Biochimica et Biophysica Acta, 592 (1980) 76—86

BBA 47869

DISTRIBUTION OF EXCITATION ENERGY BETWEEN PHOTOSYSTEM I AND PHOTOSYSTEM II IN RED ALGAE

III. QUANTUM REQUIREMENTS OF THE INDUCTION OF A STATE 2-STATE 1 TRANSITION

A. RIED and B. REINHARDT

Fachbereich Biologie (Botanik) der J.W. Goethe-Universität, Siesmayerstr. 70, 6000 Frankfurt/Main (F.R.G.)

(Received December 12th, 1979)

Key words: Photosynthesis; Excitation-energy distribution; State 1-state 2-transition; Energy transfer; (Red alga)

Summary

1. The light-induced redistribution of excitation energy between both photosystems (state 1-state 2 phenomenon) is investigated in *Halymenia latifolia* and in eight other marine red algae by measurements of slow fluorescence kinetics and of O_2-exchange in monochromatic and in flashing light.

2. A light 1 pulse (443 nm) of 0.2 s and of medium intensity is sufficient to induce complete transfer from state 2 (maximum energy transfer) to state 1 (minimum energy transfer). At inducing light periods of 3 min, light intensities as low as $2 \cdot 10^{-13}$ einstein $\cdot$ cm$^{-2} \cdot$ s^{-1} gave half-maximum effect. This low energy effect is strictly to be distinguished from another, somewhat similar effect restricted to higher light intensities (more than 10^{-10} E $\cdot$ cm$^{-2} \cdot$ s^{-1}).

3. The low-energy effect is definitely dose-dependent over a wide range of inducing illumination times. In the mean of all experiments with *Halymenia*, a photon fluence of $2.7 \cdot 10^{-11}$ E $\cdot$ cm^{-2} gave a half-maximum transfer to state 1. The dose-effect curves are always found distinctively S-shaped.

4. On the basis of light flash experiments it is calculated that in *Halymenia*, *Stenogramme* and in *Phycodrys*, 2—4 photons per electron transport chain, absorbed in surplus by Photosystem I, are sufficient to induce a half-maximum transition to state 1.

5. The quantum requirement for the induction of the inverse transition to state 2 starting with state 1 is in the same range; it tends to be slightly higher.

Abbreviations: light 1 (L_1), light 2 (L_2), light of wavelengths predominantly adsorbed by Photosystem I and Photosystem II, respectively.

6. The results are interpreted as revealing a close connection between the redox state of the electron transport chain (or of some single component of it) and the probability of energy transfer between Photosystem II and Photosystem I.

Introduction

The possibility of separating in time the light-driven transition between state 1 and state 2 in a fast inducing light reaction and a following slow dark reaction, as found in red algae (except *Bangiales* [1]) allows precise measurements of the energy requirement of the induction of the transition. Such measurements could help to elucidate the mechanism of the regulation of the distribution of excitation energy between both photosystems.

Beside the absolute quantum requirements, the relationship between the energy demands of the transitions in both directions is of special interest. The finding that the induction of a transition from state 2 to state 1 has roughly the same, very low, quantum requirement as the reverse transition makes it most unlikely that both transitions could be initiated by different mechanisms, including unequal numbers of possible energy-wasting steps. Rather, they appear to be tightly coupled to the electron transport between the photosystems.

Materials and Methods

All experiments were done with marine red algae, preferably thin laminate species, all collected (during spring or autumn) in the area of Roscoff (France). The algae were transported to Frankfurt in Dewar vessels or (packed in plastic bags) in cooling boxes and were kept until the experiments (for several weeks or months) in a climatized room at 15 or 17°C and dim daylight in flat basins or in plastic boxes with natural sea water. The algae treated in this way retained their photosynthetic capacity undiminished for many months and all other physiological characteristics tested remained unchanged (compared with data obtained in Roscoff immediately after collection) for at least several weeks.

Fluorescence was measured at an angle of 45° with an R 666 photomultiplier from Hamamatsu, equipped with an Oriel interference filter (λ_{max} 684 nm, bandwidth at half peak height, 5.2 nm) and two cut-off filters (Schott & Gen. RG 665 and RG 645). Actinic light came from two grating monochromators (Schoeffel monochromator Type HM 250 with 0.55 mm slit wide and a recalibrated Bausch and Lomb monochromator with a 0.75 mm exit slit, both equipped with 250 W/24 V iodine lamps. For the fluorescence measurements the light was further filtered by sets of interference- and cut-off filters to minimize to less than 1% the error caused by scattered actinic light. Simultaneously with the fluorescence, the rate of oxygen exchange was measured with a stationary Teflon-covered platinum electrode of the type described by Fork [2].

A state transfer was induced by pulses of light 1 (443 nm) or light 2 (550

nm) of variable length and intensity. The relative height of the initial fluorescence peak $(F_p - F_s)/F_s$ in light 2, measured after a dark period of 20—120 s (constant in every experimental series), gave a measure for the induced state. The length of the dark time was chosen to obtain maximum response [1]. Maximum peak height was taken as an indication of complete state 1. (For further details and for critical discussion of the overall scheme of the experiments see Ref. 1.)

For the calculation of the photosynthetic unit size, another type of Teflon-covered Pt| Ag/AgCl electrode, designed as an O_2-concentration electrode, was used. Light flashes of duration (measured at half-maximum intensity) 900 ns and frequency 3 Hz were produced by a Spark-Combi Flash Lamp filled with 80% Ar/20% H_2 at 4 atm. The effect of 1000—2000 flashes was averaged for each measurement and it was ascertained that the flashes were saturating. It was assumed that the number of oxygen molecules evolved by four flashes corresponded to the number of photosynthetic electron transport chains.

The primary distribution of excitation energy between both photosystems was estimated on the basis of action spectra for light reactions 1 and 2, measured with 699 nm or 550 nm background light, respectively [3]. After conversion into spectra of active absorbance [4] corrected spectra for Photosystem I were calculated assuming that with 699 nm background light (in state 1) energy transfer from Photosystem II for Photosystem I is virtually zero, whilst with 550 nm background (in state 2) upto 45% of the energy primary absorbed by Photosystem II is transmitted to Photosystem I, resulting in almost equal excitation of both photosystems. Arguments for this procedure will be given in a further communication (see also, for example, Ref. 5).

Absorption spectra of the thalli were measured with a Shimadzu UV-200 spectrophotometer using an integrating sphere. Light intensity was either measured with a calibrated silicium cell or with a photodiode PIN 5. If not mentioned otherwise, the data represent incident photon flux rates. Dose values (absorbed photon fluence) also take into account reflection by the platinum surface.

The measurements were normally made at 17°C, the highest monthly mean value of the natural environment.

Results

1. Dependence of the transfer to state 1 on the length of the inducing light pulse

We have already shown [1] that the requirement earlier reported [6—9] of prolonged illumination with light 1 or light 2 to achieve the fully developed state 1 or 2 reflects more the slowness of the transition process than the requirement for a longer inducing light period. Even at fairly low light intensities ($3 \cdot 10^{-10}$ E $\cdot$ cm$^{-2} \cdot$ s^{-1}), a light 1 pulse (443 nm) of 0.2 s induces complete transition to state 1 (Fig. 1). The slope of the curve at shorter illumination times surely does not reflect the kinetics of the induction process. As can be concluded from the following experiments, it shows only the limitation of the inducing light reaction by the applied light dose. Higher light intensities, however, were not obtainable with our equipment.

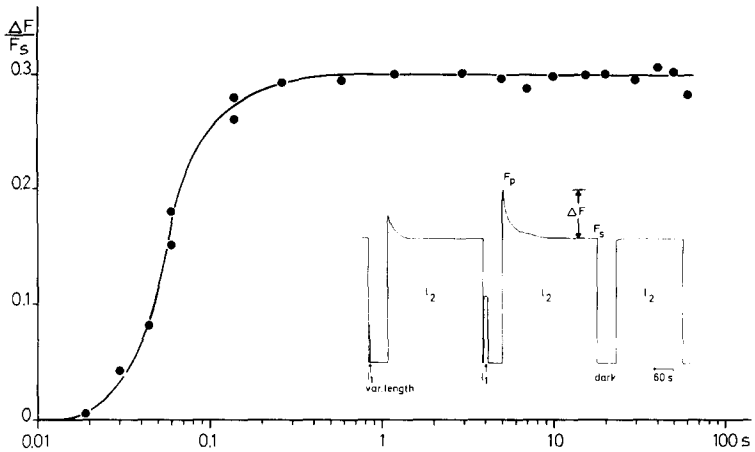


Fig. 1. Transition from state 2 to state 1 as a function of the length of the preceding exposure to inducing light of 443 nm; incident photon fluence rate is $2.89 \cdot 10^{-10}$ E · cm^{-2} · s^{-1} (L_1). As measure of the degree of state transformation in direction of state 1 the relative height of the initial fluorescence peak ($F_p - F_s$)/F_s is plotted against exposure time. Subject: *Halymenia latifolia* (as in all other figures.) Illumination schedule: 5 min $2.87 \cdot 10^{-10}$ E · cm^{-2} · s^{-1} 550 nm (L_2). 1 s dark, x s L_1, (59 — x) s dark, 5 min L_2. Inset: Time-course curves of fluorescence intensity, illustrating the experimental scheme.

2. *Dependence on light intensity*

The curves showing the height of $\Delta F/F_s$ as a measure of the extent of the state transition in dependence on the intensity of the inducing light (Fig. 2) are always found to be distinctively S-shaped. The minimum intensity which induces a significant shift in direction of state 1 depends on the illumination time and is influenced by the preconditioning of the thallus (by which the initial state 2 was established) and by the more general physiological state of the material.

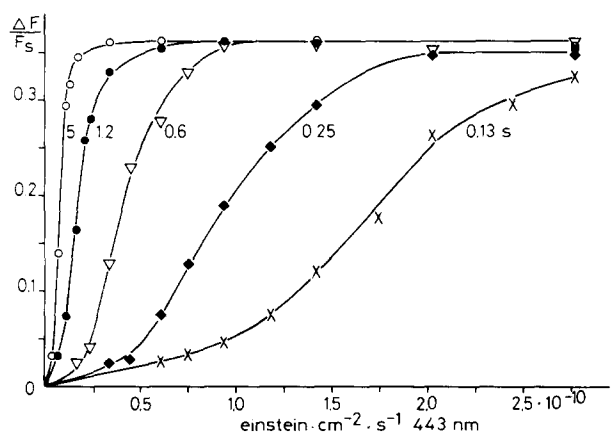


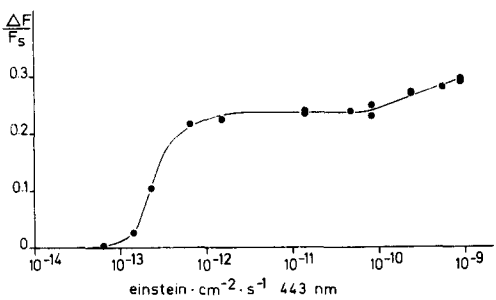
Fig. 2. Transition from state 2 to state 1 as a function of the intensity of the inducing light 1 (443 nm). Exposure times mentioned at the curves. Ordinate as in Fig. 1, abscissa: incident photon fluence rate. Illumination schedule: 5 min $1.72 \cdot 10^{-10}$ E · cm^{-2} · s^{-1} L_2, 5 s dark, x s L_1 of variable intensity, (55 — x) s dark, 5 min L_2.

When the inducing light 1 period is extended to 3 min, intensities as low as approx. $2 \cdot 10^{-13}$ E $\cdot$ cm$^{-2} \cdot$ s^{-1} are sufficient to result in a half-maximum transfer in direction of state 1 (Fig. 3). With rising intensities above about $1—2 \cdot 10^{-12}$ E $\cdot$ cm$^{-2} \cdot$ s^{-1} the effect remains approximately constant at an intensity range $10^{-12}—10^{-10}$ E $\cdot$ cm$^{-2} \cdot$ s^{-1}. Only when the intensities rise more than 100-fold is observed in some cases (but not always) a second increase of $\Delta F/F_s$. Evidently this additional effect of high intensities has to be strictly distinguished from the low-energy effect which is the only subject of this investigation. However, it seems likely that in some of the investigations on the state 1-state 2 phenomenon and on related phenomena reported in the literature such high-intensity effects are involved.

3. Dose dependency

The low energy component is characterized by a clear-cut antagonistic effect of light 1 and light 2. Furthermore, it is characterized by a distinctive dose-dependency within a wide range of illumination times (Fig. 4). Even at inducing illuminations of some minutes the effect is approximately dose-dependent.

The photon fluence necessary to induce a half-maximum transition in direction of state 1 was always found to be very small. For the experimental series shown in Fig. 4, made consecutively with the same piece of thallus, this value was $2.1 \cdot 10^{-11}$ E $\cdot$ cm^{-2}. The mean value from all experiments made with *Halymenia latifolia*, our main subject, was $2.7 \cdot 10^{-11}$ ($n = 21$, $\sigma = 1.7 \cdot 10^{-11}$). In this value as well as in the mean value of the other algae tested (see below) are included some measurements which were made several months after collecting the algae. The photosynthetic capacity of these algae and also their efficiency in weak green light had remained almost unchanged since the date of collection. However, after such a long stay in diffuse daylight some members of



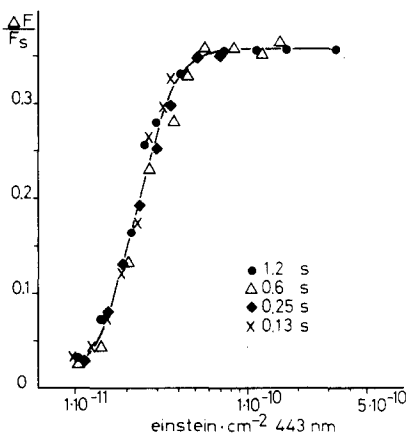


Fig. 3. As Fig. 2, time of illumination with L_1 = 3 min, $L_2 = 4.4 \cdot 10^{-10}$ E $\cdot$ cm$^{-2} \cdot$ s^{-1}.

Fig. 4. Transformation to state 1 as a function of the light dose. Ordinate as in Fig. 1, abscissa: incident photon fluence. Data from four experimental series with different periods of exposure to L_1 as explained in the figure. Illumination schedule as in Fig. 2.

the *Florideae* including *Halymenia latifolia* showed a considerable increase in photosynthetic efficiency in the spectral region of predominant chlorophyll absorption, which was accompanied by a corresponding rise in fluorescence emission, a decrease in the Emerson enhancement, and a strong increase in the quantum requirement for the induction of a transition from state 2 to state 1. It seems that a longer stay under our culture conditions leads to a gradual reduction of the initial extreme inbalance in the distribution of the chlorophyll between the two photosystems. This effect is presumably similar to the increase in the photosynthetic efficiency of chlorophyll reported from members of the *Bangiales* as a consequence of growing the algae for 10 days in red or blue light [10].

Therefore, with respect to the absolute quantum requirements of the induction of a transition, only those experiments which were made soon after the collection of the algae seem to be relevant. Measurements made in Frankfurt during the first 2 months after collection gave results identical to those obtained in Roscoff immediately after collection. If only those experiments which were carried out within this time span are evaluated, a more reliable value of only $1.8 \cdot 10^{-11}$ ($n = 15$, $\sigma = 6.6 \cdot 10^{-12}$) was obtained for the half-maximum transfer in the direction of state 1.

The results from the other eight species of *Florideae* tested in the same way (*Callophyllis laciniata*, *Rhodophyllis divaricata*, *Gymnogongrus patens*, *Stenogramme interrupta*, *Delesseria sanguinea*, *Hypoglossum woodwardii*, *Phycodrys rubens* and *Cryptopleura ramosa*, belonging to three different orders) were mostly slightly higher ($\bar{X} = 5.9 \cdot 10^{-11}$ E $\cdot$ cm^{-2}, $n = 16$, $\sigma = 2.2 \cdot 10^{-11}$) but within a similar range. Considering these values it has to be taken into account that most of these species are much more intensely coloured than *Halymenia* and that some fairly thick species such as *Gymnogongrus* or *Callophyllis* are included, and that most measurements are carried out several months after collecting the algae.

The number of electron transport chains was chosen as a meaningful reference quantity for an evaluation of these data in view of the mechanism of the induction of a state transition. The estimations of the number of electron transport chains per cm^2 were based on measurements of the amount of oxygen evolved by saturating 0.9 μs light flashes, assuming that every molecule O_2 evolved per flash corresponds to four electron transport chains (quantum yield as in green algae and in higher plants (see Ref. 11), theoretical yield 0.12). These estimates were made with a piece of the same thallus from which data on the photon fluence requirements had been obtained. The light dose, d_1, which is necessary to produce half-maximum transition to state 1 was found to be 4—6 photons per electron transport chain in *Halymenia*, approx. 3—4 photons in *Stenogramme* and approx. seven photons in *Phycodrys*.

Since action spectra of the induction of a state transfer in both directions clearly correspond to the difference spectrum between Photosystem I and Photosystem II (unpublished results), in a subsequent step allowance was made for the overlapping of the spectra of Photosystem I and Photosystem II and for photosynthetically ineffective absorption, particularly in the carotenoid region, according to the equation

$$d_1^* = t \cdot a \cdot I \cdot (1 - \delta) \cdot (1 - 2\alpha)$$

where d_1^* is the dose of photons absorbed by Photosystem I which are not balanced by a corresponding excitation of Photosystem II, required on a electron transport chain base to induce a half-maximum transfer to state 1; t is the length of the inducing light pulse; a is the fractional thallus absorption; I is the incident photon fluence rate ($h\nu \cdot cm^{-2} \cdot s^{-1}$); δ is the fraction of absorbed light that does not contribute to one of the photo-reactions (includes losses of energy transfer from carotenoids and phycobiliproteids and absorption by pigments not involved in collection of light energy for photosynthesis); α is the fraction of (photosynthetically effective) light absorbed by Photosystem II; $1 - \alpha$ is the fraction of light absorbed by Photosystem I.

The term $1 - 2\alpha$ takes into account that only that part of excitation of Photosystem I is relevant for the induction of transition to state 1 which exceeds the simultaneous excitation of Photosystem II. Since the experiment starts with state 2, the extent of energy transfer from Photosystem II to Photosystem I ($P_{T_{II \to I}}$) had to be considered, at least when short light 1 periods are used for the induction of state 1. However, the values of α_{443} being small in all our experiments (between 0.05 and 0.1), the error would scarcely exceed 10%, even if $P_{T_{II \to I}}$ attained the maximum value observed by us (of approx. $0.5\,\alpha$).

The values of α derive from spectra of active absorbance of Photosystem I and Photosystem II calculated as described in Methods. The obtained α values coincide very well with estimations made by Butler [12,13] for *Porphyridium* in a completely independent way. In addition our basic assumption of a near 50% energy transfer from Photosystem II to Photosystem I (in state 2) is supported by the work of Butler on *Porphyridium* [5]. For the estimation of δ, the sum of the spectra of active absorbance of Photosystem I and Photosystem II is compared with the absorbance spectrum of the thallus.

Estimations of d_1^* were made on the basis of experiments with *Halymenia*, *Stenogramme* and *Phycodrys* and gave values between 2.0 and 3.8 $h\nu$/electron transport chain ($\bar{X} = 3.0$, $n = 8$, $\sigma = 0.72$). This means that the number of photons required to induce a state transformation is within the range of the electron capacity of the photosynthetic electron transport chain. This does not prove a causal relationship between the redox state of the electron transport system (or of some component of it) and the state transformation, but it does allow speculation in this direction.

4. Induction of state 2

We have already shown that the transformation from state 1 to state 2 is, at least in our subjects (cf. Ref. 14), an active light-driven process, too [1]. However, during a dark time of several minutes (following a state 1-inducing light 1 period), there is a light-independent return to a dark state, which approaches state 2 very closely as observed by us in all red algae tested so far and reported also for green algae [14,15]. In the members of *Florideae*, both processes, the light 2-induced and the dark process, differ greatly in time constant. Whilst $\tau_{1/2}$ for the light induced transformation is more-or-less the same as for the reverse transformation [1], ranging from 8—30 s, (mostly between 12 and 18 s), $\tau_{1/2}$ for the dark transformation (varying considerably) has values between 2 and 15 min. Nevertheless, this dark process overlaps the light-

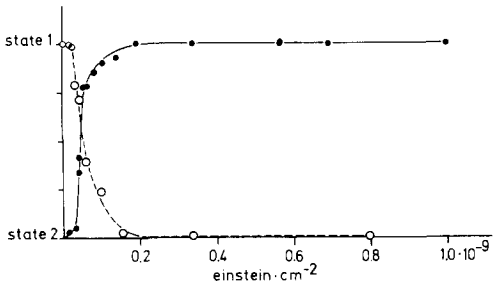


Fig. 5. Transition from state 1 to state 2 (○) and from state 2 to state 1 (●) as a function of the incident photon fluence of the inducing L_2 or L_1 illumination, respectively. Both experimental series made with the same piece of *Halymenia latifolia*. Ordinate: state finally obtained, determined as in Fig. 1.

induced transitions to some (variable) extent and therefore renders precise comparison of the quantum demand for the transition in both directions more difficult. A further problem in the experiments on the induction of state 2 seems to be — in some conditions — the achievement of a complete state 1 as the initial state. At the moment we can state only that the quantum requirement for both transitions is of the same range. From all experiments which give data for the quantum demand of both transitions from the same piece of the thallus, a mean value of $7.8 \cdot 10^{-11}$ E · cm^{-2} ($n = 11$, $\sigma = 2.4 \cdot 10^{-11}$) is found for the half-induction of state 2, and of $4.8 \cdot 10^{-11}$ ($n = 11$, $\sigma = 1.9 \cdot 10^{-11}$) for the half-induction of state 1 (experiments with *Halymenia*, *Cryptopleura*, *Phycodrys*, *Gymnogongrus*, *Rhodophyllis* and *Stenogramme*). If only those experiments (with *Halymenia*, *Stenogramme* and *Rhodophyllis*) are selected which were done within two months after collecting the algae (see p. 81), mean values $7.1 \cdot 10^{-11}$ E · cm^{-2} ($n = 5$, $\sigma = 1.9 \cdot 10^{-11}$) for the half-induction of state 2 and of $4.4 \cdot 10^{-11}$ E · cm^{-2} ($n = 5$, $\sigma = 9.3 \cdot 10^{-12}$) for the half-induction of state 1 are obtained. Considering the overlapping of the state 2 transition with the dark reaction acting in the same direction, there seems to be a tendency towards a higher quantum requirement for the induction of state 2. If one accepts that the deactivation of the S_2 and S_3 states of oxygen evolution occurs at least in part via backflow of electrons from Q^- (and possibly PQ) (cf. Refs. 16, 17) it could be supposed that the observed difference results from losses by this deactivation occurring during the illumination with low intensities of the inducing light 2, or in the following dark time. In view of the importance of precise comparative data for the understanding of the induction mechanism, further experiments on this point are in progress.

Discussion

The presented data on the quantum requirements of the initiation of a transition from state 2 to state 1 and vice versa can give some hints to the way of the linkage between primary photosynthetic reactions and the decisive, rate-limiting final step of the transition which is visualized as a conformational change of an individual protein or another structural change of the thylakoid membrane, which would lead to a redistribution of excitation energy [18,19].

Among the early photosynthetic events which could possibly induce such a process, such as electron transport, membrane potential changes, fluxes of protons and of Mg^{2+}, the last one, especially, has been thoroughly discussed during the last years, because of many similarities between the state 1-state 2 transition and the cation effect on the energy distribution in broken chloroplasts [18,20,21]. However, two well established observations are hardly compatible with this interpretation: the antagonism of light 1 and light 2 and the return in the dark to a state resembling state 2. When state 2 is so similar to the dark state, it cannot be identical with the high-energy state, as usually assumed (cf. Ref. 18) on the basis of the work on intact chloroplasts [20,22]. At least each state must be caused in a different way.

Further, it can be concluded that the primary inducing factor, the state determining factor, has similar properties in light 2 and in the dark (but differs greatly in light 1). Obviously, among the early photosynthetic events listed above, only electron transport includes some elements which could be expected to meet these requirements. Among such elements: some high-potential components ($E_0' \gtrsim 0.2$ V) of the electron transport chain or some closely connected redox compounds which attain similar redox states in the dark and light 2, are to be discussed.

There is an obvious discrepancy, however, between our constant findings about the dark state in red algae and the corresponding results of Williams and co-workers [14,15] on green algae on one side and the statement of Bonaventura and Myers [6] and of Wang and Myers [9], that state 1 evolves in the dark, on the other. It is not possible to solve this discrepancy at the moment. If the 'state' was determined by the redox state of an electron carrier, there would be some possibility that this redox state and hence the probability of excitation energy transfer could vary in the dark according to the physiological conditions. But some confusion could also arise from the secondary increase of the initial fluorescence peak after longer dark times which we do not correlate with a change in α or in $P_{T_{I \to II}}$ [1].

If the state-determining factor be represented by an electron carrier involved in or associated with the electron transport chain between both photosystems, the redox state of which controls the degree of excitation energy transfer from Photosystem II to Photosystem I, as earlier proposed by Duysens [23] (or, less probably by the distribution pattern of charges in the thylakoid membrane), the other crucial property of the in vivo regulation of excitation energy, the antagonism of light 1 and light 2, ensues by itself.

Every other concept of the linkage between the light reactions and the state transformation entails considerable difficulty in explaining this antagonism, insofar as both light reactions create the same electrochemical potential, the same proton gradient and, consquently, the same gradient of Mg^{2+} (and other ions). To account for the observed antagonism it is necessary to provide for complex feedback effects by secondary reactions as in the proposal discussed by Barber et al. [18,20]. This concept suggests different reaction chains for the transition from state 1 to state 2 and for the reverse shift. Whilst the shift to state 2 (Barber et al. assume the dark state to be identical with state 1) is seen as the simple consequence of the evolving high-energy state in the light and of the corresponding efflux of Mg^{2+} from the intra-thylakoid space, the reverse

transition to state 1 when light 1 is superimposed is explained by the accumulation of ATP produced by cyclic phosphorylation which results in a back-pumping of Mg^{2+} into the intra-thylakoid space by an ATP-dependent Mg^{2+} pump.

According to this and similar models, one should expect a distinctly higher time demand as well as quantum requirements for the initiation of a transition to state 1 than for the reverse process. However, we found both transitions to be fairly symmetrical in many respects, the energy demand being possibly even higher for the transition to state 2.

There is a great number of further facts which to us seem hardly compatible with the above proposal or with any concept providing for the formation or degradation of a Mg^{2+} or a proton gradient as an integral part of the reaction chain, but which fit very well in the idea of the determination of the probability of excitation energy transfer by the redox state of an electron carrier.

Such facts are the observed very low quantum requirements for the induction of a transition between both states, the short exposure time to light 1 or light 2 sufficient to obtain maximum response, and the capability of the system to sum small impulses over a time of minutes with only minor losses. (If a concentration gradient were involved, the steady leakage and metabolic degradation of this gradient should prevent this summation.) A special problem arises from the relative slow decay of state 1 in the dark, demonstrating long persistence of the state determining factor in the (redox) state, attained during the last illumination period. To our knowledge there are no measurements of decay kinetics of proton- and Mg^{2+}-gradients in red algae, but in all experiments made with green algae or chloroplasts from higher plants, fast degradation of the gradients starts almost immediately after darkening. On the other hand, we found in our subjects a remarkably slow dark equilibration in the electron transport chain, the reduction of cytochrome *f* in the dark after an exposure to red light having half-times in the range of a minute (unpublished results). Therefore it seems conceivable that redox compounds located near cytochrome *f* as presumably the 'Riske' $g = 1.89$ iron-sulfur center (not observed by us) could have kinetics as expected from the postulated state-determining factor (cf. Ref. 24).

The sigmoidal shape of the dose vs. effect curves is open to controversial interpretation. Considered by itself, this result could also be interpreted as a hint of the existence of a threshold value of some gradient which must be overcome to start a state transition as the cooperativity of several binding sites of a protein. However, in context with the other points of discussion we prefer the concept that it reflects the control of the light state by the redox state of an electron carrier located near the middle of the electron transport chain or of a redox compound in close connection with it.

Acknowledgements

We gratefully acknowledge the hospitality and the kind support we found for the collection of the marine algae at the Station Biologique de Roscoff (France). A minor part of the experiments was done at this Station. This work was supported by a grant from the Deutsche Forschungsgemeinschaft.

References

1 Ried, A. and Reinhardt, B. (1977) Biochim. Biophys. Acta 460, 25—35
2 Fork, D.C. (1963) Plant Physiol. 38, 323—332
3 Ried, A., Hessenberg, B., Metzler, H. and Ziegler, R. (1977) Biochim. Biophys. Acta 459, 175—186
4 French, C.S. (1977) Photochem. Photobiol. 25, 159—160
5 Ley, A.C. and Butler, W.L. (1976) Proc. Natl. Acad. Sci. U.S.A. 73, 3957—3960
6 Bonaventura, C. and Myers, J. (1969) Biochim. Biophys. Acta 189, 366—386
7 Murata, N. (1969) Biochim. Biophys. Acta 172, 242—241
8 Murata, N. (1970) Biochim. Biophys. Acta 205, 379—389
9 Wang, R.T. and Myers, J. (1974) Biochim. Biophys. Acta 347, 134—140
10 Yocum, C.S. and Blinks, L.R. (1954) J. Gen. Physiol. 38, 1—16
11 Yocum, C.S. and Blinks, L.R. (1958) J. Gen. Physiol. 41, 1113—1117
12 Ley, A.C. and Butler, W.L. (1977) in Photosynthetic Organelles (Miyachi, S., Katoh, S., Fujita, Y., Shibata, K., eds.), Special Issue of Plant and Cell Physiology pp. 33—46, Jpn. Soc. Plant Physiol.
13 Butler, W.L. (1978) Annu. Rev. Plant. Physiol. 29, 345—378
14 Williams, W.P. and Salamon, Z. (1976) Biochim. Biophys. Acta 430, 282—299
15 Williams, W.P., Futrado, D. and Nutbeam, A.R. (1979) personal communication
16 Diner, B.A. and Joliot, P. (1977) in Encyclopedia of Plant Physiology, New Series, Vol. 5 (Trebst, A. and Avron, M., eds.), pp. 187—205, Springer-Verlag, Berlin
17 Radmer, R. and Chenia, G. (1977) in Topics in Photosynthesis, Vol. 2, Primary Processes in Photosynthesis, (Barber, J., ed.), pp. 302—348, Elsevier, North-Holland Biomedical Press, Amsterdam
18 Barber, J. (1976) in Topics in Photosynthesis, Vol. 1, The Intact Chloroplast, (Baber, J., ed.), pp. 89—134, Elsevier, Amsterdam
19 Williams, W.P. (1977) in Primary Processes of Photosynthesis (Barber, J., ed.), pp. 99—147, Elsevier, North-Holland Biomedical Press, Amsterdam
20 Barber, J., Telfer, A., Mills, J. and Nicolson, J. (1974) in Proceedings of the 3rd International Congress of Photosynthesis Research (Avron, M., ed.), pp. 53—63, Elsevier, Amsterdam
21 Vernotte, C., Briantais, J.M., Armond, P. and Arntzen, C.J. (1975) Plant Sci. Lett. 4, 115—123
22 Krause, G.H. (1974) in Proceedings of the 3rd International Congress on Photosynthesis Research (Avron, M., ed.), pp. 1021—1030, Elsevier, Amsterdam
23 Duysens, L.N.M. (1972) Biophys J. 12, 858—863
24 Malkin, R. and Bearden, A. (1978) Biochim. Biophys. Acta 505, 147—181