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

II. KINETICS OF THE TRANSITION BETWEEN STATE 1 AND STATE 2

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SUMMARY

The kinetics of chlorophyll fluorescence were measured during the state 1–state 2 and the state 2–state 1 transition in some members of the Florideae (*Halymenia latifolia, Phycodrys rubens* and *Delesseria sanguinea*) and in *Porphyra umbilicalis* as a member of the Bangiales.

With the members of the Florideae it was possible to induce 70–80 % of the maximum transition in direction to state 1 (obtained by us in longtime experiments) by an illumination of only a few (2–5) seconds with medium intensities of light 1*. A complete transition back could be induced by a similar short illumination with light 2*. The transition process itself is slow with values of $\tau_{\frac{1}{2}}$ in the range of 10 to 20 s and occurs in the dark with nearly the same speed as in continuous light 1 or light 2.

The state 1–state 2 transient of chlorophyll fluorescence is kinetically clearly different from the dark-light transient phenomenon. In dark times longer than 1 min *Halymenia* (starting from state 1) slowly approaches state 2. This decay of state 1 is slower by a factor of about five in *Halymenia* than in *Porphyra*. This may explain, why in *Halymenia*, but not in *Porphyra*, the whole transition process can be resolved experimentally into a fast light reaction and a slow dark reaction.

The results are discussed on the basis of a model which assumes the rearrangement of charges in the plane of the thylakoid membrane as a primary inducing event in the state 1–state 2 transition. This may lead to a redistribution of excitation energy among Photosystems I and II by a slow dark process, which may include a conformation change of some protein(s).

INTRODUCTION

The state 1–state 2 transition (as well as the reverse process) is known as a slow process ([1–7], for earlier experimental evidence see [4]) which needs several

* Light 1, light 2: light preferentially absorbed by Photosystem I or Photosystem II, respectively [9].

minutes for completion. Red algae are suitable objects for investigations on this phenomenon, because of the minor overlapping between the spectra of both systems [8], and also because of the degree of the fluorescence changes connected with the transition [4, 8] and the relatively fast kinetics of the transition in some of these algae. With these objects we could discriminate experimentally between a fast, low-energy light reaction and a slow dark reaction. This slow dark reaction determines the time course of the whole effect and may involve several steps. In this paper we shall mainly report on the kinetics of the dark reaction.

MATERIAL AND METHODS

Thin laminate marine species of red algae were collected in the surroundings of Roscoff (France) and handled as described in ref. 8.

Equipment for measurements of chlorophyll fluorescence was also the same as in ref. 8. Measurements were carried out at a temperature of about 20 °C. During the experiments, which often lasted several days, the algae were covered with a dialyzing membrane and provided with O_2 and nutrients by a slow stream of fresh sea water. By appropriate use of filter combinations in the actinic and the background beam and in front of the photomultiplier, it was assured that the measured fluorescence light contained no more than at most 3 % scattered actinic light. It was also assured that both the actinic and background (or second actinic) beam covered exactly the same area of the thallus.

Simultaneously, oxygen measurements were carried out [8].

RESULTS

A sudden change from light 1 to light 2 as well as the addition and removement of a light 1 beam to a light 2 background produces in *Halymenia* and in other members of the Florideae the same fast chromatic transients (Blinks-effect) and slow changes in fluorescence emission and O_2 evolution (state 1–state 2 phenomenon) as described by Bonaventura and Myers [1] on *Chlorella*, by Duysens and Talens [2] on *Schizothrix calcicola* and by Murata on *Porphyridium cruentum* [3] and on *Porphyra yezoensis* [4]. It was found, that an illumination of a few seconds with light 1, inserted between longer periods of illumination with light 2, suffices to induce a strong transition in direction to state 1. Therefore, if not mentioned otherwise, the experiments were performed in the following way: We started with material in a nearly absolute state 2 obtained after irradiation for 10 to 20 min with light 2 (550 nm) of an intensity near the upper limit of linear correlation to oxygen evolution. When this state had been reached, it did not change markedly within 60 s of darkness between two 4 min-periods of illumination with 550 nm (Fig. 1 at right). During this 60 s dark period, light 1 (443 nm) of different intensities was given for 5 s in varying distance from the onset of the next period of 550 nm light. The 4-min periods of 550 nm light had the function to maintain or to restore (after illumination with 443 nm) state 2 and to serve as a detector for the transition in state induced by a preceding short illumination with 443 nm. The height of the initial fluorescence peak (F_P) in light 2 or ΔF (the difference between this peak and steady-state fluorescence F_s) gave a quantitative measure indicating the degree to which state 1 had developed (Fig. 1). For direct

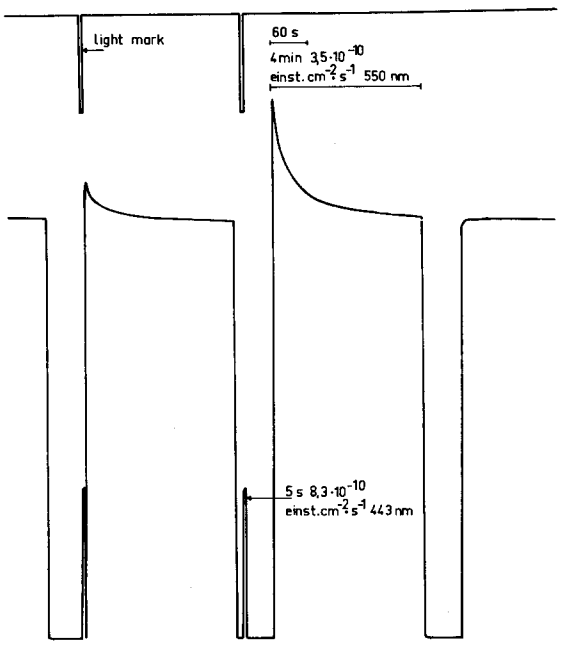

Fig. 1. Effect of a 5 s illumination with 443 nm light on the chlorophyll *a* fluorescence in a subsequent 550 nm light period in dependence on the dark-time separating both light periods. Object: *Halymenia latifolia*. At left: dark-time between the 443 nm and the 550 nm light: 2 s; middle: dark-time 45 s; at right: control, no illumination with 443 nm light, dark-time 60 s.

comparison between different series of experiments

$$\frac{\Delta F}{F_s} = \frac{F_P - F_s}{F_s}$$

was used.

The effect of a 5 s period of light 1 is strongly dependent on the distance in time from the following 4 min period of light 2. Given immediately before the 550 nm light, it has a poor effect, but if it is given at a distance of 45 s from the detector light, the effect is four-to ten fold (Fig. 1). The transition to state 1 starts with the beginning of the irradiation with 443 nm and continues nearly at the same rate in the dark as in light 1 (Fig. 2). The second (incomplete) series of measurements with *Halymenia* shows, that even an illumination of 2 s with 443 nm light of medium intensity ($8.3 \cdot 10^{-10}$ einstein $\cdot$ $cm^{-2} \cdot s^{-1}$) suffices to trigger a transition of the same proportions.

With onset of illumination with the 550 nm detecting light the evolution of the state 1 is immediately stopped and the reverse transition to state 2 is initiated. The induction of a complete transition back to state 2 also needs only a few seconds of light 2. The kinetics of this transition are roughly the same whether the whole process takes place in the light or whether it proceeds in the dark after 5 s of light 2 (Fig. 3). We did not find a first order kinetic for this process as Murata [4] did, neither with members of the Florideae nor with *Porphyra umbilicalis*. At all experi-

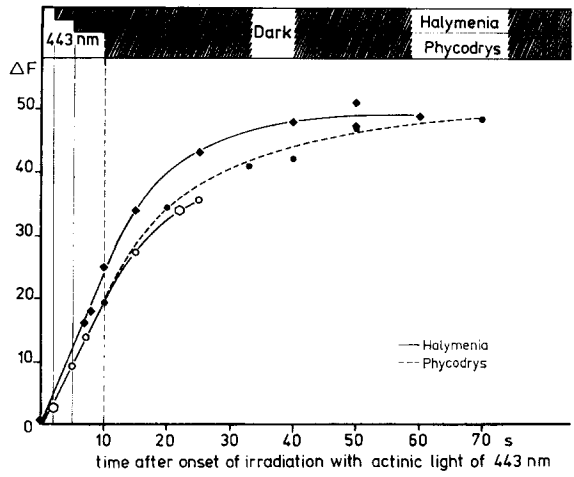

Fig. 2. Evolution of state 1 after an illumination of 2 s (◇), 5 s (◆ and ○) or 10 s (● *Phycodrys*) with light of 443 nm. The intensity of the 443 nm light was $8.3 \cdot 10^{-10}$ (*Halymenia*) respectively $6.9 \cdot 10^{-10}$ (*Phycodrys*) einstein $\cdot$ cm$^{-2} \cdot$ s^{-1}. The individual points give the values of ΔF of chlorophyll fluorescence, excited by a standard illumination with 550 nm light, $3.5 \cdot 10^{-10}$ (*Halymenia*) respectively $4.7 \cdot 10^{-10}$ (*Phycodrys*) einstein $\cdot$ cm$^{-2} \cdot$ s^{-1}. These ΔF values (in arbitrary units) are used as a relative measure for the transition in direction of state 1.

mental conditions tested, at varying intensities of 550 nm light (including very low intensities) and varying intensities of 443 nm light, we monotoneously got kinetics as shown in Fig. 4 in semilogarithmic plot.

The kinetics of transition in either direction are quite similar, as Fig. 5 shows. However in order to make a precise quantitative comparison of the kinetics of the transition in both directions, one had to make sure, that the starting points are the

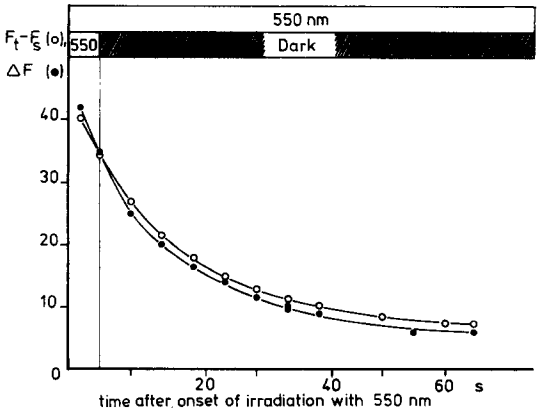

Fig. 3. Conversion of state 1 into state 2 in light 2 (○) or in the dark after a 5 s illumination with light 2 of the same intensity, $3.5 \cdot 10^{-10}$ einstein $\cdot$ cm$^{-2} \cdot$ s^{-1} 550 nm (●). An intermediate state approaching state 1 was induced by a 5 s illumination with light 1 ($8.3 \cdot 10^{-10}$ einstein $\cdot$ cm$^{-2} \cdot$ s^{-1}). F_t = fluorescence at time t, F_s = stationary fluorescence. Object: *Halymenia latifolia*. Illumination scheme: 5 s 443 nm, 20 s dark, 5 s 550 nm, 0-x s dark, 5 min 550 nm, 5 s 443 nm .....

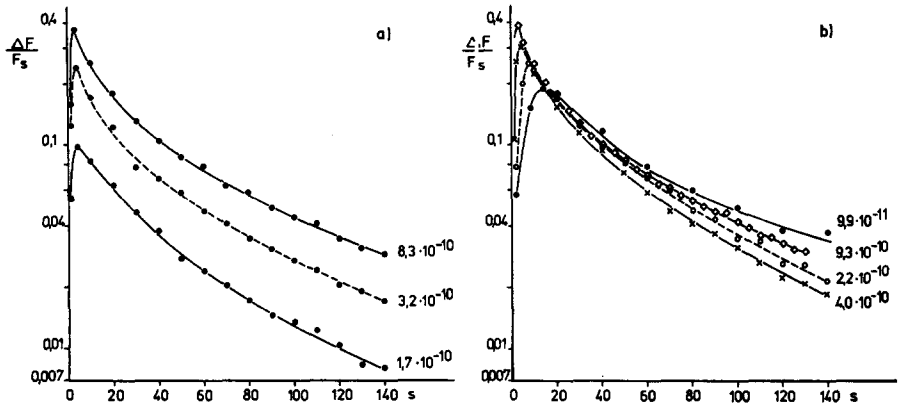

Fig. 4. Semilogarithmic plot of $\Delta F/F_s$ against time. Light 1 (443 nm) of (a) variable or (b) constant ($8.3 \cdot 10^{-10}$ einstein $\cdot$ cm$^{-2} \cdot$ s^{-1}) intensity was added to a (a) constant ($6.4 \cdot 10^{-10}$ einstein $\cdot$ cm$^{-2} \cdot$ s^{-1}) or (b) variable light-2-background (550 nm). The variable intensities are indicated at the corresponding curves. Similar kinetics are found when 443 nm and 550 nm light is given alternatively, independent of the length of the 443 nm light period. Object: *Halymenia latifolia.*

"absolute" states 1 or 2 and that no dark decay of the states takes place. Both conditions were not given in our experiments.

If the dark period following an illumination with light 1 is prolonged for more than 1 min, the initial fluorescence peak in the detecting light becomes smaller again and finally after 5 to 10 min darkness reaches a minimum value of about half the maximum (Fig. 6–8). This result corresponds with the data given by Murata [4] for *Porphyra yezoensis* (differing only in the half time of the decay), but seems to be inconsistent with some observations [1, 5] which indicate that state 1 can also be

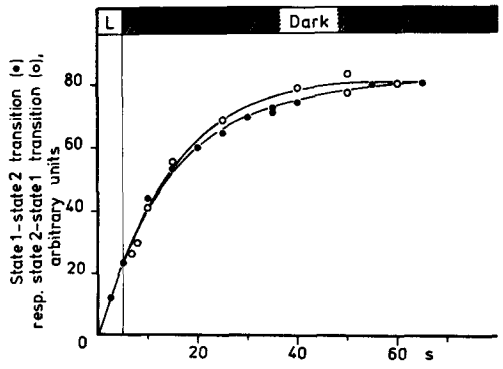

Fig. 5. Comparison of the kinetics of the evolution of state 1 during and after a 5 s illumination with 443 nm light ($8.3 \cdot 10^{-10}$ einstein $\cdot$ cm$^{-2} \cdot$ s^{-1}) (○) and of the return to state 2 during and after a 5 s illumination with 550 nm light ($3.5 \cdot 10^{-10}$ einstein $\cdot$ cm$^{-2} \cdot$ s^{-1}) (●).

Ordinate: $\frac{\Delta F \times 100}{\Delta F_{max}}$ (○) or $100 - \frac{\Delta F \times 100}{\Delta F_{max}}$ (●), respectively

Object: *Halymenia latifolia.*

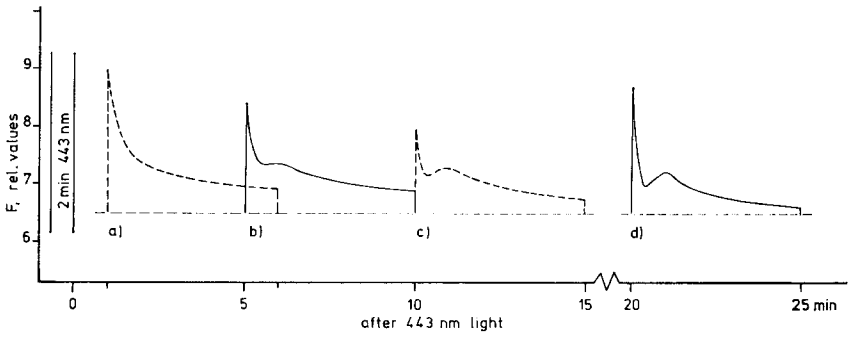

Fig. 6. Time-course curves of chlorophyll *a* fluorescence in *Halymenia latifolia* in light 2 ($3.3 \cdot 10^{-10}$ einstein $\cdot$ cm$^{-2} \cdot$ s^{-1} 550 nm) in dependence on the distance from a preceding 2 min illumination with light 1 ($8.3 \cdot 10^{-10}$ einstein $\cdot$ cm$^{-2} \cdot$ s^{-1} 443 nm). Dark interval (a) 1 min, (b) 5 min, (c) 10 min and (d) 20 min.

produced by prolonged darkness. After darkening the algae for more than 10 min the height of the initial fluorescence peak rises again and may reach, after many hours, twice the maximum peak height attained as a consequence of illumination with light 1. But the kinetics of the induction phenomenon after prolonged dark-time

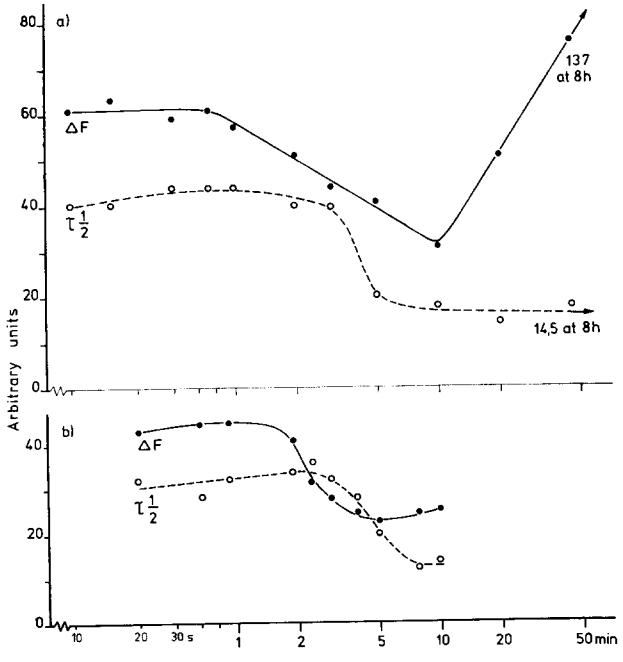

Fig. 7. Variation of ΔF and of the decay-half-time of chlorophyll *a* fluorescence in light 2 with increasing length of the dark time separating a preceding illumination with light 1 from the illumination with the measuring beam (light 2). Abscissa: Length of the dark time, logarithmic scale. Light 2 = $3.5 \cdot 10^{-10}$ einstein $\cdot$ cm$^{-2} \cdot$ s^{-1} 550 nm, light 1: (a) 2 min $8.3 \cdot 10^{-10}$ einstein $\cdot$ cm$^{-2} \cdot$ s^{-1} 443 nm, (b) 5 s 443 nm, same intensity. Object: *Halymenia latifolia*.

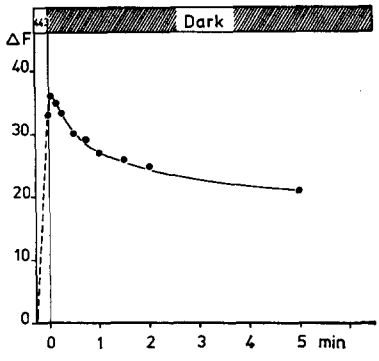

Fig. 8. Decrease of ΔF with preceding dark-time increasing, when the experiment is started with *Porphyra* in state 1. A relative state 1 (well below the absolute state 1) was obtained by a 15 s illumination with $2.1 \cdot 10^{-10}$ einstein $\cdot$ cm$^{-2} \cdot$ s^{-1} 443 nm. Measurements are made with $4.9 \cdot 10^{-10}$ einstein $\cdot$ cm$^{-2} \cdot$ s^{-1} 550 nm.

differ clearly from the kinetics of a true state 1–state 2 transition. Fig. 6 shows the gradual substitution of the kinetics of a typical state 1– state 2 transition by the kinetics of a conventional dark-light induction phenomenon (with a second flat fluorescence peak) when the dark time between the illumination with light 1 and light 2 increases. Both phenomena can be quantitatively distinguished best by their half-live time $\tau_{\frac{1}{2}}$. The gradual diminuation of the peak height of the chlorophyll fluorescence is followed, with a marked time lag, by a fairly abrupt diminuation of $\tau_{\frac{1}{2}}$. But when the peak height rises again, the values of $\tau_{\frac{1}{2}}$ remain constant for hours (Fig. 7).

The phenomena observed on members of Florideae are in principle the same as those reported from Bangiales [3, 4] or from *Chlorella* [1], they differ essentially in the rate constants of the individual processes involved in the variation of the peak height of chlorophyll *a* fluorescence (F_P) (Figs. 7, 8). In the experiments of Murata

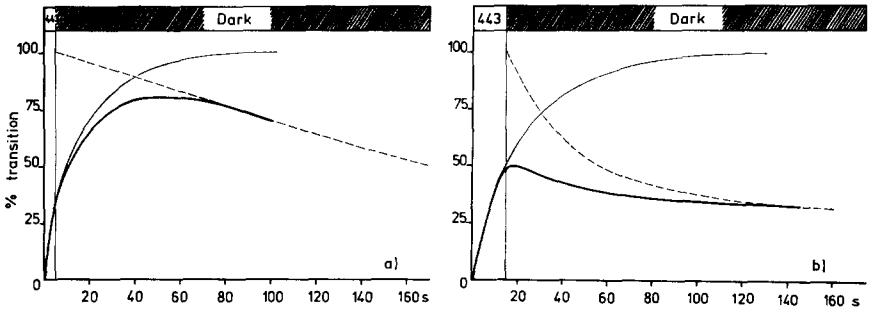

Fig. 9. Scheme: The actual state (—) varying between the initial absolute state 2 (= 0 % transition, maximum energy transfer) and the absolute state 1 (100 % transition, minimum energy transfer between Photosystems II and I) as a resultant of two counteracting processes: the conversion of state 2 into state 1 (—), induced by a short illumination with light 1 and the slow dark-decay of state 1 (– – –) which leads to an intermediate state, under our conditions approaching state 2. (a) Scheme for *Halymenia* with very slow dark decay. (b) Scheme for *Porphyra*, both counteracting processes having similar time constants.

with *Porphyra yezoensis* [4] as in ours with *Porphyra umbilicalis*, the dark decay of state 1 is much faster (by a factor of about five) than in *Halymenia* or in *Phycodrys* (Fig. 8). This may explain, as the following scheme (Fig. 9) demonstrates, why only in our experiments with members of Florideae the development of state 1 continues in the dark after a few seconds of illumination with light 1 while in *Porphyra* it does not or it continues only to a very small extent. It further explains why in *Porphyra* much longer illumination periods with light 1 are necessary for an 80 % conversion of the state than in *Halymenia*. The dark decay of state 1 may finally explain why also in *Halymenia* the full "absolute" state 1 is obtained only after illumination with light 1 of more than 1 min. In *Halymenia* as well as in *Porphyra* the $\tau_{\frac{1}{2}}$ values for the state 1–state 2 transition are greater than the $\tau_{\frac{1}{2}}$ values for the dark-light-induction phenomenon after prolonged dark time, but the difference is much greater in *Porphyra*.

DISCUSSION

The discussion of our experiments is based on the assumption that the initial enhancement of chlorophyll fluorescence in light 2 after irradiation with light 1 (respectively the slow rise of fluorescence intensity in light 1 following an illumination with light 2) is a consequence of a redistribution of excitation energy among both photosystems, as proposed initially by Bonaventura and Myers [1] and by Murata [3, 4] and as widely accepted by others in the following years (e.g. refs. 5, 7, 10, 11). The controversal interpretation of the state 1–state 2 phenomenon by Williams and Salomon [12], (variation of the quantum yield of light reactions 1 and 2) does not seem suitable to explain the fluorescence phenomena, especially the parallel rise of fluorescence yield and O_2 evolution during the state 2–state 1 transition, and, therefore, may be ignored here.

Within the scope of the first hypothesis, the relative height of the initial fluorescence peak after switching from light 1 to light 2 (represented as $\Delta F/F_s$ or, if only values of one experimental series have to be compared, as ΔF), can be used as a relative measure of the state of the object at the beginning of the illumination with light 2. This state will be in the most cases an intermediate one between state 1 and 2 (the absolute state 1: minimum energy transfer between Photosystems 2 and 1, and the absolute state 2: maximum energy transfer). It could, in the understanding of the first hypothesis, better be defined as probability of energy transfer with values between 0 and 1 (zero and maximum energy transfer). The absolute state 1 is not necessary identical with value 0 for the probability of energy transfer.

However there are some restrictions in using ΔF as a relative measure of the probability of energy transfer induced by a short light 1 period, especially if the light 2 period does not follow immediately light 1. The fluorescence yield, depending not only on the part of excitation energy diverted to Photosystem II, but also on other parameters, especially on the redox state of Q, the primary electron acceptor of Photosystem II, is therefore also a function of all factors affecting the redox state of Q. There are chiefly two facts which interfere with the effect of a change in the state on the fluorescence yield and therefore impair ΔF as a quantitative measure of the state attained after a short (triggering) light 1 period: (1) The Blinks-effect which will reduce ΔF especially if there is no time or only a short time interval between the inducing and the detecting light period, (2) a superimposed "normal"

dark-light-induction phenomenon (Fig. 6). The last effect, important only at greater distances between both light periods, is difficult to eliminate or to compensate by calculation. Also the extrapolation of the curves at zero time to get f_0 as defined by Murata [4] to eliminate the Blinks-effect does not seem practicable since the semilograthmic plots in Fig. 5 are not linear and therefore the error of an explanation may be to big. Lastly, one has to keep in mind the dark decay of the state, also being of a greater consequence only at longer dark periods between the inducing and the detecting light period (Figs. 6–8). Because all three factors may be influenced by parameters of the specific experiment in a different way, the curves of ΔF could give a more or less distorted representation of the dependency of the state on the parameter. However, the good correspondence between the kinetics of the state 1–state 2 transition with the kinetics of the state 2–state 1 transition (Fig. 5) speaks against a stronger distortion of the curves presented here.

The observation, that in *Halymenia* a light 1 period of 2 seconds suffices to induce at least a 70–80 % transition from state 2 to state 1 and that the slow process of transition goes on in the following dark time at the same or nearly the same rate than in continuous light 1 seems to us most important for the understanding of the state 1–state 2 phenomenon. It rules out some possible interpretations. The scheme in Fig. 9 gives a tentative explanation for the fact that this separation of the whole transition process in a fast light- and a slow dark-reaction was not observed with other objects like *Chlorella* [1], *Porphyridium* [3] and *Porphyra* (ref. 4 and our own experiments) and the further observation that in *Halymenia* the full transition could be obtained only with illumination times with light 1 of more than 1 min. If this interpretation is correct, it would need no more than 2 s of light 1 of medium intensity to trigger the complete transition from the absolute state 2 to the absolute state 1 if the back reaction in the dark could be prevented.

There is ample evidence for a close relationship between the light-dependent state 1–state 2 phenomenon observed in whole cells and in intact chloroplasts [10] and the light-independent effect of magnesium observed in broken chloroplasts [7, 10, 13–17]. A connection between both phenomena could be seen in the light-driven cation transport through the thylakoid membrane [10]. This concept is supported by the measurements of the light-driven cation and anion fluxes through the thylakoid membrane by Hind et al. [18], which show changes of the concentration of Mg^{2+} (and, to a smaller degree, of other ions) inside and outside the thylakoid membrane, which are of the same order of magnitude as found necessary in the experiments with broken chloroplasts to produce changes in fluorescence. Also the kinetics of these ion transport processes (in counter flow to the primary proton transport) are comparable to the slow fluorescence change. The main problem, however, for this interpretation is to explain the antagonistic effects of the two light reactions, since both generate the same electric field [19] and consequently drive an apparent influx of protons and concomitant efflux of Mg^{2+} [18, 20]. Obviously the light-induced long-term fluorescence changes, in so far as they are related to the state 1–state 2 phenomenon, do not simply indicate the high energy state or the electrochemical potential of the thylakoid membrane as Krause [16] proposes for his experiments in white light. One has to remember that the wavelength-dependent state 1–state 2 phenomenon has been shown to be kinetically distinct from the dark-light induction phenomenon for which this interpretation by Krause is given and for

which it seems very likely. The additional proposal to explain the wave length-dependence of long-term fluorescence-changes on the basis of cation fluxes, discussed in [10], that a surplus activation of Photosystem I could lead, via cyclic phosphorylation, to an increase in the chloroplast ATP pool which could stimulate the functioning of an ATP-dependent Mg^{2+} pump operating to oppose the primarily induced Mg^{2+} efflux, does not seem very likely. There is no indication of such an energy-wasting mechanism. If this mechanism would function, the steady-state electric field over the thylakoid membrane should be strongly wavelength-dependent, being much stronger in light 1. However, both photosystems contribute equally to this field [19]. Furthermore, according to this suggestion the state 1–state 2 phenomenon should vanish at low energy charge of the cell and should be replaced by an analogous wavelength-independent low-high potential phenomenon. Our finding that in some red algae a short illumination with light 1 or light 2 induces a transition in the state, which is realized in a slow reaction in the dark, seems to be another argument against a close (direct) connection between the state 1–state 2 phenomenon and the Mg^{2+} transport through the thylakoid membrane. As we will show in more detail in a following paper our results seem to be in a much better agreement with the proposal of Duysens [5], that the primary event, which induces the transition from one state to another is a change in the redox state of some components of the electron transport chains. Such a rearrangement of charges in the plane of the thylakoid membrane could induce a slow conformation change of some proteins (a process, in which the reaction of side chains with Mg^{2+} may be included). Adopting the model of Seely [21], this could lead to a reorientation of some key chlorophyll-molecules, which control the transfer of a portion of the whole absorbed energy in direction to the traps of Photosystem I or Photosystem II. Since Photosystem II of most of the red algae seems to involve only a small number of chlorophyll molecules (10 to 20 % of the number of the chlorophyll molecules of a Photosystem I unit, according to our action spectra [8], such a mechanism should work with much higher efficiency in these algae than in plants with Photosystem I and Photosystem II units of nearly equal size concerning the number of chlorophyll molecules. Functionally, this model resembles the model of Butler and Kitajima [22].

The proposed model would have the consequence, that a regulation of energy distribution among Photosystem I and Photosystem II also could be effected by a feed back from secondary photosynthetic reactions. Every change in the reduction- or the energy-charge inside the chloroplast (or rhodoplast) should react on the distribution of excitation energy by causing a rearrangement of charges in the thylakoid membrane. This mechanism would be a means to regulate not only cyclic and noncyclic electron transport, but also the energy supply of both processes. It also could explain the variable equilibrium situation in the dark.

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