Biochimica et Biophysica Acta, 766 (1984) 525–532
Elsevier

BBA 41555

PHYSIOLOGICAL ADAPTATION TO A NEWLY OBSERVED LOW LIGHT INTENSITY STATE IN INTACT LEAVES, RESULTING IN EXTREME IMBALANCE IN EXCITATION ENERGY DISTRIBUTION BETWEEN THE TWO PHOTOSYSTEMS

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(Received December 15th, 1983)

Key words: Photosynthesis; Low-light state; Excitation energy distribution; Photosystem; Photoacoustic spectroscopy; Fluorescence

In intact leaves, a new physiological state is obtained reversibly at low light intensity (typically 1 W/m^2), in which oxygen evolution yield, monitored by the photoacoustic method, approaches zero. In this 'low-light' state, irradiation with far-red ($\lambda > 700$ nm) background light immediately restores the normal oxygen yield, resulting in an unusually high Emerson enhancement ratio. Quantitative analysis of the enhancement ratio and the saturation curve of enhancement by far-red light shows that in the new state, short wavelength excitation does not reach PS I reaction centers, resulting in an extreme imbalance between the two photosystems. We suggest that adaptation to the low-light state occurs through loss of excitonic interaction between antennae of PS I and their reaction-centers. It appears also that the 'far-red' absorbing pigments do not participate in the disconnection and remain closely attached to the reaction centers of PS I. Their number is estimated to be less than 30 per reaction center. The disconnection of the antennae from the reaction center appears to be reversed by readaptation to 'normal' light levels, as well as by a brief preillumination with broad band (400–600 nm) light, acting as a trigger. In the last case, the transition to high oxygen yield state is transient. The quantum requirement of this recovery process is very small (approx. 10 *hν*/reaction center). The adaptation times after switching from higher to lower intensities and vice versa are in the range of minutes. The fluorescence yield remains virtually constant during adaptation to the low-light state in contrast to expectations, suggesting the possibility of cyclic electron flow around PS II in this state. In a chlorophyll-*b*-less barley mutant, which lacks the light-harvesting chlorophyll-*a*/*b* protein (LHC) (and possibly the newly discovered light-harvesting chlorophyll-*a*/*b* protein associated with PS I (LHC-I)), the 'low-light' state was absent. These results are consistent with the hypothesis that these antennae complexes participate directly in the adaptation to low light intensities.

Introduction

In oxygen-evolving photosynthetic organisms, it is now generally recognized that at subsaturating light intensities the distribution of excitation energy between the two photosystems is regulated in order to maintain maximal rates of photosynthesis [1]. The discovery of this regulatory mechanism, using *Chlorella pyrenoidosa*, was made by Bonaventura and Myers [2], who coined the term state 1–state 2 transitions for the readjustment in energy distribution between PS II and PS I. State 1–state 2 transitions were also observed in higher plants by changes in the fluorescence yield [3,4] and oxygen evolution yield [5,6]. In intact leaves exposed to light that is preferentially absorbed by PS II (light 2), an increase in the quantum yield of oxygen evolution, a decrease in the yield of chloro-

Abbreviations: PS I, PS II, Photosystems I and II; LHC, LHC-I, light-harversting chlorophyll *a*/*b* complex of PS II and PS I, respectively.

phyll fluorescence and a minimum in Emerson enhancement of oxygen evolution yield were found in state 2 [5,6]. The reverse transition from state 2 to state 1 occurred as a result of irradiating the leaves with far-red light which is preferentially absorbed by PS I (light 1). State 1 was characterized by maximum Emerson enhancement of oxygen evolution and higher fluorescence yield. The mechanism of the state 1 to state 2 transition in intact leaves was suggested to occur through a decrease in the absorption cross-section of PS II and an increase in that of PS I [6], and not by the operation of 'spill-over' in state 2, i.e., direct energy transfer from PS II to PS I, so that the initial light distribution is as in state 1. A controversial issue related to state 1–state 2 transitions is the identity of a state resulting from dark adaptation. In the red alga *Porphyridium curentum,* Murata [7] suggested that the dark state was the high fluorescence state (state 1). Ley and Butler [8] reported that in the same alga, the dark state was a mixed condition of states 1 and 2. By contrast, Ried and Reinhardt [9] suggested state 2 as the dark state in several species of red algae. Similarly, Satoh and Fork [10–12] suggested that the dark state is similar to state 2 in the red alga *Porphyra perforata,* in the blue-green alga *Synechococcus lividus* and in the green alga, *Scenedesmus obliquus.* In their state monitoring, by liquid nitrogen fluorescence measurements, they could not observe state transitions during light 2 illumination and proposed that either the state transitions were eliminated during the cooling process, or that Photosystem II light does not induce state transitions because the dark state was already state 2. It is clear from the above statement that low temperature fluorescence yield measurements may not be the best way to define the light distribution state. Even room-temperature fluorescence measurements are quite complex and depend on various factors besides light distribution. State 1–state 2 and similar physiological changes are much better monitored by measuring oxygen evolution and Emerson enhancement, preferably by modulation techniques [5,6,13].

In this work, by using the photoacoustic technique, it is shown that a new adaptive phenomenon occurs as a result of changes of light intensity, in the photosynthetic apparatus of higher plants in vivo. It is demonstrated that decreasing the light intensity beyond a certain threshold results in a physiological state characterized by an extremely low oxygen evolution yield and an extremely large Emerson enhancement but with almost no change in the fluorescence yield (cf. our preliminary report [5]). The transition to the low-light state is reversible. We suggest that the 'low-light' state, which approaches the 'dark' state in the limit, is obtained through a reversible detachment of main antenna complexes from PS I reaction centers.

Materials and Methods

Plant material. We used Tobacco leaves (*Nicotiana tabacum* L. var. Xanthi) for most experiments. In some experiments several other plants were investigated: pea (*Pisum sativum*), spinach (*Spinacia oleracea*), bean (*Phaseolus vulgaris*), barley (*Hardeum vulgare* var. Lyon) and the mutant of barley, missing chlorophyll *b* [14].

Photoacoustic and fluorescence set-up. The photoacoustic signal of an intact leaf is a superposition of two vectorial contributions which stem from modulated heat and modulated oxygen evolution. The two vectorial signals can be distinguished by using nonmodulated background light of constant and high intensity, in addition to the modulated light [15]. In the presence of such background light, photosynthesis is saturated, and the modulated oxygen evolution is eliminated. In this case, the photoacoustic signal is proportional to the heat generated by the total thermal conversion of the absorbed modulated light. The photoacoustic signal due to this modulated heat is then corrected by taking into account the 'photochemical loss', obtained from high frequency (e.g., 400 Hz) measurements [15]. A detailed description of our photoacoustic apparatus capable also of monitoring modulated fluorescence from the sample was given elsewhere (cf. the accompanying paper, Refs. 6 and 16).

Results

A rather surprising decrease in the quantum yield of oxygen evolution in the steady-state was observed as the intensity of the exciting light was lowered. With 640 nm modulated light, the yield dropped to 50% of the initial maximum value at

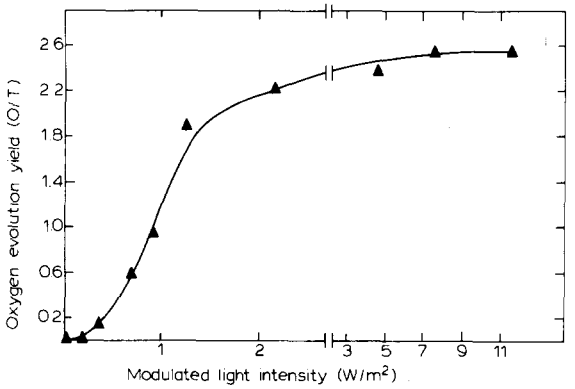

Fig. 1. Dependence of the quantum yield of oxygen evolution on the intensity of modulated 640 nm light after irradiation for 10 min at each light intensity. Modulation frequency, 15 Hz. The quantum yield is obtained as the ratio of the oxygen signal (O) to the photothermal signal (T). (Cf. Ref. 15.)

an average intensity of 1 W/m^2, and decreased to zero at intensities less than about 0.2 W/m^2 (Fig. 1). The drop in the oxygen yield was not instantaneous and was completed within 8–10 min. This new phenomenon of a decrease in oxygen evolution yield at low light intensities was entirely reversible. A typical experiment is depicted in Fig. 2. After prolonged irradiation at limiting (but not too low) light 2 intensities and achievement of a steady-state [5] characteristic of state 2 (Fig. 2a), a subsequent reduction in the light intensity by a factor of 10 resulted in a slow decrease to a very low oxygen evolution yield (Fig. 2b). Reexposing the leaf to the initial higher light intensity, resulted in slow return to the original level (Fig. 2c). This was preceded by an induction period with a characteristic lag of about 30 s, during which the oxygen yield remained low except for a small transient wave. This lag was also observed after complete dark adaptation of the leaf and depended monotonically on the dark-adaptation period (data not shown). These results suggest that the biochemical processes responsible for the decrease of oxygen evolution at low light are reversible and no permanent damage has occurred during adaptation to the low state. Fig. 2 clearly demonstrates that the change in the light intensity does not bring any instantaneous changes in yield, and that the changes in yield reflect adaptive processes.

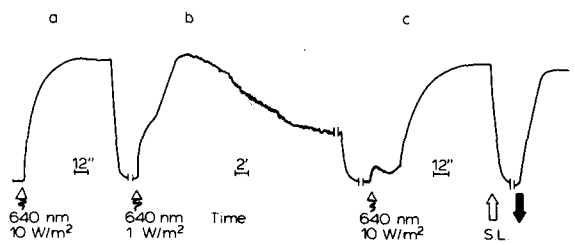

Fig. 2. Changes in oxygen evolution yield as function of irradiation period with 640 nm modulated light. (a) At intensity of 10 W/m^2. Subsequently the intensity was changed to (b) 1 W/m^2. Following low light irradiation, the intensity was changed back to (c) 10 W/m^2. Modulation frequency, 15 Hz. Saturating light (S.L.) was 300 W/m^2; band width 400–600.

We explored the effect of light 1, in the low-light state. The leaf was first adapted to the low light level, during which the oxygen evolution level dropped. Interestingly, during the drop in the oxygen yield there was almost no change in the chlorophyll-*a* fluorescence yield (Fig. 3). When the low-light steady-state level was achieved, the leaf was irradiated with 710 nm background continuous light (in addition to the weak 640 nm modulated beam). This resulted in an exceptionally large enhancement of the oxygen evolution yield, similar in all characteristics to Emerson enhancement [6]. This effect was accompanied by some fluorescence quenching (Fig. 3). The level of

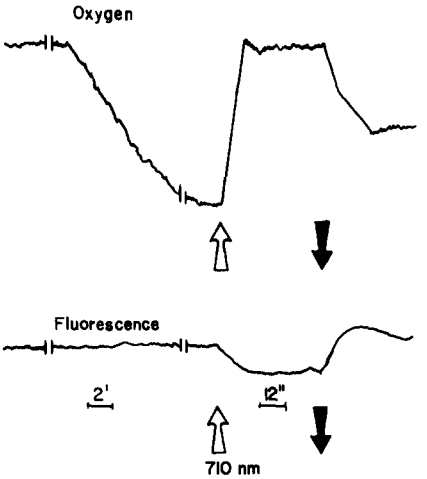

Fig. 3. Changes in oxygen evolution and fluorescence yields during the transition to the low-light state and the effect of nonmodulated far-red background light on the low-light state. Arrows indicate the switching on (⇑) and off (⇓) of the far-red light. Modulated light was 640 nm, 0.75 W/m^2. Fluorescence quenching was 10%.

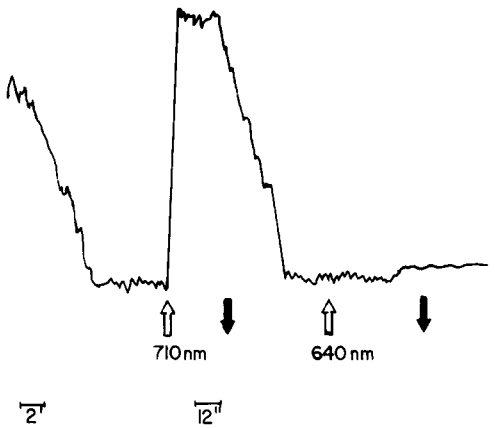

Fig. 4. A comparison of the effects of far-red and short wavelength background lights on modulated oxygen evolution yield in the low-light state, following a transition from a high-light state. Arrows indicate the switching (⇧) on and off (⬇) of either far-red light (710 nm, 2.4 W/m^2) or short wavelength light (640 nm, 1.4 W/m^2). Modulated light was 640 nm, 0.75 W/m^2, 15 Hz.

oxygen evolution yield in the presence of 710 nm background illumination was equal to or even slightly higher than the maximum yield, as obtained with the normally higher light 2 intensities (Figs. 3 and 4). When the exposure time of the 710 nm irradiation was short (less than 12 s), turning off the 710 nm, resulted in relatively immediate reversal of the oxygen yield to the original low level (Fig. 4). However, after longer exposures (e.g., 40 s), turning off the 710 nm resulted in a rather slow relaxation to a level intermediate between the low-light state and the maximum yield, reflecting some adaptation process caused by the 710 nm light itself (Fig. 3). This enhancement was specific for the far-red light, since addition of 640 nm light with equal absorbed intensity did not cause any immediate change whatsoever in the low yield of oxygen evolution (Fig. 4).

The electron transfer apparatus in the low-light state is probably intact, as the far-red light immediately (in about 300 ms or less) restored oxygen evolution. For this reason, it also appears that in the low-light state, the delivery of light 2 excitation to PS I reaction centers is severely limited since the restoring far-red light is specifically absorbed in PS I. The saturation curves of the Emerson enhancement in the low-light state and of concomitant fluorescence quenching, shown in Fig. 5, are consistent with this interpretation. In this particular case, the low-light state was not completely obtained. Assuming the separate package hypothesis, the maximum enhancement ratio is equal to the ratio between the fraction of photons delivered to PS II (β) and that delivered to PS I (α), giving $E = \beta/\alpha$ [6]. In the transition from state 2 to the low-light state, β presumably did not change, as the levels of modulated oxygen evolution in the presence of far-red light are approximately the same. Hence, from the maximal enhancement ratio in this case, $E = 3.4$, α and β are estimated to be 0.14 and 0.48, respectively. An independent estimate is based on the slope of the enhancement curve [6]. Here, we will represent this in the following simple way: at the point of the minimal intensity of the far-red light where the maximum enhancement is just obtained, there is a perfect balance of excitation between the two photosystems. The distribution of the far-red light is presumably the same in the low-light state as in the normal state (i.e., $\alpha' = 0.72$; $\beta' = 0.28$; cf. Ref. 6). For a perfect balance situation: $\beta i + \beta' I = \alpha i + \alpha' I$, from which $\beta - \alpha = (\alpha' - \beta')(I/i) = 0.44(I/i)$ is obtained (where i is the average modulated light 2 intensity and I the far-red (710 nm) intensity). The maximum ratio was found to be approx. 0.64, yielding $\beta - \alpha = 0.28$ in quite a reasonable agreement to the former estimate (0.34), considering all the uncertainties.

This experiment indicates very large imbalance between the photosystems in which PS I reaction centers receive only little 640 nm modulated exci-

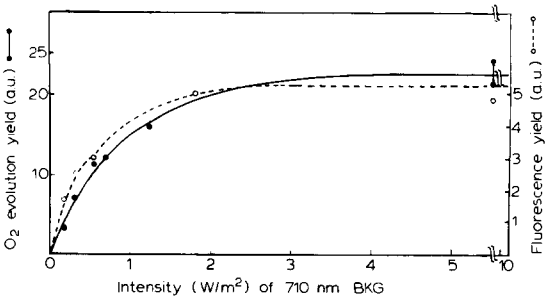

Fig. 5. Intensity dependence of far-red light enhancement of oxygen evolution (●———●) and fluorescence quenching (○- - - - -○). Exciting light was 640 nm, 1.1 W/m^2 modulated at 15 Hz. Ratio of photons absorbed at 710 and 640 nm, respectively, for equal energy fluxes was 0.67 from the corresponding photothermal signals [15]. BKG, background.

tation. In the extreme low-light state obtained at lower intensities where oxygen evolution approaches zero (actually within the experimental noise which is about 10% of the maximum level), the calculated Emerson enhancement increases to 'infinity', relfecting the tendency of α to zero.

Induction of a reverse transition by short exposures

In the low-light state, an exposure of the leaf to continuous white light of high intensity resulted, after turning off the white light, in a transient increase of the oxygen evolution yield to the maximum level, which was then followed by a subsequent decrease, back to the level of the low-light state (Fig. 6). While studying this phenomenon in more detail, it turned out that very short exposures (less than 3 s) were sufficient to obtain the maximum transient. The saturation curve for this light effect is illustrated in Fig. 7, showing the maximum yield obtained by this effect as a function of the light intensity, for a given exposure time. It was observed that the maximal transient oxygen yield could be induced by broad band (400–600 nm) light with a minimal intensity of 3.2 W/m^2. The dependence of the oxygen evolution yield on the exposure time for a given intensity is shown in

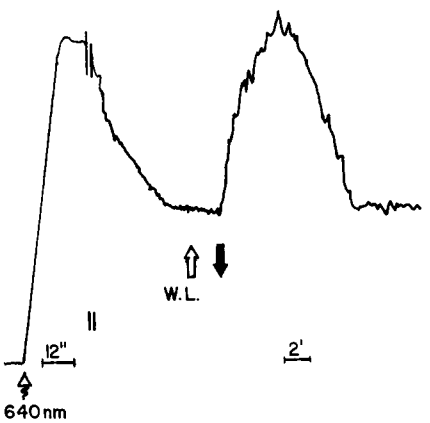

Fig. 6. The effect of intense light in the low-light state on the oxygen evolution yield. The decrease in oxygen evolution yield induced by illumination with modulated 640 nm light (0.75 W/m^2, 15 Hz) was followed by a transient increase in the yield after 2 min irradiation with saturating nonmodulated light (400–600 nm, 300 W/m^2; W.L., white light). This figure shows the total photoacoustic signal. The zero level for oxygen evolution is the level obtained with the addition of (nonmodulated) saturating light.

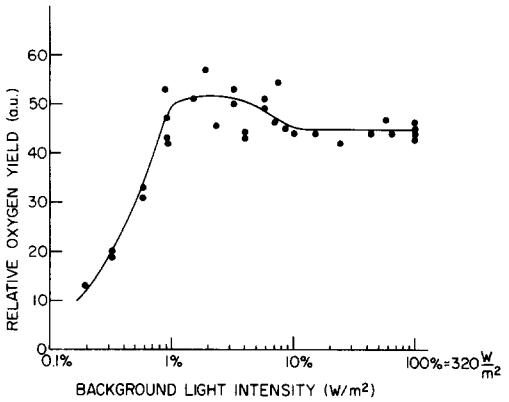

Fig. 7. Dependence of the transient peak in the O_2 yield increase, due to a short exposure in the low-light state, on the light intensity during the exposure. Exposure time 45 s; band width 400–600 nm. Modulated light, 640 nm, 0.75 W/m^2, 15 Hz.

Fig. 8. In this case, half of the maximal oxygen yield was reached with $t < 1$ s illumination period. The kinetics of the transient increase in the oxygen evolution yield was considerably slower than the time of illumination (in this case 30–40 s vs. 2 s) (Fig. 6). These results suggest that the transient increase in oxygen evolution yield, induced by the broad band background illumination, can be divided into a fast photochemical triggering reaction followed by a slow dark process. The quantum requirement for obtaining half of the maximal oxygen yield was caluclated from Figs. 7 and 8 and was approx. 2 nE/cm^2. If far-red light was added at any time during the increase in the yield of oxygen evolution, as shown in Fig. 9, the yield

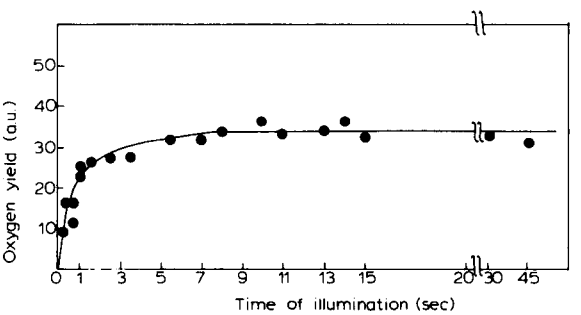

Fig. 8. Dependence of the transient peak in the O_2 evolution yield increase, due to a short exposure in the low-light state, on the duration of the exposure. Intensity during exposure with broad band light (400–600 nm) was of 23 W/m^2. Modulated light 640 nm, 0.75 W/m^2, 15 Hz.

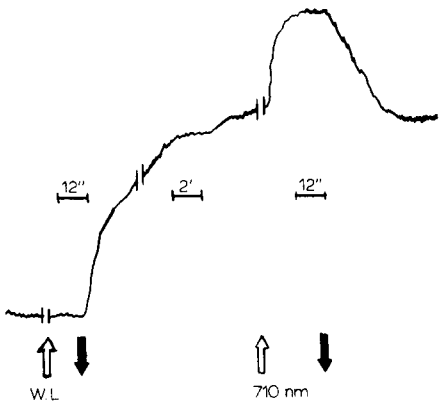

Fig. 9. Emerson enhancement of O_2 evolution yield by far-red light, following irradiation with 640 nm at a midpoint during the transient increase from the low-light state. At the low-light state, the leaf was irradiated for 2 min exposure with 400–600 nm, 20 W/m^2 (white light, W.L.). Modulated light was 640 nm, 1.1 W/m^2, 15 Hz. Nonmodulated far-red light was 710 nm, 2.4 W/m^2.

obtained was always the same maximum. This indicates that the increase of the yield after exposure to high light intensity is a true reversal of the adaptation to low light levels.

Fig. 10 illustrates that the increase in oxygen evolution yield after illumination with photosynthetically saturating light is accompanied by a simultaneous decay in the fluorescence yield. During the irradiation in the presence of the saturating light, the oxygen evolution yield could not be measured by the photoacoustic method [16]. The almost instantaneous fluorescence yield increase reflects the rapid reduction of Q. The following decrease probably has different reasons, and its level at any moment corresponds to a (varying) F_{max} [17], an indicator of a complete reduction of Q. Upon cessation of the strong background illumination, there was an immediate decrease of fluorescence, reflecting partial oxidation of Q, as its oxidation level adjusts to the weak modulated beam by rapid electron transfer from PS II reaction centers. This was followed by a slow kinetic phase during which the recovery of oxygen evolution and the further decay of fluorescence had parallel kinetics (Fig. 10) having half-time 36 and 40 s, respectively. The slow decay of fluorescence could indicate gradual oxidation of Q to completion (in this particular case from a level at which about 40% of Q is initially reduced). Thus, in this reversal from the low-light state, the oxygen evolution and fluorescence yield do change in a complementary fashion. This is in contrast to the constant level of the fluorescence yield during the decrease of the oxygen evolution yield in the transition from high to low light levels (Fig. 3).

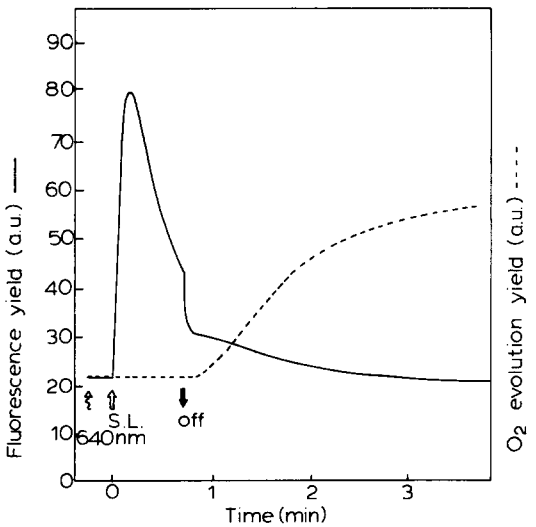

Fig. 10. Changes in fluorescence yield (———) and O_2 evolution yield (- - - - - -) with time during irradiation with nonmodulated white light (W.L., 400–600 nm, 300 W/m^2) and after switching off W.L. with the modulated 640 nm light (1.1 W/m^2, 15 Hz) alone. S.L., saturating light.

The above phenomenon of adaptation to low

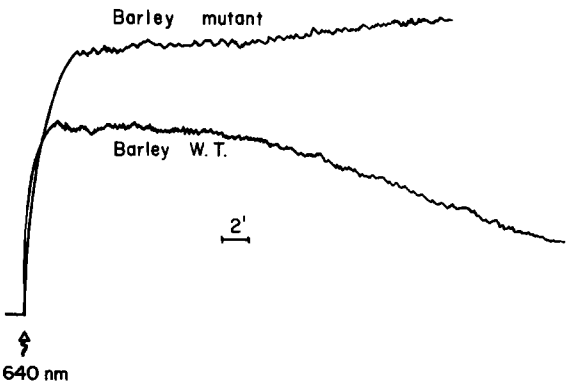

Fig. 11. Comparison of changes in oxygen evolution yield with time in barley and in chlorophyll-*b*-less barley mutant, during irradiation with weak modulated light (640 nm, 1.1 W/m^2, 15 Hz), after starting with an initial state at higher light intensity.

light levels was observed in several other higher plants such as pea, bean, spinach and barley. However, in the chlorophyll-*b*-less barley mutant [14] missing the LHC [18] and possibly also the LHC-I, the antennae of PS I [19], this adaptation to low light intensities did not occur. A comparison between barley and barley mutant after exposure to low light intensity for a prolonged period of time is shown in Fig. 11. In the barley mutant, the oxygen yield after prolonged adaptation to low light 2, even somewhat increased.

Discussion

Our results can be explained by a new physiological state in higher plants, in which at low light intensities, the photosynthetic oxygen evolution yield decreases to very low levels, approaching zero in the limit. This phenomenon appears to be general, since it was observed for several higher plant species. From the observations of the large (in the extreme case almost 'infinite') Emerson enhancement, and its far-red light saturation curve, we can conclude that the reason for the low oxygen yield in the low-light state is rooted in an extreme case of imbalance between the two photosystems, in which hardly any short wavelength light reaches PS I reaction centers. There must be a loss of interaction between the antennae of PS I and its reaction centers as required for efficient excitation transfer. However, since the far-red light remains photochemically efficient, it seems that the special pigments having the far-red absorption remain in very close contact with the reaction centers, very probably in the 'core' of PS I [19]. It is suggested that adaptation to the low-light state occurs through a detachment or a change in orientation of the main antennae of PS I with respect to their reaction centers, in an extent sufficient to abolish energy transfer from these antennae to PS I reaction centers.

The detachment of the major antennae of PS I appears to be reversed by readaptation to 'normal' light levels as well as by very short illumination with strong light, which induces a gradual restoration of the oxygen evolution yield to its initial high level in the period following low level illumination. As shown, this recovery process is triggered by a fast photochemical reaction with a quantum requirement of 2 nE/cm^2. Since the chlorophyll density in intact leaves amounts to about 40 μg Chl/cm^2 [15], it is calculated that about 1 photon per 20 chlorophyll molecules is sufficient to trigger the reversal to the 'high light' level. This number closely corresponds to the plastoquinone (PQ) pool [20]. One could speculate that it is the reduction of the PQ pool that triggers the transition from the low- to high-light state, similar to its role in the regulation of excitation transfer between the photosystems during state 1 $\leftrightarrow$ state 2 transitions [21,22].

It is interesting that in the chlorophyll-*b*-less barley mutant, which lacks the major LHC associated with PS II [18] and the LHC-I associated with PS I [19], the transition to the low-light state was absent. In this mutant, state 1 $\leftrightarrow$ state 2 transitions were missing as well [3,6]. The phosphorylation of the major LHC [21–23] and its migration from PS II-rich grana to PS I-rich stroma [24] was implicated in the control of excitation distribution through change in the absorption cross-section [6] of the photosystems. It is then suggested that LHC-I and possibly LHC are necessary for the regulation of adaptation to low light intensities, and probably are playing a direct role in this process.

During the decrease in oxygen evolution yield in the transition to the low-light state, the fluorescence yield increased only very slightly. If the 640 nm modulated light cannot be transferred to PS I, it would be expected that during the decrease in oxygen yield, fluorescence would increase tremendously, due to an expected closure of PS II reaction centers. The fact that the fluorescence remained nearly constant can be explained by appearance of cyclic electron flow around PS II, leading to no net oxygen evolution, and keeping a steady-state of low fluorescence. Immediately after short exposure to strong light, the fluorescence attains a new steady-state value indicating partial reduction of Q and therefore partial inhibition of the cyclic flow around PS II. From that point in time, the fluorescence decrease and the oxygen yield increase are correlated, as the extent of limitation set by PS I in balancing the state of PS II reaction centers, is decreasing.

A possible speculation on the order of events triggered by strong light, causing a reversal from a

low-light state, is as follows: illumination with strong light reduces the plastoquinone pool (leading to high fluorescence), which somehow triggers the reattachment of antennae to PS I. Then energy-transfer to PS I is resumed and results in the regular noncyclic electron flow. The cyclic electron flow around PS II is inhibited immediately after the strong light triggering period.

The extent of decrease to very low oxygen yield in the low-light state shows that the ratio of the (remaining) far-red pigments in PS I to the bulk pigments in PS II is at most about 1/10 (the noise level of the experiment), assuming equal specific absorption at short wavelengths. For a PS II 'classical' unit size of 300 chlorophylls, the number of far-red absorbing pigments is then less than 30, corresponding to a very small antenna core around PS I reaction centers.

Possible alternative explanations to the low-light effect must be eliminated when taking into account the entire body of data: a decrease in the oxygen yield due to the decay of S states must be rejected, as the low state is not immediately reversed by the exposure to moderately strong light 2, while a comparable or lower intensity of light 1 increased the yield momentarily. Other processes may occur as well during the decrease of oxygen evolution yield such as changes in the ATP pool, or in energy utilization by carbon assimilation [25]. However, these processes are kinetically slow and cannot provide an adequate explanation for the almost instantaneous far-red-induced enhancement of oxygen evolution to maximal yield, occurring in less than 300 ms, during which the total photon input (intensity × duration) corresponds to only about two turnovers of electron transport. Likewise, there is no adequate alternative explanation for the absence of the transition to low-level state in the barley mutant, differing from the wild type only in the light-harvesting antennae.

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