Energy transfer and charge separation in the purple non-sulfur bacterium *Roseospirillum parvum*

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Abstract

The antenna reaction centre system of the recently described purple non-sulfur bacterium *Roseospirillum parvum* strain 930I was studied with various spectroscopic techniques. The bacterium contains bacteriochlorophyll (BChl) *a*, 20% of which was esterified with tetrahydrogeranylgeraniol. In the near-infrared, the antenna showed absorption bands at 805 and 909 nm (929 nm at 6 K). Fluorescence bands were located at 925 and 954 nm, at 300 and 6 K, respectively. Fluorescence excitation spectra and time resolved picosecond absorbance difference spectroscopy showed a nearly 100% efficient energy transfer from BChl 805 to BChl 909, with a time constant of only 2.6 ps. This and other evidence indicate that both types of BChl belong to a single LH1 complex. Flash induced difference spectra show that the primary electron donor absorbs at 886 nm, i.e. at 285 cm^{-1} higher energy than the long wavelength antenna band. Nevertheless, the time constant for trapping in the reaction centre was the same as for almost all other purple bacteria: 55 ± 5 ps. The shape as well as the amplitude of the absorbance difference spectrum of the excited antenna indicated exciton interaction and delocalisation of the excited state over the BChl 909 ring, whereas BChl 805 appeared to have a monomeric nature. © 2000 Elsevier Science B.V. All rights reserved.

1. Introduction

The photosynthetic antenna system of purple bacteria usually consists of two types of light harvesting complexes, called LH1 and LH2 [1]. Both antenna complexes are embedded in the cytoplasmic membrane, where they form large circular structures. The three-dimensional structure of LH2 complexes from *Rhodopseudomonas* (*Rps.*) *acidophila* and *Phaeospirillum* (formerly *Rhodospirillum*) *molischianum* have been determined by X-ray diffraction [2,3]. The so-called B800-850 LH2 complexes of these two species were found to possess 9- or 8-fold circu-

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Abbreviations: BChl, bacteriochlorophyll; BPhe, bacteriopheophytin; DHGG, dihydrogeranylgeraniol; GG, geranylgeraniol; HPLC, high pressure liquid chromatography; LH, light harvesting complex; P, phytol; P870, primary electron donor; PMS, *N*-methylphenazonium methosulphate; Q$_A$, Q$_B$, acceptor quinones; THGG, tetrahydrogeranylgeraniol

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lar symmetry, respectively; they contain 18 or 16 bacteriochlorophylls (BChls) *a* absorbing near 850 nm and in addition nine or eight BChls absorbing near 800 nm. The structure of LH1 is not yet known at a high resolution. It forms a ring which presumably encloses the reaction centre [4,5]. The α and β subunits bind 32 (or somewhat fewer [6,7]) BChls *a*, that usually absorb near 880 nm. Some species do not possess LH2 and have only an LH1 antenna, like *Rhodospirillum* (*Rsp.*) *rubrum*.

New species and genera of purple bacteria are regularly described, indicating that the full diversity of this group is still only partially explored. Recently the purple non-sulfur bacterium *Roseospirillum* (*Rss.*) *parvum* strain 930I, with an unusual near-infrared absorption spectrum was isolated from an intertidal microbial mat [8]. Here we report an investigation of this species with various spectroscopic techniques, revealing the unusual characteristics of its light harvesting apparatus.

2. Materials and methods

Rss. parvum strain 930I was grown in 250 ml glass screw cap bottles filled with modified RS medium supplemented with 1.25 mM sulphide as described earlier [8]. Membrane fragments were prepared by sonication of cells suspended in a buffer containing 50 mM Tris-HCl and 1 M NaCl (pH 8.3) and subsequent centrifugation for 5 min at $15\,000 \times g$. The supernatant contained the membrane fragments.

For pigment analysis, the membrane fragments were extracted at 4°C with a 100-fold excess of a mixture of methanol and acetone (1:1 v/v) [7]. The extracts were analysed by reversed phase high pressure liquid chromatography (HPLC) on a C18 silica column (Chrompack Spherisorb 5 ODS2, 250×4.6 mm i.d.) using a mixture of methanol and acetone (9:1 v/v) as eluent at a flow rate of 1 ml/min. Pigment elution was monitored by means of a Jasco MD-915 diode array detector.

Room and low temperature absorption and fluorescence spectroscopy were performed with a single beam spectrophotometer described by Otte [9]. The spectral resolution was 0.5 nm for the absorption measurements, 3 nm for room temperature and 1.5 nm for low temperature fluorescence measurements.
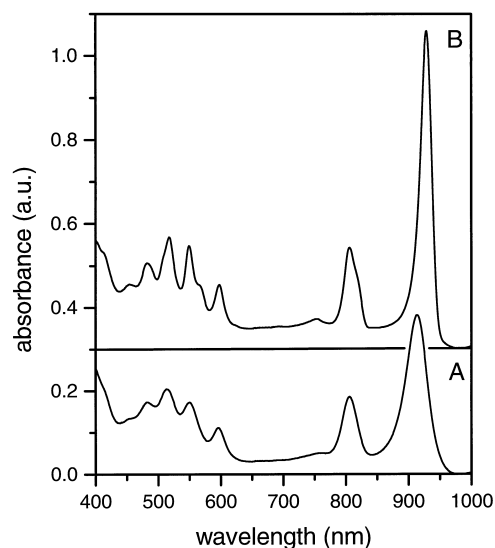

Fig. 1. Absorption spectra of membranes of *Rss. parvum* measured at room temperature (A) and at 6 K (B). Spectrum B was shifted upwards for clarity.

Flash induced absorption changes in the millisecond range were measured as described by Franken and Amesz [10]. Excitation flashes were provided by a Q-switched frequency doubled Nd-YAG laser (15 ns, 532 nm, 90 mJ per pulse). Picosecond absorption changes were measured with a home-built amplified dye laser system, operating at 10 Hz, as described earlier [11]. Kinetics of the antenna signals were fitted with deconvolution of the pulse by simultaneous analysis of the bleaching and of the excited state absorption bands. Measurements at cryogenic temperatures were performed with a Utrecs-LSO (Tartu, Estonia) or an Oxford Instruments helium flow cryostat. To obtain clear samples at low temperature glycerol (66% v/v) was added.

3. Results

3.1. Pigments and absorption spectra

Absorption spectra of membrane fragments of *Rss. parvum* strain 930I were measured at room temperature and at 6 K (Fig. 1). The room temperature spectrum (Fig. 1A) was very similar to that of whole cells (see also [8]), except that it was not distorted by scattered light. The low temperature spectrum
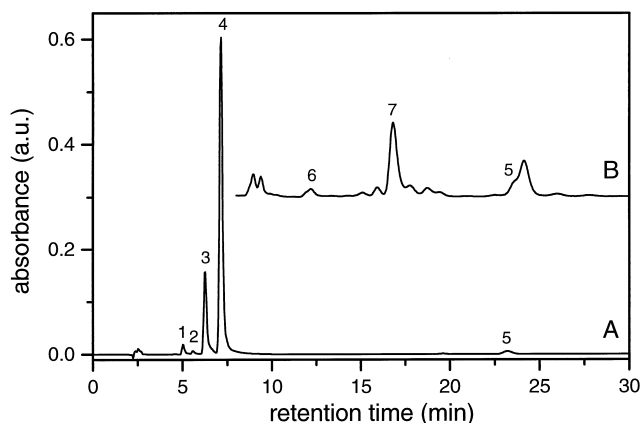
Fig. 2. HPLC elution profiles of membrane extracts detected at 760 nm (A) and at 450 nm (B). The absorbance scales are not comparable. Numbered peaks represent: (1) BChl a_{GG}, (2) BChl a_{DHGG}, (3) BChl a_{THGG}, (4) BChl a_P, (5) BPhe a_P, (6) rhodopin, (7) spirilloxanthin.

showed more clearly defined bands and these facilitated the interpretation of the spectral features.

The absorption spectrum did not resemble that of any known species of purple bacteria. In the near-infrared, the room temperature spectrum (Fig. 1A) showed peaks at 805 and 909 nm. The latter is situated at an unusually long wavelength, comparable only to *Thermochromatium* (formerly *Chromatium*) *tepidum*, which has a band at 918 nm [12]. In the visible region bands are seen at 596 nm (the Q_x transition of BChl *a*) and at 482, 514 and 549 nm. The latter three absorption maxima reflect the presence of spirilloxanthin, the main carotenoid [8]. At 6 K the longest wavelength maximum was shifted to 929 nm while the 805 nm band developed a shoulder at 820 nm (Fig. 1B). A weak band at 755 nm also became visible, due to reaction centre bacteriopheophytin (BPhe) *a*. The bands below 600 nm became more pronounced and several shoulders appeared. At 6 K they were located at 452, 481, 507 (shoulder), 518, 549, 569 (shoulder) and 598 nm. At first sight, the 805 and 820 nm bands might be ascribed to a B800-820 LH2 complex and the long wavelength band to LH1, but, as will be argued below, it is more probable that all these bands belong to a single light harvesting complex. In the following we shall refer to the pigments absorbing at 805 and 909 nm at room temperature as BChl 805 and BChl 909, respectively.

As reported earlier, BChl *a* is the only type of

bacteriochlorophyll present in *Rss. parvum*. Thin layer chromatography showed that spirilloxanthin is the main carotenoid [8]. The pigment composition of membrane fragments of *Rss. parvum* was determined in more detail by HPLC analysis (Fig. 2). They were found to contain BChl *a* esterified with phytol as the main pigment (peak 4 in Fig. 2), but in addition an unusually large amount of BChl *a* esterified with tetrahydrogeranylgeraniol (THGG) was detected (peak 3). Purple bacteria usually contain only small amounts ($< 5\%$) of BChl *a* esterified with THGG and other metabolic precursors of phytol [7,13]. In contrast, the amount of BChl a_{THGG} in *Rss. parvum* was 20% of the total BChl *a* content. BPhe *a* eluted at 23 min (peak 5); the ratio of total BChl *a* to BPhe *a* was about 20.

The HPLC analysis also confirmed that the main carotenoid, with a retention time of 17 min, is spirilloxanthin (peak 7). Minor carotenoids are probably metabolic precursors of spirilloxanthin, like rhodopin (peak 6) and the unnumbered peaks in Fig. 2B.

3.2. Energy transfer and charge separation

The properties of the primary electron donor of *Rss. parvum* were studied by means of flash induced absorbance changes. Room temperature absorbance
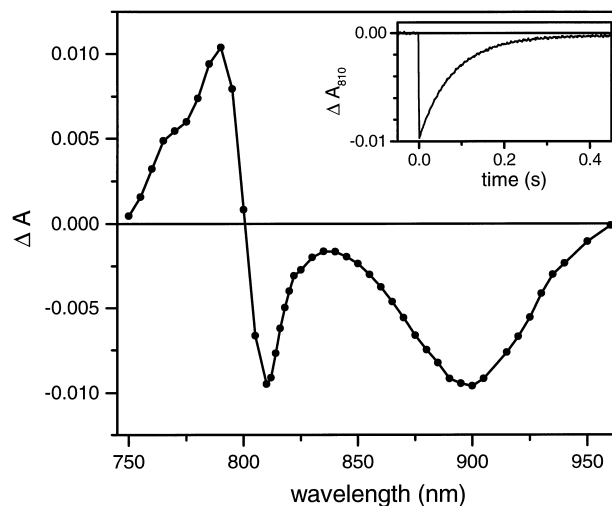

Fig. 3. Absorbance difference spectrum of membranes measured at room temperature. Inset: kinetics at 810 nm. Excitation was performed with a 532 nm 15 ns saturating laser flash. 10 mM *o*-phenanthroline was added to prevent electron transfer from Q_A to Q_B.

difference spectra of isolated membranes were obtained with saturating laser flashes in the presence of 10 mM o-phenanthroline to block electron transfer from Q_A to Q_B. An instantaneous bleaching, followed by a monoexponential decay with a time constant of 80 ms was observed (Fig. 3, inset). This decay can be ascribed to a recombination of the oxidised primary electron donor, $P870^+$ with Q_A^- (we shall use the designation P870 for the primary donor irrespective of the location of its maximum absorbance). The corresponding absorbance difference spectrum is also shown in Fig. 3. The shape of the difference spectrum is typical for $P870^+Q_A^-$ formation in purple bacteria. The bleaching of P870 is centred at 886 nm, a blue shift of the accessory BChls a is seen around 800 nm and the absorption increase at 766 nm can be ascribed to BPhe a.

Fluorescence measurements were performed to determine the efficiency of energy transfer between the BChls a and from the carotenoids to BChl a. For this purpose the excitation spectrum was compared to the corresponding $1-T$ spectrum, where T is the transmission. *Rss. parvum* showed a single emission band at 925 nm at room temperature and at 954 nm at 6 K (Fig. 4). BChl 805 did not show fluorescence at either temperature. From the fluorescence excitation spectra (Fig. 5) it can be seen that this pigment transfers its excitation energy very efficiently to BChl 909. At both temperatures the efficiency of excitation energy

Fig. 5. Fluorescence excitation (solid lines) and $1-T$ spectra (dotted) at room temperature (A) and at 6 K (B). Detection wavelengths were 927 and 954 nm, respectively. The spectra were normalised at the longest wavelength maxima.
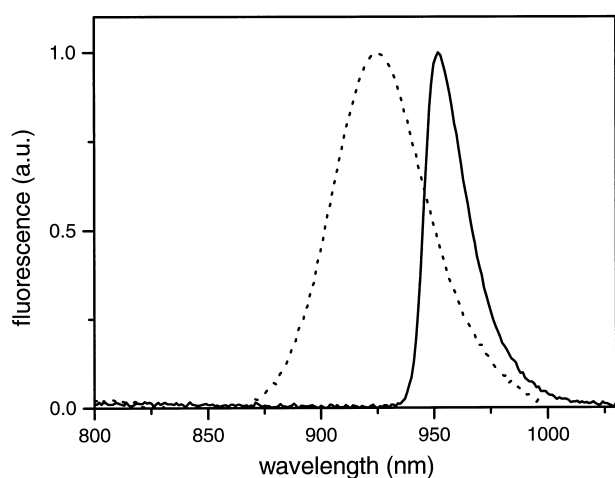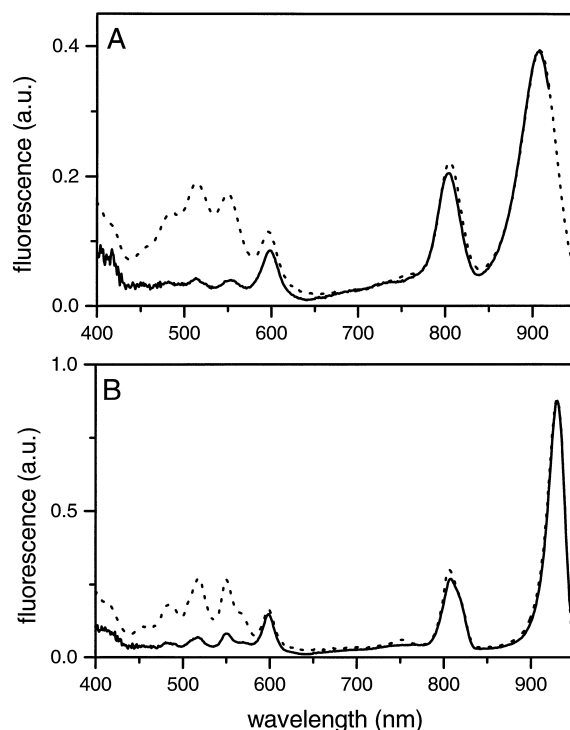

Fig. 4. Fluorescence emission spectra of membranes at room temperature (dotted line) and at 6 K (solid). The excitation wavelength was 590 nm. The spectra were normalised at their maxima.

transfer from carotenoids to BChl a is low, about 25%. Comparable efficiencies were measured for other spirilloxanthin containing purple bacteria: 30–40% in *Rsp. rubrum* [14], and 18–24% in three species of purple sulfur bacteria (M. König et al., in preparation).

In a second approach, energy transfer within the antenna system and to the reaction centre was studied by pump probe spectroscopy in the femtosecond and picosecond time range. The experiments were done at 275 K, in the presence of 10 mM ascorbate and 20 μM N-methylphenazonium methosulphate (PMS) to reduce $P870^+$ between excitation pulses. Fig. 6 shows transient absorbance difference spectra of membranes obtained at various times after excitation with 200 fs pulses at 800 nm. At first a bleaching developed at the excitation wavelength, but this bleaching was rapidly replaced by one at 918 nm, indicating an efficient energy transfer to BChl 909. Kinetics are shown in Fig. 7. A monoexponential decay with a time constant of 2.6 ps was observed at 800 nm; the bleaching at 918 nm developed

with the same time constant. This high rate of energy transfer explains why BChl 805 does not fluoresce either at room temperature or at 6 K. Once the excitation has arrived on BChl 909, the large energy gap of 1420 cm^{-1} between the two pigments will effectively prevent back transfer of excitation energy to BChl 805 and will shift the thermal equilibrium of the excited state almost completely to BChl 909, even at room temperature.

The bleaching at 918 nm reached a maximum amplitude after approx. 10 ps. It was accompanied by a positive absorbance change around 880 nm signifying excited state absorption and indicating exciton interaction between the BChls [15]. Similar excited state absorption bands have been observed with antenna complexes of various groups of photosynthetic bacteria [16–19]. The bleaching at 918 nm decayed with a time constant of 55 ± 5 ps. At 30 ps after excitation, the characteristic blue shift of the reaction centre band at 800 nm started to appear, indicating the formation of oxidised P870. Eventually the excited states of BChl 909 disappeared completely and the resulting difference spectrum with a broad

Fig. 7. (A) Kinetics of absorbance changes averaged at 797–805 nm (triangles) and 910–927 nm (circles) derived from the difference spectra. (B) Kinetics at 920 nm on a longer time scale. The lines show fits with exponential time constants of 2.6 ps (decay at 800 nm and rise at 920 nm) and 55 ps (decay at 920 nm). No attempt was made to model the kinetics at 920 nm with consecutive rise and decay components.
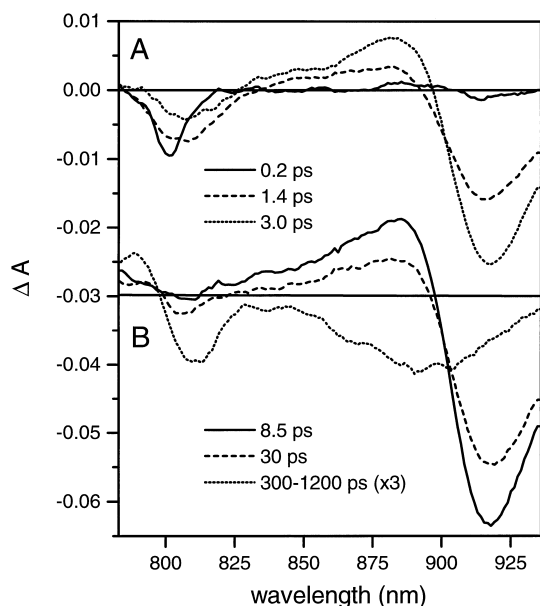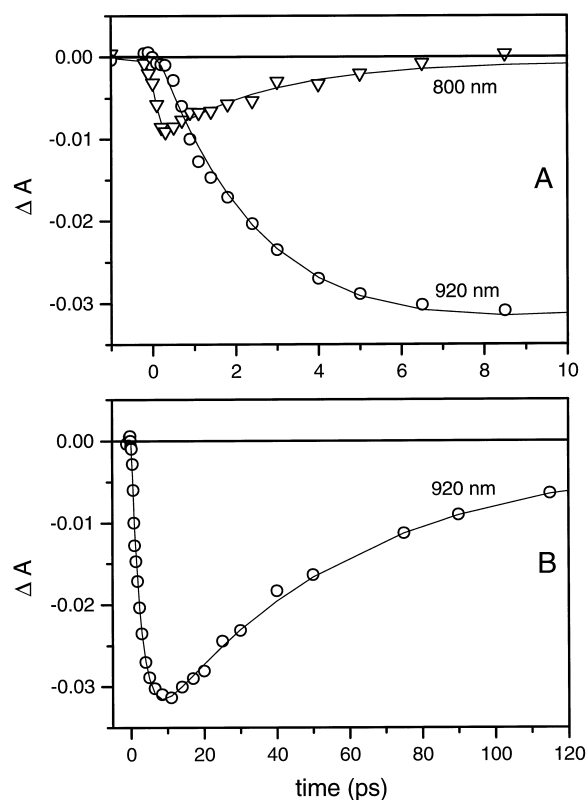

Fig. 6. Time resolved difference spectra of membranes measured at 275 K upon excitation at 800 nm (FWHM: 8 nm), (A) at delays of 0.2 ps (solid line), 1.4 ps (dashed) and 3 ps (dotted) and (B) at delays of 8.5 ps (solid line), 30 ps (dashed) and the average of the spectra recorded between 300 and 1200 ps, three times enlarged (dotted).

bleaching around 900 nm was quite similar to that of P870 photooxidation observed in the millisecond region (shown in Fig. 3). The amplitude of the bleaching of P870^{+}, however, was much smaller than that of the antenna signal, even if one takes into account that the latter contains a contribution by stimulated emission. The same has been observed with other species of purple bacteria [20,21], and this gives yet another indication for exciton interaction in the BChl 909 antenna band [22].

4. Discussion

Rss. parvum shows two clearly defined absorption bands in the BChl *a* Q$_y$ region at 805 and 909 nm, with the 805 nm band developing a shoulder at 820

nm upon cooling to 6 K. The 909 nm band is undoubtedly due to absorption by an LH1 complex. The nature of BChl 805 cannot be determined with certainty from our experiments. However, they provide evidence that BChl 805 is bound to the LH1 complex. First of all, our absorption and excitation spectra exclude the possibility that BChl 805 is part of the reaction centre. Its absorption band is much too large in comparison to that of BPhe *a* that can be observed at 766 nm in the low temperature absorption spectrum (Fig. 1B). Moreover, there is efficient energy transfer to the antenna BChl 909, while energy transfer from the accessory BChls *a* of the reaction centre to the antenna has not been observed in other species under comparable conditions [23–26].

One might speculate that the 805 nm band is due to an LH2 complex, and the observation of a shoulder at 820 nm at low temperature might be taken as evidence for the presence of an LH2 complex of the B800-820 type with a strong 800 nm band, similar to that occurring in *Allochromatium* (formerly *Chromatium*) *vinosum* [27]. However, the amount of LH2 would then be unusually small (less than one per LH1); as far as we know, this has never been observed in purple bacteria that contain both types of antenna complexes [28]. Energy transfer from BChl 805 to BChl 909 is fast compared to that between LH2 and LH1 rings in various other species, for which time constants of 3–15 ps (or even longer) have been reported [29–32].

The time resolved measurements show that the amplitude of the bleaching associated with the excited state of BChl 909 is several times larger than that of BChl 805 (Fig. 6). This phenomenon has been reported earlier in relation to the 850 and 800 nm bands of LH2 [17], and may be explained by exciton interaction and delocalisation of the excited state over several BChl 909 molecules [19]. In contrast, BChl 805 would have a monomeric nature. As mentioned above, the same explanation may apply to the large difference in the amplitudes of the bleaching due to oxidation of P870 and that due to excitation of BChl 909 (Fig. 6).

Considering the above evidence, we tentatively conclude that *Rss. parvum* contains only one type of antenna complex, an LH1 complex with two absorption bands. The structure of this complex may well be comparable to that of the B800-850 LH2 complex of e.g. *Rps. acidophila*, with two parallel rings of BChl *a*.

There are some other examples of phototrophic bacteria having an LH1 complex with more than one absorption band. In some ways, the B806-866 complex of the green filamentous bacterium *Chloroflexus aurantiacus* resembles that of LH1 of purple bacteria [1], and the same may be true for a thermophilic filamentous bacterium with absorption bands at 807 and 910 nm [33]. The BChl *b* containing purple bacteria *Halorhodospira* (*Hlr.*; formerly *Ectothiorhodospira*) *halochloris* and *Halorhodospira abdelmalekii* have room temperature absorption bands at 800 and 1020 nm [1,34,35]. These bands were shown to be part of the same antenna complex (LH1); the ratio of the amplitudes of the 800 and 1020 nm bands is similar to that of the two bands in *Rss. parvum*. The nature of the shoulder at 820 nm in *Rss. parvum* (only visible at low temperature) is not clear, but it should be noted that the 800 nm bands in *Hlr. halochloris* and *abdelmalekii* have even more conspicuous shoulders, at 830 nm [34].

The surprisingly large amount of about 20% BChl *a* esterified with THGG (BChl a_{THGG}) suggests that this particular pigment has a functional role in *Rss. parvum*, and is not just a metabolic intermediate of the synthesis of BChl *a* esterified with phytol (BChl a_P) [13,36]. Studies with *Rsp. rubrum* have shown that the degree of saturation of the alcohol side chain has an effect on the interaction with the surrounding protein and with other pigments [37]. Accordingly, different and specific protein binding sites may exist for both pigment types in *Rss. parvum*. For example, BChl a_{THGG} could be specifically associated with BChl 805 and BChl a_P with BChl 909. Only two other species of purple bacteria have been shown to have the bulk of their BChls esterified with alcohols other than phytol. *Rsp. rubrum* contains only BChl *a* with geranylgeraniol (BChl a_{GG}) [38], *Hlr. halochloris* contains BChl *b* that is esterified with a form of THGG, $\Delta 2,10$-phytadienol [39], but it appears that *Rss. parvum* is the only species containing significant amounts of BChls with two types of alcohol.

The maximum bleaching due to P870 photooxidation is located at 886 nm for membranes of *Rss. parvum* (Fig. 3). This corresponds to an energy gap between LH1 and P870 of 285 cm^{-1} at room temperature, which is the largest in any BChl *a* containing

species reported so far. Some degree of uphill energy transfer from LH1 to P870 is frequently observed in purple bacteria [24,40], but the energy differences are usually much smaller. Nevertheless, the time constant of trapping in *Rss. parvum* (55 ps) is quite normal; time constants of 40–60 ps have been observed in almost all species studied [20,21,31,41,42]. This point is not well understood and merits further investigation.

Photosynthetic characteristics of purple bacteria – presence and type of LH2, organisation of intracytoplasmic membranes, type of BChl (*a* or *b*) and carotenoid composition – do not seem to correlate with the taxonomic subdivisions based on 16S rDNA. *Rss. parvum* is no exception to this rule. It is closely related to the genus *Rhodobium*, but its antenna system appears to be unique, at least among the purple bacteria. Studies of the isolated pigment-protein complex will be necessary to elucidate the actual structural differences with other antenna complexes.

Acknowledgements

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