LIGHT-INDUCED EFFICIENCY AND PIGMENT ALTERATIONS IN RED ALGAE*

By C. S. YOCUM‡ and L. R. BLINKS

(*From the Hopkins Marine Station of Stanford University, Pacific Grove*)

(Received for publication, December 26, 1957)

ABSTRACT

The low photosynthetic efficiency of chlorophyll in freshly collected red algae, can, in the case of *Porphyra perforata*, *P. nereocystis*, and *Porphyridium cruentum*, be increased by growing the algae for 10 days in red or blue light. Exposure to darkness or to green light maintains the algae in their originally low efficiency with respect to chlorophyll, while retaining the high efficiency of phycobilins. Red- or blue-adapted algae are rapidly reversed by exposure to green light, the chlorophyll efficiency dropping to low values again in a few hours. This is assumed to account for the action spectrum of freshly gathered plants.

Some pigment changes were observed, but not in the direction of "chromatic adaptation;" and the carotenoid pigments were not activated, even by blue light, but remained as photosynthetically inactive shading filters. The higher red algae (Florideae) did not show activation of chlorophyll by red or blue light.

Chlorophyll *a* of freshly collected marine red algae sensitizes photosynthesis with an efficiency of about 0.04 molecule oxygen liberated per absorbed quantum. This is in contrast to about 0.08 for the phycobilin pigments phycocyanin and phycoerythrin in the same algae and for chlorophyll of most other organisms (1). Two mechanisms may lead to the low efficiencies: (*a*) relatively rapid (ontogenetic) response to environmental factors and (*b*) rigid genetic (phylogenetic) control. If changes of efficiency are reversible and (*a*) operates in red algae it should be possible to increase the efficiency of chlorophyll-sensitized photosynthesis by altering parameters such as temperature, nutrients, carbon dioxide, or light. Long-time breeding and selection would be necessary to demonstrate (*b*). The preliminary experiments described below provide evidence for (*a*) by showing that chlorophyll-sensitized efficiencies as high as 0.07 can be induced by growing *Porphyra* thalli in red or blue light.

Absorption spectra, photosynthetic action spectra, and quantum efficiencies were determined as previously described (1, 2) in the genus *Porphyra* and other red algae

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* Research partly supported under contract with the Office of Naval Research (Nonr 120-050).

‡ Present address: Botany Department, Cornell University, Ithaca, New York.

before and after varying periods of dark or continuous illumination in narrow wave length regions of the visible spectrum. The illumination sources consisted of CH-4 reflector spot lamps with glass and liquid filters. The green Hg line (546 mμ) was

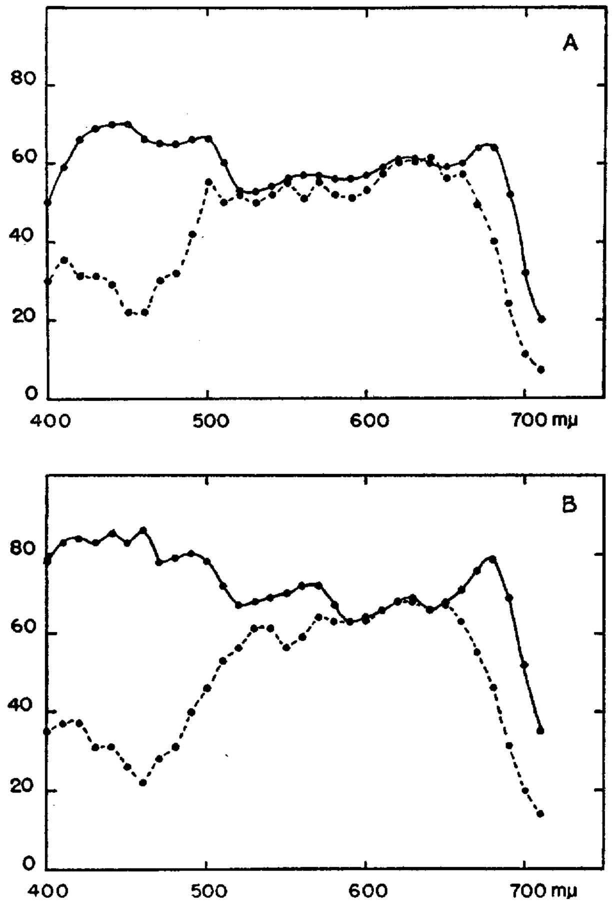

FIG. 1. Absorption spectra (solid lines) and action spectra (dotted lines) of *Porphyra perforata* thalli before and after darkening. Ordinates, per cent absorption or relative rate of photosynthesis per incident quantum; abscissae, wave lengths in mμ. A (above), freshly collected thallus; B (below), after 10 days' darkness (in running sea water, at 15°C.).

isolated with a Corning number 5120 filter and 5 cm. of water containing $K_2Cr_2O_7$ and $CuSO_4$, the blue line (436 mμ), with a Corning number 5562 filter, 3 cm. H_2O, and 2 cm. saturated solution of $NaNO_2$. The former gave an intensity of 175 ergs/mm.^{2}/sec., the latter, 240 ergs/mm.^{2}/sec. at the plane of the algae. Aerated seawater, 15°C., flowed continuously over the algae.

Changes in the relative efficiencies were estimated from the ratio of photosynthetic action/absorption before and after such illumination (or darkness) as shown in Figs. 1 and 2. The characteristics of the action and absorption spectra for the freshly collected

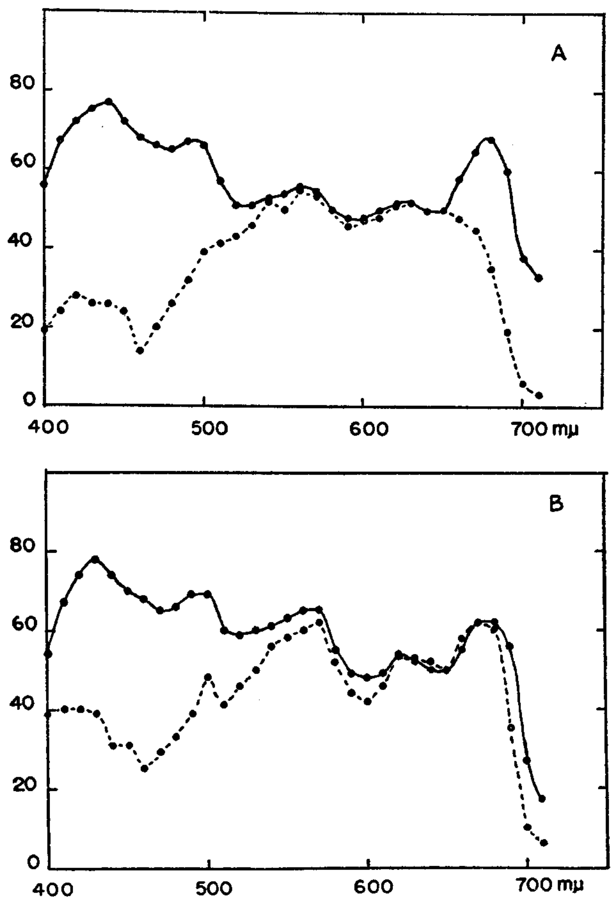

FIG. 2. Absorption spectra (solid lines) and action spectra (dotted lines) of *Porphyra perforata* thalli, previously exposed to A (above), green light (546 mμ); B (below), blue light (436 mμ) (exposures in running sea water for 10 days at 15°C.). Ordinates and abscissae as in Fig. 1.

thallus (Fig. 1 *A*) are similar to those previously reported (2). Data for all curves were obtained from adjacent sections cut from a uniform portion of one thallus.

Assuming a constant quantum efficiency of photosynthesis sensitized by phycocyanin at λ 620 mμ, there appear to be only small changes in that of phycoerythrin measured at λ 560 mμ; the largest being about a 10 per cent decrease for the thallus grown at λ 546 mμ (Fig. 2 *A*). The efficiency of chlorophyll *a*, as measured at 675 mμ, decreased in both the darkened thallus (Fig. 1 *B*) and that exposed to green light, 546 mμ (Fig. 2 *A*). These results are in contrast to those obtained from the thallus exposed to blue light, λ 436 mμ (Fig. 2 *B*). Here there is a relative increase in chlorophyll efficiency, to a value nearly equal to that of phycocyanin. The action spectrum, at the longer wave lengths, now shows a close resemblance to the absorption spectrum at the long wave length maxima of all three principal pigments instead of the two phycobilins alone (as in Fig. 1 *A*). A comparable increase of efficiency at the blue absorption maximum of chlorophyll (λ 420 mμ) was not observed however. This is presumably due to shading of chlorophyll by photosynthetically inactive pigments such as carotenoids. Similar changes in relative efficiency were observed in *Porphyra nereocystis* and the unicellular red alga *Porphyridium cruentum*. In all three organisms the blue-induced changes were partially duplicated by red light (λ 660 mμ).

That these relative results were not due to a decrease of phycobilin efficiency to the initial low level of chlorophyll was demonstrated by quantum efficiency measurements. For example, the measured values for a freshly collected *Porphyra nereocystis* thallus were 0.052 and 0.031 molecules O_2 evolved per absorbed quantum at λ 560 mμ and λ 675 mμ respectively. After exposure to red light (200 ergs/mm.^{2}/sec. λ 660 to 690 mμ) for 10 days, the corresponding values were 0.086 and 0.071—increases of 65 and 130 per cent respectively.

Reversion to the initial low chlorophyll efficiency was observed after brief exposure of such adapted red algae to green light. A thallus of *Porphyra nereocystis* initially with a phycoerythrin/chlorophyll efficiency ratio of 3.2 was exposed to red light 2.5 days, reducing the ratio to 1.3. Exposure to λ 560 mμ, 60 ergs/mm.^{2}/sec. increased the ratio to 1.9 at the end of 2 hours and to 2.8 at 9 hours. Thus the efficiency of chlorophyll-sensitized photosynthesis in red algae can be reversibly altered within certain limits by visible radiation to which they had been previously exposed. Low temperature (5°C.) and supplemental illumination during the time of measurement are also reported to increase the photosynthetic efficiency of green and red algae at long wave lengths (5–7).

During the course of the illumination and dark treatments of thalli, changes in their color appeared, related to changes in absorption spectra (Figs. 1 and 2). These spectral changes were definite and consistent enough to justify brief remark. They were interpreted, qualitatively, as resulting from altered pigment concentration and will be so described. Precise quantitative estimation of pigment content from the absorption spectra of the living thalli alone is precluded by (*a*) optical inhomogeneity caused by localization of pigments in the plastids, and (*b*) partial overlapping of the absorption bands of the various pigments. However, the overlapping is small and should not lead to serious error here since the relative amounts of each pigment changed only slightly.

The dark-treated thallus contained more phycobilins and chlorophyll per unit area than the freshly collected plants. The thallus illuminated at λ 546 mμ decreased in phycobilin and increased slightly in chlorophyll content. The thallus receiving λ 436 mμ contained more phycoerythrin but less phycocyanin and slightly less chlorophyll. These interpretations, at least for chlorophyll, were in agreement with data from quantitative solvent extractions and spectrophotometric analyses of the extracts. Chlorophyll *d* content (3) could account for less than 0.3 per cent of the total light absorption at λ 675 mμ, and changes in chlorophyll *a/d* ratio were below the limits of spectrophotometric detection.

None of the observations on pigments and apparent changes in their concentration supports the theory of (ontogenetic) complementary chromatic adaptation. According to this hypothesis (4, pp. 419–427) the thallus should increase in absorption at the specific wave length of illumination. For example green light of λ 546 mμ should specifically increase the phycoerythrin content. In fact a decrease, under the conditions of these experiments, was generally observed. However, the data from *Porphyra* thalli were not obtained from a wide enough range of conditions to permit generalizations in this controversial field.

Although parallel experiments with higher red algae (Florideae) were made, neither efficiency nor pigment changes were observed. Nor was it always possible to induce changes in *Porphyra*, a lack of response at times being presumably due to seasonal differences.

The changes described above were accompanied by increases in thallus area (growth) but no attempt as yet has been made to correlate the several events. Nor have they been studied by varying other possible parameters. However, it is apparent that the high intensity of green light in coastal waters where *Porphyra* normally grows can account for the relatively low efficiency of its chlorophyll-sensitized photosynthesis when first collected.

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