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Energy transfer in the photosynthetic antenna system of the purple non-sulfur bacterium *Rhodopseudomonas cryptolactis*

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Abstract

Energy transfer in the antenna of the purple non-sulfur bacterium *Rhodopseudomonas cryptolactis* was studied by means of fluorescence and transient absorption measurements. Different growth conditions resulted in three cultures which differed in the composition of the peripheral antenna (B800-820, B800-850 or a mixture of both). Oxidation of the primary electron donor caused an increase of the fluorescence yield of the core complex, B880, and of B800-850, but not of B800-820, indicating energy transfer from B880 to B800-850, but not to B800-820. Singlet-singlet annihilation measurements showed that the number of bacteriochlorophylls of B880 between which energy transfer can occur corresponds to one or two photosynthetic units only (40 to 70 BChls), for all the three cultures studied. These results are explained by a model for *Rps. cryptolactis* in which each B880 unit is associated with its own complement of B800-850. The B800-850 complexes do not appear to form an interconnecting network. Time-resolved transient absorption measurements showed trapping rates by open and closed reaction centres of $(50\ ps)^{-1}$ and $(200\ ps)^{-1}$, respectively. Time constants of energy transfer from B800-850 to B880 or from B800-820 to other complexes were 12–15 ps.

Keywords: Energy transfer; Antenna; Excitation annihilation; Purple bacterium; (*Rps. cryptolactis*)

1. Introduction

In purple bacteria, the antenna and reaction centre pigments are contained in pigment-protein complexes which are localised in the intracytoplasmic membrane. These membranes either form extensive invaginations or are folded into parallel, densely packed lamellae [1]. The reaction centre complexes and the antenna complexes are in close contact with each other. The main function of antenna systems is to absorb light energy and to transfer this to the reaction centres [2]. In general, the efficiency of this energy transfer, which forms the first step in all photosynthetic processes, is very high.

Little is known about the way in which the antenna complexes are organised within the photosynthetic membrane. Monger and Parson [3], on basis of experiments with *Rhodobacter sphaeroides*, proposed a model in which the core (B875)-reaction centre complexes form large aggregates, surrounded by the peripheral complexes (B800-850). However, studies of Deinum et al. [4] did not confirm this model. This paper describes a series of experiments performed on *Rhodopseudomonas cryptolactis* which is a newly described species of purple non-sulfur photosynthetic bacteria [5]. It is one of a growing group of purple bacteria, such as *Rps. acidophila* [6] and *Rps. palustris* [7], which are characterised by their ability to synthesise more than one spectral type of peripheral antenna complex (in this case B800-850 and B800-820). The type of peripheral antenna which is synthesised depends upon the light-intensity at which the cells are grown [5]. This species therefore offered us the opportunity to see whether the conclusions of our recent study on the energy

Abbreviations: BChl, bacteriochlorophyll; B800-820, B800-850, antenna complexes with Q_y-band absorption maxima at 800 nm and 820 or 850 nm, respectively; B880, antenna complex with Q_y-band absorption maximum at 880 nm; PMS, *N*-methylphenazonium metasulfate.

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transfer properties of *Rps. acidophila* [4] were generally applicable.

Changes of the fluorescence yield upon oxidation of the primary electron donor of the reaction centres and fluorescence quenching by singlet-singlet annihilation were studied. The latter measurements provided us with information about the number of antenna BChl molecules between which energy transfer can occur. The results differ from those obtained with *Rps. acidophila* [4] in that for *Rps. cryptolactis* small domains of B880 were found irrespective of the presence of a B800-850 antenna, suggesting the absence of an interconnecting network of B800-850 as in *Rps. acidophila*. Time-resolved transient absorption measurements were performed yielding information about the excitation energy transfer rates between the peripheral and core antennae and to the reaction centres.

2. Materials and methods

Rhodopseudomonas cryptolactis was grown anaerobically at 35° C in the medium THERMED [5]. Pyruvate and ammonium chloride served as the main carbon and nitrogen sources, respectively. The cultures were grown at three different light intensities, of 150, 500 and 5000 lux, respectively. This resulted in different antenna compositions, as demonstrated by the absorption spectra (Fig. 1).

Membrane fragments were suspended in a buffer containing 20 mM Tris (pH 8.0) with 30% glycerol (v/v) added in order to reduce the light scattering and to avoid centrifugation effects during the time-resolved transient absorption measurements. The fluorescence emission and annihilation measurements were performed under anaerobic conditions. For the transient absorption measurements ascorbate (40 mM) and PMS (20 μM) were used in order to keep the primary donor in the reduced state.

Fluorescence was measured by means of the spectrofluorimeter described elsewhere [8]. The sample was excited either by a frequency doubled Nd-YAG laser with a maximum pulse energy of about 5 mJ/cm^2 at 532 nm and a pulse duration of approx. 25 ps or by a low intensity xenon flash with filters providing a band width of 40 nm, centred at 520 nm. The fluorescence passed a monochromator with a resolution set at 2 or 4 nm for fluorescence emission and annihilation measurements, respectively. Continuous background illumination, filtered by a Schott BG-18 filter, was used for those experiments where the primary donor was kept in the oxidised state. The apparatus used for the absorption and the fluorescence excitation measurements was described in Ref. [9]. Transient absorption measurements were performed with a synchronously pumped dye laser in a one-colour pump-probe configuration using a rotary sample holder. The angle between the polarisation of pump and probe beams was set at the magic angle of 54.7° by means of a Glan-Thomson polariser. The instrumental time response was determined by the auto-correlation trace with a FWHM of 4–6 ps. The experimental set-up and the double modulation technique used for detection of the transient absorption signal were described elsewhere [10].

3. Results and interpretation

3.1. Absorption spectra

The absorption spectrum of the low light culture of *Rps. cryptolactis* (Fig. 1A) shows an absorption band at 822 nm (827 nm at low temperature) in the absorption spectra which can be ascribed to the presence of a B800-820 antenna complex. At low temperature, a weak absorption band at 864 nm is also visible, indicating that a small amount of B800-850 is present. The absorption band near 876 nm (894 nm at low temperature) is due to the B880

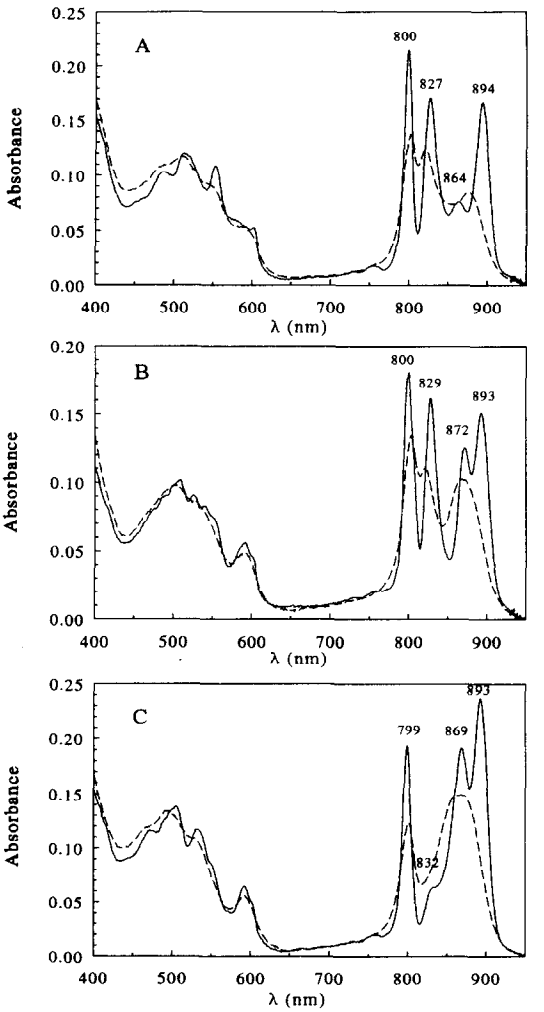

Fig. 1. Absorption spectra of membranes of *Rps. cryptolactis* grown at three different light intensities, measured at 6 K (solid line) and 298 K (dashed line). (A) Low light (150 lux); (B) intermediate light (500 lux); (C) high light (5000 lux).

core complex. The high light culture of *Rps. cryptolactis* shows an absorption band at 869 nm at low temperature (Fig. 1C) due to the presence of a B800-850 antenna complex. The presence of the B880 complex is again demonstrated by an absorption band at 894 nm. At room temperature the B880 absorption is only visible as a weak shoulder on the B800-850 absorption band which dominates the absorption spectrum, while a weak band at 832 nm reveals the presence of a small residual of B800-820. The low-temperature absorption spectrum of the intermediate light culture of *Rps. cryptolactis* (Fig. 1B) revealed the presence of all three antenna complexes.

3.2. Variable fluorescence

Upon oxidation of the primary donor of purple bacteria one generally observes an increase of the fluorescence yield due to less efficient energy transfer to the reaction centre. Fluorescence emission spectra were measured with the primary donor in the reduced and in the oxidised state, respectively. The latter condition was brought about by continuous background illumination. The sample was excited by a weak xenon flash.

The fluorescence spectra are shown in Fig. 2. The three cultures showed a fluorescence maximum near 900 nm, due to fluorescence from B880. Photooxidation of the primary donor caused an increase of the fluorescence at this wavelength by a factor of 2.5 for all three cultures when measured with an extremely weak, non actinic, xenon flash. The measurements shown in Fig. 2 were performed with a higher xenon flash intensity in order to improve the signal-to-noise ratio.

For the low light and the intermediate light culture no significant increase of the fluorescence yield was observed in the region below 830 nm upon closing the reaction centres. This indicates that back transfer of energy from the B880 complex to the B800-B820 complex is severely restricted. An increase of fluorescence was observed for the fluorescence from B800-850 (Fig. 2, B and C). However, for both the high and intermediate light culture the increase of fluorescence was somewhat lower than that of the B880 complex which can obviously be the case if energy equilibration between the two complexes is not extremely fast. This confirms the notion that only the B880 complex is in direct contact to the reaction centre complex [2].

3.3. Fluorescence spectra at high and low excitation densities

Energy transfer from pigments absorbing at shorter wavelengths to pigments absorbing at longer wavelengths will lead to a higher extent of singlet-singlet annihilation in the B880 complex than in the peripheral antenna complexes [4]. Comparison of the fluorescence spectra at low excitation densities to those obtained at high excitation densities yields information about the extent of annihilation as a function of the emission wavelength.

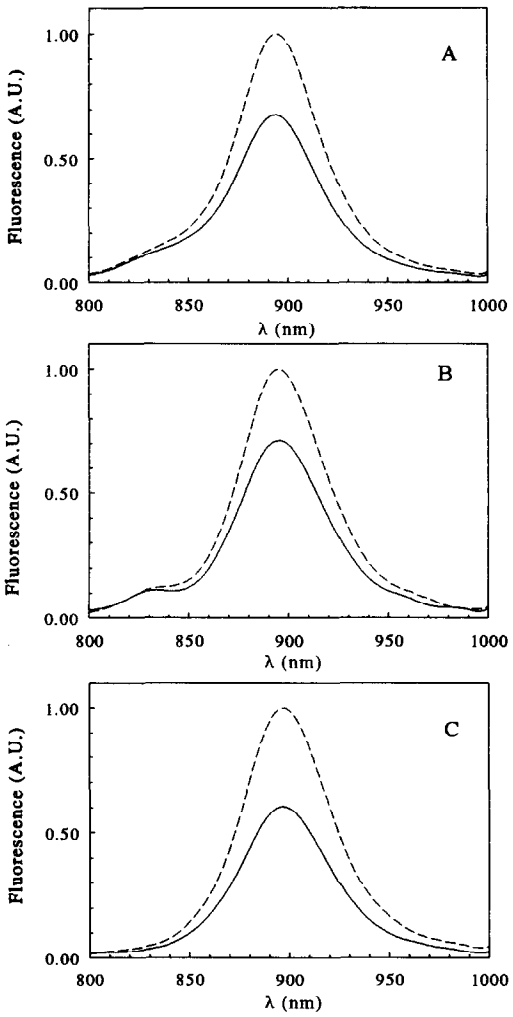

Fig. 2. Fluorescence emission spectra of the low light culture (A), the intermediate light culture (B) and the high light culture (C) obtained with a low intensity xenon flash, with the primary donor in the reduced state (solid line) and in the oxidised state (dashed line), respectively.

Fluorescence emission measurements were performed with oxidised reaction centres in the presence of continuous background illumination. In order to create high excitation densities in the antenna the sample was excited with a 25 ps laser flash with an energy of approx. 5 mJ. For the low intensity fluorescence measurements the sample was excited by a weak xenon flash.

Spectra obtained for the low light culture are shown in Fig. 3. They were normalised in the region above 900 nm where only fluorescence from the B880 complex occurs. The extent of annihilation in B880 exceeded that in B800-820. This is due to a rapid energy transfer from B800-820 to the B880 complex, resulting in a much shorter lifetime in B800-820. After subtraction of the two spectra a difference spectrum with a band around 835 nm was obtained which can be ascribed to the B800-820 complex. Similar

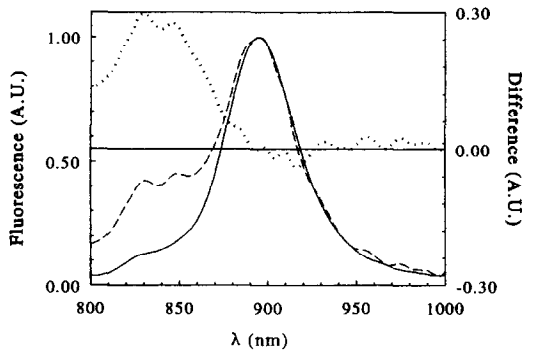

Fig. 3. Fluorescence spectra of the low light culture, obtained with a low intensity xenon flash (solid line) and with a high intensity laser flash (dashed line), respectively. The spectra were normalized in the region above 900 nm. The dotted line represents the difference of the two spectra. The reaction centres were kept in the oxidised state by means of background illumination.

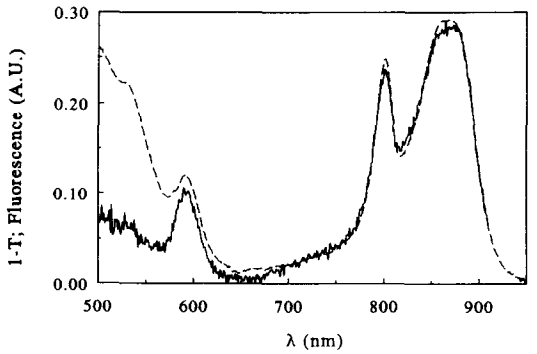

Fig. 4. Fluorescence excitation spectrum (solid line) and absorption ($1-T$) spectrum (dashed line) of the high light culture. The fluorescence was recorded at 920 nm.

results were obtained with the intermediate and high light cultures. For both cultures we observed less annihilation in B800-850 than in B880 (data not shown).

3.4. Domain sizes

The fluorescence yield measured at one specific wavelength as a function of the excitation energy can provide information about the domain size of the antenna complex, i.e., the number of BChl molecules within one complex between which energy transfer can occur. Paillotin et al. [11] derived, under certain assumptions, the following expression for the total fluorescence yield, $\phi(z)$, as a function of the average number of excitations (z) in a domain for a system with all reaction centres in a fixed state:

$$\phi(z) = \phi_o\left(1 + \sum_{k=1}^{\infty} \frac{1}{k+1} \frac{(-z)^k}{(r+1)\ldots(r+k)}\right) \qquad (1)$$

The parameter r denotes the ratio of the mono-excitation decay rate (the overall rate of decay due to trapping and loss for a single excitation on a domain) and the bi-excitation decay rate (the overall rate of decay due to annihilation for a pair of excitations on a domain). ϕ_0 describes the fluorescence yield when no annihilation occurs, i.e., at low excitation energy intensities. For various values of r we can thus calculate the fluorescence yield as a function of z. By comparing these simulations with measurements of the fluorescence yield, at one specific wavelength, versus the pulse intensity (the annihilation curves), we obtain information about the efficiency of annihilation (r) and about the domain size of the antenna complexes. It should be noted that, for values of r higher than 2–5, the curves become very similar and the calculated domain sizes must be considered to be lower limits. Our measurements were performed with the primary donor in the oxidised state. This was brought about by means of continuous background illumination.

The efficiency for energy transfer to the core antenna for photons absorbed at 532 nm was measured by comparing the fluorescence excitation spectra with the absorption spectra. As an example the fluorescence excitation spectrum of the high light culture is shown (Fig. 4). The energy transfer efficiencies for photons absorbed at 532 nm were found to be 0.27 for the low light, 0.35 for the intermediate light and 0.28 for the high light culture, respectively. Similar low efficiencies for energy transfer from carotenoids to BChl have been observed in some other species of purple bacteria [12,13]. The efficiency for energy transfer from the peripheral antennae, B800-820 and B800-850, to B880 was close to 100%. For analysing the data, the excitation energy transfer efficiencies mentioned above were used. We further assumed the extinction coefficients at the Q_y maxima to be 140 mM^{-1} cm^{-1} for the core [14] and 184 mM^{-1} cm^{-1} at the maxima near 820 and 850 for the peripheral antennae [15]. N, the number of BChl molecules per domain, was calculated from the intensity at which $z = 1$.

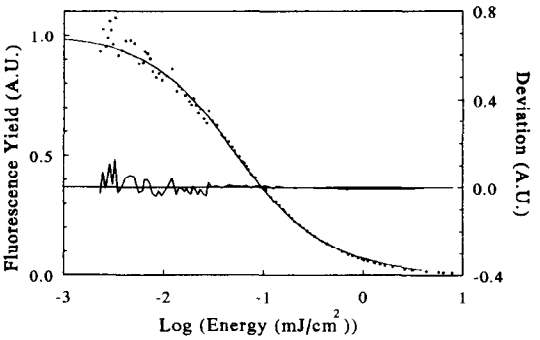

Fig. 5. The relative fluorescence yield at 930 nm of the low light culture, as a function of the incident energy density of the excitation flash, normalised at low energy densities. The primary donor was kept in the oxidised state by means of continuous background illumination. The data were fitted with Eq. (1) (see text). Deviations from the fits are also shown.

The annihilation curves were recorded at 930 nm. For the low light culture (Fig. 5), the curve could be fitted with $r = 1.3$ and the number of connected BChl molecules (N) was found to be 200 ± 40. For the intermediate and the high light cultures, higher values of r and N were obtained (data not shown).

In the above analyses it was assumed that annihilation occurs only in B880. However, only a relatively small fraction of the excitations in B880 result from direct absorption by the carotenoids of the core; most of the excitations will reach B880 by energy transfer from the peripheral complexes. This fraction is difficult to determine exactly, but as judged from the absorption spectra, at low excitation energies it will be more than 60% for all

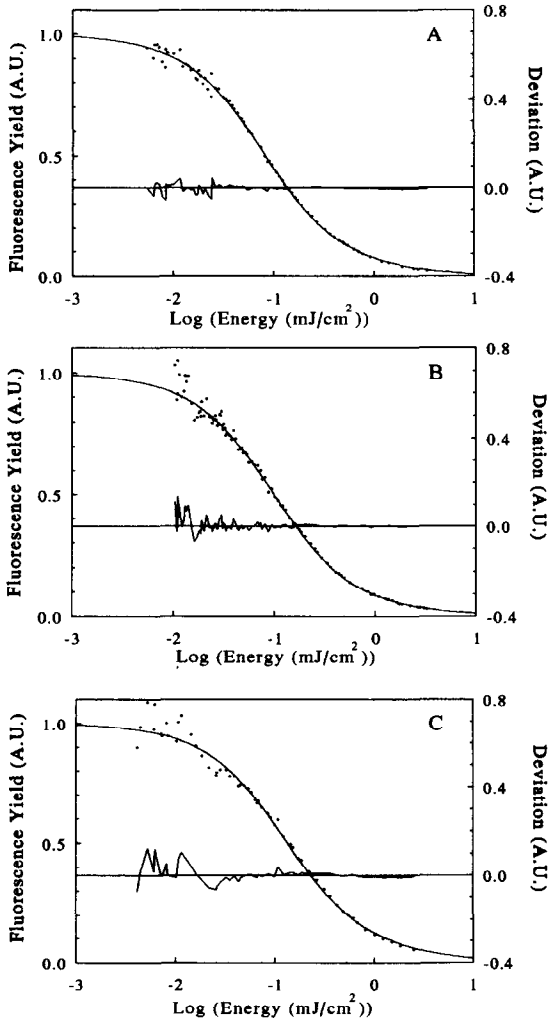

Fig. 6. The relative fluorescence yield of B880 corrected for annihilation in the peripheral antenna (see text) as a function of the incident energy density of the excitation flash. The fluorescence yield was normalised at low energy densities. It was assumed that, at low excitation densities, 60% of the excitations reached B880 by energy transfer from the peripheral antennae and that in the intermediate light culture B800-820 and B800-850 contributed in a ratio of 3:2 to energy transfer. The corrected curves were fitted with Eq. (1) (see text). (A) Low light culture; (B) intermediate light culture; (C) high light culture.

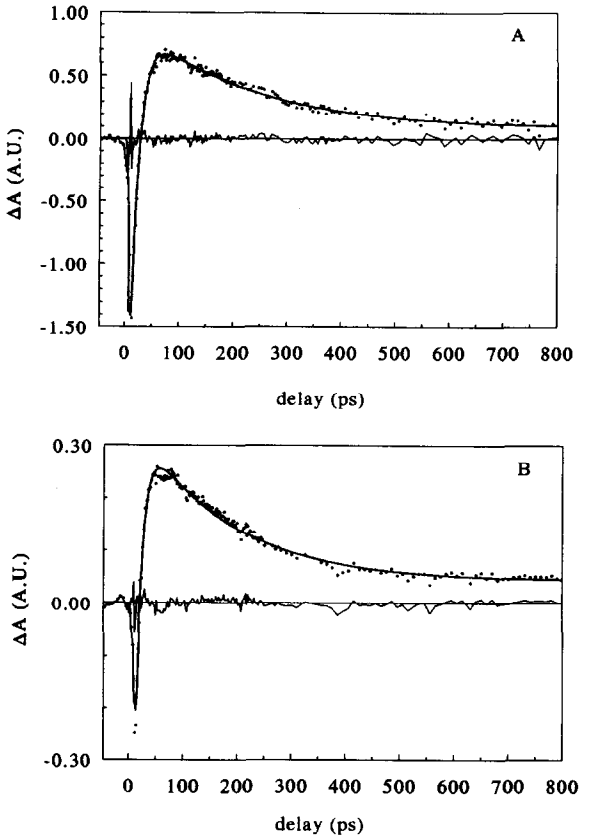

Fig. 7. One-colour time-resolved transient absorption measurements at 820 nm of the low light (A) and intermediate light (B) culture, with the primary donor in the oxidised state. In (A), the data were fitted with time constants of 15 ps for the reverse of the initial bleaching and of 220 ps for the final decay, reflecting energy transfer from B800-820 to B880 and from B880 to closed reaction centres, respectively (see text). For (B), the corresponding time constants were 12 and 170 ps, respectively. In both cases a minor long-lived component was also observed. The relative amplitudes of the three components were −1.0, 0.27 and 0.03 for (A) and −1.0, 0.38 and 0.05 for (B). The residuals of the fits are also shown.

Table 1
Domain sizes in B880

Culture	Fraction (%)	r	Domain size (BChls)
Low light	60	0.3	66
	80	0.25	55
	100	0.0	32
Intermediate light	60	0.3	53
	80	0.1	32
High light	60	0.6	73
	80	0.25	43

The data were obtained from analysis of the annihilation curves at 930 nm after correction for annihilation in the peripheral antenna (see text). The correction was calculated for different fractions of excitations reaching B880 via the peripheral antenna at low excitations densities (second column). It was assumed that in the intermediate light culture B800-820 and B800-850 contributed in a ratio of 3:2 to energy transfer.

three cultures. This means that annihilation processes in B800-820 and B800-850, albeit less than in B880 (Fig. 3), cannot be neglected. We therefore determined the annihilation curves for fluorescence emitted by B800-820 and B800-850 at 840 and 864 nm, respectively, for the three cultures (data not shown) and applied a correction to the annihilation curves at 930 nm [16]. For the purpose of this calculation it was assumed that energy transfer from B800-850 to B880 was unidirectional. Examples of such corrected curves are shown in Fig. 6. Much lower r-values could now be applied to the fits and consequently much smaller domains were obtained. It turned out that in the range above 60% the results were not very sensitive to the fraction of photons transferred from the peripheral complexes, as shown in Table 1. The lowest numbers are obtained in the (imaginary) case of no direct absorption by B880.

We conclude that the B880 antenna complex consists of relatively small units of interconnected BChls in all three cultures. The size of these units (40–70 BChls) does not appear to be much larger than the number of BChls associated with one reaction centre [17].

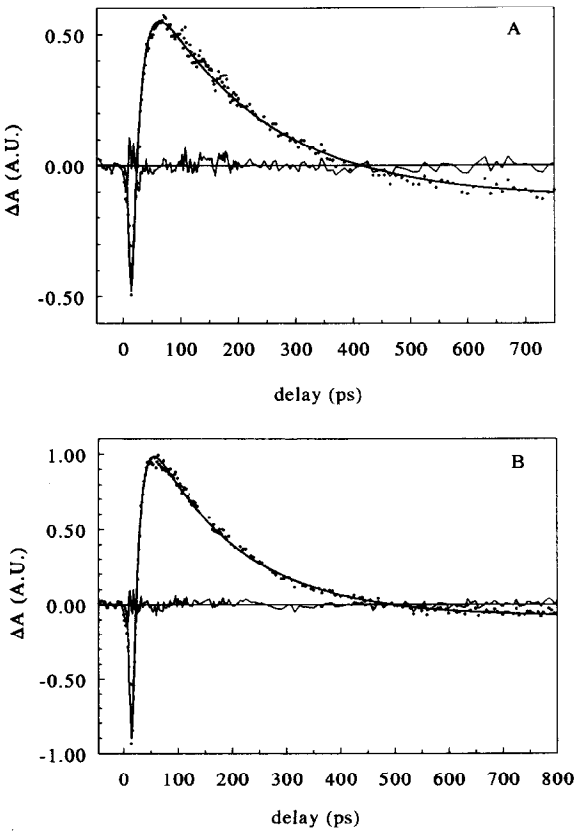

Fig. 8. One-colour time-resolved transient absorption measurements at 862 nm of the intermediate light (A) and high light (B) culture, with the primary donor in the oxidised state. In (A), the data were fitted with time constants of 15 ps for the reverse of the initial bleaching and of 200 ps for the final decay, reflecting energy transfer from B800-850 to B880 and from B880 to closed reaction centres, respectively (see text). For (B), the corresponding time constants were 12 and 165 ps, respectively. In both cases a minor long-lived component was also observed. The relative amplitudes of the three components were −1.0, 0.56 and −0.07 for (A) and −1.0, 0.45 and −0.02 for (B).

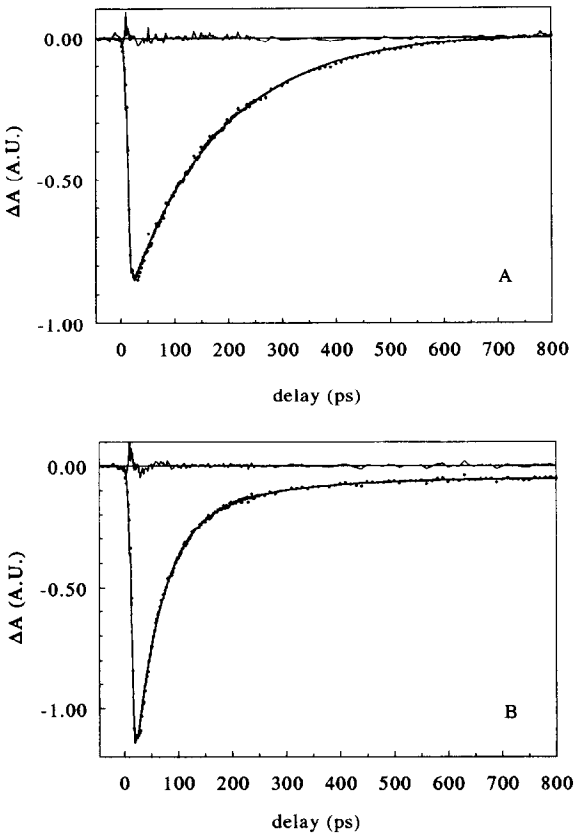

Fig. 9. One-colour transient absorption measurements performed on the intermediate light culture at 900 nm with the primary donor in the oxidised (A) and in the reduced (B) state. The data were fitted with time constants of 47 and 170 ps, reflecting energy transfer from the core antenna to open and closed reaction centres, respectively (see text), together with a long-lived component. The relative amplitudes of the three components were 0, −1.0 and 0.01 for (A) and −1.0, −0.27 and −0.05 for (B).

3.5. Transient absorption measurements

One-colour transient absorption measurements were performed on all three cultures with excitation and probe wavelengths varying from 810 to 900 nm. For those experiments where the primary donor was kept in the reduced state (open reaction centres) ascorbate (40 mM) and PMS (20 μM) was added to the sample.

The energy transfer rates between the peripheral antennae and the core antenna, for all three cultures, are illustrated in Figs. 7 and 8. For these experiments the reaction centres were in the oxidised state. For the low light culture the initial bleaching at 820 nm, due to excitation of the B800-820 antenna complex, decayed with a time constant of 15 ps due to energy transfer to the B880 antenna (Fig. 7A). The subsequent increase of the absorbance is ascribed

to excited state absorption of the core antenna and decays with a time constant of 220 ps due to energy transfer to the reaction centre. Similar kinetics were observed for the intermediate light culture, with time constants of 12 and 170 ps for excitation at 820 nm (Fig. 7B) and of 15 and 200 ps for excitation at 862 nm (Fig. 8A). For the high light culture time constants were found of 12 and 165 ps for energy transfer from B800-850 to B880 and from B880 to the reaction centre, respectively (Fig. 8B). A minor long-lived kinetic component was observed at all wavelengths. Its amplitude was only 2–7% of the fast component; we ascribe it to a small fraction of "detached" BChl 850.

All three cultures showed an increase of the energy transfer rate from he core antenna to the reaction centre when the reaction centres were kept in the reduced state. Fig. 9 shows the transient absorption signals obtained at 900 nm with the intermediate light culture for reaction centres in the oxidised and reduced state, respectively. With closed reaction centres, the data were fitted with a single exponential decay of 170 ps, in agreement with the experiments of Fig. 7B. With open reaction centres, the data had to be fitted with two time constants of 47 and 170 ps, which indicates that a fraction of the reaction centres was not in the reduced state. The amplitude of the 47 ps component, however, was almost a factor of 4 larger than that of the 170 ps component. The long-lived component in Fig. 9B may be ascribed to generation of the oxidised primary electron donor. For the high light culture (Fig. 10) both sets of measurements had to be fitted with two time constants. In Fig. 10A the dominant decay component was one of 190 ps, and presumably represents energy transfer to closed reaction centres. The presence of a 50 ps component indicates, however, that not all reaction centres were closed in this experiment. The 50 ps component was the dominant one in Fig. 10B, indicating that most of the reaction centres were open in this case. We have no ready explanation for the minor long-lived components in these experiments.

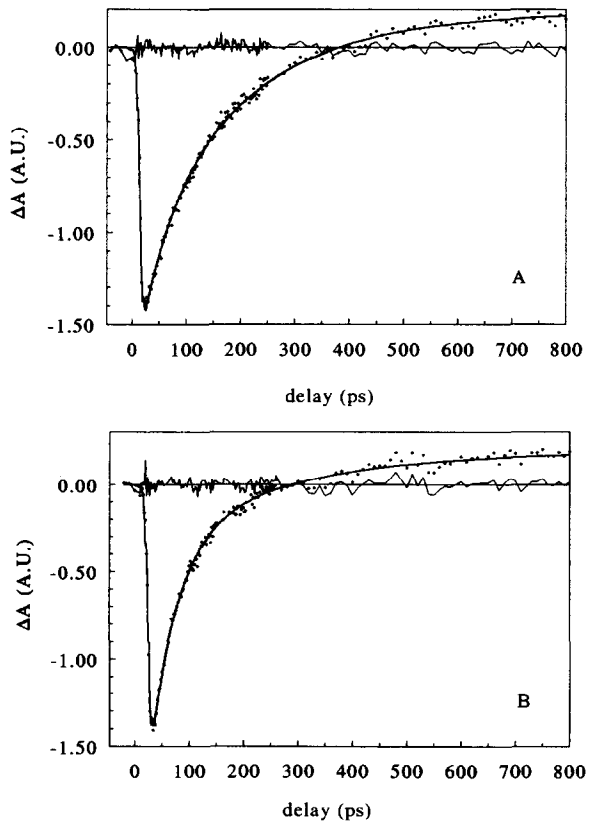

Fig. 10. One-colour transient absorption measurements performed on the high light culture at 900 nm with the primary donor in the oxidised (A) and in the reduced (B) state. The data were fitted with time constants of 50 and 190 ps and a long-lived component with relative amplitudes of −0.38, −1.0 and 0.15. For (B) the time constants were 50 and 240 ps, with relative amplitudes of −1.0 and −0.46, and 0.15 for the long-lived component.

4. Conclusions

The emission spectra of the variable and the base fluorescence (Fig. 2) clearly show that in *Rps. cryptolactis*, as in *Rps. acidophila* [4], the excitation energy can be transferred from B880 to B800-850, but not to B800-820. In contrast to *Rps. acidophila* [4], however, the domains for energy transfer for B880 appear to be about the same for the three cultures studied and to contain one or two photosynthetic units only, i.e., one or two core-reaction centre complexes. The model proposed for *Rps. acidophila*, where the B880 complexes are energetically connected by large arrays of B800-850 complexes [4] therefore does not appear to apply to *Rps. cryptolactis*. The model thus has to be replaced by one where each B880 unit is associated with its own complement of B800-850, without an extensive interconnecting network of B800-850 complexes. For wild-type *Rb. sphaeroides* no comparable information is available. However, it may be of interest to note here that in mutant M21 [18] and in *Rhodospirillum rubrum* [19], which lack the peripheral antenna, large domains for energy transfer were found. For *R. rubrum* this agrees with the "classical" experiments of Vredenberg and Duysens [20].

Our time-resolved absorption measurements show that the rate constants of trapping by open and closed reaction centres in *Rps. cryptolactis* are about the same as observed in most other species of purple bacteria [2,21–23]: for open reaction centres they are about $(50\ ps)^{-1}$ for the high and the intermediate light culture: with closed reaction centres rate constants of about $(200\ ps)^{-1}$ were observed.

Also the time constants of energy transfer from B800-850 to B880 (12–15 ps) are not very different from those usually observed with other species like *Rb. sphaeroides* [22,24], *Rb. capsulatus* [25], *Chromatium vinosum* [23] and *C. tepidum* [23]. Of particular interest is our observation that the time constant of energy transfer from B800-820

to other complexes is almost the same (15 and 12 ps) in the low and in the intermediate light culture. Since B800-850 is almost completely lacking in the low light culture, this indicates that energy transfer to B880 occurs at the same rate as to B800-850, in spite of the different overlap integrals.

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