Biochimica et Biophysica Acta, 635 (1981) 1—12
© Elsevier/North-Holland Biomedical Press

BBA 48003

THE PRIMARY CHARGE SEPARATION, CYTOCHROME OXIDATION AND TRIPLET FORMATION IN PREPARATIONS FROM THE GREEN PHOTOSYNTHETIC BACTERIUM *PROSTHECOCHLORIS AESTUARII*

T. SWARTHOFF, K.M. VAN DER VEEK-HORSLEY and J. AMESZ

Department of Biophysics, Huygens Laboratory of the State University, P.O. Box 9504, 2300 RA Leiden (The Netherlands)

(Received September 8th, 1980)

Key words: Bacteriochlorophyll; Triplet formation; Cytochrome oxidation; Charge separation; Bacterial photosynthesis; (Prosthecochloris aestuarii)

Summary

Flash-induced absorbance changes were measured in intact cells and subcellular preparations of the green photosynthetic bacterium *Prosthecochloris aestuarii*. In Complex I, a membrane vesicle preparation, photooxidation of the primary electron donor, *P*-840, and of cytochrome *c*-553 was observed. Flash excitation of the photosystem pigment complex caused in addition the generation of a bacteriochlorophyll *a* triplet. Triplet formation was the only reaction observed after flash excitation in the reaction center pigment -protein complex. The triplet had a lifetime of 90 μs at 295 K and of 165 μs at 120 K. The amount of triplet formed in a flash increased upon cooling from 295 to 120 K from 0.2 and 0.5 per reaction center to 0.45 and nearly 1 per reaction center in the photosystem pigment and reaction center pigment-protein complex, respectively. Measurements of absorbance changes in the near infrared in the reaction center pigment-protein complex indicate that the triplet is formed in the reaction center and that the reaction center bacteriochlorophyll *a* triplet is that of *P*-840. Formation of a carotenoid triplet did not occur in our preparations.

Illumination with continuous light at 295 K of the reaction center pigment-protein complex produced a stable charge separation (with oxidation of *P*-840 and cytochrome *c*-553) in each reaction center, but with a low efficiency. This low efficiency, and the high yield of triplet formation is probably due to damage of the electron transport chain at the acceptor side of the reaction center of the reaction center pigment-protein complex.

Abbreviations: BChl, bacteriochlorophyll; BPh, bacteriopheophytin; PP complex, photosystem pigment complex; RCPP complex, reaction center pigment-protein complex; *P*-840, reaction center bacteriochlorophyll *a* absorbing near 840 nm.

The halftime for cytochrome c-553 oxidation in Complex I and the photosystem pigment complex was 90 μs at 295 K; below 220 K no cytochrome oxidation occurred. At 120 K $P\text{-}840^+$ was rereduced with a halftime of 20 ms, presumably by a back reaction with a reduced acceptor.

Introduction

During the last years, studies on the bacterial photosynthetic membrane and reaction center have mainly been restricted to cells and subcellular preparations of purple bacteria, and relatively little attention has been paid to the green sulfur bacteria. This is partly due to technical difficulties caused by the high antenna bacteriochlorophyll to reaction center ratio of about 1500 BChl *c* + *a* per reaction center [1,2] in these species, compared to 50—100 BChl *a* per reaction center in purple bacteria. Recently we reported the isolation of photochemically active reaction center preparations from the green photosynthetic bacterium *Prosthecochloris aestuarii* [3]. Starting from Complex I, a membrane vesicle preparation [1,4,5], two different pigment-protein complexes were isolated. The photosystem pigment (PP) complex contains about 75 BChl *a* molecules per reaction center. By removal of the antenna BChl *a* protein complex [6,7], the reaction center pigment-protein (RCPP) complex was obtained, which contains about 35 BChl *a* molecules per reaction center. Both complexes are free of BChl *c*, which pigment is located in the chlorosomes [8,2], and contain about one photooxidizable cytochrome *c*-553 per reaction center, as compared to about three in Complex I [1,3].

In this paper we report a study of the photochemical reactions caused by continuous illumination or flash excitation, both at room temperature and at 80 or 120 K. By comparison of the properties of intact cells, Complex I, the PP complex and the RCPP complex, information was obtained concerning the electron transport in the reaction center and about the structural integrity of the reaction center in the isolated pigment-protein complexes.

Materials and Methods

Prosthecochloris aestuarii, strain 2 K, was grown anaerobically in a mixed culture known as *'Chloropseudomonas ethylica'* [9] as described by Holt et al. [10]. The membrane preparation Complex I, and the reaction center preparations PP and RCPP complex were prepared as previously described [3]. The light-induced absorbance changes were measured as described elsewhere [11, 12]. Xenon flashes (duration at half maximum intensity 13 μs) or continuous light were used as actinic illumination. Infrared light was provided by a combination of Schott RG 715 and RG 780 filters for measurements in the region 370—690 nm; orange light filtered by a Schott AL 606 interference filter for the region 670—900 nm. Suitable interference and absorbance filters were used to protect the photomultiplier from stray actinic light. For measurements at 80 or 120 K, glycerol (50% v/v) was present to prevent crystallization upon cooling.

Results

Fig. 1 shows the kinetics of the absorbance changes at 610 and 553 nm induced by continuous illumination. For Complex I and the PP complex the light-on response at 610 nm, due to $P\text{-}840^+$ formation, was too fast to be measured with the time resolution of the apparatus used for these experiments. The light-on response of the RCPP complex was much slower, which is probably due to a low efficiency of the formation of a stable charge separation, as will be discussed below. The total amount of the photooxidizable cytochrome *c*-553 was about one per reaction center in the PP and RCPP complexes [3]. It was about three per reaction center in Complex I, but two of these cytochromes were only very slowly oxidized by $P\text{-}840^+$, as can be seen from the kinetics at 553 nm. By kinetic analysis of the absorbance changes in Complex I, the spectrum of the relatively rapid phase in the $P\text{-}840^+$ reduction (Fig. 2, solid curve) and the oxidized minus reduced spectrum of cytochrome *c*-553 (Fig. 2, broken curve) were obtained. Below 650 nm, the *P*-840 spectrum was similar to that of *P*-870 in reaction center particles from purple bacteria [13,14], except for a trough at 435 nm.

Fig. 3 shows the light-induced difference spectrum of the PP complex measured at 80 K. A very similar spectrum was obtained upon illumination of Complex I. Except for low temperature sharpening of the bands and the absence of cytochrome oxidation, the spectrum shows the same features as that obtained at room temperature [3]. Thus we may assume that it is due to oxidation of *P*-840 together with the reduction of an acceptor, of which the absorbance changes are probably dominated by those of *P*-840 oxidation. The absorbance changes were completely reversible. The amplitude of the absorbance changes induced by saturating light was about half of that obtained at room temperature [3]. In case of the RCPP complex, absorbance changes at 80 K were only obtained upon illumination with much higher intensities than those used with the PP complex, as will be discussed below.

The difference spectrum at 295 K of the RCPP complex, measured 50 μs after a flash is shown in Fig. 4. The shape of this spectrum is similar to that of

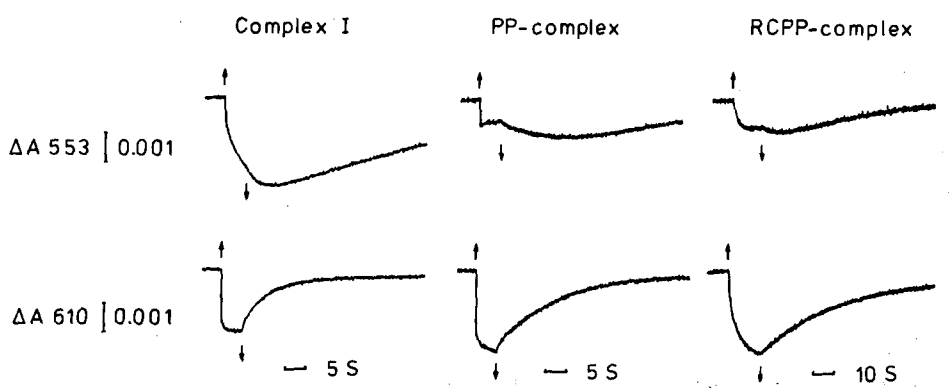

Fig. 1. Kinetics of light-induced absorbance changes at 553 and 610 nm at 295 K of Complex I (A_{810} = 0.80), the PP complex (A_{810} = 1.08) and the RCPP complex (A_{813} = 0.50). Illumination with infrared light; intensity: 20 mW/cm^2.

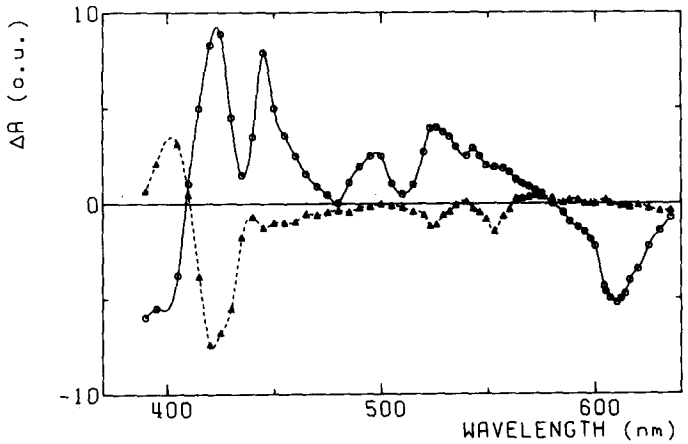

Fig. 2. Absorbance difference spectra (not normalized), obtained by kinetic analysis of the absorbance changes induced by continuous light of Complex I at 295 K.

the spectrum obtained by Monger et al. [15] and Parson et al. [16,17] in preparations of *Rhodopseudomonas sphaeroides* R-26, which spectrum was ascribed to the formation of a BChl *a* triplet. We therefore assume that also in our case a BChl *a* triplet is formed upon illumination in the RCPP complex. The kinetics (Fig. 5) showed a monophasic decay with a halftime of about 90 μs. The amount of triplet formed was about 0.5 per reaction center, assuming that $\Delta\epsilon_{510} = 11\ mM^{-1} \cdot cm^{-1}$ [15]. No stable charge separation could be observed in the RCPP complex after a flash.

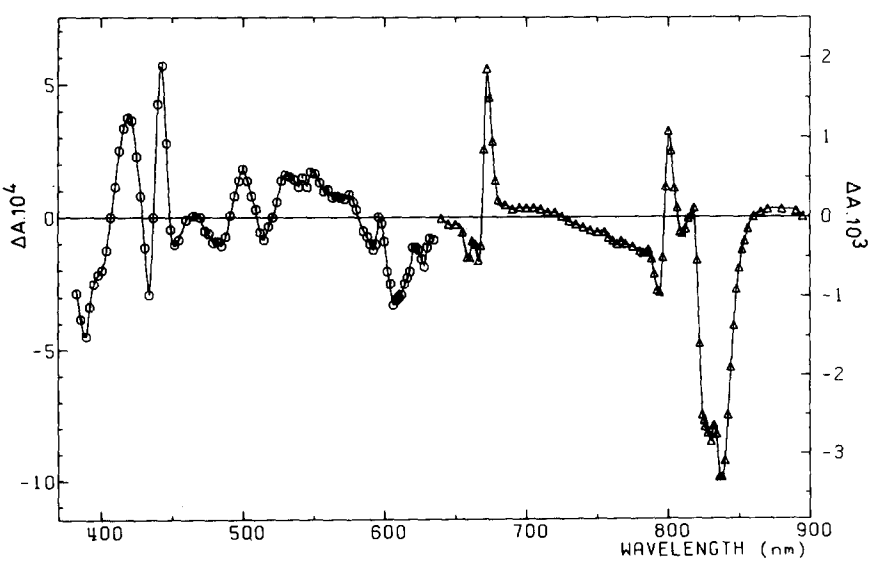

Fig. 3. Spectrum of the absorbance changes at 80 K induced by saturating continuous illumination of the PP complex ($A_{810} = 0.35$). Illumination for 3 s with orange light (intensity: 3 mW/cm^2) for the region 670—890 nm and with infrared light (intensity: 2 mW/cm^2) for the region 380—690 nm. Circles: left hand scale; triangles: right hand scale. Each point is the average of four to eight measurements.

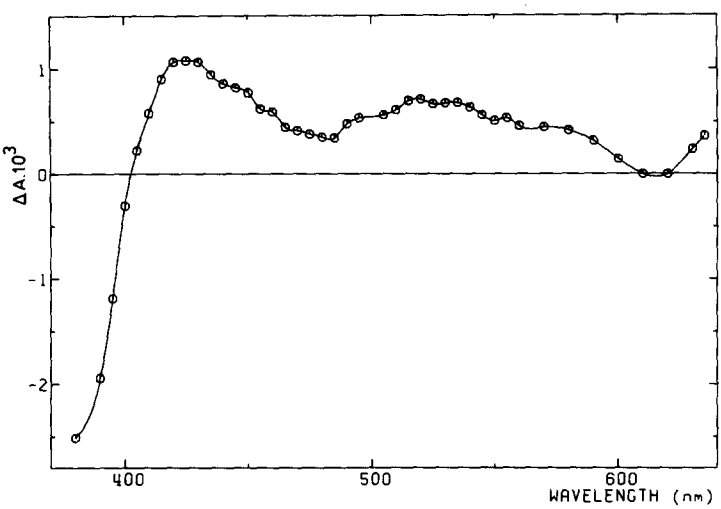

Fig. 4. Flash-induced absorbance difference spectrum at 295 K of the RCPP complex (A_{813} = 0.42), measured 50 μs after the flash. Excitation every 20 s with an infrared flash; each point is the average of 16—32 flashes, depending on the wavelength.

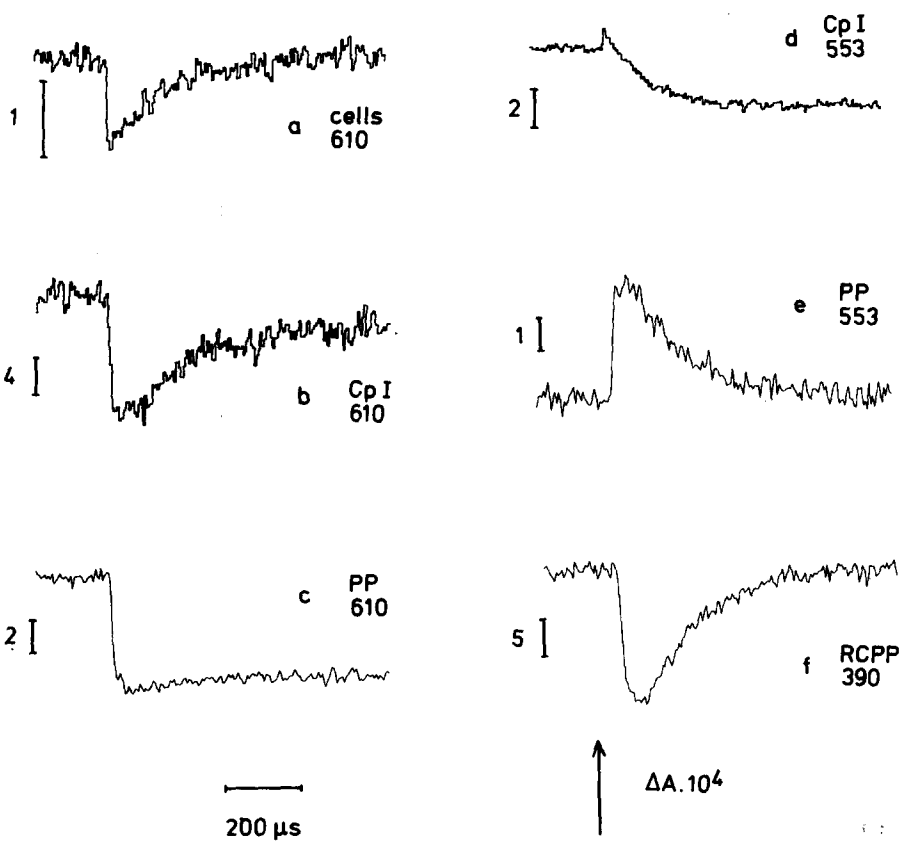

Fig. 5. Kinetics of absorbance changes at 295 K upon flash excitation. Recordings a, b and c: kinetics at 610 nm of intact cells (A_{745} = 1.35), Complex I (A_{810} = 1.35) and the PP complex (A_{810} = 0.8), respectively. Recordings d and e: kinetics at 553 nm of Complex I and the PP complex, respectively. Recording f: kinetics at 390 nm of the RCPP complex (A_{813} = 0.42). Flash duration: 13 μs at half maximum intensity. Time constant of the apparatus: 10 μs. Excitation every 20 s with an infrared flash. The traces are the average of 32—512 flashes, depending on the wavelength and on the preparation.

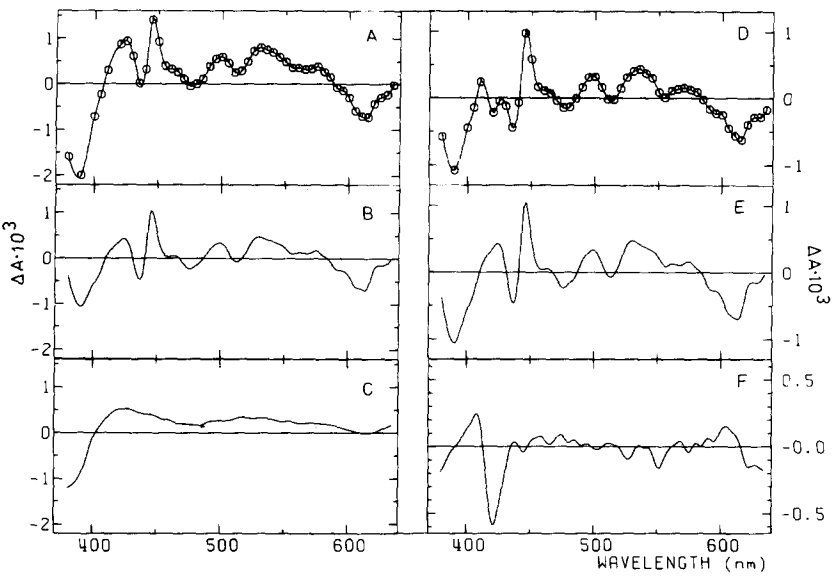

Fig. 6. Absorbance difference spectra of the flash-induced changes in the PP complex ($A_{810} = 0.80$) at 295 K, measured 50 μs after the flash (A) and 700 μs after the flash (D). Excitation with infrared flashes; each point is the average of 16—32 flashes, depending on the wavelength. The 50 μs spectrum is analyzed in a spectrum reflecting the charge separation P-840$^+$X$^-$ (B) and a spectrum due to the BChl *a* triplet (C) similar to that obtained with the RCPP complex. The 700 μs spectrum is analyzed in two spectra, due to P-840$^+$X$^-$, which is still partly present (E) and to oxidation of cytochrome *c*-553 (F).

The kinetics upon flash illumination at 295 K of intact cells, Complex I and the PP complex at 610 nm, where *P*-840 oxidation is measured and of Complex I and the PP complex at 553 nm, at the α band of cytochrome *c*-553, are shown in Fig. 5. Fig. 6, A and D, shows the difference spectra of the PP complex, measured 50 μs and 700 μs after the flash, respectively. The troughs at 420 and 555 nm in the 700 μs spectrum indicated cytochrome oxidation by *P*-840$^+$. The difference spectrum of the changes occurring between 50 and 700 μs, however, could not be attributed to cytochrome oxidation and *P*-840 reduction alone. Further analysis showed that it also contained a component reflecting the decay of a BChl *a* triplet with a spectrum similar to that of the KCPP complex (Fig. 6C). The decay of the triplet and the oxidation of cytochrome *c*-553 were kinetically indistinguishable and appeared to have the same halftime of about 90 μs (see Fig. 5). If the triplet spectrum was subtracted from the spectrum measured after 50 μs, a difference spectrum was obtained (Fig. 6B), which showed the same features as that shown in Fig. 2 (solid curve) and which was probably due to oxidation of *P*-840 and the reduction of an acceptor. If extrapolated to saturating intensity the amount of *P*-840$^+$ produced by a flash was about 0.5 per reaction center. The cytochrome spectrum (Fig. 6F) was similar to that obtained from kinetic analysis of the light-off response after continuous illumination (Fig. 2, broken curve). Depending on the preparation, 20 to 50% of the *P*-840$^+$ formed was reduced with a halftime of 90 μs by cytochrome *c*-553. The remaining part was reduced with a halftime of about 30 ms, as judged from the decay of the remaining fraction of *P*-840$^+$. The amount of BChl *a* triplet formed was about 0.2 per reaction center.

In Complex I about 60—70% of $P\text{-}840^+$ was reduced by cytochrome *c*-553 with a halftime of 90 μs; the remaining part of $P\text{-}840^+$ was reduced in about 25 ms. The amount of oxidized *P*-840, formed in a saturating flash was again about 0.5 per reaction center. No significant amount of BChl *a* triplet could be detected in Complex I after the flash. In intact cells of *P. aestuarii*, the kinetics at 610 nm showed that nearly all $P\text{-}840^+$ was rereduced with a time constant of 90 μs after the flash (Fig. 5). These results suggest that the slow phase of $P\text{-}840^+$ reduction may be due to a damage of the donor side of the reaction center as a result of the preparation methods used.

The kinetics after a flash measured at about 120 K are shown in Fig. 7. The PP complex showed a biphasic decay, consisting of two components with half-

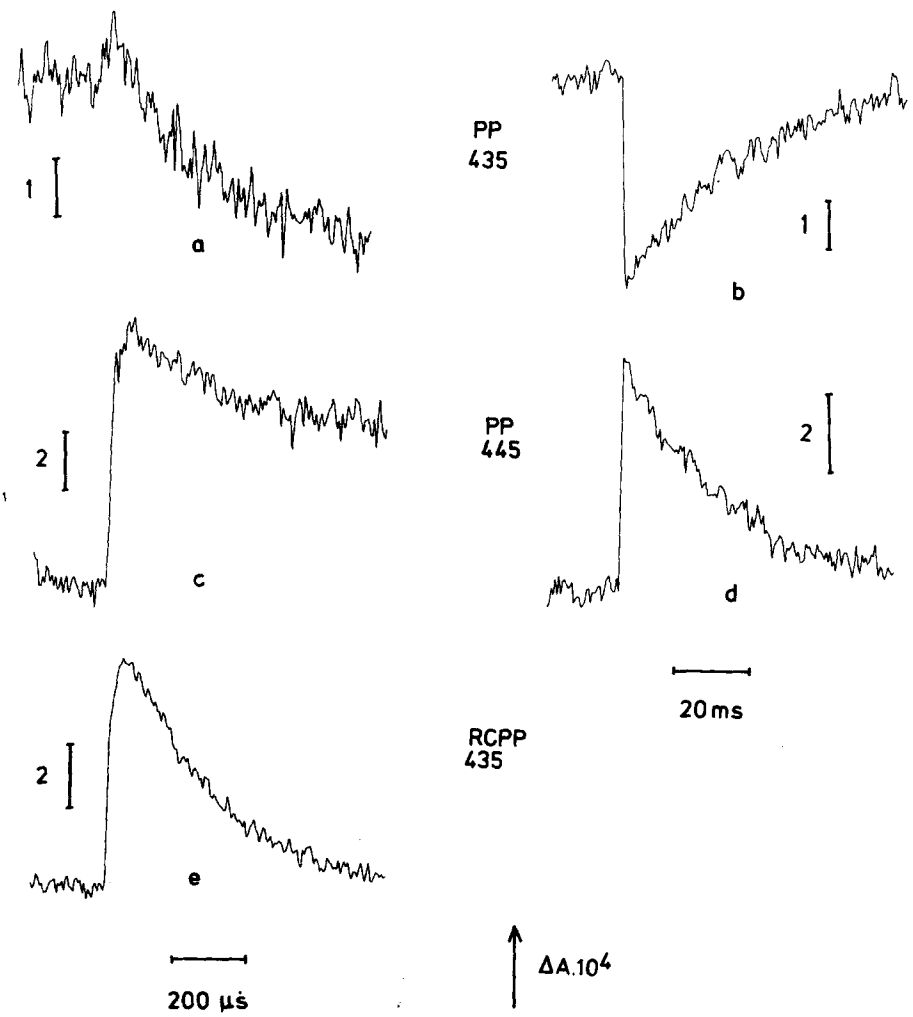

Fig. 7. Kinetics of absorbance changes at 120 K, upon flash excitation. Recordings a—d: PP complex (A_{810} = 0.35) and e: RCPP complex (A_{813} = 0.2); recordings a, b and e: 435 nm; recordings c and d: 445 nm. Excitation with infrared flashes, separated by 15 s. Each trace is the average of 32—128 flashes, depending on the wavelength and the preparation.

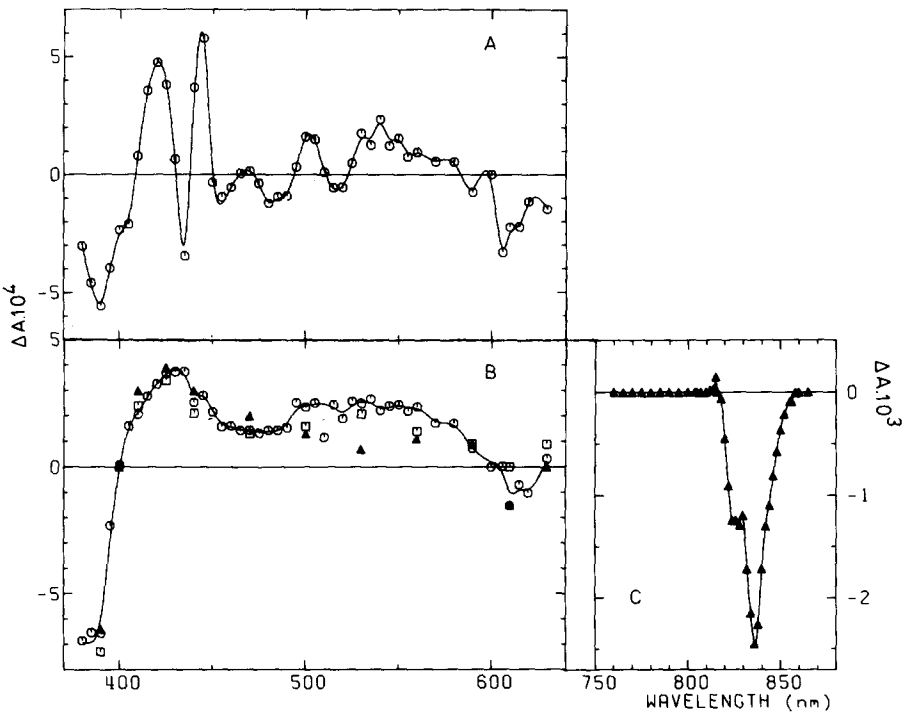

Fig. 8. (A) Absorbance difference spectrum at 120 K of the 20 ms decay component after a flash of the PP complex (A_{810} = 0.35). (B) Circles: absorbance difference spectrum at 120 K of the 165 μs decay component after a flash of the PP complex. Squares: flash-induced absorbance changes at 120 K of the RCPP complex (A_{813} = 0.1). Conditions as Fig. 7. Triangles: absorbance changes at 80 K, induced by high intensity continuous illumination of the RCPP complex (A_{813} = 0.1). Short illumination periods (0.3 s) with infrared light were used to prevent irreversible changes due to heating of the sample. Each point is the average of 32 illumination periods, separated by 10 s. The absorbance changes induced in the RCPP complex by continuous and flash illumination are normalized to those of the PP complex at 425 nm. (C) Absorbance difference spectrum of the RCPP complex (A_{813} = 0.22) at 80 K, induced by high intensity continuous light. Illumination for 3 s with orange actinic light (intensity: 25 mW/cm^2). Each point is the average of 8—16 measurements.

times of about 165 μs and 20 ms, respectively. The decay of the RCPP complex was monophasic with a halftime of about 165 μs. The spectra of the two components in the PP complex are shown in Fig. 8. The 20 ms spectrum (Fig. 8A) is very similar to that obtained at 80 K with continuous illumination, indicating a back reaction between *P*-840$^+$ and the reduced acceptor with a halftime of 20 ms at 120 K; at 80 K the halftime had increased to about 25—30 ms. The 165 μs spectra (Fig. 8B) of the PP complex (circles) and of the RCPP complex (squares) were similar and are probably due to the BChl *a* triplet that was also observed at 295 K.

Fig. 9 shows the flash intensity dependence of the two components of the PP complex and of the 165 μs component of the RCPP complex. Both components of the PP complex showed a similar intensity dependence, suggesting that they result from the same light reaction. The amount of BChl *a* triplet that was formed at the highest flash intensity available was about 0.45 per reaction center in the PP complex, assuming that $\Delta\epsilon_{510}$ is the same at 295 K and at 120 K. The amount of *P*-840$^+$ formed was about 0.5 per reaction center; the

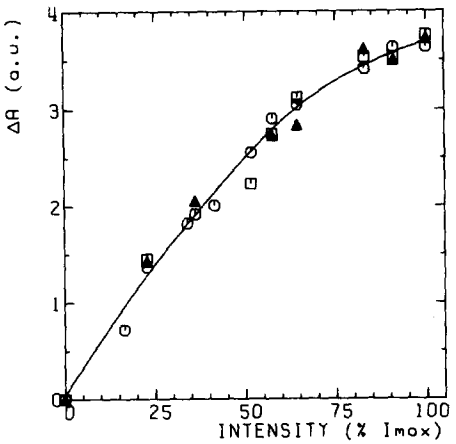

Fig. 9. Intensity dependences of flash-induced absorbance changes at 120 K, measured at 425 nm. Circles: RCPP complex. Squares and triangles: PP complex, contribution due to the 165 μs and 20 ms component, respectively. The changes were normalized at 100% intensity of incident light. Conditions as for Fig. 7.

same as observed at 295 K. The amplitude of the flash-induced changes in the RCPP complex at 120 K suggested the formation of about 0.8 BChl *a* triplet per reaction center.

The triangles in Fig. 8B represent the absorbance changes obtained at 80 K in the RCPP complex at high intensity of continuous illumination. The difference spectrum obtained in this way was similar to the triplet spectrum measured in a flash. Under similar conditions, a bleaching around 836 nm was observed at 80 K in the RCPP complex (Fig. 8C), presumably likewise due to the formation of the BChl *a* triplet. The absorbance changes could not be saturated with the highest intensities of continuous light available. The amount of triplet observed in continuous light in the RCPP complex did not exceed 0.1 per reaction center. Although all preparations contained relatively large amounts of carotenoid [3], formation of a carotenoid triplet was not observed.

Discussion

At 295 K the oxidized reaction center bacteriochlorophyll *a* of *Prosthecochloris aestuarii*, *P*-840$^+$, is reduced by cytochrome *c*-553. The light-induced absorbance difference spectrum at 295 K clearly reflects the oxidation of *P*-840, indicated by a bleaching at 810—850 and 610 nm, and the oxidation of cytochrome *c*-553 [13,18]. Additional signals were observed at 790 nm and around 670 nm; the latter change was ascribed to BPh *c* [3]. The difference spectrum obtained by continuous illumination at 80 K of Complex I or the PP complex (Fig. 3) probably reflects the oxidation of *P*-840 together with the reduction of an acceptor, the charges of which recombine in about 25 ms in the dark. In the infrared region, the spectrum shows a bleaching at 836 nm, probably due to *P*-840$^+$ and a red shift of a BChl *a* absorbing at 797 nm; the latter was only visible as a bleaching at 793 nm at 295 K [1,3]. The difference spectrum between 810 and 850 nm is quite complicated and not easily resolved in individual components. In contrast to measurements of Whitten et al. [19] in

Complex I prepared from *Chlorobium limicola*, no red shift of a BChl *a* absorbing at 816 nm was observed. The positive band of the BPh *c* signal shifted from 678 nm at 295 K [3] to 672 nm at 80 K; the negative band was resolved in two peaks at 659 and 666 nm upon cooling. The spectrum may be analyzed in shifts of BPh *c* molecules absorbing at about 665 and 670 nm, respectively; these different forms of BPh *c* were also visible in the linear dichroism spectra of Complex I and the pigment-protein complexes [20]. In the Q_x region of BChl *a*, negative bands are visible at 592, 606 and 628 nm, probably resulting from a bleaching of *P*-840 at about 610 nm and BChl *a* band shifts. The absorbance changes in the 450—530 nm region might be due to a shift of a carotenoid belonging to the pool that absorbs at relatively long wavelength [20]. Absorbance changes due to cytochrome *c*-553 were not observed; at temperatures below 220 K the oxidation of this component by *P*-840$^+$ did not occur (Ref. 21 and Swarthoff, T., unpublished experiments). At 295 K, cytochrome *c*-553 oxidation appears to be biphasic in Complex I and in the PP complex with halftimes of 90 μs and about 25—40 ms, respectively. These results differ from observations of Prince and Olson [22], who found a biphasic cytochrome oxidation with halftimes of 5 and 50 μs in Complex I from *C. limicola*.

The absence of *P*-840 and cytochrome oxidation after a flash in the RCPP complex is probably due to the low efficiency of stable charge separation. This may be caused by the destructive action of guanidine-HCl on the acceptor side of the reaction center complex, resulting in a very inefficient transfer of electrons from the primary acceptor to secondary acceptors. Thus, the situation in the RCPP complex is comparable to that in reaction centers of purple bacteria when the secondary quinone has been reduced before illumination, a condition which favors the formation of a reaction center BChl *a* triplet [15—17].

The relative amount of cytochrome *c*-553 that was oxidized with a halftime of about 90 μs decreased and the amount of BChl *a* triplet increased progressively from intact cells to Complex I, to the PP and to the RCPP complex. It is likely that the amount of BChl *a* triplet that is formed in a flash, and the efficiecny of *P*-840 oxidation in continuous light are an indication for the structural integrity of the acceptor side of the reaction center complex, whereas the relative amount of the 90 μs reduction of *P*-840$^+$ by cytochrome *c*-553 may be used as a measure of the integrity of the donor side of the reaction center complex.

It is conceivable that the BChl *a*-triplet is formed in a similar way as was proposed for triplet formation in purple bacteria [16,23], by means of a fast back reaction of the electron from I^-, the first electron acceptor, to *P*-840$^+$ from the triplet state of the radical pair. The slow-light-on kinetics of *P*-840 and cytochrome oxidation in continuous light at 295 K of the RCPP complex (Fig. 1) is in agreement with this, and indicates that the low efficiency of stable charge separation is due to the fast recombination of the primary charge separation *P*-840$^+$ I^-. Eventually, a stable charge separation was produced in all reaction centers at 295 K; however, at 80 K the electron transfer from I to secondary acceptors is probably completely inhibited. Therefore, no stable charge separation is observed in the RCPP complex at this temperature. A similar reasoning may be applied to the PP complex, where in part of the reaction centers the

electron transport at the acceptor side may be damaged. This results in the formation of a relatively low amount of stable charge separation (about 0.5 per reaction center) upon flash illumination at 295 and 120 K and continuous illumination at 80 K, compared to the amount obtained upon continuous illumination at 295 K. The amount of triplet produced by a saturating flash in the PP complex increased from about 0.2 to 0.45 molecule per reaction center upon cooling from 295 to 120 K. This indicates that the efficiency of triplet formation by the back reaction increased upon cooling. A similar increase was also observed in preparations from carotenoidless mutants of purple bacteria [16,17]. In the RCPP complex the maximum amount of BChl *a* triplet that could be formed in a strong flash at 120 K appeared to be close to one per reaction center. The flash intensity dependences for *P*-840 oxidation and BChl *a* triplet formation at 120 K in the PP complex (Fig. 9) were the same. This strongly suggests that the triplet is produced in the reaction center. The position of maximum bleaching in the near-infrared at 836 nm (Fig. 8C) is in agreement with this notion and indicates that the BChl *a* triplet formed is that of *P*-840.

The similar intensity dependences for the PP and RCPP complex (Fig. 9) would suggest a similar absorption cross-section for both preparations, although the numbers of BChl *a* molecules per reaction center are about 75 and 35, respectively. Preliminary experiments indicate that at least part of this effect may be due to losses occurring in the transfer of energy from the antenna BChl *a* protein to the reaction center in the PP complex.

The halftime of the decay of the reaction center BChl *a* triplet (90 μs at 295 K) was of the same order of magnitude at that of the state P^R (50 μs) in the reaction centers of *Rhodospirillum rubrum* G9 [24] and of antenna BChl *a* triplet (70 μs) in *R. rubrum* G9 and *Rps. sphaeroides* R-26 [15], but much longer than those of P^R of reaction centers of *Rps. sphaeroides* R-26 and in chromatophores of *R. rubrum* G9 (6 and 10 μs, respectively) [15].

The most conspicuous difference between our preparations and those of carotenoid containing purple bacteria, is the absence of the formation of a carotenoid triplet. In preparations of wild-type purple bacteria (except perhaps for reaction center preparations of *Rps. viridis*, which may contain carotenoid [25,26]), a reaction center carotenoid triplet is formed in 10—40 ns by triplet-triplet energy transfer from the BChl *a* triplet [15,16,24], whereas antenna triplets are formed from the excited singlet state of BChl *a* without interference of the reaction center [15,27]. This indicates that in the reaction centers of *P. aestuarii* no carotenoid is present in the direct environment of the reaction center BChl *a*. In purple bacteria such a carotenoid is needed for protection against the destructive action of the combination of light and oxygen, by preventing the formation of singlet O_2 [15]. In this connection it is also interesting to note that the light-harvesting BChl *a* protein does not contain carotenoid, in contrast to light-harvesting chlorophyll complexes of other classes of organisms [28—30]. This suggests that a protective role of carotenoid in the antenna is not necessary in green bacteria either. The reason may be that *Chlorobiaceae* are strictly anaerobic, their natural habitat being the deeper and dimly lit layers of ponds ands ditches [31], a situation in which formation of singlet oxygen is excluded.

Acknowledgements

The authors are indebted to Mrs. L.M. Blom for skillful preparative work, to A.H.M. de Wit for carefully culturing the bacteria and to Mrs. M. Bokhorst for assisting with some of the low temperature experiments. Thanks are also due to H.N. van der Wal for valuable advice and to Dr. R. van Grondelle for reading the manuscript. The investigation was supported by the Netherlands Foundation for Chemical Research (SON), financed by the Netherlands Organization for the Advancement of Pure Research (ZWO).

References

1 Fowler, C.F., Nugent, A. and Fuller, R.C. (1971) Proc. Natl. Acad. Sci. U.S.A. 68, 2278—2282
2 Pierson, B.K. and Castenholz, R.W. (1978) in The Photosynthetic Bacteria (Clayton, R.K. and Sistrom, W.R., eds.), pp. 179—197, Plenum Press, New York
3 Swarthoff, T. and Amesz, J. (1979) Biochim. Biophys. Acta 548, 427—432
4 Olson, J.M., Philipson, K.D. and Sauer, K. (1973) Biochim. Biophys. Acta 292, 206—217
5 Olson, J.M. and Thornber, J.P. (1979) in Membrane Proteins and Energy Transducation (Capaldi, R.A. et al., eds.), pp. 279—340, Marcel Dekker, New York
6 Fenna, R.E., Matthews, B.W., Olson, J.M. and Shaw, E.K. (1974) J. Mol. Biol. 84, 231—240
7 Matthews, B.W., Fenna, R.E., Bolognesi, M.C., Schmid, M.F. and Olson, J.M. (1979) J. Mol. Biol. 131, 259—285
8 Cruden, D.L. and Stanier, R.Y. (1970) Arch. Mikrobiol. 72, 115—134
9 Olson, J.M. (1978) Int. J. Syst. Bacteriol. 28, 128—129
10 Holt, S.C., Conti, S.F. and Fuller, R.C. (1966) J. Bacteriol. 91, 311—323
11 Visser, J.W.M. (1975) Thesis, University of Leiden
12 Van Grondelle, R. (1978) Thesis, University of Leiden
13 Romijn, J.C. and Amesz, J. (1977) Biochim. Biophys. Acta 461, 327—338
14 Slooten, L. (1972) Biochim. Biophys. Acta 275, 208—218
15 Monger, T.G., Cogdell, R.J. and Parson, W.W. (1976) Biochim. Biophys. Acta 449, 136—153
16 Parson, W.W. and Monger, T.G. (1977) Brookhaven Symp. Biol. 28, 195—212
17 Parson, W.W., Clayton, R.K. and Cognell, R.J. (1975) Biochim. Biophys. Acta 387, 265—278
18 Olson, J.M., Prince, R.C. and Brune, D.C. (1977) Brookhaven Symp. Biol. 28, 238—246
19 Whitten, W.B., Pearlstein, R.M. and Olson, J.M. (1979) Photochem. Photobiol. 29, 823—828
20 Swarthoff, T., de Grooth, B.G., Meiburg, R.F., Rijgersberg, C.P. and Amesz, J. (1980) Biochim. Biophys. Acta 593, 51—59
21 Sybesma, C. and Vredenberg, W.J. (1964) Biochim. Biophys. Acta 88, 205—207
22 Prince, R.C. and Olson, J.M. (1976) Biochim. Biophys. Acta 423, 357—362
23 Hoff, A.J., Rademaker, H., van Grondelle, R. and Duysens, L.N.M. (1977) Biochim. Biophys. Acta 460, 547—554
24 Cogdell, R.J., Monger, T.G. and Parson, W.W. (1975) Biochim. Biophys. Acta 408, 189—199
25 Holten, D., Windsor, M.W., Parson, W.W. and Thornber, J.P. (1978) Biochim. Biophys. Acta 501, 112—126
26 Trosper, T.L., Benson, D.L. and Thornber, J.P. (1977) Biochim. Biophys. Acta 460, 318—330
27 Rademaker, H. (1980) Thesis, University of Leiden
28 Cogdell, R.J. and Thornber, J.P. (1979) in CIBA Foundation Symp. 61 (New Ser.), pp. 61—69, Excerpta Medica, Amsterdam
29 Sauer, K. and Austin, L.A. (1978) Biochimistry 17, 2011—2019
30 Thornber, J.P., Markwell, J.P. and Reinman, S. (1979) Photochem. Photobiol. 29, 1205—1216
31 Pfennig, N. (1978) in The Photosynthetic Bacteria (Clayton, R.K. and Sistrom, W.R., eds.), pp. 179—197, Plenum Press, New York