Emerson Enhancement Effect in Synchronous *Scenedesmus* Cultures

THE photosynthetic activity and quantum efficiency of synchronized cultures of *Scenedesmus obliquus* maintained on a 14 : 10 h light–dark regime are maximal at the eighth hour after the onset of illumination and minimal at the sixteenth hour just before separation of the mother cells into autospores[1]. Similar results have been reported in synchronized cultures of *Scenedesmus sp.*[2] and for various strains of *Chlorella*[3,4]. The variation apparently resides in photosystem II, for the Hill reaction using quinone as oxidant (a photosystem II reaction) parallels the photosynthetic activity, whereas photoreduction of CO_2 (a photosystem I reaction) is unchanged throughout the life cycle[1]. We have investigated the level of Emerson enhancement in these synchronized cells to see if this also follows the variation in quantum efficiency and photosynthetic capacity. The literature provides only inferential evidence about the influence of different developmental stages on the effect of the Emerson enhancement[5,6].

The Emerson enhancement effect, discovered by Emerson and co-workers[7–10], describes the fact that the sum of photosynthetic activity caused by light absorbed by shorter wavelength (chiefly system II) and longer wavelength (chiefly system I) is less than the activity produced by simultaneous irradiation with both wavelengths. The current interpretation is that this is caused by a series reaction between the two distinct primary photochemical reactions of the two photosystems.

To measure the Emerson enhancement effect samples of 30 µl. packed cell volume were taken at selected times from the synchronous cultures, washed and resuspended in 3 ml. of 0·2 M Warburg's carbonate–bicarbonate buffer No. 9[11]. Photosynthetically evolved O_2 was measured in a Gilson respirometer with the all-glass differential volumometer. The contents of the reaction and compensation vessel on respective sides of the differential manometer were identical. The compensation vessel was maintained in complete darkness to compensate for dark respiration. The respirometer was modified to allow either separate or simultaneous irradiation with two different wavelengths of monochromatic light into the reaction vessel. The irradiation of cells was carried out according to the schedule of Table 1. Because some of the samples were selected during the dark phase of the culture, all the samples were exposed to white light to avoid the spurious effect of varied induction phenomena. We are well aware that the ratio of long to short wave response affects the amplitude of the Emerson enhancement effect[12,13]. In the conditions reported in Table 1 oxygen evolution under long wave irradiation was 25–60 per cent less than under short wave light. The measurable Emerson enhancement effect would have been even more pronounced if a smaller ratio of short to long wave light could have been used. The percentage enhancement reported in Fig. 1 was calculated by the following equation

Table 1. SEQUENCE AND INTENSITY OF IRRADIATION FOR MEASUREMENT OF THE EMERSON ENHANCEMENT EFFECT

Time in min*		Light quality †	Erg/cm²/s
10	*A*	White	5×10^5
5	*A*	704 nm	1×10^4
15	*M*	704 nm	1×10^4
5	*A*	640 nm	$2{\cdot}8 \times 10^3$
15	*M*	640 nm	$2{\cdot}8 \times 10^3$
5	*A*	704 + 640 nm	
15	*M*	704 + 640 nm	

* *A* = time of adaptation; *M* = time of measurement.
† To obtain monochromatic irradiation, line-interference filters (Type PIL, Schott and Gen., Mainz, Germany) were used.

$$E(\%) = \frac{O_2\,(704+640) - O_2\,(704) - O_2\,(640)}{O_2\,(704) + O_2\,(640)} \times 100$$

where O_2 stands for the amount of oxygen evolved. The wavelengths of the irradiation causing the O_2 evolution are given in parentheses.

Alternative methods for calculating the Emerson enhancement effect are used by Myers[14], Myers and Graham[12] and Bedell and Govindjee[5].

The degree of enhancement obtained at different stages of a synchronized life cycle is shown in Fig. 1; the pattern closely resembles that seen for the photosynthetic activity. In both cases the maximum effect occurs at the eighth hour and the minimum at the sixteenth hour. Parallel decreases of the Emerson enhancement to the activity of photosystem II could be the result of insufficient electron transport from system II to system I. Both phenomena could, however, be the result of an actual disengagement of the two photosystems, perhaps through structural modifications within the chloroplast membranes or to a greater degree of overlap of the total absorption spectra of the separate photosystems. The latter explanation would make it difficult to evaluate experimentally the Emerson enhancement effect because of the half-band widths of the interference filters used in the measurements. The negative values for the Emerson enhancement around the sixteenth hour might be the result of a photoinhibition by far-red light as reported by Govindjee *et al.*[15].

The precise mechanism of the alternation in the Emerson enhancement during a synchronous life cycle of certain green algae remains unexplained, but it is a factor that must be considered in enhancement studies with algae.

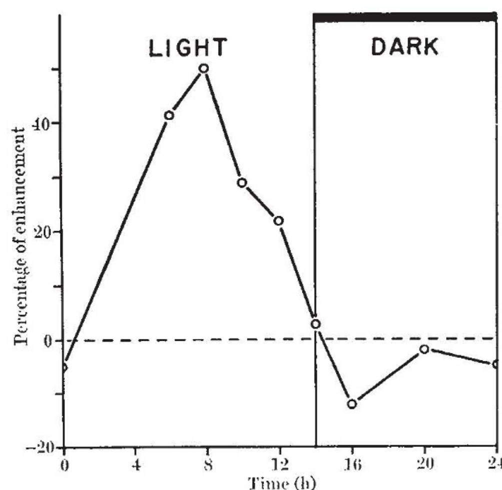

Fig. 1. Emerson enhancement effect in a culture of *Scenedesmus obliquus* during a synchronous life cycle. Each point of the curve represents the average of two, the maximum and minimum each of six different experiments. For the extremes the values and standard deviations in per cent are: max, 50 ± 23·4; min, −13·0 ± 9·2.

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1 Senger, H., and Bishop, N. I., *Nature*, **214**, 140 (1967).
2 Bongers, L. H. J., *Meded. Landb. Hoogesch. Wageningen*, **58**, 1 (1958).
3 Tamiya, H., *Ann. Rev. Plant Physiol.*, **17**, 1 (1966).
4 Pirson, A., and Lorenzen, H., *Ann. Rev. Plant Physiol.*, **17**, 439 (1966).
5 Bedell, G., and Govindjee, *Science*, **152**, 1383 (1966).
6 Soeder, C. J., *Ann. Rep., Dept. Plant Biol. Carnegie Inst.*, 477 (1964).
7 Emerson, R., Chalmers, R., and Cederstrand, C., *Proc. US Nat. Acad. Sci.*, **43**, 133 (1957).
8 Emerson, R., *Ann. Rev. Plant Physiol.*, **9**, 1 (1958).
9 Emerson, R., *Science*, **127**, 1059 (1958).
10 Emerson, R., and Rabinowitch, E. I., *Plant Physiol.*, **35**, 477 (1960).
11 Warburg, O., *Biochem. Z.*, **100**, 230 (1919).
12 Myers, J., and Graham, J. R., *Plant Physiol.*, **38**, 105 (1963).
13 Bannister, T. T., and Vrooman, M. J., *Plant Physiol.*, **39**, 622 (1964).
14 Myers, J., in *Photosynthetic Mechanism of Green Plants*, 301 (Nat. Acad. Sci.—Nat. Res. Council, Washington DC, Pub. No. 1145, 1963).
15 Govindjee, Rabinowitch, E. I., and Thomas, J. B., *Biophys. J.*, **1**, 361 (1960).

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