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Oxygen photoreduction and variable fluorescence during a dark-to-light transition in *Chlorella pyrenoidosa*

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When dark-adapted (5 min in the dark) *Chlorella* cells were deposited on a bare platinum electrode, treated with DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea) and illuminated, O_2 was consumed after a lag time of about 250 ms. The comparison of the O_2 consumption kinetics with the fluorescence O-I-D-P-S transition (the fast change in chlorophyll fluorescence which occurs after the onset of illumination of dark-adapted algae and is over within 2 s) observed in untreated algae indicates that no O_2 is consumed during the fluorescence rise and that O_2 uptake is initiated approximately when the maximum level of fluorescence P is reached. Mass spectrometry measurements of O_2 exchange (using $^{18}O_2$) were performed during dark to light transition with DCMU-untreated *Chlorella* cells. Under these conditions, O_2 reduction began after a lag time (about 200–400 ms) and stopped after about 5 s of illumination. The above experiments clearly show that the reduction of O_2 starts nearly at the same time that the fluorescence P-S decline. On the other hand, we show that the reduction of CO_2 does not interfere in the fluorescence O-I-D-P-S transient. We found the same apparent affinity for O_2 (about 57 μM) for both the fluorescence P-S decline and the reduction of O_2. At least three consecutive short (2 μs) saturating flashes were required to affect the fluorescence transient significantly and also to induce a significant uptake of O_2. Moreover, parabenzoquinone, an artificial Photosystem I electron acceptor, inhibited both the fluorescence D-P rise and the 250 ms lag time observed in the reduction of O_2. We conclude from the above results that in the early stages of the illumination of dark-adapted algae, some Photosystem I electron acceptors are in an inactive form. In this form, the electron transport chain is unable to reduce either O_2 or CO_2. This would lead to the accumulation of electrons on the Photosystem II acceptors (principally Q_A^- and the plastoquinone pool) and therefore explains the fluorescence D-P rise. The light activation, probably achieved through the reduction of at least two electron acceptors, first allows the reduction of O_2, and therefore explains the P-S fluorescence decline. By accepting electrons before the site of regulation and mediating rapid O_2 reduction, parabenzoquinone avoids the accumulation of electrons and therefore inhibits the D-P fluorescence rise.

Abbreviations: PS I, Photosystem I; PS II, Photosystem II; CCCP, carbonyl cyanide *m*-chlorophenylhydrazone; DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea; O-I-D-P-S transition, the fast change in chlorophyll fluorescence which occurs after the onset of illumination of dark-adapted algae and is over within 2 s; O, initial level; I, intermediate level; D, dip; P, peak; S, quasi-steady-state level.

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Introduction

When dark-adapted green cells or chloroplasts are illuminated with strong light, rapid changes in the chlorophyll fluorescence intensity (Kautsky effect) occur [1–5]. The D-P-S transient (according to the terminology given in Ref. 4) which

appears in this induction process has been reported to be due to a regulation of the electron flow at the reducing side of PS I [6–8]. The D-P fluorescence rise has been attributed to a transitory 'traffic jam' of electrons on the acceptors of PS I because of their inactive form in the dark. The subsequent P-S fluorescence decline has been considered as the result of the activation of the electron carriers in the light [6]. By using oxidants accepting electrons at different potentials, Satoh and Katoh [7] have located a site of regulation after ferredoxin and before NADP, probably at the ferredoxin-$NADP^+$ reductase level [9]. Anoxia has been reported to inhibit the fluorescence P-S decline [2,10,11], but the actual role of oxygen in the activation process is at present unknown.

By an other way, transitory oxygen uptake processes related to the activity of PS I have been reported to occur following the illumination of algae [12–16]. In *Scenedesmus*, Radmer and Kok [16], using $^{18}O_2$ and mass spectrometry, observed an important O_2 uptake during the first 20 s of illumination. Moreover, bare platinum electrode measurements allowed the existence of an O_2 uptake in *Ulva* [12] and in *Chlorella* [13,14] to be shown. We have previously reported that in *Chlorella* cells, at least three consecutive flashes were necessary to induce a significant O_2 uptake, thus indicating the probable existence of an activation phenomenon [13].

In the present work, we investigate the activation processes taking place at the PS I level following the illumination of dark-adapted *Chlorella*. For this purpose, we compare the properties of the D-P-S fluorescence transient to those of the O_2 uptake. We report that the fluorescence P-S decline is strongly related to the reduction of O_2 and that the fluorescence D-P rise is the consequence of an inactive form of the electron transport unable to reduce O_2 in the early stages of the illumination.

Materials and Methods

Algae *(Chlorella pyrenoidosa)* were grown phototrophically as described previously [17]. After 4–5 days of growth, algae were harvested by low speed centrifugation ($1500 \times g$) and resuspended in a 0.05 M Tris (pH 7.2) containing 0.1 M KCl. 1 ml of the algal suspension containing about 30 μg/ml chlorophyll was deposited on the platinum electrode of the three electrode system described by Schmid and Thibault [18]. The cells were allowed to settle for at least 30 min before O_2 exchange measurements were made. The circulation of gas mixtures containing various concentrations of O_2 at the surface of the sample allowed the dissolved O_2 concentration in the sample to be controlled.

Measurements of O_2 exchange were also performed using a mass spectrometer (type 1480, VG Instruments). 4 ml of the algal suspension described above were deposited at the bottom of a closed vessel (total volume of about 40 ml) on a gas permeable membrane allowing the diffusion of dissolved gases towards the mass spectrometer for analysis; after bubbling the sample with N_2 to remove the $^{16}O_2$ present, 10 ml of $^{18}O_2$ (98.1% ^{18}O) were injected in the gas phase and 1 mM $NaHCO_3$ was injected in the liquid phase. Algae were then allowed to settle for at least 15 min before measurement. The concentrations of the gases dissolved in the sample were analyzed by continuously and simultaneously recording masses 32 ($^{16}O_2$) and 36 ($^{18}O_2$) or 36 and 44 (CO_2). Under these conditions, O_2 concentration stabilized in the dark at a constant level resulting from the equilibrium between gas consumption (due to the mass spectrometer and algal respiration) and diffusion from the gas phase to the liquid phase.

The electrode system and the mass spectrometer vessel were covered by a conic reflector in which apertures for xenon flash, optic fiber and photodiod were adapted. A xenon flash (EG and G, FX 201, 2 μs duration) was used to provide flash illumination. Continuous light was obtained from a 150 W halogen lamp and was passed through a Schott filter BG-39. Fluorescence emission was measured at the same time as gas exchange (measured either by amperometry or by mass spectrometry) by means of a photodiod (PIN 10 DP, United Detector Technology) protected with a red filter (Kodak 89 B). Both the fluorescence and the amperometric signals were recorded after amplification with a storage screen oscilloscope (Tektronix 5115). Parabenzoquinone was used dissolved in ethanol and was purchased from Aldrich.

Results

To investigate the relationship between the reduction of O_2 and the fluorescence transient, we have first compared the kinetics of the two phenomena. Fig. 1A shows the classical fluorescence O-I-D-P-S transition (according to the terminology given in Ref. 4) observed when dark-adapted (5 min in the dark) *Chlorella* cells were illuminated. In order to compare, under good conditions, the kinetics of the fluorescence transient with the kinetics of the O_2 uptake, it was necessary to measure O_2 exchange with a sufficiently low response time. For this purpose, we have used a bare platinum O_2 electrode (with a response time of about 5 ms) and algae were treated with 10 μM DCMU to completely inhibit O_2 evolution. In these conditions, transitory O_2 uptake was still occurring (see Ref. 13) which was probably due to the existence of a sufficient pool of donors for PS I (principally the plastoquinone pool). We observed that after a lag time of about 250 ms, the O_2 concentration decreased and reached a minimum value after about 1 s of illumination (Fig. 1B). The comparison of the O_2 curve with the fluorescence transient (Fig. 1A) measured in dark-adapted algae (but not treated with DCMU) during a dark to light transition clearly shows that no O_2 is consumed during the fluorescence D-P rise and that the reduction of O_2 takes place nearly at the same time that the fluorescence P-S decline. One can however argue that the comparison of these two experiments is difficult due to the fact that the measurements were performed under different conditions (i.e., in the absence and in the presence of DCMU). The following mass spectrometric experiments were therefore undertaken in order to answer this question.

The use of mass spectrometric techniques and

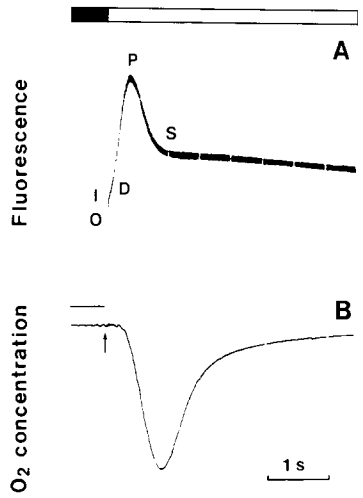

Fig. 1. Chlorophyll fluorescence and O_2 uptake during a dark to light transition; (A) the fluorescence transient was first recorded; (B) cells were then treated by 10 μM DCMU to inhibit O_2 evolution and O_2 uptake was measured by using the bare platinum electrode system.

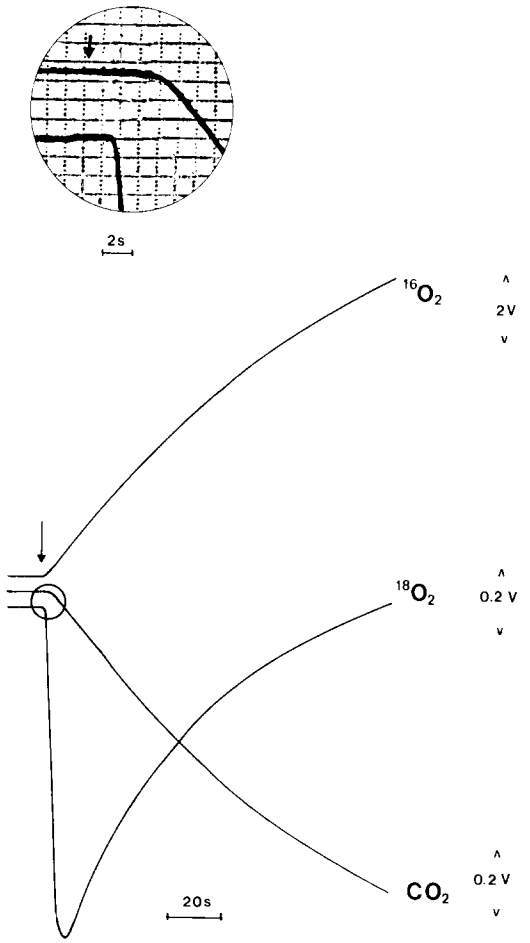

Fig. 2. Oxygen production, oxygen and CO_2 uptakes measured by mass spectrometry during a dark to light transition in dark-adapted *Chlorella* cells. Light was switched on when indicated (↓); $^{18}O_2$ ($m/e = 36$), $^{16}O_2$ ($m/e = 32$) and CO_2 ($m/e = 44$) were simultaneously and continuously recorded.

of $^{18}O_2$ allows the determination of O_2 uptake in the presence of O_2 evolution. Fig. 2 shows that, following the illumination of dark-adapted cells, $^{16}O_2$ is evolved (from the photolysis of water: $H_2{}^{16}O$) and $^{18}O_2$ is consumed. Whereas $^{16}O_2$ is continuously evolved during the light period, $^{18}O_2$ uptake stops after less than 10 s of illumination and the $^{18}O_2$ concentration progressively increases to its initial value. However, due to the relatively important response time of the membrane inlet system used (about 1 s), it was not possible to directly measure the kinetics of the O_2 uptake process. In order to free oneself of the response time of the apparatus, we varied the length of the light period and measured the integral of the light-induced variation of the $^{18}O_2$ signal (Fig. 3). The O_2 uptake rate was constant from 0.5 s to about 2.5. s and then progressively decreased to stop after about 5 s of illumination. Consequently, even in the absence of DCMU, conditions where the PS I electron donors are not limited, the O_2 uptake is transitory but stops after 5 s of illumination (compared to 1 s in the presence of DCMU – see Fig. 1). Moreover, we note (Fig. 3) that the extrapolation of the linear part of the O_2 uptake curve towards zero does not intercept with the axis at zero time, thus indicating the existence of a delay (about 200–400 ms) in the reduction of O_2

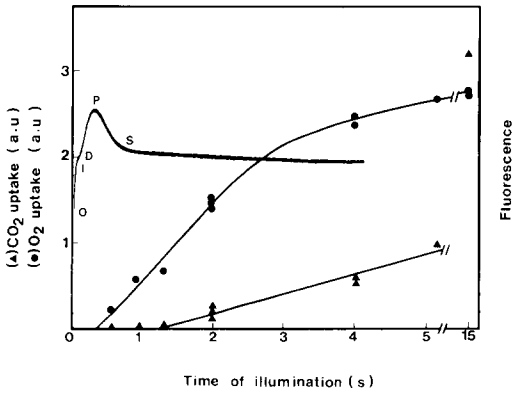

Fig. 3. Oxygen uptake, CO_2 uptake and chlorophyll fluorescence during a dark to light transition in dark-adapted *Chlorella*. Oxygen and CO_2 uptakes were measured by mass spectrometry by recording masses 36 and 44; after different times of illumination, the area of the light-induced variation of the 36 signal (O_2 uptake) and of the 44 signal (CO_2 uptake) were measured. Chlorophyll fluorescence was measured under continuous light in the same conditions as O_2 and CO_2 uptakes.

even when algae were not treated with DCMU.

Variations in the CO_2 concentration ($m/e = 44$) have also been recorded during the mass spectrometric experiments shown in Figs. 2 and 3. The concentration of CO_2 continuously decreased during the light period (Fig. 2). Moreover, we found that CO_2 uptake was delayed by about 2 s, compared to the uptake of O_2. This was confirmed by the experiment shown in Fig. 3. We observed no significant CO_2 uptake when the time of illumination was shorter than 2 s. Such a delay in the utilization of CO_2 as terminal acceptor has already been observed during the induction phase of photosynthesis in the green alga *Scenedesmus* [15]. In that species, the lag time in the reduction of CO_2 was however quite a bit longer (about 20 s). Note that because the 'S' fluorescence level is reached after about 1 s, the reduction of CO_2 probably does not interfere in the fluorescence transient.

Consequently, it appears from these experiments that the reduction of O_2 (but not the reduction of CO_2) might be related to the fluorescence P-S decline. In order to definitively establish a link between these two transitory phenomena, we have further compared some of their properties.

In agreement with earlier studies [2,10,11], the P-S fluorescence decline was found to be sensitive to O_2 concentration. When the O_2 concentration was decreased, it was progressively slowed down. The effect of various O_2 concentrations on the intensity of the O_2 uptake and on the fluorescence decline rate are shown on Fig. 4. We found that the apparent K_m (O_2) for the fluorescence decline (K_m (O_2) = 57.5 μM) was similar to the one measured for the O_2 uptake (K_m (O_2) = 57.1 μM). This value is in the same range as the K_m values generally found for O_2 uptake when measured with in vivo photosynthetic systems (50–100 μM – see Refs. 19–21).

In an earlier report [13] we noticed that dark-adapted DCMU-treated *Chlorella* cells, when illuminated by a series of short saturating flashes (2 μs duration), required at least three consecutive flashes to consume O_2. This is also true in the absence of DCMU (see Fig. 5). In the same way, a significant inhibition of the fluorescence D-P-S transient (measured as the P-S decline rate) was only recorded when at least three flashes were

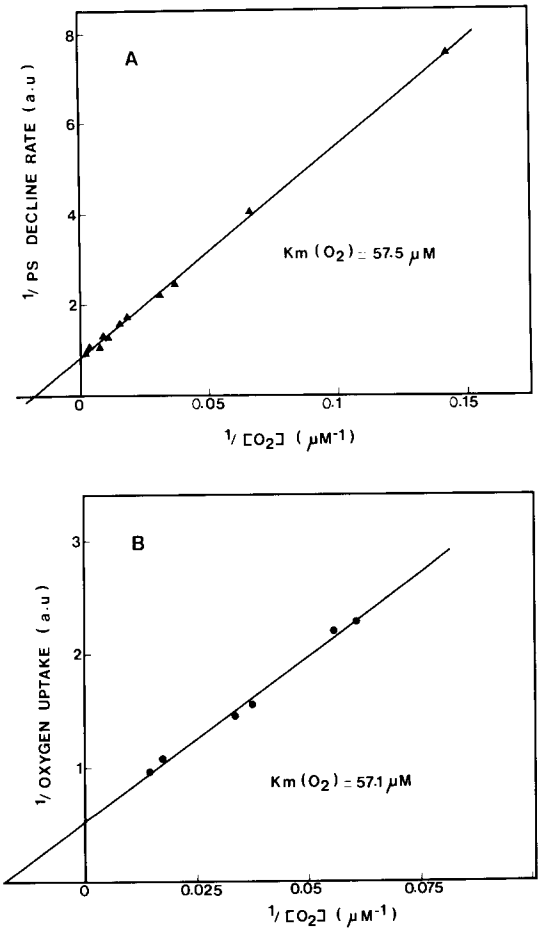

Fig. 4. Apparent affinity for O_2 of the fluorescence P-S decline rate (A) and of O_2 uptake (B). (A) algae were placed in a Clark-type O_2 electrode chamber, and the P-S fluorescence decline rate was measured at different O_2 levels. (B) O_2 uptake was measured by mass spectrometry (amplitude of the light-induced variation of the mass 36 signal) at different $^{18}O_2$ levels following a 4 s illumination.

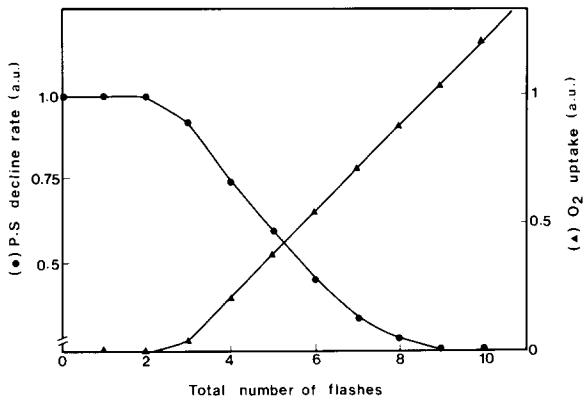

Fig. 5. ●, Effect of flash-preillumination on the fluorescence P-S decline rate; 0.1 s before continuous light, various numbers of saturating flashes spaced by 0.1 s were fired. ▲, O_2 uptake measured by mass spectrometry after flashes.

fired before continuous light (Fig. 5). The inhibition increased as a function of the number of flashes and was maximal after a nine-flash preillumination. Consequently, the three consecutive flashes which are required to initiate the reduction of O_2 are also required to significantly change the fluorescence D-P-S transient.

Parabenzoquinone, like methylviologen has been shown to accept electrons at the reducing side of PS I and to mediate a rapid photoreduction of O_2 [18]. At a concentration of 1.5 mM, parabenzoquinone inhibited the fluorescence D-P rise (Fig. 6B). This effect of parabenzoquinone on the fluorescence transient, similar to that observed for methylviologen [2], indicates that the site of regulation of the electron flow responsible for the D-P-S fluorescence transient is located after the site where parabenzoquinone accepts the electrons from PS I. When 1.5 mM parabenzoquinone was added to DCMU-treated algae, O_2 uptake was observed under continuous illumination (Fig. 6D). However, in contrast to the O_2 uptake observed in the absence of parabenzoquinone, which occurred after a lag time of about 250 ms in continuous light (Fig. 6C) and was significant after only three flashes, this one occurred without delay in continuous light (Fig. 6D) and appeared from the first flash (Fig. 6F). Thus, in the presence of parabenzoquinone, both the fluorescence D-P rise and the lag time in the reduction of O_2 were suppressed. Note that parabenzoquinone did not induce rapid O_2 uptake after flash illumination of a *Chlamydomonas* mutant lacking PS I activity (data not shown), thus indicating that, at the concentration used, parabenzoquinone was not reduced by PS II activity.

Fig. 7 shows that the lag time for O_2 reduction of about 250 ms which occurs when dark-adapted algae are illuminated with continuous light is strongly shortened (to about 60 ms) when a five-flash preillumination was performed (compare Fig.

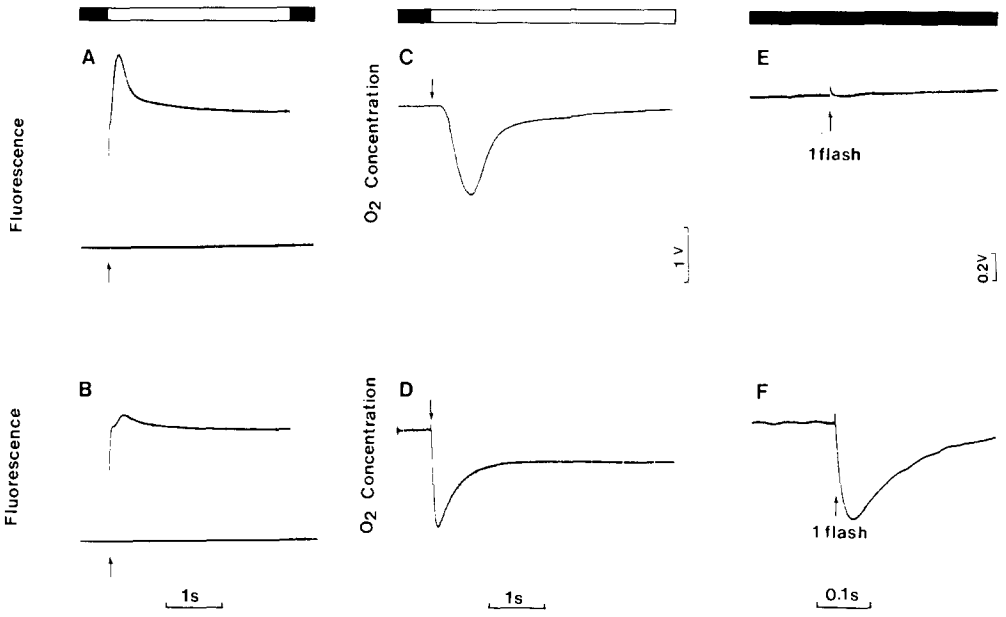

Fig. 6. Effect of parabenzoquinone on the fluorescence transient measured in dark-adapted *Chlorella* (A, B), and on the O_2 exchange measured in DCMU-treated algae under continuous light (C, D) or after one flash (E, F); (A, C, E) control; (B, D, F) in the presence of 1 mM parabenzoquinone.

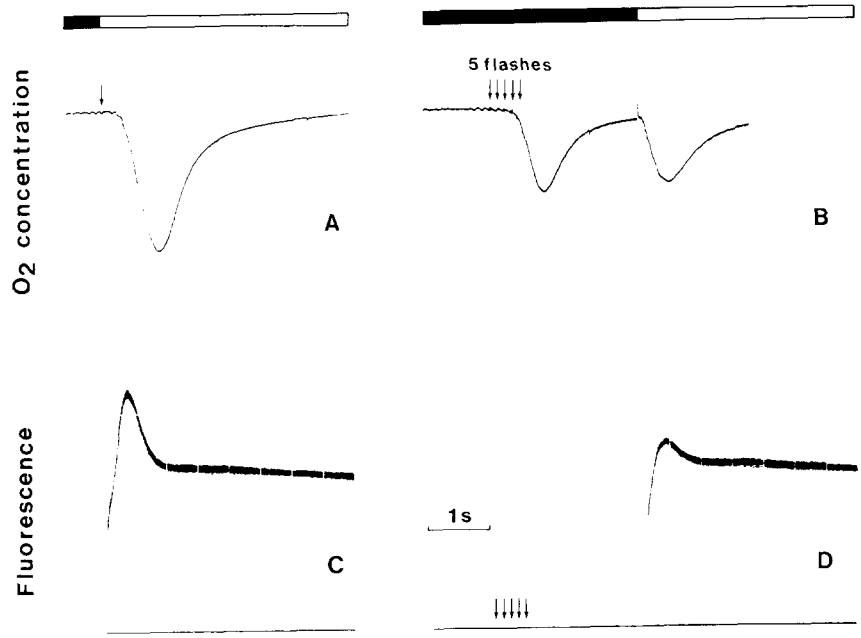

Fig. 7. Effect of a five flash preillumination on the O_2 uptake lag time (A, B) and on the fluorescence transient (C, D) in dark-adapted *Chlorella*. (A) O_2 uptake was measured by amperometry following continuous illumination of DCMU-treated algae. (C) fluorescence transient was measured under the same conditions as in (A), but in the absence of DCMU. (B) O_2 uptake was measured in DCMU-treated algae on a five-flash illumination and on a subsequent continuous illumination delayed by 2 s. (D) fluorescence transient was measured under continuous illumination in the same conditions as in (B), but in the absence of DCMU.

7A and 7B). After such a preillumination, the D-P-S fluorescence transient was dramatically inhibited (compare Fig. 7C and 7D). Moreover, the dark time necessary for the fluorescence transient to recover its maximal amplitude (about 2 min) was found to be similar to the one necessary for the observation of the maximum lag time of about 250 ms in the reduction of O_2 (data not shown). We conclude from these experiments that the duration of the lag time observed before the reduction of O_2 directly depends on the activation state of the electron transport. Note that after the five-flash preillumination, the intensity of the O_2 uptake measured during the subsequent continuous illumination was smaller than the one measured in the control experiment. However, the latter was virtually equal to the added O_2 uptake measured after the preillumination and after continuous light. This indicates that, in the presence of DCMU, the reduction of O_2 is probably limited by the pool of electron donors (principally the plastoquinone pool), partially exhausted following flashes and completely exhausted after continuous light.

Discussion

The results presented in this paper support the evidence that the fluorescence P-S decline and the reduction of O_2 which occur during the first seconds of the illumination of dark-adapted *Chlorella* cells are closely related: (1) reduction of O_2 occurs nearly at the same time as the fluorescence decline, (2) the reduction of O_2 and the fluorescence decline have the same apparent affinity for O_2, (3) at least three consecutive saturating flashes are required to significantly affect the fluorescence transient and also to induce a significant reduction of O_2.

According to the Q hypothesis first proposed by Duysens and Sweers [5], the easiest way to explain a link between the P-S fluorescence decline and the reduction of O_2 is to consider that O_2, by acting as an electron acceptor at the reducing side of PS I, allows the reoxidation of the PS II acceptors (the plastoquinone pool and Q_A^-) and thus reduces the fluorescence level from P to S. However, O_2 does not act as an acceptor during the first 250 ms of the illumination, as shown by the lag time observed in O_2 reduction (see Figs. 2 and 3). This inability of the electron transport chain to reduce O_2 probably causes, under conditions where CO_2 fixation does not occur, the reduction of the PS I electron acceptors followed by the reduction of Q_A. This would explain the fluorescence increase from the D level to the P level. Thereafter, the electron transport chain would be activated by light, thus allowing the reduction of O_2. This would lead to the reoxidation of the PS I then of the PS II electron acceptors and would therefore explain the fluorescence decrease from P to S. This interpretation, based on the existence of an activation site at the level of the PS I electron acceptors, is supported by the inhibitory effect of parabenzoquinone on the fluorescence transient. By accepting electrons from PS I before ferredoxin and mediating O_2 reduction without significant delay, parabenzoquinone bypasses the site of activation and therefore avoids the electron 'traffic jam'.

Because O_2 uptake occurs after a lag time in continuous light or after at least three consecutive flashes under flash illumination, we propose that the reduction of at least two acceptors is necessary for the activation to occur. This hypothesis is in agreement with the results of Satoh obtained on *Bryopsis* chloroplasts permeable to small molecules [10]. This author observed that the fluorescence D-P-S transient was inhibited completely by dithionite, partially by dithiothreitol, but not by ascorbate, and concluded that the photoreduction of a very low potential component should be involved in the photoactivation process. One may for instance speculate that the photoactivation is achieved by the reduction of a disulfide bridge. The LEM_1 system, which has been reported to accept electrons from the electron transport system at a site on the reducing side of PS I prior to ferredoxin [22] therefore appears as a possible mediator of the activation process.

An alternative hypothesis to explain the lag time would be to consider that the modification in the ability to reduce O_2 is not due to the pre-reduction of two electron transport components, but is the consequence of a light-induced variation of pH. This interpretation is supported by the fact that, in *Bryopsis* chloroplasts, the P-S transient was found to be sensitive to uncouplers and to

variations of the pH [23]. It was suggested that the activation of the electron transport was due to a light-induced alkalinization of the stroma. This hypothesis appears unlikely however, at least in the case of intact *Chlorella* cells. Indeed, we found that the fluorescence D-P-S transient was insensitive to the uncoupler CCCP (data now shown).

If we admit, as already suggested [9], that the site of regulation is located at the ferredoxin-$NADP^+$ reductase level and because the electron transport has to be activated before reducing O_2, this implies that the site of O_2 reduction is either ferredoxin-$NADP^+$ reductase itself (in the active form) or NADPH. The latter is however unlikely because of the slow auto-oxidation rates of NADPH. This conclusion conflicts with the widely accepted scheme in which photoreduction of O_2 is thought to be mediated by ferredoxin [24,25]. However, recent in vitro kinetics studies indicated that the direct reduction of O_2 by ferredoxin was too slow to make this reaction the predominant route of post-PS I O_2 reduction [26]. In this context, the possible existence of an O_2 reduction site on the acceptor side of PS I different from ferredoxin appears as a reasonable hypothesis to consider. Clearly, additional experiments are required to determine the nature of the electron carrier interacting with O_2.

One may easily conceive that O_2 is reduced because the Calvin cycle is not operative at the beginning of the illlumination [27]. However, as shown in Fig. 2A, O_2 reduction persists for at least 4 s even after the beginning of the CO_2 uptake. This behaviour is different from that observed in the green alga *Scenedesmus* by Radmer and Kok [16]. In this species, a strict competition between O_2 and CO_2 was observed, O_2 reduction decreasing as the fixation of CO_2 was initiated. This could indicate that, at least in the case of *Chlorella*, O_2 reduction does not take place, for the sole reason that CO_2 reduction is not operative, but participates in the accomplishment of a physiological function. This one could be, for instance, to supply extra ATP for CO_2 fixation by pseudocyclic photophosphorylations [28,29]. Indeed, CO_2 fixation requires a higher ATP/NADPH ratio than produced by linear electron flow [28]. However, because light-induced O_2 uptake stops after about 5 s of illumination, this ATP supply would be limited to the induction phase of photosynthesis. In this context, a more likely role for O_2 reduction might be, as already suggested [30], to poise the electron transport system, thus allowing the functioning of cyclic electron transport. Indeed, cyclic electron flow has been shown to require an appropriate poising for its initiation [31]. In this connection, Ziem-Hanck and Heber [30] reported that a pulse of O_2 was sufficient to release the inhibition of photosynthesis observed under anaerobic conditions and that photosynthesis could thereafter function at a high rate in the presence of a very low O_2 concentration. Oxygen reduction, by regulating the redox state of some electron carriers (poising) and preventing over-reduction would permit the initiation of cyclic electron flow. With this view in mind, we suggest that O_2 uptake would stop as the cyclic electron transport is initiated.

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