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Mutations Affecting Chromatic Adaptation in the Cyanobacterium *Fremyella diplosiphon*

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The chromatically adapting cyanobacterium, *Fremyella diplosiphon*, when grown in cool white fluorescent light, contains phycoerythrin as its predominant phycobiliprotein. When grown on agar plates with cool white illumination, mutant colonies deficient or devoid of phycoerythrin can be visibly distinguished from the wild type. A total of 25 anomalously pigmented strains were isolated and examined for their ability to chromatically adapt. Based on absorption spectra of cell extracts and on fluorescence emission spectra of intact filaments, we assigned each mutant to one of three classes. In green mutants (16 strains), the photoinduction of phycoerythrin synthesis by green light was lost or impaired, whereas the photorepression of phycocyanin synthesis by green light still functioned as in the wild type. In blue mutants (eight strains), both the ability to photoinduce phycoerythrin synthesis and the ability to photorepress phycocyanin synthesis were lost or impaired. Filaments of blue mutants exhibited a high fluorescence emission at 660 nm. A black mutant (one strain) exhibited partial induction of phycoerythrin and partial repression of phycocyanin in both red and cool white light. From the data, we suggest that in information transduction for chromatic adaptation, early events are common to both phycoerythrin and phycocyanin regulation and that blue mutants possess lesions in these early events. The lesions in green mutants occur in a subsequent branch of the information transduction pathway which is specific for phycoerythrin photoinduction.

In the cyanobacteria, phycobiliproteins serve as the major light-harvesting pigments for oxygenic photosynthesis. All members of this phylum contain phycocyanin and allophycocyanin (absorption maxima, 615 and 650 nm, respectively) and lack chlorophyll *b*. Many cyanobacteria synthesize a third major phycobiliprotein, phycoerythrin, which absorbs maximally in the green region of the spectrum (565 nm). These phycobiliproteins are organized into membrane-bound organelles, the phycobilisomes (8), which facilitate the absorption and efficient transfer to chlorophyll of those photons which would otherwise be only weakly absorbed by chlorophyll itself. In some of the cyanobacteria which synthesize phycoerythrin, the relative rates of phycoerythrin and phycocyanin synthesis are determined by the spectral quality of the light in which the organism is growing; phycoerythrin synthesis predominates in green light and phycocyanin synthesis in red. This phenotypic tuning of phycobilisome absorbance to match the spectral quality of ambient light is known as chromatic adaptation (4). Of those cyanobacteria which chromatically adapt, two groups can be distinguished (21); in one group, only the synthesis of phycoerythrin is subject to photoregulation, and in the other group, the synthesis of both phycoerythrin and phycocyanin is under photocontrol.

In this laboratory, we have chosen *Fremyella diplosiphon* for a systematic study of chromatic adaptation since the organism grows rapidly (25), shows extreme regulation of both phycoerythrin and phycocyanin synthesis (21), grows heterotrophically in the dark (7), and shows little tendency to clump or adhere to surfaces during growth in liquid culture. Furthermore, for this organism, detailed action spectra for chromatic adaptation have already been determined (11, 22), and techniques have been devised for the isolation of intact phycobilisomes (9). Other investigators have extensively examined chromatic adaptation in the wild type of *F. diplosiphon* (2, 3, 10, 13, 16). Mutants of *F. diplosiphon* showing altered patterns of phycobiliprotein synthesis have not to date been reported; in this paper we describe the isolation of such mutants.

MATERIALS AND METHODS

Maintenance and growth of organisms. *F. diplosiphon* (UTEX 481) was obtained from the Culture Collection of Algae, University of Texas at Austin, and was maintained at 30°C on slants containing 1%

agar and BG-11 (17) illuminated with grolux fluorescent tubes (Sylvania GTE; F15T8-GRO) at an intensity of 8 $\mu E\ m^{-2}\ s^{-1}$. To prepare slants, 2% agar and double-strength BG-11 were autoclaved separately (1) and combined in equal volumes.

For growth in liquid culture, 250-ml Erlenmeyer flasks containing 100 ml of BG-11 were incubated at 30°C in a rotary shaker operating at 150 rpm. Above the rotary shaker was mounted one of two types of lighting fixture. Red light was obtained by filtering the emission of four 60-W incandescent bulbs through a red-transmitting cutoff filter (10% transmittance at 615 nm and 50% transmittance at 650 nm; Roscolene Medium Red, no. 823; Rosco, Port Chester, N.Y.). The cutoff filter was supported by a plate of frosted, colorless glass, and the bulbs were positioned approximately 30 cm from the top of the Erlenmeyer flasks. This lighting is subsequently referred to as red light and was at an intensity of 10 $\mu E\ m^{-2}\ s^{-1}$ at the surface of the cultures.

The alternative fixture consisted of one cool white fluorescent tube (Sylvania GTE; F15T8-CW), the emission of which is strong in the green region of the spectrum and low in the red. The light was of suitable spectral composition without the use of color filters and was dispersed through a colorless plate of frosted glass. The tube was positioned approximately 30 cm above the top of the Erlenmeyer flasks, and at this distance, the intensity of cool white illumination at the surface of the cultures was 12.5 $\mu E\ m^{-2}\ s^{-1}$.

Measurement of light intensities. The fluence rate (intensity) of photosynthetically active radiation was measured with a LiCor Quantum Meter (Li-185A) and a Quantum Sensor (Li-190S) from Lambda Instruments Corp., Linden, Nebr. This sensor only responds to light in the wave band of 400 to 700 nm.

Isolation of mutants. Wild-type filaments from a liquid culture grown in red light were spread on plates (100 by 15 mm) containing 1% agar and BG-11 (autoclaved separately) to give approximately 2,000 filaments per plate. Plates thus spread were exposed to the emission of a 14-W cold-cathode germicidal (UV) lamp (Westinghouse; WL-782-L-20) for periods of up to 5 min at a distance of 55 cm. This lamp is rated at 20 μW at a distance of 1 m. Plates were then sealed with Parafilm and incubated in cool white light (4 $\mu E\ m^{-2}\ s^{-1}$) at 30°C for 3 weeks. Anomalously pigmented filaments were detected by eye, replated, and purified from the wild type and other contaminating microorganisms where necessary by picking off those filaments which had grown across the agar surface into sterile areas of the plate. Mutant strains were maintained in axenic culture as described above for the wild type.

Strain numbers. We have assigned the general prefix CHRO to all strains with altered patterns of chromatic adaptation. This strain prefix cannot be confused with a gene locus symbol (6) since it has four nonitalicized capital letters. The specific strain number which follows this prefix reflects the order in which the strains were isolatd.

Absorption spectra of total pigments. Filaments were suspended in buffer (15 mM KH_2PO_4, 1 mM mercaptoethanol, and 1% Triton X-100 adjusted to pH 7.8 with KOH) and then sonicated for three 20-s bursts with intermittent cooling on ice (Biosonik; Bronwill Scientific Inc., Rochester, N.Y.; probe, 12 mm in diameter). Under these conditions, the filaments are totally disrupted. Centrifugation of the sonically treated material at 2,000 × *g* for 15 min yields a nonscattering supernatant containing total cell pigments. Absorption spectra were recorded with a model 3600 Beckman spectrophotometer.

Absorption spectra of phycobiliproteins. Filaments suspended in the buffer described above, but with Triton X-100 omitted, were incubated with 0.05% lysozyme for 30 min at room temperature and then frozen and thawed twice. The supernatant obtained after centrifugation at 2,000 × *g* for 15 min contains the phycobiliproteins free of chlorophyll and carotenoids. The relative concentrations of the three major phycobiliproteins were determined from absorption spectra of these phycobiliprotein solutions.

Fluorescence measurements on intact filaments. Liquid cultures were stood on the bench for 1 h, and the sedimented filaments were resuspended in the supernatant to an apparent absorbance value of 0.2 at 750 nm. Emission spectra were obtained with a Perkin-Elmer spectrofluorimeter (model 650-10s) and were not corrected for the differential spectral sensitivity of the instrument. Filaments grown in cool white light were excited at 560 nm and those grown in red light at 600 nm. Both excitation and emission slit widths were set at 2 nm. Emission spectra were recorded at room temperature both in the presence and absence of 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) at a final concentration of 50 μM. DCMU was added from a stock solution of 10 mM dissolved in acetone.

Sources of chemicals. DCMU (purity, >99%) was a gift from E. I. du Pont de Nemours & Co., Inc., Wilmington, Del. Agar (150 mesh) was obtained from Calbiochem, La Jolla, Calif. Triton X-100 and lysozyme were purchased from Sigma Chemical Co., St. Louis, Mo. All other chemicals were Analar grade where possible. Water used throughout was singly distilled in glass.

RESULTS

Isolation of mutants. The method above permits the isolation of photoautotrophically competent strains with anomalous pigmentation. It is, however, unclear as to the importance of UV irradiation in their induction since 12 of the 27 isolates were found on control plates which received no UV treatment. Some mutants grew poorly on slants in cool white light. As an effective method for the maintenance of all strains, grolux fluorescent tubes were used. These tubes have blue and red emission bands which closely match the absorption bands of chlorophyll. The wild-type and mutant strains grow rapidly in this illumination. Only 2 of the 27 isolates could not be maintained photoautotrophically under these conditions and were lost. The 25 photoautotrophically viable strains appear to be genetically stable, and all attempts to detect reversion have to date been unsuccessful.

Chromatic adaptation. To examine the ability of mutant strains to chromatically adapt, cultures were grown in flasks; filaments grown in red light were compared with those grown in cool white light. Chromatic adaptation in the

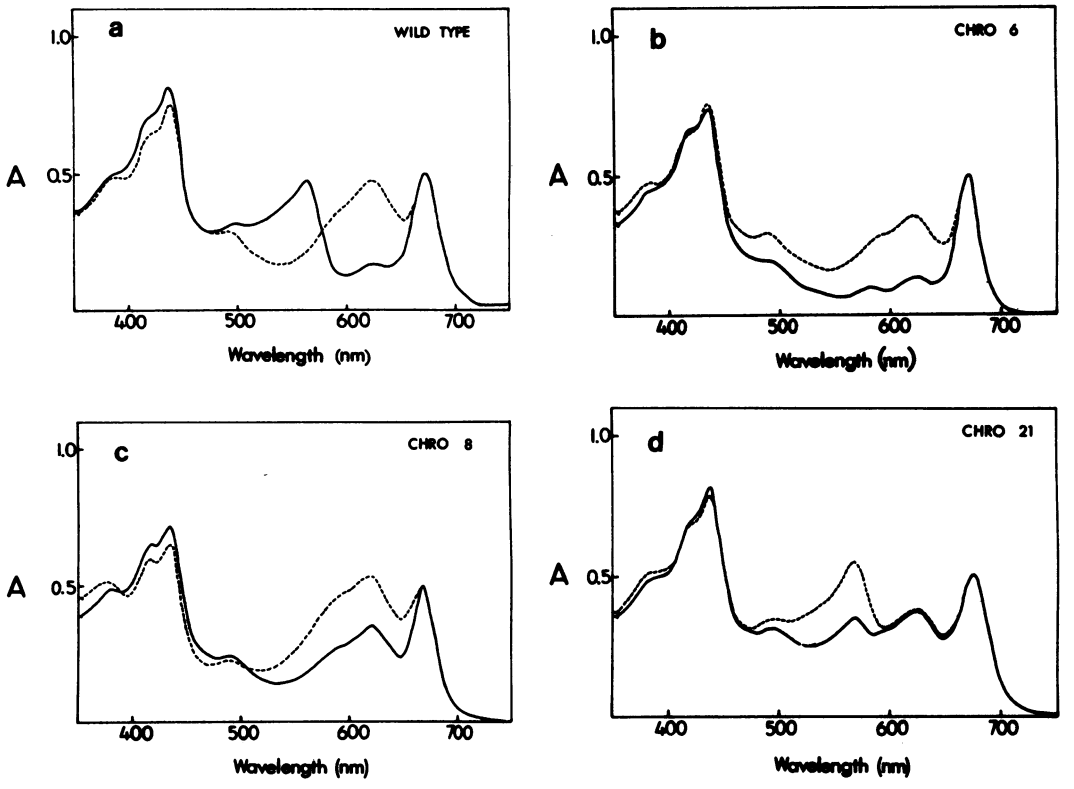

FIG. 1. Chromatic adaptation in the wild type and in three mutant strains of *F. diplosiphon*. Extracts containing total cell pigments were prepared from filaments grown in cool white light (solid line) or red light (broken line) as described in the text. Spectra were normalized for absorbance (A) at 672 nm. (a) Wild type, (b) CHRO 6, (c) CHRO 8, (d) CHRO 21.

wild type is illustrated in Fig. 1a. Here the absorption spectrum for total pigments synthesized in red light is compared with the spectrum for pigments synthesized in cool white light; the two spectra have been normalized for absorption at 672 nm (absorption peak for chlorophyll *a* in the presence of 1% Triton X-100). Typical absorption spectra which illustrate chromatic adaptation in three mutant strains are shown in Fig. 1b to d. All 25 strains were tested for chromatic adaptation by this procedure. From the absorption spectra, absorption values at 565 nm (maximum wavelength for phycoerythrin absorption), 615 nm (maximum wavelength for phycocyanin), and 672 nm (maximum wavelength for chlorophyll) were measured, and absorption ratios were calculated (Table 1). All mutant strains when grown in cool white light show a ratio, A_{565}/A_{672} (absorbance at 560 nm/absorbance at 672 nm), lower than that found for the wild type. In many strains grown in cool white light, the ratio A_{615}/A_{672} is higher than that of the wild type. In comparing strains grown in red light, a striking feature is the high value of A_{565}/A_{672} found for CHRO 21 (Fig. 1d).

Pigment ratios. To more accurately determine the ratio of phycoerythrin to phycocyanin in our mutant strains, we prepared cell extracts free of chlorophyll and carotenoids (see above). Ab-

TABLE 1. Absorbance characteristics of total pigments solubilized with Triton X-100

Strain	Absorbance ratios when grown in:			
	Cool white light		Red light	
	A_{565}/A_{672}	A_{615}/A_{672}	A_{565}/A_{672}	A_{615}/A_{672}
Wild type	0.93	0.30	0.20	0.31
Wild type	1.02	0.28	0.42	0.91
CHRO 5	0.35	0.73	0.74	1.08
CHRO 6	0.13	0.26	0.41	0.71
CHRO 7	0.37	0.32	0.42	0.84
CHRO 8	0.37	0.68	0.67	1.12
CHRO 11	0.37	0.59	0.60	0.98
CHRO 16	0.23	0.27	0.30	0.42
CHRO 17	0.29	0.41	0.33	0.53
CHRO 18	0.61	1.03	0.70	0.80
CHRO 19	0.47	0.67	0.51	0.61
CHRO 21	0.67	0.72	1.12	0.73
CHRO 26	0.21	0.30	0.23	0.36

TABLE 2. Absorbance characteristics of extracts which contain the phycobiliproteins free of chlorophyll and carotenoids

Strain	A_{565}/A_{615}	
	Cool white light	Red light
Wild type	5.28	0.46
Wild type	5.47	0.48
CHRO 5	0.62	0.50
CHRO 6	0.50	0.49
CHRO 7	1.37	0.42
CHRO 8	0.48	0.51
CHRO 11	0.58	0.48
CHRO 16	0.99	0.55
CHRO 17	0.59	0.56
CHRO 18	0.49	0.53
CHRO 19	0.54	0.61
CHRO 21	1.09	1.73
CHRO 26	0.70	0.63

sorption spectra were recorded, and an absorption ratio, A_{565}/A_{615}, was calculated. Values for this ratio are listed in Table 2. Every strain when grown in cool white light showed an A_{565}/A_{615} value lower than that for the wild type, indicating a decreased phycoerythrin-to-phycocyanin content. In the wild type and in all mutant strains except one, phycoerythrin was virtually undetectable in extracts from filaments grown in red light. The exceptional strain (CHRO 21) appears to synthesize more phycoerythrin in red light than in cool white light.

Fluorescence emission spectra. To further characterize the mutant strains, we recorded fluorescence emission spectra of intact filaments (see above). Typical emission spectra are shown for the wild type grown in red (Fig. 2a) or in cool white light (Fig. 2b). Fluorescence emission increased in the presence of DCMU (12), a potent and specific inhibitor of photosystem II. The increase in emission from chlorophyll *a* (emission at 680 nm) was greater than the increase from allophycocyanin (emission at 660 nm). Most mutant strains were similar to the wild type in their emission spectra and in their response to DCMU. A different pattern of emission was found for eight of the strains. CHRO 8 is a typical strain in this group (Fig. 3); the emission at 660 nm is severalfold stronger than that recorded for the wild type, and the apparent response to DCMU is much decreased.

For each strain, a fluorescence emission ratio, F_{680}/F_{660}, was calculated from emission spectra recorded with and without added DCMU. Typical data are shown in Table 3. The strains which

TABLE 3. Effect of DCMU on fluorescence emission from intact filaments

Strain	F_{680}/F_{660}			
	Excitation at 560 nm; filaments grown in cool white light		Excitation at 600 nm; filaments grown in red light	
	Control	With DCMU	Control	With DCMU
Wild type	0.44	0.84	0.86	1.10
Wild type	0.64	0.88	0.66	1.12
CHRO 5	0.33	0.42	0.37	0.49
CHRO 6	0.54	0.88	0.88	1.04
CHRO 7	0.47	0.77	0.61	1.15
CHRO 8	0.31	0.40	0.39	0.55
CHRO 11	0.32	0.44	0.39	0.47
CHRO 16	0.44	0.80	0.58	0.98
CHRO 17	0.68	1.04	0.63	0.95
CHRO 18	0.33	0.53	0.38	0.49
CHRO 19	0.33	0.46	0.36	0.49
CHRO 21	0.42	0.88	0.78	1.10
CHRO 26	0.46	0.84	0.50	0.85

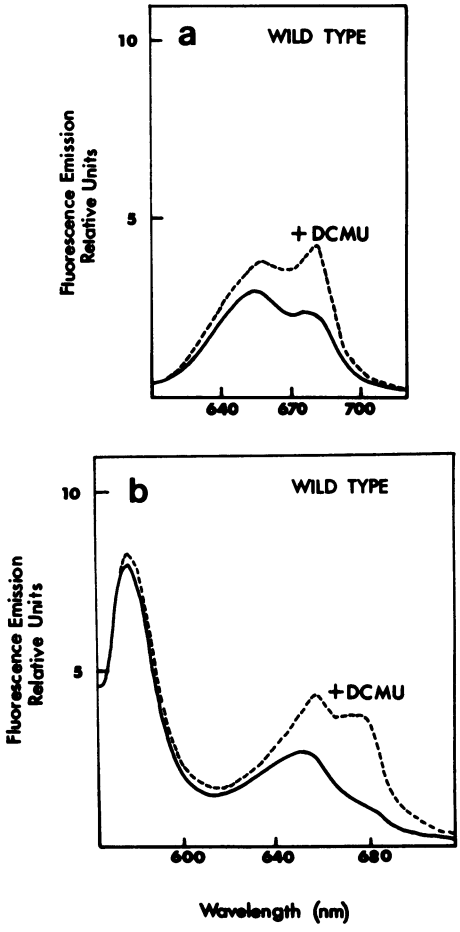

FIG. 2. Fluorescence emission spectra of intact filaments of wild-type *F. diplosiphon*. Filaments grown in red light (a) or cool white light (b) were scanned in the absence (solid line) or presence (broken line) of DCMU. Conditions for fluorescence were as described in the text.

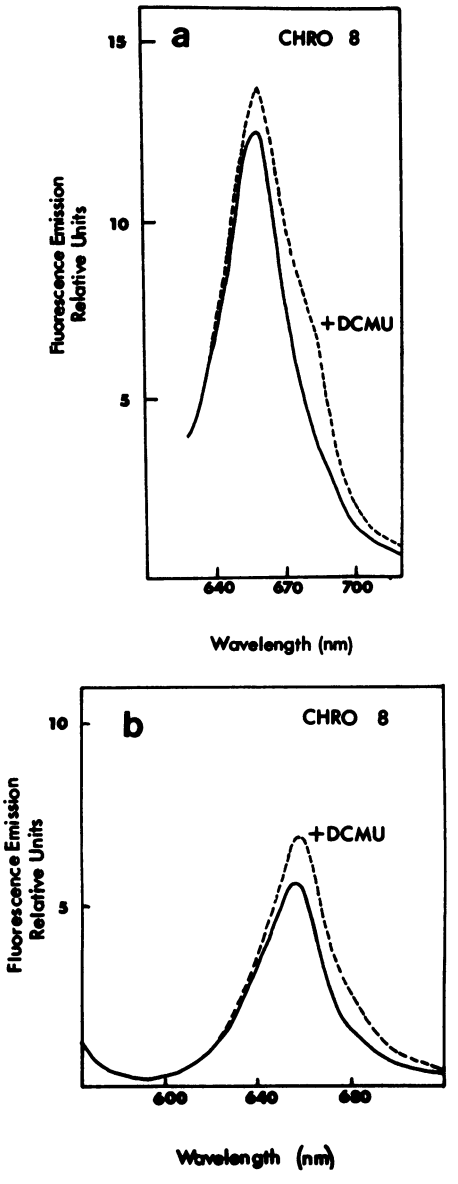

FIG. 3. Fluorescence emission spectra of intact filaments of a typical blue mutant of *F. diplosiphon* (CHRO 8). Filaments grown in red light (a) or cool white light (b) were scanned in the absence (solid line) or presence (broken line) of DCMU. Conditions for fluorescence were as described in the text.

show a different pattern of fluorescence emission can be most clearly distinguished from the rest by considering the far right column where the F_{680}/F_{660} ratio is listed for red-grown filaments treated with DCMU. For the wild type and for some of the mutant strains, F_{680}/F_{660} is close to unity. The remaining strains show a value close to 0.5. With cool white illumination for growth, the strains with anomalous fluorescence can be distinguished from the rest since in both the absence and presence of DCMU they exhibit the lowest F_{680}/F_{660} values (Table 3). The anomalously fluorescing strains are also outstanding in Table 1, where they show the highest values of A_{615}/A_{672} for filaments grown in cool white light. Although the one strain synthesizing phycoerythrin in red light (CHRO 21) also exhibits a high A_{615}/A_{672} value when grown in cool white light, its pattern of fluorescence emission and its response to DCMU are similar to those of the wild type.

Classification. In Table 4 is summarized our classification of mutant strains. Green mutants are similar to the wild type except for a partial or complete inability to synthesize phycoerythrin in cool white light. Their ability to effectively photoregulate phycocyanin synthesis is suggested in Table 1. This was confirmed by examining for each strain the effect of red and cool white light on the concentration of phycocyanin relative to that of allophycocyanin. A change in the ratio of these two phycobiliproteins results in a change in the absorbance ratio, A_{615}/A_{650}, as calculated from absorption spectra of the phycobiliprotein solutions free of chlorophyll and carotenoids. In the wild type this ratio was larger for red-grown than for cool-white-grown filaments, indicating an increased synthesis of phycocyanin in red light. For all green mutants the photoregulation of phycocyanin synthesis was similar to that in the wild type. In contrast, blue mutants have lost the ability to photoregulate phycocyanin synthesis, since for these strains, A_{615}/A_{650} values did not depend on the type of illumination during growth; the values obtained were always close to that found for the wild type grown in red light (data not shown). In CHRO 21, A_{615}/A_{650} values for filaments grown in red or cool white light were always lower than that for the wild type grown in red light and higher than that for the wild type grown in cool white light.

DISCUSSION

In this study no attempt was made to determine either the percent killing or the frequency of mutation under the conditions used for mutagenesis. These calculations are difficult since *F. diplosiphon* is filamentous and, when grown on plates, produces diffuse colonies which soon overlap and are then indistinguishable. The fact that the mutant strains we describe were isolated from approximately 500 plates gives some indication of mutation frequency. We have, however, now isolated in our laboratory a mutant of *F. diplosiphon* which chromatically adapts normally but forms colonies which remain small and discrete (K. Motamed-Larijani, unpublished

TABLE 4. Classification of mutant strains of *F. diplosiphon* according to phenotypes

Classification of mutant	CHRO mutant strain no.	Characteristics
Green mutants	1, 2, 4, 6, 7, 9, 10, 13, 15, 16, 17, 20, 24, 25, 26	When grown in cool white illumination, deficient or devoid of phycoerythrin but otherwise similar to the wild type in phycobiliprotein composition. When grown in red illumination, phycobiliprotein composition similar to that of the wild type. In filaments inhibited with DCMU, the fluorescence emission ratio, F_{680}/F_{660}, was similar to that of the wild type.
Blue mutants	5, 8, 11, 12, 18, 19, 22, 27	Markedly deficient in or devoid of phycoerythrin when grown in cool white illumination. High phycocyanin-to-chlorophyll *a* ratio when grown in cool white illumination. In filaments inhibited with DCMU, the fluorescence emission ratio, F_{680}/F_{660}, is approximately half that of the wild type.
Black mutant	21	Synthesizes phycoerythrin in both cool white and red illumination. Phycocyanin synthesis in either red or cool white illumination is less than that of the wild type grown in red light and more than that of the wild type grown in cool white light. In filaments inhibited with DCMU, the fluorescence emission ratio, F_{680}/F_{660}, is similar to that of the wild type.

data). Quantitative aspects of mutagenesis will be described in a later publication.

Mutants with altered phycobiliprotein composition have previously been isolated from cyanobacteria (15, 18, 20, 24), and their photosynthetic capabilities have been compared with those of the wild types (14, 19, 23). However, none of the species examined in these studies show chromatic adaptation with photoregulation of both phycoerythrin and phycocyanin. Sherman and Cunningham (18, 19) have isolated highly fluorescing mutants of *Synechococcus cedrorum*, but since detailed fluorescence emission spectra at room temperature were not reported, we cannot at present compare their strains to the blue mutants described here.

Bryant (5) has reported that in *F. diplosiphon* two discrete forms of phycocyanin can exist; one form is synthesized in either red or cool white light, while the other is only present in filaments grown in red light. When *F. diplosiphon* is grown in the dark in BG-11 supplemented with 2% glucose and 1% amino acids (acid-hydrolyzed casein), phycoerythrin is not synthesized, and the ratio of phycocyanin to allophycocyanin is identical to that found for filaments grown photoautotrophically in red light (unpublished data). This is generally found for facultative heterotrophic cyanobacteria which photoregulate the synthesis of both phycoerythrin and phycocyanin (21). Bryant has further shown (5) that *F. diplosiphon*, when grown heterotrophically in the dark, synthesizes both forms of phycocyanin. From all of these observations it can be concluded that in *F. diplosiphon* green light induces phycoerythrin synthesis and represses the synthesis of that form of phycocyanin which is subject to photoregulation. These green-light effects which occur at the level of gene transcription (10) are presumably mediated by a photoreversible dichroic photoreceptor as proposed by Vogelmann and Scheibe (22).

An intriguing feature of chromatic adaptation yet to be explained is the mechanism by which the rate of phycoerythrin synthesis is inversely related to the rate of phycocyanin synthesis. This relationship is disrupted in green mutants, some of which (CHRO 17 and 26) synthesize no detectable phycoerythrin. We conclude, therefore, that phycoerythrin does not itself act as a repressor of phycocyanin synthesis. It also seems highly unlikely from our data that a specific repressor for phycocyanin synthesis is cosynthesized with phycoerythrin. Our data, however, are compatible with the possibility that a specific repressor for phycoerythrin synthesis is cosynthesized with that form of phycocyanin which is subject to photoregulation. We suggest, therefore, as a working hypothesis that genes encoding photoregulable phycocyanin and a repressor for phycoerythrin synthesis are genetically adjacent and that green light causes an attenuation in their expression. This simple model is attractive in that it explains the inverse relationship between phycoerythrin and phycocyanin synthesis in the wild type of *F. diplosiphon* and is compatible with the patterns of phycobiliprotein synthesis in both green and blue mutants and yet requires only a single

genetic locus which is directly responsive to the signal transduced from the photoreceptor for chromatic adaptation.

To date we have employed only one mutagenic agent and have selected for mutants with unusual pigmentation in cool white light. We are at present testing other mutagens and selecting for mutants with anomalous pigmentation when grown in red light.

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