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Role of Protein Synthesis in Regulation of Phycobiliprotein mRNA Abundance by Light Quality in *Fremyella diplosiphon*[1]

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ABSTRACT

If green light-acclimated *Fremyella diplosiphon* cultures are transferred to red light, the transcription from the inducible phycocyanin gene set increases at least 30-fold within 60 minutes. This effect is inhibited completely by the protein synthesis inhibitors chloramphenicol and spectinomycin. Application of chloramphenicol 30 minutes after transfer of cultures to inductive red light prevents further phycocyanin mRNA accumulation within 10 minutes. If red light-acclimated cells are transferred to green light, the phycocyanin transcript level declines by about 70% within 1 hour. Most of the green light-dependent decline results from the rapid cessation of transcription from the PC gene set. Chloramphenicol slows the decline to some extent by decreasing the rate of mRNA degradation in a light-independent manner. The accumulation of phycoerythrin mRNA after transfer of red light-acclimated cells to green light is also inhibited by chloramphenicol. However, there is no red light-dependent mechanism that rapidly halts phycoerythin mRNA synthesis after transfer of cultures from green to red light. Therefore, at least three light-dependent processes are involved in regulating phycobiliprotein-gene expression: chloramphenicol-sensitive processes required for the activation of phycocyanin and phycoerythrin gene sets and a chloramphenicol-insensitive process which blocks phycocyanin mRNA synthesis after transfer of cells from red to green light.

The phycobilisome is the major light-harvesting complex of eukaryotic red algae and procaryotic cyanobacteria (1, 6–8). It is composed of two domains: the core, which is attached to the thylakoid membranes and includes the major biliprotein AP,[2] and the rods, which are associated with the core and contain either PC alone or PC and PE. Some cyanobacteria, such as *Fremyella diplosiphon,* alter the components of their phycobilisomes in response to changes in the wavelengths of light in their environment, a phenomenon termed complementary chromatic adaptation (1). R promotes PC synthesis while G promotes PE synthesis (1). Using gene-specific DNA fragments as hybridization probes, we have previously shown that transcripts encoding PC are barely detectable in G- and very abundant in R-grown cells, while the level of PE mRNA is high in G- and low in R-grown cells (11). Although both transcript levels increased rapidly upon exposure of cells to inductive illumination, only PC mRNA decreased rapidly (*i.e.* nondetectable within 2 h) after transfer of cultures to noninductive light. The PE transcript level declined relatively slowly and was reduced by only 50% even 16 h after the transfer of the cultures from G to R. Since the half-lives of the PC and PE transcripts are between 10 and 30 min and independent of R and G (11), changes in the steady state levels of these mRNAs are controlled by the rate of transcription.

Although it is unknown whether the PE and PC gene sets are controlled by a positive or negative regulatory element, the gradual decline in the level of PE mRNA after switching cultures from G to R may result from the dilution of a relatively stable cellular factor important in promoting expression from the PE gene set (11). The more rapid decline in the rate of transcription from the inducible PC gene set suggests that control is either by a negative regulatory element which becomes effective after the cells are transferred from R to G or a positive regulatory element that is unstable in G. We have analyzed the effect of CAP, an inhibitor of protein synthesis on 70S ribosomes, on phycobiliprotein gene expression. The results are consistent with both the hypothesis that transcription from the PC and PE gene sets are controlled by different positive regulatory elements and with the hypothesis that both elements are relatively stable under inductive light conditions. The rapid decline in the transcription of the PC gene set after transfer the cultures from R to G appears to be caused by a third, G-dependent mechanism which is not sensitive to CAP. This G-dependent process may cause a rapid inactivation (either via degradation or modification) of the positive regulatory element.

MATERIALS AND METHODS

Growth Conditions

Fremyella diplosiphon (Calothrix sp., PCC 7601), a subculture of UTEX No. 481, was grown for 5 d at 32°C in 40 mL of BG-11 medium (9) in an atmosphere of 3% CO_2 in air. Cultures were illuminated with 15 μmol m^{-2} s^{-1} of R or G. The light conditions have previously been described (11).

Hybridization of DNA Fragments Encoding Phycobiliproteins to RNA

The gene-specific DNA fragments used for these experiments (a 3.7 kb *Hin*dIII fragment encoding the inducible PC

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[2] Abbreviations: AP, allophycocyanin; bp, base pair; kb, kilobase pair; G, green light; PC, red-light inducible phycocyanin; PE, phycoerythrin; R, red light; CAP, chloramphenicol; SPEC, spectinomycin.

subunits, a 294 bp *Xba*I fragment encoding the PE subunits, and a 693 bp *Pst*I fragment encoding the AP subunits) have been described previously (11). RNA was isolated from the cells (4) and either resolved by electrophoresis on a 1.5% agarose gel under denaturing conditions and transferred to nitrocellulose or directly bound to nitrocellulose paper for slot blot hybridizations (4, 5, 11). The 3.7 kb *Hin*dIII fragment was hydrolyzed to 400 to 800 bp by boiling in 0.5 M NaOH for 5 min and neutralized before use. Hybridizations were performed at 67°C (15–18 h, 10^4 Cerenkov counts/slot) in 0.5 M NaCl, 0.1 M NaH_2PO_4, 0.1 M Tris, 2 mM EDTA, 0.1% SDS. Filters were washed three times (10 min each) in 0.01 M phosphate buffer (pH 7) 0.02 M EDTA, 0.1% SDS at room temperature and once at 67°C for 2 min with the same buffer except that the phosphate concentration was 0.05 M, and exposed to Kodak XAR-5 film (−80°C, 3–8 h). Under these conditions the PE-specific probe hybridizes to an mRNA of 1500 bases, the AP-specific probe to a predominant mRNA of 1400 bases (11), and the PC-specific probe to an predominant mRNA of about 1600 bases and a minor species of 3800 bases (see Fig. 2).

Application of Inhibitors

Cells were grown to midexponential phase in either R or G (A_{650} = 0.8–1.0). CAP was dissolved in ethanol and spectinomycin in water, both at concentrations of 100 μg/mL. R- and G-acclimated cultures were placed in either the same light in which they were grown, or complementary light 5 min after the addition of the protein synthesis inhibitors. For experiments shown in Figures 3 to 7, 10 μg CAP/mL culture medium was used.

Determination of Protein Synthesis

Counts of 10^7 of [^{35}S]sulfate were applied to growing cells 5 min after the application of protein synthesis inhibitors. The cells were incubated for 30 min and aliquots were removed, placed in two volumes of TCA (25%, w/v) to precipitate protein, vortexed, and kept on ice for 1 h. Precipitated protein was collected on a Whatman GF/C-filter and washed with five volumes of 8% TCA prior to liquid scintillation counting. Application of rifampicin (RIF, 50 μg/mL culture medium) was performed as described previously (11).

From two to five independent experiments were used to obtain the data presented in the figures (for details see ref. 11).

RESULTS

Effect of CAP and SPEC on Protein Synthesis

Figure 1 shows that both CAP (■) and SPEC (♦), inhibitors of protein synthesis on 70S ribosomes (3), prevent the incorporation of [^{35}S]sulfate into TCA-precipitable material in a dose-dependent manner. Ten μg/mL culture medium of CAP and 30 μg/mL culture medium of SPEC reduce the incorporation of radioactivity into TCA precipitable material by about 90%. For these concentrations the incorporation of [^{35}S]sulfate into protein is almost fully restored if the cultures are washed with inhibitor-free medium (Fig. 1, □ and ◇).

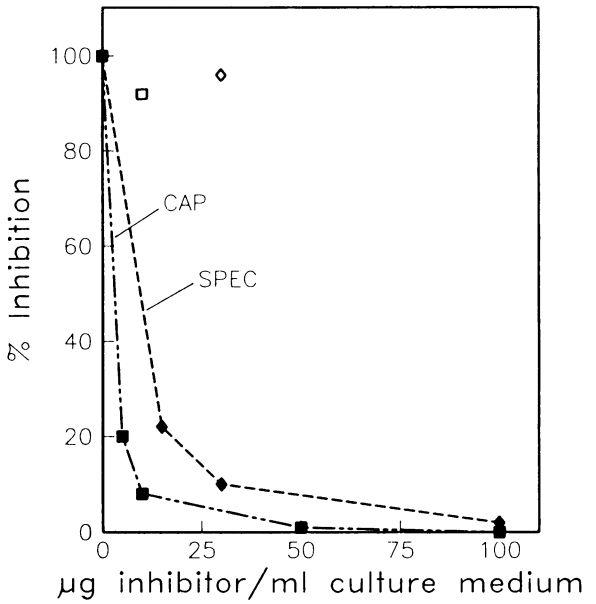

Figure 1. Dose-response relationship of the effect of CAP (■) and SPEC (♦) on the incorporation of [^{35}S]sulfate into TCA precipitable material. The protein synthesis inhibitors were added to the cultures 5 min prior to the addition of 10^7 cpm of [^{35}S]sulfate. After a 30-min incubation, incorporation of radioactivity into TCA-precipitable material was determined as described in "Materials and Methods." The data are expressed as percent of the incorporation of radioactivity in inhibitor-free control cells (between 1–5 × 10^4 counts). Cells were incubated with CAP (□) or SPEC (◇) for 1 h and washed three times with inhibitor-free growth medium before determination of incorporation of radioactivity into TCA precipitable material.

Effect of Protein Synthesis Inhibitors on PC-mRNA induction

In agreement with previous observations (11), little PC mRNA is detectable in G-acclimated *Fremyella diplosiphon* cultures while in R-acclimated cultures the PC-mRNA level is high (Fig. 2, lanes 1 and 2). After transfer of G-acclimated cells to 1 h of R the PC-mRNA level increases rapidly (Fig. 2, lane 3). The inductive effect of R on the PC-mRNA level is almost completely inhibited if 5 μg/mL CAP is included in the medium 5 min prior to the transfer of cultures to 1 h of R (Fig. 2, lane 4). Complete inhibition is achieved with 10 μg CAP/mL culture medium (Fig. 2, lane 5). At 30 μg/mL culture medium, SPEC also prevents PC-mRNA induction by R (Fig. 2, lane 6). Since both inhibitors at low levels prevent the accumulation of PC mRNA in R, and the inducibility is reestablished if cells treated for 1 h with 10 μg/mL and 30 μg/mL CAP or SPEC, respectively, are washed under a G safelight with inhibitor-free growth medium prior to transfer to R (Table I), PC-mRNA synthesis in R probably requires protein synthesis.

The effect of 10 μg/mL CAP on PC, PE, and AP transcript levels has been analyzed quantitatively by slot blot hybridizations (Fig. 3). Cells were either grown in R or G or transferred from R to 1 h of G (R + G) or from G to 1 h of R (G + R). For the results in Figure 3 labeled (+CAP), CAP was added to the medium 65 min before the isolation of RNA (5 min before shifting light conditions). A more detailed time

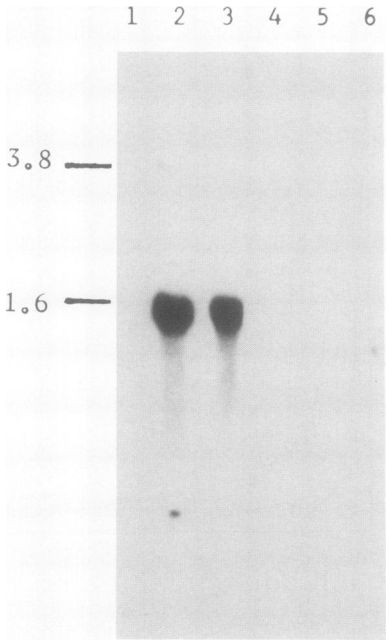

Figure 2. Hybridization of a 3.7 kb *Hin*dIII fragment encoding the inducible PC gene set to RNA from *F. diplosiphon* cells grown in G (lane 1) or R (lane 2) or G-acclimated cells transferred to R for 1 h (lanes 3–6). Five min prior to the transfer the cells received no inhibitor (lane 3, control), 5 μg/mL CAP (lane 4), 10 μg/mL CAP (lane 5), or 30 μg/mL culture medium SPEC (lane 6). Equal amounts of RNA (5 μg) were separated on denaturing agarose gels (5). Sizes of the hybridizing RNA species, in kb, are given to the left. The 1600-base transcript encodes the β and α subunit of PC and the 3800-base transcript encode the PC subunits plus 3 linker polypeptides (10).

Table I. *Reversibility of CAP and SPEC Treatments on the Induction of PC-mRNA*

G-Acclimated cells received CAP (10 μg/mL) or SPEC (30 μg/mL) for 1 h. After this incubation the cells were washed three times with inhibitor-free growth medium and transferred back to G for 2 h (G) or to 1 h of G followed by 1 h of R (R). Control: Cells which were treated in the same way except that they did not receive CAP or SPEC. Quantitations, as described in legend to Figure 4, were done using RNA from two independent extractions. The highest value of this set of experiments was taken as 100%.

Inhibitor	Light Conditions after Removal of Inhibitor	Relative Amount of PC-mRNA
		%
CAP-treated	G	4
	R	100
SPEC-treated	G	2
	R	82
Control (without CAP)	G	3
	R	94

course based on densitometrical scanning of autoradiograms similar to those shown in Figure 3 is presented in Figure 4. These results lead to three conclusions: (a) The PC transcript level in R-grown cells and the PE transcript level in G-grown cells are not affected for at least 65 min by CAP. (b) Both the accumulation of PC mRNA in 1 h of R and the accumulation of PE mRNA in 1 h of G are completely blocked by CAP. (c)

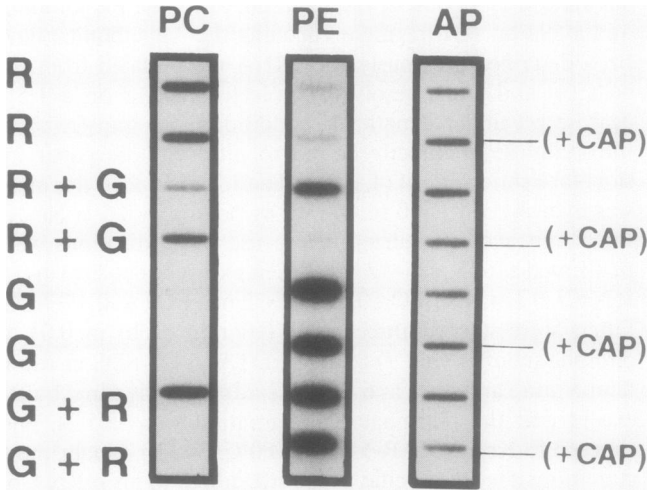

Figure 3. Slot blot hybridization of RNA (5 μg in each slot) to a 3.7 kb *Hin*dIII fragment encoding PC, a 294 bp *Xba*I fragment encoding PE, and a 693 bp *Pst*I fragment encoding AP. Cells were either grown in R (R) or in G (G), or R-acclimated cells were transferred to G for 1 h (R + G) and G-acclimated cells to R for 1 h (G + R). For the slots labeled (+CAP), 10 μg/mL CAP was added to the growth medium 65 min before isolating RNA.

Neither R nor G, in the presence or absence of CAP 1 h prior to RNA isolation, affects AP transcript levels. These results suggest that only the *de novo* accumulation of PC and PE transcripts is prevented if protein synthesis is blocked. Transcript levels established prior to CAP application are relatively unaffected.

This conclusion was confirmed by the results of the experiment shown in Figure 5. If CAP is applied 30 min after the transfer of G-acclimated cells to R, further accumulation of PC mRNA is inhibited within 10 min and the PC mRNA level remains stable thereafter.

Effect of CAP on PC and PE mRNA Decay after Transfer of *F. diplosiphon* Cultures to Noninductive Light Conditions

The high PC mRNA level drops rapidly after transfer of cultures from R to noninductive G (Fig. 3; Fig. 4 upper panel; for details see ref. 11). Application of CAP 5 min prior to the transfer from R to G does not prevent the PC mRNA disappearance, but leads to a significant reduction in the rate of its decay. By contrast, little decay of PE mRNA can be detected within 1 h after the transfer of G-acclimated cells to R, and the PE transcript levels are not significantly affected by CAP (Figs. 3 and 4, lower panel).

Effect of CAP on PC mRNA Degradation

To investigate whether the alleviating effect of CAP on PC mRNA decay after transfer of R-acclimated cells to G is the consequence of a decrease in the rate of PC mRNA degradation or the maintenance of a high rate of PC mRNA synthesis, we have determined the rate of mRNA degradation in the presence and absence of CAP. The background for this experiment has been described previously (11): the application

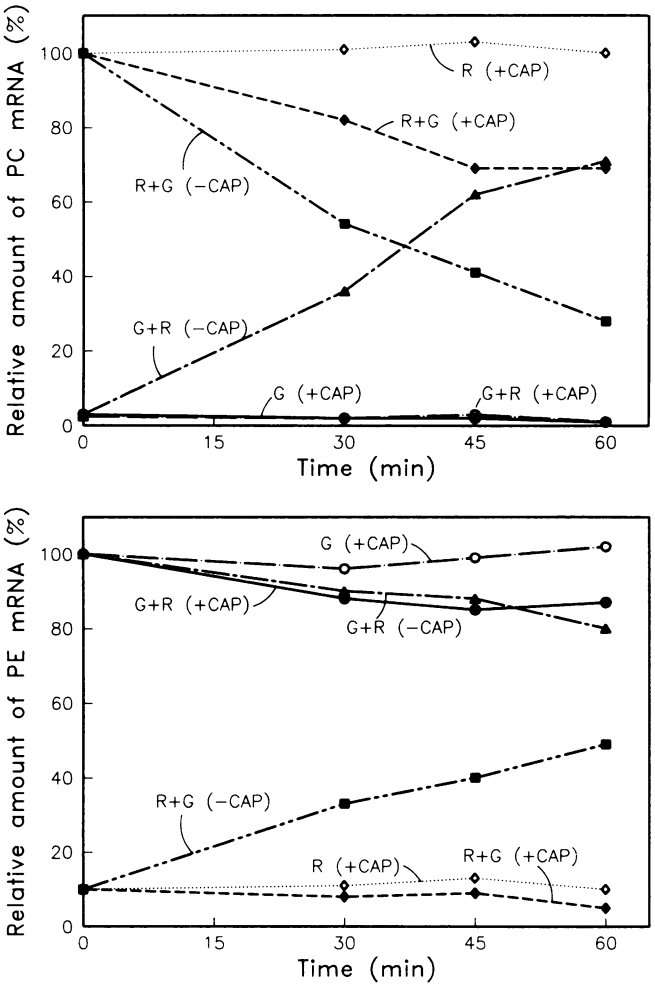

Figure 4. Upper panel, Time course for the relative amount of PC mRNA based on three independent RNA extractions and slot blot hybridizations. Cells were either grown in R or G, or R-acclimated cells were transferred to G (R + G) and G-acclimated cells to R (G + R) at 0 time. (+CAP), Cultures received CAP (10 μg/mL culture medium) 5 min prior to the onset of the time course, *i.e.* at −5 min; (−CAP); no CAP added. The hybridization signals obtained by autoradiography were quantitated with a scanning densitometer (Hoefer Scientific Instruments, USA). The level of PC mRNA in R-acclimated cells at time 0 (operationally the signal obtained by scanning the autoradiogram) was taken as 100% and all other levels are expressed with reference to this value. Lower panel, Similar to upper panel, but PE mRNA was quantitated. The same RNA samples used for the quantitation of PC mRNA were used. The PE-mRNA level in G at time 0 was taken as 100%. Variation in the data was between 2 and 17%.

of rifampicin, which blocks mRNA synthesis in *F. diplosiphon,* allows us to directly measure the rate of degradation of PC mRNA. Figure 6 shows the levels of PC mRNA between 0 and 45 min after rifampicin application. If CAP is included in the culture medium 20 min prior to rifampicin application (◇), a significant reduction in the rate of PC-mRNA degradation is observed. Moreover, no significant differences in the rates of PC-mRNA degradation can be detected between cultures that were kept in R (upper panel) and cultures that were transferred from R to G 20 min prior to rifampicin

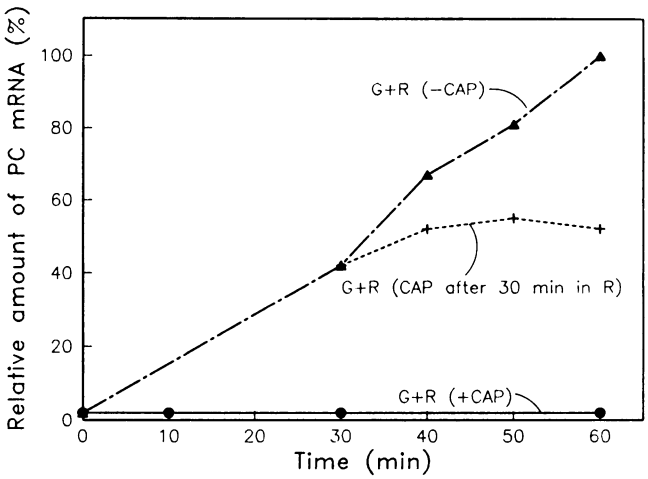

Figure 5. Relative amounts of PC mRNA after transfer of G-acclimated *F. diplosiphon* cells to R. (●), Cultures which received CAP (10 μg/mL) 5 min prior to transfer to R; (+), CAP was applied 30 min after transfer to R; (▲), no CAP applied. The highest mRNA level (the level detectable in G-acclimated cultures which were transferred to R for 1 h without inhibitor) was taken as 100%. Results are based on three different RNA extractions, variation in the data was between 6 and 14%.

application (lower panel). Under both light conditions CAP causes an increase in the half-life of PC mRNA from between 13 and 15 min to approximately 20 to 23 min (see legend of Fig. 6). Thus, application of CAP reduces the rate of PC mRNA degradation in a light-independent manner.

Effect of CAP on PC mRNA Synthesis

On the basis of the steady state PC mRNA levels shown in Figure 4 (upper panel) and the decay of PC mRNA presented in Figure 6, the rate of PC mRNA synthesis can be calculated (for details see ref. 11). Figure 7 shows that PC mRNA synthesis increases rapidly after transfer of G-acclimated cells to R (■). This increase is completely prevented if CAP is included in the growing medium 5 min prior to transfer of the cells to inductive R (◆). The rate of PC mRNA synthesis in R-acclimated cells (□, taken as 100%) is slightly reduced in the presence of CAP (◇). After 30 min of incubation with CAP, 88% of the control level of PC mRNA synthesis still occurs. In contrast, a rapid decrease in the rate of PC mRNA synthesis is observed after transfer of R-acclimated cells to G in the presence or absence of CAP (compare ○ and △). Therefore, a CAP-insensitive, G-dependent process has to be responsible for depressing transcription from the inducible PC gene set.

DISCUSSION

Even though we do not know at present the exact mechanism by which CAP affects PC and PE mRNA synthesis, the data presented here allow several conclusions with regard to the regulation of phycobiliprotein transcripts in R and G.

(a) *De novo* induction of PE mRNA synthesis by G and PC mRNA synthesis by R is inhibited in the presence of CAP. This is consistent with the hypothesis that a positive regulatory

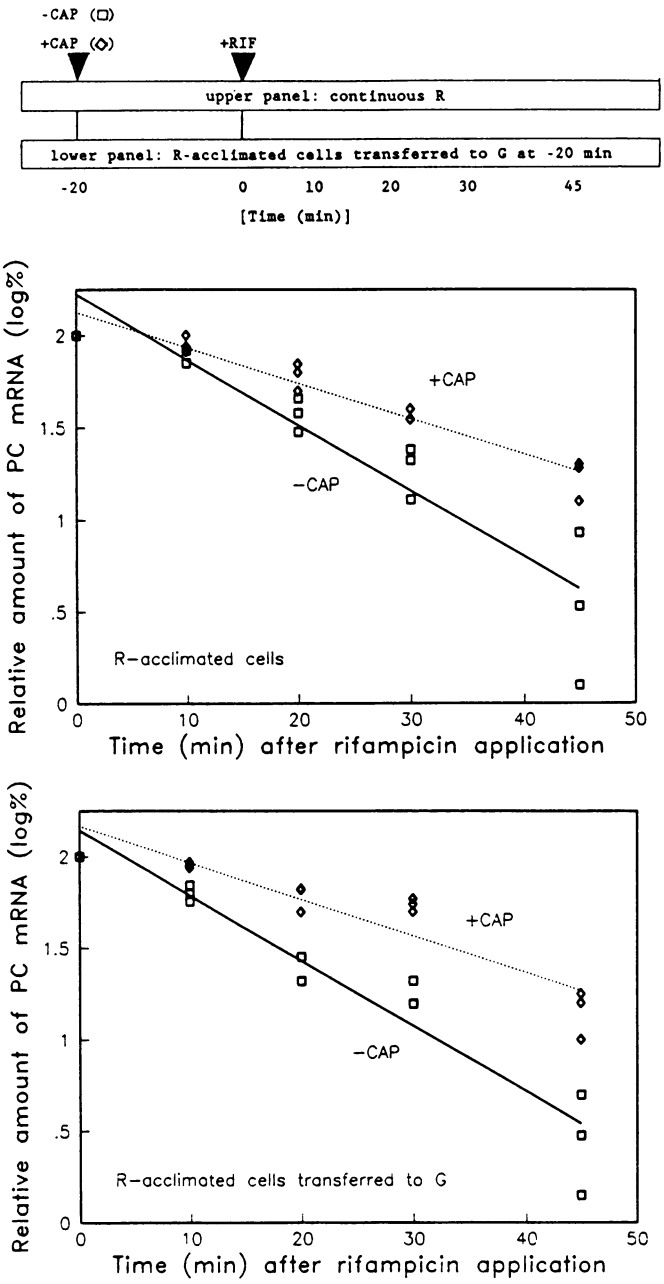

Figure 6. Effect of CAP (10 μg/mL) on PC-mRNA degradation. The diagram on top of the figure represents a time scale and shows the sequence of inhibitor applications and light treatments. Upper panel, R-acclimated cells received rifampicin (50 μg/mL) at time point 0 and the PC-mRNA levels were determined over the next 45 min. For the data labeled +CAP, CAP was added to the growth medium 20 min prior to rifampicin application. The amount of PC mRNA detectable at time 0 was taken as 100% and all other values expressed with reference to this value. Lower panel, the same protocol as described for the upper panel, except that the cultures were transferred from R to G at the time of CAP application. To show the variation in the data all of the measurement are shown in the graph. Probabilities of the regression lines between 0.81 and 0.93, $t_{1/2}$ values as calculated from the slopes are: upper panel: −CAP (15 min), +CAP (23 min); lower panel: −CAP (13 min), +CAP (22 min).

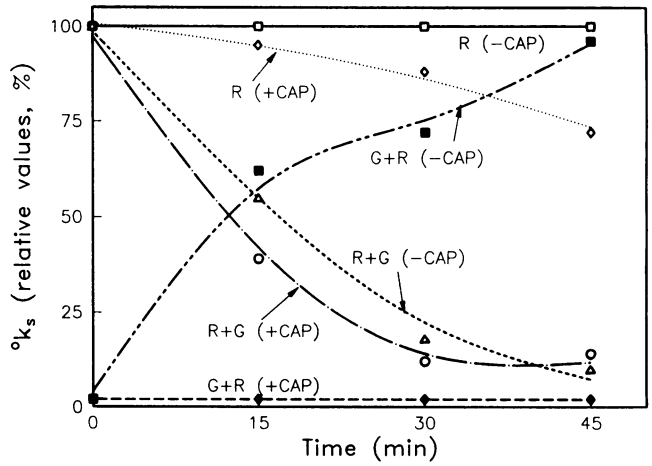

Figure 7. Estimations of the rate of PC mRNA synthesis [operationally $^{o}k_s$ (t)] in R and after transfer of R-acclimated cells to G (R + G) and vice versa (G + R) as affected by CAP. The data are based on the results of Figures 4 (upper panel) and 6. The rate of PC mRNA synthesis in R-acclimated cells was taken as 100% and all other values expressed with reference to that. (+CAP), CAP at 10 μg/mL culture medium final concentration was added to the cultures 5 min prior to the first measurement; (−CAP), control cultures with no inhibitor. These estimations are based on the equation

$$^{o}k_s\,(t) = d(\text{mRNA})\,(t)/dt + {}^{1}k_d\,(\text{mRNA})\,(t),$$

where $^{o}k_s(t)$ is the zero-order rate constant of synthesis at time t and $^{1}k_d$ the first order rate constant of degradation at time t. For details see Oelmüller *et al.* (11).

element is required for the transcription of the PE and PC gene sets. Since accumulation of PC mRNA is inhibited almost immediately if CAP is included in the growth medium 30 min after transfer of the cells to R (Fig. 5), PC mRNA accumulation may be limited by the amount of this regulatory element until the maximum rate of PC mRNA synthesis is achieved. Once synthesized, these postulated regulatory elements may be fairly stable (over at least 60 min) since the PC and PE mRNA levels, in *Fremyella diplosiphon* maintained under inductive light conditions, are not detectably affected by CAP (Figs. 3 and 4) and the calculated rate of PC mRNA synthesis declines only 12% within 30 min after its application (Fig. 7).

(b) The rate of PC mRNA synthesis drops rapidly after transfer of R-acclimated cells to G (reduction of more than 75% within 30 min, see Fig. 7). This decline occurs in the presence or absence of CAP demonstrating that a CAP-insensitive, G-light dependent process is responsible.

(c) A mechanism which rapidly blocks PE mRNA synthesis after transfer of *F. diplosiphon* cells from G to R (analogous to that found for the PC mRNA on transfer from R to G) seems to be absent. The PE transcript level decreases only slowly and is not affected by CAP. Thus, the postulated positive regulatory element required for PE mRNA induction is relatively stable (at least over 60 min) in G and after transfer of cultures from G to R (Figs. 3 and 4, lower panel). The decay in transcription from the PE gene set appears to follow the cell generation time, suggesting that the regulatory element is diluted out during growth (11).

(d) It has been suggested that a photoreversible photosystem(s) similar to phytochrome is involved in controlling phycobiliprotein transcript accumulation (1, 8, 12). The data shown here make it unlikely that a single intermediate in the signal-transduction chain (between the perception of light and an alteration in the rate of gene expression) can act as an inducer for the PE gene set and a repressor for the PC gene set. For example, while induction of PE mRNA synthesis after transfer of the cultures from R to G is sensitive to CAP, the accompanying inhibition of PC mRNA synthesis is insensitive to CAP. Furthermore, mutants that regulate PC normally but cannot regulate PE (and vice versa) have recently been isolated and characterized (2).

Thus, at least three light-dependent mechanisms must be involved in the regulation of phycobiliprotein gene expression during chromatic adaptation: two CAP-sensitive processes that are required for transcription of the PC and PE gene sets and one CAP-insensitive process which rapidly depresses transcription from the PC gene set in G.

The data shown in Figure 6 indicate that inhibition of protein synthesis by CAP leads to a significant shift in the half-life of the PC-mRNA (from about 13–15 min in the absence of CAP to 20–23 min in the presence of CAP; see legend of Fig. 6). This shift is the same for cultures kept in R and those transferred from R to G at the time of CAP application. We do not known at present whether this is a specific effect on PC transcripts or whether it reflects a general reduction in the degradation of cellular RNA. However, the data make it very unlikely that a specific protein synthesized after the shift to G is involved in PC mRNA degradation. If a specific G-induced ribonuclease were synthesized soon after the switch from R to G, the half-life of the PC mRNA would be shorter after a 20 min preincubation in G than in R. This is not the case; pretreatment with R or G did not affect the half-life of the mRNA. Treatment with CAP did increase the half-life of the mRNA, but this effect was independent of the light quality used during the pretreatment, suggesting that the inhibitor reduces the rate of transcript turnover in a general rather than a specific manner. These results together with previous observations (11) argue that light-regulated changes in the level of phycobiliprotein transcripts are exclusively mediated by changes in the rate of transcription.

The main conclusions from results presented here are that at least three different light-dependent processes, two CAP sensitive and one CAP insensitive, are involved in controlling chromatic adaptation in *F. diplosiphon.* CAP sensitivity suggests that protein synthesis is required for at least two of the processes. Unspecific effects of the inhibitors are unlikely for several reasons. (a) The CAP concentration (10 μg/mL culture medium) is low and PC mRNA induction by R is reestablished if the inhibitor is washed from the cells (Table I). (b) Other inhibitors of protein synthesis such as SPEC also prevent the accumulation of PC and PE transcripts under inductive conditions. (c) CAP treatment for 1 h has little effect on the levels of PC and PE mRNAs if the cultures were maintained continuously in inductive illumination. (d) Finally, CAP has little effect, over a period of 1 h, on the level of AP mRNA in cultures maintained in either R or G.

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