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Photoreversible absorbance changes in solutions of allophycocyanin purified from *Fremyella diplosiphon*: Temperature dependence and quantum efficiency

(phycobilins/blue-green algae/chromatic adaptation/photochromism)

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ABSTRACT **Preparations of allophycocyanin isolated from the alga *Fremyella diplosiphon* show light-induced optical absorbance changes that suggest the presence of a photoconvertible component**

$$\left(P_r \underset{\text{green light}}{\overset{\text{red light}}{\rightleftharpoons}} P_g\right)$$

similar to the algal pigments described by J. Scheibe [(1972) *Science* 176, 1037–1039]. At pH < 4 the allophycocyanin has an absorption maximum at 620 nm. Red illumination causes a loss of absorbance in the red, centered at 620 nm, and subsequent green illumination restores the lost absorbance. We have studied this photoconversion at temperatures between 200 K and 307 K, analyzing the results in terms of photostationary states established under red (640 nm) and green (550 nm) light. As the temperature was lowered to 260 K, the state P_r became progressively favored; the reaction $P_r \rightarrow P_g$ induced by red light was attenuated but the reaction $P_g \rightarrow P_r$ induced by green light was not. Decreasing the temperature from 260 K to 200 K had no further effect. Two distinct and simple models can account for this curious temperature dependence. By analyzing the kinetic and steady-state data, with reasonable estimates of the molar extinction coefficients of P_r and P_g, we computed quantum efficiencies greater than 15% for the photoconversion at 300 K. We deduced that a conversion of "all P_r" to "all P_g" should produce a fractional absorbance change $\Delta A/A$ at 620 nm equal to 0.1. If the chromatic adaptation response of intact *F. diplosiphon* shows the unusual temperature dependence reported here, the system $P_r \rightleftharpoons P_g$ will be implicated in mediating this response.

Fractions extracted from a variety of algae contain photoconvertible pigments (P) such that exposure to red light induces a loss of absorbance in the red, often near 650 nm, and exposure to green light restores this absorbance (1–4):

$$P_r \underset{\text{green light}}{\overset{\text{red light}}{\rightleftharpoons}} P_g,$$

in which P_r has the greater absorbance in the red. These pigments have received the generic name "phycochromes," perhaps suggested by the photoconvertible phytochromes of higher plants.

Some blue-green and red algae exhibit chromatic adaptation (5–7). When grown in green light they synthesize the phycobiliproteins phycoerythrin, phycocyanin, and allophycocyanin (APC). When grown in red light they cease making phycoerythrin and accumulate relatively more phycocyanin and APC. It is not known whether the phycochromes are involved in mediating this chromatic adaptation response.

Ohad *et al.* (4), studying extracts of the alga *Fremyella diplosiphon*, found the photoconvertible absorbance change $P_r \rightleftharpoons P_g$ in fractions that contained the phycobiliproteins. This activity was abolished by antisera that precipitated APC selectively, but not by antisera specific toward phycoerythrin or phycocyanin. The activity was present in purified APC fractions, and the spectrum of the absorbance change was like the absorbance spectrum of APC. This spectral correspondence persisted when the pH was changed; both the absorbance and the light-induced change showed a maximum at 620 nm at pH $\leq$ 4, shifting to 650 nm at pH 7. In purified APC solutions the light-induced change of absorbance did not exceed about 2% of the total absorbance, suggesting that a minor component in the preparation, perhaps a special configuration or state of aggregation of APC, was photoconvertible between the states P_r and P_g. In less highly purified fractions of phycobiliproteins the light-induced change in the red was usually accompanied by a smaller complementary (reverse) change near 520 nm. The magnitude of the change near 520 nm was variable; it could be dissociated from the main effect in the red as exhibited by purified APC.

This report describes the temperature dependence of the photoconversion $P_g \rightleftharpoons P_r$ in solutions of APC purified from *F. diplosiphon*. We have found that the reaction induced by red light,

$$P_r \xrightarrow{\text{red light}} P_g,$$

is inhibited as the temperature is lowered from 300 K to about 260 K, whereas the reverse reaction,

$$P_g \xrightarrow{\text{green light}} P_r,$$

is not inhibited at temperatures down to 200 K. We found no evidence for transient intermediates that might have been stabilized at low temperature. From the kinetics of these reactions, analyzed in terms of transitions between photostationary states, we estimate a quantum efficiency greater than 15% for the interconversion in each direction at 300 K. We present two alternative models that can account for the unusual temperature dependence of $P_r \rightleftharpoons P_g$. If this photoconvertible system mediates chromatic adaptation, a similar unusual temperature dependence might be found for the induction of the chromatic adaptation response in living cells of *F. diplosiphon*.

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Abbreviations: P, photoconvertible pigment; APC, allophycocyanin.

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MATERIALS AND METHODS

F. diplosiphon cells were grown as described by Bennet and Bogorad (8). The cells were harvested by centrifugation and stored at −20°C until use. Extracts containing the phycobiliproteins were prepared by sonication of cells suspended in distilled water (three times for 15 sec each, Branson Sonifier, with microtip operated at 100 W at 0°C). The homogenate was centrifuged at 81,000 × *g* for 60 min. The supernatant was dialyzed against distilled water overnight and then used for isolation of APC by the method described by Bennet and Bogorad (8). The purified APC dissolved in distilled water was diluted with glycerol (final concentration 60% vol/vol), and the pH was adjusted to 3.8 by adding acetic acid. A flocculent blue precipitate exhibiting absorption bands at both 620 and 650 nm was removed by centrifugation. All of the photochemical activity was retained in the supernatant, which showed an absorption maximum at 620 nm but no perceptible band at 650 nm (Fig. 1). At pH 6.5–7.0 this fraction showed a main absorption peak at 650 nm, as described before (4).

The material prepared as described above, at pH 3.8, was used in all the experiments described here. The photochemical activity of a sample declined slowly over several days; this was taken into account when correlating the data of experiments made on different days.

Absorbance spectra and light-induced difference spectra were measured with a home-made split-beam spectrometer (9) in conjunction with a Tracor–Northern (Middletown, WI) TN-1500 signal averager. Some absorbance spectra were also measured with a Cary 14R spectrophotometer. For control of temperature the samples were mounted in the optical chamber of a helium refrigerator (Cryogenics Technology, Inc., Waltham, MA). Actinic light from a 600-W tungsten/iodine lamp passed through 2.5 cm of water and an interference filter, either 550 or 640 nm, of about 20-nm band width. The intensity of the actinic light at the sample was 2.6 mW/cm^2 (0.72 × 10^{16} quanta/cm^2 sec) at 550 nm (green filter) and 4.7 mW/cm^2 (1.50 × 10^{16} quanta/cm^2 sec) at 640 nm (red filter). In every experiment except those shown in Fig. 4 we used a standard exposure of 45 sec with either the red or the green filter. This was sufficient to produce a maximal effect.

RESULTS

The absorbance spectrum of a sample of APC at 300 K and the change in absorbance induced by red light (640 nm, 45 sec) after prior exposure to green light are shown in Fig. 1. In the range 400–750 nm the light-induced difference spectrum showed no features other than the bleaching of a band centered at 620 nm. Subsequent exposure to green light (550 nm, 45 sec) exactly nullified the change induced by red light.

We explored the temperature dependence of the photoconversion of the pigment with various illumination programs. In our first protocol (○ in Fig. 2) the sample was given green light, then red, then green, at 300 K. The temperature was then brought to a different value and the green, red, green sequence was repeated. At each temperature we recorded the absorbance change induced by red after green, and verified that this change was reversed by green after red. In a variation of this protocol (● in Fig. 2) we exposed the sample to green light at 300 K, then brought it to a new temperature in the dark, and then exposed it to the green, red, green sequence. We recorded the absorbance changes induced by each exposure, and (as expected) found that the first exposure to green light at any temperature, following green at 300 K, caused no change. The extent of the reversible absorbance change, shown in Fig. 2, declined strongly with falling temperature between 307 K and 270 K, and was

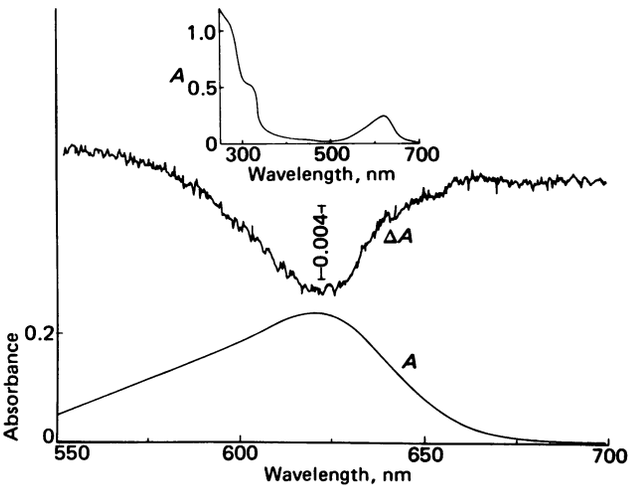

FIG. 1. Absorbance spectrum of a solution of APC purified from *F. diplosiphon* (lower curve) and the spectrum of the absorbance change induced by red (640 nm) light at 300 K (upper curve). (*Inset*) Absorbance spectrum at shorter wavelengths as well. This change is attributed to the conversion of a component of APC from a state P_r to a state P_g. Details of the preparation and actinic illumination are in the text. APC in glycerol/H_2O (60/40, vol/vol) adjusted to pH 3.8 with acetic acid.

then constant down to 200 K. Thus, there appeared to be a temperature-independent component underlying a temperature-sensitive one. For the latter, an Arrhenius plot gave a pseudo-activation energy of 6 kcal/mol (1 cal = 4.184 J). In these data about 10% of the absorbance change at low temperature (240 K) might be discounted as due to greater absorption band intensity, judging from the change of the absorbance spectrum with temperature.

The foregoing protocols measured the reversible absorbance

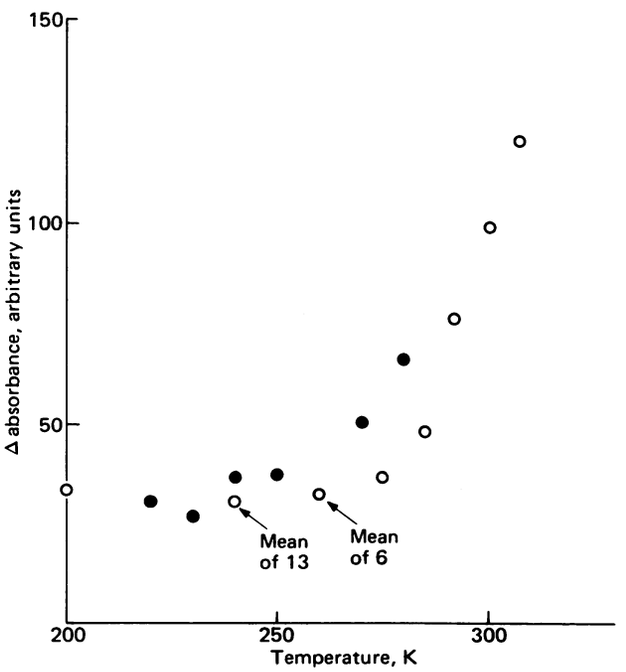

FIG. 2. Temperature dependence of the reversible photoconversion in a preparation of APC purified from *F. diplosiphon*, as measured by the change of absorbance at 620 nm. Two experimental protocols using alternate red and green actinic light are described in the text; ○ and ● pertain to the first and second of these protocols, respectively.

change attending the $P_g \rightleftharpoons P_r$ interconversion. The temperature dependence of Fig. 2 reflects correctly the variation of $P_r \rightarrow P_g$ (the reaction to red light) with temperature, but we found that the reverse reaction, induced by green light, is not suppressed by lowering the temperature. We exposed the sample to red light at 300 K, cooled it in the dark to 240 K, recorded its absorbance spectrum again, and then exposed it to green light. The resulting absorbance change was as great as the response to green light at 300 K, as shown in Fig. 3, spectrum a (compare Fig. 1). Subsequent red illumination at 240 K gave only the small red light response expected at that temperature from Fig. 2. In a complementary experiment, with exposure to green light at 300 K followed by cooling in darkness to 240 K, we found only small responses on successive exposures to red, green, and red light (Fig. 3, spectrum b).

Results of some control experiments were as follows: We gave green light at 300 K and cooled to 240 K, then exposed the sample to green light, followed by red light. The green light at 240 K gave no response, and the subsequent red light gave a small response as in Fig. 3, spectrum b. This response did not grow as the sample was warmed to 300 K in the dark; this could be tested by comparing the final spectrum at 300 K with the original one (prior to cooling, but after exposure to green light at 300 K). In fact, any state established at a lower temperature remained stable when the sample was brought in darkness to a higher temperature, regardless of the illumination program prior to rewarming. We found no evidence for an intermediate in the conversion between P_r and P_g, trapped at low temperature but released upon warming. In another test we applied green light to a sample at 300 K, brought it to 285 K, and then gave red light to produce a moderate response (see Fig. 2). The response recorded 1–2 min after the red light exposure had not changed when recorded again 10 min later, arguing against a temperature-dependent rate-limiting step in the conversion of P_r to P_g. Finally, simply changing the temperature of the sample from 300 K to 240 K and back to 300 K, all in the dark, caused no change in its absorbance spectrum.

A paradoxical result is shown in Fig. 3, spectrum c. A sample was exposed to red light at 300 K, brought to 240 K in the dark, and then exposed once more to red light (45 sec, 640 nm, as usual). The result was a typical green light response, nearly as great as the one shown in Fig. 3, spectrum a. The reaction $P_r \rightarrow P_g$, normally driven by red light, was blocked at 240 K except for the small temperature-insensitive component. The temperature-independent reaction $P_g \rightarrow P_r$ was apparently being driven by a "green-effective" component in the 640-nm light. The interference filters used for excitation transmitted very little light outside the 20-nm band width of each (at 550 and 640 nm, respectively). The fact that the 640-nm actinic light could have a "green" effect, converting P_g to P_r, then implies that the action spectrum for $P_g \rightarrow P_r$, although maximal in the green part of the spectrum, extends well into the 640-nm region. This conclusion is compatible with action spectra reported by Ohad *et al.* (4). Light at 640 nm can drive both $P_r \rightarrow P_g$ and $P_g \rightarrow P_r$. Usually the net effect of 640-nm light is to convert P_r to P_g, but when this reaction is inhibited at low temperature, the reverse change can occur.

P_g apparently drifts slowly toward the state P_r in darkness. We found that, after 24 hr of dark adaptation at room tem-

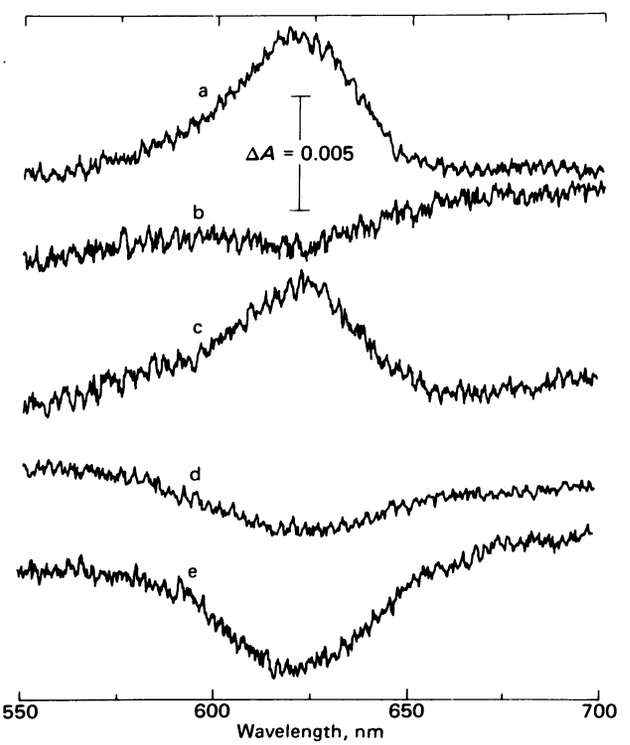

FIG. 3. Light-induced absorbance changes of the preparation shown in Fig. 1 under various conditions. Spectrum a, response to green illumination at 240 K after exposure to red light at 300 K and cooling in the dark. Spectrum b, response to red illumination at 240 K after exposure to green light at 300 K and cooling in the dark. Spectrum c, response to red illumination at 240 K after exposure to red light at 300 K and cooling in the dark. Spectrum d, response to green illumination at 300 K after 24-hr dark adaptation. Spectrum e, response to red illumination after green illumination at 300 K after 24-hr dark adaptation. Red and green illumination are defined in the text.

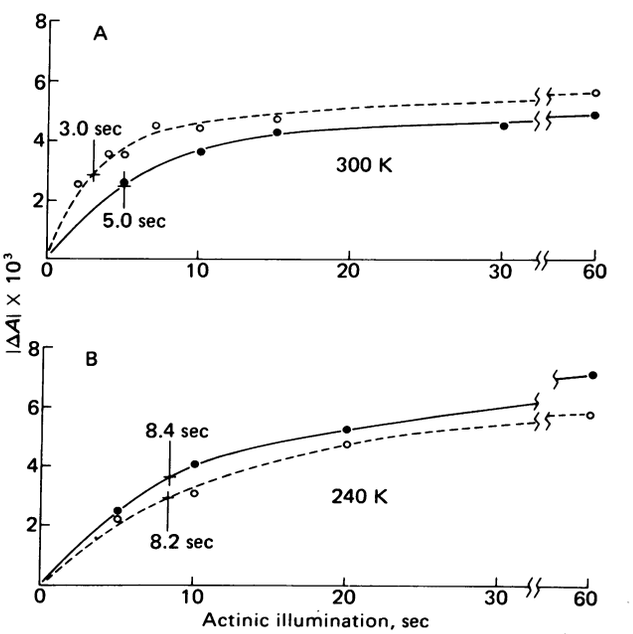

FIG. 4. Absorbance changes, at 620 nm, of the preparation shown in Fig. 1. (*A*) Cumulative responses to successive increments of exposure to green (●) or to red (○) light at 300 K. The abscissa shows the cumulative seconds of exposure to the actinic light. With green actinic light the sample had first been exposed for 45 sec to red light, and with red actinic light the sample had been conditioned by 45-sec exposure to green light. (*B*) The sample was exposed to red light for 45 sec at 300 K and then cooled in darkness to 240 K. Cumulative responses to successive increments of red (○) or green (●) actinic illumination were then measured. The absorbance changes were negative for red illumination after green at 300 K and positive for the other three cases. Half-times are indicated for each curve.

perature, a sample reached an equilibrium in which the ratio of P_r to P_g was greater than in the photostationary state produced by green (550 nm) light. This is shown in Fig. 3, spectra d and e (all at 300 K). The first exposure to green light after dark adaptation had a small red light effect (Fig. 3, spectrum d); the photostationary state established in green light represented a net conversion of P_r to P_g. The conversion of P_r to P_g was carried further when red light was then applied (Fig. 3, spectrum e). If dark adaptation was followed by red light rather than green, the response (not shown) was equal to the sum of those shown in Fig. 3, spectra d and e.

Finally, we measured the kinetics of the photoconversion by recording the absorbance changes produced by successive increments of actinic illumination. At 300 K we applied short periods of green light after a saturating exposure to red light, plotting the cumulative absorbance change as in Fig. 4*A*. The same was done with increments of red light after prolonged green illumination. We also exposed the sample to red light at 300 K, cooled it in the dark to 240 K, and then measured the responses to successive increments of green or red light (Fig. 4*B*). The times for half-maximal response, $t_{1/2}$, are indicated on the figure.

DISCUSSION

The reactions $P_r \rightleftharpoons P_g$ in our preparations of APC from *F. diplosiphon* showed a remarkable dependence on temperature, becoming nearly unilateral ($P_g \rightarrow P_r$) as the temperature was lowered. We found no evidence that this behavior involved the stabilization of intermediates between P_r and P_g. Absorbance changes induced at any temperature remained stable when the sample was held at that temperature or brought to room temperature, except for a slow drift toward P_r after many hours.

Our observations can be accommodated by at least two distinct and simple models. We shall develop one of these in some detail and then describe the other. Suppose that the excitation of either P_r or P_g produces a common intermediate (excited state) X that decays spontaneously to P_r or to P_g with rate constants k_r and k_g:

$$P_r \underset{k_r}{\overset{h\nu}{\rightleftarrows}} X \underset{k_g}{\overset{h\nu}{\leftrightarrows}} P_g.$$

Then if the quantum efficiencies for the light reactions $P_r \rightsquigarrow X$ and $P_g \rightsquigarrow X$ are ϕ_r^o and ϕ_g^o, respectively, the overall quantum efficiencies for $P_r \rightarrow P_g$ and $P_g \rightarrow P_r$ are

$$\begin{aligned}\phi_r(P_r \rightarrow P_g) &= \phi_r^o k_g/(k_r + k_g)\\ \phi_g(P_g \rightarrow P_r) &= \phi_g^o k_r/(k_r + k_g).\end{aligned} \quad [1]$$

The temperature dependence can then be ascribed to a change of k_g/k_r with temperature. As the temperature is lowered, k_g/k_r decreases. When k_g becomes much smaller than k_r, X decays preferentially to P_r after any illumination program, and any light-induced conversion of P_r to P_g is small. There is a small residual $P_r \rightarrow P_g$ reaction below 270 K, at least down to 200 K (Fig. 2). This could imply a residual (nonzero) value of k_g at low temperature.

To develop this model quantitatively we must deal with the kinetics of transitions between different photostationary states. We shall use the following notation: The concentrations of P_r and P_g are $[P_r]$ and $[P_g]$, with $[P_r] + [P_g] = [P]$, the total concentration of photoconvertible pigment. The fraction of pigment in each state is $x_r = [P_r]/[P]$ and $x_g = [P_g]/[P]$. We have assumed that there is no significant accumulation of any intermediate between P_r and P_g, so that $x_r + x_g = 1$. We shall express light intensity I in quanta/cm^2 sec, and correspondingly use an effective cross section for absorption, S = cm^2 per molecule. S is related to the molar extinction coefficient (as usually used in computing absorbance) by

$$S\ (\text{cm}^2) = 3.8 \times 10^{-21}\ \epsilon\ (\text{M}^{-1}\ \text{cm}^{-1}). \quad [2]$$

Subscripts will denote the state of the pigment, and superscripts the color of the actinic light. For example, S_r^G is the absorbance cross section of P_r (and any antenna pigments that transfer energy to P_r) at the wavelength of the green actinic light, 550 nm.

With the dilute samples used here (see Fig. 1), allowing for attenuation of incident actinic light by absorption and by reflections, the average intensity I in the sample was approximately 0.9 I_o at 550 nm and 0.8 I_o at 640 nm. Here I_o is the intensity incident on a sample of absorbance 0.175 at 640 nm and 0.05 at 550 nm (Fig. 1). Using the values of I_o stated in *Materials and Methods*, I^G (550 nm) = 0.6×10^{16} quanta/cm^2 sec and I^R (640 nm) = 1.2×10^{16} quanta/cm^2 sec.

The rates of interconversion are $[P_r]\phi_r S_r I$ for $P_r \rightarrow P_g$ and $[P_g]\phi_g S_g I$ for $P_g \rightarrow P_r$, with ϕ_r and ϕ_g given by Eqs. 1. The reactions are described by the differential equation $dx_r/dt = -dx_g/dt = x_g\phi_g S_g I - x_r\phi_r S_r I$, or, with $x_g = 1 - x_r$,

$$dx_r/dt = I\ \phi_g S_g - x_r(\phi_g S_g + \phi_r S_r). \quad [3]$$

In the steady state,

$$x_r/x_g = \phi_g S_g/\phi_r S_r. \quad [4]$$

For the transition from one photostationary state to another, integration of Eq. 3 gives

$$0.7/t_{1/2}I = \phi_g S_g + \phi_r S_r, \quad [5]$$

provided that I can be treated as a constant, as it was in our experiments. Eqs. 3–5 can be written separately for red and green actinic light; for example $0.7/t_{1/2}I^R = \phi_g S_g^R + \phi_r S_r^R$, etc.

These equations can be used to estimate quantum efficiencies and to describe the photostationary states (ratios of P_r to P_g) produced by green or red illumination, provided that we can estimate the absorption cross sections S_r^R, etc. If the photoconversions of P_r and P_g are assisted by energy transfer from nearby molecules, the values of S_r^R etc. include the contributions of these antenna pigments. Having no way to evaluate this possibility, we shall ignore it for the present and assume that each molecule of P_r and P_g sensitizes its own photoconversion without the help of energy transfer from neighbors. Phycobilins have molar extinction coefficients (ϵ) of the order of 3×10^4 M^{-1} cm^{-1} at their absorption maxima. Then if P_r is a special component of APC, or a molecular complex similar to APC, we can estimate $\epsilon = 3 \times 10^4$ M^{-1} cm^{-1} and (from Eq. 2) $S = 10^{-16}$ cm^2 for P_r at its absorption maximum, presumably at 620 nm in our preparations. From the absorption spectrum of Fig. 1 we can then guess that S_r^R (at 640 nm) = 0.6×10^{-16} cm^2 and S_r^G (at 550 nm) = 0.2×10^{-16} cm^2. There is no change of absorbance at 550 nm when P_r is converted to P_g, so S_g^G can be assigned the same value as S_r^G; 0.2×10^{-16} cm^2.

At 240 K the reaction $P_r \rightarrow P_g$ is attenuated strongly, whereas $P_g \rightarrow P_r$ is not. It follows that $\phi_r S_r \ll \phi_g S_g$, and Eq. 5 can be written $0.7/t_{1/2}I = \phi_g S_g$. The reactions at 240 K with green and red actinic light (Fig. 4*B*) gave $t_{1/2}$ = 8.4 sec (green illumination) and 8.2 sec (red). With $I^G = 0.6 \times 10^{16}$ and $I^R = 1.2 \times 10^{16}$ quanta/cm^2 sec, we have $0.7/8.4(0.6 \times 10^{16}) = \phi_g S_g^G$ and $0.7/8.2(1.2 \times 10^{16}) = \phi_g S_g^R$. With S_g^G estimated at 0.2×10^{-16} cm^2, the first of these equations gives $\phi_g = 0.7$ at 240 K. With this value of ϕ_g, the second equation gives $S_g^R = 0.1 \times 10^{-16}$ cm^2. Now, applying Eq. 5 at 300 K (Fig. 4*A*), using the foregoing values of S and multiplying the equations by 10^{16}, we have for green illumination $0.7/5(0.6) = 0.2\phi_g + 0.2\phi_r$ and for red, $0.7/3(1.2) = 0.1\phi_g + 0.6\phi_r$. The simultaneous solution of these equations gives $\phi_g = 1.0$ and $\phi_r = 0.16$ at 300 K.

These estimates of quantum efficiencies are crude, being based on guesses as to the optical cross sections of P_r and P_g at 640 and 550 nm. If P_r and P_g are served by antenna pigments, the values of S may have been grossly underestimated and the quantum efficiencies correspondingly overestimated. Taken at face value, the reactions $P_r \rightleftharpoons P_g$ are more or less balanced: $P_r \rightarrow P_g$ combines a large absorption coefficient with a small quantum efficiency, and for $P_g \rightarrow P_r$ a small absorption coefficient is compensated by a higher quantum efficiency (compare ref. 2).

The photostationary states established at 300 K with green or red illumination can be computed from Eq. 4, using the foregoing values of ϕ and S. After red illumination $x_r = 0.51$ (and $x_g = 0.49$); after green illumination $x_r = 0.86$ and $x_g = 0.14$. The change induced by red light after green, or vice versa, is $|\Delta x_r| = 0.86 - 0.51 = 0.35$. The observed absorbance change (ΔA) at 620 nm, from Fig. 1, was about 3% of the total absorbance (A) at that wavelength. If one could effect a complete conversion of P_r to P_g or vice versa, corresponding to $|\Delta x_r| = 1.0$, one could expect an absorbance change at 620 nm equal to $\Delta A/A = 0.1$. Presumably we could have observed a greater $\Delta A/A$, approaching 0.1, at higher temperature (judging from Fig. 2), or by choosing more widely separated wavelengths of excitation.

An entirely different model for the dependence on temperature can be framed as follows: The photoconvertible pigment exists in two (allosteric?) forms. In one form the interconversion of P_r and P_g is bilateral; in the other the reaction can proceed from P_g to P_r but not from P_r to P_g (unilateral). The proportion of pigment in the bilateral form decreases as the temperature is lowered, but a residual fraction of the bilateral form persists below 260 K. Specifying the fractions of unilateral and bilateral forms as u and v (with $u + v = 1$), we can denote the quantum efficiencies as ϕ_{rv} and ϕ_{gv} for the bilateral form, and ϕ_{gu} for $P_g \rightarrow P_r$ in the unilateral form (by definition, $\phi_{ru} = 0$). The average quantum efficiencies are then $\phi_g = u\phi_{gu} + v\phi_{gv}$ for $P_g \rightarrow P_r$, and $\phi_r = v\phi_{rv}$ for $P_r \rightarrow P_g$. As the temperature falls, v diminishes and so does ϕ_r. The formalism of Eqs. 2–5, and the numerical conclusions that follow, remain as before. The only difference is in how we interpret the decline of ϕ_r at low temperature. We have no plausible basis for choosing between these two models.

The unusual temperature dependence of photoconversion between P_r and P_g provides a way of asking whether this pigment system mediates chromatic adaptation in the living cell: Does the chromatic adaptation response show the same curious temperature dependence? This might be tested by giving programs of illumination to the living cells at temperatures down to 273 K, or perhaps lower with the help of glycerol, and measuring the subsequent responses in darkness at a chosen temperature. In cells depleted of phycoerythrin after prolonged growth in red light, the earliest synthesis of phycoerythrin (in response to green light) might be detected fluorometrically or by means of radioisotopes, even under conditions that do not favor sustained growth.

We have found that the effect of temperature on the balance between P_r and P_g is strong over the "physiological" range, above 273 K, and slight below the freezing point of water. At lower temperatures the state P_r is favored under all conditions of illumination; this would correspond to a chromatic adaptation response in which the synthesis of phycoerythrin is favored. For algae that exhibit chromatic adaptation, is a higher phycoerythrin content found in cells growing in colder waters?

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