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Electron transfer from high-potential iron-sulfur protein and low-potential cytochrome *c*-551 to the primary donor of *Rubrivivax gelatinosus* reaction center mutationally devoid of the bound cytochrome subunit

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Abstract

The electron transfer reactions from low-potential cytochrome *c*-551, high-potential iron-sulfur protein (HiPIP) and cytochrome *c*′ to the photosynthetic reaction center mutationally devoid of the bound cytochrome subunit in the C244 mutant of the purple bacterium *Rubrivivax gelatinosus* were investigated using time-resolved optical spectroscopy. Cytochrome *c*-551 was the best electron donor. Both HiPIP and low-potential cytochrome *c*-551 can also react with the bound cytochrome subunit, but in this case HiPIP appeared to be more efficient than cytochrome *c*-551. Identification of soluble immediate electron donors to the bacteriochlorophyll dimer indicates that in *Rvi. gelatinosus* the bound cytochrome subunit is not essential for photosynthetic electron transport and growth. The presence of high- and low-potential electron carriers (HiPIP, $E_m = 330$ mV, and cytochrome *c*-551, $E_m = 50$ mV) involved in the reduction of the bacteriochlorophyll dimer and the bound cytochrome subunit suggests that two alternative electron transfer pathways to the photosynthetic reaction center may exist in *Rvi. gelatinosus*. © 1997 Elsevier Science B.V.

Keywords: Reaction center mutant; Cytochrome subunit; HiPIP; Cytochrome *c*-551; Electron transfer; (*Rubrivivax gelatinosus*)

1. Introduction

The initial step of the photosynthetic electron transfer pathway in purple bacteria involves the light-driven excitation of a bacteriochlorophyll dimer within the reaction center (RC) complex. Depending on species, two types of cytochrome *c* act as an electron donor to the photo-oxidized bacteriochlorophyll dimer. In some species (e.g., *Rhodobacter*

Abbreviations: RC, reaction center; HiPIP, high-potential iron-sulfur protein; E_m, midpoint redox potential; PVDF, polyvinylidene fluoride; DAD, 2,3,5,6-tetramethylphenylenediamine; Mops, 3-morpholinopropanesulfonic acid; SDS, sodium dodecyl sulfate; PAGE, polyacrylamide gel electrophoresis; *Rvi*., *Rubrivivax*; *Rba*., *Rhodobacter*; *Rps*., *Rhodopseudomonas*; *Rfx*., *Rhodoferax*; *Rcy*., *Rhodocyclus*; *Chr*., *Chromatium*

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sphaeroides, *Rba. capsulatus*, *Rhodospirillum rubrum*, *Rhodopseudomonas palustris*) it is soluble cytochrome c_2, in others (e.g., *Rps. viridis*, *Rhodospirillum molischianum*, *Rubrivivax gelatinosus*, *Rhodoferax fermentans*, *Chromatium vinosum*, *Rhodopseudomonas acidophila*) it is a tetraheme cytochrome *c* subunit bound to the RC core complex (see [1–4] for reviews). Since the re-reduction of the bound cytochrome heme occurs from water-soluble electron carrier proteins (cytochromes or HiPIP's) it is generally admitted that this subunit does not replace mobile mediators, but instead appears to be an additional component in the electron transfer pathway [4]. The significance of this subunit and its physiological importance are still not fully clarified.

One contribution to the understanding of the role of the tetraheme cytochrome subunit was made by examining the effect of its removal (both biochemically and genetically) from RC complexes in *Rubrivivax* (*Rvi.*) *gelatinosus* [5,6]. In *Rvi. gelatinosus* the tetraheme cytochrome is less tightly bound to LM subunits in RC core complexes [7,8], and can be eliminated by detergent treatment [8]. An almost unchanged rate of oxidation of soluble cytochrome *c* by RC chemically devoid of the cytochrome subunit indicated the possibility that this subunit does not have an obligatory role in the photosynthetic electron transfer pathway and that direct electron transfer from soluble electron carrier proteins to the bacteriochlorophyll dimer would also be possible if the bound cytochrome subunit was lost by mutation [5]. It has been suggested through phylogenetic analysis that the cytochrome subunit has become less necessary in some species and subsequently lost during the course of evolution [4,9]. A support to this theory came recently when *Rvi. gelatinosus* C244, a mutant lacking the reaction center bound cytochrome subunit, exhibited the ability to grow photosynthetically, demonstrating that the shortcut electron transfer may occur in vivo, in growing cells [6].

Here we analyze this electron transfer pathway, focusing on the participation of soluble electron mediators in the direct re-reduction of photo-oxidized bacteriochlorophyll dimer in RCs mutationally devoid of the cytochrome subunit. Three major mobile electron carriers present in the periplasmic space of *Rvi. gelatinosus*: HiPIP, cytochrome *c*-551 and cytochrome *c*′ were purified and tested for their reactivity with the bacteriochlorophyll dimer in mutated RCs.

2. Materials and methods

2.1. Purification of the soluble electron carrier proteins and preparation of membranes

Rvi. gelatinosus strains: IL144 (wild type [10]) and C244 (mutant lacking bound cytochrome subunit [6]) were grown anaerobically at 30°C in the light, in PYS medium (0.5% polypeptone, 0.1% yeast extract, 0.5% sodium succinate and minerals, pH 7.0). Harvested cells were suspended in 10 mM Mops-NaOH (pH 7.0), 0.4 M NaCl, disrupted by sonication and centrifuged at $10\,000 \times g$ for 20 min to remove cell debris. Membrane fragments were collected by ultracentrifugation at $40\,000 \times g$ for 90 min. Soluble electron transfer proteins were purified from the remaining supernatant. The fraction sedimenting between 40 and 100% saturation of ammonium sulfate was dialyzed against 10 mM Mops-NaOH pH 7.0 and applied to a CM fast-flow column (Pharmacia LKB) equilibrated with the same buffer. Using a stepwise salt gradient, HiPIP, cytochrome *c*-551 and cytochrome *c*′ were eluted from the column at 50, 75 and 100 mM NaCl, respectively. Each fraction was concentrated, dialyzed against 10 mM Mops-NaOH pH 7.0, 25 mM NaCl and purified by gel filtration on Sephadex S-100 (Pharmacia LKB) column. The final purity of each protein was checked by SDS-PAGE. Horse heart mitochondrial cytochrome *c* (type IV) was purchased from Sigma.

2.2. Amino-acid sequencing

Amino-acid sequencing of *Rvi. gelatinosus* cytochrome *c*-551 and HiPIP was performed using an automatic sequencer (Applied BioSystem 477A) with the sample blotted on PVDF membrane (Atto Clear Blot Membrane-p).

2.3. Redox potentiometry

The redox midpoint potential of cytochrome *c*-551 was determined through the redox-dependent absorbance change in the α-band region recorded on Shimadzu UV-3000 spectrophotometer [11].

2.4. Kinetic spectrophotometry

Xenon-flash-induced absorbance changes were measured using a single-beam spectrophotometer assembled in our laboratory [12]. The measurements for HiPIP and mitochondrial cytochrome *c* were performed aerobically in 1 mM Mops-NaOH (pH 7.0) in the presence of 0.5 mM ascorbate and DAD (20 μM for wild type membranes, 2 μM for C244 mutant membranes). The measurements for low-potential cytochromes (*c*-551 or *c*′) were carried out in 1 mM Mops-NaOH (pH 8.5) in the presence of 1 mM ascorbate and DAD (same concentrations as above) anaerobically in an argon-purged cuvette in the case of C244 mutant membranes or semi-aerobically with prior degassing of the sample under vacuum in the case of wild type membranes. A low concentration of DAD (2 μM) was chosen for measurements with C244 mutant membranes as preliminary results indicated that in the absence of any soluble electron carrier, the decay of the RC change was dependent on the concentration of DAD, having however no effect on the second order kinetics observed after addition of soluble electron donors. When low-potential cytochromes were used, the ambient redox potential was lowered as described above in order to maintain these proteins in the reduced state during the period of flash measurements. In these experiments pH 8.5 was chosen to maintain stable redox conditions in the presence of ascorbate. In each measurement the concentration of membranes was adjusted to $A_{870} = 1.0$.

3. Results

Wild type IL144 and mutant C244 cells of *Rvi. gelatinosus* grown photosynthetically on PYS medium express HiPIP, cytochrome *c*′ and cytochrome *c*-551 in proportions consistent with the content of soluble fraction reported for other strains of *Rvi. gelatinosus*: ATCC 17011 [13,14] and TG-9 [15] (i.e., abundant amount of HiPIP, significantly less cytochrome *c*′, and a small amount of cytochrome *c*-551).

N-terminal amino-acid sequences up to position 12 for HiPIP and cytochrome *c*-551 revealed no difference with the corresponding sequences previously described for ATCC 17011 strain [13,16]. The redox midpoint potential of cytochrome *c*-551 has been determined to be 50 mV, confirming previous observations that it is a low-potential cytochrome [15,17].

Purified electron transfer proteins were added separately in micromolar concentrations to membrane fractions prepared from mutant C244 cells and wild type IL144 cells. Kinetics of the electron transfer reaction of HiPIP and cytochrome *c*-551 with RCs in C244 membranes are presented in Fig. 1. The reduction rate of photo-oxidized bacteriochlorophyll dimer (absorbance decrease at 542 nm) was strongly increased upon addition of HiPIP (Fig. 1A) or cytochrome *c*-551 (Fig. 1B) in the reduced form. The corresponding oxidation of cytochrome was also observed (as the decrease in the difference absorbance, 551–542 nm) when cytochrome *c*-551 was added (Fig. 1B). The light-induced changes of the spectra recorded before and after the addition of cytochrome *c*-551 are shown in Fig. 2, confirming the oxidation

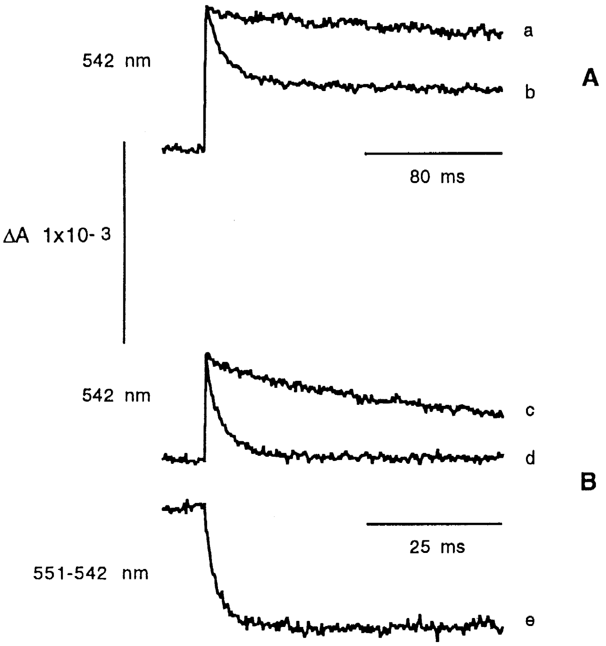

Fig. 1. Effects of HiPIP (A) and cytochrome *c*-551 (B) on flash-induced absorbance changes in purified membrane fragments isolated from C244 mutant of *Rvi. gelatinosus*. Time courses show absorbance changes in membranes without addition of any soluble electron donor (traces a,c), supplemented with 2 μM HiPIP (trace b), supplemented with 1 μM cytochrome *c*-551 (traces d,e). Experimental conditions are described in Section 2. Extent of shifted baseline (trace b) is attributed to the contribution of oxidized HiPIP at 542 nm.

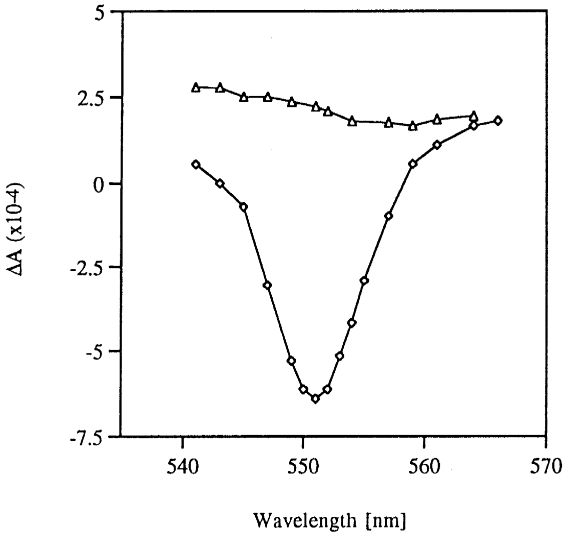

Fig. 2. Spectra of flash-induced changes in purified membrane fragments isolated from C244 mutant of *Rvi. gelatinosus.* Absorbance changes recorded 25 ms after the flash in the absence of soluble electron donors (△) and after addition of cytochrome *c*-551 (◇) were plotted vs wavelength from measurements similar to those in Fig. 1B.

of this cytochrome. The second order rate constants were calculated to be $5.4 \cdot 10^7\ \mathrm{M}^{-1} \cdot \mathrm{s}^{-1}$ and $5.0 \cdot 10^8\ \mathrm{M}^{-1} \cdot \mathrm{s}^{-1}$ for HiPIP and cytochrome *c*-551, respectively, demonstrating that both proteins are efficient electron donors to the bacteriochlorophyll dimer in RC complexes. Cytochrome *c*′ also interacted with RC in C244 mutant membranes, but with a lower rate constant of $1.0 \cdot 10^7\ \mathrm{M}^{-1} \cdot \mathrm{s}^{-1}$ (data not shown). Horse heart mitochondrial cytochrome *c* reduced photo-oxidized bacteriochlorophyll dimer with a rate constant of $8.0 \cdot 10^7\ \mathrm{M}^{-1} \cdot \mathrm{s}^{-1}$.

Comparative kinetics measurements were carried out in membranes isolated from wild type IL144 cells. As shown in Fig. 3, the re-reduction of the bound tetrahemic cytochrome was observed in the presence of HiPIP or cytochrome *c*-551 (absorbance increase at 555 nm and 557 nm measured for HiPIP and cytochrome *c*-551, respectively). When the ambient redox potential was poised properly, HiPIP efficiently donated electrons to the bound cytochrome with the second order rate constant of $1.1 \cdot 10^8\ \mathrm{M}^{-1} \cdot \mathrm{s}^{-1}$ (Fig. 3A). The interaction of cytochrome *c*-551 was clearly observed when ambient redox potential was lowered to partly reduce cytochrome *c*-551 prior to the flash. In the absence of soluble electron donors, under the low redox conditions the fast (sub ms) phase with the absorption decrease peak around 551–552 nm came mostly from low-potential hemes in the tetraheme subunit which remained oxidized (data not shown). In the presence of cytochrome *c*-551 additional secondary electron transfer occurred from soluble cytochrome to the bound cytochrome subunit (Fig. 3B: slow increase at 557 nm and concomitant decrease at 548 nm) with an apparent second order rate constant of $3.1 \cdot 10^7\ \mathrm{M}^{-1} \cdot \mathrm{s}^{-1}$, although the real value should be larger, since under these conditions a part of cytochrome *c*-551 was oxidized prior to the flash. These data demonstrate that HiPIP and low-potential cytochrome *c*-551 can donate electrons to the tetraheme cytochrome when added in micromolar concentrations to suspended membranes isolated from wild type IL144 cells. Cytochrome *c*′ was also tested as potential electron donor to the tetraheme subunit, however, we found no indication of the oxidation of this protein by the bound cytochrome, even under the low ambient redox potentials. The oxidation of mito-

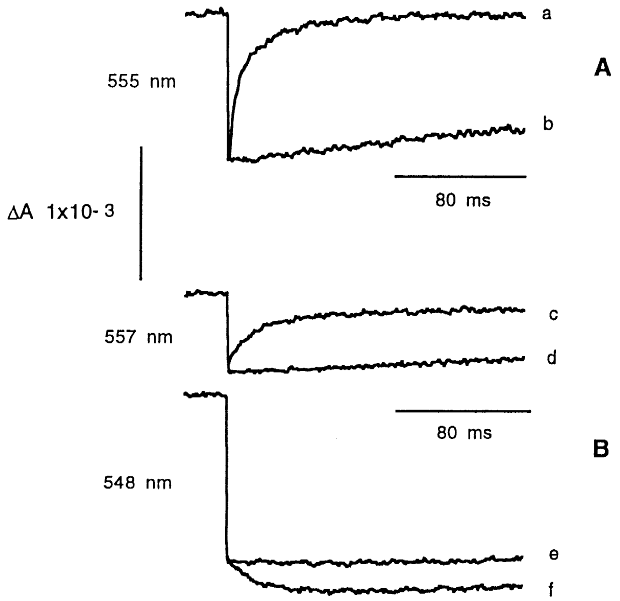

Fig. 3. Effects of HiPIP (A) and cytochrome *c*-551 (B) on flash-induced absorbance changes in purified membrane fragments isolated from wild type IL144 cells of *Rvi. gelatinosus.* Time courses show absorbance changes in membranes without addition of any soluble electron donor (traces b,d,e), supplemented with 1 μM HiPIP (trace a), supplemented with 2.4 μM cytochrome *c*-551 (traces c,f). Experimental conditions are described in Section 2.

chondrial cytochrome *c* by RC complexes present in wild type membranes was much slower, with a second order rate constant of $0.9 \cdot 10^6\ M^{-1} \cdot s^{-1}$ (data not shown).

The electron donations from soluble electron carriers to RC complexes in membranes derived from C244 mutant and wild type IL144 cells were dependent on the ionic strength. As shown in Fig. 4 increasing the NaCl concentration retarded the oxidation of HiPIP and cytochrome *c*-551 in both types of membranes. The ionic strength dependence suggests that electrostatic attractive interactions contribute to the formation of functional complex between the RC and soluble components. Although the interaction domains of HiPIP and cytochrome *c*-551 have not been yet elucidated, it seems plausibly to assume that both proteins have positively charged residues on their encounter surface which attract to negatively charged groups on the reaction sites of RC complexes (mitochondrial cytochrome *c* in the reaction with RC core complexes displayed the same type of ionic strength dependence).

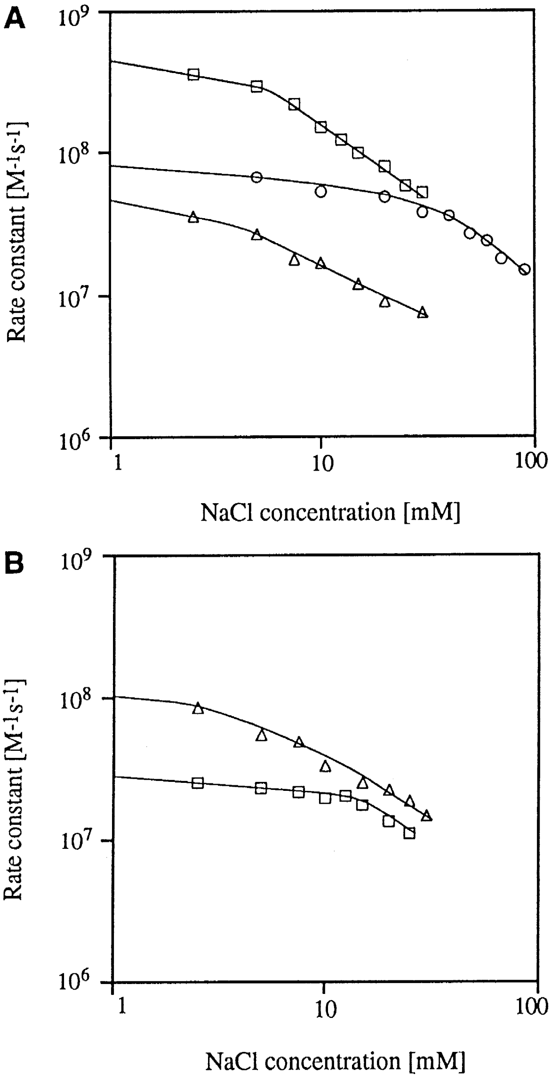

Fig. 4. Effects of NaCl concentration on the observed second order rate constant for the reaction of soluble electron donors with RCs in membranes isolated from C244 mutant cells (A) and wild type IL144 cells (B). Curves represent the interaction with cytochrome *c*-551 (□), HiPIP (△) and mitochondrial cytochrome *c* (○).

4. Discussion

Our previous study showed that mutational loss of the bound cytochrome subunit from RC complexes does not result in serious damage to bacterial photosynthetic growth, having presumably no significant effect on the in vivo electron transfer from periplasmic soluble components to the photo-oxidized special pair of bacteriochlorophyll *a* [6]. The reconstitution experiments with purified membranes prepared from the C244 mutant of *Rvi. gelatinosus* presented in this study support this hypothesis. Low-potential cytochrome *c*-551, HiPIP and cytochrome *c*′ can all act as soluble electron donors to the photo-oxidized RC bacteriochlorophyll dimer and cytochrome *c*-551 appeared to be the most efficient donor among these proteins.

Recently, in some species (*Rvi. gelatinosus* [15], *Rfx. fermentans* [18,19] and *Rcy. tenuis* [20]) HiPIP was shown to fulfil the role of cytochrome c_2 in the electron donation to the bound cytochrome subunit. In our study, the bound tetraheme cytochrome present in the wild type membranes can accept electrons from both HiPIP and cytochrome *c*-551 (in this reaction HiPIP displayed better efficiency), but not from cytochrome *c*′. Thus the cytochrome subunit may provide an additional level of specificity for the reduction of bacteriochlorophyll dimer.

The existence of two proteins with significantly different redox midpoint potentials (HiPIP, $E_m = 330$ mV and cytochrome *c*-551, $E_m = 50$ mV) engaged in the same step of the *Rvi. gelatinosus* photosynthetic electron transfer pathway may have physiological significance. Considering the relative amounts of HiPIP and cytochrome *c*-551 present in *Rvi. gelatinosus* cells it could be assumed that the major electron donation to RC complexes comes from HiPIP and that the concentration of cytochrome *c*-551 may be below that needed to allow rates of RC reduction required for cells growth. As cytochrome *c*-551 presumably would not be able to efficiently accept electrons from the cytochrome bc_1 complex, its low potential may be advantageous in the oxidation of low-potential compounds (e.g., sulfur compounds) allowing the alternative electron transfer route to occur. The function of HiPIP seems clearer since its re-reduction by the bc_1 complex has been observed in *Rvi. gelatinosus* TG-9 cells [15].

Based on an amino-acid sequence homology, soluble *Rvi. gelatinosus* cytochrome *c*-551 (in spite of its low redox potential) has been classified with the high-potential cytochromes c_8 (as designated by Ambler [21]; for alternative nomenclature, see [22,23]). Cytochromes of the c_8 family have also been identified in *Rhodocyclus tenuis*, *Rfx. fermentans* and *Rcy. purpureus* and proposed to function in a manner analogous to cytochrome c_2 of purple bacteria from the α-subgroup [24] in reducing the oxidized tetraheme subunit [[3], Zannoni, D., personal communication]. A similar function was suggested for cytochrome c_8 recently identified in the purple-sulfur bacterium *Chromatium purpuratum* [25]. The amino-acid seqeunce of soluble cytochrome *c*-551 from *Chr. vinosum*, which was found to mediate electron transfer between cytochrome bc_1 complex and the RC [26,27], revealed that this cytochrome also belongs to the cytochromes c_8 family [28]. *Rvi. gelatinosus* cytochrome *c*-551 may present a new example of an c_8-type cytochrome, one able to functionally replace cytochrome c_2 , although its midpoint potential is abnormally low within cytochromes c_8 so far examined. Flash kinetic spectroscopy demonstrated its possible role in photosynthesis, although the low content of this cytochrome in bacterial cells makes it difficult to evaluate its actual significance in vivo.

RC with the bound cytochrome subunit and RC mutationally devoid of this subunit in *Rvi. gelatinosus* present an interesting example of transmembranous protein complexes which can accept electrons from two different types of soluble electron carriers. It will therefore be worthwhile to locate the binding sites for HiPIP and cytochrome *c*-551 on the surface of *Rvi. gelatinosus* RCs. Considering redox midpoint potentials of *Rvi. gelatinosus* cytochrome subunit [8,29], any of high-potential hemes *c*-555 ($E_m = 320$ or 300 mV) may be the preferred site of the interaction for HiPIP or soluble cytochrome *c*-551. However, the low potential of cytochrome *c*-551 may also allow direct electron donation to the low-potential hemes of the cytochrome subunit (heme *c*-551; $E_m = 70$ mV). In the related case of the *Rps. viridis* bound tetraheme cytochrome, each of respective heme vicinities (high-potential hemes *c*-559, *c*-556 and low-potential heme *c*-554) are predicted as electrostatically suitable docking areas for charged soluble protein molecules [30–32]. The ionic strength dependence shown here confirms that electrostatics plays a significant role in stabilizing the formation of functional complex between HiPIP or cytochrome *c*-551 and RC complexes.

Cytochromes c_2 of species with RCs without bound cytochrome subunit (e.g., *Rba. spheroides*, *Rba. capsulatus*) show fast, first-order components in their electron transfer kinetics [33–36]. As the rate constants for the reaction of these cytochromes c_2 with simple RCs are comparable to the values for the reaction of the bound cytochrome with bacteriochlorophyll dimer [37–39], it was proposed that only the acquisition of highly reactive cytochrome c_2 in some species may have made the bound cytochrome subunit superfluous and subject to deletion [30,40]. In C244 mutant membranes of *Rvi. gelainosus* no fast phase was observed when HiPIP and cytochrome *c*-551 were oxidized by RCs without the bound cytochrome subunit. These proteins, being able to mediate the electron transfer to RCs mutationally devoid of the tetraheme subunit sustain the photosynthetic capability of C244 cells, albeit with a growth rate significantly slower than the wild type cells [6]. The lack of rapid re-reduction of the photo-oxidized special pair in the absence of the bound cytochrome subunit may partially explain the nature of this growth inhibition. Observed in vitro kinetics of the re-reduction by cytochrome *c*-551 or HiPIP may be too slow to compete with the back reaction from the primary quinone acceptor (Q_A) under highly reduced environmental conditions. In this context the *Rvi. gelatinosus* tetraheme cytochrome subunit, which appears to be dispensable to sustain the photosynthetic growth capability of C244 cells, may not be compensated by soluble cytochrome *c*-551 nor HiPIP in preventing the electron back transfer from quinone to the oxidized special pair in RC devoid of the bound cytochrome subunit.

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