

Photosynthetic genes in *Rhodobacter capsulatus* can be regulated by oxygen during dark respiratory growth with dimethylsulphoxide

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In the purple non-sulphur bacterium *Rhodobacter capsulatus*, genes encoding structural polypeptides of the light-harvesting (LH) and reaction center (RC) complexes incorporated into an intracytoplasmic photosynthetic membrane are induced upon lowering the oxygen tension in the media of aerobically growing cultures. When cultures are grown microaerophilically in the dark, an intracytoplasmic photosynthetic membrane develops gratuitously if a terminal oxidant, such as dimethylsulphoxide (DMSO) is present in the medium. The purpose of the present study was to determine whether in these conditions, photosynthetic genes are completely derepressed or whether they are still inducible in response to a lowering of oxygen tension. Oxygen induction of mRNA for the *puf* and *puc* operons was compared in dark aerobic cultures (20% O₂) shifted to low oxygen conditions (3% O₂) allowing growth microaerophilically with or without DMSO as an accessory terminal oxidant. The extent of the induction was similar in both growth conditions, 6 to 12-fold for *pufA* mRNA and at least 400-fold for *pucB* mRNA which encode the light-harvesting I (LHI α) and light-harvesting II (LHII β) polypeptides, respectively. The *puf* and *puc* operons were also induced by low oxygen tension in a mutant strain blocked in an early step of bacteriochlorophyll (BChl) synthesis, suggesting that the presence of BChl may not be a prerequisite for the normal oxygen regulation of the genes encoding the structural polypeptides of the photosynthetic apparatus.

Introduction

Rhodobacter capsulatus is a metabolically versatile purple non-sulphur bacterium, capable of photosynthetic or chemoheterotrophic growth according to environmental conditions. It grows photosynthetically in an illuminated environment only when oxygen tension drops below 3% (Oelze & Drews, 1972). Furthermore, in the dark, *R. capsulatus* is capable of anaerobic growth on non-fermentable sources of carbon when the medium is supplemented by either dimethylsulphoxide (DMSO) or trimethylamine-*N*-oxide (TMAO) (Yen & Marrs, 1977; Cox *et al.*, 1980; Madigan *et al.*, 1980; Schultz & Weaver,

1982; McEwan *et al.*, 1985) or with nitrous oxide (McEwan *et al.*, 1984). These alternative terminal oxidants stimulate the growth of non-photosynthetic cultures and allow the gratuitous formation of an intracytoplasmic photosynthetic membrane (Yen & Marrs, 1977). Thus it is possible to propagate non-photosynthetic mutants in conditions in which they can express components of the photosynthetic apparatus, but where photosynthetic growth is not required. The pattern of photosynthetic gene expression during microaerophilic respiratory growth with an alternative terminal oxidant has not been previously studied. The observation that an intracytoplasmic membrane develops during dark anaerobic growth (Yen & Marrs, 1977) implies that genes for the photosynthetic polypeptide components of the integral membrane BChl-protein complexes are expressed to some extent. We wished to determine whether bacterial cultures maintained oxygen regulation of photosynthetic gene expression in the presence of an alternative terminal oxidant. In the present paper, we have compared the growth properties of cultures of *R. capsulatus* shifted from 20% to 3% oxygen tension both in the presence and in the absence of DMSO as an accessory terminal oxidant.

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Abbreviations: BChl, bacteriochlorophyll; LH, Light-harvesting complex; PS, photosynthetic; RC, reaction-center; RCV medium, DL-malate as the carbon source, ammonium sulphate as the nitrogen source, phosphate buffer, thiamine hydrochloride, and mineral salts; RCV⁺ medium, RCV supplemented with 50 mM-DMSO, 0.6% glucose and 0.5% pyruvate.

Methods

Bacterial strains, media, and growth conditions. *R. capsulatus* rifampicin-resistant strain SB1003 (Marrs, 1981) and its *bchD::Tn5.7* derivative KZR8E12 (Zsebo & Hearst, 1984) were used. Strains were grown on malate-minimal RCV medium (Weaver *et al.*, 1975) in 250 ml side-arm flasks at 30 °C or in RCV supplemented with 50 mM-DMSO, 0.6% glucose and 0.5% pyruvate (RCV⁺). Neither glucose nor pyruvate supports fermentative growth of *R. capsulatus*, but they greatly enhance dark anaerobic growth when DMSO is added to RCV medium (Yen & Marrs, 1977). Overnight dark inocula were sparged with N₂/O₂/CO₂ (78:20:2, by vol). When cultures reached early exponential growth, the sparging gas mixture was changed to low oxygen conditions of either 95:3:2 or 98:0:2. The gas flow rates were approximately 250 cm³ min⁻¹ for each culture. Gas flow rate and composition were controlled using a Matheson Gas Products Multiple Dyna-blender, model 8219. Growth rates were monitored using a Bausch and Lomb Spectronic 21 spectrophotometer.

RNA isolation and hybridization. Total RNA was extracted as described by Zhu & Kaplan (1985). At each time-point, 5 µg RNA was dot-blotted onto a GeneScreen membrane (New England Nuclear) or a nitrocellulose membrane (Schleicher and Schuell) using a mini-fold dot-blot apparatus (Schleicher and Schuell). Blots were probed either with nick-translated pDC100 (Cook *et al.*, 1989) which carries the *fbc* operon encoding the cytochrome b/c1 complex (Gabellini & Sebald, 1986), or with recombinant M13 phage derivative T319 containing a portion of the *pufA* gene which codes for the α subunit of the LHI antenna complex (Youvan *et al.*, 1984) labelled by primer-extension, or with a 5' end-labelled 15-mer oligonucleotide complementary to the *pucB* gene encoding the LHII-β subunit of the LHII antenna complex (Zhu & Hearst, 1986). To account for fluctuations in the amounts of RNA dotted, serial dilutions of each RNA stock were probed with nick-translated pRC1 plasmid which encodes *R. capsulatus* rRNA genes (Yu *et al.*, 1982). After hybridization and autoradiography, dots were quantified by scintillation counting in 5 ml of Opti-Fluor (Packard) in a Packard model 3385 scintillation counter, or by scanning autoradiograms in their linear response range with a Hoefer GS-300 transmittance-reflectance densitometer. Data for mRNA hybridizations were normalized based on rRNA hybridization using pRC1 as a probe.

Results

Dark respiratory growth of *R. capsulatus* strains in the presence of DMSO at low-oxygen concentrations

Strain SB1003, which is wild-type for the photosynthetic genes, and its derivative KZR8E12, which lacks BChl (Zsebo & Hearst, 1984), were grown on a non-fermentable medium in the presence (RCV⁺) or absence (RCV) of added DMSO. KZR8E12 carries a *bchD::Tn5.7* mutation and is blocked in one of the first two reactions of BChl biosynthesis starting from protoporphyrin IX (Biel & Marrs, 1983). Cultures were maintained in the dark throughout the experiment. When cells reached early exponential phase, they were shifted from a 20% to a 3% oxygen concentration. This drop in oxygen tension is sufficient to allow induction of photosynthetic genes in the wild-type strain when grown without illumination on unsupplemented RCV medium

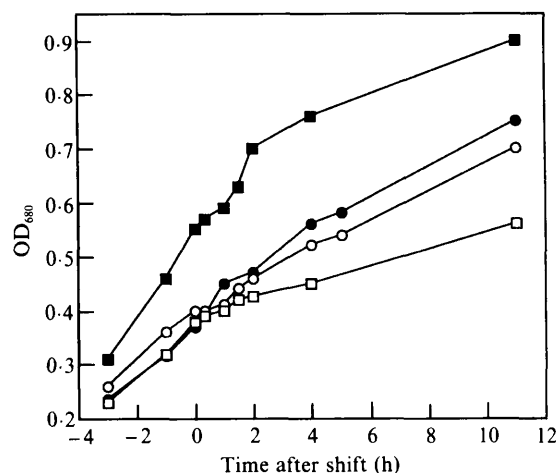


Fig. 1. Growth curves during dark shift from 20% to 3% oxygen concentration of *R. capsulatus* strain SB1003 in RCV (■) and RCV⁺ (●), and strain KZR8E12 in RCV (□) and in RCV⁺ (○).

(Oelze & Drews, 1972). We chose a shift to 3% O₂ for our studies because we observed no growth of SB1003 or KZR8E12 cultures when they were shifted to 0% O₂ in the dark unless DMSO was present in the medium, as has been previously reported (Schultz & Weaver, 1982; Richardson *et al.*, 1988). Growth of the cultures was monitored for 11 h after the shift from 20% to 3% O₂. The doubling time in 20% oxygen was about 4 h for both SB1003 and KZR8E12, whether the medium was supplemented with DMSO or not (Fig. 1). When oxygen tension dropped to 3%, the cultures resumed growth at a slower rate with only a short adaptive period compared to the 90–120 min lag phase observed when shifting a wild-type *Rhodobacter* culture to strictly anaerobic photosynthetic growth conditions (Gray, 1967; Cook *et al.*, 1989). The longer lag-phase in the latter experiments can be explained by the more dramatic nature of the shift from respiratory to photosynthetic conditions. After the shift from 20% to 3% O₂, cultures grew with an average doubling-time of 14 h for SB1003 and 18 h for KZR8E12 in RCV medium (Fig. 1) indicating slow respiratory growth with 3% O₂ in the absence of alternate terminal oxidants. When the medium was supplemented with DMSO, growth subsequent to the O₂ step-down resumed with a generation time of 6 h and 10 h for strains SB1003 and KZR8E12, respectively. The generation times were averaged over three experiments and are in accord with published values for growth on supplemented malate medium in a completely anaerobic environment, which range from 7 to 14 h, depending on strain type (Schultz & Weaver, 1982; Richardson *et al.*, 1988). Cultures of the same strains in RCV⁺ shifted to 0% oxygen had similar growth rates as when shifted to 3% oxygen concentration (data not shown). The presence of low levels of oxygen in

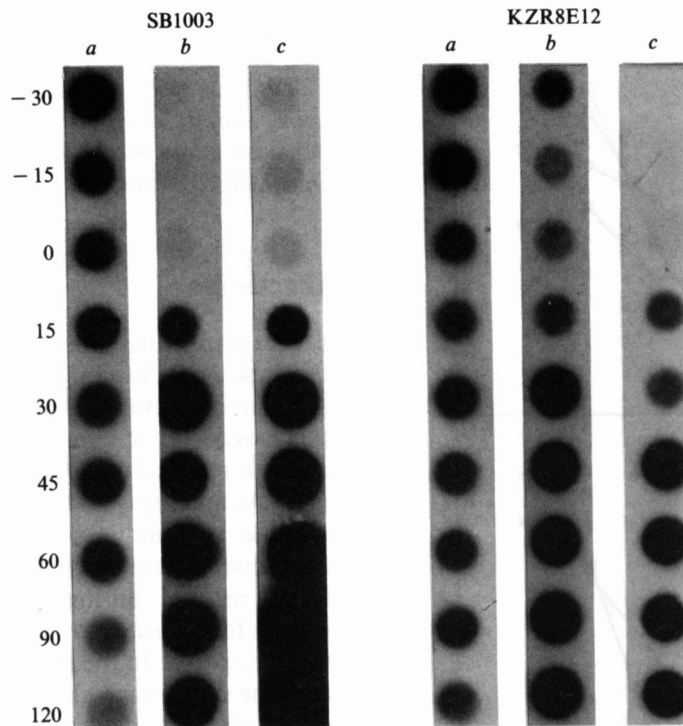


Fig. 2. Dot-blot hybridization of *R. capsulatus* strains SB1003 and KZR8E12 with probes for *fbc* (a), *puf* (b) and *puc* (c) operons. Total RNA was collected at the time indicated (min) following the shift in oxygen tension from 20% to 3%, and 5 μ g was dotted for hybridization. Autoradiograms obtained from cultures grown in RCV⁺ and RCV were similar, and only data corresponding to the shift in RCV⁺ are shown.

the RCV⁺ cultures thus did not grossly disturb the metabolic balance established by the use of the alternative DMSO respiratory pathway.

Expression of fbc mRNA for the cytochrome b/c1 complex remains constant

Amounts of mRNA for the cytochrome b/c1 complex encoded by the *fbc* operon (Gabellini & Sebald, 1986) have been shown to remain constant throughout shifts from aerobic to anaerobic photosynthetic growth conditions in strain SB1003 (Cook *et al.*, 1989). Since the cytochrome b/c1 complex is used during both photosynthetic and aerobic growth, but not during growth with the alternative DMSO respiratory pathway (Daldal, 1988), we first examined whether *fbc* expression was also constitutive during a dark shift in DMSO-supplemented media. Fig. 2 shows that when both the wild-type and the *bchD* mutant KZR8E12 strains are shifted from 20% to 3% O₂ in the presence of added DMSO the amount of *fbc* mRNA remains constant.

The puf operon induction is similar in the wild-type and a BChl-minus mutant

We next investigated whether expression of other genes necessary for photosynthesis was constitutive or induc-

ible during dark respiratory growth (3% O₂) with DMSO, with respect to levels of mRNA found during dark aerobic respiration (20% O₂). Transcript accumulation from the *puf* operon encoding LHI antenna and RC structural polypeptides was monitored over a 2 h period after reducing the oxygen tension. The *puf* operon both in SB1003 and its *bchD* derivative KZR8E12 showed transcriptional responses to the lowering of the oxygen tension in both unsupplemented and DMSO supplemented media (Figs 2 and 3a). The increase in *pufA* mRNA was 6 to 15-fold over the basal levels observed before the shift for all four cultures. Amounts of *pufA* mRNA in strain KZR8E12 were on the average 36% higher than in the wild-type. However, there was no significant difference in accumulation of *pufA* mRNA between the wild-type and the BChl-less mutant strain in the conditions used in this study.

puc mRNA induction differs in the wild-type and a BChl-less mutant

We also probed for mRNA from the *puc* operon, encoding the LHII antenna polypeptides (Youvan & Ismael, 1985), since the pattern of accumulation of the *puc* mRNA is different from that of *puf* mRNA in wild-type strains. Maximal *puc* mRNA accumulation occurs

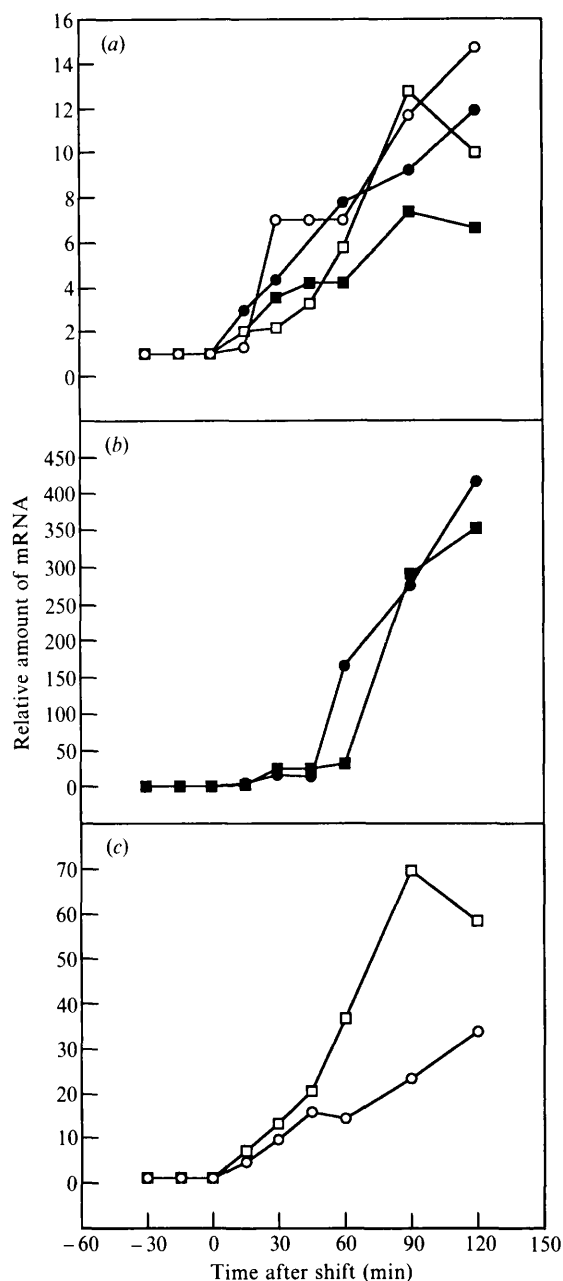


Fig. 3. Time-course of *puf* (a) and *puc* (b and c) mRNA accumulation for dark-shifted cultures of SB1003 (filled symbols) and KZR8E12 (open symbols), respectively, in RCV and RCV⁺ media. mRNA values are relative to basal levels for each culture. After autoradiography, dots were quantified by scintillation counting.

30 min later than maximal *puf* mRNA accumulation during development of the photosynthetic membrane (Klug *et al.*, 1985). We observed that transcription in the wild-type strain was induced similarly in both RCV and RCV⁺ media, with mRNA amounts 120 min post-shift up to 400-fold higher than the pre-shift values. For both cultures, induction of the *puc* operon was delayed when compared to that of the *puf* operon (Fig. 3b and c), in

agreement with the results obtained by Klug *et al.* (1985). Although the magnitude of *puc* mRNA accumulation at 120 min post-shift is reduced when compared to wild-type, the BChl-less strain KZR8E12 also showed a substantial mRNA induction of 30-fold in RCV and 70-fold in RCV⁺ media.

Discussion

The experiments we describe in this paper show that in the dark, under low oxygen tension in the presence of an alternative terminal oxidant such as DMSO, photosynthetic genes in *R. capsulatus* are not fully derepressed, and still respond to O₂ regulation. The accumulation of mRNAs for the *puf* and *puc* operons is similar whether or not the medium is supplemented with DMSO. The magnitude of mRNA accumulation is comparable to levels reached during adaptation to photosynthetic growth for the *puf* operon, whereas it is much higher for the *puc* operon. In the presence of DMSO, growth slows after the shift from high to low oxygen concentration, but unlike photosynthetic cultures, no marked lag-time for adaptation is observed. In these growth conditions, bacteria develop a chromatophore membrane gratuitously, but do not need to wait for its completion to resume growth. They rely on an energy-generating mechanism which is already in place, but which is less efficient in generating cell mass when compared to aerobic growth (Fig. 1). The initial controversy as to the role of added oxidants such as DMSO, as either electron sinks to maintain favourable cellular redox potentials (Marrs & Gest, 1973; Cox *et al.*, 1980; Madigan *et al.*, 1980; Zannoni & Marrs, 1981) or as participants in an electrogenic pathway (Yen & Marrs, 1977; Schultz & Weaver, 1982; McEwan *et al.*, 1983) has only recently been clearly resolved. *Rhodobacter capsulatus*, like many non-photosynthetic bacteria, has two proton-translocating respiratory pathways. One pathway can function in complete anaerobiosis as well as in microaerophilic conditions, and uses either DMSO, TMAO, nitrate or nitrous oxide as terminal oxidants instead of oxygen (McEwan *et al.*, 1984; Richardson *et al.*, 1988). It has been determined that during anaerobic respiration, electrons pass from the NADH dehydrogenase to the quinone pool, by-passing the cytochrome b/c1 complex, and proceed to the DMSO/TMAO or the nitrous oxide reductase. This electron transport is coupled to ATP production (Richardson *et al.*, 1986).

The increase in *pufA* mRNA for the photosynthetic wild-type strain SB1003 was comparable to the 8 to 15-fold range previously reported by several authors (Bauer *et al.*, 1987; Klug *et al.*, 1986; Cook *et al.*, 1989). In the 2 h induction experiments we describe here, *pucB*

mRNA continued to increase up to about 400-fold at the end of the time-course, three-fold higher than any *puc* mRNA increase reported previously. Differences in amounts of *puc* mRNA between high and low oxygen cultures vary widely in the literature, ranging from 6-fold to 100-fold (Klug *et al.*, 1984; Klug *et al.*, 1985; Zhu & Hearst, 1986). We attribute these differences to experimental procedures, *puc* mRNA being much more sensitive than *puf* mRNA to environmental factors (Zhu *et al.*, 1986), and to differences in the bacterial strains. When we shifted a dark, aerobically-grown SB1003 culture to totally anaerobic conditions, we observed a maximal increase of *puc* mRNA accumulation of only 20-fold compared to pre-shift levels (data not shown). It thus appears that the maximal inducibility of *puc* mRNA occurs at oxygen tensions greater than 0% in spite of the faster degradation rate reported for *puc* mRNA in cells exposed to fully aerobic conditions (Zhu *et al.*, 1986).

The *puf* and *puc* operons in strain KZR8E12, a *bchD::Tn5.7* derivative of SB1003 blocked in one of the first two reactions of BChl biosynthesis after protoporphyrin IX, show a qualitatively wild-type response at the transcriptional level to a drop in oxygen tension. *pufA* mRNA induction was similar to that of the wild-type strain. This result is in accord with that of Bauer *et al.* (1987), who observed oxygen regulation of *puf* operon expression in BChl mutants using plasmid-borne *lacZ* transcriptional gene fusions to monitor promoter activity. In the case of the *puc* operon, the level of induction was ten-fold lower in the *bchD* strain than in the wild-type in RCV, and partially compensated for by the addition of DMSO to the media. This differential regulation of the *puf* and *puc* operons cannot be attributed to the *crtD* carotenoid biosynthesis point-mutation also carried by KZR8E12, since this latter mutation does not affect expression of genes encoding the LHI and LHII polypeptides (Armstrong, 1989). A differential regulation between *puf* and *puc* mRNA was also seen by Klug *et al.* (1986) for strain YS, a *bchC* mutant. In their case, however, these authors observed no induction of the *puc* operon and only a slight induction of *puf* mRNA. We conclude that the requirements for the normal accumulation of mRNA for the structural components of the LHI and LHII antenna complexes are different. Neither mature Bchl nor a precursor beyond Mg-protoporphyrin IX monomethyl ester is required for induction of mRNA for the LHI complex. In contrast, while we observe a 30 to 70-fold increase of *puc* mRNA in the *bchD* mutant KZR8E12 2 h after lowering the oxygen tension, the full 400-fold accumulation of this mRNA with wild-type kinetics is dependent on the presence of a compound participating in the biosynthesis of Mg-porphyrins. Whether the effect is exerted on overall mRNA levels, or merely affects the rate of

mRNA accumulation, is outside the scope of our shift experiments.

Growth shifts were performed in the dark, using conditions where cultures of both the wild-type and the BChl mutant strains could continue to grow after lowering the oxygen tension. Although both strains grew at different rates subsequent to the shift to 3% oxygen in RCV and RCV⁺ media, transcriptional control of the *puf* and *puc* operons was retained, proving that dark respiration with DMSO is compatible with the regulation of photosynthetic gene expression by oxygen tension. Gene regulation of the *puf* and *puc* operons is therefore independent of the ATP-producing pathway, be it photosynthesis, or aerobic respiration at oxygen tensions as low as 3% with or without an accessory terminal oxidant in the form of DMSO. Both TMAO and DMSO are naturally occurring compounds considered to be intermediates in the global sulphur cycle (Lovelock *et al.*, 1972). They are generated mainly as by-products of phytoplankton activity and are present in ecosystems which host *Rhodospirillaceae*. Recently a DMSO reductase has been purified and characterized from *R. capsulatus* (McEwan *et al.*, 1985, 1989). Mixed forms of ATP-generation are therefore compatible with normal photosynthetic gene regulation, and can indeed be postulated to take place *in vivo* in low light environments, where energy supply by light-driven proton translocation is limited.

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