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# ON THE LONG-WAVE DECLINE OF THE QUANTUM YIELD OF PHOTOSYNTHESIS IN THE RED ALGA *PORPHYRIDIUM CRUENTUM*

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## Introduction

The quantum yield of photosynthesis, $\Phi$ in the far red, instead of remaining constant until a region is reached where chlorophyll *a* no longer absorbs at all, declines with increasing wavelength (8, 9). Emerson and coworkers (cf. 3) found that the wavelength at which this decline starts varies with the pigment composition of the photosynthetic system. They also observed that irradiation with light of shorter wavelengths can restore the reduced quantum yield to its full value (6, 7). This "Emerson effect" was interpreted as evidence of a need for cooperation in photosynthesis of an excited auxiliary pigment with an excited chlorophyll *a*. It was noted (5) that the amount of activation by auxiliary light depends on the intensity ratio of auxiliary light and far red light. No effect occurred unless this ratio exceeded a certain minimum.

The published data do not prove whether, in the case of exclusive excitation of chlorophyll *a*, the rate of photosynthesis becomes zero, or has a certain small finite value. (The smallest value measured by M. Brody and R. Emerson (2) with *Porphyridium* was $\phi = 0.01$ in a narrow band centered at 700 m$\mu$). The present study was intended to answer this question.

## Methods

We wanted to be able to vary the composition of the incident light so that the proportion of energy absorbed by auxiliary pigments could change in small steps. To this purpose, an organism had to be used in which the auxiliary pigments absorbed well outside the red chlorophyll *a* band (which has a peak between 670 and 680 m$\mu$).

This requirement is met by red algae, which contain chlorophyll *a*, but not chlorophyll *b*. The main auxiliary pigments are the phycocyanin, absorbing around 625 m$\mu$, and the phycoerythrin, absorbing from 565 to 500 m$\mu$. The red alga, *Porphyridium cruentum*, was grown over fluorescent white light tubes in the medium described by M. Brody and Emerson (1). Gradual removal of light absorbed by the phycobilins was obtained by filtering the incident white light through cuvettes containing aqueous phycobilin extracts of increasing concentration. As a light source, a 225-watt ribbon-filament, incandescent lamp was used. Care was taken to remove, as far as possible, the infrared radiation (not absorbed by the algae), by using a 6-inch water layer and two American Optical IR-absorbing glass filters. A correction was applied to account for the remainder of the radiation beyond 720 m$\mu$.

The phycobilin extracts were prepared by storing thalli of *Porphyra perforata* in distilled water in the dark at room temperature (about 23°C) for at least five days. In this time the cells died and the phycobilins, but not the chlorophyll and the carotenoids, were released. The extract was partly purified by filtering through a Seitz filter, centrifuging, and repeated precipitation with ammonium sulfate. The final preparation was highly concentrated, but clear, showing only very little light-scattering. Our thanks are due to Dr. L. R. Blinks for providing us with the algal material, and to Mr. C. Cederstrand for measuring true (scattering-free) absorption of the *Porphyridium* suspensions in an integrating sphere set-up.

Photosynthetic oxygen production was measured manometrically, while the incident energy was determined with a bolometer, as described by Emerson and Chalmers (4).

## Results and Discussion

The results of six consecutive experiments are shown in Fig. 1, in which quantum yield in percentages of that in full light is plotted against the fraction of total incident light absorbed by the phycobilin filter. The curve consists of three sections. In the first section, the quantum yield does not change as the absorption of the phycobilin filter is raised from 0 to 20%. Further increase of the filter density up to 80% absorption leads to a linear decline of the quantum yield. When the concentration is increased still further, the quantum yield declines more steeply, until, at about 95% absorption, photosynthesis ceases to be measurable (—0.24 ± 0.25 $\mu$l $O_2$/hour). However, the Emerson effect can still be observed: if a background of orange light

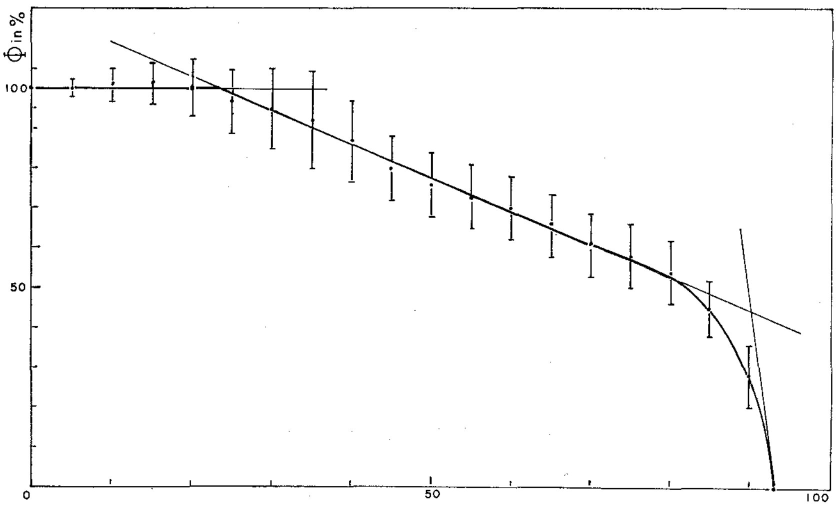


Fig. 1. Relation between quantum yield and light absorption by phycobilin filters.

is provided, the light transmitted by the 95% filter clearly shows a measurable photosynthetic effect (+ 1.66 ± 0.30 μl $O_2$/hour). This shows that the disappearance of photosynthetic activity in light filtered through the 95% filter was not due to the residual light being practically unabsorbable by chlorophyll *a*. The same conclusion can also be derived by calculation, using the energy distribution curve of the incident light, the absorption curve of the filter, and the absorption curve of the cell suspension (determined in an integrating sphere and therefore free from scattering effects). This calculation shows that much of the transmitted light falls into the region 680-700 mμ, and is largely absorbed by the cell suspension.

The effect of removal of light predominantly absorbed by phycobilins, shown in Fig. 1, may be explained in terms of the dependence of Φ on the intensity ratio of auxiliary light to far red light, as noted by Emerson and coworkers. As long as the phycobilin filter absorbs less than 20% of the incident light, this ratio may remain above the critical value, and the maximal quantum yield is maintained. If more than 20% but less than 80% of light is absorbed in the filter, the quantum yield becomes dependent on the intensity ratio; i.e., light energy absorbed by chlorophyll *a* produces photosynthesis only in proportion to the energy absorbed by the auxiliary pigment. When the intensity ratio declines below another critical value, no enhancement of the quantum yield in the far red by light of shorter wave is possible. One would then expect the yield either to become constant, or to decline to zero, depending on whether the light absorbed only by chlorophyll *a* (or, more precisely, the form of chlorophyll *a* responsible for the absorption in this region) does or does not produce by itself a finite yield of photosynthesis. The curve in Fig. 1 suggests that the latter is the case.

However, according to a suggestion made by Dr. E. I. Rabinowitch, the situation may be more complex. The measurements by Brody and Emerson (2) (and confirmed by Govindjee) suggest that $\phi$ remains measurable in the narrow spectral bands centered at 695 m$\mu$ and even 700 m$\mu$. Why, then, should there be no photosynthesis at all in the "5% band" which extends from 680 m$\mu$ to longer waves? Perhaps there exists in photosynthesis, as in many other photobiological phenomena, a "counter-effect" caused by extreme red light, which deactivates some of the intermediates in photosynthesis. The amount of this light in the "5% band" may be sufficient to reduce the photosynthesis to zero. Further experiments are in progress to check this tentative suggestion.

## Summary

The relation between quantum yield and white light from which the wavelengths predominantly absorbed by both phycobilins were removed was established for the red alga *Porphyridium cruentum*. It proved possible to obtain incident light of such a spectral composition that no photosynthesis could be measured in it at all, although a significant part of it was absorbed, and while the Emerson effect still occurred.

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