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Occurrence and Nature of Chromatic Adaptation in Cyanobacteria

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Forty-four axenic strains of cyanobacteria that synthesize phycoerythrin were screened to ascertain the effect of light quality on pigment synthesis. Cellular pigment compositions were determined after photoautotrophic growth with low light fluxes (7.0×10^2 ergs/cm^2 per s) of green, red, and white light, and in the case of facultative heterotrophs, after dark growth at the expense of sugars. Twelve strains did not adapt chromatically: the cells contained fixed proportions of phycoerythrin, phycocyanin, and allophycocyanin under the growth conditions used. In the remaining strains, the cellular ratio of phycoerythrin to phycocyanin was much higher after growth in green than in red light. Quantitative data on the cellular pigment contents, supplemented by measurements of the differential rates of pigment synthesis on representative strains, show that chromatic adaptation may involve a light-induced modulation either of phycoerythrin synthesis alone (7 strains) or of both phycoerythrin and phycocyanin synthesis (25 strains). Facultative heterotrophs able to adapt chromatically have a phycobiliprotein composition after dark growth which closely resembles that after growth in red light. Light quality does not affect the differential rate of chlorophyll synthesis. The physiological and taxonomic implications of these findings are discussed.

The phycobiliproteins play a major role as light-harvesting pigments in cyanobacteria and red algae: a large fraction of the light energy used to drive photosynthesis, and virtually all that channelled to photosystem II, is absorbed by these chromoproteins (2, 8, 17, 19, 21, 28). All members of both groups synthesize phycocyanin and allophycocyanin. The overlapping visible absorption bands of these two pigments lie in the red region, extending from approximately 600 to 660 nm. Cellular light absorption in this spectral region is mainly attributable to phycocyanin, since allophycocyanin is usually a minor pigment. Nearly all red algae and many cyanobacteria also synthesize phycoerythrins, which have visible absorption bands at much shorter wavelengths, situated between 520 and 580 nm in the green region.

In 1902, Engelmann and Gaidukov (7, 13) reported that the pigmentation of certain cyanobacteria can be modified by light quality: the growth of such organisms behind a series of filters of different colors causes increased light absorption by the cells in the specific spectral region to which they have been exposed, a phenomenon which these authors termed "complementary chromatic adaptation." However, the existence of such a chromatic response was questioned by several investigators, who were unable to repeat the observations of Engelmann and Gaidukov on other strains of cyanobacteria. The controversy was resolved by Boresch (4), who was the first to confirm the results of Engelmann and Gaidukov and who showed that the chromatically induced change in the color of the cells is largely (and perhaps entirely) attributable to a change in phycoerythrin-phycocyanin ratio. Phycocyanin predominates after growth in red light and phycoerythrin predominates after growth in green light, the transition occurring at a wavelength of approximately 590 nm. Consequently, chromatic adaptation can occur only in cyanobacteria that synthesize phycoerythrin. Furthermore, as Boresch also discovered, the ability to synthesize phycoerythrin is a necessary, but not a sufficient, cause: several phycoerythrin-producing cyanobacteria that he studied did not adapt chromatically. The phenomenon is not known to occur in red algae.

More recent studies of chromatic adaptation, reviewed by Bogorad (3), have been conducted with two filamentous cyanobacteria, *Tolypothrix tenuis* and *Fremyella diplosiphon*. Two main conclusions have emerged from this work. The chromatically induced modification of the

phycoerythrin-phycocyanin ratio involves de novo protein synthesis, not turnover (1). There is evidence, both indirect (6, 9–12) and direct (5, 27), which suggests that the relative rates of phycoerythrin and phycocyanin synthesis are controlled by a regulatory pigment analogous to, but not identical with, phytochrome. This regulatory pigment appears to exist in two forms, interconvertible by irradiation with specific wavelengths of light.

We shall describe experiments that bear on two general questions concerning chromatic adaptation. (i) How widespread is the phenomenon among cyanobacteria that contain phycoerythrin when grown in white light? Information on this point has been obtained by Engelmann and Gaidukov (7, 13) and Boresch (4) for a limited number of impure strains of cyanobacteria. Other than this, no systematic analysis has been made of strains belonging to different cyanobacterial genera. (ii) Do all cyanobacteria that adapt chromatically respond in the same fashion to growth in red and green light? Little information is available regarding this since extensive quantitative studies of the pigment changes that underlie the adaptative response have been conducted only with two cyanobacteria (*T. tenuis* (9–12, 16) and *F. diplosiphon* (1)), both of which adapt chromatically for both phycoerythrin and phycocyanin.

MATERIALS AND METHODS

Biological material. The 44 axenic cultures examined include most of the phycoerythrin-producing cyanobacteria in the strain collection maintained by our laboratory. Strain histories and an explanation of the generic terminology will be the subject of a future publication (R. Rippka, manuscript in preparation). It should be noted that the two strains used in recent studies on chromatic adaptation, *T. tenuis* and *F. diplosiphon*, are here referred to by our strain numbers (Paris Culture Collection 7101 and 7601, respectively).

Conditions of cultivation. Freshwater strains were grown in medium BG-11 (29), modified by increasing the concentration of Na_2CO_3 to 0.04 g/liter. Strains of marine origin (7301-03, 7305, 7307, 7310, 7312, 7314, 7317, 7319, 7320, 7322, 7325–27, 7375, 7376, 7437, 7438, 7440) were grown in medium MN (J. Waterbury and R. Y. Stanier, Bacteriol. Rev., in press) which consists of half-strength medium BG-11 prepared in 75% (vol/vol) seawater. Unless otherwise stated, all cultures were grown at 25°C.

For comparative studies of the effect of light quality on pigmentation, 40 ml of liquid cultures were grown in 100-ml Erlenmeyer flasks without gassing in white light under a light flux of 3.0×10^2 ergs/cm^2 per s, in green light under a light flux of 7.0×10^2 ergs/cm^2 per s, and in red light under a light flux of 5.0×10^2 ergs/cm^2 per s. The light source for these experiments was an Osram Universal white fluorescent lamp, chromatic illumination being provided by the interposition of plastic filters. The transmission spectra of the two filters used are shown in Fig. 1. Facultatively heterotrophic strains were grown in unshaken liquid cultures in the dark, in the basal medium used for photoautotrophic growth supplemented with filter-sterilized glucose, fructose, or sucrose at a final concentration of 0.2% (wt/vol). Pigment analyses were standardly performed on light-grown cultures after 2 to 3 weeks of incubation and on dark-grown cultures after 6 weeks of incubation. Since many of the strains grow in liquid culture as aggregates, it has not been possible routinely to determine for each strain used its growth stage at harvesting. However, in those cases where such analysis was possible the cells were at the beginning of stationary phase, having undergone ap-

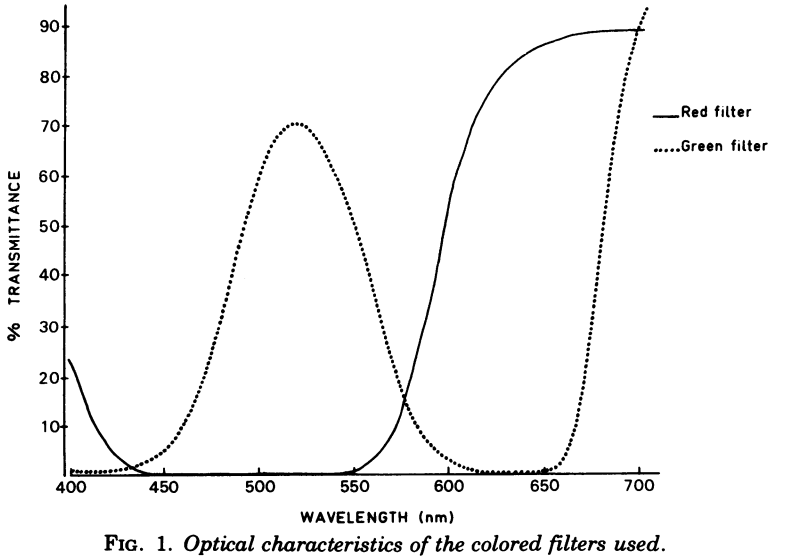

FIG. 1. *Optical characteristics of the colored filters used.*

proximately three cell divisions since inoculation.

Differential rates of phycobiliprotein synthesis (ratio of the net amount of phycobiliproteins synthesized to the net amount of protein synthesized within the same period of time [23]) during exponential growth under different light regimes were measured for three strains. Strains 6701 and 7409 were grown in medium BG-11, at 35°C and 30°C, respectively; strain 7376 was grown in medium MN containing 4 μg of vitamin B_{12} per liter, at 30°C. In both media, the concentration of Na_2CO_3 was 0.2 g/liter, and the cultures were gassed continuously with air -1% CO_2. In order to prevent a change in growth rate as a result of overshadowing during the course of the experiments, the cultures were diluted several times with fresh medium. For each organism, the differential rates of pigment synthesis were measured over approximately four generations, growth being followed turbidimetrically by the measurement of optical density at 750 nm with a Zeiss spectrophotometer. Chromatic illumination was provided by the plastic filters previously described (Fig. 1). Since the relative growth rates of cyanobacteria in green and in red light are determined by the cellular content of phycobiliproteins, which differed markedly in the three strains studied, the same intensities of green and red light could not be used in each experiment. For each strain, the distance of the light source (Mazda-fluor, Blanc Industrie) from the green and red filters was adjusted empirically in preliminary experiments until the growth rates under the two light regimes were nearly identical; these light fluxes were then used in the experiments described. In each experiment, the inoculum for the culture grown in green light was taken from a preculture in red light and vice versa. All light fluxes were measured with a radiometer (YSI-Kettering, model 65).

Extraction and determination of phycobiliproteins. Under both the cultivation conditions described above, cultures were harvested by centrifugation at 27,000 $\times$ *g* for 15 min at 4°C, and the pellets of packed cells were stored at -25°C until analysis. The thawed pellet was resuspended to a volume of 5.0 ml in 0.01 M phosphate buffer (pH 7.0) containing 0.15 M NaCl and subjected to two passages through a French pressure cell at 1,330 atm. The crude cell-free extract was centrifuged at 12,000 $\times$ *g* for 10 min at 4°C, and the pellet was resuspended in the same volume of buffer and again centrifuged. The two supernatant fractions were combined and a portion (2 ml) was centrifuged at 81,000 $\times$ *g* for 45 to 75 min at 4°C in order to sediment finely divided chlorophyll-containing membrane fragments. The washed pellet resuspended in phosphate buffer did not contain spectrophotometrically detectable phycobiliproteins. The amounts of phycoerythrin, phycocyanin, and allophycocyanin in the clarified supernatant fraction were calculated from measurements of optical density at 562, 615, and 650 nm, using the simultaneous equations developed by Bennett and Bogorad (1), with an absorption coefficient of 12.7 for phycoerythrin (15) instead of 9.62 used by these authors. The calculated values for allophycocyanin are subject to considerable inaccuracy, since this pigment is usually a minor constituent and its absorption spectrum largely overlaps that of phycocyanin. The equations are probably correct for the measurement of phycocyanin and allophycocyanin in all cyanobacteria, since these two cyanobacterial pigments have remarkably uniform spectral properties (14). The phycoerythrins of most of the strains included in this study have not been purified and spectrally characterized. For certain strains, accordingly, the calculated phycoerythrin values may be subject to a systematic numerical error, since some cyanobacteria are known to contain phycoerythrins that differ spectrally from the C-phycoerythrin type (24, 26). Even if this were so, it would not affect the interpretation of the experimental results, since the interpretation rests on a comparison of the pigment composition of each organism studied after growth under different conditions.

In kinetic experiments where phycobiliprotein analyses had to be performed on small cell samples, the extraction procedure was slightly modified. The cell pellets were all resuspended in buffer to the same optical density. Each sample was then broken by treatment for a standard time (previously determined for each strain) in an 150-W sonic oscillator (Measuring & Scientific Equipment, Ltd., London) and further treated as previously described.

Determination of chlorophyll *a*. The cell suspension was centrifuged and the pellet was extracted with 90% (vol/vol) methanol, at 4°C, in dim light, followed by centrifugation. The chlorophyll *a* content was calculated from the absorbance of the methanolic extract at 665 nm, using the extinction coefficient of 13.9 (30).

Protein determination. The cells were precipitated with 10% (wt/vol) trichloroacetic acid and centrifuged. The pellet was resuspended in 1 N NaOH, boiled for 30 min, cooled, and then recentrifuged to eliminate light-scattering material. The protein content of the supernatant was determined by the method of Lowry et al. (22), using bovine serum albumin as a standard.

RESULTS

Effects of growth in red and green light on cellular pigment composition. The strains examined include representatives of nearly every major taxonomic subgroup among the cyanobacteria (Table 1). At the low light fluxes used, the cellular content of chlorophyll *a* (expressed on a protein basis) is unaffected by light quality: cultures of each strain grown in green and red light do not differ significantly in specific chlorophyll *a* content.

The strains examined can be divided into three physiological groups with respect to the effect of chromatic adaptation on their phycobiliprotein contents (Table 1). Group I strains do not adapt chromatically. The ratio of phycoerythrin contents under the two light regimes, red and green, and the ratio of phycocyanin

TABLE 1. *Physiological groups of chromatic adapters and nonadapters among 44 strains of phycoerythrin-containing Cyanobacteria*

Genera	Group I Strains that do not adapt chromatically	Group II Strains that adapt chromatically by modification of phycoerythrin synthesis	Group III Strains that adapt chromatically by modification of both phycoerythrin and phycocyanin synthesis
Chroococcales			
Synechocystis		6701, 6808	
Gloeothece	6501, 6909, 7109, 73108		
Gloeocapsa	7501		
Chamaesiphonales			
Chamaesiphon			6605
Pleurocapsales			
Dermocarpa	7301		7302, 7303, 7437, 7438
Xenococcus			7305, 7307
Dermocarpella			7326
Chroococcidiopsis			6712
Pleurocapsa	7310, 7317, 7327		7312, 7314, 7319, 7320 7322, 7325, 7440
Hormogonales			
Nonheterocyst formers			
Oscillatoria type	7112		
Pseudanabaena type			6802
Phormidium type	7375, 7376	7113	6409, 6703, 7409
Heterocyst formers			
Nostoc		73102	
Calothrix		6303	7101, 7103, 7415, 7504
Generic identity uncertain		6305, 6601	7601

contents under the same regimes are both within the limits of experimental error, equal to 1.0. Figure 2 shows the results obtained for the 12 strains belonging to this group, no strain varying for either the phycocyanin or phycoerythrin ratios of 1.0 by more than 20%.

The remaining 32 strains examined all adapt chromatically as shown by the marked diminution of phycoerythrin content under red light conditions (i.e., phycoerythrin ratios ≤ 0.5) (Fig. 2). Two groups can, however, be distinguished on the basis of the association of this change with that of phycocyanin content. In group II strains, the specific phycoerythrin content of the cells is alone modified by light quality, the specific phycocyanin content being scarcely affected (Fig. 2). The phycocyanin content of these strains is at most 20% lower after growth in green light than after growth in red light, a difference of questionable significance. In group III strains, the response to chromatic illumination involves major changes of the specific cellular content of both phycoerythrin and phycocyanin. As can be seen from Fig. 2, the phycoerythrin ratios of strains of this group vary from 0 to 0.5 and the phycocyanin ratios from 1.6 to 3.7.

Detailed quantitative data on the phycobiliprotein composition of selected representative strains belonging to groups I, II, and III are shown in Fig. 3, 4, and 5. Cells of strain 6701, which belongs to group II, when grown in white light have a pigment composition closely resembling that of cells grown in green light (Fig. 4). The other strains of this group have not been analyzed after growth in white light. Figure 5 shows that growth in green light, in addition to greatly enhancing the phycoerythrin content, diminishes the phycocyanin content to a level that ranges, for the strains examined, from about one-third to slightly over one-half of that characteristic of cells grown in red light. Several strains of group III, as shown in Fig. 2 and 5 (strains 6802, 7103, and 7409), do not synthesize detectable phycoerythrin when grown in red light. This behavior is not shown by any strains of group II. The phycobiliprotein composition of cells of strain 7409 grown in white light is roughly intermediate between the compositions characteristic of cells grown in red and in green light (Fig. 5). Other strains of group III have not been analyzed after growth in white light.

It has proved possible to subdivide group I into three subgroups I_A, I_B, and I_C according to the relative proportions of phycoerythrin and phycocyanin of the different strains. The results of this classification are shown in Table 2.

Kinetics of pigment synthesis by strains belonging to the three physiological groups. The

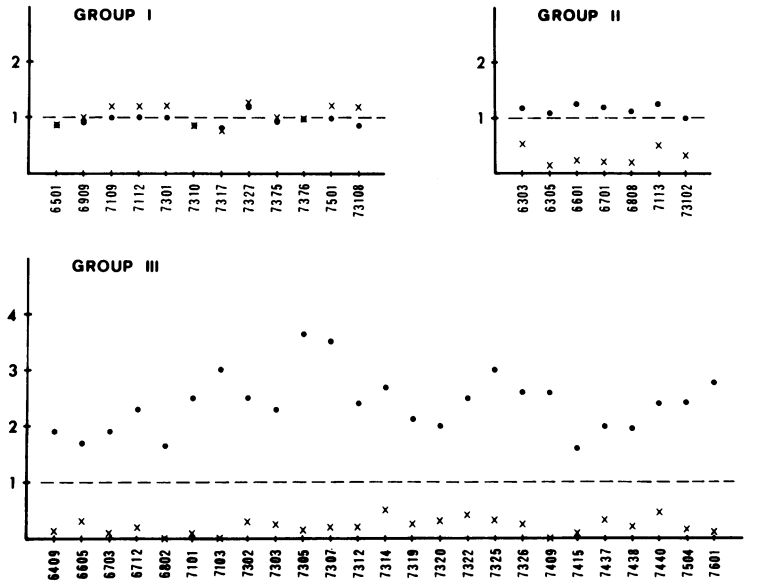

FIG. 2. *Effect of red and green light regimes on the phycoerythrin and phycocyanin contents of the 44 strains examined and classified into groups I, II, and III. Symbols: ●, ratio of phycocyanin contents after growth in red and green light [PC (red)/PC (green)]; ×, ratio of phycoerythrin contents after growth in red and green light [PE (red)/PE (green)].*

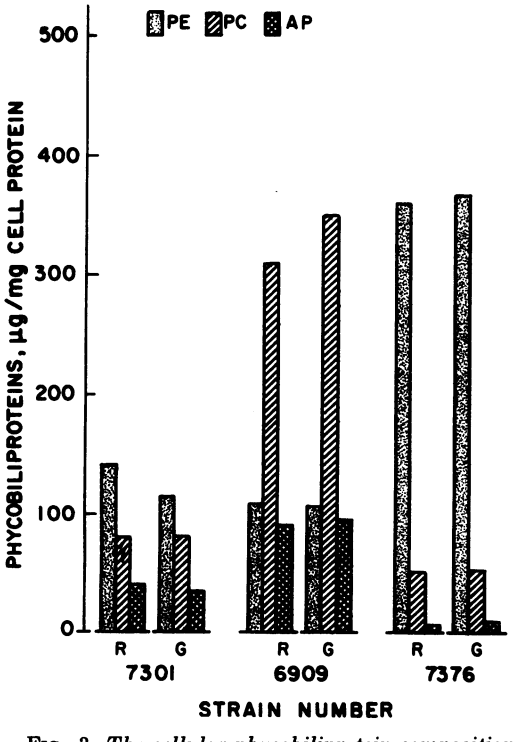

FIG. 3. *The cellular phycobiliprotein composition of three nonadapting strains (group I) after growth in red (R) and green (G) light. Abbreviations: PE, phycoerythrin; PC, phycocyanin; AP, allophycocyanin.*

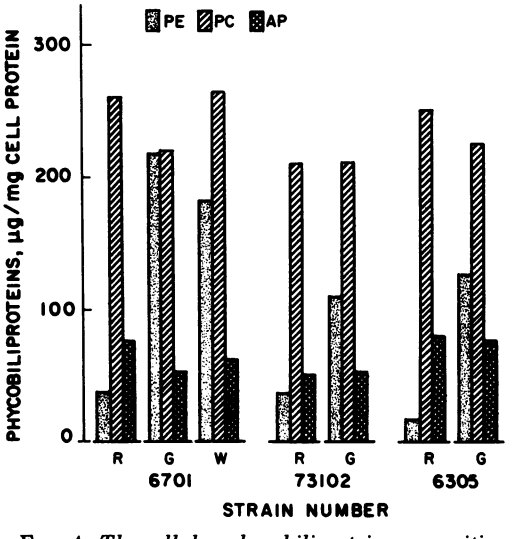

FIG. 4. *The cellular phycobiliprotein composition of three chromatically adapting strains (group II) after growth in red (R), green (G), and white (W) light. Abbreviations: PE, phycoerythrin; PC, phycocyanin; AP, allophycocyanin.*

three different types of response to chromatic illumination revealed by the analyses of pigment composition after growth under red and green light were confirmed by kinetic experiments with one strain representative of each physiological group. The differential rates of

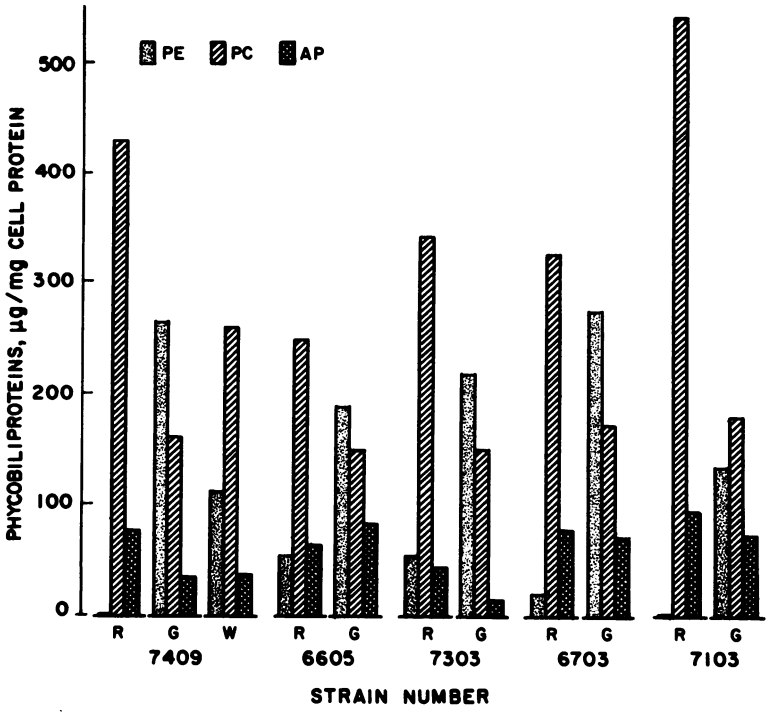

FIG. 5. *The cellular phycobiliprotein composition of five chromatically adapting strains (group III) after growth in red (R), in green (G), and white (W) light. Abbreviations: PE, phycoerythrin; PC, phycocyanin; AP, allophycocyanin.*

TABLE 2. *Classification of group I strains into subgroups I_A, I_B, and I_C according to their relative phycoerythrin and phycocyanin contents*

Subgroup	Percentage		Strain no.
	PE[a]	PC[b]	
I_A	25 ± 5	75 ± 5	6501, 6909,[c] 7109
I_B	50 ± 10	50 ± 10	7112, 7301,[c] 7310, 7317, 7327, 7501, 73108
I_C	90	10	7375, 7376[c]

[a] PE, Phycoerythrin content expressed as percentage of total phycobiliprotein (PE × 100/PE + PC).

[b] PC, Phycocyanin content expressed as percentage of total phycobiliprotein (PC × 100/PE + PC).

[c] Strains for which detailed quantitative data are presented in Fig. 3.

phycobiliprotein synthesis were measured in parallel cultures, growing exponentially under light fluxes of red and green light that supported near-identical growth rates (Table 3). As also shown in this table, cultures of each strain growing in green and in red light had the same specific chlorophyll contents, a confirmation that the rate of chlorophyll synthesis is unaffected by light quality.

In strain 7376, representative of group I (Fig. 6), the differential rates of phycoerythrin, phycocyanin, and allophycocyanin synthesis were not experimentally distinguishable in cultures growing in green and in red light. In strain 6701, representative of group II (Fig. 7), the differential rate of phycoerythrin synthesis in red light was approximately 25% of that in green light, whereas phycocyanin and allophycocyanin were synthesized at experimentally indistinguishable rates under both light regimes. In strain 7409, representative of group III (Fig. 8), phycoerythrin was not synthesized at all in red light, but was synthesized at a far higher differential rate than phycocyanin in green light. Both phycocyanin and allophycocyanin were synthesized by this strain in green light at differential rates about 30% of those in red light.

The inocula for the parallel growth experiments with each strain in chromatic light came from cultures grown under different light regimes: the inoculum for growth in green light came from a culture in red light, whereas the inoculum for growth in red light came from a culture in green light. Consequently, in the

TABLE 3. *Chlorophyll a content of cultures grown in red light or in green light*

Strain no.	Red light			Green light		
	Light flux (ergs/cm² per s)	Generation time (h)	Chlorophyll *a*, specific content[a]	Light flux (ergs/cm² per s)	Generation time (h)	Chlorophyll *a*, specific content[a]
7376	2.0×10^3	34	4.3	1.5×10^3	34	4.7
6701	3.0×10^3	15	3.9	1.5×10^3	23	3.9
7409	2.0×10^3	34	5.7	2.0×10^3	28	5.5

[a] Determined as micrograms of chlorophyll *a* per unit of cell mass, the latter measured turbidimetrically at 750 nm.

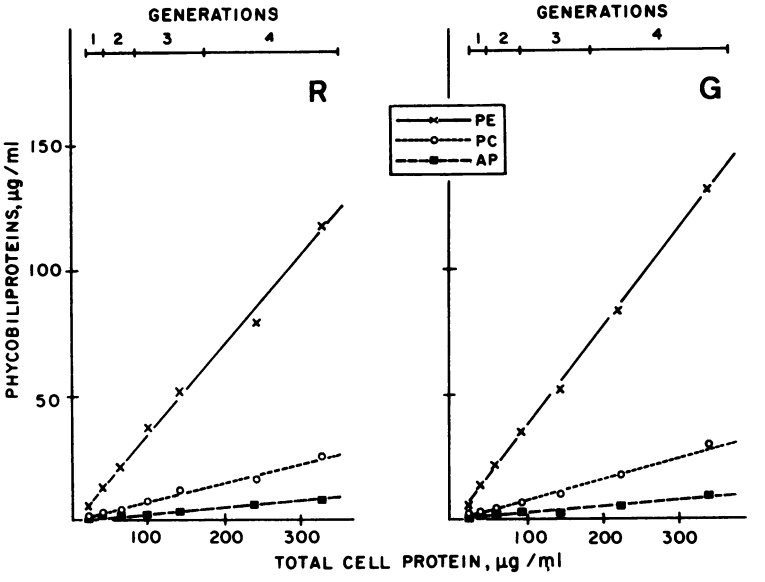

FIG. 6. *The differential rates of phycoerythrin (PE), phycocyanin (PC), and allophycocyanin (AP) synthesis of a nonadapting strain 7376 (group I) grown for four generations with light fluxes of red (R) and green (G) light that support approximately equal growth rates.*

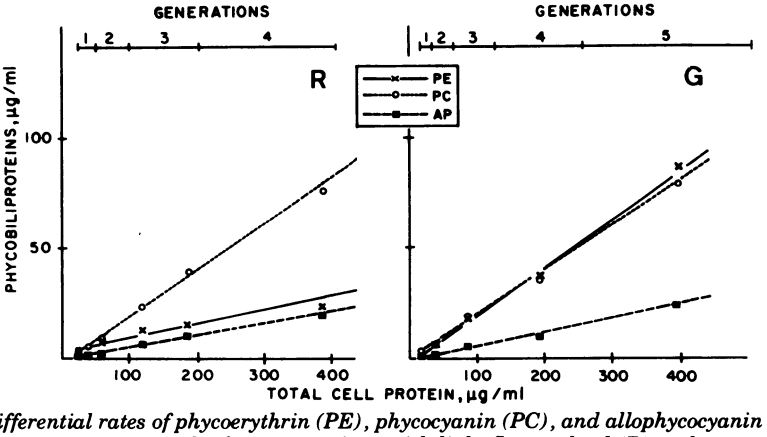

FIG. 7. *The differential rates of phycoerythrin (PE), phycocyanin (PC), and allophycocyanin (AP) synthesis of strain 6701 (group II) grown for four generations with light fluxes of red (R) and green (G) light that support approximately equal growth rates.*

case of the two strains that adapt chromatically (6701 and 7409), the inocula had phycobiliprotein compositions markedly different from these subsequently established in the course of growth. As shown by measurements made 2 h after transfer, the cells start to synthesize phy-

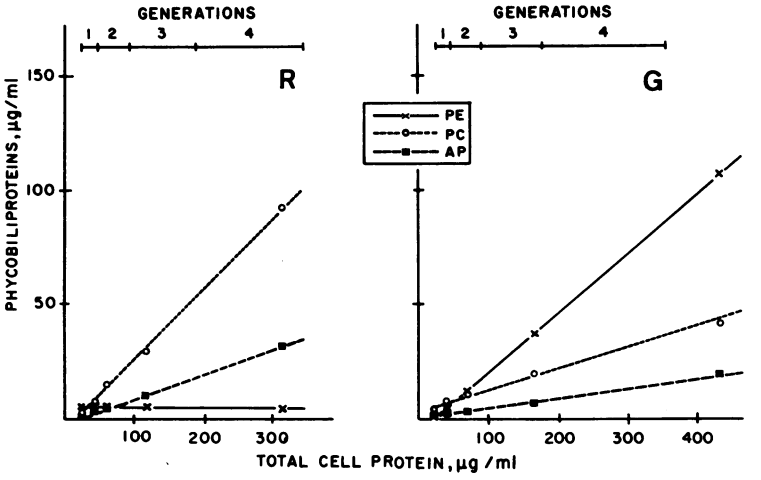

FIG. 8. *The differential rates of phycoerythrin (PE), phycocyanin (PC), and allophycocyanin (AP) synthesis of strain 7409 (group III) grown for four generations with light fluxes of red (R) and green (G) light that support approximately equal growth rates.*

cobiliproteins at the differential rates imposed by the changed light regime without any apparent lag.

A second kinetic experiment similar to that portrayed in Fig. 8 was performed with strain 7409, using chromatic light fluxes about one-half as great. The same differential rates of phycobiliprotein synthesis were obtained. Over this very limited intensity range, accordingly, light intensity does not modify the specific chromatic response.

Phycobiliprotein synthesis in the dark. For two facultatively heterotrophic strains of group I (strains 7317 and 7327; J. Waterbury and R. Y. Stanier, Bacteriol. Rev., in press) and eight facultative heterotrophic strains of group III (strains 6712 [25], 7101 [20], 7307, 7319, 7325, 7326, 7437, and 7438; J. Waterbury and R. Y. Stanier, Bacteriol. Rev., in press), phycobiliprotein composition was also determined on dark-grown cultures. Representative data for one strain belonging to each group are shown in Fig. 9 and 10. Strain 7317 (group I), like the other strain of this group examined, retains a phycobiliprotein composition during dark growth identical to that of light-grown cells (Fig. 9). Strain 7319 (group III) maintains a phycobiliprotein composition during dark growth closely similar to that of cells grown in red light, a behavior shared by the other facultative heterotrophic strains. The total rate of phycobiliprotein synthesis remains high during dark growth. The total phycobiliprotein content of dark-grown cells of strains 7317 and 7319 is similar to that of cells grown photoautotrophically in red and in green light. The percentages (expressed as percentage of the total cell pro-

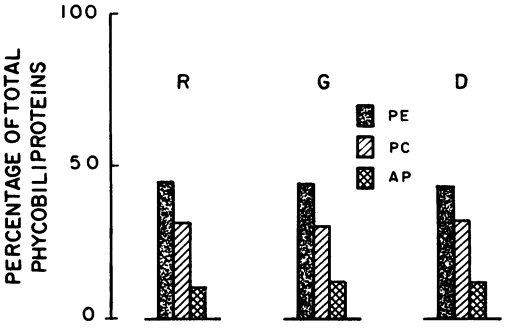

FIG. 9. *A comparison of the phycobiliprotein composition of a facultatively heterotrophic strain 7317 (group I), after autotrophic growth in red (R) and green (G) light and after heterotrophic growth with glucose in the dark (D).*

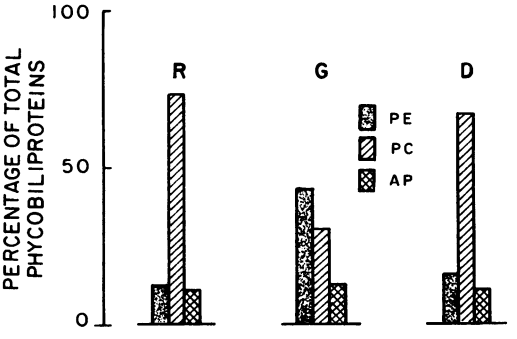

FIG. 10. *A comparison of the phycobiliprotein composition of a facultatively heterotrophic strain 7319 (group III), after autotrophic growth in red (R) and green (G) light and after heterotrophic growth with sucrose in the dark (D).*

tein) were 18, 19, and 26% for strains 7317, 37, and 39, respectively, and 44% for strain 7319.

DISCUSSION

This work has confirmed the early report (4) that not all phycoerythrin-containing cyanobacteria can adapt chromatically. No adaptation was observed in 12 of the 44 strains examined. In such cyanobacteria (group I) the relative rates at which the three phycobiliproteins are synthesized seem to be constant and characteristic for each strain, whether grown in white light, in chromatic light, or in the dark. As shown by the representative data in Fig. 3, such nonadapting strains may differ widely from one another in phycobiliprotein composition, some containing phycoerythrin as the major pigment and others containing phycocyanin. It is conceivable that the pattern of phycobiliprotein synthesis in these strains might be modifiable to some degree by other factors, such as light flux or temperature, but this aspect of the problem has not been examined. Since many cyanobacteria containing phycoerythrin are markedly light sensitive, light flux cannot be varied very widely without introducing the risk of photochemical bleaching. It is for this reason that all the experiments described here were conducted at very low light fluxes: $<10^3$ ergs/cm^2 per s.

Among cyanobacteria that do adapt chromatically, two physiological groups can be distinguished. In seven strains (group II) only the synthesis of phycoerythrin is significantly affected, the rate of its formation being much higher in green than in red light. However, phycoerythrin synthesis never ceases completely in red light. This mode of chromatic adaptation, exhibited by strains of widely different taxonomic position, has not been previously described. In 25 strains (group III) light quality affects both phycoerythrin and phycocyanin synthesis: in green light, the differential rate of phycoerythrin synthesis is much higher than in red light, whereas that of phycocyanin is much lower. Some of these strains cease to synthesize phycoerythrin in red light, whereas phycocyanin synthesis is never completely arrested in green light. The kinetic data for one strain of this group (7409) suggest that allophycocyanin synthesis is light regulated in the same fashion as phycocyanin synthesis. However, in view of the inaccuracy of our allophycocyanin determinations, it cannot yet be concluded that synthesis of the two pigments is really coordinated. The two strains of cyanobacteria so far used for experimental studies on chromatic adaptation, *T. tenuis* (strain 7101) and *F. diplosiphon* (strain 7601), both belong to this category of chromatic adapters.

Hoare et al. (18) showed that cultures grown in the dark are pigmented but that the proportion of phycoerythrin is relatively higher in light- than in dark-grown cultures. Fujita and Hattori (10) observed that the phycobiliprotein composition of *T. tenuis* grown in the dark with sugars closely resembles that of cultures grown in red light. We have found this to be true for many other facultative heterotrophs in which both phycoerythrin and phycocyanin synthesis are photoregulated; they include cyanobacteria that are taxonomically distant from *T. tenuis*.

As mentioned in the introduction, both direct and indirect evidence support the view that chromatic control of phycobiliprotein synthesis is mediated by a regulatory pigment that exists in two forms, interconvertible photochemically. Since the cellular phycobiliprotein composition of chromatically adapting strains is the same after growth in the dark and in red light, it follows that only one state of the regulatory pigment (i.e., that produced by irradiation with green light) is active in modulating phycobiliprotein synthesis. The observations reported here indicate that in all cyanobacteria that adapt chromatically, the active form of the regulatory pigment increases the differential rate of phycoerythrin synthesis. In some, it also diminishes the differential rate of phycocyanin (and perhaps also of allophycocyanin) synthesis.

The pigment composition of cyanobacteria is usually determined after growth in white light. Under these conditions, many cyanobacteria do not contain phycoerythrin. We have attempted to induce phycoerythrin synthesis in 12 strains of this type (6301, 6307, 6714, 6715, 6901, 7203, 7321, 7425, 7430, 7431, 7432, and 7434) by exposure to green light (see Fig. 1 for the transmission spectrum of the filter used). Although all were able to grow under these conditions, none synthesized detectable phycoerythrin. Hence, the absence of phycoerythrin from cells of a cyanobacterium grown in white light appears to constitute good evidence of its inability to synthesize this pigment.

A secondary purpose of this study was to determine the possible utility of chromatic adaptation as a taxonomic character in cyanobacteria. As shown in Table 1, several genera (e.g., *Dermocarpa, Pleurocapsa*) contain both adapting and nonadapting representatives; in such subgroups, the character might at best help to discriminate between species. None of the unicellular cyanobacteria of the order *Chroococcales* so far examined adapts through regula-

tion of both phycocyanin and phycoerythrin synthesis. Four strains of *Gloeothece* are nonadapters and two strains of *Synechocystis* adapt through regulation of phycoerythrin synthesis. However, a much larger number of strains must be examined in order to evaluate the taxonomic significance of these facts.

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