JOURNAL OF BACTERIOLOGY, Feb. 1988, p. 877–882
0021-9193/88/020877-06$02.00/0

Vol. 170, No. 2

Posttranscriptional Regulation by Light of the Steady-State Levels of Mature B800-850 Light-Harvesting Complexes in *Rhodobacter capsulatus*

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Received 7 August 1987/Accepted 23 November 1987

Photosynthetic organisms exhibit a variety of responses to changes in light intensity, including differential biosynthesis of chlorophyll-protein complexes. Cultures of *Rhodobacter capsulatus* grown anaerobically with a low intensity of light (2 W/m^2) contained about four times as much B800-850 light-harvesting complex as cells grown under high light intensity (140 W/m^2). The mRNA transcripts encoding B800-850 beta and alpha peptides were analyzed by Northern blot (RNA blot), S1 nuclease protection, and capping with guanylyl transferase. It was found that the steady-state levels of B800-850 mRNAs in high-light-grown cultures were about four times as great as in cells grown under low light intensity. Therefore, the lesser amounts of mature B800-850 peptide gene products found in cells grown with high light intensity are the result of a posttranscriptional regulatory process. It was also found that there are two polycistronic messages encoding the B800-850 peptides. These messages share a common 3′ terminus but differ in their 5′-end segments as a result of transcription initiation at two discrete sites. Moreover, the half-lives of B800-850 mRNAs were about 10 min in cells grown with high light and approximately 19 min in cultures grown with low light. It is concluded that there must be more frequent initiations of transcription of B800-850 genes in cells grown with high light than in those grown with low light, and that the relative amounts of B800-850 complexes under these conditions are controlled by a translational or a posttranslational mechanism.

Rhodobacter capsulatus (formerly known as *Rhodopseudomonas capsulata* [9]) is a purple nonsulfur photosynthetic bacterium that is capable of growth by use of several different modes of energy generation, including aerobic respiration in darkness and anaerobic photosynthesis (8). During respiratory growth with high concentrations of oxygen, *R. capsulatus* cells are indistinguishable from nonphotosynthetic bacteria in many respects. However, with a reduction in the amount of oxygen available to cultures, cells develop an intracytoplasmic membrane system that contains the components of the photosynthetic apparatus. There are three distinct photosynthetic pigment-protein complexes made by *R. capsulatus*: the reaction center (RC), light-harvesting I (B870), and light-harvesting II (B800-850) complexes. The relative amounts of RC and B870 complexes are believed to remain relatively constant with changes in growth conditions, whereas the amounts of B800-850, relative to RC and B870 complexes, increase in response to a reduction in light intensity during photosynthetic growth (7, 12, 17).

The B800-850 light-harvesting complex of *R. capsulatus* contains two peptides that bind bacteriochlorophyll *a* (Bchl) (18). The genes encoding the pigment-binding peptides, designated alpha and beta, have been cloned, and their DNA sequence was determined (21). The B800-850 beta and alpha genes are located very close to each other and have been assumed to form an operon (24). A third peptide, the 14-kilodalton peptide, has been found to copurify with the alpha and beta peptides, but it does not bind pigments and its function is obscure (8, 18).

In this investigation, we used segments of the cloned B800-850 genes as probes to determine the approximate transcriptional start and termination sites of B800-850 mRNAs and their relative steady-state amounts, under photosynthetic conditions of growth with either excess or growth-rate-limiting levels of light. The relative amounts of B800-850 mRNAs were compared with the relative amounts of the complexes, and a posttranscriptional regulatory mechanism is proposed to explain the relationship between mRNA levels and the amounts of mature B800-850 complexes.

MATERIALS AND METHODS

Bacterial strain and growth conditions. *R. capsulatus* B10 (15, 20) was used throughout this study. Inocula for both high- and low-light-grown samples were grown to stationary phase under low aeration at 34°C in RCV medium (20) (supplemented with 0.1% yeast extract and 9.6 mM potassium phosphate buffer) to induce the synthesis of the photosynthetic apparatus. The cells were then transferred to a completely filled 20-ml screw-cap tube and incubated at 34°C with either 140 (high-light) or 2 W/m^2 (low-light) incandescent tungsten illumination. Cells were harvested at a density of 3×10^8 CFU/ml to minimize the effects of self-shading.

In experiments determining the half-life of the B800-850 mRNA, 800 ml of cells was grown photosynthetically, with either high- or low-light illumination, in a 1-liter Roux bottle at 34°C. The medium was bubbled continuously with 95% N_2–5% CO_2. When cells reached a density of 3×10^8 CFU/ml, a 25-ml sample was removed, transcription initiation was stopped by the addition of rifampin (200 μg/ml) to the culture, and subsequent samples were then taken at 20, 40, 60, and 80 min for RNA extraction.

Plasmid and probe constructions. The 5′ probe used in S1 protection experiments was an antisense RNA molecule, which was transcribed by T7 RNA polymerase. The 270-

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nucleotide (nt) *Sma*I-*Cla*I fragment of pRPSLHII (21) (labeled 5′ in Fig. 2) was subcloned into the pT7-2 vector (Pharmacia), which contains the T7 promoter. The 3′ probe was obtained as the 800-nt *Apa*L1-*Sma*I segment (indicated as 3′ in Fig. 2) from pRPSLHII. The *Apa*L1 site was filled in (14) by incubation with the Klenow fragment of DNA polymerase I and with dATP, dCTP, dGTP, and 50 μCi of [α-^{32}P]TTP (10 μCi/μl; New England Nuclear Corp.).

In vitro transcription of RNA probes. To produce homogeneously labeled 5′ RNA probes, 1 to 2 μg of linearized DNA template was used with T7 RNA polymerase, as recommended by the commercial supplier (Pharmacia), and incubated at 37°C for 1 h. Samples were then extracted with phenol-chloroform (1:1), and the nucleic acids were precipitated twice from ethanol. The pellet was washed with 70% ethanol, dried, dissolved in 100 μl of DNase I buffer (20 mM sodium acetate, 10 mM $MgCl_2$, 10 mM sodium chloride, pH 4.5) with 23 U of DNase I (Boehringer Mannheim Biochemicals), and incubated at 22°C for 30 min. The sample was then extracted with phenol, and the RNA was precipitated with ethanol. Usually 10 to 20 μg of RNA was obtained from 1 to 2 μg of linearized DNA template, with a specific activity of 0.5×10^6 to 1.0×10^6 dpm/μg of RNA.

RNA isolation, blotting, and hybridization. Isolation of RNA from *R. capsulatus* was done as described previously (19). The blotting procedure was done as follows: 5 μg of *R. capsulatus* RNA was dissolved in running buffer (20 mM MOPS [morpholinepropanesulfonic acid], 1 mM EDTA, 5 mM sodium acetate, pH 7.0) supplemented with 50% formamide and 2.2 M formaldehyde, heated to 70°C for 3 min, cooled, and loaded onto a 1% agarose–6.6% formaldehyde gel which was run at 20 to 40 mA. The gel was then blotted for 16 h onto a sheet of nitrocellulose paper which had been soaked in 20× SSC (1× SSC is 0.15 M NaCl plus 0.015 M sodium citrate) (14). The filter was baked for 2 h at 80°C. Prehybridizations were done in 200 μg of denatured salmon sperm DNA per ml, 5× SSPE (14), 0.3% sodium dodecyl sulfate, and 50% formamide at 42°C for 1 to 2 h. This mixture was supplemented with 10^6 dpm of radioactive probe for hybridizations of 12 to 16 h at 42°C. The filters were washed three times, for 7 min each, at 70°C in 0.1× SSPE–0.1% sodium dodecyl sulfate.

Capping of RNA with guanylyl transferase. Unfractionated RNA (10 μg) from *R. capsulatus* cells grown with high light, was incubated in guanylyl transferase buffer (25 mM Tris hydrochloride, 2 mM $MgCl_2$, 1 mM dithiothreitol [pH 7.5]) with 150 μCi [α-^{32}P]GTP (10 μCi/μl) and 10 U of guanylyl transferase (Bethesda Research Laboratories, Inc.) in a total volume of 100 μl at 37°C for 30 min. The RNA was extracted twice with phenol-chloroform, ethanol precipitated four times, washed, and dried. The pellet was dissolved in 100 μl of diethylpyrocarbonate-treated (14) sterile distilled water.

S1 nuclease protection experiments. A 5-μg sample of *R. capsulatus* RNA was ethanol precipitated with 0.2 to 0.4 μg of the 5′ probe or 5 ng of the 3′ probe and 5 μg of yeast tRNA. The pellet was washed in 70% ethanol and dried. The sample was dissolved in 30 μl of hybridization buffer (0.4 M sodium chloride, 0.04 M sodium phosphate, 0.4 mM EDTA [pH 6.5]), heated to 95°C for 5 min, quickly transferred to 70°C, and incubated for 16 h. S1 nuclease (1,500 U) in 300 μl of S1 buffer (0.28 M sodium chloride, 0.03 M sodium acetate, 4.5 mM zinc sulfate [pH 4.5]) was added, and the sample was incubated at 37°C for 1 h. Then, 50 μl of a solution of 4 M ammonium acetate–0.1 M EDTA, with 20 μg of carrier tRNA was added, followed by extraction with 350 μl of buffered phenol-chloroform (1:1). After the phenol extraction, 400 μl of isopropanol was added to precipitate the nucleic acids. The RNA pellet was washed, dried, dissolved in sample buffer (80% formamide, 0.5× TBE [14], 0.02% bromphenol blue, 0.02% xylene cyanol), heated to 95°C for 5 min, cooled, and loaded onto a 5% polyacrylamide–7 M urea gel in 0.5× TBE. After electrophoresis the gel was dried and exposed to X-ray film.

When capped RNA and unlabeled probe were used in S1 protection experiments, the procedure was modified slightly. *R. capsulatus* RNA (10 μg) and the 5′ probe (0.2 μg) were ethanol precipitated and then dissolved in hybridization buffer, heated to 95°C, cooled to 70°C, and incubated for 12 to 16 h. The sample was then digested with 1,500 U of S1 nuclease for 1 h, followed by incubation with 25 ng of RNase A for 15 min at 20°C. The RNA was phenol extracted, ethanol precipitated, and subsequently dissolved in sample buffer. It was then heated to 95°C, cooled to 0°C, and loaded onto a 5% polyacrylamide–7 M urea gel.

Analytical methods. The light intensity was measured with a Li-Cor quantum sensor (model Li-185B). To measure total cell protein, a version of the Lowry (13) protein assay was performed in which cells were boiled in 0.05 M NaOH for 1 min and then cooled before adding the other reagents. The protein standard used was crystalline bovine serum albumin. Spectral scans were done on 5 ml of cells that had been suspended in 1 ml of 22.5% bovine serum albumin (Sigma Chemical Co.). Autoradiograms were scanned with a Quick Scan Jr. (Helena Laboratories Corp.) densitometer, and the area under the peaks was measured by weighing the appropriate cut-out regions.

RESULTS

Effects of different levels of illumination on photosynthetic growth of *R. capsulatus* cells. There were substantially greater amounts of pigments found in cells grown in low light than with high light (Fig. 1). The A_{860} is due to a combination of B800-850, B870, and RC complexes, whereas nearly all the 800-nm peak is due to B800-850 light absorption (22). Therefore, the area under the 800-nm peak is proportional to the number of B800-850 pigment-protein complexes in the *R. capsulatus* membrane. A comparison of the 800-nm peaks from the spectral scans (Fig. 1) revealed that there were fourfold more B800-850 complexes in cells grown with low light than with high light.

The culture turbidity and protein content of equal numbers of CFU in cultures grown under both levels of illumination were within 10% of each other, indicating that there were not

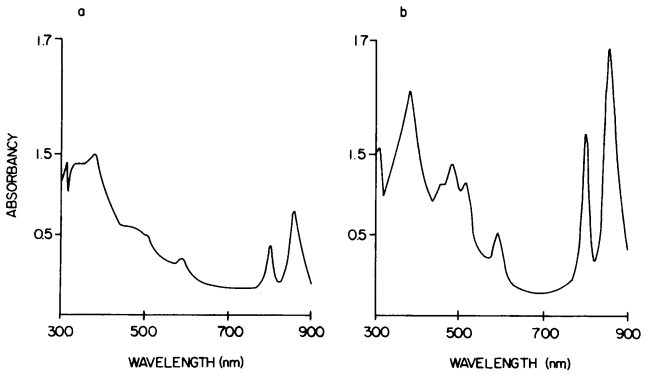

FIG. 1. Spectral scans of (a) high- and (b) low-light-grown *R. capsulatus* cells.

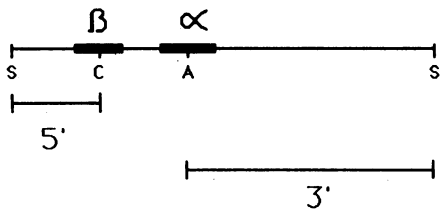

FIG. 2. Representation of the 3′ and 5′ probes used in S1 protection experiments. At the top of the figure is a representation of a 1.25-kilobase *Sma*I fragment from pRPSLHII (21). The B800-850 alpha and beta structural genes, which are transcribed from left to right, are indicated (▬). The endpoints of the 5′ probe (270 nt) and the 3′ probe (800 nt) are shown below. Abbreviations: S, *Sma*I; A, *Apa*L1; C, *Cla*I.

major differences in cell size. However, the growth rate, expressed as the time required for a doubling in cell number, was 12 h for cultures grown with low light and 2 h for cultures grown with high light.

It has been observed that the RNA content of *R. capsulatus* cells is proportional to the growth rate (1), and it was found that cells grown with high light contained about three times as much total RNA as cells grown with low levels of illumination (that is, 7.5 μg of total RNA per 3×10^8 CFU in high light and 2.5 μg of total RNA per 3×10^8 CFU in low light).

Sizing and end-mapping of B800-850 transcripts. The approximate length of B800-850 transcripts was estimated by Northern (RNA blot) blot analysis of RNA from *R. capsulatus* grown with either high- or low-light intensities. A radioactive antisense RNA probe was obtained by in vitro transcription of the 270-nt DNA fragment designated 5′ in Fig. 2, which extends from a *Cla*I site in the B800-850 beta gene to a *Sma*I site 190 nt before the start codon of this gene. Transcripts of about 530 nt in length were present under both growth conditions tested (Fig. 3). Although this transcript was long enough to encode both the alpha and beta B800-850 peptides, it was possible that a second transcript was derived from the alpha peptide gene, for the probe was complementary only to the beta gene. To distinguish between these possibilities and learn more about the transcription of these genes, 5′- and 3′-end mapping experiments were done.

The 5′ probe (Fig. 2) was protected from S1 nuclease digestion by hybridization with *R. capsulatus* RNA, and the protected fragments were visualized by gel electrophoresis and autoradiography. Two distinct RNA molecules hybridized with the 5′ probe (Fig. 4A), suggesting that both of the B800-850 genes might be encoded by polycistronic transcripts with different 5′ ends. The two 5′ ends would be separated by approximately 15 nt, with the end of the longer segment being about 125 nt upstream of the start codon of the beta structural gene.

The probe used to map the 3′ end of the B800-850 mRNA in S1 protection experiments was an end-labeled DNA molecule, which extends from an *Apa*L1 site within the alpha structural gene to a *Sma*I site 700 nt downstream of the alpha gene stop codon (Fig. 2). This 800-nt fragment was labeled at the *Apa*L1 site. One DNA segment, of about 120 nt, was protected from nuclease digestion by the RNA in both high- and low-light samples (Fig. 4B).

There seemed to be slightly more RNA from low-light-grown cells that was homologous to the 5′ probe in the Northern blot experiment shown in Fig. 3, but the amount of protected probe in the two growth conditions was about equal in the end mapping experiments (Fig. 4). To quantitatively measure the relative amounts of B800-850 mRNA in high- and low-light-grown cells, saturation hybridization experiments were performed as described in the following section.

Saturation hybridization and half-life determination of B800-850 mRNAs. Although the end-mapping experiments implied that cells cultured in each growth condition contained equal amounts of B800-850 mRNA, it is possible that the concentration of the probe was too low to drive the homologous hybridizations to completion. Either 0.2 or 0.4 μg of ^{32}P-labeled 5′ probe was used in an S1 protection experiment with 5 μg of high- and low-light RNA samples (Fig. 5). Because there was no increase in the amount of RNA hybridized to the probe when the amount of probe was increased, it was concluded that the amounts of B800-850 mRNAs detected in this experiment are accurate measurements of the relative steady-state levels of these transcripts in cells grown with the two conditions of illumination. Densitometric scans showed that there was approximately 1.4-fold more B800-850 mRNA (per microgram of total RNA) in cells grown with high light compared with that in low-light-grown cells. Because the faster-growing high-light cells contained about three times as much total RNA as low-light-grown cells, the steady-state levels of B800-850 mRNA in cells grown with high illumination would then seem to be four times as great as in cultures grown under low levels of light.

Since the steady-state levels of RNAs are in part a function of their decay rates, it was of interest to determine the half-lives of the B800-850 mRNAs. The decay rates of these transcripts were derived from densitometric scanning of autoradiograms, such as the one shown in Fig. 5, in which the 5′ probe was used. The half-lives were found to be 10 min (± 1.0 min) for RNAs from cells grown with high light and 19 min (± 2.5 min) for RNAs from cells grown with low levels of light. The rates of decay of both of the transcripts detected with this probe were the same. Thus, although the steady-state levels of B800-850 mRNAs were fourfold greater in cells grown with high light, the rates of decay were also greater, so there must be more frequent initiations of tran-

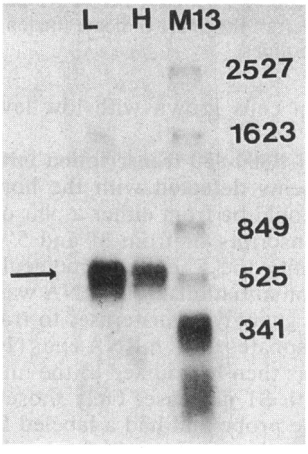

FIG. 3. Northern blot of RNA isolated from *R. capsulatus* grown with either high (H) or low (L) light illumination. The blot was hybridized with the in vitro-transcribed 5′ RNA probe. Radioactively labeled *Hae*III-cut M13mp11 single-stranded DNA fragments (M13) were used as molecular weight markers. The values to the right of the figure indicate the lengths of the marker molecules in nucleotides. The arrow indicates the transcripts present under the two conditions of illumination.

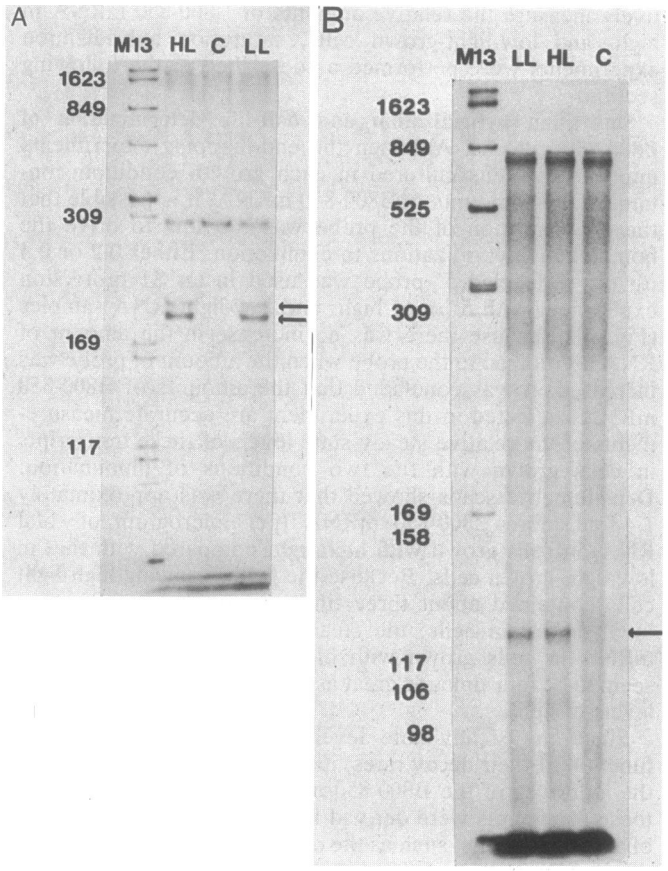

FIG. 4. End mapping analysis of B800-850 mRNA isolated from high- and low-light-grown *R. capsulatus* cells. (A) The results from the 5'-end mapping, which show two protected fragments of 200 and 185 nt (indicated by arrows). The undigested probe (seen in all three lanes) ran as a 280-nt fragment. (B) The 3'-end mapping shows a single 120-nt protected segment (indicated by the arrow) and the 800-nt end-labeled probe. Molecular weight markers were *Hae*III-cut M13mp11 radioactively labeled single-stranded DNA molecules (M13). Abbreviations: HL, high light; LL, low light; C, control (probe incubated with yeast tRNA before S1 nuclease treatment). The values to the left of the figure indicate the lengths of the marker molecules in nucleotides.

scription than in cells grown with low levels of illumination.

Localization of B800-850 transcription initiation sites. The RNA end segments detected with the homogeneously labeled 5' probe could be from either a pair of overlapping 5' segments of transcripts or from 3' and 5' RNA ends. To specifically identify the 5' ends of molecules that resulted from transcription initiations, total RNA was incubated with [α-^{32}P]GTP and guanylyl transferase, to transfer [^{32}P]GMP to di- and triphosphates on 5' mRNA ends (16). The resultant labeled RNA was then hybridized to the unlabeled 5' probe and digested with S1 nuclease. Only those transcripts that hybridized to the probe and had a labeled 5' end (that is, a transcription initiation site) would be detected by gel electrophoresis and autoradiography after S1 digestion. It was found that the 5' probe protected two capped RNA molecules that must correspond to the two 5' ends detected in the previous S1 experiments (Fig. 6). There was greater variation between independent experiments in the relative intensities of the two capped transcripts (perhaps due to variation in the efficiency of capping) than there was in the standard S1 experiments. Therefore, it was concluded that the standard S1 protection experiments provided a more accurate estimate of the relative amounts of the two transcripts. The difference in sequence composition and the presence of the additional 5'-5' linked (16) nucleotide probably account for the differences in electrophoretic mobility of these RNA segments, relative to the segments of the S1-protected RNA probe run in the adjacent lane. These results show that there are two sites, separated by 10 to 15 nt, at which transcription of the B800-850 genes initiates.

DISCUSSION

The mapped 3' and 5' ends of the two B800-850 mRNAs give overall transcript lengths of about 505 and 491 nt, which corresponds well to the size of the mRNA species found in the Northern blot. Since the resolution of nucleic acids of this size in agarose gels is poor compared with that in polyacrylamide gels, the Northern blot could not distinguish between the two RNA transcripts, which may be why previous reports have only mentioned a single transcript of the B800-850 genes (23, 24).

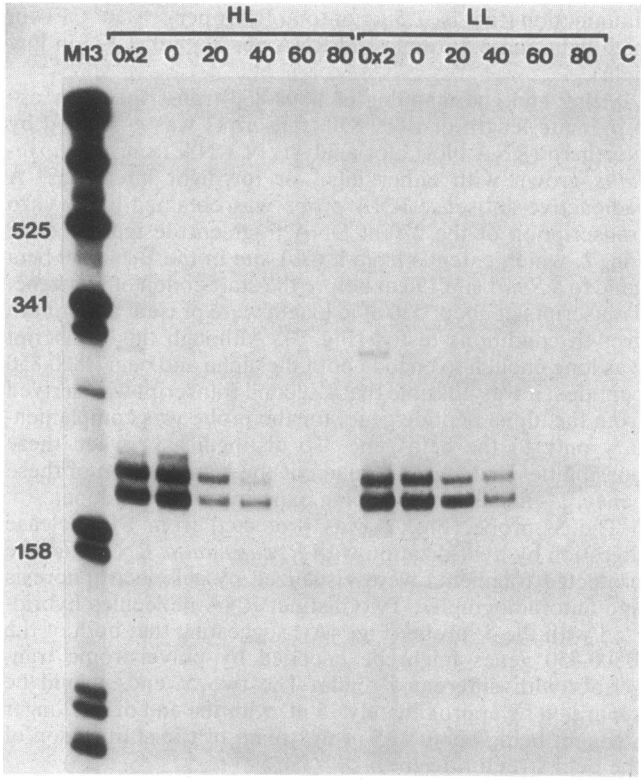

FIG. 5. Determination of the relative steady-state levels and half-lives of B800-850 mRNAs. S1 protection experiments were performed on 5 μg of *R. capsulatus* RNA from each time point, by using 0.2 μg of the 5' RNA probe (0.4 μg on lanes labeled 0×2) with samples taken at the indicated times (in minutes) after rifampin addition. Although only one representative autoradiogram is shown here, the half-lives of the B800-850 mRNAs were determined by averaging the measurements from three separate experiments. *Hae*III-cut M13mp11 radioactively labeled single-stranded DNA fragments (M13) were used as molecular weight markers. Abbreviations: HL, high light; LL, low light; c, control (probe incubated with yeast tRNA before S1 nuclease digestion). The values to the left of the figure indicate the lengths of the marker molecules in nucleotides.

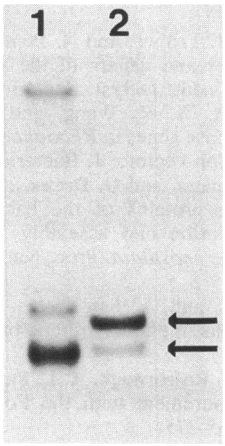

FIG. 6. Autoradiogram of the gel used for separation of capped mRNA segments protected from S1 digestion by hybridization with the 5′ probe. Lane 1 contains the radioactive 5′ RNA probe and the two segments protected by hybridization with the B800-850 mRNAs (compare with Fig. 4A). In lane 2 are the two radioactively capped mRNAs (indicated by arrows) protected from S1 digestion by hybridization with the same nonradioactive 5′ RNA probe.

We have also identified two transcription initiation sites of the B800-850 genes. Both transcripts had the same decay rate, and their relative amounts, although slightly variable between different experiments, were usually about equal. Also, there appeared to be no change in this pattern between cells grown with high light and cells grown with low light. There could either be two promoters (one for each transcript) or a single promoter that directs transcription initiation at two sites. Upon examination of the nucleotide sequence upstream of the start sites, no sequences like those centered at −10 or −35 in *Escherichia coli* could be found. This was expected, as all *R. capsulatus* promoters tested thus far have failed to function in *E. coli* (10). However, there exists a direct repeat of "ACACTTG" in the DNA sequence upstream of where the 5′ end of the longer B800-850 mRNA transcript maps (Fig. 7). The centers of these repeated sequences are separated by 14 nt, which is the approximate distance between the 5′ ends of the two B800-850 mRNAs. Moreover, the center of the most upstream repeated sequence is approximately 25 nt from the start site of the longer transcript, whereas the center of the downstream sequence is about 26 nt from where the initiation site of the shorter transcript maps. The spacing of the repeated sequences in relation to each other and to the B800-850 5′ mRNA ends suggest that these sequences may be involved in transcription initiation. The 3′ terminus of the B800-850 transcript is in the region of a potential stem-loop structure of 10 base pairs (8 of which are G-C bonds), which may serve as a transcriptional terminator (Fig. 7).

When *R. capsulatus* cultures were grown photosynthetically, four times as much B800-850 mRNA was found in cells grown with high light as in cells grown with low light. The steady-state levels of mRNAs depend on both the rates of transcription and mRNA decay. In this study, the B800-850 mRNAs isolated from cells grown with high light had a half-life of 10 min, whereas the same transcripts found in low-light-grown *R. capsulatus* cells had a half-life of 19 min. As the B800-850 mRNAs isolated from high-light-grown *R. capsulatus* were degraded more rapidly, yet were present at greater steady-state amounts than in low-light-grown cells, the frequencies of transcription initiation must be greater in cells exposed to saturating light intensity. Despite this difference in the amount of B800-850 mRNAs per cell, low-light-grown cells were found to contain four times as many B800-850 complexes.

If it is assumed that the amounts of B800-850 peptides parallel the amounts of the mRNAs, then there would have to exist a pool of these light-harvesting peptides that had not yet bound Bchl in high-light-grown cells. It has been shown by Dierstein (5, 6) that the turnover rate of the B800-850 alpha peptide in a Bchl-less mutant strain of *R. capsulatus* and in wild-type cells exposed to inhibitors of Bchl synthesis, is much greater than in untreated wild-type cells. Therefore, in the presence of Bchl, the B800-850 peptides may be protected from degradation, perhaps because the apopeptides exist in a protease-sensitive conformation that changes to a protease-resistant conformation after binding Bchl (5, 6). We have found that cells grown with saturating light intensity have the capacity to produce fourfold more B800-850 peptides than cells grown with low light (due to the higher levels of B800-850 mRNA). However, since less Bchl is produced in high-light-grown *R. capsulatus*, more of the newly translated peptides would be turned over, as they would be unable to bind Bchl molecules. No free Bchl is detected in normal cells of photosynthetic bacteria, so the ratio of pigment-binding peptides to Bchl must be equal to or greater than 1. It has been well established that the total Bchl content of anaerobically grown *R. capsulatus* increases as the light intensity decreases (1, 3, 7, 8, 12, 17); therefore, when cells are shifted from a high- to a low-light environment, more Bchl is produced, which could bind to preexistent components of a B800-850 apopeptide pool. These protein-pigment complexes would be more resistant to proteolytic degradation and could then function in light absorption.

However, it is also possible that there is control of translation of B800-850 mRNAs, so that translation would be less efficient in cells grown with high light intensity. Additional experiments would be necessary to distinguish between translational and posttranslational regulatory mechanisms. It should be noted that with either model the amount of B800-850 complexes in the membranes of anaerobically grown *R. capsulatus* is limited by the availability of Bchl.

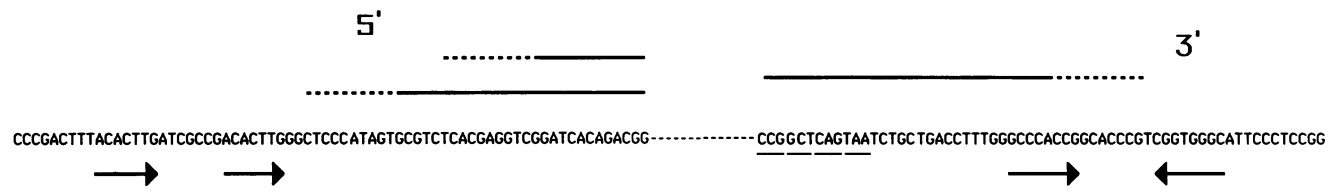

FIG. 7. Sequence of the 5′ and 3′ regions flanking the B800-850 alpha and beta genes (21). The approximate positions of the 5′ and 3′ ends of the B800-850 transcript are shown by the lines above the sequence. Since there is some uncertainty in the interpretation of the sizes of the S1-protected segments of the probes, a possible error of ± 5 nt is indicated (– – –). The repeated sequence of "ACACTTG", which may be involved in transcription initiation, is indicated (→→), as is the palindromic sequence (→←) near where the 3′ ends of the B800-850 mRNAs map. The last four codons of the alpha gene are underlined.

The regulation of Bchl accumulation by light also seems to be largely posttranscriptional (3).

It has been found that cells grown in darkness with high aeration contained significant levels of B870 and RC peptide mRNAs although the cells did not have detectable levels of absorbancy in the range of 800 to 900 nm (2; unpublished observations), and Dierstein (5) has shown that the RC L peptide, although more rapidly degraded than with Bchl, also can be immunologically detected in cells without Bchl. Therefore, it seems that a translational or posttranslational mechanism may be significant for both oxygen and light regulation of biogenesis of other photosynthetic complexes in *R. capsulatus*, as a supplement to the previously described transcriptional and posttranscriptional control processes (2, 4, 11, 23, 24). An advantage of this sort of posttranscriptional regulation might be that it would allow a very rapid increase in light-harvesting capability, because the rate of that increase would be limited by the catalytic activity of the enzymes in the Bchl biosynthetic pathway and would not require de novo initiation of transcription of genes encoding pigment-binding peptides.

ACKNOWLEDGMENTS

We thank Douglas C. Youvan for providing plasmid pRPSLHII, Joel G. Belasco and Chyi-Ying A. Chen for providing information and advice on S1 experiments, and Gabrielle Klug for helpful comments.

This research was supported by grant A-2796 from the Natural Sciences and Engineering Research Council of Canada, Ottawa, Ontario.

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