BBA 43166

Energy transfer between photosynthetic units of system 1 in algae

A photosynthetic unit can be defined as a reaction center and those pigment molecules (chlorophylls, carotenoids, *etc.*) which transfer their excitation energy preferably to that reaction center. Experiments to measure the efficiency of conversion of light into chemical energy as a function of the fraction of reaction centers which were operative, have indicated that energy transfer occurs between photosynthetic units in purple bacteria[1,2] and in photosystem 2 of algae[3,4]. When excitation energy reaches a photosynthetic reaction center that is inactive, *e.g.*, because of a photochemical reaction shortly before, the energy can be transferred to another reaction center.

To investigate the existence and extent of energy transfer in system 1 in algae, we have measured both the relative efficiency of photosynthesis and the level of oxidation (bleaching) of the presumed reaction center, P_{700}, as a function of light intensity in a number of algal species.

Fig. 1 shows the results of an experiment with the red alga *Cryptopleura violacea*. The steady-state rate of O_2 evolution, measured with a Teflon-covered platinum electrode[5], was measured as a function of light intensity. An adjacent thallus piece was used under the same conditions to measure the oxidation levels of P_{700} and the *f*-type cytochrome. This was done by measuring with an apparatus described previously[6] the increase in absorption at 705 and 420 mμ upon turning off the light after several minutes of illumination, when photosynthesis proceeded at a steady rate. Difference spectra in the red and blue region at high and low intensities of actinic light confirmed the identity of these compounds. Green light, more strongly absorbed by system 2 than by system 1, was used so that photochemistry in system 1 occurred at maximum efficiency. During the experiments the algae were in sea water; the gas phase was 1.5 % CO_2 in air and the temperature was 21°.

As Fig. 1 shows, P_{700} remained practically completely in the reduced state at intensities where photosynthesis proceeded at maximum rate; only at intensities where photosynthetic efficiency began to decline, did an accumulation of oxidized P_{700} occur. This is in agreement with the hypothesis that P_{700} is a reaction center: when part of the reaction centers are inoperative, photosynthetic efficiency is less than maximal. On the contrary, cytochrome *f* was already partly oxidized at intensities that gave maximum efficiency, indicating that cytochrome is not a primary reactant.

For a more quantitative evaluation, the relative efficiency of O_2 evolution was plotted from the curves of Fig. 1 as a function of the level of reduced P_{700} and cytochrome (Fig. 2). The relative efficiency corresponding to the dashed line in Fig. 1 was normalized at unity. The total amount of oxidizable P_{700} and cytochrome present in the alga was determined by measuring the maximum changes in absorbance that could be obtained with blue or red exciting light and in the presence of DCMU. The shaded areas indicate the estimated uncertainty. At high level of reduced P_{700} or cytochrome the uncertainty was mainly determined by the measurement of the

---

Abbreviations: DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea; CMU, 3-(*p*-chlorophenyl)-1,1-dimethylurea.

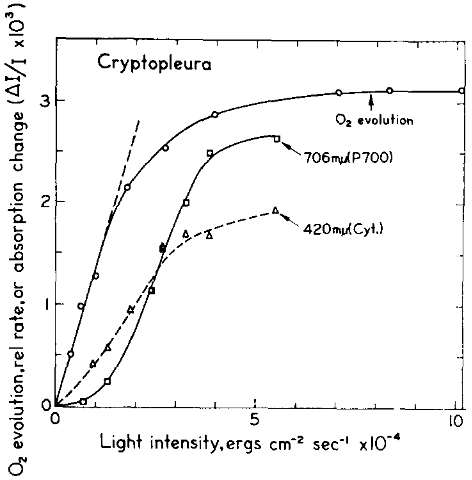

Fig. 1. Steady-state level of oxidation of P_{700}, *f*-type cytochrome, and steady-state rate of O_2 evolution in *C. violacea* as a function of the intensity of green light (540 mμ max; 40 mμ half-band width). The maximum signal obtained in red or blue light was $\Delta I/I = 3.6 \cdot 10^{-3}$ for P_{700} and $1.9 \cdot 10^{-3}$ for the cytochrome.

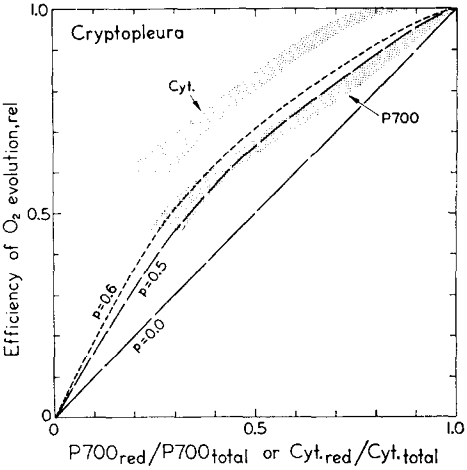

Fig. 2. Relative efficiency of O_2 evolution as a function of the level of reduction of P_{700} and of the *f*-type cytochrome in *C. violacea*. Green actinic light as for Fig. 1. The dashed lines show computed curves for transfer probabilities (P) of 0, 0.5 and 0.6 (ref. 3).

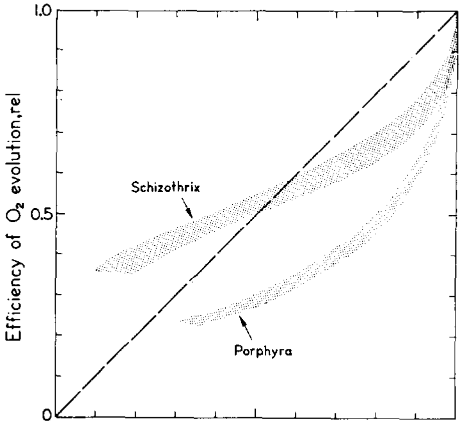

Fig. 3. Relative efficiency of O_2 evolution as a function of the level of reduction of P_{700} in *S. calcicola* and *P. perforata*. Green actinic light, 535 mμ max; 100 mμ half-band width.

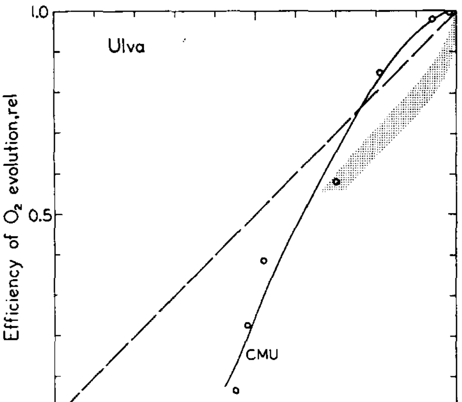

Fig. 4. Relative efficiency of O_2 evolution as a function of the level of reduction of P_{700} in *U. lobata*. The shaded area was obtained from experiments done as for Figs. 1 to 3, the open circles (solid line) represent an experiment at $6 \cdot 10^3$ erg·cm^{-2}·sec^{-1} where photosynthetic efficiency was lowered by adding increasing amounts of CMU. Blue actinic light, 450 mμ max; 80 mμ half-band width.

relative photosynthetic efficiency; at low level of reduction by the measurement of the total amount of oxidizable P_{700} or cytochrome. The diagonal dashed line gives the relation which could be expected when no transfer between photosynthetic units occurred; the photosynthetic efficiency would be linearly proportional to the level of reduced P_{700}. The shaded band for P_{700} lies consistently above this line, indicating that energy transfer occurs. The dashed curves give the calculated[3] relation for probabilities, P, of 50 and 60 %, respectively, for excitation energy to be transferred to a second reaction center (active or inactive) when the first one visited is inactive. Our data agree reasonably well with a probability for transfer to a second reaction center of 50–60 %.

Fig. 3 shows results obtained with *Porphyra perforata* and with the blue-green alga *Schizothrix calcicola*. For Schizothrix the left part of the band lies above the diagonal, suggesting energy transfer between reaction centers. However, in the right side of the figure (low light intensities) the band drops below the diagonal line. For Porphyra the whole band lies below the diagonal. The most plausible explanation for these results is that a concomitant "cyclic" reaction between the oxidized and reduced photoproducts of system 1 occurs. There is some evidence for such a reaction in blue-green and red algae[7]. A cyclic reaction would give rise to a higher rate of photochemistry in system 1 than measured from O_2 evolution alone. Results similar to those with Porphyra were obtained with the green alga *Ulva lobata* (Fig. 4).

The experiments with Cryptopleura indicate that P_{700}, but not the *f*-type cytochrome, is a primary reactant, and suggest for system 1 a probability of 50–60 % for transfer of excitation energy to a second reaction center when the first one visited is inoperative. This would be of obvious importance to the plant, because it enables it to use absorbed light more efficiently when part of the reaction centers are inoperative, such as occurs at high light intensities. The number of 50–60 % may give a lower limit, since the true rates of photochemistry may be higher than measured, because of "cyclic" reactions of P_{700}.

No correlation has been found[8] between fluorescence of system 1 and the oxidation level of P_{700}. For this reason it has been assumed[9] that energy from the bulk chlorophyll is transferred to the reaction center *via* a special weakly fluorescent chlorophyll present in small amounts and located near the reaction center. Back transfer of energy from this chlorophyll to the bulk chlorophyll would be negligible so that bleaching of P_{700} would not affect the fluorescence yield of the bulk chlorophyll. A consequence of this hypothesis would be that energy transfer between reaction centers would occur *via* the special chlorophyll which should form a more or less continuous structure containing the reaction centers.

Department of Plant Biology,
Carnegie Institution of Washington,
Stanford, Calif. (U.S.A.)

DAVID C. FORK
JAN AMESZ*

1 W. J. VREDENBERG AND L. N. M. DUYSENS, *Nature*, 197 (1963) 355.
2 R. K. CLAYTON, *Photochem. Photobiol.*, 5 (1966) 807.
3 A. JOLIOT AND P. JOLIOT, *Compt. Rend.*, 258 (1964) 4622.
4 A. JOLIOT, *Biochim. Biophys. Acta*, 126 (1966) 587.
5 D. C. FORK, *Plant Physiol.*, 38 (1963) 323.
6 Y. DE KOUCHKOVSKY AND D. C. FORK, *Proc. Natl. Acad. Sci. U.S.*, 52 (1964) 232.
7 J. AMESZ AND W. J. VREDENBERG, in T. W. GOODWIN, *Biochemistry of Chloroplasts*, Vol. II, Academic Press, London, 1967, p. 593.
8 W. J. VREDENBERG AND L. N. M. DUYSENS, *Biochim. Biophys. Acta*, 94 (1965) 355.
9 L. N. M. DUYSENS, *Arch. Biol. Liège*, 76 (1965) 251.

Received February 8th, 1967

---

* On leave from the Biophysical Laboratory, University of Leiden, Leiden, The Netherlands.