Evidence that phosphorylation and dephosphorylation regulate the distribution of excitation energy between the two photosystems of photosynthesis *in vivo*: Photoacoustic and fluorimetric study of an intact leaf

(state 1/state 2/Emerson enhancement/photosystems I and II)

ORA CANAANI, JAMES BARBER*, AND SHMUEL MALKIN

Biochemistry Department, Weizmann Institute of Science, Rehovot 76100, Israel

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ABSTRACT State 1–state 2 transitions in an intact tobacco leaf were monitored by the photoacoustic method. Modulated oxygen evolution yield and its enhancement by continuous far-red light (“Emerson enhancement”) were used to characterize the balance of light distribution between the two photosystems. These measurements were additionally supported by fluorimetry. Adaptation of the leaf to far-red light ($\lambda \geq 700$ nm), mainly absorbed in photosystem I (light 1), results in state 1, where short-wavelength light (light 2) is distributed in favor of photosystem II. This is shown by a low yield of oxygen evolution, a high extent of Emerson enhancement, a concomitantly high extent of fluorescence quenching by far-red light, and a low ratio of the 77 K emission peaks at 730 and 695 nm. The magnitudes of these parameters were reversed when the leaf was adapted to light 2 (state 2), indicating a change towards a more equal distribution of the excitation between the two photosystems. Preincubation of an intact leaf with NaF, a specific phosphatase inhibitor, stimulated the extent of adaptation to light 2, shown by all the above criteria, and completely abolished adaptation to light 1. Light 1 preillumination prior to NaF treatment resulted initially in state 1, but then a transition to state 2 was irreversibly induced by any light. The NaF effect was specific because NaCl did not affect the state 1–state 2 transitions. Leaching out the NaF restored the original physiological transitions of the leaf. NaF presumably acts here in the same way as it acts in isolated thylakoids—by blocking the dephosphorylation of membranal proteins (particularly the chlorophyll a/b–protein complex) phosphorylated by a light 2-activated kinase. Our results give direct support to the suggestion [Allen, J. F., Bennett, J., Steinback, K. E. & Arntzen, C. J. (1981) *Nature (London)* 291, 25–29] that it is the phosphorylation level of thylakoid proteins that controls the light distribution between the two photosystems *in vivo*, shown previously in isolated thylakoids.

Photosynthetic noncyclic electron transport of oxygen-evolving organisms is mediated by two light reactions acting in series and driven by two photosystems, I and II (PSI and PSII). A balanced distribution of absorbed excitation energy between the two photosystems is required for maximum efficiency. If one of the photosystems is excited more frequently than the other, the excess excitation energy is then dissipated as heat and fluorescence, resulting in a smaller quantum efficiency for electron transport, a situation that can be detected by the “Emerson enhancement” effect (1, 2).

In response to the light spectral composition, there are physiological adaptation processes by which photosynthetic organisms can regulate the distribution of absorbed excita-

tion energy between PSI and PSII. These were first described in algae (3–5) and are commonly known as state 1–state 2 transitions (2–8). State 1 results from illumination that over-excites PSI (light 1—e.g., far-red light, $\lambda \geq 700$ nm). In this state, shorter-wavelength light (light 2—most typically 650 nm) will be initially distributed so that PSII receives excess excitation relative to PSI. Conversely, state 2 results from an adaptation of an initial over-excitation of PSII by light 2, leading towards a more balanced distribution. These changes are reflected in the levels of oxygen evolution, chlorophyll a fluorescence, and the immediate effect of far-red light on them: enhancement of oxygen evolution (Emerson enhancement) and quenching of fluorescence. The extent of the immediate far-red light effect indicates the degree of over-excitation in PSII relative to PSI. These changes are also reflected in the low-temperature (77 K) chlorophyll a emission spectrum (5). In state 2 the longer wavelength emission peak (between 715 and 730 nm), originating from PSI, is enhanced relative to the shorter wavelength peaks (≈ 684 and ≈ 695 nm) associated with PSII, compared to those of cells adapted to state 1. In leaves, state 1–state 2 transitions were also observed, but only by room-temperature fluorimetry (9).

The molecular mechanism behind the above transitions is still not resolved conclusively. It has been suggested (7) that these transitions could stem from controlled changes in the concentration of (various) cations in the vicinity of the photosynthetic membranes; these changes in isolated thylakoids were shown to affect the balance between the two photosystems (8). More recently it was alternatively shown that effects similar to state 1–state 2 transitions were artificially induced in isolated thylakoids by changing the phosphorylation level of their membranal proteins. When thylakoids were supplied with ATP, membranal proteins, notably the light-harvesting chlorophyll a/b protein (LHChl), were phosphorylated (10–12) by a protein kinase and dephosphorylated (13) by a phosphatase (14). This reversible phosphorylation of LHChl was accompanied (with similar kinetics) by a decrease in the chlorophyll fluorescence yield (15). This and changes in partial reactions of PSII and PSI indicated that, as the extent of phosphorylation increases, smaller and larger proportions of the absorbed excitation energy reach PSII and PSI, respectively (15–20). It was shown that the initial state of balance between the two photosystems is sensed by the redox level of an intermediate electron carrier, possibly plastoquinone (17, 18, 20, 21), which transmits a control signal to activate the kinase when the photosystems

Abbreviations: PSI and PSII, photosystems I and II, respectively; LHChl, Light-harvesting chlorophyll a/b protein.

*Permanent address: ARC Photosynthesis Research Group, Department of Pure and Applied Biology, Imperial College, Prince Consort Road, London SW7 2BB U.K.

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are imbalanced. The changes in the balance between the two photosystems have been mostly explained by opposite changes in the cross sections for light absorption of the photosystems caused by partial migration of antennae (possibly LHChl) from one photosystem to the other, and vice versa (22–24). Such migration possibly arises from changes in electrostatic interactions induced by the charged phosphoryl group (25).

There is a strong tendency to relate the *in vivo* state 1–state 2 transitions to the transitions between nonphosphorylated to phosphorylated state of the membrane proteins, based on similarities of fluorescence phenomena accompanying these transitions. For example, a similar time course as well as the effect of light 1 were found for the light-induced fluorescence decrease from isolated thylakoids in the presence of ATP and for the light-induced fluorescence change in a leaf (9, 15). However, the evidence is still circumstantial. Moreover, there were persistent claims that there is no relevance of the thylakoid protein phosphorylation to the state 1–state 2 transitions, based on direct measurements of changes in the phosphorylation level *in vivo* (26, 27), which yielded negative results. Considering that such changes are difficult to detect directly, we reexamined whether phosphorylation plays a role in the state 1–state 2 transitions by looking at the effect of the phosphatase inhibitor NaF (14, 28) *in vivo*, expecting, in this case, the attainment of maximum of phosphorylation. We demonstrate that, in the presence of NaF, which is incorporated into a leaf, only state 2 is reached, and the transition to state 1 is inhibited. This is direct experimental proof that, *in vivo* (in an intact leaf), protein phosphorylation brings about the transition to state 2, and its dephosphorylation brings about the transition to state 1.

An important feature of our studies is that the quantum efficiency of photosynthesis in both states has been mainly monitored by the yield of oxygen evolution rather than by chlorophyll fluorescence, as was mostly done previously. Fluorescence can be influenced by various irrelevant parameters, whereas oxygen yield measurements allow direct and quantitative evaluation of the activity ratios between PSI and PSII. We have been able to accomplish this in an intact leaf by using modulated light coupled to microphone detection. The modulation technique allows, in this case, direct measurements of the relative oxygen-evolution quantum yield and effects of added various (nonmodulated) illuminations on it.

MATERIALS AND METHODS

We recently developed the photoacoustic method as a tool to measure the yield of oxygen evolution from a leaf (29–31). It is based on the absorption of modulated light followed by its partial dissipation as heat and, independently, the generation of oxygen by the photosynthetic process. Heat and oxygen fluxes are partially modulated at the same frequency as is the exciting light. They are transferred by diffusion from the chloroplasts to the cell surface and cause a layer of the inner air space near the cell surface to expand and contract periodically, creating acoustic waves that propagate outside the leaf. At low modulation frequency (≤ 100 Hz), the major contribution to the photoacoustic signal arises from modulated oxygen evolution. A separation of the oxygen and the thermal signals can be achieved as described (30).

A combined photoacoustic and fluorimetric set-up was used as described (29). A circular leaf section (diameter, 1 cm) was cut and placed in a hermetically closed cavity connected through a channel to a microphone. Modulated light 2 (in most cases 650 nm, $4 \text{ W} \cdot \text{m}^{-2}$) was provided from a 450 W dc Xenon lamp, chopper, and a monochromator (10-nm bandpass). Background illumination, either far-red (710 nm)

operating as light 1 or strong, saturating wide-band (400–600 nm) light, was provided from a dc projector. The modulated and background lights were combined onto the leaf by means of a triple-branched light guide with a common end. The third branch was used to pass modulated fluorescence from the sample into a photovoltaic detector. Fluorescence emission was filtered from the exciting light by a 680-nm interference filter combined with 645-nm long-pass and 700-nm short-pass filters. The photoacoustic and fluorescence signals were analyzed simultaneously with two lock-in amplifiers and recorded. Low-temperature fluorimetry was performed conventionally in a spectrofluorimeter (Perkin-Elmer) equipped with a Dewar. The leaf was placed in a copper block, cooled by liquid nitrogen, and oriented 45° to the exciting light. Front surface fluorescence was collected.

Leaf discs of tobacco plants (*Nicotiana tabacum* L. var. Xanthi) were subjected to the different treatments prior to the experiments by immersing them in a buffer containing 10 mM mannitol and 30 mM phosphate (pH 7.4) and continuing as described in figure legends.

RESULTS AND DISCUSSION

Fig. 1 gives an example of the enhancement of modulated oxygen-evolution yield obtained when background nonmodulated light 1 (far-red) was added to modulated light 2 (Emerson enhancement; cf. also ref. 32). Light 2 was distributed in excess in favor of PSII, with distribution fractions α and β to PSI and PSII, respectively (i.e., $\beta > \alpha$). Without far-red background light, the rate of light absorption in PSI was limiting, and the modulated oxygen yield was proportional to α . However, when excess far-red light, which is absorbed almost exclusively in PSI, removed this limitation, the modulated oxygen yield was proportional to β . Hence, the relative extent of the enhancement effect is $(\beta - \alpha)/\alpha$. The far-red light, being nonmodulated, does not induce any acoustic signal by itself.

A similar but opposite effect occurs with the (modulated) fluorescence level. A certain quenching occurred upon addi-

FIG. 1. Simultaneous photoacoustic and fluorescence traces demonstrating Emerson enhancement in an intact leaf. Modulated light 2 (in this example 480 nm, $4 \text{ W} \cdot \text{m}^{-2}$) excites photoacoustic (—) and fluorescence (---) signals. Upon addition of background nonmodulated light 1 (710 nm, $18 \text{ W} \cdot \text{m}^{-2}$), the photoacoustic signal immediately increases, and the fluorescence is quenched. These effects reverse upon turning off the modulated light. The zero level for the contribution of the oxygen evolution to the photoacoustic signal is established by adding strong saturating light (SL; 400–600 nm, $400 \text{ W} \cdot \text{m}^{-2}$), which eliminates the modulated oxygen evolution. This is marked as zero on the vertical scale for oxygen evolution (ox).

FIG. 2. State 1-state 2 transitions in intact leaves and the effect of NaF on them. The state transitions were monitored by the changes in the far-red light-induced Emerson enhancement and fluorescence quenching (see Fig. 1). Modulated light was 650 nm, $4 \text{ W} \cdot \text{m}^{-2}$; far-red background light was 710 nm, $18 \text{ W} \cdot \text{m}^{-2}$. (a) Control, after incubation for 20 min in the presence of NaCl (125 mM). Similar results were obtained from an untreated leaf. (b) After incubation for 20 min in the presence of NaF (125 mM) and illumination for 10 min with modulated light 2. (c) After illumination for 10 min with light 1 followed by NaF treatment as in b. (d) After NaF treatment as in b, followed by leaching out the NaF by incubating for 3 hr more in a buffer that did not contain NaF. Arrows correspond to switching on (upward) or off (downward) of the modulated light (wavy arrow) and the various background illuminations.

tion of the far-red light because of the oxidation of the electron acceptor Q of PSII, which had been partly reduced when PSII was excessively excited.

Fig. 2a shows a typical experiment of state 2-state 1 transition. The experiment starts with a certain initial level of oxygen-evolution yield, where the base line is approximately defined by the level of the photoacoustic signal in the presence of strong, nonmodulated, photosynthetically saturating light (SL). When illumination with light 2 (650 nm) was maintained for about 15 min, there was first a slow rise in oxygen evolution with a concomitant slow decrease in fluorescence, until a steady state was achieved. This is defined as state 2 (Fig. 2a). In this state, subsequent addition of nonmodulated light 1 (710 nm) caused only a small immediate increase in oxygen evolution (small Emerson enhancement) and a simultaneous small decrease in fluorescence intensity, indicating only a slight imbalance in the distribution of the excitation energy of light 2 in favor of PSII. Prolonged illumination (15 min) with excess nonmodulated 710-nm light in addition to the 650-nm light brought about a transition to state 1. This transition was characterized by a slow increase of the oxygen evolution yield and a concomitant slight increase in fluorescence intensity in the presence of the far-red light. When state 1 was achieved and light 1 was turned off, there was an immediate substantial decrease in oxygen evolution (reflecting the "off" part in the Emerson enhancement experiment) to a level somewhat lower than that achieved in state 2. At the same time, there was a rapid increase in fluorescence yield to a much higher level than that achieved in state 2.

These results indicate that during the prolonged illumination with light 1, there was a considerable change in the distribution of the modulated light 2 in favor of PSII. The reverse transition from state 1 to state 2 was achieved by light 2 alone. State 1-state 2 transitions could be repeated reversibly several times with the same leaf disc as reported previously (9, 32). The Emerson enhancement in each state could also be repeated several times by switching on and off the far-red light repeatedly.

Assuming that the transition to state 1 requires dephosphorylation of LHChl by the phosphatase enzyme, it should be inhibited by NaF (14). A tobacco leaf was incubated for 20 min in 125 mM NaF in the dark prior to the photoacoustic measurement, and its oxygen evolution was brought to a steady state with modulated 650-nm light (state 2). This treatment resulted in a virtually undetectable Emerson enhancement and no far-red fluorescence quenching (Fig. 2b), as expected for a "pure" state 2. Further illumination with 710-nm background light for several minutes, which otherwise results in state 1, did not bring about any change; turning off the 710-nm light did not affect the level of the oxygen evolution or the fluorescence yield. These results indicate that, upon incubation of the leaf with NaF, no transition to state 1 could occur, and the system was blocked irreversibly in state 2.

In another experiment (Fig. 2c), an untreated tobacco leaf was brought to state 1 by illumination with 710-nm light before the NaF treatment. The leaf was then incubated for 20 min in 125 mM NaF in the dark. After this incubation the

Table 1. Emerson enhancement (E) and the extent of fluorescence quenching ($-\Delta F/F$) induced by addition of light 1 (710 nm) background after adaptation to preillumination and various treatments

Treatment	Preillumination		A_{ox}/A_T^*	E	$-\Delta F/F$
	λ , nm	Time, min			
Intact tobacco leaf, control	650	15	30	0.06	0.023
	650 + 710	14		0.45	0.250
+ NaF (125 mM, 20 min)	650	10	23	0.06	0.013
	650 + 710	10		0.02	0.031
+ NaF (250 mM, 15 min)	650	10	15	0.02	0
	650 + 710	12		0.02	0.012
+ NaCl (125 mM, 20 min)	650	10	31	0.09	0.061
	650 + 710	10		0.47	0.290
+ NaCl (250 mM, 45 min)	650	10	9	0.14	0.025
	650 + 170	10		0.51	0.200
+ NaF (125 mM, 20 min, then 3 hr in buffer with no NaF)	650	10	17	0.22	0.014
	650 + 710	10		0.40	0.163
+ NaF (250 mM, 15 min, then 2 hr in buffer with no NaF)	650	10	12	0.36	0.030
	650 + 710	10		0.79	0.070

E is the additional fractional extent of oxygen evolution (i.e., $\Delta A_{ox}/A_{ox}$) and $-\Delta F/F$ is the fractional extent of fluorescence decrease induced by addition of light 1 background (710 nm) after adaptation to light 2 (650) or to light 2 with excessive light 1 (650 + 710).

* A_{ox} , oxygen evolution signal amplitude; A_T , amplitude of the heat (photothermal) effect. The ratio A_{ox}/A_T is proportional to the oxygen evolution quantum yield.

initial state was still close to state 1, but an irreversible transition to state 2 occurred upon prolonged irradiation with modulated light 2, even in the presence of excess nonmodulated light 1, as indicated by the change in enhancement ratio. When a leaf was treated with NaF as in Fig. 2*b* but then reincubated in a buffer containing no NaF for 3 hr, it regained the regular pattern of state 1–state 2 transitions (Fig. 2*d*), indicating the reversible nature of the NaF effect. In all of the above experiments, the typical state 2 parameters were more emphasized after NaF treatment, with almost zero Emerson enhancement and zero light 1-induced fluorescence quenching. The effect of NaF on the transition from state 2 to state 1 is not due to an increased salt concentration: the control experiment shown in Fig. 2*a* was carried out with leaves previously treated with 125 mM NaCl, which gave exactly the same results as those of untreated leaves (32).

Table 1 summarizes the above experiments in a quantitative manner. As a typical example, the Emerson enhancement in oxygen evolution after prolonged irradiation with additional 710-nm light was about 45% in the control and decreased to as little as 2% in the NaF-treated leaf. In parallel,

the extent of fluorescence quenching decreased from 25% in state 1 in the control to 3% in the NaF-inhibited leaf.

It could be thought that NaF has some direct effect on the oxygen-evolving system itself, canceling the additional activity of PSII by light 1 and thus eliminating the Emerson enhancement effect. Indeed, with NaF there was a decrease of the photoacoustic oxygen signal (in 125 mM NaF to 80% and in 250 mM NaF to 50% of the control; cf. Table 1, A_{ox}/A_T column). However, for a leaf treated with NaCl, a similar decrease was also noted, particularly with 250 mM NaCl (to 50%). Nevertheless, even at this NaCl concentration, the Emerson enhancement in state 1 was at least as high as that for untreated leaves (50–60%), and state 1–state 2 transitions were observed in a normal manner. Thus, it appears that the decrease of signal is related to a general salt effect, and its origin is not relevant to the present issue. The fact that a complete restoration of the transition to state 1 occurred after dialyzing out the NaF makes it unlikely that any permanent damage of the oxygen-evolving system occurred.

The NaF effect was further examined by low-temperature (77 K) spectrofluorimetry. A change in the distribution of

Table 2. Ratio of intensity of fluorescence (F) peaks at 77 K from intact tobacco leaf under various treatments

Exp.	Treatment	Illumination, * nm	$F_{730}/F_{695}^\dagger$	SD
1	Intact tobacco leaf, control	640	3.7	0.2
		710	2.7	0.05
	+ NaF (125 mM, 20 min)	710	3.7	0.5
	+ NaF (125 mM, 20 min), then in buffer with no NaF (3 hr)	710	2.7	0.4
2	Intact tobacco leaf, control	640	5.0	0.2
		710	4.6	0.1
	+ NaF (125 mM, 20 min)	640 _{pre} + 710	5.9	0.1
	+ NaCl (125 mM, 20 min)	640 _{pre} + 710	4.4	0.07
3	Intact tobacco leaf, control	640	3.1	0.1
		710	2.8	0.1
	+ NaF (125 mM, 20 min)	640	4.1	0.2
	+ NaCl (125 mM, 20 min)	640	4.3	0.2

*Treatment of samples was conducted in the dark, except for experiment 2, where samples were illuminated during treatment (designated 640_{pre}). Consequently, samples were illuminated, as indicated, for 10 min. Illumination was continued during cooling (≈ 10 min) until low temperature was attained.

[†]Each ratio determination is an average of five measurements on the same leaf.

excitation energy in favor of PSI is reflected in an increase in PSI-associated chlorophyll emission (730-nm band) relative to PSII-associated chlorophyll emission (685- and 695-nm bands). Table 2 demonstrates that illumination at room temperature with light 2 resulted in a larger ratio of the PSI peak to the PSII peak compared to the case obtained with illumination with light 1 (Table 2, experiment 1 control). However, when light 1 was given after NaF incubation, the ratio of PSI/PSII emission peaks was the same as in state 2 (rather than state 1) of the control. Again, the effect of NaF was completely abolished when the NaF was leached out (Table 2, experiment 1). Another experiment (Table 2, experiment 2) produced essentially the same results, comparing the effects of NaCl vs. NaF treatments, which were carried out in the presence of light 2 and followed by light 1 illumination. After NaCl treatment and illumination with light 1, a lower ratio of PSI/PSII emission peaks was obtained compared to the case of NaF treatment. This effect can be compared to that of another experiment carried out with light 2 illumination (Table 2, experiment 3) in which both NaCl- and NaF-treated leaves gave similar high ratios. The above results show again that NaF is involved specifically in blocking the transition to a state where the distribution of excitation energy is in favor of PSII.

Because of the destructive nature of low-temperature experiments, the results reported in Table 2 required a number of measurements on different sections from the same leaf in order to approach meaningful averages. From the standard deviations and number of measurements, it seems likely that the average values for each experiment are significant. However, it was not generally possible to compare emission ratios obtained from different leaves because of too large variations, possibly caused by significant differences in their fluorescence reabsorption properties. Thus, one should not compare values between the different experiments in Table 2. The control values for the fluorescence emission peaks in state 2 for experiments 2 and 3 were lower compared to that obtained with NaF treatment. It may be assumed that, in this case, the control represents a state "midway" between states 1 and 2, whereas the NaF treatment leads to "pure" state 2. The trend, however, is always in the expected direction and is reinforced by the comparison between NaF and NaCl treatments.

CONCLUSIONS

It is shown here for an intact leaf that NaF interferes with the state 1-state 2 transitions, blocking the light 1-induced transition to state 1 and facilitating the achievement of state 2 by either lights 1 or 2. This effect is exerted mainly in the light because, after incubation with NaF in the dark in state 1, the characteristics of state 1 could be maintained initially. Consistent with work on isolated thylakoids, this effect is formulated as follows, with implication of the LHChl.

NaF inhibits the phosphatase. The kinase is switched on by light 2, leading to an increased excitation of PSI at the expense of PSII, and is switched off when PSI is excited in excess.

The work presented in this paper was necessitated by the claim that phosphorylation does not play a role in the state 1-state 2 transitions *in vivo*. Our results strongly indicate that the phosphorylation/dephosphorylation phenomenon shown *in vitro* occurs also *in vivo* and is closely linked to the state 1-state 2 transitions. In a separate work we show, from

a mathematical analysis of Emerson enhancement data, that state 1-state 2 transitions are associated with significant changes in the light-absorption cross sections of the two photosystems rather than with the operation of resonance energy transfer from PSII to PSI. It is inferred that LHChl is mobile in the membrane and can be associated with or dissociated from the two photosystems according to its phosphorylation state (22-24, 33, 34), thus causing changes in the cross section of light absorption in PSI and PSII.

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