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FLUORESCENCE EMISSION BY WILD-TYPE- AND MUTANT-STRAINS OF *RHODOPSEUDOMONAS CAPSULATA*

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Summary

Absorption and fluorescence emission spectra of *Rhodopseudomonas capsulata*, strains 37b4 (wild type), A1a$^+$ (blue-green mutant strain), Y5 (phototroph negative, having only *B*-800—850 bacteriochlorophyll-carotenoid-protein complex) at 4 K, 77 K and 300 K were measured. The fluorescence emission at 890 nm of the *B*-870 bacteriochlorophyll band dominates the emission of other spectral forms of the strains 37b4 and A1a$^+$, while in strain Y5 a fluorescence emission band at 865 nm of the *B*-850 bacteriochlorophyll dominates. Very little fluorescence was observed at 805 nm. A linear relation between relative fluorescence intensity and the exciting light intensity was observed. The integrated fluorescence yield increased as the temperature was lowered from 300 K to 4 K. The results are discussed in the light of the arrangement of pigment molecules in the membrane and the process of energy migration within the photosynthetic apparatus.

Introduction

The organization of the bacterial photosynthetic apparatus has been reviewed recently [1—3]. One type of photosynthetic apparatus, which is found besides others, in cells of *Rhodopseudomonas capsulata*, *Rhodopseudomonas palustris* and *Rhodopseudomonas sphaeroides*, is localized in intracyto-

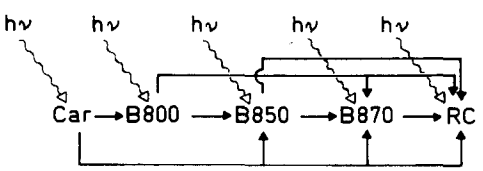
Abbreviation: BChl, bacteriochlorophyll.

plasmic membranes and contains the photochemical reaction center and two light-harvesting antenna components: the *B*-870 and *B*-800—850 complexes [1—3]. All three pigment complexes have been isolated from *Rps. capsulata* and partially characterized [4,5]. The *B*-800—850 complex, which is characterized by two near infrared absorption bands of bacteriochlorophyll (BChl) *a* at 800 and 855 nm, contains bacteriochlorophyll (BChl) *a*, carotenoids and three polypeptides (M_r 14 000, 10 000, and 8000) in the molar ratio 6 : 2 : (1—2) : 2 : 2 [5,6,7]. A sequential degradation of the polypeptides with trypsin followed by dodecyl sulfate polyacrylamide gel electrophoresis under mild conditions, has shown that the pigments are associated with the two smaller polypeptides [6,8]. The absorption spectra after partial degradation indicate that two molecules of BChl (*B*-850) are associated with the 10 000 polypeptide, while one BChl molecule (*B*-800) and one carotenoid molecule are associated with the 8000 polypeptide [5,6,8].

The number of antenna *B*-870 molecules per reaction center (approx. 25) seems to be constant under various culture conditions [9—12]. In contrast the molar ratio of antenna *B*-800—850 to reaction center is variable [3,9—12]. The size of the photosynthetic unit, i.e. the total amount of BChl molecules per reaction center is variable between 15 and more than 100 due to changes in oxygen partial pressure, light intensity and other external factors [1—3,9—12]. Since the BChl-carotenoid ratio of the three pigment complexes differs, the BChl-carotenoid ratio of the photosynthetic unit varies under different growth conditions. Hence, the fraction of light quanta absorbed directly by each of the pigment complexes varies and depends on the wavelength of the incident light. In cells, grown under low incident light flux, most of the light quanta are absorbed by the pigments of the *B*-800—850 complex.

The excitation energy might be transferred from the antenna pigments to the reaction center by a dipole-dipole resonance mechanism [13,14] in the sequence given in Scheme I. Although the energy transfer from *B*-800 and

Scheme I.



B-850 to the reaction center most likely goes through *B*-870 [15], direct transfer from *B*-800 or *B*-850 to the reaction center should not be excluded. Excitation energy which is not used by photochemistry in the reaction center is lost as prompt or delayed fluorescence [16], triplet formation or heat. The course and efficiency of the migration of excitation energy between the pigment complexes depends on the turnover of energy and the redox state of reaction centers and arrangement of pigment complexes within the membrane [14—18].

In this paper we describe data on fluorescence emission spectra at different temperatures (4 K—300 K) of the wild-type strain 37b4 and mutant strains defective in the photochemical apparatus. Moreover, the relative fluorescence yield on a BChl basis of the isolated complex *B*-800-850 and whole cells of wild

type and mutant strains irradiated with different light fluxes has been measured.

The results show large differences in the emission spectra and in the relative fluorescence intensity depending on the exciting light intensity and relative proportions of the two light-harvesting complexes. This will be discussed in terms of energy migration in the photosynthetic apparatus.

Materials and Methods

The following strains of *Rhodopseudomonas capsulata* have been used: 37b4 (German collection of micro-organisms, Göttingen, strain number 938), wild type, A1a$^+$ (*crt*$^-$, *B*-800—850$^-$*pho*$^+$) [4]; Y5, reaction center (RC) lacking, *B*-870$^-$ *pho*$^-$ [5]; A1a$^+$*pho*$^-$ (*crt*$^-$, RC$^-$, *B*-870$^+$, *B*-800—850$^-$ [19]. The bactera were cultivated and the *B*-800—850 complex isolated as described [5].

Absorption spectra were recorded using a cryostat described elsewhere [20,21]. For the measurement of the fluorescence emission spectra the monochromator was shielded from the scattered actinic light by Schott KV 550 and RG 715 filters. The bandwidth was set at 1.6 nm. The photomultiplier used for measuring the fluorescence (EMI 9684 B) was mounted in a thermostated liquid N_2 cooled socket (Products for Research Inc., Danvers, MA) and operated at 170 K, to suppress the thermal noise.

A combination of an absorption filter (Schott BG 18) with a broad band interference filter (Balzer filtraflex) either K 3, maximal transmission at 505 nm, or K 5, maximal transmission at 590 nm, was used to select the excitation wavelength band. The former combination excites mainly the carotenoids (if present), the latter the BChl of the various preparations. The intensity of the exciting light was varied with Schott neutral density filters.

For the fluorescence experiments samples were used, which always had an absorbance of less than 0.2 in the main long wavelength absorption peak to prevent reabsorption of fluorescence.

The sample was contained in a perspex vessel of 1 mm thickness. Before measurements at low temperature the photosynthetic material in buffer was mixed with glycerol to a ratio 1 : 2 (v/v). To this solution 1 M sucrose was added. This resulted in clear samples at all temperatures. Computer programs were used to plot the fluorescence emission spectra (after correction for the wavelength dependent sensitivity of the apparatus), the absorbance spectra, and to calculate the integrated fluorescence and the overlap integrals. All calculations mentioned in this paper were performed on a PDP 11/45 computer.

For the measurement of the fluorescence emission, detailed in Figs. 3—6, the light of an Osram-halogen-Bellaphot lamp (24 V, 240 watt) was passed through a combination of filters (BG 38 + KG 3, Schott + Gen., Mainz). The fluorescence emitted from the sample (10 ng—2.72 μg bacteriochlorophyll was passed through a monochromator (Gamma Scientific, model 700 31 IRTM) and detected by a S_1-photocathode. The dynode voltage of the photomultiplier was controlled and amplified by a control module (Gamma Scientific, model 820-1S). The amplified signals were displayed on a Kipp + Zonen B 30 *X*/*Y*/*t* recorder. The emission spectra were not corrected for the wavelength dependent sensitivity of the detector. Lamp, sample and monochromator were optically connected by fiber flass optics.

Results

Fig. 1 shows the absorption spectra of the wild type and mutant strains of *Rps. capsulata* defective in one or more pigment complexes. At low temperature the single absorption bands are considerably sharpened. The position of the absorption maxima is nearly independent from the temperature as shown with the isolated complex *B*-800—850 (Fig. 2). This was, however, also observed with the wild type membrane. At all temperatures the bands at 800, 850 and 870 nm are assymmetric, which may indicate that these bands do not represent single pigment species.

The emission spectrum of the wild type cells of *Rps. capsulata* at room temperature shows a broad asymmetric peak at 883—891 nm and a shoulder at 863/864 nm (Fig. 3 a + b). At increased sensitivity a small peak at 805 nm becomes visible. The spectrum shows that all light-harvesting bands at 800, 850 and 870 nm contribute, although in quite different ratios, to the fluorescence emission. The correlation between pigment complex and emission spectrum is possibly in comparison with mutant strains (see below). At 77 K the emission

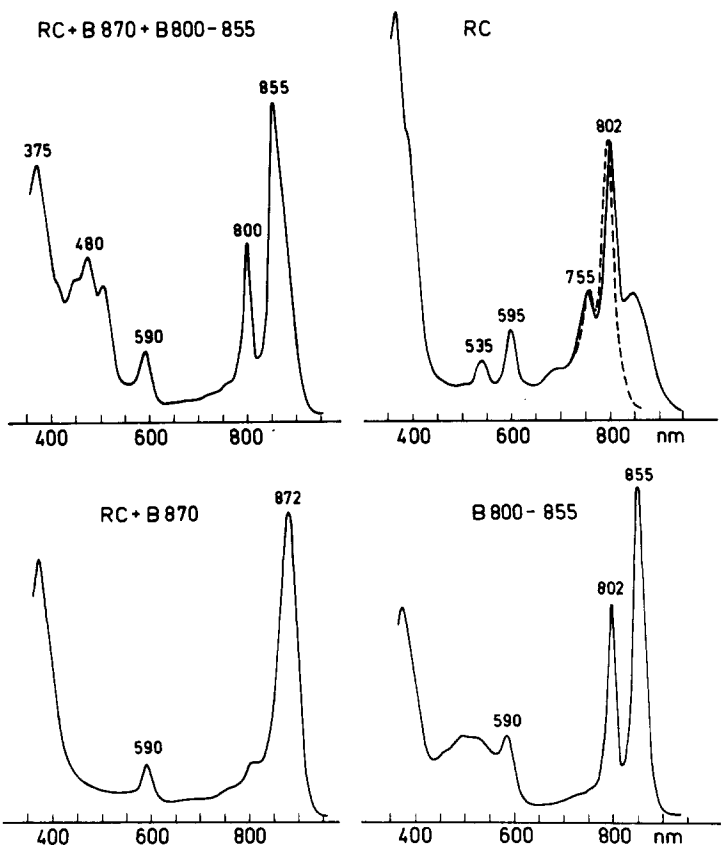


Fig. 1. Absorption spectra of membranes from *R. capsulata*, strains 37b4 (reaction center (RC) + *B*-870 + *B*-800—855), A1a$^+$ (RC + *B*-870), Y5 (*B*-800—855) and reaction center preparations (RC; dotted line shows infrared region of bleached reaction centers).

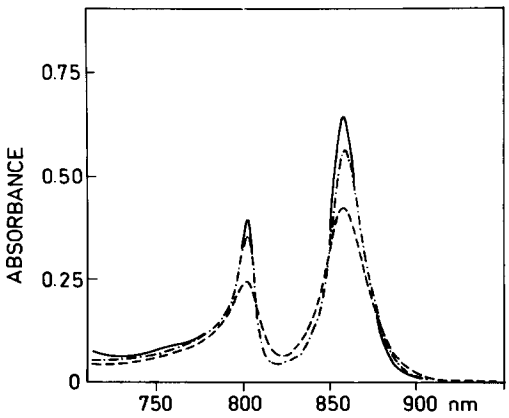


Fig. 2. Absorption spectrum of the isolated light harvesting complex *B*-800—850 from *Rps. capsulata*, strain Y5 at room temperature (- - - - -), at 100 k (· — · — ·) and 4 K (———).

peaks are sharpened and shifted to longer wavelengths. The fluorescence emission of the *B*-870 light-harvesting component dominates (Fig. 3 a + b). A comparison with the emission spectrum of the mutant A1a$^+$, which possesses *B*-870 as the only light harvesting BChl component (Fig. 1), indicates that the 891 nm emission band at room temperature, and the 915 nm band at 77 K of the wild type cells are due to *B*-870 complex (Fig. 4).

The *B*-800—850 complex, when located either in the membrane or in the isolated state, emits fluorescence light around 864 nm at room temperature and around 890 nm at 77 K. Again a weak band is visible at 805 nm (Fig. 5a). The 805 nm emission band most likely stems from the *B*-800 in the light-harvesting complex *B*-800—850. The amplitude of the *B*-800 emission relative to the *B*-850 emission is about 1%, the halfwidth of this band at 300 K is approx. 15—20 nm compared with a halfwidth of 35—40 nm for the *B*-850 emission band at 870 nm. The integrated *B*-800 emission is therefore about 0.5% of the *B*-850 emission. If the temperature is 120 K the *B*-800 emission disappears completely; may be on carotenoid excitation (see Materials and Methods) a small shoulder can be observed, but the amplitued of this emission is less than 0.04% of the *B*-850 fluorescence. This decrease of the *B*-800 emission can be explained by assuming that the distribution of excitation energy over both antenna pigment pools is governed by a Boltzmann factor (see Discussion), which strongly depends on the temperature.

Lowering the temperature to 4 K makes the *B*-800 emission again visible. The absolute amplitude increases at least a factor 5 between 120 K and 4 K, the amplitude relative to *B*-850 emission (at 886 nm halfwidth 20 nm) is 0.07%. It should be noted that the *B*-850 emission increases a factor 3 on lowering the temperature from 120 K to 4 K (see Fig. 8). The peak of the *B*-800 emission is now at 807 nm, the halfwidth is about 8 nm, which means that the *B*-800 fluorescence yield relative to the *B*-870 fluorescence yield is: $\phi(B\text{-}800)/\phi(B\text{-}850) = 4 \cdot 10^{-4}$. Both at room temperature as at 4 K the ratio $\phi(B\text{-}800)/\phi(B\text{-}850)$ is independent on the type of excitation light used (bacteriochlorophyll excitation or carotenoid excitation).

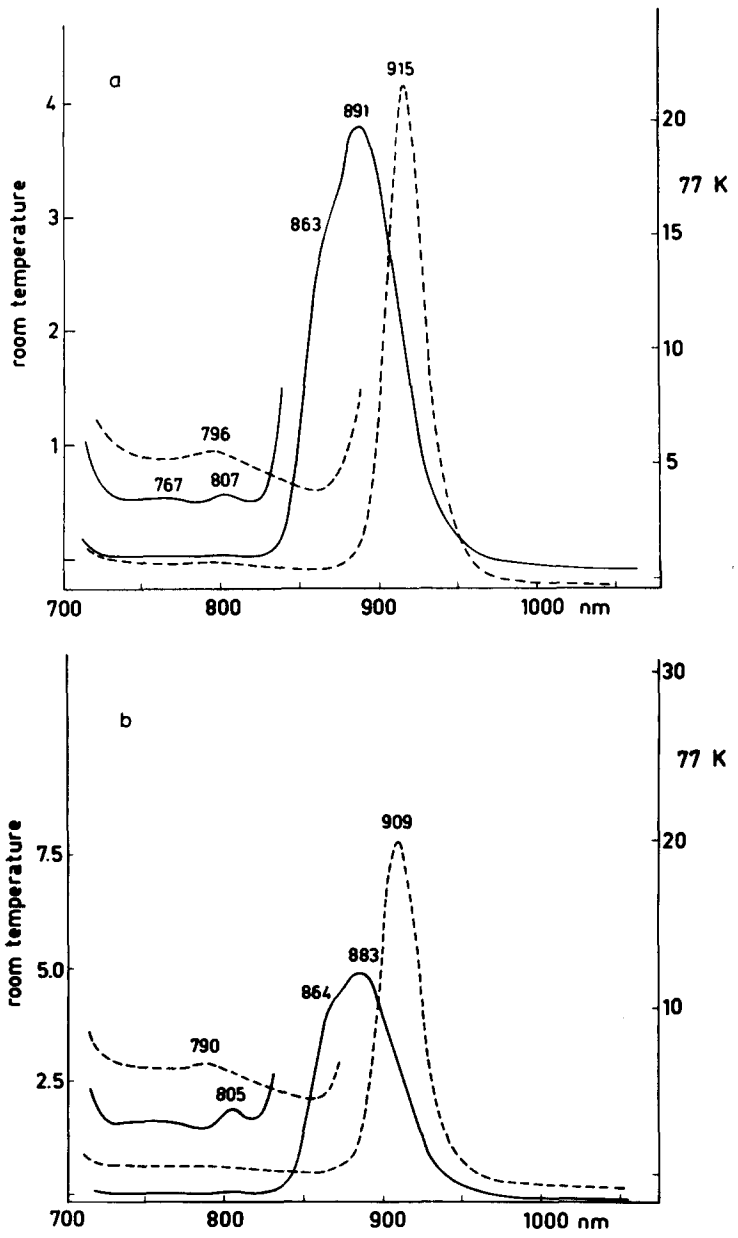


Fig. 3. Fluorescence emission spectra of wild type cells (37b4) of *Rps. capsulata*. (a) Grown anaerobically in the light. (b) Grown semiaerobically in the dark. Full line, room temperature, broken line 77 K. The upper curves between 720 and 850 nm are taken at higher amplification of the phototube. See also Fig. 1.

In most experiments the preparations were excited with a broad region of the visible spectrum. Hence, due to the presence or absence of carotenoids in wild type cells and A1a$^+$ cells, respectively, different amounts of light quanta were absorbed by cells of the various strains. However, the relative fluorescence intensity from equal amounts of BChl reflects the presence or absence of traps

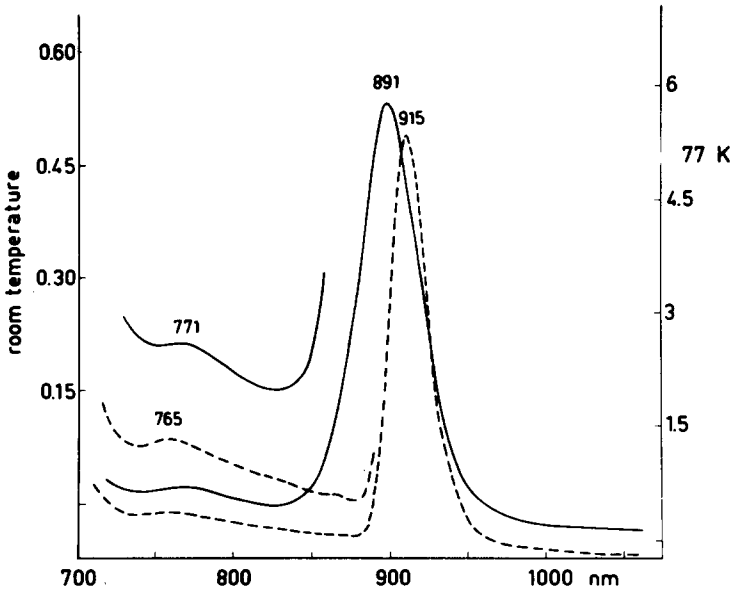


Fig. 4. Fluorescence emission spectrum of cells from *Rps. capsulata*, strain A1a$^+$, see legend of Fig. 3 for further explanation.

(Fig. 6a). The relative fluorescence is proportional to the exciting light intensity in the isolated *B*-800—850 complex (Y5). The dependence of the relative fluorescence on the intensity of the exciting light, however, is biphasic in bacteria which contain a reaction center. The slopes of the curves are about 1.4 times smaller under low light intensities than under higher intensities (Fig. 6b; factors of increase: 1.35, 37b4 semiaerobic; 1.4, 37b4 anaerobic; 1.45, A1a$^+$). The highest relative fluorescence intensity was observed in membranes of strain Y5 and in isolated *B*-800—850 complex, the lowest was observed in A1a$^+$ due to absence of carotenoids and a low ratio of light-harvesting BChl to reaction center (*B*-800—850 is missing, see Figs. 1 and 4). Interestingly in semiaerobically grown cells of the wild type strain the relative fluorescence intensity is higher than for anaerobically grown cells. This may be due to a less effective coupling between reaction center and light-harvesting pigments and different sizes of photosynthetic units [1,18].

A decrease of temperature to 77 K (Figs. 3—5) and to 4 K (Fig. 7) increased the fluorescence yield of a light-harvesting *B*-800—850 complex, which has a molecular weight of about 150 000 (Shiozawa, J. and Drews, G., unpublished results) and contains approximately 12 bacteriochlorophyll and 4 carotenoid molecules per particle. Fig. 8 shows the temperature dependence of the integrated emission between 120 K and 4 K of the complex. At temperatures below 4 K the fluorescence yield of the *B*-800—850 complex approaches a value of about 25%, which is close to fluorescence yield of bacteriochlorophyll *a* in vitro [16]. The relative increase in fluorescence yield as a function of temperature is identical for predominantly carotenoid or BChl exciting light (Fig. 8), which means that the efficiency of the transfer of excitation energy from the carotenoid to the light-harvesting *B*-800—850 is constant over the

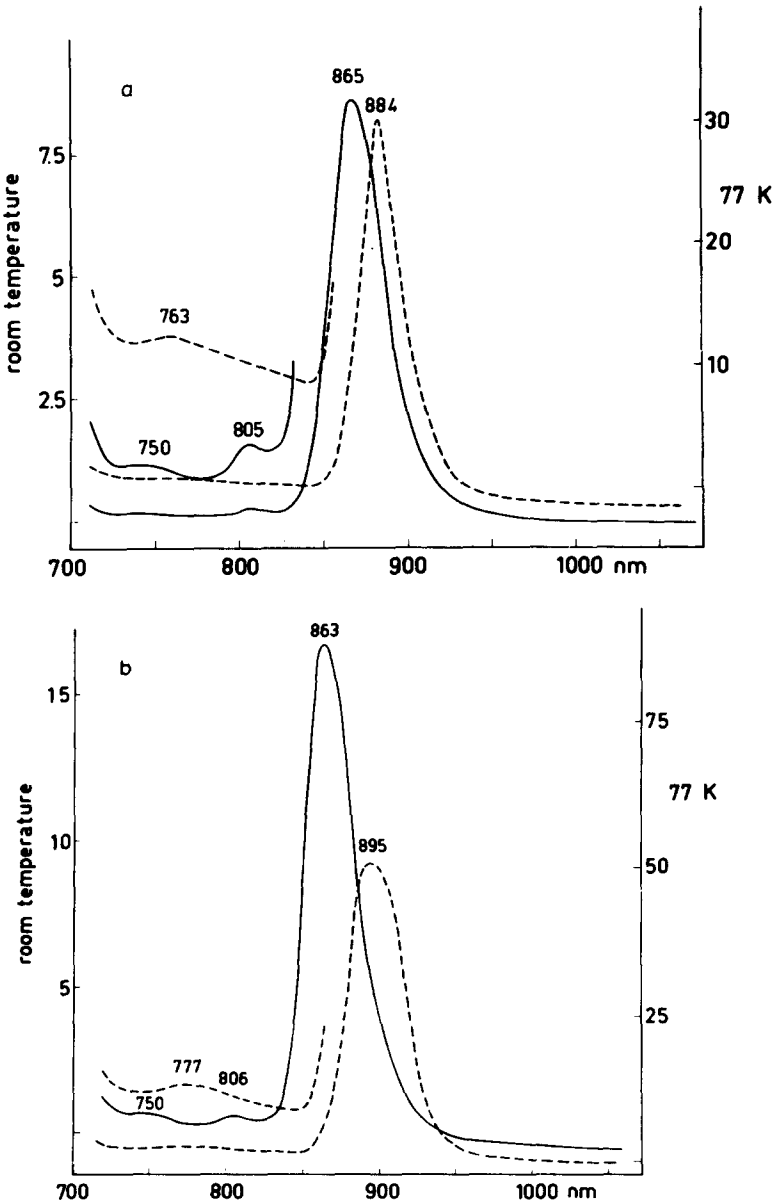


Fig. 5. Fluorescence emission spectrum of cells from strain Y5 (a) and from isolated complex *B*-800—850 (b); see legend of Fig. 3.

whole temperature range. At all temperatures this efficiency is about 90% which is similar to that observed for the wild type cells (Rijgersberg, C.P. and van Grondelle, R., unpublished observations). The 3-fold increase in the integrated fluorescence yield, which is observed if the temperature is lowered from 300 K to 4 K is very similar to that observed in intact systems for the maximum fluorescence, obtained when all the reaction centers are photochemically closed [22].

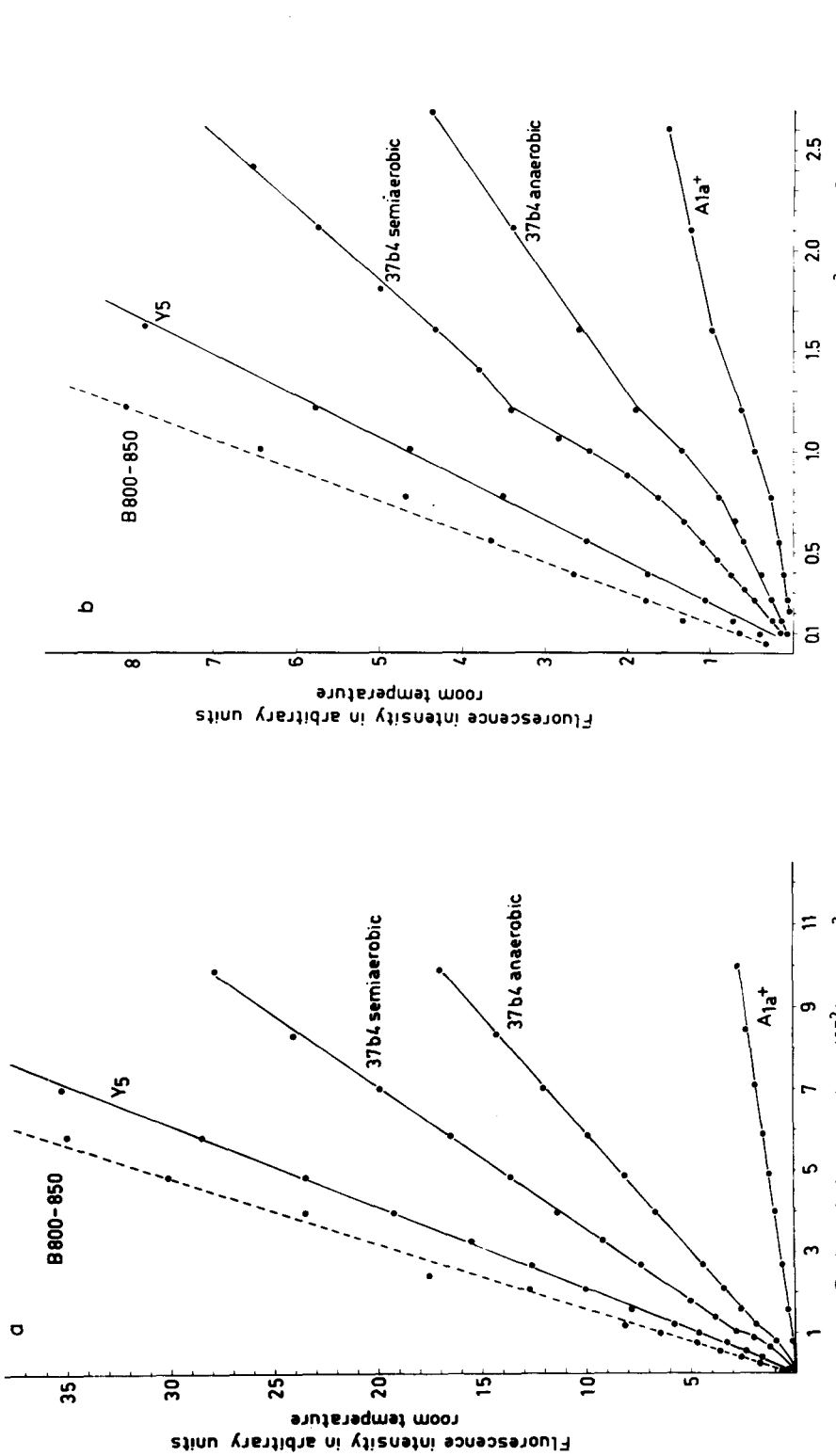


Fig. 6. Relative fluorescence intensity at various exciting light fluencies. A1a$^+$, cells of *Rps. capsulata* strain A1a$^+$; 37b4, cells of wild type strain anaerobically in the light (see Fig. 3a) and semiaerobically in the dark (see Fig. 3b); Y5, cells of the phototroph negative mutant Y5; B-800—850 isolated light harvesting complex B-800—850 from membranes of *Rps. capsulata*, strain Y5. Excited at higher (a) and lower (b) light intensities.

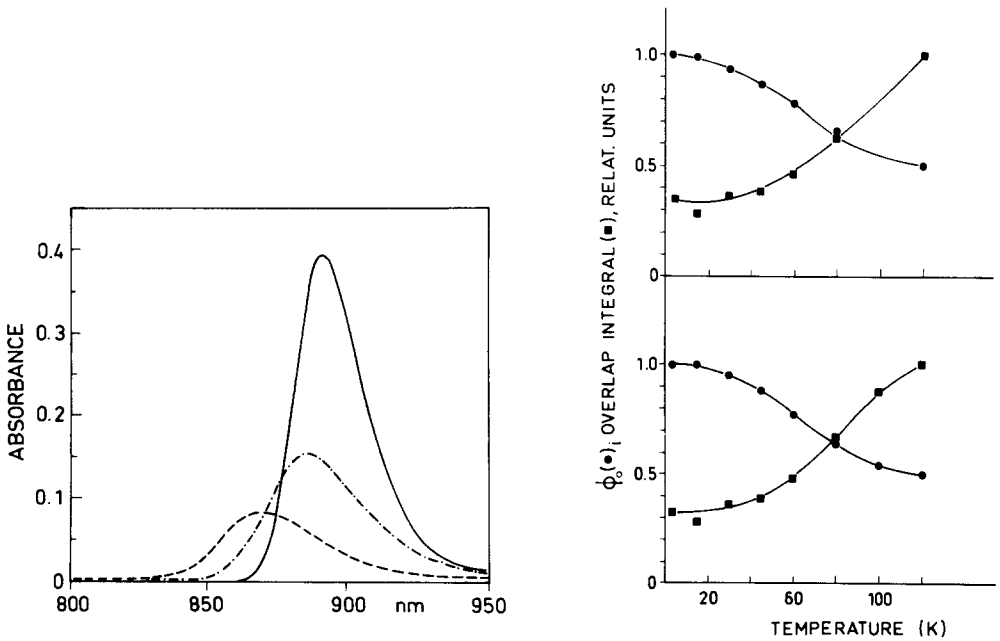


Fig. 7. Fluorescence emission spectrum of the light harvesting complex *B*-800—850, from *Rps. capsulata*, strain Y5 measured at room temperature (- - - - -), at 100 K (· — · — ·) and at 4 K (———). In contrast to the absorption spectrum (Fig. 2) the peaks shift to longer wave lengths with decreasing temperature.

Fig. 8. Overlap integral (■) and integrated fluorescence (ϕ_0; •) of the isolated *B*-800—850 light harvesting complex, excited at 590 nm (bacteriochlorophyll excitation; Balzer Filtraflex K5), top figure and 505 nm (carotenoid excitation; Balzer Filtraflex K3), lower figure. The overlap integral was calculated from the absorption and fluorescence emission spectra at specific temperatures. Normalized to 1 at 4 K.

In this case the increase of the fluorescence was found to be correlated to a decrease of the rate of energy transfer k_{ET} as given by the Förster equation

$$k_{ET} = \frac{\phi_D}{\tau} \frac{1}{R^6} \frac{3}{4\pi} \int_0^\infty \lambda^4 F_D(\omega) \sigma_A(\omega) \, d\omega \qquad (1)$$

where ϕ_D is the fluorescence yield of the donor in the absence of an acceptor, τ is the lifetime in the absence of an acceptor, $\lambda = \lambda/2\pi n$ where λ is wavelength and n the index of refraction, $F_D(\omega)$ is the normalized fluorescence emission spectrum of the donor on an angular frequency scale, $\sigma_A(\omega)$ is the absorption cross-section of the acceptor. Therefore we have calculated from the absorption and emission spectra at different temperatures the value of the resonance integral (Fig. 8). The rate of energy transfer decreases about 3-fold in the same temperature range in which the fluorescence rises and the two effects are abviously correlated.

Discussion

The fluorescence emission spectrum of cells which contain reaction centers and two antenna pigment complexes shows three emision bands (Fig. 3). The highest fluorescence yield was obtained from the *B*-870 complex, especially

at 77 K although *B*-870 is mostly a minor antenna component [1—3]. *B*-870 is thought to be directly associated with reaction centers [1—3,15]. Thus, most of the energy, which cannot be used for photochemistry is delivered as fluorescence from the antenna complex *B*-870.

In all preparations which contain the *B*-800—850 complex *B*-800 fluorescence is observed at room temperature. From the assumption that the excitation density in both pigment pools will be rapidly equilibrated before any significant loss of excitation energy has occurred, which is especially true for the isolated *B* 800—850 complex or the reaction center-less mutants it follows that:

$$R(T) = \left(\frac{\phi(B\text{-}800)}{\phi(B\text{-}850)}\right)_T = \frac{N800}{N850} \cdot e^{-\Delta E/kT} \tag{2}$$

assuming equal rate constants for fluorescence in *B*-800 and *B*-850. In Eqn. 2 $r(T)$ has been defined as the ratio of $\phi(B\text{-}800)$ to $\phi(B\text{-}850)$ at a certain temperature T, ΔE is the energy difference between *B*-800 and *B*-850, $N800$ and $N850$ are the concentrations of *B*-800 and *B*-850, respectively. If $N800/N850 = 0.5$ it follows that $r(300) = 0.015$. Experimentally the ratio of fluorescence yields at 300 K was found to be 0.005; this may indicate that a thermal equilibrium has not been established or that the rate constants for fluorescence from *B*-800 and *B*-850 are not identical. The former possibility must be taken quite seriously as the rate constant for back transfer from *B*-850 to *B*-800 may easily be of the same order of magnitude as the rate constant for excitation deactivation in *B*-850 and thus give rise to an increased *B*-850 fluorescence relative to *B*-800.

The *B*-800 emission disappears completely if the temperature is lowered from 300 K to 100 K. This decrease must in large part be ascribed to the decrease of the temperature dependent factor in Eqn. 2, or:

$$\frac{r(100)}{r(300)} = \frac{e^{-\Delta E/k \cdot 100}}{e^{-\Delta E/k \cdot 300}} \simeq \frac{1}{1200}$$

This result is of course based on the assumption that the excitation distribution among both pigment pools is in equilibrium before deexcitation occurs. Although that may not be absolutely true, the temperature dependent factor in Eqn. 2 is certainly the predominant factor for the reduction of *B*-800 emission in the temperature range 300 K to 100 K.

Further lowering of the temperature to 4 K results in a small increase of the *B*-800 emission, $r(4) \simeq 4 \cdot 10^{-4}$, which is rather low but clearly observable. This increase of the *B*-800 emission in this temperature region is most likely due to a slowing down of the rate of energy transfer from *B*-800 to *B*-850 at these low temperatures. The rate of energy transfer depends strongly on the value of the overlap integral in the Förster equation, due to band sharpening this overlap integral may decrease rather dramatically [22].

The rate of energy transfer from *B*-800 to *B*-850 at 4 K is of course still rather high, as more than 99% of the absorbed excitation energy arrives in *B*-850. Energy transfer from *B*-800 to *B*-850 at these low temperatures is almost irreversible due to the large thermal factor involved. The following model is assumed for energy transfer in the *B*-800—850 light-harvesting pigment protein. A *B*-800 molecule can only transfer its excitation energy to a

neighbouring *B*-850 molecule, at a rate k_{ET} or loose the energy as fluorescence, heat or triplet formation, rate k_L. If energy transfer from *B*-800 to *B*-850 is considered irreversible at 4 K the following simple equation can be derived for the rate of energy transfer from *B*-800 to *B*-850.

$$k_{ET} = \frac{\alpha k_L}{r(4)}$$

where α fraction of excitations absorbed by *B*-800 either directly or via carotenoid absorption. Using $r(4) = 4 \cdot 10^{-4}$; $k_L = 2.2 \cdot 10^8\ s^{-1}$ and $\alpha \simeq \frac{1}{3}$ for 590 nm excitation light it follows that $k_{ET} = 2 \cdot 10^{11}\ s^{-1}$ still a fairly large number.

It seems not impossible that this rate decreases a factor of ten upon cooling from 300 K to 4 K [17,20,22], which means that at room temperature $k_{ET} \simeq 10^{12}$—$10^{13}\ s^{-1}$ for *B*-800 to *B*-850 energy transfer.

From these results it is possible to deduce some geometrical properties of the *B*-800—850 light-harvesting complex. The *B*-850 moiety contains presumably two molecules BChl per 10 000 polypeptides, while the *B*-800 moiety seems to contain one molecule BChl and one molecule carotenoid [6,8]. The fact that at all temperatures $\phi(B\text{-}800)/\phi(B\text{-}850)$ is independent of the wavelength of excitation (carotenoid or bacteriochlorophyll) suggests that an excited carotenoid molecule can transfer its excitation energy with about equal probabilities to either *B*-800 or *B*-850 and this means that the carotenoid may be arranged such that the *B*-800 and the *B*-850 molecules are at about equal distances from the carotenoid. Further studies on the molecular arrangements of pigment and protein molecules in light-harvesting complexes may help to understand in more detail the deexcitation mechanisms active in *B*-870, *B*-850, *B*-800 and the carotenoid molecules [23].

Membranes containing only *B*-800—850 complex show a linear relation between the intensity of excitation light and relative fluorescence yield over a large range of exciting light intensities (Fig. 6b). Under our experimental conditions saturation was not observed. The different slopes observed with strains equipped with reaction centers suggest that in the lower range of exciting light energy the reaction centers are active and use a considerable portion of excitation energy while at higher light intensities most of the excitation energy is finally lost as fluorescence or be radiation-less deexcitation (Fig. 6b). This idea is supported by the observed fluorescence yield at low temperatures (Fig. 8).

The result that the fluorescence increases, observed in the isolated *B*-800—850 light-harvesting complex, match the decrease of the rate of energy transfer in *B*-800—850 complexes argues strongly for the existence of a quencher in the light-harvesting complex, which apparent activity becomes less if the rate of energy transfer in the complex decreases upon lowering the temperature. If the process of energy transfer is considered a diffusion type process, then the average number of BChl molecules visited during the lifetime of the excitation depends strongly on k_{ET}. If the quencher is considered to be one of the antenna BChl molecules of the complex than the probability that the excitation gets near this quenching antenna molecule depends on k_{ET}. An exact description of the process will depend on the exact value of k_{ET}, the efficiency of the quencher, the molecular arrangement of the pigments in the aggregate etc. As the observed effects in the light-harvesting complex occur in the same temperature

range and have approximately an equal magnitude as similar effect observed in intact systems, with their reaction centers inactive (for example P^+X^-), we might tentatively conclude that energy transfer in the isolated *B*-800—850 aggregate proceeds in the same way as in the intact antenna [6,22,23].

Acknowledgements

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