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DETERMINATION AND MODIFICATION OF THE REDOX STATE OF THE SECONDARY ACCEPTOR OF PHOTOSYSTEM II IN THE DARK

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Summary

The redox state of the secondary electron acceptor B of Photosystem II was studied using fluorescence measurements. Preillumination of algae or chloroplasts with a variable number of short saturating flashes followed rapidly by the addition of 3-(3,4-dichlorophenyl)-1,1-dimethylurea induces oscillations of the initial level of fluorescence. The phase of these oscillations is characteristic of a given B/B^- ratio in the dark-adapted samples.

We conclude from our results that about 50% of the secondary electron acceptors are singly reduced in the dark in *Chlorella* cells, but that more than 70% are fully oxidized in the dark adapted chloroplasts.

Benzoquinone treatment modifies this distribution in *Chlorella* leading to the same situation as in chloroplasts, i.e. more than 70% of the secondary acceptors are oxidized in the dark.

The same ratio is observed if these algae are illuminated and then dark-adapted, unless an artificial donor (hydroxylamine) is added before this illumination. In that case about 50% B^- is generated and stabilized in the dark.

Introduction

Variable fluorescence is controlled by the redox state of the primary acceptor and the primary donor of Photosystem II [1,2]. Fluorescence yield is high only when both are in a reduced state. In addition, the two following charge storage systems modify, either directly or indirectly, the fluorescence yield:

(i) The "S" states, involved in the oxygen-evolving mechanism on the donor side, which induce changes of the initial level of fluorescence as well as changes in its maximum level [3—5].

Abbreviation: DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea.

(ii) The secondary acceptor B (or R) which, after addition of DCMU, induces changes of the initial level of fluorescence [6].

In the present paper, we analyse the initial level of fluorescence after a variable number of preilluminating flashes followed by the addition of DCMU. We studied the redox state of the secondary acceptor assuming the following hypotheses:

The charge storage system on the donor side is described according to the "S" state model [7]. Thus only S_0 and S_1 are stable in the dark. The ratio S_1/S_0 depends on the biological material studied.

The secondary acceptor is a 2 electron carrier [8]. It is stable in states B and B^-; it transfers reducing equivalents to the plastoquinone pool in state $B^=$ only.

The addition of DCMU, which inhibits Photosystem II, changes the relative redox potential of Q and B, displacing the equilibrium $QB^- \rightleftharpoons Q^-B$ to the right [6].

Thus, in the absence of DCMU, there are only four possible redox states in the dark: S_0QB, S_0QB^-, S_1QB, S_1QB^-.

Materials and Methods

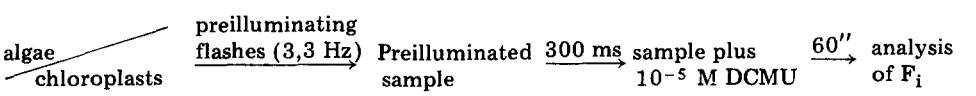
Fluorescence induction was detected at room temperature under continuous illumination in a 56 µl cuvette to which was connected a mixing apparatus. 200 µl of both the inhibitor and the sample studied were mixed for each measurement. The incident light was filtered by two blue Schott BG 38 filters and the emitted fluorescence was detected through complementary filters: Wratten 70 ($\lambda > 650$ nm) and Ulano Rubylith. Preillumination was performed with Stroboslave flashes (General Radio, model 1539A) with a 3 µs width at half height. All flashes were saturating. Fluorescence induction was followed on a Tektronix oscilloscope or a CAT 400C.

Chlorella pyrenoidosa were grown in the usual medium previously described [9]. Prior to use, the cells were suspended in 0.1 M phosphate buffer at a final chlorophyll concentration of 40 µg/ml.

Chloroplasts were prepared from market spinach according to the method of Avron [10] and stored at −70°C in 0.05 M Tris · HCl buffer, pH 7.8, containing 0.01 M NaCl, 0.4 M sucrose, 1% albumin and 5% dimethylsulfoxide. Prior to use they were suspended in 0.1 M phosphate buffer, pH 7, containing 0.4 M sucrose, 0.01 M NaCl, at a final chlorophyll concentration of 40 µg/ml.

Results

The procedure is the same for all the experiments discussed in this paper. It can be summarized as follows:



Our results were analysed with the aid of two additional hypotheses which permit the best fit between the theoretical and experimental curves: A back reaction occurs between Q^- and S_2 and S_3 only. This is supported by lumines-

cence experiments [11]. Since there is a damping in the oscillations we are studying, as is the case with the oscillations of the oxygen yield for a series of saturating flashes [7], we assume that there are "misses" responsible for these phenomena with the same origin, which is consistent with Bouges-Bocquet's results [8]. As an example, the redox successive states resulting from flash excitation of S_1QB would be:

	initial state	state after addition of DCMU	state after the back reactions	
dark	S_1QB	⟶	S_1QB	quenching states
1 flash	S_2QB^-	S_2Q^-B ⟶	S_1QB	
2 flashes	S_3QB	⟶	S_3QB	—
3 flashes	S_0QB^-	S_0Q^-B ⟶	S_0Q^-B	non quenching state

Distribution of B/B^- in Chlorella intact cells in the dark

As shown in a previous paper [12], some secondary acceptors are singly reduced in the dark.

Fig. 1b shows that after addition of DCMU, the initial level of fluorescence (F_i) oscillates as a function of the number of preilluminating flashes with a periodicity of 4. These oscillations, 180° out of phase with those due to the "S" states alone [4] are similar to one of the computed oscillations in Fig. 1a. The theoretical curves, resulting from the interaction between the donor and the acceptor side, differ in their initial B/B^- dark ratios. They have been computed with given values of S_1/S_0 ratio and misses (data from Bouges-Bocquet). It is assumed that the reduction of Q by B^- is quantitative after addition of DCMU. Thus, changes in F_i are mainly due to changes in B/B^- ratio after each flash. When compared with the experimental oscillations, they indicate that

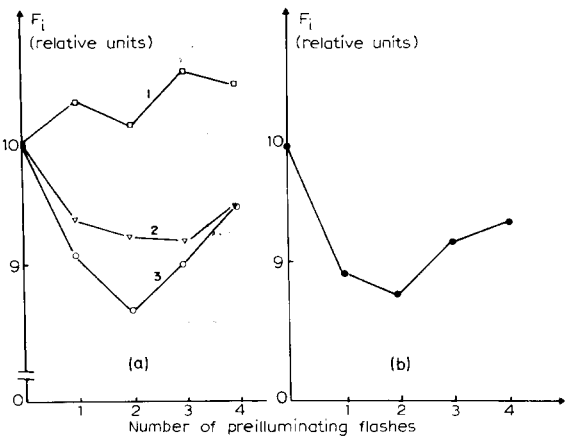


Fig. 1. Oscillations of the initial level of fluorescence F_i in *Chlorella* after a variable number of preilluminating flashes followed by the addition of 10^{-5} DCMU. (a) Theoretical oscillations calculated for different fractions of $[B^-]^-$ using α = 22%, S_0 = 28%, S_1 = 72% (data from Bouges-Bocquet). 1 $[B^-]^-$ = 0%; 2 $[B^-]^-$ = 100%; 3 $[B^-]^-$ = 50%. (b) Algae dark-adapted for 10 min, were preilluminated with a variable number of saturating Stroboslave flashes, 300 ms apart. They were then incubated for 1 min in the dark with 10^{-5} M DCMU. Temperature = 20°C.

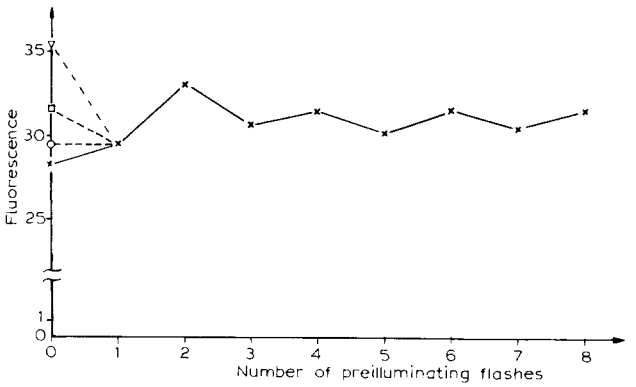


Fig. 2. F_i sequence in *Chlorella* incubated in the dark in the presence of 10^{-2} M NH_2OH. Otherwise, the procedure is the same as in Fig. 1b. The F_i of the dark adapted algae varies with the dark adaptation time when the cells are first illuminated with 10 saturating flashes (□, 3 min; ○, 5 min; X, 10 min). The evolution of the 0 flash yield does not change the subsequent oscillations. ▽, computed initial level of fluorescence of dark adapted algae for α = 19%; see hypotheses in the text.

about 50% of the total number of secondary acceptors are singly reduced in the dark.

If this were the case, one would expect to observe only very small oscillations of periodicity 2, or even no oscillations at all, when the oxygen evolving site is replaced by an artificial donor. This experiment is shown in Fig. 2 where 10^{-2} M hydroxylamine is used. As expected, we observed an oscillation of small amplitude of periodicity 2, whose phase indicates a slight excess of B^- in the dark.

The F_i level of algae dark-adapted for at least 10 min, is lower than would be expected from the phase of the subsequent oscillations. As these oscillations have misses (α) of about 19% (computed from the damping between the 1st and the 6th flash), it was possible to compute the expected level of F_i for dark adapted algae. Thus, the observed rise of F_i between 0 and 1 preilluminating flash indicates that some quenching species which could be different from Q (see Fig. 8b) disappear upon illumination.

When the algae were left for a short time in the dark (3 min) the F_i after the addition of DCMU was closer to the theoretical value we have computed than it is when the time of dark adaptation is increased to 10 min. Therefore, the F_i decreases to a limiting value which we take as the F_i of dark-adapted algae.

Distribution of B/B^- in spinach chloroplasts in the dark

Bouges-Bocquet has measured the quantity of methyl viologen reduced by System I under flash illumination when the plastoquinone pool is oxidized [8]. An oscillation of periodicity 2 demonstrates that in the dark in spinach chloroplasts $B/B^- >> 1$.

Using Tris-washed chloroplasts with *p*-phenylenediamine as an artificial donor, Velthuys and Amesz arrived at the same conclusion. When DCMU was added after a variable number of preilluminating flashes, they saw an oscillation of a periodicity 2 of the F_i indicating a major fraction of B oxidized in the dark [6].

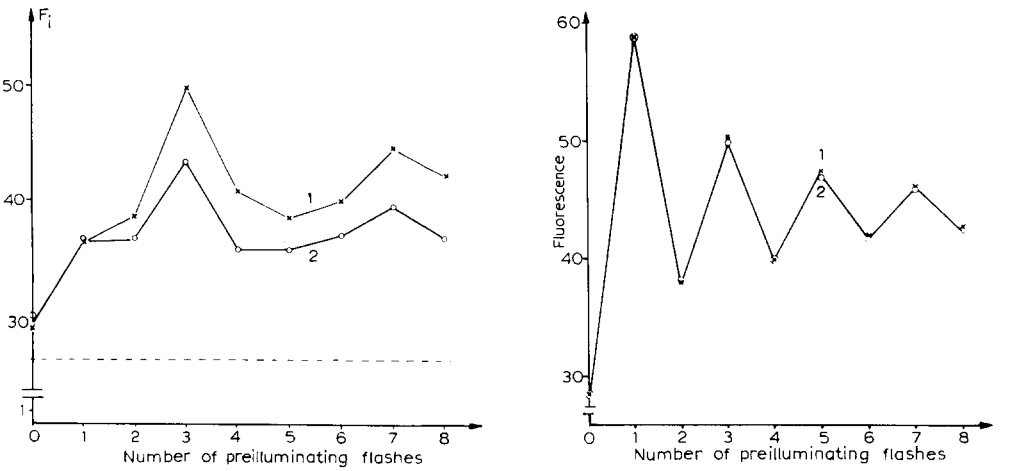


Fig. 3. F_i sequence in chloroplasts when no artificial donor is added. (X———X), curve 1: same procedure as in Fig. 1b; (o———o), curve 2: $2 \cdot 10^{-4}$ M benzoquinone is added; (- - - - -), F_i level of in dark adapted chloroplasts before the addition of DCMU.

Fig. 4. F_i sequence in chloroplasts in the presence of 10^{-2} M NH_2OH. (X———X), curve 1: same procedure as in Fig. 1b; (o———o), curve 2: chloroplasts are incubated 5 min in the presence of $2 \cdot 10^{-4}$ M benzoquinone before the addition of 10^{-2} M NH_2OH. F_{max} = 95.5 (relative units).

We checked this distribution with our experimental procedure using both untreated chloroplasts where the "S" states are the natural donors (Fig. 3, curve 1) and chloroplasts with hydroxylamine as an artificial donor (Fig. 4, curve 1). Fig. 4 confirms that there is a large excess of B in the dark. The difference between the F_i after one preilluminating flash and the F_{max} level indicates that part of the secondary acceptors must be reduced in the dark. The average number of misses of this sequence is about 12%.

The sequence shown in Fig. 3, curve 1, peaks on the 3rd and the 7th flashes. It is consistent with 100% oxidation of B in the dark 70% oxidation of B, for example, would give rise to oscillations which more closely resemble those of Fig. 1a (50% oxidations of B). This discrepancy between the analysis of Figs. 3 and 4 will be discussed in the last part of this paper.

This figure shows also that the addition of the inhibitor induces an increase of F_i of about 5% of the variable fluorescence.

Modification of the redox state of B in the dark by addition of benzoquinone

A number of properties of algae are modified by benzoquinone treatment. Their fluorescence is quenched [13,14], they show fewer misses [15] and the permeability of the membranes surrounding the thylakoids is increased. These last two properties are shared by untreated broken chloroplasts. As the midpoint potential of benzoquinone is 320 mV at pH 7, while it is close to 0 for the System II acceptors [16], we attempted to see if B could be oxidized by such treatment.

Fig. 5, curves 3 and 1, shows the effect of $2 \cdot 10^{-4}$ M benzoquinone with and without 10^{-2} M hydroxylamine. It shows that the secondary acceptor has been oxidized relative to the situation described in Figs. 1 and 2. It is not, however,

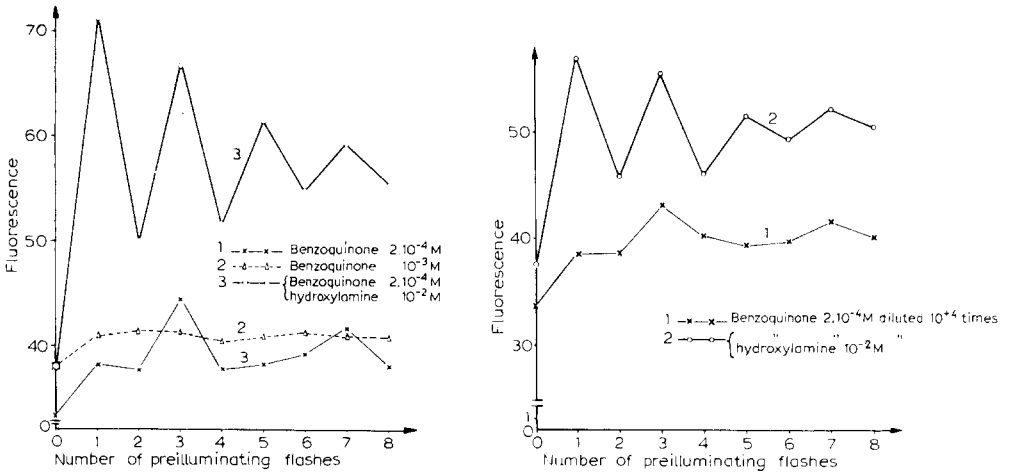


Fig. 5. F_i sequence in *Chlorella* treated with benzoquinone before flash illumination and addition of DCMU. (X———X), curve 1: cells were dark adapted 5 min with $2 \cdot 10^{-4}$ M benzoquinone; (△———△), curve 2: cells were dark adapted 5 min with 10^{-3} M benzoquinone; (○———○), curve 3: cells were dark adapted 5 min with $2 \cdot 10^{-4}$ M benzoquinone before addition of 10^{-2} M NH_2OH. $F_{max} = 107$.

Fig. 6. F_i sequence in *Chlorella* washed out with benzoquinone $2 \cdot 10^{-4}$ M. (X———X), curve 1: cells were incubated 5 min in the dark with $2 \cdot 10^{-4}$ M benzoquinone; the oxidizing agent is then removed by centrifugation and 10 saturating flashes are given to the algae followed by 10 min dark adaptation. (○———○), curve 2: same procedure as curve 1. 10^{-2} M NH_2OH is added 2 min before proceeding to flash preillumination followed by addition of DCMU.

possible to discriminate between a total and a partial oxidation since we are faced with the same discrepancy as for chloroplasts (the remaining difference between the 1st flash yield and F_{max}). Neither an increase in the incubation time nor an increase in the concentration of the oxidizing agent changes the amplitude of these oscillations in the presence of hydroxylamine (curve 3). However, the oscillations in the absence of an artificial donor (curve 1) change when the concentration of benzoquinone is increased to 10^{-3} M. This change is shown by curve 2 where the oscillations have still a periodicity of 4 but no maximum on the 3rd flash. They are similar to oscillations due to the "S" states only [3], indicating that the acceptors are oxidized by benzoquinone before the back reaction with the donors occurs.

We checked to see if the secondary acceptor remained oxidized after washing out the benzoquinone. Three washings via centrifugation corresponding to a dilution 10^4 times were used. Ten actinic flashes were then given to the algae to reduce the benzoquinone in case some of it was bound to the thylakoïd membrane. After 10 min of dark adaptation, we performed the experiment shown in Fig. 6. The secondary acceptor is still oxidized in the dark. Thus, an irreversible change in the redox state of the acceptors has occurred after treatment with benzoquinone.

Figs. 3 and 4, curve 2, show the effect of benzoquinone treatment on chloroplasts, which causes no further oxidation of B. Use of 10^{-4} M ferricyanide, produces the same result (not shown). It was thus not possible to destroy the remaining quenching revealed by one preilluminating flash in the presence of

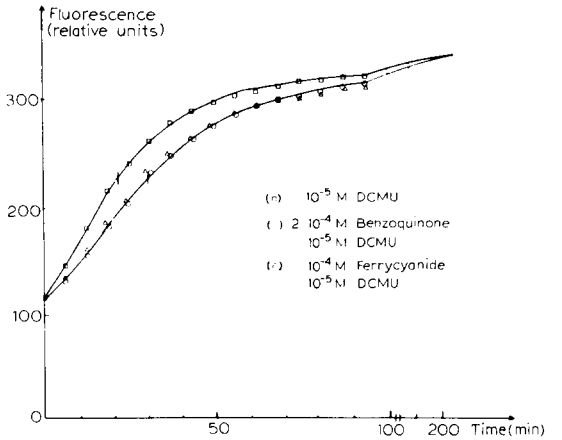


Fig. 7. Effect of the addition of 10^{-4} M ferricyanide and $2 \cdot 10^{-4}$ M benzoquinone on the induction of fluorescence of chloropkast. (□———□), 10^{-5} M DCMU; half-time = 22.5. (△———△), 10^{-4} M ferricyanide. (●———●), $2 \cdot 10^{-4}$ M benzoquinone. Half-time = 30 ms. There is an increase of about 30% of the half-time of the fluorescence rise in the presence of the oxidizing agents. (The curves are normalized to the same variable fluorescence).

hydroxylamine either in *Chlorella* cells treated with benzoquinone or in chloroplasts.

Nevertheless, benzoquinone as well as ferricyanide slow down the fluorescence induction curves of chloroplasts in the presence of DCMU (Fig. 7). These treatments increase by 30% the half-time of the fluorescence rise which is consistent with Joliot's previous results [17] but less then the 100% increase reported by Ikegami [18].

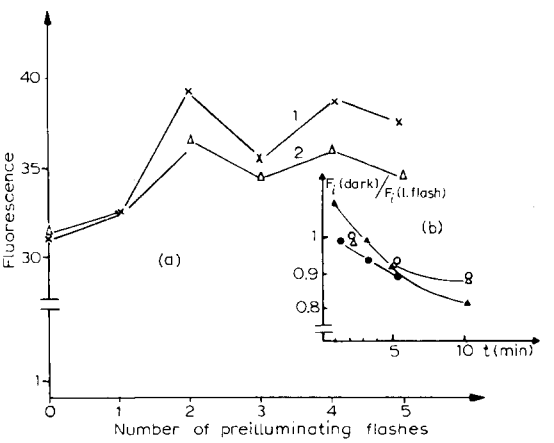


Fig. 8. Effect of an illumination by 10 actinic flashes followed by a variable time of darkness before the procedure of flash illumination followed by addition of DCMU. (a) The illumination is given in the presence of 10^{-2} M NH_2OH followed by 10 min of darkness. The same procedure as in Fig. 1b. About 50% of B^- has been generated. Curve 1: $2 \cdot 10^{-4}$ M benzoquinone. Curve 2: $2 \cdot 10^{-4}$ M benzoquinone washed out via centrifugation. (b) The illumination is given in the absence of NH_2OH. The F_i level of dark-dapted algae decreases in the first 10 min of darkness. The subsequent oscillations (not shown) are not changed, i.e., the redox state of B is not modified by this illumination. (▲———▲), Chloroplasts. (●———●), Chloroplasts treated with $2 \cdot 10^{-4}$ M benzoquinone. (○———○), *Chlorella* treated with $2 \cdot 10^{-4}$ M benzoquinone. (△———△), *Chlorella* washed out with $2 \cdot 10^{-4}$ M benzoquinone.

Effect of an illumination in the presence of hydroxylamine

Algae treated with benzoquinone were illuminated by 10 flashes in the presence of 10^{-2} M hydroxylamine. After 10 min of dark adaptation we performed the experiment of flash preillumination followed by the addition of DCMU. Fig. 8a shows that about half the secondary acceptors are now singly reduced in the dark adapted samples (cf. with Fig. 6). When the dark incubation time was increased to 30 min, the results were the same. This effect is similar to that described by Bennoun and Li [19]. They preilluminated with continuous light chloroplasts which had been treated with hydroxylamine. After dark incubation times of 5 and 40 min, they observed the same reduced area between the fluorescence induction curve and its F_{max} asymptote.

Thus, when the natural donors are replaced by hydroxylamine, an illumination irreversibly changes the redox state of the secondary acceptors. This does not happen in the absence of hydroxylamine, i.e., when the "S" states can interact with the acceptor side. In this case, only the F_i decreases to a limiting value reached after 10 min of dark adaptation (Fig. 8b). There are no changes in the subsequent oscillations (not shown), which indicate that the redox state of B has not been modified.

Discussion

The experiments described in this paper allowed us to study the redox state of the secondary acceptor without having to modify the donor side. This made it possible to verify several hypotheses proposed in the recent years concerning the characteristics of the two charge storage systems and the action of inhibitors like DCMU.

The mere comparison between the phase of the experimental oscillations in the absence of an artificial donor and that of the oscillations computed for various B/B^- ratios permits us to estimate the redox state of the secondary acceptor. This estimated B/B^- ratio is then approximately confirmed by the oscillations of a period 2 obtained with hydroxylamine as an artificial donor.

In *Chlorella* the inhibitor closes about half of the centers, those which are linked to acceptors in the state QB^-. The subsequent acceleration of the induction curve has been shown by Joliot and Joliot [17] in an experiment which is in fact an independent proof of the 50% B^- found in the dark adapted algae. They observed a decrease of about 50% of the half-time of the fluorescence induction rise at low temperature after the addition of DCMU. It is now clear that in addition to the inhibition of electron transport between Q and B due to the lowering of temperature, DCMU closes about half of the centers, i.e., that there is about 50% B^- in the dark.

The B/B^- ratio in *Chlorella* is very different from that of spinach chloroplasts, since the latter contains a major fraction of oxidized B. We therefore tried to induce changes in the redox state of the secondary acceptor. Benzoquinone has the ability to oxidize the acceptors in *Chlorella* cells placing B in the same redox state as in chloroplasts.

Two conditions seem to control the changes in the B/B^- ratio from 1 (*Chlorella*, intact cells) to more than 2.3 (Chloroplasts, *Chlorella* treated with benzoquinone).

The loss of an endogenous reductant

Since the outer membranes of the chloroplasts are damaged during preparation, it is likely that the chemical composition of the interthylakoid space is modified. It is then possible that an endogenous reductant is lost at that time.

In *Chlorella* benzoquinone may oxidize this endogenous reductant or B directly. In any case, this treatment produces exactly the same fraction of oxidized secondary acceptors as in chloroplasts.

The integrity of the donor side

When chloroplasts or algae treated with benzoquinone are illuminated and then dark adapted for 10 min, the addition of DCMU reveals that they still contain a high ratio of B/B^-. On the other hand, about half of the centers contain B^- if hydroxylamine is added before the preillumination. This shows that once B is singly reduced it is stable unless reoxidized by a pathway involving the "S" states.

We computed the average misses from the oscillations observed in the presence of hydroxylamine, with algae or chloroplasts. This leads to values of 19% for *Chlorella* cells, 12% for chloroplasts, 13% for quinone treated algae. These results are consistent with the values computed from oscillations in the oxygen field for a series of saturating flashes [11,20]. Thus the similarity in the percentage of misses seen in the oscillations due to the donors and the acceptors successive states, make it likely that the mechanism responsible for the damping is common to both sides of the chain.

With reference to Lavorel's analysis of damping phenomena [21], our results favour unconservative misses rather than conservative ones. The latter would induce differences between the damping of the oscillations due to the acceptor and to donor side activities.

It is of interest to note that this computation of misses is done on oscillations produced by 10^{-2} M hydroxylamine treated chloroplasts or algae. As misses from the donor side are computed without an artificial donor, it is likely that the photochemical primary reaction has the same efficiency with and without hydroxylamine.

There is a good agreement, in *Chlorella*, between experiments done in the presence and in the absence of hydroxylamine. In both cases, we conclude that there is about the same proportion of B^- and B in the dark. However, the case of chloroplasts is different. When the "S" states are the natural donors, F_i peaks after the 3rd and the 7th flashes of preillumination which is consistent with 100% of B oxidized in the dark. The addition of hydroxylamine should then lead to the reduction of about 90% of the primary acceptors on the first flash (for $\alpha = 10\%$). This was not observed. After one preilluminating flash, there remains about 30% of the total area, bounded by the fluorescence induction curve and its F_{max} asymptote [22,23].

Several observations are consistent with a partial reduction of B in dark adapted chloroplasts:

A rise of F_i representing about 5% of the variable fluorescence is observed after the addition of DCMU to chloroplasts. This should be produced by some B^- which is stable in the dark and which is sensitive to the action of DCMU.

When the low temperature experiment of Joliot and Joliot (described

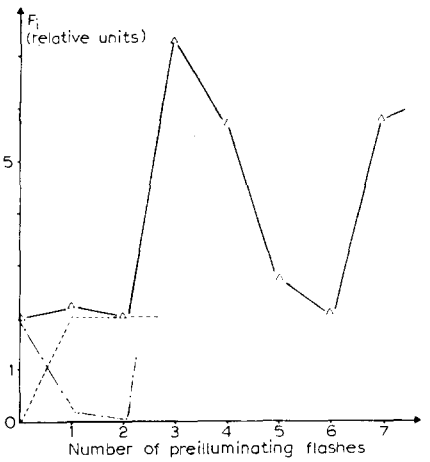


Fig. 9. Computed oscillations of the initial level of fluorescence using the following hypotheses: In this example, there are in the dark: 100% S_1, 12% α and $B/B^- = 4$ 20% double hits (β) occur on the first flash. They involve an auxiliary acceptor with the same quenching properties as Q_1, but they do not affect the oxygen evolution (i.e., the "S" states sequence). This produces oscillations which have a phase similar to that resulting from B, 100% oxidized in the dark. They are produced by the superimposition of a change between the quenching state of dark adapted and illuminated chloroplasts (- - - - - -) and oscillations due to 80% oxidized B in the dark (— · — · —).

already in the first part of this section) is performed on chloroplasts, it yields a half-time of fluorescence rise up to 40% faster [17] after addition of DCMU. Therefore, some centers blocked at low temperature must be linked to a singly reduced secondary acceptor revealed by the action of DCMU.

If a change in F_i between dark-adapted and illuminated algae is superimposed on oscillations corresponding to 70% B and 30% B^- in the dark, we expect, in the absence of hydroxylamine, oscillations which peak on the 3rd and the 7th flash as shown in Fig. 9.

This change in F_i may involve an auxiliary acceptor with the following characteristics: (a) at least part of this auxiliary acceptor is oxidized in the dark; (b) it is reduced on the first flash in addition to the main acceptor Q; (c) it is reoxidized within 10 min of darkness thus protected from rapid reoxidation via S_2 or S_3.

(a) and (b) are consistent with Joliot and Joliot's results [24], (c) gives a life time similar to that found by Diner [25] with Tris-washed chloroplasts.

However, partial contribution of other phenomena to the remaining quenching in chloroplasts and in quinone-treated algae, after one preilluminating flash in the presence of hydroxylamine, cannot be excluded. They are based on the following hypothesis:

(i) The equilibrium constant between QB^- and Q^-B, which is about 18 [26], might be changed after addition of DCMU without becoming infinite. Thus a fraction of the secondary acceptors would remain singly reduced in the presence of the inhibitor. This hypothesis would also explain why the amplitudes of the oscillations presented in this paper are surprisingly small although their phase fit with our theoretical model. This is expected if only a fraction of the centers linked to QB^- is involved in the oscillations.

(ii) There might be two types of centers both of which are blocked by

DCMU, one where Q is linked to B and the other where electron transfer after Q bypasses B. These are then not sensitive to the action of DCMU on QB equilibrium.

However, it will not be possible to evaluate the relative contribution of hypothesis (i) and (ii) to the quenching properties of Photosystem II in the presence of DCMU until better characterisation of a possible auxiliary acceptor is provided.

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References

1 Duysens, L.N.M. and Sweers, H.E. (1963) in Microalgae and Photosynthetic Bacteria, pp. 352, University of Tokyo Press
2 Butler, W.L. (1972) Proc. Natl. Acad. Sci. U.S. 69, 3420—3422
3 Joliot, P. and Joliot, A. (1972) in Proc. IInd Int. Congr. Photosyn. Res., pp. 26—38, W. Junk, N.V., The Hague
4 Delosme, R. (1972) in Proc. IInd Int. Congr. Photosyn. Res., pp. 187—195, W. Junk, N.V., The Haque
5 Etienne, A.L. (1974) Thèse de Doctorat d'Etat, Orsay
6 Velthuys, B.R. and Amesz, J. (1974) Biochim. Biophys. Acta 333, 85—94
7 Kok, B., Forbush, B. and McGloin, M. (1970) Photochem. Photobiol. 11, 457—475
8 Bouges-Bocquet, B. (1975) in Proc. IIIrd. Int. Congr. Photosyn. Res. (Avron, M., ed.) pp. 579—588, Elsevier Publishing Company, Amsterdam
9 Joliot, P. (1960) Thèse de Doctorat d'Etat, Paris
10 Avron, M. (1960) Biochim. Biophys. Acta 40, 257—272
11 Joliot, P., Joliot, A., Bouges, B. and Barbieri, G. (1971) Photochem. Photobiol. 14, 287—305
12 Wollman, F.A. (1976) C.R. Acad. Sci. Paris 283D, 1345—1348
13 Delosme, R. (1967) Thèse de Doctorat d'Etat, Paris
14 Kitajima, M. and Butler, W.L. (1975) Biochim. Biophys. Acta 376, 105—115
15 Diner, B. and Joliot, P. (1976) Biochim. Biophys. Acta 423, 479—498
16 Bendall, D.S. (1977) in Int. Rev. Biochemistry, Plant Biochemistry II (Northcote, ed.) Vol. 13, pp. 41—79, University Park Press, Baltimore, Md.
17 Joliot, P. and Joliot, A. (1973) Biochim. Biophys. Acta 305, 302—316
18 Ikegami, I. and Katoh, S. (1973) Plant Cell Physiol. 14, 829—836
19 Bennoun, P. and Li, Y.S. (1973) Biochim. Biophys. Acta 292, 162—168
20 Forbush, B., Kok, B. and McGloin, M. (1970) Photochem. Photobiol. 11, 457
21 Lavorel, J. (1976) FEBS Lett. 66, 164—167
22 Bennoun, P. (1970) Biochim. Biophys. Acta 216, 357—363
23 Joliot, A. and Joliot, P. (1964) C.R. Acad. Sci. Paris, 258D, 4622—4625
24 Joliot, P. and Joliot, A. (1978) Biochim. Biophys. Acta, in press
25 Diner, B. (1978) in Proc. IVth Int. Congr. Photosyn. Res. Reading, in the press
26 Diner, B. (1977) Biochim. Biophys. Acta 460, 247—258