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ENERGY TRANSFER IN THE B800-850-CAROTENOID LIGHT-HARVESTING COMPLEX OF VARIOUS MUTANTS OF *RHODOPSEUDOMONAS SPHAEROIDES* AND OF *RHODOPSEUDOMONAS CAPSULATA*

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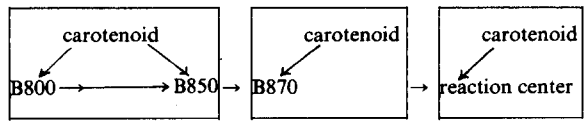
Key words: Light-harvesting complex; Energy transfer; Bacterial photosynthesis; Carotenoid; (Rps. sphaeroides, Rps. capsulata)

Emission and absorption spectra in the temperature range 4–300 K have been obtained for bacteriochlorophyll light-harvesting complexes (B800-850 complexes) from several mutants of *Rhodopseudomonas sphaeroides* and a nonphotosynthetic mutant of *Rhodopseudomonas capsulata*. The energy-transfer properties of these complexes were remarkably similar despite differences in carotenoid composition. Between 300 and 200 K the excitation densities in B800 and B850 are in thermal equilibrium, indicating rapid energy transfer from B800 to B850 and vice versa. The temperature dependence of the ratio of the B800 and B850 emission yields allows the determination of the ratio of the number of B800 and B850 molecules in the complex which is close to 0.5. Below 200 K thermal equilibrium no longer exists. At 4–100 K the B800 emission yield increases with decreasing temperature and becomes dependent on the wavelength of excitation. From the B800 emission yield at 4 K the B800-850 dipole-dipole distance was calculated to be equal to or smaller than 21 Å for all B800-850 complexes. Excitation spectra for B800 and B850 emission show that the overall energy-transfer efficiencies from carotenoid and B800 to B850 are greater than 90% at all temperatures. At 4 K the carotenoid transfers its excitation energy preferentially to B850. Experiments with chromatophores indicated that the energy-transfer properties of the B800-850 complexes were not modified by the isolation procedures.

Introduction

The light-harvesting antennae of the photosynthetic purple bacteria *Rhodopseudomonas sphaeroides* and *Rps. capsulata* are known to be composed of two types of pigment-protein complexes, the B800-850 and the B870 complex [1,2]. Especially the properties of the first of these have been extensively investigated [3–12]. The functional arrangement of these pigment-protein complexes is such that the B800-850 complex surrounds the B870 'lake' in which several reaction centers are embedded, and energy transfer is thought to occur according to the following scheme [13–15]:



Earlier experiments using chromatophores of several purple bacteria [16] showed that the rate of energy transfer in the antenna decreases signifi-

Abbreviations: B800, B850 and B870, bacteriochlorophyll molecules having an absorption maximum at 800, 850 and 870 nm, respectively; BChl, bacterioclorophyll; B800-850 complex, light-harvesting complex containing B800, B850 and carotenoid.

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cantly upon lowering the temperature to 4 K. For *Rps. sphaeroides* this was observed for energy transfer from B850 to B870 and from B870 to the reaction center. Similar experiments using the isolated B800-850 complex of *Rps. capsulata* Y5 [17] indicated that the rate of energy transfer between the B850s was strongly inhibited at 4 K. The weak B800 emission detected at 4 K was thought to represent the fraction of excitations lost by the excited B800 before energy transfer occurred to B850 [17].

Room-temperature excitation spectra of the B850 emission were obtained for B800-850 complexes of several mutants of *Rps. sphaeroides* and the carotenoid-to-B850 energy transfer was variously reported to be greater than 90% [18] or 70% [19].

The organization of the B800-850 complex has been studied by means of linear dichroism and fluorescence polarization to obtain the orientation of the chromophores [20–22]. However, so far the exact angles are known only to a limited extent. If in addition the rates of energy transfer in the complex could be obtained, a calculation of the distances of the various transition moments is possible using the well known Förster equation.

The most important object of this work is to obtain the energy-transfer rate from B800 to B850 from the B800 emission yield at 4 K. This allows calculation of the maximum B800-850 dipole-dipole distance for the B800 and B850 dipoles parallel to the connecting vector R.

From the excitation spectra of the B800 and B850 emissions at 4 K we also calculated the efficiencies of energy transfer from carotenoid to B800 and B850. Part of these results has been presented in a preliminary form elsewhere [23].

Material and Methods

Rps. sphaeroides and *Rps. capsulata* were grown as described elsewhere [16]. Chromatophores were prepared using a French press at 3 atm or by 10 min sonication at 0°C. The B800-850 complexes of *Rps. sphaeroides* WT, G1C and GA were prepared using the method of Clayton and Clayton [6]. The preparation was done in the dark at 4°C to avoid the formation of a substantial amount of bacteriochlorophyll emitting at 790 nm. Usually 790 emission levels of less than 1–of the B850 emission yield were obtained. The B800-850 complex of *Rps. capsulata* Y5 (a kind gift of Dr. R. Dierstein, Albert-Ludwigs-Universität, Freiburg, F.R.G.) was prepared according to the method of Feick and Drews [5].

Low-temperature emission and absorption spectroscopy was performed using a single-beam spectrophotometer described elsewhere [16]. To keep the samples clear upon cooling, the complexes, suspended in 10 mM Tris buffer and 0.1% lauryldimethylamine *N*-oxide were mixed with 60% (v/v) glycerol and 0.5 M sucrose.

Results

Emission spectra and emission yields in the temperature range 4–300 K

In all B800-850 complexes examined at 293 K at least three emission bands were observed. The predominant peak at about 865 nm (863 nm for *Rps. sphaeroides* WT, 866 nm for *Rps. capsulata* Y5) arises from B850. An emission band at about 807 nm is due to B800 and a weak broad band at 790 nm stems from some nonspecifically bound BChl. The intensity of the latter band varied from preparation to preparation and this emission was only excited by light of wavelengths shorter than 780 nm. We used only those preparations for which the 790 emission yield was less than 1‰ of the B850 emission yield. Fig. 1 shows the emission spectra of the B800-850 complexes of *Rps.*

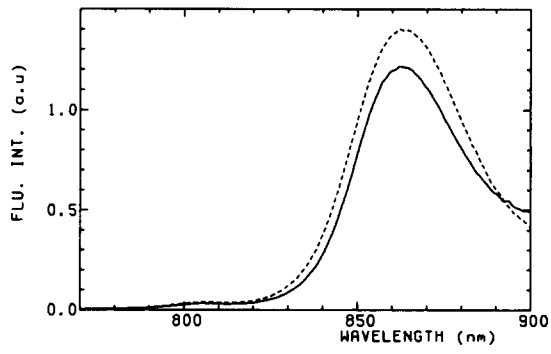

Fig. 1. Emission spectrum of B800-850 complex of *Rps. capsulata* Y5 (— — —) and *Rps. sphaeroides* WT (———) taken at 300 K. Excitation wavelength 540 nm for *Rps. capsulata* Y5 and 510 nm for *Rps. sphaeroides* WT. FLU. INT., fluorescence intensity; a.u., arbitrary units.

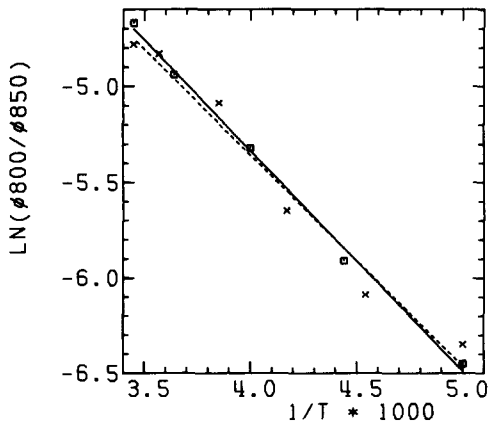

Fig. 2. Temperature dependence of the ratio of the B800 (ϕ_{800}) and B850 (ϕ_{850}) emission yields. The emission spectra of B800 and B850 were deconvoluted by assuming that the short-wavelength side of B850 emission peak was Gaussian shaped. The spectra were integrated to calculate the emission yields. (×———×) B800-850 complex of *Rps. capsulata* Y5, excited at 540 nm; (□———□) B800-850 complex of *Rps. sphaeroides* WT, excited at 510 nm.

sphaeroides WT and *Rps. capsulata* Y5, both excited in the carotenoid region at 515 and 540 nm, respectively. The ratio of B800 to B850 emission was independent of the excitation wavelength in the temperature range 200–300 K.

The temperature dependence of the ratio of the B800 and B850 emission yields (ϕ_{800}/ϕ_{850}) is shown in Fig. 2 for the B800-850 complexes of *Rps. sphaeroides* WT and *Rps. capsulata*. The linear relation obtained from Fig. 2 where $\ln(\phi_{800}/\phi_{850})$ is plotted vs. the reciprocal of the temperature means that the ratio ϕ_{800}/ϕ_{850} in the range 200–300 K can be described by an equation based on thermal equilibrium between the excitation densities in B800 and B850:

$$\frac{\phi_{800}}{\phi_{850}} = \frac{N_{800}}{N_{850}} c^{-\Delta E/kT} \qquad (1)$$

where N_{800}/N_{850} is the ratio of B800 to B850 molecules in the complex, ΔE the energy difference between the excited states of B800 and B850 and k Boltzmann's constant. Equal fluorescence rate constants are assumed for B800* and B850*. Thus, from Fig. 2 the slope of $\ln(\phi_{800}/\phi_{850})$ vs. T^{-1} gives $\Delta E = 0.1$ eV, extrapolation to $T^{-1} \rightarrow 0$ yields $N_{800}/N_{850} = 0.5$ for *Rps. sphaeroides* WT. A similar calculation gives $\Delta E = 0.1$ eV and $N_{800}/N_{850} = 0.4$ for *Rps. capsulata* Y5. These values are in excellent agreement with ΔE values calculated from the absorption spectra which are $\Delta E_{800\text{-}850} = 0.09$ eV for *Rps. sphaeroides* WT and $\Delta E_{800\text{-}855} = 0.1$ eV for *Rps. capsulata* Y5.

Fig. 3 shows the temperature dependence of the B800 and B850 emission in the range 200–4 K. The intensities of the B800 and B850 emissions as a function of the temperature indicate the absence of a thermal equilibrium in this temperature range. The fluorescence yield of B800 went through a minimum at about 120 K and became dependent on the wavelength of excitation. The emission yield of B850 increased with decreasing temperature and reached a value close to 90% at 4 K. At this temperature ϕ_{800}/ϕ_{850} for the various B800-850 complexes ranged between 1 and $5 \cdot 10^{-4}$ (see Table II). Fig. 4 shows the emission spectra at 4 K using 590 nm excitation light for the B800-850 complex of *Rps. sphaeroides* WT (Fig. 4A). The spectrum between 770 and 830 nm is amplified. In this spectrum the band at 803 nm can be ascribed to B800 emission; this sharp band is usually superimposed on a broad 790 nm emission. Fig. 4B

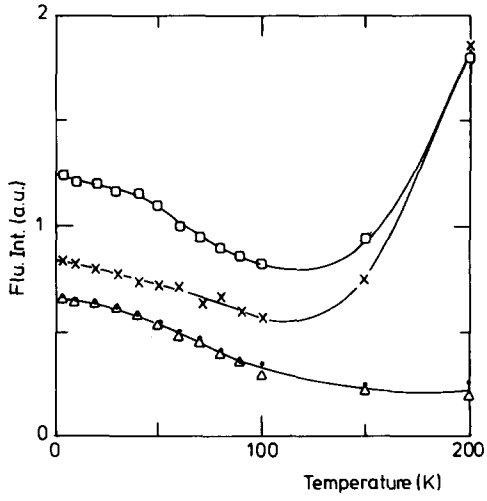

Fig. 3. Temperature dependence of B800 and B850 emission yields in the temperature range 200–4 K of the B800-850 complex of *Rps. sphaeroides* WT. (□———□) ϕ_{800}, $\lambda_{exc} = 590$ nm; (×———×) ϕ_{800}, $\lambda_{exc} = 510$ nm, (△———△) ϕ_{850}, $\lambda_{exc} = 590$ nm, (●———●) ϕ_{850}, $\lambda_{exc} = 510$ nm.

shows the emission spectrum obtained at 4 K in chromatophores of *Rps. sphaeroides* WT using 590 nm excitation light. Emission peaks at 910, 880 and 803 nm can be distinguished and assigned to B870, and B800, respectively, and a weak band at 790 nm due to the BChl absorbing at about 770 nm. The B870 and B850 peaks have been observed earlier [16], but the B800 peak was not observed before at 4 K in chromatophores. The yield of the B800 emission relative to the total emission is about $8 \cdot 10^{-4}$ for 590 nm excitation and 25% lower for 515 nm excitation. Similar emission spectra were obtained for the B800-850 complexes and chromatophores of *Rps. sphaeroides* G1C and GA and *Rps. capsulata* Y5. The presence of the B800 emission band in the chromatophores shows that this emission is the isolated complex is not due to an artefact of the preparations. The higher relative B800 emission yield in chromatophores upon 590 nm excitation compared to the complex (Table II), is probably due to a much lower total emission yield. Even with all the reaction centers inactive the fluorescence yield in chromatophores at 4 K is at most 8% [16].

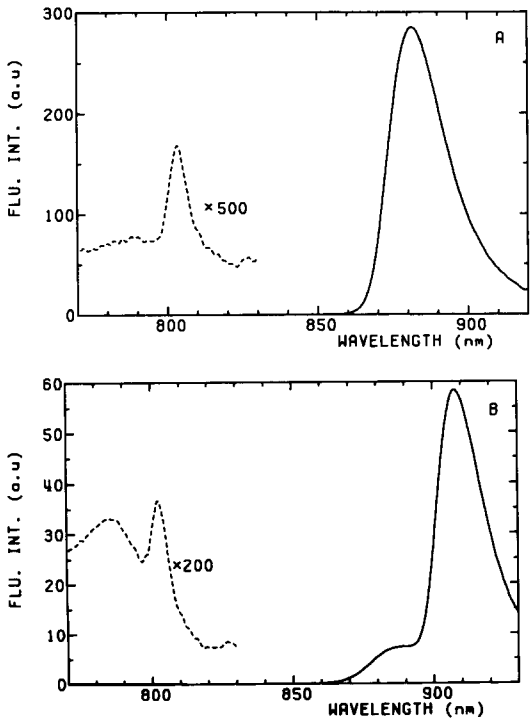

Fig. 4. Emission spectra at 4 K of the B800-850 complex (A) and of chromatophores (B) of *Rps. sphaeroides* WT. Excitation wavelength 590 nm. The dashed lines show the B800 emission spectra at 4 K, the amplification factor is given in each figure.

Absorption spectra

In Fig. 5 the absorption spectra of the B800-850 complexes of *Rps. sphaeroides* WT and G1C and *Rps. capsulata* Y5 at 4 K are shown. The positions of the main peaks are summarized in Table I. The differences in position of the 850 nm absorption band between the B800-850 complex of *Rps. capsulata* Y5 and the two *Rps. sphaeroides* complexes should be noted. Both the B800 and B850 peaks in the absorption spectra shift only very little if at all upon lowering the temperature to 4 K. Note the splittings of the middle and higher energy carotenoid absorption bands at 480 and 450 nm for *Rps. sphaeroides* WT and at 460 and 430 nm for *Rps. sphaeroides* G1C.

Excitation spectra of B850 and B800 fluorescence emission

At room temperature the excitation densities in

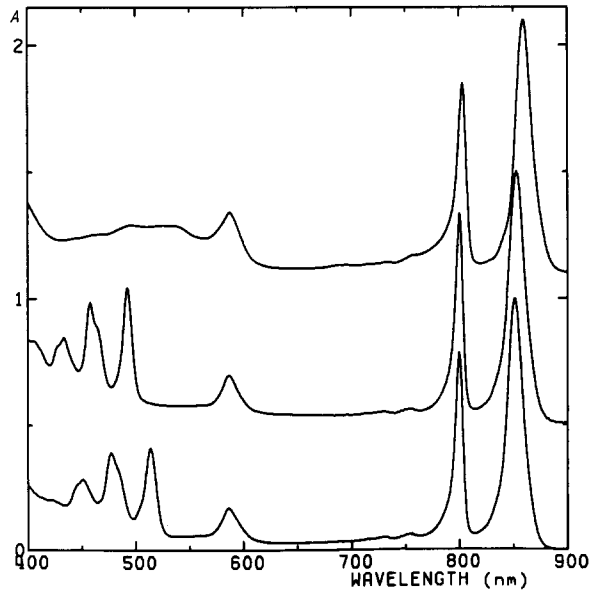

Fig. 5. Absorption spectra at 4 K of the B800-850 complex of *Rps. capsulata* Y5 (upper spectrum), *Rps. sphaeroides* G1C (middle spectrum) and *Rps. sphaeroides* WT (lower spectrum). All spectra have been normalized to an absorbance of 1 at the long-wavelength bacteriochlorophyll absorption band. The baselines have been shifted by 0.5 and 1.1 absorbance unit for the middle and upper spectrum, respectively.

TABLE I

POSITIONS OF THE PEAKS (nm) IN THE ABSORPTION (Abs) AND EMISSION (Em) SPECTRA OF THE VARIOUS B800-850 COMPLEXES AND OF CHROMATOPHORES OF *RPS. SPHAEROIDES* WT AND *RPS. SPHAEROIDES* G1C AT 4 K

	Abs	Em	Abs	Em	Abs	Em	Abs	Em
Rps. capsulata Y5 B800-850			855	888	800	807		792
Rps. sphaeroides WT B800-850			848	882	797	803		
Rps. sphaeroides G1C B800-850			849	887	797	802		790
Rps. sphaeroides WT chromatophores	≈ 880	908	≈ 850	882	797	803		786
Rps. sphaeroides G1C chromatophores	≈ 880	903	≈ 850	885	797	802		787

B800 and B850 are in thermal equilibrium and the ratio of their amplitudes is independent of the wavelength of excitation. The excitation spectra of B850 emission at 300 K for the various B800-850 complexes in the region 400–600 nm deviate only slightly from the absorption spectra in the same wavelength region, which indicates that overall energy-transfer efficiencies from excited carotenoid molecules to B850 (possibly via B800) exceed 90%, in agreement with earlier findings [17,18]. In addition, excitation spectra were obtained at 4 K and these show that the overall efficiency for energy transfer from excited carotenoid to B850, either directly or via B800, in all preparations studied is not greatly dependent on temperature. Fig. 6 shows as an example the 4 K excitation spectrum of the fluorescence detected at 880 nm (due to B850) for the B800-850 complex of *Rps. sphaeroides* WT. This can be compared with the absorption spectrum shown in Fig. 5.

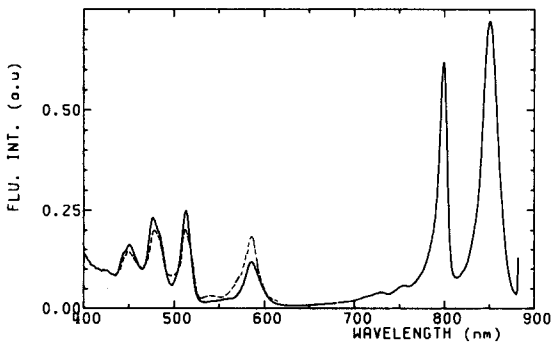

Fig. 6. Excitation spectra of the B800 (— — —) and B850 emission (———) at 4 K of the B800-850 complex of *Rps. sphaeroides* WT. The emissions were monitored at 805 nm for B800 and 890 nm for B850. The B800 excitation spectrum was recorded at a 400× higher amplification.

The measurement of an excitation spectrum of the B800 emission at 4 K allows a direct estimate of the efficiency of energy transfer from carotenoids to either B800 or B850. If the excited carotenoid transfers all its energy to B800 a 3-fold higher B800 emission will be expected upon excitation in the carotenoid region than upon excitation at 590 nm where about one-third of the absorption is due to B800. If, on the contrary, all the light absorbed by the carotenoid is transferred to B850 no B800 emission will be observed. At 4 K no back-transfer from B850 to B800 occurs as was checked with 850 nm excitation and 803 nm detection.

In Fig. 6 the dashed curve shows the excitation spectrum at 4 K of the fluorescence detected at 803 nm (due to B800) for the B800-850 complex of *Rps. sphaeroides* WT. The relatively low contribution of the carotenoids in this excitation spectrum (Fig. 6) indicates that excited carotenoids preferentially transfer their energy to B850. The same situation was encountered in all the B800-850 complexes investigated. Table II summarizes the results for the various preparations. Although there was some variation from one preparation to another the overall picture was consistent. Direct energy transfer from an excited carotenoid molecule to B850 seems to be the most favorable process in all these B800-850 complexes, in spite of the fact that different carotenoids are present in

TABLE II

RELATIVE B800 EMISSION YIELDS AT 4 K, CALCULATED FROM THE EMISSION SPECTRA AT 4 K, AS SHOWN IN FIG. 4

Sometimes the B800 emission spectrum was superimposed on a broad emission peak centered at 790 nm, which then was assumed to be symmetrical around 790 nm and subtracted from the observed emission spectrum. The rate of energy transfer from B800 to B850, K_{ET}, is calculated from Eqn. 2, R_0 is defined in the text. The B800-850 dipole-dipole distance is given for the maximum value of the orientation parameter k^2, which assumes that the B800 and B850 dipoles both are parallel to the vector R connecting the two dipoles.

Species	Carotenoid λ_{ex} (nm)	ϕ_{800}/ϕ_{total} ($\times 10^4$)	BChl λ_{ex} (nm)	ϕ_{800}/ϕ_{total} ($\times 10^4$)	K_{ET} ($\times 10^{-11}$) (s^{-1})	R_0 ($k^2 = 4$) (Å)	R (Å)
Rps. sphaeroides G1C	490	1.4	590	1.9	3.8	89	21
Rps. sphaeroides WT	510	1.5	590	2.6	2.8	83	21
Rps. sphaeroides Ga	490	1.3	590	3.1	2.4	89	22
Rps. capsulata Y5	540	3.2	590	4.9	1.5	76	21
Rps. sphaeroides WT (chromatophores)	510	6	590	8			

these preparations. If we assume that in the case of 590 nm excitation 33% of the excitations start off in B800, then upon carotenoid excitation only between 15 and 25% of the excitation energy is transferred directly to B800, the remainder directly to B850. The excitation spectrum in Fig. 6 of the B800 emission at 4 K indicates that the absorption spectrum of the carotenoid transferring to B800 is not different from that of the total carotenoid. Even the splitting of the peak at 490 nm can be observed. The results obtained with chromatophores of *Rps. sphaeroides* WT were in quantitative agreement with those obtained with the isolated complex.

Calculation of the B800-850 pigment-pigment distance

To calculate the distance between the transition dipoles of B800 and B850 involved in the energy transfer in the various complexes several assumptions have to be made. The first is that at 4 K energy transfer from B800 to B850 is irreversible. The fact that upon 850 nm excitation at 4 K no B800 emission is observed supports this hypothesis. The second assumption is that only one B850 is involved in the energy transfer from B800 and B850 selected either by a relative short distance to B800 or by a favorable orientation. We will return to this point later. From these assumptions it follows that the rate of energy transfer K_{ET} from B800 to B850 can be expressed as:

$$K_{ET} = \alpha K_L \frac{\phi_{850}}{\phi_{800}} \tag{2}$$

where K_L is the decay rate of B800* if no energy transfer occurs ($K_L = 2.2 \cdot 10^8\ s^{-1}$ was used, corresponding to a fluorescence lifetime of 4.5 ns if no additional quenching occurs [24]) and α the fraction of excitations starting off in B800 either by direct absorption or via carotenoid absorption followed by energy transfer ($\alpha = 0.33$ for 590 nm excitation). The values obtained for K_{ET} for the various complexes are listed in Table II. From the Förster equation [25] for long-distance dipole-dipole energy transfer we obtain [26]:

$$K_{ET} = \frac{9 \ln 10}{128\pi^5} K_F \frac{k^2 c^4}{\eta^4 N_1 R^6} \frac{\int \epsilon_{850}(\nu) F_{800}(\nu)\, d\nu}{\nu^4} = K_F \left[\frac{R_0}{R}\right]^6 \tag{3}$$

where ν is the frequency, ϵ_{850} the absorption spectrum is extinction units of the B850 involved in the transfer process, $F_{800}(\nu)$ the normalized emission spectrum of B800, K_F the B800 emission rate ($K_F = 5.6 \cdot 10^7\ s^{-1}$), η the index of refraction of the medium ($\eta = 1.5$ was used), k^2 an orientation factor ($0 \leqq k^2 \leqq 4$), $N_1 = 6 \cdot 10^{20}$, $c = 3 \cdot 10^8\ ms^{-1}$ and R the distance between B800 and the B850 involved. The B850 absorption spectrum was ob-

tained assuming that both B850s in the complex have the same absorption spectrum and that the extinction coefficient at 850 nm at 300 K was 184 $mM^{-1} \cdot cm^{-1}$ [10]. The B850 absorption profile between 790 and 825 nm was extrapolated using the 4 K absorption bands of *Rhodospirillum rubrum* WT and *Rps. sphaeroides* R-26 as examples. We estimated the error introduced in the calculation of the overlap integral to be less than 20% which leads to a 3% error in the distance. A possible splitting of the B850 absorption band into two exciton components [20] was not considered. The maximum value of 21 Å for the B800-850 dipole-dipole distance is obtained for an orientation of the B800 and B850 dipoles both parallel to the connecting vector R. All other orientations yield distances smaller than 21 Å. Linear dichroism and fluorescence polarization data have indicated angles of about 30 and 120° between the B800 dipole and the two B850 dipoles [21]. This gives maximum distances of 20 and 17 Å, respectively, assuming that either the first or the second B850 is involved in energy transfer from B800, and that in each case at least one of the dipoles is parallel to the connecting vector R. For the same choice of the orientation factor k^2 the B800-850 dipole-dipole distance is almost the same for all complexes (Table II). If by coincidence both B850s in the complex participate in the energy-transfer process from B800 with equal probability, this would increase the calculated distance by 12% as compared to the case when only a single B850 is involved.

Discussion

This work describes a study on the emission and absorption spectra of three B800-850 complexes of *Rps. sphaeroides* (WT, GA, G1C) and a B800-850 complex of *Rps. capsulata* Y5. Although the preparations are very different with respect to their carotenoid composition, mainly sphaeroidene in *Rps. sphaeroides* WT, neurosporene in GA and G1C and a mixture of sphaeroidenone and sphaeroidene in *Rps. capsulata* Y5 no differences were observed in their energy-transfer properties both at 300 and at 4 K. The dependence on the temperature of the B800 and B850 emissions was identical for all complexes. All our results indicate that the structural properties of the B800-850 complexes are not modified upon removal of the complex from the chromatophore membrane.

The temperature dependence of the ratio ϕ_{800}/ϕ_{850} between 200 and 300 K can be described by assuming a thermal equilibrium between the excitation densities in B800 and B850. This means that the rates of energy transfer from B800 to B850 and vice versa are at least 10-times larger than the rate of loss of excitations from the complex. At 300 K the fluorescence yield of the B800-850 complex is about 10%, indicating a loss rate of $5 \cdot 10^8$ s^{-1} [24] or K_{ET} (B850 → B800) $\geqq 5 \cdot 10^9$. This gives K_{ET} (B800 → B850) $\geqq 5 \cdot 10^{11}$. The lower value calculated at 4 K (Table II) can be explained by a decrease in the overlap integral in the expression for the Förster energy-transfer rate [16]. The extrapolated B800 : B850 stoichiometry favors 1 B800 : 2 B850, in agreement with earlier suggestions [3,7,10] and seems to exclude a ratio of 2 B800 : 3 B850 [10].

For all complexes we find that the B800-B850 dipole-dipole distance is less than or equal to 21 Å and for most configurations the distance is between 13 and 21 Å. Much shorter distances do not seem very likely in our opinion as there is little or no effect of the presence of the B800 absorption band on the B850 absorption band [10] and because of the absence of a circular dichroism signal in the B800 band [7,10]. For a certain choice of the orientation of the pigments, all complexes yield the same B800-850 dipole-dipole distance, indicating that they have a similar structure. The small differences observed in ϕ_{800} at 4 K for the various complexes do not seem to be due to structural differences but to small spectral differences between the pigments attached to these complexes which are reflected by small variations in the parameter R_0 (Table II). If the distance between two energy-transferring BChls becomes as close as 20 Å or less a correction has to be made to the energy-transfer rate as calculated by eqn. 3 [27]. For the case that both dipoles are parallel to the connecting vector R at 21 Å the correction in the distance is only small ($\pm 2\%$).

At all temperatures the overall efficiency for energy transfer from carotenoid to B850 is high (greater than 90%), in agreement with other results [18]. For the preferential direct energy transfer from carotenoid to B850 we observed at 4 K

several explanations may be suggested. From linear dichroism and fluorescence polarization measurements it has been concluded that the carotenoid transition moment is more parallel to the Q_x transition of B850 and more or less perpendicular to the Q_x transition of B800 [21]. So the orientation factor in Eqn. 3 might favor energy transfer to B850. Alternatively, it has been assumed that carotenoid-to-BChl energy transfer occurs by exchange energy transfer [28,29], which implies the carotenoid must be situated at 4 Å or less from the BChl molecule [29]. In that case we would have to assume two carotenoid pools: 15–25% close to B800, 75–85% close to B850. However, it is not clear how such a structure should be reconciled with the finding that the carotenoid and B800 are associated with the same polypeptide [11,12].

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