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CHANGES IN THE REDOX STATE OF THE SECONDARY ACCEPTOR OF PHOTOSYSTEM II ASSOCIATED WITH LIGHT-INDUCED THYLAKOID PROTEIN PHOSPHORYLATION *

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Thylakoid membrane protein phosphorylation affects photochemical reactions of Photosystem II. Incubation of thylakoids in the light with ATP leads to: (1) an increase in the amplitude of three components (4–6, 25–45 and 280–300 μs) of delayed light emission after a single flash without any change in their kinetics; (2) a reduction of the flash-dependent binary oscillations of chlorophyll *a* fluorescence yield associated with electron transfer from the primary quinone acceptor, Q, to the secondary quinone acceptor, B; (3) an increase in the B^-/B ratio resulting from an increase in stability of the semiquinone anion during dark adaptation; and (4) no change in the redox state of the plastoquinone pool as determined by flash-induced photooxidation of the Photosystem I reaction center, P-700. All the above observations are reversible upon dephosphorylation of the thylakoid membranes. These data are explained by a protein phosphorylation-induced stabilization of the bound semiquinone anion, B^-. It is proposed that this increased stability may be due to an alteration in the accessibility of an endogenous reductant to B, or to an increase in dissipative cycling of charge around Photosystem II.

Introduction

It has recently been shown [1–3] that the light-harvesting antenna chlorophyll-protein complex of PS II (LHC II) is reversibly phosphorylated on a threonyl residue of a surface-exposed portion of the complex. The LHC II is phosphorylated by a protein kinase [4,5] and dephosphorylated by a membrane-bound phosphatase [3]. It has been shown [6,7] that in chloroplasts phosphorylation of LHC II, just as cation depletion [8,9], regulates the distribution of absorbed excitation energy between PS I and PS II. Phosphorylation of LHC II has been suggested to control excitation energy distribution in vivo [10–12]. It has been suggested [10,13] that the protein kinase is controlled by the redox state of the plastoquinone pool in vivo, which ultimately leads to excitation energy distribution effects similar to that of altering cation concentrations [9,14], however, phosphorylation-induced changes are suggested to operate under physiological ion concentrations and without the major structural rearrangements (i.e., destacking) seen

* The mention of firm names or trade products does not imply that they are endorsed or recommended by the U S Department of Agriculture over other firms or similar products not mentioned

Abbreviations PS, photosystem, Chl, chlorophyll, Tricine, *N*-tris(hydroxymethyl)methylglycine, TMPD, *N,N,N',N'*-tetramethylphenylene-*p*-diamine, diuron, 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU)

upon cation depletion [15]. In addition to LHC II, several other PS II polypeptides have been shown to be phosphorylated in pea thylakoids [16].

In this paper we report a secondary effect of protein phosphorylation on the primary photochemistry of PS II. We have related the results reported here to a single event: a change in the redox state of the secondary acceptor, B, of PS II [17]. Biological strategy is discussed for an alteration of the redox state of semiquinone anion under conditions that promote LHC II phosphorylation and distribution of absorbed excitation energy preferentially to PS I

Materials and Methods

Chloroplast preparation and phosphorylation Broken chloroplasts were isolated from leaves of 14–21-day-old dwarf peas (*Pisum sativum* var. Progress 9) by a method published elsewhere [11]. The isolated membranes were diluted to a concentration of 200 μg Chl/ml in a reaction medium consisting of 10 mM $MgCl_2$, 10 mM NaCl, 10 mM Tricine (pH 7.8) and 100 mM sorbitol. NaF (10 mM) was included in samples to be phosphorylated to inhibit the phosphatase activity and to allow complete phosphorylation of the chloroplast membranes. Phosphorylation was initiated by the addition of ATP (200 μM) and illumination with a tungsten-halogen lamp (200 W/m^2). Phosphorylation was carried out for 10 min at room temperature, following which the sample remained in the dark for 10 min prior to placement on ice for storage until the measurements were made. Dephosphorylated samples were prepared as above, but with no NaF in the medium, and nonphosphorylated samples received no light treatment. Phosphorylation and dephosphorylation of chloroplasts were demonstrated to have taken place by the characteristic changes in the Chl *a* fluorescence transients described earlier [11] and by fluorescence emission spectra at 77 K described by Steinback et al. [16]. To obtain reliable phosphorylation and dephosphorylation, freshly prepared chloroplasts were used, and all glassware was washed with 0.1 M HCl and rinsed thoroughly with deionized-distilled water.

Fluorescence yield The Chl *a* fluorescence yield was measured by the two-flash method [18] The actinic flash was provided by a General Radio Strobotac 1538 A and filtered through a Corning CS 4-96 blue filter. The delayed analytic flash was identical to the actinic flash but reduced in intensity by a 1% neutral density filter. Fluorescence was detected by a Hamamatsu R 928 photomultiplier that was shielded from the actinic light with a Corning CS 2-64 red-cutoff filter The analog photomultiplier output was digitized by a Biomation 805 waveform recorder and transferred to a Heath H8 minicomputer for peak-height determination

Dark reoxidation of B^-. The redox state of the secondary acceptor was determined by the diuron-induced Chl *a* fluorescence increase as described by Velthuys and Amesz [17]. The low-intensity measuring flash was provided by a xenon flashlamp filtered through a Corning CS 4-96 blue filter. The fluorescence signal was detected 90° from the analytic beam as described above

Delayed light emission. Delayed light emission was measured in the range of 12 μs to 1 ms [19] For the 12–100 μs range, saturating flashes were provided by a Phase-R model 1100 dye laser. The laser was operated with Phase-R LD490 dye in ethanol (peak emission = 479 nm). The laser pulse was 300 ns at half-height. In the 140–1000 μs range, saturating flashes were provided by a xenon flash through a Corning CS 4-96 glass filter. The photomultiplier was gated off electronically by a factor of $5 \cdot 10^3$ during the actinic flash. Further protection of the photomultiplier from the actinic source was provided by a Corning CS 2-64 glass filter. Signal artifacts from scattered light and sample fluorescence during the actinic flash were less than 1% of the delayed light emission signal amplitude Data were digitized as in the fluorescence measurement and converted to numerical form by the minicomputer.

Oxygen flash yields These were measured with a rate electrode as previously described [20]. Flashes were provided by two xenon flashlamps Rates of S-state relaxation are determined by varying the time between two flashes and measuring the effect this has on the oxygen yield on the third flash [21]

700 nm absorption change Absorption changes at 700 nm were measured with a single-beam spectrophotometer, which had a 200 μs electronic rise time. Single saturating flashes were provided by xenon flashlamps on each side of the sample

cuvette that were triggered simultaneously. The analytic light was generated from a Bausch and Lomb high-intensity monochromator adjusted to 1 nm bandwidth and operated with a regulated d.c. power supply. The analytic beam passed through an electronic shutter that was opened 60 ms prior to the actinic flash to void any excitation by the analytic light The photomultiplier was protected from the actinic beam by a 700 nm interference filter.

Results

Delayed light emission from chloroplasts is sensitive to many of the reactions associated with charge separation and stabilization in the PS II reaction center [22,23]. The effects of protein phosphorylation on delayed light emission following a single flash are shown in Fig. 1. First-flash illumination was used to minimize the modulation of delayed light emission by other phenomena such as membrane potential and proton gradients [24] and the build up of higher S-states of the oxygen-evolving system [25]. Three components were observed with half-times of decay of 4–6, 35–45 and 280–300 μs (Fig. 1) in agreement with previous results [22]. These decay rates were found to be unchanged by phosphorylation. The amplitudes, however, were enhanced 2-fold for the two most rapid components and approx. 40% for the 300 μs component in the phosphorylated membranes This enhancement of delayed light emission amplitudes was found to be reversible to a large extent upon dephosphorylation.

Because protein phosphorylation caused changes in the amplitudes of delayed light emis-

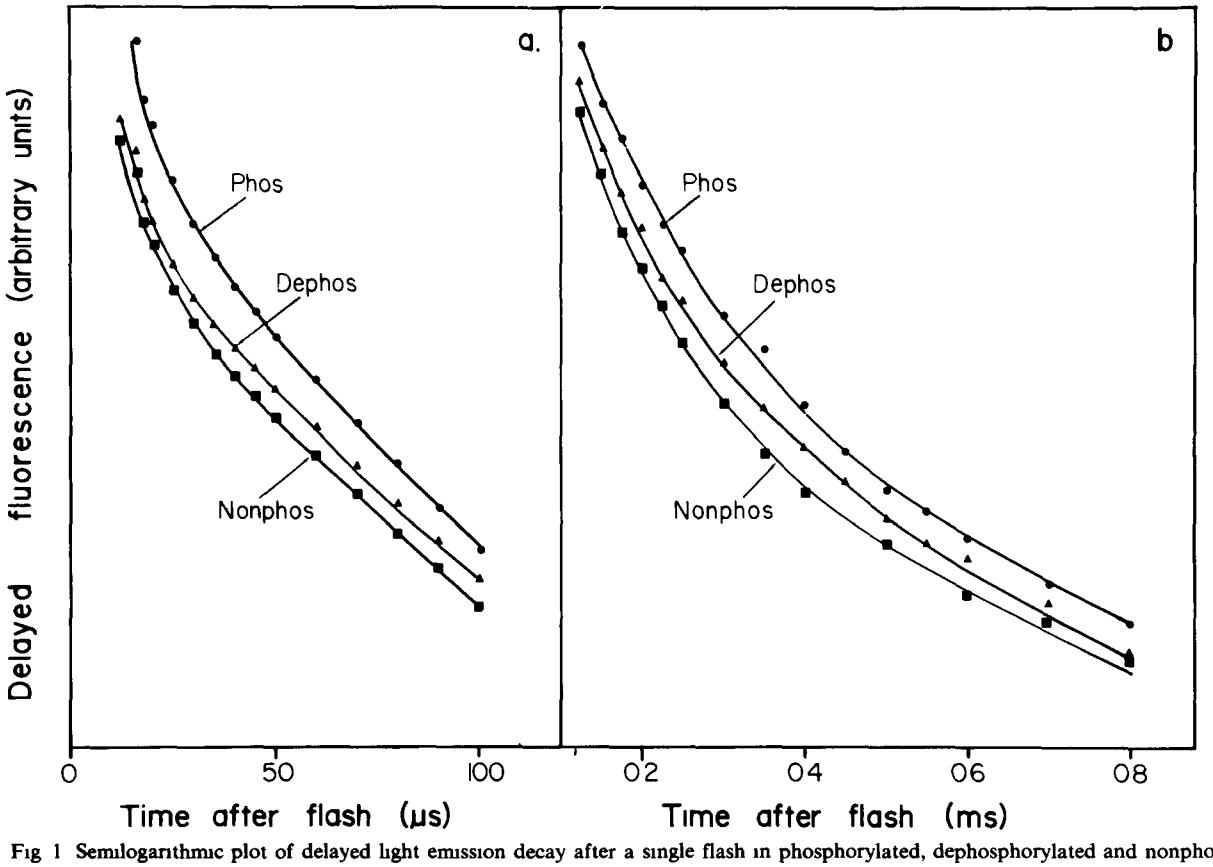

Fig 1 Semilogarithmic plot of delayed light emission decay after a single flash in phosphorylated, dephosphorylated and nonphosphorylated chloroplast samples that were dark adapted for 10 min or longer Saturating excitation flashes were generated by a dye laser (a) or a xenon flashlamp (b) See Materials and Methods for details Measurements were made at a chlorophyll concentration of 10 μg/ml

sion rather than in kinetics and were observed on the first flash, effects on the rapid charge stabilization reactions on the donor side of PS II seem unlikely However, an alteration in the state of reduction of components on the acceptor side of PS II should give the observed results.

The decay of Chl *a* fluorescence yield, following a flash given to a dark-adapted sample, is known to be biphasic [26,27] with components having half-times of approx. 200 μs and 1 ms [27] An analysis of the fluorescence decay curves after one or more excitation flashes of phosphorylated, nonphosphorylated and dephosphorylated samples is presented in Table I. The flash-number dependence of representative time points in the decay is shown in Fig 2 For the nonphosphorylated and dephosphorylated samples, the amplitudes of the fluorescence oscillates with a cycle-of-two, being low on the first flash. This is due to a high proportion of the 100–130 μs component on the first flash (Table I). This fast component has been attributed to the transfer of an electron from the reduced primary acceptor of PS II to the fully oxidized secondary acceptor [28,29] ($Q^-B \rightleftarrows QB^-$).

In phosphorylated chloroplasts, the cycle-of-two oscillation is barely discernible (Fig. 2), and the portion of the fast component changes little with flash number (Table I). According to earlier interpretations [28,29], this behavior of fluorescence decay indicates that the B^-/B ratio that occurs during dark adaptation is much greater in phosphorylated than in nonphosphorylated or dephosphorylated chloroplasts.

After many flashes, the B^-/B ratio will approach a steady-state value of unity [17]. For the dephosphorylated and nonphosphorylated samples, the portion of the 100–130 μs component after many flashes becomes approx 30–35% (Table I) It is noteworthy that this is the proportion of the fast component observed on the first flash in phosphorylated chloroplasts.

The amount of the singly reduced secondary acceptor of PS II (B^-) present in the dark can be detected by observing the level of Chl *a* fluorescence yield after diuron injection [17,30] to samples preilluminated with a series of flashes. Complications due to quenching by oxygen-evolution S-states were eliminated by incubation of the chloroplasts for at least 10 min in the dark at room temperature with 5 mM NH_2OH [30] Membrane protein phosphorylation leads to a higher level of diuron-induced Chl *a* fluorescence with no preilllumination flashes and significantly dampens the binary oscillation of this fluorescence with flash number (Fig. 3). In the nonphosphorylated and dephosphorylated samples, the dark fluorescence level is low, and pronounced binary oscillations occur.

Based on the data in Fig. 3 and assuming a constant miss parameter for flash photochemistry in all samples of 0.1 [20], estimates can be made for the B^-/B ratio in the dark. The ratio for chloroplasts that are nonphosphorylated is 0.16 0.84, but it is 0.34 : 0.66 for phosphorylated and 0.13 . 0.87 for dephosphorylated samples. The values for nonphosphorylated and dephosphory-

TABLE I

AMPLITUDES AND HALF-TIMES FOR THE TWO EXPONENTIALS IN THE Chl *a* FLUORESCENCE DECAY FROM 50 μs TO 2 4 ms

The fluorescence decay curves were analyzed by computer, using a two-component exponential-fit program, and the tabulated values represent the minimum-error fit The amplitude values (A) are the amplitudes of the variable fluorescence extrapolated back to the time of the flash The variable fluorescence is calculated as follows $\Delta F = (F_t - F_0)/F_0$ where F_t is the fluorescence level at time t after the last excitation flash, and F_0 is the fluorescence level before any excitation flashes Multiple flashes were given at a rate of 1 Hz All measurements were done at a chlorophyll concentration of 10 μg/ml

Flash	$A_{(1)}$	$T^{(1)}$ (μs)	$A_{(2)}$	$T^{(2)}$ (ms)
Nonphosphorylated				
1	1 54 (53%)	105	1 37 (47%)	1 51
2	0 66 (25%)	110	2 03 (75%)	1 38
3	0 81 (33%)	116	1 66 (67%)	1 36
Many	0 80 (30%)	101	1 87 (70%)	1 30
Phosphorylated				
1	0 58 (36%)	113	1 05 (69%)	2 64
2	0 45 (28%)	127	1 16 (72%)	2 41
3	0 53 (34%)	130	1 03 (66%)	2 58
Many	0 55 (34%)	123	1 09 (66%)	2 87
Dephosphorylated				
1	1 12 (50%)	100	1 10 (50%)	1 68
2	0 64 (27%)	105	1 72 (73%)	1 64
3	0 62 (31%)	110	1 36 (69%)	1 66
Many	0 60 (34%)	106	1 46 (66%)	1 52

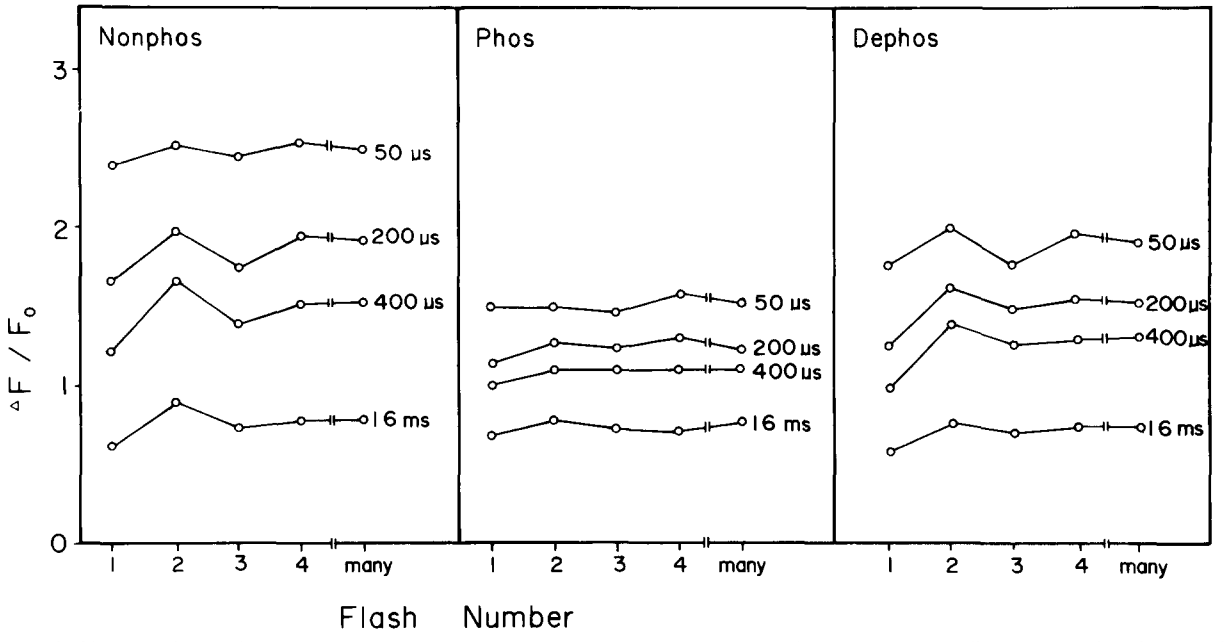

Fig 2 Variable Chl *a* fluorescence yield vs flash number at various times after the last excitation flash in nonphosphorylated, phosphorylated and dephosphorylated chloroplast samples $\Delta F = (F_t - F_0)/F_0$ where F_t is the fluorescence at time t after the flash (t is indicated in the figure), and F_0 the fluorescence level measured before any excitation flashes Multiple flashes were given at a rate of 1 Hz See legend to Fig 1 for other details

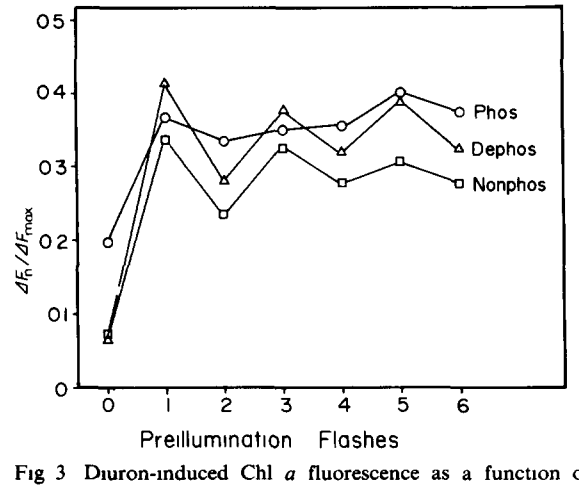

Fig 3 Diuron-induced Chl *a* fluorescence as a function of preillumination flash number in phosphorylated, dephosphorylated and nonphosphorylated chloroplast samples Measurements were made at a chlorophyll concentration of 10 µg/ml, and diuron was injected within 2 s after the last preillumination flash to give a final concentration of 10 µM Preillumination flashes were given at a rate of 1 Hz Chloroplasts were incubated with 5 mM NH_2OH for 10 min in the dark $\Delta F = (F - F_0)/F_0$ where F is the fluorescence level measured 30 s after diuron injection and F_0 the fluorescence level measured before preillumination flashes or diuron injection $\Delta F_{max} = (F_{max} - F_0)/F_0$ where F_{max} is the fluorescence level measured after the sample had diuron added and 15 excitation flashes were given

lated chloroplasts are in good agreement with previous reports [30]. A high amount of B^- in the dark appears to be associated with polypeptide phosphorylation.

The difference in the B^-/B ratio of phosphorylated and nonphosphorylated samples is established rapidly after exposure to continuous illumination to achieve a steady-state B^-/B ratio The time dependence of the B^-/B ratio, as indicated by the diuron-induced increase in Chl *a* fluorescence, is shown in Fig. 4. The B^-/B ratio is significantly larger for the phosphorylated (○——○) than for the nonphosphorylated samples (■——■) even as soon as 5 min after preillumination. This apparently is due to a more rapid reoxidation of B^- in the nonphosphorylated sample. During preillumination, the sample called dephosphorylated become phosphorylated, explaining the high initial $\Delta F_t/\Delta F_{max}$ in Fig. 4 In the dark on ice, dephosphorylation of this sample occurs in about 120 min (▲——▲) as can be seen by the merging of the dephosphorylation and nonphosphorylation curves in Fig. 4 However, at 20°C

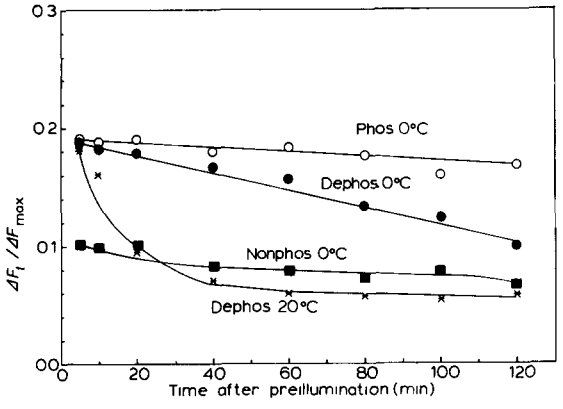

Fig 4 Diuron-induced Chl *a* fluorescence as a function of time after preillumination with continuous light for 10 min The phosphorylated (○——○), dephosphorylated (●——●) and nonphosphorylated (■——■) samples were kept on ice in the dark after preillumination For the one dephosphorylated sample (☆——☆) the dark adaptation took place at 20°C ΔF is as defined in the legend to Fig 3

(☆——☆), the dephosphorylation and consequent B^- oxidation are largely complete within 30 min (Fig. 4).

It is possible that changes in the B^-/B ratio were due to shifts in the redox potential of the medium during preillumination. To determine if this was the case, an experiment similar to that of Fig. 4 was carried out with a reaction medium that contained 10 μM TMPD and had its redox potential adjusted to +260 mV on the hydrogen scale. The $\Delta F_t/\Delta F_{max}$ at 1 min after preillumination was 0 180 for the phosphorylated and dephosphorylated samples and 0.109 for the nonphosphorylated sample. The presence of the redox mediator TMPD does not eliminate the effect of the increase in the B^-/B ratio caused by phosphorylation.

It is also conceivable that the increased stability of the bound plastosemiquinone anion (B^-) may be due to an increased level of reduction of the free plastoquinone pool by protein phosphorylation. This was tested by observing the number of flashes required to oxidize completely the plastoquinone pool and P-700 in chloroplasts in the presence of diuron, used to block electron flow into the plastoquinone pool. Five flashes were required to remove all the charge from the plastoquinone pool and P-700 regardless of the phosphorylation treatment (Fig. 5). A sample with its plastoquinone pool fully reduced by preillumination without diuron or methyl viologen takes 12 flashes to remove the charge (Fig. 5). Thus, it appears that protein phosphorylation does not change the extent of the plastoquinone pool reduction, but it does affect the level of reduction of the bound quinone (B) rather specifically.

Since it has been shown [30,31] that oxidized S-states are essential for B^- oxidation, it was possible that changes in the B^-/B ratio due to phosphorylation might also be reflected in changed S-state relaxation. But phosphorylation has no sig-

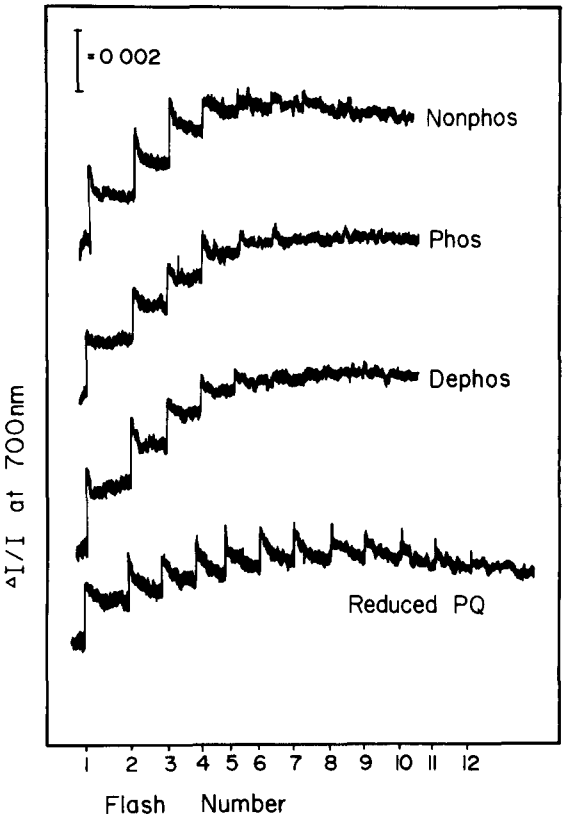

Fig 5 Flash-induced absorption changes at 700 nm in nonphosphorylated, phosphorylated and dephosphorylated chloroplast sample Chloroplast samples were dark adapted for 10 min before addition of diuron (4 μM) and methyl viologen (100 μM) The lowest curve represents nonphosphorylated chloroplasts in which the plastoquinone pool was first reduced by preillumination with 30 saturating flashes before the addition of diuron and methyl viologen Flashes were given at a rate of 1 Hz, and all measurements were made at a chlorophyll concentration of 25 μg/ml PQ, plastoquinone

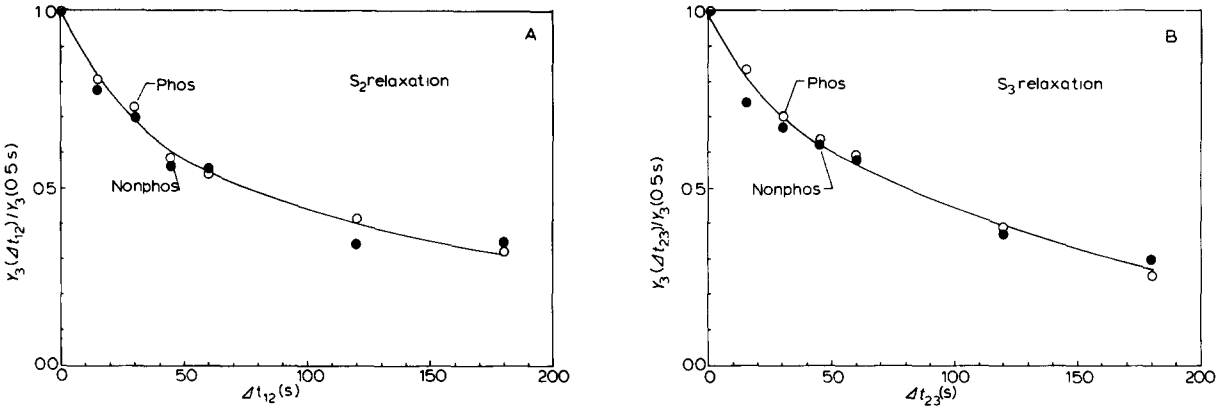

Fig 6 Oxygen yield on flash three (Y_3) as a function of time between flashes one and two (Δt_{12}) (A) and flashes two and three (Δt_{23}) (B) in phosphorylated and nonphosphorylated sample All other flashes are given at a rate of 2 Hz These samples were resuspended in reaction medium that had 100 μM NADP present as an acceptor Samples were loaded onto the electrode at a chlorophyll concentration of 0 5 mg/ml

nificant effect on S_2 and S_3 relaxation rates (Fig. 6A and B). Apparently, although B^- can recombine with the oxygen system S-states, any changes in the rates of S-state relaxation due to phosphorylation are insignificant compared to interactions with other oxidants and reductants that are endogenous to chloroplasts.

Discussion

The data presented in this paper suggest that thylakoid membrane protein phosphorylation is associated with an elevated level of reduction of B^- in the dark. In algae, it is known that the B^-/B ratio in the dark depends on the balance between an endogenous reductant and oxidation by oxygen [32,33]. In chloroplasts, this endogenous reductant is apparently absent, or at least not able to reduce significantly B or the plastoquinone pool [33]. However, some form of reductant does exist in chloroplasts and is capable of fully reducing P-700 and plastocyanin and partially reducing cytochrome *f* [34]. The increase in dark equilibrium of B^-/B in phosphorylated samples may be due to an alteration in the availability of the secondary acceptor to this endogenous reductant A similar effect has been shown on the availability of an exogenous acceptor (ferricyanide) to reoxidize the reduced primary acceptor, Q [15]. The latter case was explained by a surface charge effect with a protein phosphorylation-induced increase in the local negative surface charge around PS II.

The reversibility of the phosphorylation-induced high level of B^- was demonstrated at 20°C to occur during 30 min of dephosphorylation. This time course matches that for the dephosphorylation of LHC II, whereas that of other labeled PS II polypeptides have a somewhat longer time scale for dephosphorylation [16]. We cannot, therefore, rule out the possibility that the increase in the local negative surface charge around PS II caused by the phosphorylation of LHC II that affects the ability of an endogenous reductant to interact with B.

Another explanation for the high B^-/B ratio may be that protein phosphorylation enhances a cycling of charge around the PS II reaction center. This would be similar to the electrogenic back-reaction between $P\text{-}680^+$ and Q^- as proposed by Renger and Wolff [35] for Tris-treated chloroplasts. A cycle of this type may act as a safety valve for dissipating excess energy, when the plastoquinone pool is fully reduced and ATP levels are high, and thereby decrease photooxidation of the PS II trap and buildup of the oxygen-evolution S-states. The level of B^- in the dark is known to be dependent upon the existence of S-states [30,31]. Therefore, enhanced dissipative cycling around PS II would lead to higher stability of B^- in the dark Although these data also could be interpreted to

mean that the redox potential of B may have been altered by phosphorylation, preliminary evidence on the titration of the binary oscillations of fluorescence decay with flash number indicate that the redox potential of B is unaffected by phosphorylation (Robinson, H, Crofts, A and Kyle, D., and independently by Jursinic, P, unpublished data)

At this time we are unable to determine if the increase in the B^-/B ratio induced by protein phosphorylation is due to a surface charge effect that increases ability of an endogenous reductant to interact with B, or to the promotion of a cycle around PS II involving B The latter explanation is teliologically acceptable, since it represents a physiological mechanism that would control pressure of electron delivery to the plastoquinone pool and thereby work in concert with the phosphorylation of LHC-II, which changes the distribution of absorbed quanta to excite preferentially PS I [12]

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