Proc. Natl. Acad. Sci. USA
Vol. 83, pp. 3924–3928, June 1986
Genetics

Genes encoding major light-harvesting polypeptides are clustered on the genome of the cyanobacterium *Fremyella diplosiphon*

(phycobilisome/allophycocyanin/phycocyanin/chromatic adaptation/light-regulated RNA)

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Communicated by Winslow R. Briggs, January 31, 1986

ABSTRACT **The polypeptide composition of the phycobilisome, the major light-harvesting complex of prokaryotic cyanobacteria and certain eukaryotic algae, can be modulated by different light qualities in cyanobacteria exhibiting chromatic adaptation. We have identified genomic fragments encoding a cluster of phycobilisome polypeptides (phycobiliproteins) from the chromatically adapting cyanobacterium *Fremyella diplosiphon* using previously characterized DNA fragments of phycobiliprotein genes from the eukaryotic alga *Cyanophora paradoxa* and from *F. diplosiphon*. Characterization of two λ-EMBL3 clones containing overlapping genomic fragments indicates that three sets of phycobiliprotein genes—the α- and β-allophycocyanin genes plus two sets of α- and β-phycocyanin genes—are clustered within 13 kilobases on the cyanobacterial genome and transcribed off the same strand. The gene order (α-allophycocyanin followed by β-allophycocyanin and β-phycocyanin followed by α-phycocyanin) appears to be a conserved arrangement found previously in a eukaryotic alga and another cyanobacterium. We have reported that one set of phycocyanin genes is transcribed as two abundant red light-induced mRNAs (1600 and 3800 bases). We now present data showing that the allophycocyanin genes and a second set of phycocyanin genes are transcribed into major mRNAs of 1400 and 1600 bases, respectively. These transcripts are present in RNA isolated from cultures grown in red and green light, although lower levels of the 1600-base phycocyanin transcript are present in cells grown in green light. Furthermore, a larger transcript of 1750 bases hybridizes to the allophycocyanin genes and may be a precursor to the 1400-base species.**

In prokaryotic cyanobacteria and eukaryotic red algae, phycobilisomes are macromolecular complexes that harvest light energy and transfer this energy to the photosynthetic reaction centers (1). They can provide 30–50% of the light-harvesting capacity of the cells and can comprise 60% of the total soluble protein (2). Although functionally analogous to light-harvesting chlorophyll–protein complexes in higher plants, the phycobilisome is water soluble and only peripherally associated with photosynthetic membranes. The complex is composed of chromophoric and nonchromophoric polypeptides arranged into two domains: a central core anchored to the photosynthetic membranes and rods that radiate from the core (3, 4). There are three major chromophoric proteins (phycobiliproteins) in the phycobilisome—allophycocyanin (APC), phycocyanin (PC), and phycoerythrin—as well as nonchromophoric linker polypeptides that maintain the structure and allow efficient energy transfer among the components of the complex (5). Each phycobiliprotein is composed of two related subunits, α and β, to which one or more tetrapyrole chromophores are attached (4), conferring upon each phycobiliprotein a characteristic light-absorption and emission spectrum. Amino acid (6–13) and DNA (14–16) sequence data show considerable sequence conservation among the various phycobiliproteins (APC, PC, and phycoerythrin) as well as between the α and β subunits of a given phycobiliprotein. These findings suggest that phycobiliprotein genes arose via duplications of an ancestral sequence (8).

By a mechanism termed complementary chromatic adaptation (2), certain cyanobacteria can modulate PC and phycoerythrin levels, enabling them to maximize absorption of prevalent wavelengths of light. At least two different sets of PC subunits are present in phycobilisomes isolated from such organisms grown in red light while only one set is found in phycobilisomes from cells grown in green light (17). We have characterized in *Fremyella diplosiphon* a PC gene set (α- and β-subunit genes) whose mRNAs are very abundant in cells maintained in red light but not detectable in cells maintained in green light (18). In this report, we describe the use of phycobiliprotein gene probes (18, 19) for the isolation, mapping, and transcriptional characterization of *F. diplosiphon* genomic fragments encoding two sets of PC subunits and one set of APC subunits.

MATERIALS AND METHODS

Materials. All chemicals were of reagent grade. Restriction enzymes were from Bethesda Research Laboratories, New England Biolabs, and Boehringer Mannheim; calf intestine alkaline phosphatase, DNA polymerase I, and the Klenow fragment of DNA polymerase I were from Boehringer Mannheim; T4 DNA ligase was from Bethesda Research Laboratories; [α-^{32}P]dCTP (800 Ci/mmol; 1 Ci = 37 GBq) and [α-[^{35}S]thio]dCTP (650 Ci/mmol) were from Amersham.

Bacterial Strains, Vectors, and Culture Media. *F. diplosiphon*, a subculture of UTEX#481, was grown in Gorham's medium (20) in an atmosphere of 5% CO_2/95% air and illuminated at 40 microeinsteins·m^{-2}·s^{-1} (1 einstein = 1 mol of photons). *F. diplosiphon* genomic DNA was cloned into λEMBL3 (21); *Escherichia coli* strains Q358 and Q359 were used to grow nonrecombinant and recombinant phage, respectively (21). Fragments were inserted into pUC8 (22) and into the M13 vectors mp18 and mp19 (23) and transformed into *E. coli* strains JM83 (22) and JM101 (23), respectively.

Isolation of Cyanobacterial DNA and Library Construction. Genomic DNA from *F. diplosiphon*, isolated by the method of Curtis and Haselkorn (24), was digested with *Sau*3A for varying lengths of time to generate a randomly sized population of molecules, and fractionated on sucrose gradients. Fragments from 13 to 20 kilobases (kb) were ethanol precipitated from 0.3 M NaOAc, resuspended in TE (0.01 M Tris·HCl, 0.001 M EDTA, pH 7.5) and treated with alkaline

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Abbreviations: kb, kilobase pair(s); bp, base pair(s); APC, allophycocyanin; PC, phycocyanin.

phosphatase (following the specifications of the supplier) before ligation into λ-EMBL3.

Phage and phage DNA were purified according to Maniatis *et al.* (25). DNA was ligated (ref. 21, specifications of the supplier) at 200 μg/ml, and various molar ratios of λ arms to insert from 1:1 to 4:1 were used. The ligated DNA was packaged using a commercial packaging extract (Packagene, Promega Biotec, Madison, WI) as specified by the supplier. Recombinant phage, selected as *spi*$^-$, were screened directly without amplification.

Screening of λ Library. λ-EMBL3 phages containing *F. diplosiphon* genomic DNA were screened by plaque hybridization (26) with the following DNA sequences encoding phycobiliprotein genes: a 1.4-kb fragment encoding α- and β-APC from *Cyanophora paradoxa* (19), a 0.8-kb fragment encoding predominantly β-PC from *C. paradoxa* (27), and a 3.8-kb fragment encoding α- and β-PC from *F. diplosiphon* (18). Two clones, which hybridize to phycobiliprotein sequences designated 37 and 4-10, were characterized in detail.

Southern Hybridizations and Restriction Mapping. DNA from clones 37 and 4-10 was isolated (25), digested with restriction enzymes (*Sal* I, *Hin*dIII, *Eco*RI, and *Pst* I) (following specifications of the supplier), and electrophoresed on a 0.8% agarose gel in TEA buffer (0.04 M Tris·acetate, 0.002 M EDTA, pH 8.0) (25), and the restriction fragments were transferred to nitrocellulose (25). DNA fragments used as hybridization probes were radiolabeled by nick-translation using DNA polymerase I and [α-^{32}P]dCTP (25). Hybridizations were performed, and filters were washed as described (18). Regions of homology to the phycobiliprotein gene probes were then mapped by restriction analysis.

Subcloning of Phycobiliprotein Genes from λ-EMBL3 Clones. DNA from clone 4-10 was digested with *Eco*RI and electrophoresed on a 0.8% agarose gel in TBE buffer (0.089 M Tris·borate, 0.089 M boric acid, 0.002 M EDTA, pH 8.0) (25). The region of the gel containing a 4.1-kb fragment was excised, and the DNA was electroeluted and ligated into pUC8 that had been digested with *Eco*RI and treated with alkaline phosphatase. Plasmid DNA from transformants (22) (Lac$^-$ phenotype) was isolated (25), digested with *Eco*RI, electrophoresed on a 0.8% agarose gel, transferred to nitrocellulose, and hybridized with the 0.8-kb DNA sequence from *C. paradoxa* encoding β-PC. A positively hybridizing clone was used for restriction analysis and sequencing. A 3.45-kb *Eco*RI fragment from clone 37 containing the α- and β-APC genes was subcloned in a similar manner. Subcloning of the 3.8-kb *Hin*dIII fragment encoding the "inducible" PC gene set has been described (18).

Sequencing of Phycobiliprotein Genes. The 4.1-kb *Eco*RI fragment was digested with *Hin*dIII, ligated into mp18 DNA, and transformed into JM101 (28). Plaques containing the phycobiliprotein genes were identified by hybridization to either a β-PC-specific probe (19) or a fragment encoding mostly α-PC from *C. paradoxa* (insert from pCPC 2368) (27). The 3.45-kb *Eco*RI fragment was digested with *Pst* I and ligated into mp18 and mp19. Resulting plaques were screened with α- and β-APC-specific probes (two *Msp* I fragments, 0.9 and 0.5 kb, generated from the 1.4-kb *C. paradoxa* fragment encoding APC). The 3.8-kb *Hin*dIII fragment, contained within clone 37 and encoding α- and β-PC (18), was digested with *Pst* I and cloned into mp18 and mp19. Template preparations, dideoxy-sequencing reactions, and gel electrophoresis were carried out according to Messing (28).

Hybridizations with RNA. RNA was isolated, and samples were electrophoresed as described except the cells were pressed through a French pressure cell (1500 psi; 1 psi = 6.89 kDa) immediately following resuspension in guanadine·HCl (18). The 4.1-kb *Eco*RI fragment was radiolabeled by nick-translation and hybridized to RNA isolated from *F. diplosiphon* grown in either red or green light (18). A single-stranded mp18 clone encoding α-APC, the intergenic region, and the amino terminus of β-APC was used as a template in the synthesis of a labeled complementary second strand according to Church & Gilbert (29). Prior to use in hybridizations, the reaction mixture was passed over a Sephadex G-50 column that had already been equilibrated with 20 μg of tRNA.

RESULTS

Identification and Characterization of λ-EMBL3 Genomic Clones Encoding Phycobiliproteins. Two λ-EMBL3 genomic clones (designated 37 and 4-10) that hybridized with DNA fragments encoding phycobiliprotein sequences were further characterized. Fig. 1 shows the results of hybridizations designed to localize and identify phycobiliprotein-related sequences present on λ clone 37. An APC-specific DNA sequence from *C. paradoxa* (19) hybridizes strongly with a 3.5-kb *Eco*RI fragment, with a 2.95- and a 2.55-kb *Pst* I fragment, and with a 5.9-kb *Hin*dIII fragment from clone 37 DNA (Fig. 1*A*). The α-APC gene was localized utilizing a 0.5-kb *Msp* I fragment encoding only α-APC from *C. paradoxa* (19). Under conditions of ≈40% mismatch, this fragment only hybridizes to the 2.55-kb *Pst* I fragment (the 3.45-kb *Eco*RI and the 5.9-kb *Hin*dIII fragments in the other digests also hybridize) (data not shown). A predominantly

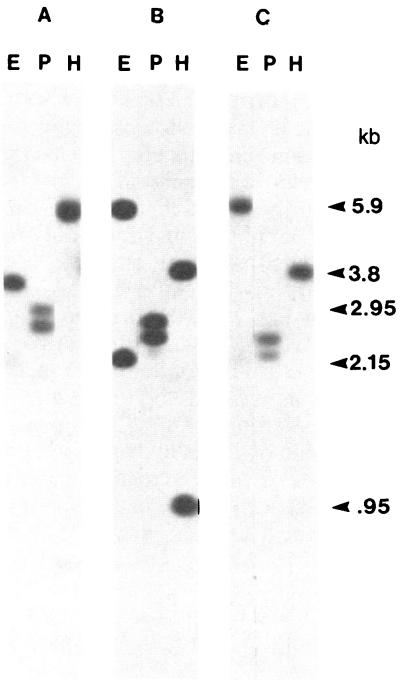

FIG. 1. Hybridizations of clone 37 DNA with heterologous and homologous phycobiliprotein gene fragments (APC and PC). DNA from clone 37 was digested with *Sal* I (which excises the insert DNA) and a second restriction endonuclease and electrophoresed on a 0.8% agarose gel in TEA buffer (25), and then the restriction fragments were transferred to nitrocellulose. (*A*) Autoradiogram of a hybridization to a nick-translated 1.4-kb (*Bam*HI–*Bgl* II) fragment encoding α- and β-APC from *C. paradoxa* (19). (*B*) Autoradiogram of a hybridization to a nick-translated 0.8-kb fragment (*Eco*RI–*Pst* I fragment) from pCPC4067 encoding all but 17-amino-terminal amino acids of β-PC and the amino-terminal one-third of α-PC from *C. paradoxa* (27). (*C*) Autoradiogram of a hybridization to a nick-translated 3.8-kb *Hin*dIII fragment encoding the red light-induced PC genes from *F. diplosiphon* (18). Hybridizations in *A* and *B* were carried out at 55°C (≈40% mismatch), while in *C*, hybridization was at 65°C (≲30% mismatch). For all hybridizations, 500,000 Cerenkov cpm of nick-translated DNA were used per filter. Filters were washed as described (27).

β-PC-specific probe hybridizes to two *Eco*RI fragments (5.9 and 2.0 kb), two *Pst* I fragments (2.55 and 2.35 kb), and two *Hin*dIII fragments (3.8 and 0.95 kb) (Fig. 1*B*). The fragments of clone 37 encoding the red light-induced α- and β-PC genes were identified utilizing a previously characterized 3.8-kb fragment from *F. diplosiphon* encoding those genes (18). This sequence hybridizes to the 5.9-kb *Eco*RI fragment, to the 2.35-kb and 2.15-kb *Pst* I fragments, and to the 3.8-kb *Hin*dIII fragment (Fig. 1*C*). Based on these results, we conclude that clone 37 contains APC-related sequences and two different PC-related sequences.

Similar experiments were performed with DNA from another λ clone, clone 4-10 (data not shown). No detectable hybridization of an APC-specific probe with clone 4-10 was observed under conditions of ≈30% mismatch. Using a β-PC-specific probe and the 3.8-kb *F. diplosiphon* fragment to localize α- and β-PC genes, fragments of the same size as clone 37 hybridize at identical stringency. Based on these hybridization experiments and the coincidence of restriction sites, we conclude that clone 4-10 contains part of the same genomic region as clone 37 and that this region contains two different sets of PC-related sequences but no APC-related sequences. A restriction map showing overlap of these clones and the positions of the genes encoding phycobiliprotein subunits is presented in Fig. 2. These positions were confirmed by sequence analysis (see below). To preclude the possibility of fragment scrambling in the APC region during genomic library construction, two fragments located between the APC and the inducible PC gene sets (*Hin*fI fragments from the *Eco*RI–*Pst* I region, see Fig. 2) were hybridized to total genomic DNA. In each of three restriction digests (*Eco*RI, *Pst* I, and *Hin*dIII), the two *Hin*fI fragments hybridized to fragments of identical size predicted from the map (data not shown), confirming the contiguous arrangement of the APC and PC genes in the genome.

Identification of Phycobiliprotein Subunit Genes. Sequencing portions of the 3.45-kb *Eco*RI fragment from clone 37 confirmed the presence of genes encoding α- and β-APC (*apcA* and *apcB*, respectively), and the direction of transcription is as indicated in Fig. 2. The amino acid sequences of the carboxyl terminus of α-APC and the amino terminus of β-APC, derived from the nucleotide sequence, are presented in Fig. 3*A*. For comparison, the analogous amino acid sequences from a eukaryotic alga, *C. paradoxa* (16, 19) are shown. The intergenic region is 69 base pairs (bp) with stop codons present in two of the three reading frames. A possible Shine–Dalgarno sequence (30) is located 9 bp upstream from the initiator codon for the β-APC gene.

We have reported the characterization of the red light-induced α- and β-PC gene set (*pcyA1* and *pcyB1*, respectively) (18); the sequences of the carboxyl terminus of β-PC, the intergenic region, and the amino terminus of α-PC are presented here (Fig. 3*B*). A second set of α- and β-PC genes (*pcyA2* and *pcyB2*, respectively), termed "constitutive"

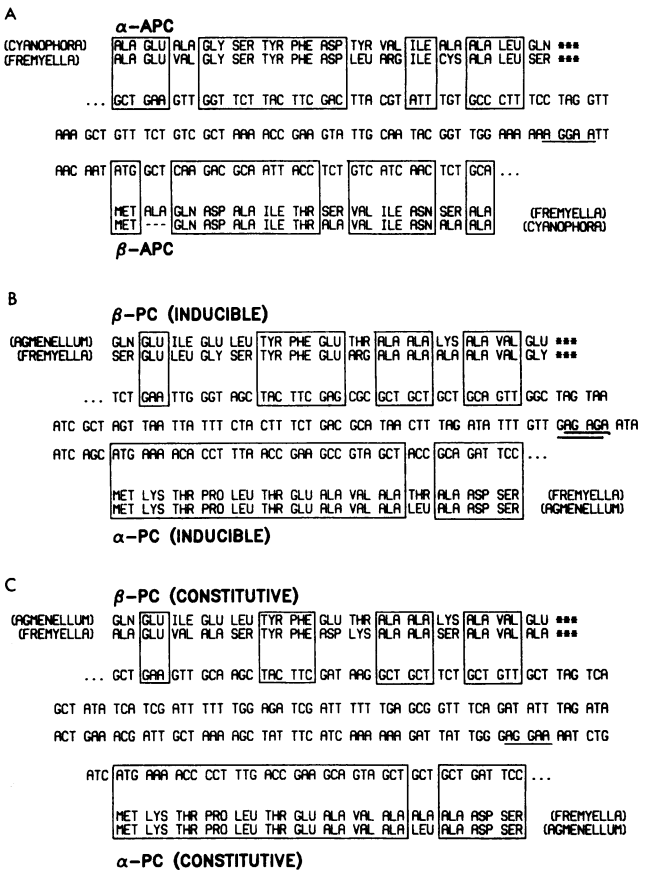

FIG. 3. Nucleotide sequences of the intergenic and portions of the coding regions of the APC and two PC gene sets and predicted amino acid sequences. (*A*) Nucleotide sequence of the carboxyl terminus of α-APC, the intergenic region (69 bp), and the amino terminus of β-APC. For comparison, the amino acid sequence derived from the nucleotide sequence of APC from *C. paradoxa* (16, 19) is shown after (CYANOPHORA). (*B*) Nucleotide sequence of the carboxyl terminus of the inducible β-PC, the intergenic region (72 bp), and the amino terminus of the inducible α-PC. (*C*) Nucleotide sequence of the carboxyl terminus of the constitutive β-PC, the intergenic region (123 bp), and the amino terminus of the constitutive α-PC. The amino acid sequence derived from the nucleotide sequence in *A*, *B*, and *C* is shown after (FREMYELLA). For comparison, the amino acid sequence of α- and β-PC from *A. quadruplicatum* are shown after (AGMENELLUM) in *B* and *C*. Amino acids in common between the two sequences are boxed in *A*, *B*, and *C*; possible ribosome binding sites are underlined and terminator codons are indicated by ***.

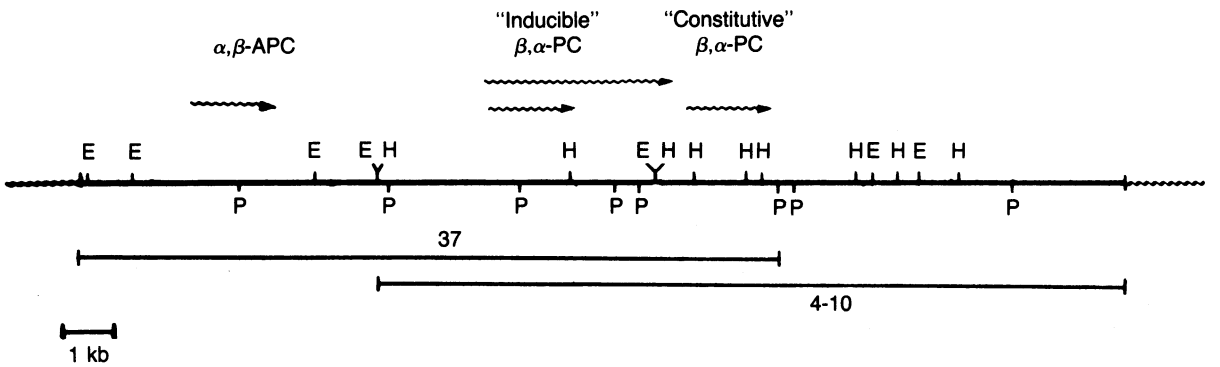

FIG. 2. Restriction enzyme maps of *F. diplosiphon* genomic clones 37 and 4-10 containing APC and PC genes. The restriction map was determined by digestion of DNA from λ-EMBL3 clones 37 and 4-10. The direction of transcription and size of the transcripts are indicated by arrows. The length of clones 37 and 4-10 are indicated by horizontal bars below the map. Not all the *Pst* I sites are indicated on the map. Abbreviations: H, *Hin*dIII; P, *Pst* I, E, *Eco*RI.

based on data presented below, was partially sequenced and sequences of the carboxyl terminus of β-PC, the intergenic region, and the amino terminus of α-PC are shown (Fig. 3*C*). For both PC gene sets, analogous amino acid sequences from another cyanobacterium, *Agmenellum quadruplicatum* (14, 15), are shown for comparison. The intergenic region for the inducible PC subunit genes is 72 bp, whereas that for the constitutive PC subunit genes is 123 bp, and both regions have stop codons present in all reading frames. Possible Shine–Dalgarno sequences are located 10 or 11 bp upstream from the initiator codon for the inducible α-PC gene (Fig. 4*B*) and 10 bp upstream from the initiator codon for the constitutive α-PC gene (Fig. 3*C*). The direction of transcription is the same (see map in Fig. 2) for all three gene sets.

RNA Hybridization Analyses. We have reported that the red light-induced PC gene set is encoded on two mRNA species (3800 bases and 1600 bases) (18). The more abundant 1600-base species encodes both α- and β-PC, while the 3800-base message contains additional sequences at the 3′ end of these genes that encode at least one inducible linker polypeptide (T.L.L., P.B.C., J. Schilling, and A.R.G., unpublished data). The 4.1-kb *Eco*RI fragment from clone 4-10 (encoding the second set of PC genes) was hybridized to RNA isolated from *F. diplosiphon* grown in either red or green light (Fig. 4*B*). This fragment hybridizes to a major mRNA species of ≈1600 bases, a size sufficient to encode both β- and α-PC. We have designated this 4.1-kb PC set "constitutive" and the 3.8-kb PC set "inducible" to be consistent with the original designations of Bryant (17). The differences (about a factor of 3) in RNA levels between red- and green-grown cultures for the constitutive set indicates that transcription from this gene set is also red light-induced but to a lesser extent than the other PC set. When an α- or β-APC specific probe is hybridized to RNA from cultures grown in red and green light there is hybridization to an abundant mRNA species of ≈1400 bases (sufficient to encode both β- and α-APC) (Fig. 4*C*). A low level of hybridization to a 1750-base transcript is also observed. Both transcripts are present at approximately the same level in RNA from cultures grown in red and green light.

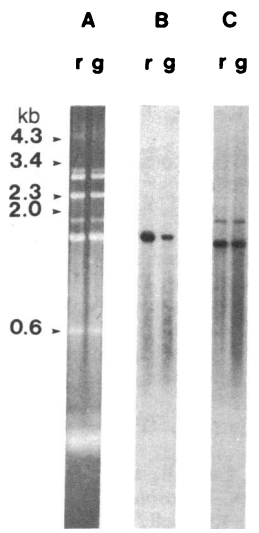

FIG. 4. Hybridization of PC and APC gene sequences to RNA isolated from cultures of *F. diplosiphon* grown in red and green light. (*A*) Photograph of a stained agarose gel with RNA from cultures grown in red (r) and green (g) light. (*B*) Autoradiogram of a hybridization of a nick-translated 4.1-kb *Eco*RI fragment encoding α- or β-PC hybridized to RNA isolated from cultures grown in red (r) and green (g) light. (*C*) Autoradiogram of hybridization of a labeled (29) single-stranded template encoding α-APC, the intergenic region, and the 13-amino-terminal amino acids of β-APC to RNA from cultures grown in red (r) and green (g) light. At least 10^6 Cerenkov cpm per filter were used in each hybridization. Hybridizations were at 65°C (≈30% mismatch). Filters were washed as described (18). Molecular size standards indicated at the left of the figure (in kilobases, kb) were λ DNA digested separately with *Hin*dIII, *Sal* I, and *Eco*RI.

DISCUSSION

We have used heterologous and homologous fragments encoding PC and APC subunits as probes to localize phycobiliprotein genes on the cyanobacterial genome of *F. diplosiphon*. Genes encoding one set of APC subunits and two sets of PC subunits are clustered on the genome and each gene set is likely to be encoded in a dicistronic message [and, in some cases, multicistronic messages (18)]. Dicistronic messages encoding phycobiliprotein subunits have also been observed for both APC and PC genes in the eukaryotic alga *C. paradoxa* (19) and for PC genes in the cyanobacterium *A. quadruplicatum* (14). Encoding both α and β subunits on a single transcript provides a possible mechanism by which the subunits can be synthesized in a 1:1 ratio, the ratio in which they are found in the functional phycobilisome (31). The cluster of phycobiliprotein genes spans a region of ≈13 kb from the beginning of the structural gene for α-APC to the end of the structural gene for the constitutive α-PC. There are ≈5 kb between the APC gene set and the inducible PC gene set and ≈3.5 kb between the inducible and constitutive PC gene sets. The direction of transcription along the cyanobacterial genome of all three gene sets is the same (left-to-right in Fig. 2) and, hence, all are transcribed from the same strand. Analysis of the sequence in the 5-kb region following the APC gene set reveals a gene for the 9-kDa APC-associated linker polypeptide present in the phycobilisome core (32); this DNA fragment hybridizes to a 370-base mRNA and a 1750-base species present in RNA from cultures grown in red and green light (S. Robbins, P.G.L., P.B.C., A.R.G., unpublished data). An oligonucleotide probe specific for the amino terminus of a red light-induced PC-associated linker polypeptide (17) hybridizes to the 3.5-kb region between the two PC gene sets, and analysis of preliminary sequence data from this region reveals amino acid homologies to a PC-associated linker polypeptide (T.L.L., P.B.C., J. Schilling, A.R.G., unpublished data). These findings suggest that additional genes for phycobilisome constituents may be clustered in this region of the cyanobacterial genome.

Both sets of PC genes hybridize well to heterologous fragments encoding most or all of α- or β-PC, but only the red light-induced PC gene hybridizes under stringent conditions to a 63-bp probe that encodes the second chromophore binding site of β-PC from *C. paradoxa* (18). This suggests that the carboxyl-terminal regions of the two β-PC genes may have diverged. Additional screening of the genomic library with PC-specific probes permitted isolation of an additional λ clone containing amino acid sequences homologous to α- and β-PC (data not shown). The relationship of these genes to those already characterized has not been determined.

Both sets of PC genes are transcribed with the β-PC followed by the α-PC, a conserved arrangement also seen in the eukaryotic alga *C. paradoxa* (19) and in the cyanobacterium *A. quadruplicatum* (14); the order of transcription of the APC genes, α-APC followed by β-APC, is also conserved between the eukaryotic alga (19) and *F. diplosiphon*. All three sets of genes have sequences located in the intergenic regions that may serve as ribosome binding sites. The sequence AGGAA occurs 9 and 10 bp upstream of the initiator codon for the β-APC and α-PC (constitutive) genes, respectively. This same sequence is found 9 bp upstream from the initiator ATG for the β-APC gene in *C. paradoxa* (19). There are two possible ribosome binding sites located 10 and 11 bp upstream of the initiation site for the inducible α-PC gene, but

none that are identical to that seen with α-PC (constitutive) and β-APC. The sequences for these possible ribosome binding sites are similar to those found in other prokaryotic organisms (33).

It has been proposed, based on amino acid composition and protein analyses, that there are at least two sets of PC genes in certain chromatically adapting cyanobacteria, one constitutively expressed and the other expressed only in red light (17). Our data represent the first proof that two PC gene sets have distinctly different transcriptional properties. The PC subunits encoded on the 4.1-kb *Eco*RI fragment are transcribed as a single detectable 1600-base mRNA species present in cultures grown in red and green light (although more abundant in red light by a factor of 3). In contrast, the PC subunit genes on the 3.8-kb *Hin*dIII fragment are encoded on two different mRNA species detectable only in RNA isolated from cultures grown in red light (18). The observed differences in steady-state abundance of both red light-induced transcripts in red versus green light is probably a result of control by light on the initiation of transcription although differences in message stability cannot be ruled out. Since the transcript levels are different in red and green light for constitutive PC but not for APC, our data indicate that the mRNA levels transcribed from the PC gene set are affected to a limited extent by light quality, whereas the mRNA levels transcribed from the APC gene set are not.

The 1600-base mRNA species that hybridizes with the constitutive PC subunit genes probably encodes only the α and β subunits. The inducible PC genes are encoded in two red light-induced transcripts; one (1600 bases) is only large enough to encode both PC subunits, while the second (3800 bases) contains additional 3′ sequences that encode at least one linker polypeptide associated with the inducible PC subunits. Although there is a linker polypeptide associated with the constitutive PC subunits in the phycobilisome (17), detectable hybridization of the constitutive PC gene set to a larger mRNA species was not observed. Therefore, if this linker polypeptide is encoded near the constitutive genes, it may be transcribed under the control of its own promoter. The APC genes hybridize to a 1750- and 1400-base transcript. The larger transcript is a possible precursor to the 1400-base species plus an abundant 370-base species, the latter encoding a small linker polypeptide associated with the core.

The authors thank Glenn Ford for his expert help with nucleotide sequence analysis and graphic illustration, Sabrina Robbins for excellent technical assistance, Laura Green and Eugenio DeHostos for helpful comments and discussions, and Loretta Tayabas for excellent secretarial assistance. P.B.C. was supported by a Carnegie Institution of Washington fellowship. P.G.L. was supported by a Carnegie Institution of Washington fellowship and a grant from the National Institutes of Health (GM 33436-01). T.L.L. was supported by a Plant Molecular Biology postdoctoral fellowship from the National Science Foundation (DMB-8312552). A.R.G. was supported by the Carnegie Institution of Washington and a grant from the National Institutes of Health (GM 33436-01). This is Carnegie Institution of Washington, Department of Plant Biology Publication No. 905.

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