Planta 143, 233–239 (1978)

Planta

Action Spectra for Chromatic Adaptation in the Blue-green Alga *Fremyella diplosiphon*

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Abstract. Action spectra for chromatic adaptation in *Fremyella diplosiphon* Drouet have been determined using techniques previously described. Action maxima are at 540 nm, with a half-band width of 80 nm, for induction of phycoerythrin synthesis (green action) and at 650 nm, with a half-band width of 90 nm, for reversal of induction of phycoerythrin synthesis (red action). The red-action spectrum includes a secondary action band centered at ca. 360 nm. Red and green action overlap from 570 to 590 nm with an isosbestic point in the vicinity of 580 nm. Shoulders are present at 520 and 630 nm. Red light is more active than green light. The 540:650-nm quantum effectiveness ratio is 1:7. There is relatively little action of either kind in the blue. The 387:540 nm and 460:650-nm quantum effectiveness ratios are zero. These results contrast strongly with previous determinations in the same organism, with major activity indicated in the blue; they are consistent with the control of photomorphogenesis in the Cyanophyta by a master pigment, analogous to phytochrome.

Key words: Adaptation (chromatic) – Chromatic adaptation – Cyanophyta (cyanobacteria) – Phycobiliproteins – Phytochrome.

Introduction

The phycobiliproteins phycoerythrin (PE), phycocyanin (PC), and allophycocyanin (APC) are widely distributed throughout three phyla: Cyanophyta, Rhodophyta and Cryptophyta. They function as photosynthetic accessory pigments, delivering excitation energy to Photosystems I and II (Jones and Myers, 1964; Wang et al., 1977). They absorb light in the green and orange regions of the spectrum and transfer this energy to chlorophyll, presumably by resonance transfer. The direction of energy transfer is from PE to PC to APC and finally to chlorophyll a (Duysens, 1951; French and Young, 1952; Tomita and Rabinowitch, 1962; Lemasson et al., 1973; Gantt et al., 1976).

In phycobiliprotein-containing organisms PC and APC are usually, if not always, present, whereas PE is sometimes present. Some organisms possess the ability to alter their biliprotein composition in accordance with the quality of ambient light. This phenomenon is called chromatic adaptation and at present has been rigorously demonstrated to occur only in the Cyanophyta, although it may occur in the other phyla as well.

Investigations of chromatic adaption with the blue-green algae *Tolypothrix* (Fukita and Hattori, 1960a), *Fremyella* (Bennett and Bogorad, 1973; Haury and Bogorad, 1977), *Synechocystis, Nostoc, Phormidium, Pleurocapsa* and others (Tandeau de Marsac, 1977) show that under continuous red light predominantly PC is synthesized, whereas under green light or light from cool-white fluorescent lamps both PE and PC are synthesized. APC is synthesized in smaller amounts, apparently independently of light quality. When many species of blue-green algae that can chromatically adapt are grown in complete darkness, PC and APC are synthesized, but PE is not (Fujita and Hattori, 1960a; Kiyohara et al., 1960; Tandeau de Marsac, 1977), indicating that light is needed for induction of synthesis of PE, but not of PC or APC.

The nature of the photocontrol of PE synthesis was first characterized for the blue-green alga *Toly-*

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Abbreviations: APC = allophycocyanin; PC = phycocyanin; PE = phycoerythrin

0032-0935/78/0143/0233/$01.40

pothrix tenuis (Hattori and Fujita, 1959; Fujita and Hattori, 1960a, 1962a; Diakoff and Scheibe, 1973). In these experiments dilute filament suspensions were subjected to a preirradiation period under photosynthetic conditions in the absence of a source of combined nitrogen. Under these conditions much of the existing phycobiliproteins underwent apparent destruction as evinced by a decrease in absorbance (bleaching), but the levels of chlorophyll and carotenoids remained about the same. When nitrate was added to bleached cells phycobiliproteins were subsequently synthesized during a period of ca. 15 h in complete darkness under aerobic conditions (Hattori and Fujita, 1959; Fujita and Hattori, 1960a, 1962a; Diakoff and Scheibe, 1973).

The quality of light preceding the period of dark synthesis determines the final phycobiliprotein composition; after red light PC is synthesized, whereas after green light both PE and PC are synthesized. Moreover, a relatively brief irradiation (flash) with green or red light immediately preceding dark incubation is sufficient to potentiate subsequent synthesis of PE or PC, respectively. This response is repeatedly photoreversible (Fujita and Hattori, 1960a), reciprocity is valid (Diakoff and Scheibe, 1973), and the response is independent of temperature during the irradiation period (Fujita and Hattori, 1962b). Action spectra have action maxima at 550 nm for the induction of PE synthesis and 660 nm for reversal of induction of PE synthesis. Minor peaks for induction and reversal of induction of PE synthesis exist at 350 and 360 nm, respectively (Diakoff and Scheibe, 1973). These action spectra resemble the absorption spectra of certain, known biliproteins. These findings strongly indicate that chromatic adaptation is controlled by a photoreversible pigment analogous to phytochrome, but the photoreceptor is probably not identical with phytochrome, because the active spectral regions are green and red rather than red and far-red.

Action spectra that have recently been developed for chromatic adaptation in the blue-green alga *Fremyella diplosiphon* are radically different from those for *Tolypothrix* (Haury and Bogorad, 1977). In that work, *Fremyella* was irradiated with continuous monochromatic light for 6 h; the cells were then extracted and the increase in PE and PC was determined. The values so obtained were used to determine action spectra for chromatic adaption. Maximal activity was reported at 387 and at 550 nm for promotion of PE production, with approximately equal quantum effectiveness at the 2 wavelengths. Similarly, the action spectrum for production of PC had action maxima at 463 and 641 nm with a 463:641-nm quantum effectiveness ratio of 1.8. The principal difference between these action spectra for *Fremyella* and those for *Tolypothrix* is the existence of major action bands in the blue for *Fremyella*. Two different photoreceptors have been proposed to govern chromatic adaptation in the two species (see review by Bogorad, 1975).

We have re-examined chromatic adaptation in *Fremyella diplosiphon* under conditions similar to those used to develop the action spectra for the same process in *Tolypothrix* and have found no essential difference in the behavior of the two organisms. The data are consistent with the hypothesis that the same photoreceptor governs this process in both organisms.

Material and Methods

Culture of the Organism

Fremyella diplosiphon Drouet was obtained from the Indiana University (Bloomington, Ind., USA) Culture Collection (IU 481) and was grown at 32° C in 950-ml glass prescription bottles in the growth medium described by Diakoff and Scheibe (1973). Both during growth and the light-bleaching procedures described below the filament suspensions were aerated continuously with air enriched with 1% CO_2 and filtered through a Koby PMC-2 filter (Koby Corp., Boston, Mass., USA) and an MSA airline filter (Mine Safety Appliances, Pittsburg, Pa., USA) to remove trace impurities. The flow rate through the cell cultures was 2 l min^{-1}. Continuous light was supplied by two 40-W cool-white fluorescent tubes. The tubes were located 3 cm from the algal cultures.

New cultures were started by inoculating freshly autoclaved growth medium with a 50-ml aliquot from an established culture. Newly inoculated cultures rapidly entered log-phase growth and were used in experiments after about 10 d.

Light-bleaching in the Absence of Nitrate

F. diplosiphon filaments were collected by centrifugation at 5860 × *g* for 5 min; after this, the growth medium was decanted, and the filaments were resuspended to a standard absorbance of 0.15 at 750 nm in bleaching medium. Bleaching medium is identical to growth medium except that K_2SO_4 is substituted for KNO_3 on a mole-equivalent basis with respect to potassium. The resulting filament suspension was transferred to 950ml glass prescription bottles and placed 1 cm from two 40-W cool-white fluorescent tubes. The filaments were incubated for 36 h at 21° C under continuous aeration with CO_2-enriched air.

Preirradiation with Broad-band Green and Red Light

Light-bleached filaments were collected by centrifugation and resuspended to a standard absorbance of 0.6 at 750 nm in growth medium containing 0.05% citrulline as an additional nitrogen source. Filament suspensions 1 cm in depth were preirradiated for 20 min with broad-band red light at 12 W m^{-2} or 20 min with broad-band green light at 6 W m^{-2}. The spectral emissions of the red and green broad-band sources were as described in Diakoff and Scheibe (1973). Fluence rate was measured with an Eppley thermopile (No. 6581; Eppley Laboratory, Newport, R.I., USA) for all light sources. All monochromatic wavelengths were obtained using a locally constructed high-dispersion xenon spectrograph which has been previously described by Balegh and Biddulph (1970).