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Effects of oxidants and reductants on the efficiency of excitation transfer in green photosynthetic bacteria

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The efficiency of energy transfer in chlorosome antennas in the green sulfur bacteria *Chlorobium vibrioforme* and *Chlorobium limicola* was found to be highly sensitive to the redox potential of the suspension. Energy transfer efficiencies were measured by comparing the absorption spectrum of the bacteriochlorophyll *c* or *d* pigments in the chlorosome to the excitation spectrum for fluorescence arising from the chlorosome baseplate and membrane-bound antenna complexes. The efficiency of energy transfer approaches 100% at low redox potentials induced by addition of sodium dithionite or other strong reductants, and is lowered to 10–20% under aerobic conditions or after addition of a variety of membrane-permeable oxidizing agents. The redox effect on energy transfer is observed in whole cells, isolated membranes and purified chlorosomes, indicating that the modulation of energy transfer efficiency arises within the antenna complexes and is not directly mediated by the redox state of the reaction center. It is proposed that chlorosomes contain a component that acts as a highly quenching center in its oxidized state, but is an inefficient quencher when reduced by endogenous or exogenous reductants. This effect may be a control mechanism that prevents cellular damage resulting from reaction of oxygen with reduced low-potential electron acceptors found in the green sulfur bacteria. The redox modulation effect is not observed in the green gliding bacterium *Chloroflexus aurantiacus*, which contains chlorosomes but does not contain low-potential electron acceptors.

Introduction

The green photosynthetic bacteria are non-oxygen-evolving prokaryotes that contain bacteriochlorophyll (BChl) *c*, *d* or *e*, located in a membrane-attached antenna complex known as a chlorosome [1–4]. There are two families of green bacteria, the Chlorobiaceae, or green sulfur bacteria, and Chloroflexaceae, or green gliding bacteria [5–6]. The obligately photoautotrophic green sulfur bacteria are anaerobic organisms that photooxidize sulfur compounds with concomitant reduction of CO_2 [7].

In the past decade, antenna structure [8,9] and energy transfer [10–15] in the green bacteria have been extensively studied. Models for the overall structure of chlorosomes and associated membranes for the green bacteria are shown in Fig. 1. Each chlorosome contains roughly 10000 bacteriochlorophyll BChl *c* (*d* or *e*) that probably are organized as pigment oligomers [16–21]. In addition, chlorosomes contain approx. 500 molecules

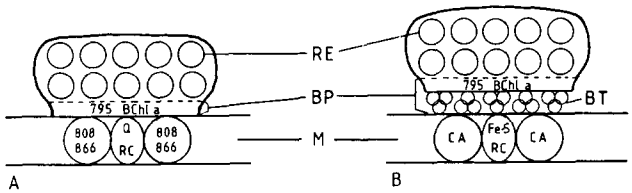

Fig. 1. Model showing cross-sections through chlorosomes and underlying photosynthetic membranes of Chloroflexaceae (A) and Chlorobiaceae (B) taken from Ref. 4. Abbreviations: 808/866.BChl *a*-protein with absorption maxima at 808 and 866 nm; BP, baseplate; BT, BChl *a*-protein trimers; CA, core antenna; Fe-S/RC, reaction center with iron-sulfur electron acceptor; M, membrane; Q/RC, reaction center with quinone electron acceptor; RE, rod element in chlorosome composed of BChl *c* oligomers and protein.

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Abbreviations: BChl, bacteriochlorophyll; DTT, dithiothreitol; PMSF, phenylmethylsulfonyl fluoride; TMPD, 2,3,5,6-tetramethyl-*p*-phenylenediamine.

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of the 790–795 nm absorbing BChl *a* that is part of the membrane attachment site known as the baseplate [22–24]. The BChl *a* 790–795 in green sulfur bacterial chlorosomes is attached to the membrane by a trimeric pigment protein complex absorbing maximally at 809 nm [25]. This complex is not found in the green gliding bacteria.

In contrast to the similarities of the chlorosomes of the two families of green bacteria, the membrane-bound antennas and reaction centers are very different. The membranes of the green sulfur bacteria contain a core antenna complex with an absorption maximum at approx. 810 nm and an Fe-S acceptor-containing reaction center with reversible photobleaching at 840 nm (P840) [26,27]. In the green gliding bacteria an integral membrane antenna complex accepts excitations directly from the chlorosome baseplate and delivers them to a quinone acceptor-containing reaction center similar to that found in purple photosynthetic bacteria [27–29]. While the two families of green bacteria contain very different types of reaction centers and membrane-bound antenna complexes, and are not closely related based on 16 S ribosomal RNA analysis [30], the chlorosomes from the two families are surprisingly similar in pigment content and organization. However, a common evolutionary origin of chlorosomes from the two families is suggested by the finding that there is approximately a 30% amino-acid identity in 5.6–6.3 kDa chlorosome proteins isolated from the two families [31].

Previous spectroscopic studies on membranes and isolated antenna complexes of green sulfur bacteria have found that the intensity of fluorescence emission arising from the chlorosome pigments was highly quenched under aerobic conditions and the intensity of this emission was greatly increased by the addition of the strong reductant sodium dithionite [32–34]. The results have been interpreted mainly in terms of the dithionite removing highly quenching impurities from the chlorosome, presumably by chemically reducing them. Flash annihilation studies have found that the size of BChl *c* domains accessible to excitations are from 10- to 50-fold larger in the presence of dithionite than in its absence in chlorosomes from green sulfur bacteria [34]. Dithionite has little or no effect on the fluorescence properties of chlorosomes from *Chloroflexus aurantiacus* [11].

The large effect of dithionite on the fluorescence properties of antenna complexes from green sulfur bacteria has never been investigated in whole cells, nor has any possible functional role been proposed for this quenching. In this study, we have carried out energy transfer efficiency measurements on whole cells, membranes and isolated chlorosomes of several species of green bacteria and propose that redox modulation of energy transfer efficiency is a possible cellular control mechanism.

Materials and Methods

Chlorobium vibrioforme f. *thiosulfatophilum* strain 8327 was obtained from the Microbiology Institute of the University of Bonn, F.R.G., and *Chlorobium limicola* f. *thiosulfatophilum* (ATCC 17092) was obtained from the American Type Culture collection. Both were grown from 1 to 5 days in a culture medium containing sulfide and thiosulfate, prepared as described by Olson et al. [35]. *Chloroflexus aurantiacus* was grown photoheterotrophically as described in Ref. 23. The buffer used to dilute whole cells for absorption and fluorescence measurements was 10 mM Tris-HCl (pH 8). An anaerobic suspension was prepared by removing the cells from the growth bottles under anaerobic conditions and injecting them directly into the fluorescence cuvette which contained buffer without oxygen. All anaerobic operations were performed in a glove bag filled with argon or in an anaerobic chamber filled with 10% hydrogen, 85% nitrogen and 5% carbon dioxide.

Chlorosomes were prepared as described by Gerola and Olson [24]. Membranes with attached chlorosomes were prepared by sonicating ice-cold whole cells in the presence of a 5 mM concentration of the proteinase inhibitor phenylmethylsulfonyl fluoride (PMSF), centrifuging for 10 min at $12000 \times g$ to remove unbroken cells and cell wall fragments and for 2 h at $240000 \times g$ to sediment the membranes with attached chlorosomes.

When present, sodium dithionite, sodium ascorbate and dithiothreitol (DTT) were added to the cell suspension to give a final concentration of 10 mM. Glucose oxidase was used at a final concentration of 0.3 mg/ml. When fresh growth medium (containing Na_2S) was used for suspending the cells, the final Na_2S concentration was 2.3 mM. The stock solutions of benzoquinone (2 mM) and 2,3,5,6-tetramethyl-*p*-phenylenediamine (TMPD) (50 mM) used alcohol as the solvent. The aqueous iodine solution contained 50 mM I_2 and 100 mM NaI. The concentration of the ferricyanide stock solution was 0.5 M.

Fully corrected, steady-state fluorescence excitation and emission spectra at room temperature were measured on the instrument described in Ref. 12. Absorption spectra were measured at room temperature with the same instrument as described above, using a Labsphere IS060-WR 6 inch diameter integrating sphere with a UDT PIP-10DP/SB Si photodiode detector. A buffer sample was used as a reference in an independent scan. The spectral band width for both fluorescence excitation and emission spectra was 9 nm, and 4.5 nm for absorption spectra.

Results

Fig. 2 shows a set of absorption spectra of the whole cells of *C. vibrioforme*, *C. limicola*, and *C. aurantiacus*.

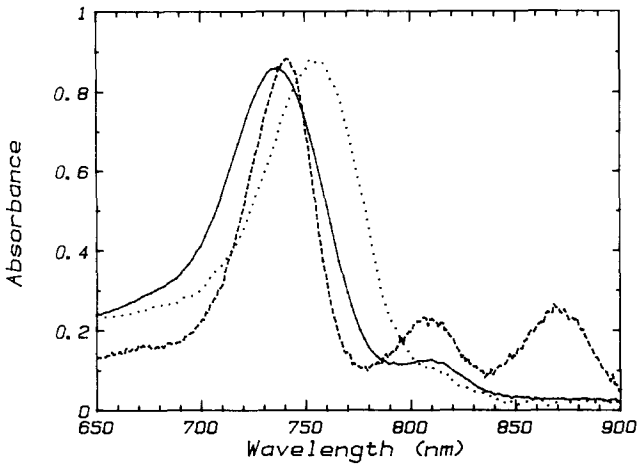

Fig. 2. Absorption spectra of whole cells in Tris-HCl (pH 8): ———, *Chlorobium vibrioforme* f. *thiosulfatophilum*. The 730 nm absorption is due to BChl *d*. · · · · · ·, *Chlorobium limicola* f. *thiosulfatophilum*. The 750 nm absorption is due to BChl *c*. – – – – –, *Chloroflexus aurantiacus*. The 740 nm absorption is the Q_y band of BChl *c*, while the 808 and 866 nm absorptions are due to the B808/866 BChl *a* antenna protein.

The strong absorption bands at 755 nm in *C. limicola* and 740 nm in *C. aurantiacus* are due to BChl *c*. The corresponding 730 nm absorption band in *C. vibrioforme* is due to BChl *d*.

Fluorescence emission and excitation spectra as well as absorption spectra of whole cells of *C. vibrioforme* are shown in Fig. 3. Without dithionite, it can be seen from Fig. 3A that the ratio of the BChl *d* peak at 730 nm to the BChl *a* shoulder at 810 nm is much higher in the absorption spectrum than in the excitation spectrum. Excitation and absorption spectra were normalized at 810 nm. By making a comparison between the fluorescence excitation and absorption spectra at 730 nm, the efficiency of excitation transfer from the BChl *d* to the BChl *a* was found to be 10%. The emission spectrum of this sample was dominated by a band at 760 nm due to BChl *d* with a weaker maximum at 816 nm due to BChl *a*.

After adding dithionite, the absorption spectrum was not changed, but the fluorescence excitation and emission spectra were very different. The intensities of 835 nm fluorescence excited at 730 nm (where BChl *d* absorbs) and 810 nm (where BChl *a* absorbs) increased about 50- and 5-fold, respectively. A comparison between the excitation and absorption spectra showed that the efficiency of excitation transfer was approx. 100% (see Fig. 3B). Similarly, the intensity of fluorescence emission at 760 nm increased by a factor of 10 and that at 816 nm increased by a factor of 30 when excitation was at 460 nm. For the green sulfur bacterium *C. limicola*, the fluorescence spectra before and after adding dithionite to an aerobic cell suspension exhibited behavior similar to that of the *C. vibrioforme* spectra (data not shown).

Other strong reducing agents such as dithiothreitol (DTT) and Na_2S (present in the culture medium) also increased the efficiency of energy transfer from the BChl *c* or *d* to BChl *a* to about 100% (data not shown).

In addition to these strong reducing agents, the effect of a mixture of glucose and glucose oxidase or ascorbate on the efficiency of excitation transfer was tested. The addition of these compounds to aerobic whole cells caused an increase in energy transfer efficiency from 10–20% up to nearly 100%, but a much longer time (at least 3 h) was required for the effect to be observed. In addition, they were ineffective in restoring high efficiencies of energy transfer in membranes and isolated chlorosomes (see below).

The fluorescence spectra of anaerobic cells of *C. vibrioforme* were identical to those of the cells in the presence of dithionite. When dithionite was added to

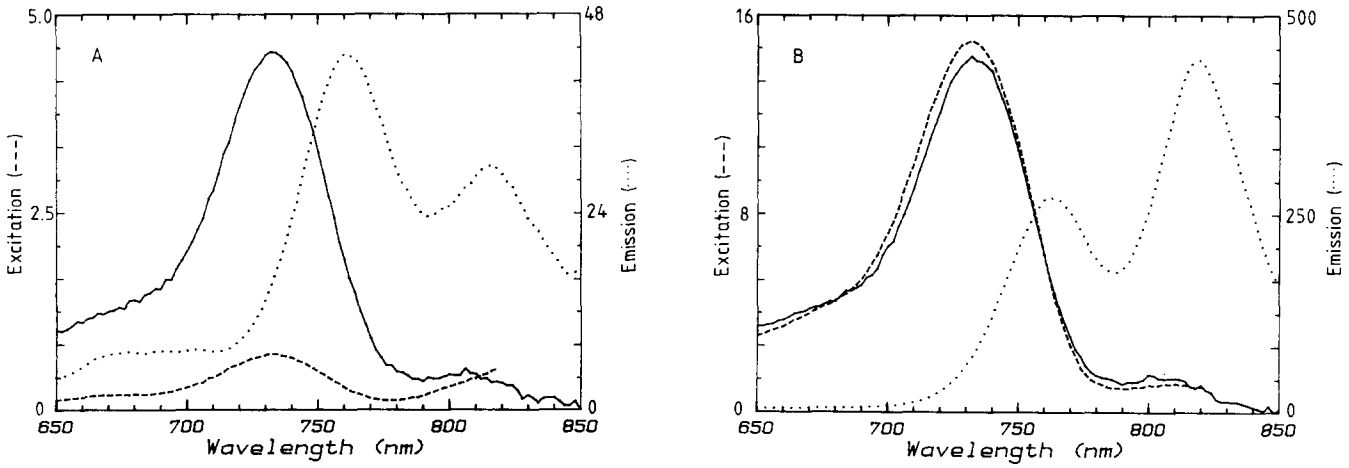

Fig. 3. Absorption (———), and fluorescence excitation (------) and emission (· · · · · ·) spectra of *C. vibrioforme* whole cells. (A) Aerobic conditions. (B) After adding dithionite. Fluorescence was monitored at 835 nm for the excitation spectrum (units on left ordinate). The emission spectrum (units on right ordinate) was obtained using 460 nm exciting light. The units for fluorescence intensity are proportional to the output of the R928 photomultiplier, and are directly comparable to those in Figs. 5 and 6, in which the same detector was used. $A_{730} = 0.2$.

the anaerobic cells, no change occurred in the fluorescence spectra of the cells (data not shown). This experiment indicates that dithionite affects the fluorescence yield and the efficiency of excitation transfer in these cells only in the presence of oxygen (or other oxidants – see below).

Experiments to study further the effect of oxygen on the energy transfer of green sulfur bacteria were done by injecting 1 μl volumes of air into a 3 ml suspension of *C. vibrioforme* cells in anaerobic buffer. Initially, the sample exhibited an efficiency of energy transfer near 100%. Injecting the first 3 μl of air into the solution did not affect the efficiency of excitation transfer, perhaps because small amounts of endogenous reductants consumed the added O_2. With the 4th and the 5th μl of air injected into the solution, the efficiency decreased rapidly, and with more air injected into the solution, the efficiency began to level off at a value of about 10%. Fig. 4 illustrates the efficiency of energy transfer as a function of amount of air added. The experiments demonstrate that the presence of oxygen, even in slight amounts, inhibits excitation transfer in green sulfur bacteria. (4 μl of air in 3 ml corresponds to an O_2 concentration of about 1.2 μM.)

Following a decrease in the efficiency of excitation transfer to 10% due to injected air, oxygen was removed by bubbling with nitrogen for 0.5 h. The efficiency of excitation transfer was again found to be 100% (data not shown).

In place of oxygen, the oxidants iodine, benzoquinone, ferricyanide, and ferricyanide + TMPD were tested in order to investigate their effects on the efficiency of excitation transfer from BChl *d* to BChl *a* in *C. vibrioforme*. Table I shows measurements of the efficiency of excitation transfer of samples exposed to

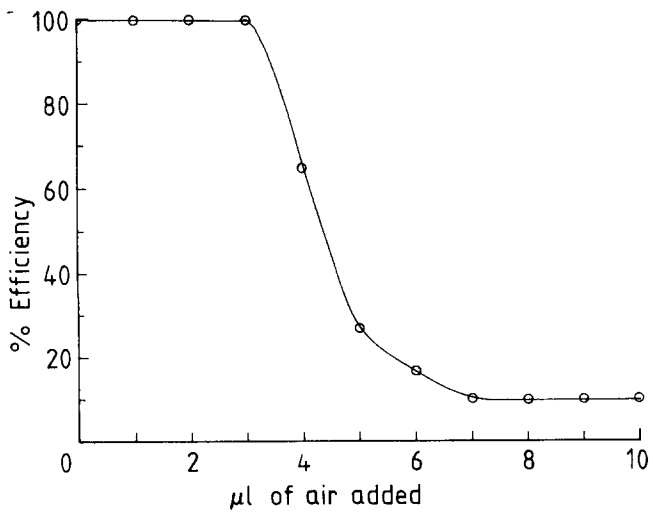

Fig. 4. Efficiency of excitation transfer in whole cells of *C. vibrioforme* (sample volume = 3 ml) as a function of the volume of air added. The time interval between air injections was 40 min.

TABLE I

Efficiency of excitation transfer (%) in Chlorobium vibrioforme

A_{730} = 0.12–0.15. The anaerobic *C. vibrioforme* cells used in these experiments initially had a 100% efficiency of excitation transfer, and all reagents were added anaerobically.

Oxidant	Concentration (μM)	%	+ Ascorbate (%)	+ Dithionite (%)
I_2	600	40	100	–
I_2	750	20	–	100
Benzoquinone	7	10	100	–
Benzoquinone	3	10	–	100
TMPD	600	100	–	–
$K_3Fe(CN)_6$	4000	100	–	–
$K_3Fe(CN)_6$	600			
+ TMPD	60	16	100	–
$K_3Fe(CN)_6$	400			
+ TMPD	75	10	–	100

different oxidants and reductants. From Table I, one can see that even a high concentration of ferricyanide (4 mM), dissolved in an anaerobic medium containing cells, had little or no effect on the efficiency. However, less ferricyanide (400–600 μM) in the presence of TMPD decreased the efficiency substantially. TMPD added alone did not quench fluorescence or inhibit excitation transfer, showing that these effects were caused specifically by the oxidized, and not the reduced form of TMPD. In contrast to ferricyanide, iodine and benzoquinone affected excitation transfer without added mediators. The effects of oxidants on whole cells were reversed by subsequent addition of dithionite or ascorbate (Table I), indicating that the oxidant-induced change was reversible.

Results similar to those found with whole cells were also observed with isolated membranes. Membranes with attached chlorosomes of *C. vibrioforme*, diluted with Tris-HCl (pH 8), are not very stable. A 664 nm band due to BPh *d* (and possibly free BChl *d*) increased rapidly over a period of hours, while the 730 nm band of chlorosomal BChl *d* decreased concomitantly. The efficiency of excitation transfer from BChl d_{730} to BChl a_{810} had a maximal value of 85% in the presence of dithionite (see Fig. 5A), compared to 10–20% without dithionite (see Fig. 5B).

In order to test whether the effects of oxidants and reductants on energy transfer efficiency were mediated by the redox state of the reaction center, similar measurements were performed using isolated chlorosomes. Before dithionite was added, the efficiency of excitation transfer from BChl *d* to BChl a_{795} was 20–30% (see Fig. 6A). After dithionite was added, the efficiency was close to 90% (see Fig. 6B).

Similar experiments were carried out with the thermophilic green gliding bacterium *Chloroflexus aurantiacus*. In contrast to the results found for green

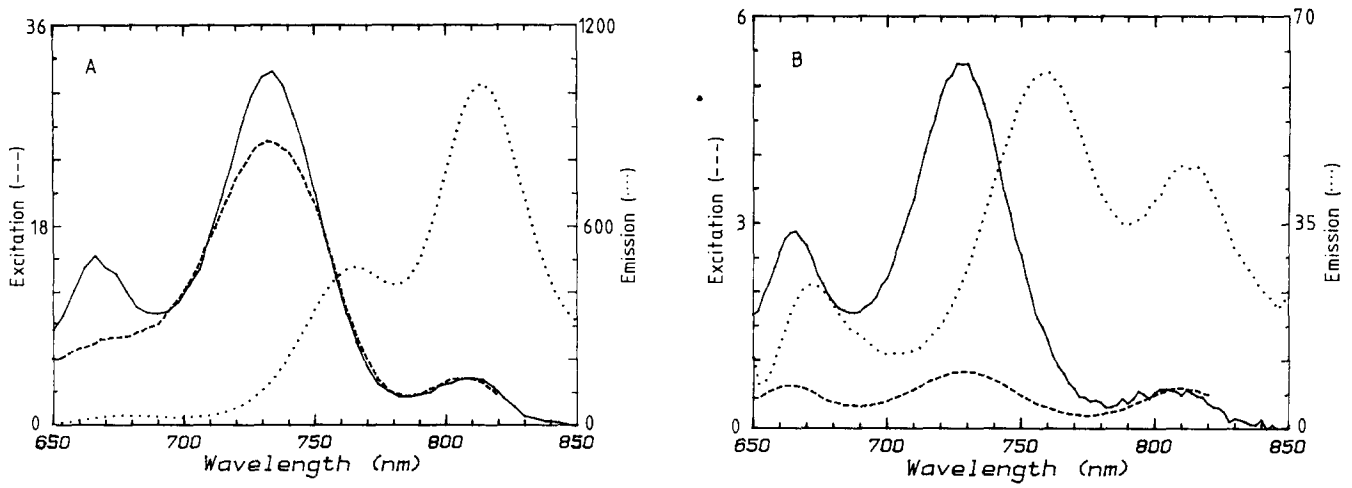

Fig. 5. Absorption (———), and fluorescence excitation (------) and emission (·····) spectra of *C. vibrioforme* membranes with attached chlorosomes. (A) After adding dithionite. (B) Aerobic conditions. Measurement conditions and fluorescence units as in Fig. 3. $A_{730} = 0.2$.

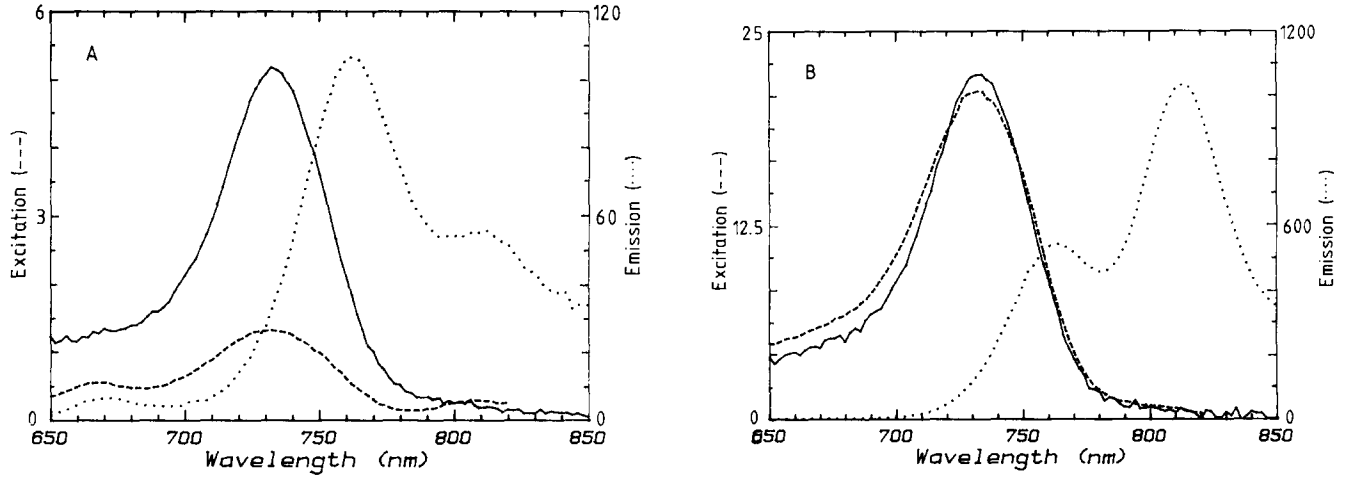

Fig. 6. Absorption (———), and fluorescence excitation (------) and emission (·····) spectra of *C. vibrioforme* chlorosomes. (A) Aerobic conditions. (B) After adding dithionite. Measurement conditions and fluorescence units as in Fig. 3. $A_{730} = 0.2$.

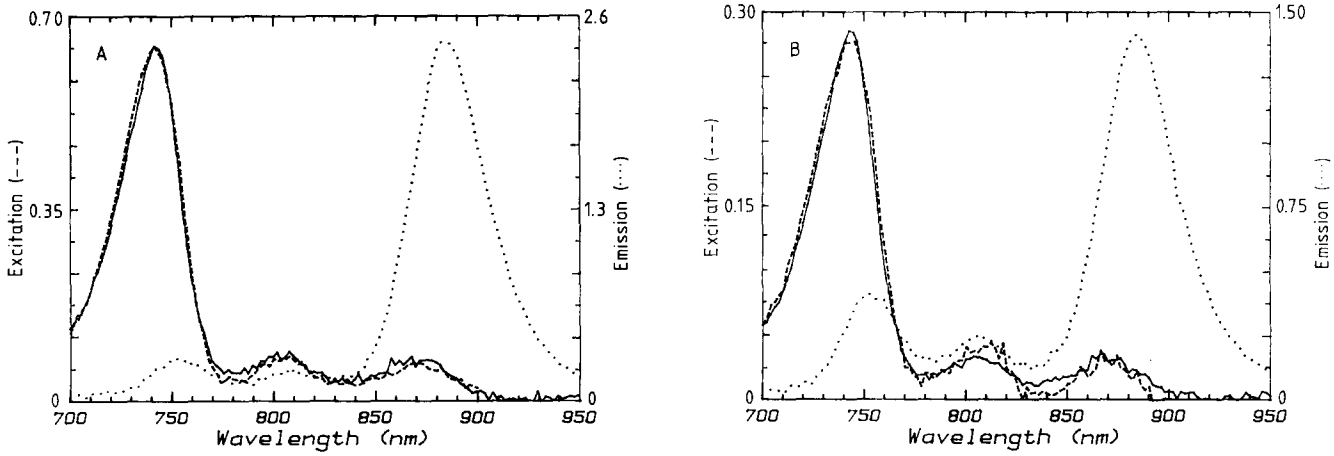

Fig. 7. Absorption (———), and fluorescence excitation (------) and emission (·····) spectra of whole cells of *C. aurantiacus*. (A) Aerobic conditions. (B) After adding dithionite. Fluorescence was monitored at 920 nm for the excitation spectrum, and 460 nm exciting light was used for the emission spectrum. Fluorescence was measured using a photodiode detector. Fluorescence intensity units are proportional to the output of the photodiode and are not directly comparable to the units used in the previous figures. $A_{740} = 0.17$.

sulfur bacteria, the excitation transfer efficiency in *Chloroflexus* cells was high and not sensitive to oxygen (see Fig. 7A). A slight increase in chlorosome fluorescence emission at 755 and 805 nm was observed when dithionite was added to *Cfx. aurantiacus* cells, but this effect was much smaller than that seen with *C. vibrioforme* cells and it was not accompanied by a noticeable change in the efficiency of excitation transfer (Fig. 8B). As discussed by Wittmershaus et al. [8], the fluorescence excitation beam can cause closing of *Cfx. aurantiacus* reaction centers at room temperature (the physiological temperature is 50 °C). This actinic effect of the excitation beam is greatest at absorption maxima and may cause artificially high apparent energy transfer efficiencies. This effect should not be a problem with *Chlorobium* because room temperature is the physiological growth temperature.

Discussion

The data presented in Table I clearly indicate that the dramatic effect of oxygen on the efficiency of energy transfer is a result of oxidizing conditions and not a specific effect of oxygen. Furthermore, the lack of an effect by the highly charged oxidizing species ferricyanide strongly suggests that the oxidant must penetrate the cell to be effective. When combined with low concentrations of the lipophilic redox mediator TMPD, ferricyanide decreased the energy transfer efficiency in a manner similar to the neutral oxidants O_2, I_2 and *p*-benzoquinone.

We interpret our experimental results in terms of a direct effect of oxidants on the energy transfer efficiency within the chlorosome antenna complex, rather than an indirect effect on the antenna mediated by the redox state of the reaction center. We propose that the oxidants induce highly quenching centers in the chlorosome, which are reversibly inactivated by reaction with endogenous or exogenous reductants. Current work is directed at a more precise characterization of the redox properties and chemical identity of the quenching species. The lack of an effect of the weak reductant ascorbate in membranes and isolated chlorosomes suggests that the midpoint potential of the component is less than 0 V.

The pattern of the effects observed in this study, with oxidants causing a decrease in both the level of fluorescence and the energy transfer efficiency, is what is expected if oxidants induce efficient excited state quenchers in the antenna complexes. A very different pattern would be observed if, for example, the oxidants blocked energy transfer by dissociating the chlorosomes from the membrane. In this case, the fluorescence from the baseplate BChl *a* would be expected to increase rather than decrease. Brune et al. [12] observed this effect in detergent-treated membranes of *Chloroflexus aurantiacus*.

A variety of evidence indicates that the BChl *c*, *d* or *e* in chlorosomes is present in the form of closely interacting pigment oligomers. Antenna pigments organized in such a way may be particularly vulnerable to the presence of quenchers or defective pigments. Excited states in large oligomers of pigments will almost certainly be described using a delocalized exciton model. The quenching efficiency of an impurity embedded in such an oligomer can be many times larger than a quencher present in solution [15,36]. In the latter case, diffusion limits the quenching effectiveness by restricting the number of excited states that the quencher contacts.

Fluorescence lifetime experiments on aerobic and anaerobic cells and isolated chlorosomes are currently underway in an effort to test the model proposed above. Preliminary results support the view advanced above, that under aerobic conditions, the excitations are quenched within the bulk chlorosome pigments and most never arrive at the baseplate (Causgrove, T., Wang, J., Brune, D., Wittmershaus, B. and Blankenship, R.E., unpublished data).

In contrast to the results found with the strictly anaerobic Chlorobiaceae, fluorescence from cells of the facultatively aerobic green bacterium *Chloroflexus aurantiacus* was not very sensitive to oxygen and dithionite. Anaerobic and aerobic cells of *Chloroflexus* have essentially the same fluorescence spectra. The fact that excitation transfer in *Chlorobium* is more sensitive to O_2 than is that in *Chloroflexus* may be correlated with differences in photosynthetic electron transport pathways between the two organisms. Shill and Wood [37] have shown that membranes from *C. limicola* can photoreduce O_2 to form superoxide radicals. This occurs because the Fe-S centers that act as electron acceptors in *Chlorobium* reaction centers have a sufficiently low redox potential to transfer electrons to O_2 when photoreduced. The superoxide product is highly reactive and participates in reactions that are destructive to biological materials [38]. In *Chloroflexus*, on the other hand, electrons from the photoexcited reaction center BChl *a* are rapidly transferred to quinone acceptors, which are insufficiently strong reductants to reduce O_2 to O_2^-. Thus, the interruption of excitation transfer within the BChl *c* antenna of *Chlorobium* chlorosomes may actually serve a protective function.

Our results might also explain the observation of Takabe and Akazawa [39] that photosynthesis in *C. limicola* f. *thiosulfatophilum*, as measured by CO_2 fixation, is strongly inhibited by O_2. Unlike the situation in *Chromatium vinosum*, in which the inhibition of photosynthesis by O_2 was shown to be due to photorespiratory reaction of O_2 with ribulose 1,5-bisphosphate, photorespiration was shown not to occur in *C. limicola*

[39]. In agreement with our results, the inhibition of photosynthesis by small amounts of O_2 was transitory, probably due to removal of O_2 by endogenous reductants. Earlier work demonstrating O_2 uptake by suspensions of *Chlorobium* cells and the ability of *Chlorobium* to survive periods of exposure to light and O_2 has been reviewed by Pierson and Castenholz [6].

Acknowledgments

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