum at 4 K in *Rps. sphaeroides* R26 (see below). At room temperature, the absorption will be at a correspondingly shorter wavelength.

In the isolated B875, which has been shown to consist of small units of about six connected BChl 875 molecules (Ref. 25; Pennoyer, J.D., unpublished data) and is proposed to form a hexameric unit, the increase of the polarization is present both at room temperature and at 4 K. In the membranes, however, the polarization increase across the absorption band is absent at room temperature. This indicates that BChl 896 forms an integral part of the antenna complex and that efficient energy transfer between BChl 875 and BChl 896 occurs. Thus, one may expect that at low temperature, all emission will originate from BChl 896, analogous to what is observed in the BChl *a* protein of green bacteria [17], and energy transfer from BChl 875 to BChl 896 will be irreversible. At room temperature, where the Boltzmann energy (kT) is large compared to the difference in energy levels, a thermal equilibrium exists between the two spectral forms of BChl and most of the emission will originate from BChl 875.

The *p*-value of 0.12 found at the short-wave side of the B875 absorption band in all the complexes studied (Figs. 2, 5 and 6), both at room temperature and at 4 K, indicates that the Q_y transition moments of the BChl 875 molecules and also of the long-wavelength component, BChl 896, lie approximately in one plane. By analogy to the B800-850 complex [7] and in agreement with the linear dichroism spectra of chromatophores [5,26], we propose that this plane is defined by the histidines of the apoproteins of the complex, and is parallel to the membrane plane. It follows from the negative value of the polarization in the Q_x band that the Q_x transitions must be approximately perpendicular to this plane. At 4 K, emission excited by light quanta absorbed by BChl 875 will be depolarized by energy transfer among the BChl 875 molecules in the complex and to BChl 896, yielding a *p*-value which is close to the theoretical value of 0.13 for a circularly degenerate system. However, quanta absorbed directly by BChl 896 will give rise to a strong polarization of the emission because at 4 K energy transfer back to BChl 875 does not occur.

We fitted the low-temperature absorption and polarization spectra with two gaussian components of variable bandwidth and position, assuming that all the emission originates from the long-wave component which has a polarization of 0.13 or 0.42 when quanta are absorbed by the short- or the long-wave components, respectively. The best fit was obtained by two components 12 nm apart with the same bandwidth of 16 nm and with a ratio of about 6 to 7 in amplitude. The asymmetry of the absorption bands on the short wave-side was disregarded. Fig. 9 shows the results obtained of *Rps. sphaeroides* R26. The same result was obtained for *Rhs. rubrum* (not shown). If it is assumed that the difference in the peak positions is not changed at room temperature, then 60–70% of the emission will come from BChl 875, independent of the excitation wavelength. The polarization of this emission will be low (0.13). The emission of BChl 896 upon excitation in the BChl 896 absorption band, however, will be high if no energy transfer occurs between the different units of about 6 BChl 875 molecules, as is apparently the case in the isolated complex. In the membrane, energy transfer among a large number of B875 complexes occurs [25] and this causes depolarization of the fluorescence to a constant value, independent of the wavelength of excitation.

A heterogeneity of the B880 complex of *Rhs. rubrum* has been suggested by Borisov et al. [27] and Gomez et al. [28,29]. Borisov et al. suggested that a special long-wave antenna complex, B905, exists that connects the B880 antenna with the reaction center. In their view, even at room tem-

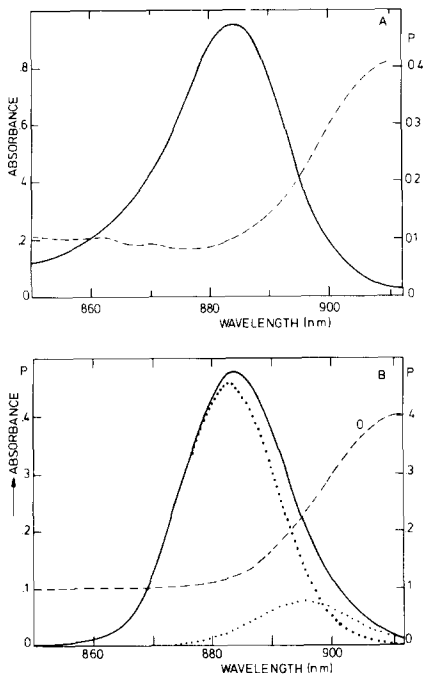

Fig. 9. Measured (A) and simulated (B) absorption (———) and fluorescence polarization spectra (— — —) of chromatophores of *Rps. sphaeroides* R26 at 4 K.

perature all the excitations will be rapidly localized on B905, from which the fluorescence is emitted. The absorption band of B905 was rather narrow (about 15 nm at 300 K) and its oscillator strength corresponded to 3–5 BChl molecules per reaction center. Neither the proposed localization of the excitations on B905 nor the narrow bandwidth agree quantitatively with the fluorescence emission and polarization data reported here. Gomez et al. [28], on the basis of the fourth derivative absorption spectrum at 300 and 77 K, proposed that the B880 antenna of *Rhs. rubrum* contains at least one other band, at 890 nm. They suggested that about 30% of the antenna BChl belongs to this special long-wave antenna which is also thought to exhibit an ESR signal at a *g*-value of 2.0025 upon dark oxidation [29]. Although their estimate of the number of BChl 890 molecules is rather large, their proposal in principle agrees with the conclusions from our work. This heterogeneity in the *Rhs. rubrum* antenna was also interpreted to reflect the existence of a second pigment-protein complex [27–29] but this is neither in accord with our model for B875 pigment organization presented above, nor with the presence of only two B875 polypeptides in isolated antenna complexes [8,12,15].

The fluorescence polarization of isolated B875 upon excitation in the main absorption peak (Fig. 2) is the same as that observed in the membrane (Fig. 5), where energy transfer among a large number of B875 complexes occurs. This indicates a very regular arrangement of the B875 complexes in the membrane. The same conclusion may be drawn for the B800-850 complex. The polarization of fluorescence was approximately the same upon excitation in the BChl 850 absorption band as upon excitation in BChl 875 in chromatophores of *Rps. sphaeroides* (Fig. 5). This indicates that the Q_y transitions of these BChls lie in the same plane, which is approximately parallel to the membrane [7] in agreement with the conclusion obtained above.

The CD spectra of Figs. 7 and 8, reveal clear differences in pigment interaction and structure of B875 in *Rps. sphaeroides* (strains 8253 and R26) and of B880 in *Rhs. rubrum*. The *Rps. sphaeroides* complex shows a negative band flanked by two equally strong positive bands in the near-infrared region which can be thought to be composed of two conservative CD signals, of opposite chirality. Explanation by a trimer-exciton split seems less likely because in that case the location of the long-wave CD spectrum does not match that of either of the two component absorption bands. The short-wave signal, centered at 883 nm in R26, might be mainly due to interaction between the BChl 875 molecules within the hexameric unit, whereas the other signal centered at 897 nm may reflect interactions between BChl 896 molecules from different units, or between BChl 896 and the other BChls.

As no CD signal is expected from interacting molecules when their transition moments lie in one plane, one has to assume that the Q_y transition moments of the BChl 875 molecules are not exactly in one plane. The molecules may be arranged in such a way that they form a one-turn helix. It should be noted that the intensity of the CD signals is weaker than those of the B800-850 or the reaction center complex as can be seen from the

spectra of Figs. 7 and 8. The CD spectrum in the visible region of the wild-type strain indicates fairly strong interaction between the carotenoid (spheroidene) molecules. Such interaction was also observed in the B800-850 complex [9]. The near-infrared CD spectrum of B875 from the wild-type strain and from the carotenoidless mutant R26 are very similar, which indicates that a contribution due to interaction beteen carotenoid and BChl in the CD spectrum in this region can only be small. Nevertheless, the distance between carotenoid and BChl 875 must be close in view of the rather high efficiency of energy transfer.

The CD spectrum of B880 of *Rhs. rubrum* shows a strong signal with a positive peak at 894 and negative peak at 906 nm, similar to that observed earlier at room temperature [24], which may be mainly due to B896. Note that the chirality is opposite to that of the long-wave CD band of *Rps. sphaeroides* B875. In the carotenoid region in *Rhs. rubrum,* the CD signals were very weak, indicating that carotenoid interaction is almost absent. The low efficiency of energy transfer from carotenoid to BChl of only 30% in *Rhs. rubrum* also indicates a different structure for the B880 complex of this species.

Although the absorption and fluorescence polarization spectra of the isolated B875 from *Rps. sphaeroides* were similar to those of the native complex, the CD spectrum in the near-infrared region was strongly altered and showed a weak broad negative band centered at 878 nm at 77 K. This either indicates a structural change upon isolation or that the much stronger and quite different CD signals observed in the native complex mainly reflect interaction between BChls belonging to different units.

Acknowledgements

This work was supported by the Netherlands Organization for the Advancement of Pure Research (ZWO) via the Foundations for Biophysics and for Chemical Research (SON), by U.S. National Science Foundation grants PCM79-03665 and PCM82-09761 and by a Predoctoral Fellowship award to J.D.P. from the Charles and Johanna Busch Memorial Fund Award to the Rutgers Bureau of Biological Research.

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