Oxygen dependence of photosynthetic electron transport in a bacteriochlorophyll-containing rhizobium

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Abstract Bacteriochlorophyll-containing rhizobia, which form nitrogen-fixing nodules on the stems and roots of the legume *Aeschynomene*, grow photosynthetically only in the presence of oxygen or auxiliary electron acceptors. We show that, in whole cells of the *Rhizobium* strain BTAi 1, a single-turnover excitation flash photooxidized *c*-type cytochrome under aerobic but not anaerobic conditions. Light-induced fluorescence yield changes show that under anaerobic conditions, the primary acceptor quinone, Q_A, is predominantly in the reduced state and so unable to accept electrons. Thus, as is the case for the aerobic photosynthetic bacterium *Roseobacter denitrificans*, over-reduction of Q_A likely prohibits photosynthesis under anaerobic conditions.

Key words: Rhizobium; Photosynthesis; Nitrogen fixation; Reaction center

1. Introduction

Several legume genera include species which have nitrogen-fixing nodules on their stems as well as on their roots [1–4]. The stem nodules of some of these plants fix nitrogen effectively even when their roots are flooded or nitrogenous fertilizer has been added to the soil [5]. Consequently such plants are grown in flooded rice fields to furnish fixed nitrogen for the rice [6,7]. Stem nodulation has been reviewed recently by Boivin et al. [8].

Rhizobia isolated from stem nodules of many species of the tropical and subtropical legume *Aeschynomene* contain bacteriochlorophyll [9–14]. Photosynthetic systems have been found both in stem nodule endophytes and in the isolated rhizobia growing in free-living culture ([9,14,15], D. Fleischman, D. Kramer and S. Shanmugasundaram, unpublished observations). Some of the isolates have been shown to contain DNA homologous to the *puf* operon (which contains photosynthesis genes) of *Rhodobacter capsulatus* [16]. Phylogenetic analyses based on 16S ribosomal RNA sequences and taxonomic studies based on phenotypic characteristics suggest that the *Aeschynomene* stem nodule rhizobia are closely related to *Bradyrhizobium japonicum* and somewhat less closely to the purple photosynthetic bacterium *Rhodopseudomonas palustris* [14,17–19]. Bacteriochlorophyll-containing rhizobia have been reviewed by Fleischman et al. [20].

The first rhizobium shown to form bacteriochlorophyll was isolated from a stem nodule that formed spontaneously on an *Aeschynomene indica* plant at the Boyce Thompson Institute at Cornell, and was named BTAi 1 [21,22]. It has been studied in most detail, and was the object of the present study. When grown under appropriate conditions, it forms bacteriochlorophyll and photochemically active photosynthetic reaction centers; light enhances $^{14}CO_2$ assimilation by free-living BTAi 1 cells, prolongs their viability and enhances acetylene reduction (an indication of nitrogenase activity) by BTAi 1 in stem nodules and in microaerobic culture [9,23]. All of the bacteriochlorophyll-containing rhizobia described thus far are unable to grow photosynthetically in the absence of oxygen. In this respect, they resemble the aerobic anoxygenic phototrophs ('aerobic photosynthetic bacteria'), which have been reviewed by Shimada [24]. Intact cells of the aerobic photosynthetic bacterium *Roseobacter denitrificans* (formerly *Erythrobacter* OCh 114) display light-induced oxidation of cytochrome c_{551} and reaction center bacteriochlorophyll, light-induced proton extrusion and photophosphorylation in the presence of oxygen but not under normal anaerobic conditions [25,26]. It was suggested that under anaerobic conditions their electron transport systems become overreduced. In support of this idea, light-induced electron transport was restored in the presence of auxiliary oxidants such as nitrate, nitrite, trimethylamine *N*-oxide (TMAO) and chlorate, and the bacteria grew anaerobically in the presence of TMAO [27,28].

Like *R. denitrificans*, BTAi 1 will grow anaerobically in the presence of TMAO [29]. Illumination elevates the ATP content of BTAi 1 cells, but only in the presence of oxygen [30]. The objective of the present study was to determine whether photosynthetic electron transport in BTAi 1 cells requires oxygen and to evaluate the redox state of the electron acceptors under anaerobic conditions.

2. Materials and methods

2.1. Bacteria

Rhizobium strain BTAi 1 was obtained from A.R.J. Eaglesham of the Boyce Thompson Institute. Cells were grown at room temperature in 2.5 l batches with magnetic stirring in air under cyclic illumination (12 h light/12 h dark) provided by two 100 W tungsten bulbs at a distance of 6 in. A mineral salts medium [31] supplemented with 0.15% glutamic acid and 0.05% yeast extract, buffered at pH 6.75 with 16 mM phosphate, was employed; Ca^{2+} was omitted. The bacteria were collected by centrifugation at the end of exponential growth, about 7 days after inoculation.

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Abbreviations: bc_1 complex, the ubiquinol:cytochrome *c* oxidoreductase; I, the pheophytin electron acceptor in the bacterial reaction center; P, the primary chlorophyll electron donor of a bacterial photosynthetic reaction center; Q_A, the primary quinone acceptor of a type-1 bacterial reaction center; Q_B, the secondary quinone acceptor of a bacterial reaction center; TMAO, trimethylamine *N*-oxide

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2.2. Measurement of absorption spectra and kinetics

BTAi 1 cells form highly scattering suspensions, making spectrophotometric measurements difficult. Consequently a sensitive kinetic spectrophotometer, designed for measurements on intact leaves and constructed in-house, was employed [32]. Based on principles suggested by Joliot and coworkers [33,34], it employs a high-intensity, short-duration light pulse to drive photochemistry, and a series of low-intensity, short-duration pulses at programmed intervals to measure absorbance. Actinic illumination was provided by a xenon flashlamp filtered with a 665 nm color glass filter (RG665, Schott). The pulse duration of the flashes was approximately 4 μs. It was concluded that the actinic flashes were saturating since decreasing their intensity by ca. 50% had little effect on the extents or kinetics of the flash-induced signals (not shown). Aerobic conditions were achieved by stirring the cells in the instrument under air; after cessation of stirring or superfusion of the cells with argon, oxygen was depleted in a few minutes by cellular respiration.

2.3. Measurement of fluorescence yield kinetics

Measurement of fluorescence yield kinetics employed a kinetic fluorimeter based on that described by Kramer et al. [35], and modified as described by Kramer and Crofts [36]. Short-duration, high-intensity flashes or steady light served to drive photochemistry, while a series of low-intensity, short-duration (2–3 μs) pulses of 640 nm light from a bank of seven light-emitting diodes (LEDs, HLMP 8103, Hewlett Packard), filtered with an interference filter (640DF70, Omega Optical) were used to probe the fluorescence yield. Each probe pulse excited less than 0.2% of the reaction centers as judged by the rate of increase in fluorescence yield upon application of successive probe pulses in the presence of 1 mM ascorbic acid and 5 mM *o*-phenanthroline to block Q_A reoxidation (not shown). Fluorescence was measured by a photodiode filtered with an appropriate long-wavelength pass filter set (two layers of Kodak Wratten 89B and one layer of Schott RG695) as described by Kramer et al. [37]. Saturating flashed actinic illumination was provided by a xenon flashlamp (FX201, EG and G) filtered with one 2 mm thick layer of a blue glass filter (Schott BG-18) and an IR cutout filter (57401, Oriel). Continuous actinic illumination – 200 μmol photons/m^2/s blue-green light as measured as 'photosynthetically active radiation' (for higher plants) by a Licor Quantum Li-185B sensor and meter – was provided by a quartz halogen lamp filtered with a hot mirror (57401, Oriel) and one layer of a blue glass filter (51710, Oriel), and shuttered with an electromechanical shutter constructed in-house.

3. Results

3.1. Flash-induced absorbance changes in whole cells of BTAi 1

Fig. 1 shows time-resolved spectra of absorbance changes that occurred after flash excitation of aerobic and anaerobic BTAi 1 cells. In aerobic cells, relatively large absorbance changes, consistent with an operational photosynthetic apparatus, were observed. After a single flash, the rapid (20 μs) spectrum is consistent with the formation of the oxidized reaction center special pair, or primary donor [9]. By 6 ms this had been replaced by a difference spectrum characteristic of the oxidation of *c*-type cytochromes. The latter spectrum had largely decayed by 60 ms. A comparison of the light-induced difference spectrum with the oxidized-minus-reduced difference spectra of the membrane and soluble fraction of BTAi 1 cells (data not shown) suggests that the absorbance changes represent the oxidation of *c*-type cytochromes, probably involved in a cyclic electron transfer chain, e.g. cytochromes c_1 and c_2 of purple photosynthetic bacteria. The reduced-oxidized difference spectrum of the membrane fraction also indicated the presence of membrane-associated *c*- and *b*-type cytochromes as evidenced by an absorbance band at 550 nm and a distinct shoulder at about 560 nm. The flash-induced redox kinetics of *c*-type cytochromes, presumably cytochromes c_1 and c_2 associated with the cyclic electron transport

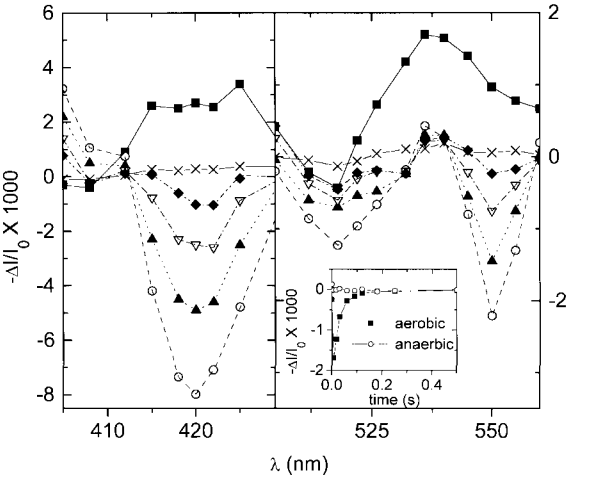

Fig. 1. Light-induced absorbance changes in aerobic BTAi 1 cells. Time dependence of absorbance changes following a single flash in aerobic (traces a–e) and anaerobic (trace f) BTAi 1 cells. Anaerobic cells were maintained under flowing (but not bubbling) argon for 60 min in the dark prior to experiments. Spectra were recorded at the following times after single-turnover excitation: a, 10 μs (■); b, 6 ms (○); c, 17 ms (▲); d, 30 ms (▽); e, 60 ms (◆); f, 6 ms (anaerobic conditions, ×). The inset shows the flash-induced kinetics of cytochrome redox changes in aerobic (■) and anaerobic (○) cells.

chain, estimated by taking the difference between the absorbance changes at 550 nm and the average of those at 540 and 560 nm, are shown in the inset to Fig. 1. The half-time for cytochrome rereduction was approximately 10 ms, and we suggest that these kinetics represent the turnover of the cytochrome bc_1 complex, as extensively studied in purple bacterial systems (reviewed in e.g. [38,39]). The flash-induced absorbance changes in anaerobic BTAi 1 cells were below the noise level. The spectrum of absorbance changes at 6 ms after a single flash is shown in Fig. 1, trace e and the deconvoluted changes in cytochrome *c* redox state are shown in the inset to Fig. 1.

We speculated that under anaerobic conditions the photosynthetic electron transport chain might have been over-reduced in the dark, so that no acceptors were available to receive electrons during subsequent illumination. In order to compare the size of the pools of available electron acceptors under aerobic and anaerobic conditions, fluorescence yield kinetics were observed in the dark or upon application of continuous exciting light. The fluorescence yield is defined as $(F-F_0)/F_0$, where F is the fluorescence yield at any time and F_0 is the fluorescence yield in the dark under aerobic conditions, when all reaction centers are expected to be in open states (i.e. with reduced primary chlorophyll donor and oxidized Q_A acceptor). The yield of fluorescence in purple bacterial systems depends upon the redox states of the reaction centers (reviewed in [40]). It is low when the centers are in the PQ_A and PI^- states, and high when either the primary donor is oxidized or Q_A is reduced. Fig. 2A shows that the fluorescence yield starts out low in the dark under aerobic conditions, consistent with the reaction centers being in the PQ_A state, but increases upon progressive depletion of oxygen (presumably by respiration) from the medium. Since oxidation of P is not expected in the dark under anaerobic conditions because a highly oxidizing potential would be required, the increase in fluorescence yield is interpreted as reflecting a reduction of Q_A. The kinetics of fluorescence increase are sig-

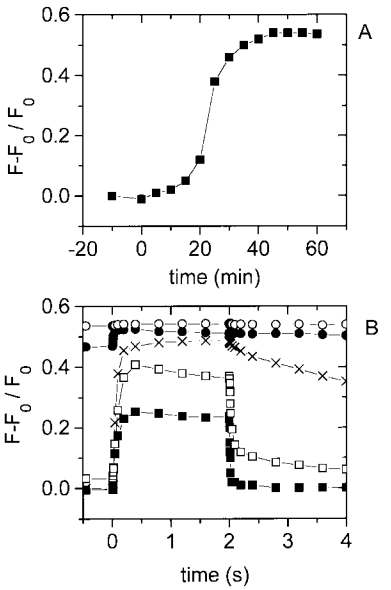

Fig. 2. Fluorescence yield kinetics in aerobic and progressively anaerobic BTAi 1 cells. A: Relative fluorescence yields of cells in the dark measured with a weak probe pulse. Cells were dark-adapted for 20 min with stirring in air prior to the start of the experiments. O_2 was removed at time zero. B: Changes in fluorescence yield upon excitation with 200 μmol photons/m^2/s blue-green light after different times of exposure to anaerobic conditions (see Section 2 for details). Illumination began at time zero and ended after 2 s. Traces were taken in air (■); after 15 (□), 25 (●), and 60 (○) min exposure to anaerobic conditions, or under aerobic conditions but in the presence of 1 mM *o*-phenanthroline (×).

moidal, with a lag of approximately 10–15 min followed by a steep increase which saturated after between 40–50 min. We interpret the lag as reflecting the time required to deplete O_2 from the medium and to reduce pools of more oxidizing electron acceptors, e.g. the quinone pool, prior to the reduction of Q_A.

Upon illumination of aerobic cells with continuous light, the fluorescence yield rose, reaching a steady level within a few milliseconds (Fig. 2B, solid squares). We interpret this as reflecting the establishment of a steady-state fraction of reaction centers in high fluorescence states during turnover of a cyclic electron transfer pathway. Upon cessation of illumination, the fluorescence yield dropped to the dark-adapted level within 100 ms (Fig. 2B, solid squares). After 15 min of anaerobiasis, the dark fluorescence yield as well as the light-induced increase in fluorescence yield had increased. This probably reflects a partial reduction of the quinone pool, resulting in a small population of reduced Q_A in the dark and a slower rate of Q_A^- reoxidation during steady-state illumination. After further incubation in the absence of oxygen, the dark fluorescence levels further increased, but the light-induced rise in fluorescence yields decreased. Our interpretation is that, as the internal redox poise of the quinone pool became more reducing in the absence of oxygen, Q_A became predominantly reduced. Illumination could not further increase the fluorescence yield since electron transfer from P to Q_A would have been blocked by prereduction of Q_A. Thus, we estimate that, after 60 min of anaerobiasis, essentially 100% of Q_A had become reduced. Reintroduction of O_2 into the cuvette, by agitating the culture in air, resulted in an immediate return to the aerobic state (not shown).

Addition of 1 mM *o*-phenanthroline to aerobic cells resulted little change in the dark fluorescence yield, but a dramatic increase in the steady-state fluorescence yield. *o*-Phenanthroline blocks the Q_B site, and thus is expected to lead to an accumulation of Q_A^- in the light. The maximum fluorescence yield in the presence of *o*-phenanthroline was somewhat lower than that achieved under fully anaerobic conditions. We suggest that *o*-phenanthroline may have secondary effects, such as a direct interaction with the antenna, which could have lowered the maximal fluorescence yield. Alternatively, illumination in the presence of *o*-phenanthroline should have resulted in reduction of Q_A without full reduction of the pool quinone. It is known that oxidized quinone species can act as fluorescence quenchers by direct interaction with the antenna system (e.g. [41,42]) and therefore the differential concentrations of oxidized pool quinone may have affected the maximum fluorescence yield.

4. Discussion

BTAi 1 cells exhibited light-induced absorbance changes, apparently due to the oxidation of a *c*-type cytochrome, only in the presence of oxygen. Thus their behavior is similar to that of the aerobic photosynthetic bacterium *R. denitrificans* [25]. The absence of measurable photosynthetic electron transport in the absence of oxygen explains the inability of BTAi 1 to grow phototrophically under anaerobic conditions.

Fluorescence induction kinetics suggest that photosynthetic electron transfer could not proceed under anaerobic conditions because the electron acceptor Q_A was prereduced. A comparison of the fluorescence yields of dark-adapted aerobic and anaerobic cells (Fig. 2A,B) strongly suggests that essentially all of Q_A is reduced before illumination in anaerobic cells. During continuous illumination, the fluorescence yield rises as the acceptor pools become filled, allowing a stable fraction of Q_A^- and P^+. Since the fluorescence yield of the aerobic cells during continuous illumination never reached the level even of that in dark-adapted anaerobic cells, it is clear the acceptor pools in the aerobic cells do not become completely reduced even after prolonged illumination under these conditions. This is expected for a purely cyclic electron transfer system since the total number of electrons on the redox carriers is constant, and the rise in fluorescence yield reflects only the movement of these electrons from P to more reducing acceptors.

In bacteria, electrons may be added to the photosynthetic electron transfer system or removed from it by peripheral processes such as oxidation of substrates and reduction of NAD^+ and O_2. Since full reduction of Q_A or full oxidation of P would prevent cyclic turnover, it is essential to have an operational redox 'poising system' to maintain the intermediate carriers in states that allow turnover of the whole cycle (reviewed in [43]). From previous results on related species [25] and our results on BTAi 1, it appears that aerobic photosynthetic bacteria are incapable of maintaining Q_A in the oxidized form in the absence of O_2, but it is yet unclear why this is the case. In *R. denitrificans*, Q_A appears to have a more positive midpoint potential (+35 mV) than is typical of purple photosynthetic bacteria [25]. If this is true in BTAi 1 as well, the redox equilibrium between Q_A and subsequent acceptors may be such that Q_A is largely reduced even when the quinone pool is only partially filled. Alternatively, the aerobic photo-

synthetic bacteria may maintain the redox state of their quinone pools via oxidative processes involving cytochrome oxidase or alternate oxidases and may lack other acceptor pools present in photosynthetic bacteria that are capable of anaerobic growth. A third possibility is that they may lack a mechanism to assure that the flow of electrons by non-photosynthetic processes into and out of the quinone pool occur at the same rate under anaerobic conditions. Chloroplasts of higher plants may utilize the cytochrome *bf* complex to sense the redox state of the plastoquinone pool and use protein kinases to adjust electron transfer rates appropriately [44]. A similar mechanisms might operate in photosynthetic bacteria, which possess cytochrome bc_1 complexes and protein kinases [45]. This might function differently in the aerobes and anaerobes.

Aerobic photosynthetic bacteria are found in several genera [24], and many of these are not closely related phylogenetically. The bacteriochlorophyll-containing rhizobia belong to the *Rp. palustris* branch of the α subdivision of the *Proteobacteria* [17,18]. *R. denitrificans* shares a different branch with *Rhodospirillum rubrum*. So aerobic and anaerobic photosynthetic bacteria may have diverged numerous times from common ancestors.

The behavior of the electron transport system in bacteroids also remains to be determined. The environment within stem nodules is expected to be microaerobic, because of the oxygen sensitivity of nitrogenase. Perhaps the bacteroid photosynthetic system is adapted to function optimally under microaerobic conditions.

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