Russian Journal of Plant Physiology, Vol. 52, No. 2, 2005, pp. 235–241. Translated from Fiziologiya Rastenii, Vol. 52, No. 2, 2005, pp. 266–273.

Effects of Glucose during Photoheterotrophic Growth of the Cyanobacterium *Calothrix* sp. PCC 7601 Capable for Chromatic Adaptation

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Received January 12, 2004

Abstract—Photoheterotrophic growth of a filamentous cyanobacterium *Calothrix* sp. PCC 7601, which is capable for complementary chromatic adaptation, in the presence of glucose was accompanied by changes in the content of phycobiliproteins. Glucose, a source of energy and a metabolism regulator, differently affected the level of major phycobilisome pigments, phycocyanin (PC) and phycoerythrin (PE) in the cells. When red light enhanced PC synthesis, glucose enhanced it additionally. When green light suppressed PC synthesis, glucose did not affect it. Under both light regimes, glucose inhibited PE synthesis. Thus, glucose oppositely affected the content of two major phycobiliproteins. Glucose not only affected the ratio between phycobiliproteins but also decreased the content of carotenoids, inhibited activity of photosystem II, and affected cell sizes. A stereochemical analog of glucose, 2-deoxy-D-glucose, induced effects similar to those of glucose. A comparison with the effects of red and green light demonstrated that glucose acted on *Calothrix* similarly to red light and oppositely to green light.

Key words: Calothrix sp. PCC 7601 - complementary chromatic adaptation - phycoerythrin - phycocyanin - glucose - 2-deoxy-D-glucose

INTRODUCTION

Complementary chromatic adaptation (CCA) induced by light of different quality is manifested in the changes in the pigment composition of cyanobacteria [1, 2]. CCA was detected in approximately one third of cyanobacteria with phycobilisomes containing both PC and PE [3]. Red light induces the synthesis of PC and prevents the accumulation of PE. Green light exerts an opposite action: it enhances PE synthesis and suppresses PC synthesis [4]. CCA optimizes light absorption under varying light quality because PC absorbs efficiently red light and PE, green light. CCA occurs due to light absorption by a phytochrome-like photoreceptor [5] and manifested at the level of the expression of genes for polypeptide subunits of PC and PE [6]. Phosphorylation/dephosphorylation of protein transcription factors is a necessary prerequisite for CCA [5, 7].

Light spectral composition is a regulatory factor that operates along with biochemical ones. Biochemical factors are the components of the whole regulatory system in the cell including light-dependent reactions as well. However, there is no evidence about the interaction between CCA and other regulatory factors in cyanobacteria. At the same time, in higher plants and some algae, carbohydrates affect gene expression along with light [8]. Glucose control is believed one of the principal components of the photosynthesis regulation. Glucose, produced during photosynthesis or absorbed from the external medium, suppresses PSII functioning, inhibits the activities of the Calvin cycle enzymes, and affects transcription of various photosynthesis-related genes [8, 9].

A primary acceptor for the glucose regulatory signal is hexokinase [10], which phosphorylates glucose. The most probable model of regulation is the operation of hexose phosphate at the transcriptional level [9, 10]. In order to elucidate glucose regulatory functions, 2dDg is widely used because this stereochemical analog of glu-

Abbreviations: AP—allophycocyanin; CCA—complementary chromatic adaptation; 2dDg—2-deoxy-D-glucose; PC—phycocyanin; PE—phycoerythrin; PSI—photosystem I; PSII—photosystem II.

cose can be phosphorylated like glucose and trigger the hexokinase signal transduction pathway but cannot be metabolized by the cell and does not serve as an energetic glucose analog [10, 11].

In the cells of facultative photoheterotrophs, sugar activity is the issue of particular interest because both light and glucose are energy sources and simultaneously active regulators of metabolism. Cyanobacteria are natural photoautotrophs. However, about half of strains tested can also consume glucose or other carbohydrates for heterotrophic growth [12]. The phenomenon of CCA was predominantly studied for *Calothrix* sp. PCC 7601 [2, 7] capable for photoheterotrophy [13]. PC and PE comprise a bulk (30–60%) of soluble proteins of cyanobacteria; therefore, the cell spends a considerable part of its energy resources for the synthesis of these proteins. It is naturally to expect that the syntheses of PC and PE have to be glucose-dependent. The effect of glucose on the content of phycobiliproteins, i.e., on CCA, is easily detectable because it results in the changes in cell pigmentation.

The objective of this work was to investigate the interaction between light and glucose as regulatory factors in cyanobacteria.

MATERIALS AND METHODS

A filamentous cyanobacterium *Calothrix* sp. PCC 7601 (*Fremyella diplosiphon* UTEX 481, called further as *Calothrix*) was cultured at 28°C in 150-ml flasks containing 40 ml of BG-11 growth medium [12]. Cell suspension (3 ml) grown under red or green light was inoculated into fresh medium. Cells were cultured under red or green light (15 μE/(m^2 s) and bubbled with air. Glass filters (for red light, 10% of transmission at 615 nm and 50% of transmission at 650 nm; for green light, 10, 60, and 15% of transmission at 550, 580, and 620 nm, respectively) were placed between the flask and fluorescent LB18 lamp of white light (an analog is OSRAM L18W/15 lamp). Three types of growth conditions were used: (1) photoautotrophy, (2) photoheterotrophy with the addition of 1% (wt/v) glucose (Sigma, United States), and (3) photoautotrophy with the addition of 0.5% (wt/v) 2dDg (Merck, Germany). Cells grew for 5 days until the beginning of the stationary growth phase until the chlorophyll content achieved 1.5–3.0 μg/ml. For this time, in the treatment with glucose, cell suspension weight increased by 70%, whereas in treatment with 2dDg, it decreased by 10% as compared to autotrophic culture under either red or green light. The cells were examined with a Jevenal light microscope (Carl Zeiss, Germany) at the 400× magnification.

Absorption spectra of *Calothrix* cells were measured using a Hitachi 550 spectrophotometer (Japan) as described earlier [14]. In order to estimate pigment content, the cells were sedimented in a Hacksley microfuge (Gallenkamp, United Kingdom) at 12000 *g* for 15 min. The pellet was resuspended in 0.01 M Na-phosphate buffer, pH 7.8, and the cells were destroyed with ultrasound for 2 min, alternating 0.5-min periods of destruction with 0.5-min periods of cooling. The homogenate obtained was centrifuged at 65000 *g* for 45 min. The concentrations of AP, PC, and PE in the supernatant were measured using known coefficients of absorption [15]. Chlorophyll and carotenoids were extracted from the pellet with 80% acetone, and their concentrations were measured as described in [16].

The action spectra of PSI and PSII were measured polarographically from the changes in the rate of O_2 exchange at monochromatic irradiation of samples with 1-s light flashes (0.2 μE/(m^2 s), a spectral half-interval of 1–3 nm) and 20–60-s dark intervals, as described earlier [17, 18]. The cell layer in 50 mM Na-phosphate buffer containing 50 mM KCl, pH 6.8, on the platinum electrode had a surface chlorophyll concentration of 1–2 μg/cm^2. The rate of O_2 evolution by PSII under monochromatic irradiation was measured under weak background irradiation at 680 nm. The rate of the photoinhibition of respiration mediated by PSI activity was measured in the same experiment in the presence of 10 mM diurone suppressing PSII activity. Relative contents of functionally active PSI and PSII reaction centers were estimated as the total O_2 yield in the reactions of water oxidation and photoinhibition of respiration, which was calculated per saturating 1.8-μs light flash [17, 18].

In order to obtain RNA, *Calothrix* cells were sedimented by centrifugation at 5000 *g* for 2 min and placed in liquid nitrogen. The pellet was thawed and resuspended in 500 μl of buffer containing 0.1 M Na-acetate, pH 8.0, 1 mM Na_2:EDTA, and 4% SDS. Equal volume of a hot (65°C) mixture of phenol and chloroform (1 : 1, v/v) was added, the mixture was thoroughly shaked and incubated at 65°C for 10 min. The suspension was centrifuged at 8000 *g* for 10 min. Extraction was repeated three times. Thereafter, RNA-containing water layer was collected, 2.5 volumes of ethanol and 0.1 volume of 5 M Na-acetate were added, and the mixture was incubated at –20°C for 12 h. RNA was sedimented by centrifugation at 14000 *g* for 10 min. The pellet was washed with 70% ethanol, dried in the vacuum-desiccator, and dissolved in 20–50 μl of sterile water. RNA was fractionated in 1.2% agarose gel containing 0.6 M formaldehyde, transferred to the GeneScreen Plus membrane by capillary blotting, and fixed by membrane keeping at 80°C for 2 h. The *Eco*RI/*Xba*I fragment of the *cpeBA* gene 1.1 kb in length was used as a probe for hybridization; this fragment was cut from the pPM 64 plasmid [19] and contained regions encoding α- and β-polypeptide subunits of PE. The fragment was labeled with ^{32}P-dATP using a BstI set for DNA polymerase reaction (Takara, Japan). Hybridization was performed in the formamide-containing solution

(50% formamide, 1% SDS, and 1 M NaCl) at 42°C for 12 h. Then the membrane was washed twice in 1% SDS at 60°C for 30 min. The membrane was dried, and radioactive autograph was obtained on a photofilm.

RESULTS

Absorption spectra of *Calothrix* cells grown autotrophically under red or green light were typical of cyanobacteria capable for CCA [4, 13]. Under green light (Fig. 1a), the PE peak at 565 nm was comparable in size with that of chlorophyll at 678 nm, whereas the PC peak at 625 nm was much less pronounced. Under red light (Fig. 1b), the PC peak increased sharply and the PE peak decreased substantially. Absorption at 440 nm in blue part of the spectrum corresponds to the Soret's band of chlorophyll; a broad band in the region of 480–500 nm is determined by carotenoids (Fig. 1).

In photoheterotrophic *Calothrix* culture grown under green light, absorption of PE and carotenoids decreased, whereas the ratio between PC and chlorophyll peaks remained unchanged (Fig. 1a). In photoheterotrophic culture grown under red light, absorption by PC increased and that by carotenoids decreased (Fig. 1b). The addition of 2dDg to photoautotrophic culture induced similar changes as glucose; however, under green light, a decrease in the carotenoid absorption was stronger (Fig. 1).

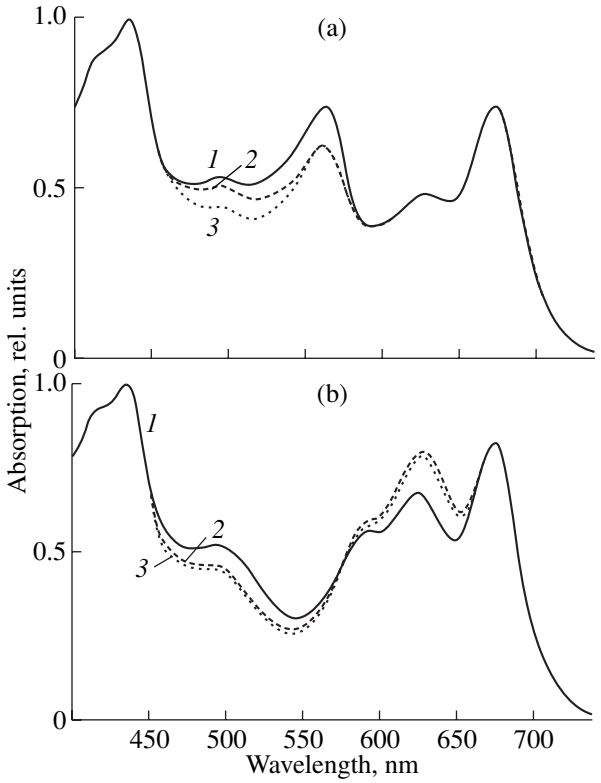

Fig. 1. Absorption spectra of *Calothrix* cells grown under (a) green and (b) red light and various conditions of culturing: (*1*) autotrophic growth; (*2*) photoheterotrophic growth in the presence of 1% glucose; (*3*)growth in the presence of 0.5% 2dDg. Spectra are normalized to 678 nm.

Table 1 sums the data about pigment composition in *Calothrix* cells grown under various regimes of culturing. Photoautotrophic cells grown under red light contained less pigments than those under green light: chlorophyll by 1.6 times, carotenoids by 1.9 times, and phycobiliproteins by 1.4 times. Thus, light quality affected not only the relative but also absolute content of pigments in *Calothrix* cells. The presence of glucose or 2dDg did not affect the content of chlorophyll, although decreased the content of carotenoids under both green and red light (Table 1). The degree of CCA development can be evaluated from the relative contents of phycobiliprotein pigments (PE : PC : AP) but not their absolute content in the cell [1, 2]. The molar ratio between PE, PC, and AP in *Calothrix* cells grown under green light was 2.6 : 1.0 : 1.0. In the photoautotrophic culture grown under red light, these ratios were 0.5 : 2.5 : 1.0. The addition of glucose or 2dDg to the growth medium changed these ratios into 2.1 : 1.0 : 1.0 under green light and 0.4 : 2.7 : 1.0 under red light (Table 1). Thus,

Table 1. The ratio between photosynthetic pigments per biomass unit of *Calothrix* cells grown under different growth conditions*

Growth conditions	Chl**	Chl/Car	PE/AP	PC/AP	Chl/PBS
GL, autotrophy	1.0	4.1 ± 0.5	2.6 ± 0.4	1.0 ± 0.15	370 ± 50
GL + 1% glucose	1.0 ± 0.12	3.9 ± 0.6	2.1 ± 0.3	1.0 ± 0.15	370 ± 50
GL + 0.5% 2dDg	1.0 ± 0.12	3.8 ± 0.6	2.0 ± 0.3	1.0 ± 0.15	370 ± 50
RL, autotrophy	0.7 ± 0.1	4.8 ± 0.8	0.6 ± 0.1	2.5 ± 0.4	330 ± 40
RL + 1% glucose	0.7 ± 0.1	4.6 ± 0.7	0.4 ± 0.05	2.7 ± 0.4	330 ± 40
RL + 0.5% 2dDg	0.7 ± 0.1	4.6 ± 0.8	0.4 ± 0.05	2.7 ± 0.4	330 ± 40

* The content of Chl in *Calothrix* cells grown under green light was taken as 1. The weight ratios of Chl and Car and molar ratios of Chl and phycobiliproteins are presented. To obtain the ratio Chl/PBS, the molar ratio Chl/AP (data not presented) was divided by 36 because each *Calothrix* phycobilisome contains 36 α-polypeptide monomers of AP. The mean values from three independent experiments and their standard errors are presented.

** Chl—chlorophyll; Car—carotenoids; PBS—phycobilisomes; GL—green light; RL—red light.

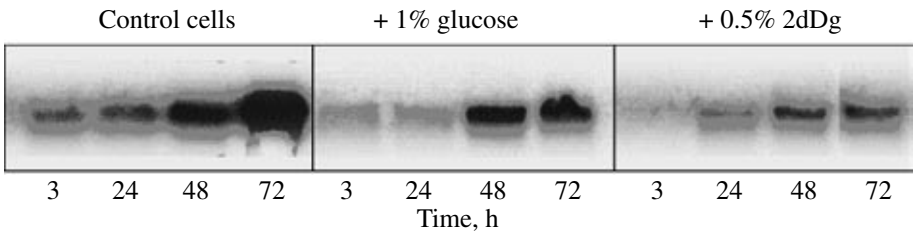

Fig. 2. Northern-blotting of *cpeBA* mRNA in *Calothrix* cells grown under green light and various conditions of culturing. Equal amounts of total cell mRNA (5 μg) were loaded into each electrophoretic well. Time of sampling after cell inoculation into growth medium containing glucose or 2dDg is indicated below blots.

glucose decreased PE content under both red and green light and increased PC content under red light.

Light control of the content of phycobiliproteins during CCA is exerted at the transcriptional level [6]. In higher plants and algae, glucose is known to control transcription as well [9, 11]. Therefore, the effects of glucose and 2dDg on CCA of cyanobacteria might manifest at the level of mRNAs encoding corresponding phycobiliproteins. It turned out that, under green light, autotrophic cells synthesized a great amount of *cpeBA* mRNA for polypeptide subunits of PE (Fig. 2), which was correlated with the abundance of PE in the cells under these light conditions (Table 1). Glucose and 2dDg suppressed *cpeBA* mRNA accumulation. The changes in the mRNA content became notable as soon as 3 h after the addition of these compounds to the growth medium. After 72 h of growth in the presence of these compounds, the amount of *cpeBA* mRNA was considerably lower than in control cells (Fig. 2), which evidently was the cause for the reduction of PE content in the cells in the presence of glucose.

CCA is most bright but not a solely aspect of the regulatory action of the light spectral composition in cyanobacteria. Green and red light affect *Calothrix* cell dimensions: under green light, cell length increases, and under red light, it reduces [4]. Our results supported these observations: under green light, *Calothrix* cells were 7–8 μm in length, whereas, under red light, their length did not exceed 6.5 μm (Table 2). Glucose and 2dDg also affected cell morphology. In the presence of these compounds, cell dimensions were reduced under both light regimes (Table 3). These changes occurred in parallel with the changes in the content of PE and PC in the cells.

Table 2. Dimensions (width × length, μm) of *Calothrix* cells grown under different growth conditions

Growth conditions	Green light	Red light
Autotrophy	4.5 × (7.0–8.0)	5.0 × (6.0–6.5)
+ 1% glucose	4.5 × (6.0–7.0)	5.0 × (5.0–6.0)
+ 0.5% 2dDg	4.5 × (5.5–6.5)	5.0 × (4.0–6.0)
Autotrophy[a]	5.0 × (8.0–10.0)	5.0 × 5.5

Note: Cell dimensions are mean values for 60 independent measurements. [a] Data of Bennett and Bogorad [4] for *F. diplosiphon*.

The action spectra of PSI and PSII of *Calothrix* cells contained bands characteristic of phycobiliproteins (Fig. 3). Under green light, the typical PE peak at 565 nm was present like in the absorption spectrum. Under red light, PC peak at 620 nm prevailed. Thus, phycobiliproteins fulfill functions of the pigment antenna during *Calothrix* growth under each light regime. As judged from the action spectra, the ratio of phycobiliproteins to chlorophyll was substantially lower in PSI than in PSII under both light regimes (Fig. 3). Light quality affected the ratio between two photosystems: under red light predominantly absorbed by PSI, the relative content of PSII increased twofold, which is explained by the demand of balanced light absorption by the two photosystems (Table 3). Under both red and green light, the content of the PSI active centers was not changed after transition of *Calothrix* cells to photoheterothrophic conditions since the presence of glucose in the growth medium does not affect PSI activity. However, glucose reduced the PSII activity and diminished the content of PSII active centers by 1–8 times. As distinct from glucose effect on pigments and cell morphology, it affected PSII immediately after its addition to the medium. 2dDg affected PSII activity much weaker than glucose. Under green light, 2dDg did not affect it at all (Table 3).

In general, the regulatory action of glucose on the ratio of PE to PC, the content of carotenoids, and *Calothrix* cell dimensions was similar to the effects of red light and opposite to the action of green light. 2dDg exerted similar action on these indices. However, glucose and red light effects on PSII activity were oppositely directed, and glucose and 2dDg effects on PSII differed substantially.

DISCUSSION

In this work, we demonstrated the regulatory action of glucose and its stereochemical analog on the development of CCA in cyanobacteria. We also confirmed some earlier found and some new effects of red and green light on CCA in cyanobacteria.

Electron microscopy shows that, under red light, phycobilisomes of *Calothrix* have an AP nucleus and three hexamers of PC in each side cylinders, but they do not contain PE. Under green light, each side cylinder comprises four hexamer disks of PE and one disk of PC. Thus, the molar ratios of pigments in phycobilisomes are 3 PC : 1 AP under red light and 4 PE : 1PC : 1AP under green light [20]. Our data on the content of phycobiliproteins in the *Calothrix* cells under red and green light are close to these values (Table 1). Thus, the changes in the phycobiliprotein content in the cells, we observed, are typical for the development of CCA. CCA manifested itself also in the total decrease in the content of photosynthetic pigments in the cells grown under red light as compared to cells grown under green light (Table 1).

These results are in good agreement with a 1.6-fold decrease in the chlorophyll level in *Calothrix* cells grown under red light as compared to control cells under white light, which has been observed earlier [4]. The autotrophic *Calothrix* cells adapted to red light were 1.2–1.4-fold shorter and more rounded than the cells grown under green light (Table 3). Similar changes have been earlier described for *F. diplosiphon* [4].

The action spectra of PSI and PSII of *Calothrix* cells contained distinct bands of phycobilisomes. In both PSI and PSII spectra, the PC peak prevailed in cyanobacteria grown under red light and the PE peak prevailed in cyanobacteria grown under green light, which corresponds to the changes in the band intensities of the absorption spectra and indicates that PE and PC are functionally active within the phycobilisomes. Structural chromatic adaptation of phycobilisomes, manifested in the changes of their pigment composition, was evidently accompanied by functional adaptation of these complexes. Another fact observed was a decrease in the content of carotenoids by approximately 15% under red light as compared to green light (Table 1). In intact *Calothrix* cells, this difference was masked by the partial overlapping of the PE and carotenoid bands (Fig. 1). The effect of light quality on the carotenoid content might be explained by a difference in the PSI/PSII ratio (Table 2) because it is known that the two photosystems differ in the content of carotenoids.

Most interesting result of this study is the involvement of glucose in the control of PE and PC syntheses. Glucose affected differently the content of the two pigments in phycobilisomes. Under green light, it decreased the content of PE; under red light, it increased the content of PC. Glucose stereochemical analog 2dDg acted similarly, indicating the regulatory role of hexoses in this process. These results are supported by the direct data on the accumulation of *cpeBA* mRNA. Light spectral composition is a principal factor of CCA, which determines the ratio of phycobiliproteins in the cells of cyanobacteria; glucose also changes their accumulation, although to a lesser degree (Fig. 1, Table 1). Under green light, we could not observe any regulation of PC synthesis by glucose because of mighty suppression of this synthesis by the light conditions. Regretfully, it is impossible to investigate the glucose regulatory action, which is not mediated by illumination. Like most facultative heterotrophic cyanobacteria, *Calothrix* strain used is only capable of "light-induced heterotrophic growth" [22] but cannot grow on glucose-containing medium in complete darkness [13].

Table 3. Relative content of the PSII reaction centers as estimated from light-induced O_2 evolution and PSI reaction centers as estimated from light-induced inhibition of respiration (in the presence of 10 μM diurone for suppression of PSII activity) in *Calothrix* cells grown under different growth conditions

Growth conditions	PSI	PSII	PSI/PSII
GL, autotrophy	1.0*	0.23	4.3
GL + 1% glucose	0.9	0.15	6.0
GL + 0.5% 2dDg	0.9	0.25	3.6
RL, autotrophy	0.85	0.4	2.1
RL + 1% glucose	1.1	0.05	20.0
RL + 0.5% 2dDg	1.0	0.22	4.5

* The content of PSI in cells grown autotrophically under green light was taken as 1.
GL—green light; RL—red light.

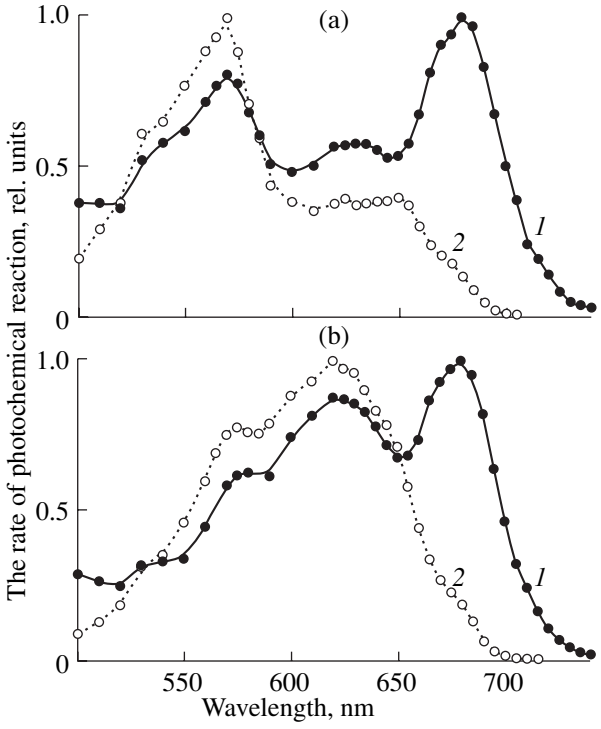

Fig. 3. Action spectra of chromatically adapted *Calothrix* cells grown under (a) green and (b) red light. (*1*) PSI action spectrum; (*2*) PSII action spectrum.

The results concerning glucose involvement in the CCA may seem contradictory since glucose oppositely affected the levels of PE and PC, i.e., glucose induced (PC) or repressed (PE) the synthesis of two homologous protein pigments with similar light-harvesting functions. However, a comparison of glucose and light effects shows that glucose acted like red light, which also induced PC and repressed PE synthesis. Both glucose and 2dDg affected carotenoid synthesis and cell morphology also like red light acted. *Calothrix* cell adaptation to light spectral composition and glucose is related to the occurrence of close or similar regulatory mechanisms. The work with *Calothrix* pigment mutants showed that CCA was under the control of at least three regulatory phosphorylable proteins, RcaE, RcaF, and RcaC [2, 22]. RcaE is a phytochrome-like protein functioning as a photoreceptor differently activated by green and red light. RcaC contains a DNA-binding domain, and RcaF is an intermediate in the photo- and phosphoregulatory chain. RcaF phosphorylation and activation can occur not only by phosphate transfer from RcaE but also from various other small donors of phosphate [22]. Such a model [22] suggests the simultaneous involvement of light and phosphorylated metabolites in the control of gene expression. Our data permit a supposition that glucose (glucose-6-phosphate to be more precise) functions as one of such phosphate donors, controlling CCA in the cells like red light. Glucose is evidently only one of possible phosphate donors involved in the CCA regulation. For example, when nitrate in the growth medium was replaced with ammonium, the latter reduced the content of PE and enhanced PC synthesis under white light, similarly as glucose or red light [19]. CCA is controlled by some other regulatory proteins with uncertain functions and position in the phosphorylation chain [7, 23]. The elaboration of their functions helps better understand the mechanism of glucose action in CCA. It is worth mentioning that the interaction between light and sugar action was observed also for the higher plant phytochrome system [8]. Changes in *Calothrix* cell morphology, which is under the control of numerous genes, indicate that CCA is only one of cell processes controlled by glucose in cyanobacteria.

Other interrelations between light, glucose, and its nonmetabolized analog were observed in photoheterotrophically grown *Calothrix* cells in relation to PSII inactivation (Table 2). As distinct from red light and 2dDg, glucose suppressed oxygen evolution. In photoheterotrophic culture of green alga *Chlorella*, PSII inactivation occurred similarly [24]. The most probably cause for the inhibition of photosynthesis by glucose is believed to be electron transfer from the respiratory chain to PSI, which reduces the electron flow from PSII [25]. It is especially difficult to separate various effects of glucose in cyanobacteria because, in these photosynthesizing organisms, photosynthesis and respiration have common regions of the electron-transport chain.

The effects of glucose accompanying photoheterotrophy of cyanobacteria are the manifestation of the endogenous regulation of the photosynthetic apparatus and physiological activity of actively growing cells. This is the difference between glucose control and the action of unfavorable environmental factors, such as mineral nutrition deficiency, extreme temperatures, or other stresses. We can speak about three types of glucose action on the cyanobacterial cell: (1) a well known glucose role as an energy source, which was not considered here; (2) the role of metabolite repressor or inducer of various genes, including those of the photosynthetic apparatus; and (3) glucose-induced inhibition of the primary photosynthetic processes, especially PSII activity, at the excess of carbohydrate metabolism products.

ACKNOWLEDGMENTS

The authors are grateful to Prof. Nicole Tandeau de Marsac for providing us with *Calothrix* sp. PCC 7601 strain and pPM64 plasmid containing the part of *cpeBA* gene.

The work was supported by the Russian Foundation for Basic Research, project nos. 01-04-49231, 01-04-48387, 03-04-49061, and 04-04-49407.

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