

O₂ Uptake in the Light in *Chlamydomonas*

EVIDENCE FOR PERSISTENT MITOCHONDRIAL RESPIRATION

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ABSTRACT

The nature of the process responsible for the stationary O₂ uptake occurring in the light under saturating CO₂ concentration in *Chlamydomonas reinhardtii* has been investigated. For this purpose, a mass spectrometer with a membrane inlet system was used to measure O₂ uptake and evolution in the algal suspension. First, we observed that the O₂ uptake rate was constant (about 0.5 micromoles of O₂ per milligram chlorophyll per minute) during a light to dark transition and was not affected by 3-(3,4-dichlorophenyl)-1,1-dimethylurea. Salicylhydroxamic acid had no effect on O₂ uptake in the dark or in the light, but was found to have the same inhibitory effect either in the dark or in the light when added to cyanide-treated algae. The stimulation of the O₂ uptake rate due to the uncoupling effect of carbonyl cyanide *m*-chlorophenylhydrazone was about the same in the dark or in the light. From these results, we conclude that mitochondrial respiration is maintained during illumination and therefore is not inhibited by high ATP levels. Another conclusion is that in conditions where photorespiration is absent, no other light-dependent O₂ uptake process occurs. If Mehler reactions are involved, in *Chlamydomonas*, under conditions where both photosynthetic carbon oxidation and reduction cycles cannot operate (as in cyanide-treated algae), their occurrence in photosynthesizing algae either under saturating CO₂ concentration or at the CO₂ compensation point appears very unlikely. The comparison with the situation previously reported in *Scenedesmus* (R. J. Radmer and B. Kok 1976 Plant Physiol 58: 336-340) suggests that different O₂ uptake processes might be present in these two algal species.

Mass isotope studies using ¹⁸O₂ provided evidence that O₂ uptake was occurring during photosynthesis both in algae (6, 15, 18, 26) and in higher plants (7, 13). This O₂ uptake process was recognized to be of a different nature from that taking place in dark respiration (18, 19). Oxygenase activity of Rubisco¹ and the associated metabolism of glycolate were shown to be involved in this light O₂ consumption (1, 4, 9). The effects of CO₂ concentration on oxygenase activity *in vitro* (3) and metabolite flux through the glycolate pathway (4, 25) allow the conclusion that these reactions (termed the photorespiratory glycolate pathway or photosynthetic carbon oxidation cycle) are responsible for that part of the O₂ uptake which is sensitive to CO₂ concentration (7, 13, 25). In the light, under saturating CO₂ concentration, conditions where the oxygenase activity of Rubisco should be completely inhibited and the glycolate pathway stopped, residual O₂

uptake still occurs (7, 14, 25). The nature of this remaining O₂ uptake is at present unknown.

Mitochondrial dark respiration could be responsible for this CO₂-insensitive O₂ uptake (14). However, the first isotope experiments on microalgae and cyanobacteria illuminated by low light intensities were interpreted as showing an inhibition by light of dark respiration (18). On the other hand, reports of studies of the labeling of tricarboxylic acid cycle intermediates (16), or of the correlation between CO₂ compensation point and CO₂ efflux from respiration (2), concluded that tricarboxylic acid cycle was not affected by light. Hence, the question is whether or not the reducing power which should continue to be produced within the mitochondria in the light is reoxidized through the mitochondrial respiratory chain.

It has also been shown that direct O₂ photoreduction (*i.e.* Mehler reactions) can be involved in O₂ uptake processes in the light (22). Such reactions could play an important role in green cells in supplying sufficient ATP for CO₂ fixation (10, 23). However, in spite of the occurrence of Mehler reactions in isolated chloroplasts (10, 22), their existence in intact cells remains questionable (23).

Thus, the participation of mitochondrial respiration or Mehler reactions to O₂ uptake in the light are presently not elucidated. The aim of this work was to determine, in the green alga *Chlamydomonas reinhardtii*, the nature of the O₂ uptake processes present in the light under CO₂ saturation when no photorespiration occurs. For this purpose, we studied the effects on O₂ exchanges of respiratory oxidase inhibitors and of an uncoupler of oxidative phosphorylation. Our results provide evidence that dark respiration is not inhibited by light and that Mehler reactions do not occur during CO₂ fixation.

MATERIALS AND METHODS

Chlamydomonas reinhardtii (wild type 137 c) was grown axenically and phototrophically as previously described (24). Air was bubbled through the culture at a flow rate of about 20 l · h⁻¹. Cells were harvested by centrifugation and then resuspended in the culture medium lacking NH₄⁺. The pH of the medium was 6.0. Chl concentration was between 25 and 40 μg Chl · ml⁻¹. Algal suspension was bubbled with air in a thermostated (25°C) flask, under a light intensity of 1000 μE · m⁻² · s⁻¹ (400-700 nm), for at least 60 min. Then, the cell suspension was transferred to a thermostated (25°C) reaction vessel (a cylindrical cavity made of Plexiglas). The vessel was stirred with a magnetic bar and illuminated with incandescent light to obtain an incident quantum flux of 1000 μE · m⁻² · s⁻¹ (400-700 nm). A polypropylene membrane at the bottom of the reaction vessel allowed dissolved gases to be introduced into the mass spectrometer (MAT Atlas CH₄). After bubbling the algal suspension with N₂ in the light, ¹⁸O₂ (98.1% ¹⁸O from CEA Saclay, France) was injected to obtain an initial O₂ concentration of about 20% O₂. Then, the reaction

¹ Abbreviations: CCCP, carbonyl cyanide *m*-chlorophenylhydrazone; Rubisco, ribulose-1,5 biphosphate carboxylase/oxygenase; DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea; SHAM, salicyl hydroxamic acid.

vessel was closed, and NaHCO_3 was added (10^{-2} M final concentration). The response time of the system was about 25 s. O_2 evolution and uptake were measured by alternately recording $^{16}\text{O}_2$ ($m/e = 32$) and $^{18}\text{O}_2$ ($m/e = 36$). Each cycle lasted about 30 s. O_2 uptake rate (U_o) and gross O_2 evolution rate (E_o) were calculated from the expressions:

$$U_o = \left(\frac{\Delta[^{18}\text{O}_2]}{\Delta t} - k[^{18}\text{O}_2] \right) \left(\frac{[^{18}\text{O}_2] + [^{16}\text{O}_2]}{[^{18}\text{O}_2]} \right)$$

$$E_o = \left(\frac{\Delta[^{16}\text{O}_2]}{\Delta t} - k[^{16}\text{O}_2] \right) + U_o \left(\frac{[^{16}\text{O}_2]}{[^{16}\text{O}_2] + [^{18}\text{O}_2]} \right)$$

where k is the rate constant of O_2 decrease due to the mass spectrometer consumption. This rate constant was measured in the absence of algae and was equal in our experimental conditions to 0.011 min^{-1} . The mass spectrometer signal was calibrated on the basis of the equilibrium with air ($258 \mu\text{M}$ at 25°C). $[^{16}\text{O}_2]$ and $[^{18}\text{O}_2]$ represent, respectively, the amounts of each molecular species expressed in $\mu\text{mol O}_2 \cdot \text{mg}^{-1} \text{ Chl}$, and Δ means that the difference between two successive values (time interval Δt) was used in the calculations.

For the experiment performed only in the dark, the algal suspension was bubbled with air, then the vessel was closed. Respiration rates were measured by recording $^{16}\text{O}_2$ ($m/e = 32$) and were calculated from the expression:

$$R = \frac{\Delta[^{16}\text{O}_2]}{\Delta t} - k[^{16}\text{O}_2]$$

In one experiment carried out to determine the optimal CCCP concentration, dark respiration and net photosynthesis were measured with a Clark-type O_2 electrode (Rank Brothers). Chl content was determined after extraction with 90% methanol (v/v) as previously described (24).

RESULTS

In a previous study on *Chlamydomonas* (25), we reported that after switching on the light, the O_2 uptake rate decreased from an initial value of about $2 \mu\text{mol O}_2 \cdot \text{mg}^{-1} \text{ Chl} \cdot \text{min}^{-1}$ to a stationary value. The stationary level was reached about 1 h after the beginning of illumination and was shown to depend on the CO_2 concentration. On the other hand, the process responsible for the initial decreasing O_2 uptake is insensitive to CO_2 concentration and will be studied later. Here, we are interested in the nature of the stationary uptake that remains even under saturating CO_2 concentrations. For this purpose, algae were pretreated at least 1 h in the light in order to suppress the decreasing O_2 uptake process. Algal suspension was then transferred into an illuminated vessel and O_2 exchanges were measured as described in "Materials and Methods."

Figure 1 shows O_2 uptake (U_o) and gross evolution rates (E_o) in the light and in the following dark period. Stationary O_2 evolution rate was about $2 \mu\text{mol O}_2 \cdot \text{mg}^{-1} \text{ Chl} \cdot \text{min}^{-1}$. O_2 uptake rate in the light was $0.5 \mu\text{mol O}_2 \cdot \text{mg}^{-1} \text{ Chl} \cdot \text{min}^{-1}$ and no significant change was observed after switching off the light. Addition of DCMU ($50 \mu\text{M}$ final concentration) in the light was found to have the same effect on O_2 exchanges as switching off the light in the control. Such a continuity in the O_2 uptake rate suggests that the same process occurs in the light and in the dark and that this process does not depend on photosynthetic electron transport. Mitochondrial respiration is known to be the main process responsible for O_2 uptake in the dark. In order to test the hypothesis that such respiration persists in the light, we studied the effects of mitochondrial respiration inhibitors (cyanide and SHAM) on O_2 exchanges in the light in comparison with their effects in the dark.

In the dark (Fig. 2), cyanide (1 mM final concentration) was shown to inhibit O_2 uptake rate by about 20%, whereas SHAM (1 mM final concentration) alone had no effect. When SHAM was added to cyanide-treated algae, respiration rate was inhibited by about 80% of the initial rate. The extent of the SHAM-induced decrease in O_2 uptake was $0.30 \mu\text{mol O}_2 \cdot \text{mg}^{-1} \text{ Chl} \cdot \text{min}^{-1}$.

In the light (Fig. 3), addition of cyanide first stimulated O_2 uptake rate to a value of about $0.9 \mu\text{mol O}_2 \cdot \text{mg}^{-1} \text{ Chl} \cdot \text{min}^{-1}$, and then O_2 uptake decreased and stabilized at a level of about $0.6 \mu\text{mol O}_2 \cdot \text{mg}^{-1} \text{ Chl} \cdot \text{min}^{-1}$. After a short lag period, O_2 evolution rate was progressively reduced to the same level as the O_2 uptake rate. From this moment net O_2 evolution was completely inhibited. Addition of SHAM (1 mM final concentration) to cyanide-treated algae was found to inhibit O_2 evolution and O_2 uptake to the same extent. The decrease due to SHAM addition was about $0.35 \mu\text{mol O}_2 \cdot \text{mg}^{-1} \text{ Chl} \cdot \text{min}^{-1}$. Addition of SHAM to untreated algae was found to have no effect on O_2 exchanges (Fig. 4). We note that after cyanide and SHAM additions, residual O_2 uptake rate in the dark was very low (about $0.08 \mu\text{mol O}_2 \cdot \text{mg}^{-1} \text{ Chl} \cdot \text{min}^{-1}$; Fig. 2), whereas in the light (Fig. 3) it remained at a relatively high value (about $0.3 \mu\text{mol O}_2 \cdot \text{mg}^{-1} \text{ Chl} \cdot \text{min}^{-1}$). This remaining O_2 uptake was completely suppressed by addition of $50 \mu\text{M}$ DCMU to the algal suspension (Fig. 5).

The effect of the uncoupler CCCP on O_2 exchanges was studied in the dark and in the light. The first experiment was performed to determine the CCCP concentration which could induce a maximum uncoupling effect in the dark with a minimal effect on net O_2 evolution in the light. To avoid any memory effect of light on the uncoupling by CCCP, algae were preincubated in the dark for at least 1 h. In this condition, basal respiration rate was found to be lower ($0.22 \mu\text{mol O}_2 \cdot \text{mg}^{-1} \text{ Chl} \cdot \text{min}^{-1}$) than the one observed after 1 h of illumination (Figs. 1 and 2). An uncoupling effect on dark respiration was significant for a CCCP concentration of $0.1 \mu\text{M}$ and was maximum at $2 \mu\text{M}$, corresponding to an increase of the dark respiration rate of about $0.33 \mu\text{mol O}_2 \cdot \text{mg}^{-1} \text{ Chl} \cdot \text{min}^{-1}$ (Fig. 6). CCCP concentrations higher than $2 \mu\text{M}$ strongly decreased the respiration rate. Inhibitory effect of CCCP on net O_2 evolution was first observed at a concentration of $1 \mu\text{M}$. We, therefore, chose a CCCP concentration of $1 \mu\text{M}$ to perform experiments on O_2 exchanges in the light. Figure 7 shows that CCCP stimulated O_2 uptake from 0.54 up to $0.80 \mu\text{mol O}_2 \cdot \text{mg}^{-1} \text{ Chl} \cdot \text{min}^{-1}$ without effect on gross O_2 evolution. The stimulation ($0.26 \mu\text{mol O}_2 \cdot \text{mg}^{-1} \text{ Chl} \cdot \text{min}^{-1}$) was about the same as that observed in the dark (Fig. 6).

DISCUSSION

Many contradictory reports have been published on the question of the persistence of 'dark' respiration in green cells in the light. This topic has been recently reviewed by Graham (16). Initial studies on the blue-green alga *Anacystis* concluded that the dark respiration was inhibited by low light intensities whereas high light intensities induced an increase in the O_2 uptake rate. The increase was later attributed to photorespiration (18). In the same way, the Kok effect was considered to be the consequence of the inhibition of dark respiration by light due to an increase in the ATP/ADP ratio (18). However, this later interpretation was contested by Healey and Myers (17) who observed that CCCP did not inhibit the Kok effect in *Chlamydomonas*.

The aim of our work was to reconsider the question of the participation of mitochondrial respiration to O_2 uptake in the light under conditions where any complication due to the presence of photorespiratory O_2 uptake was eliminated. Therefore, we performed our experiments under high CO_2 concentrations. Under such conditions, the glycolate pathway was previously reported to be completely inhibited (25). We first observed that

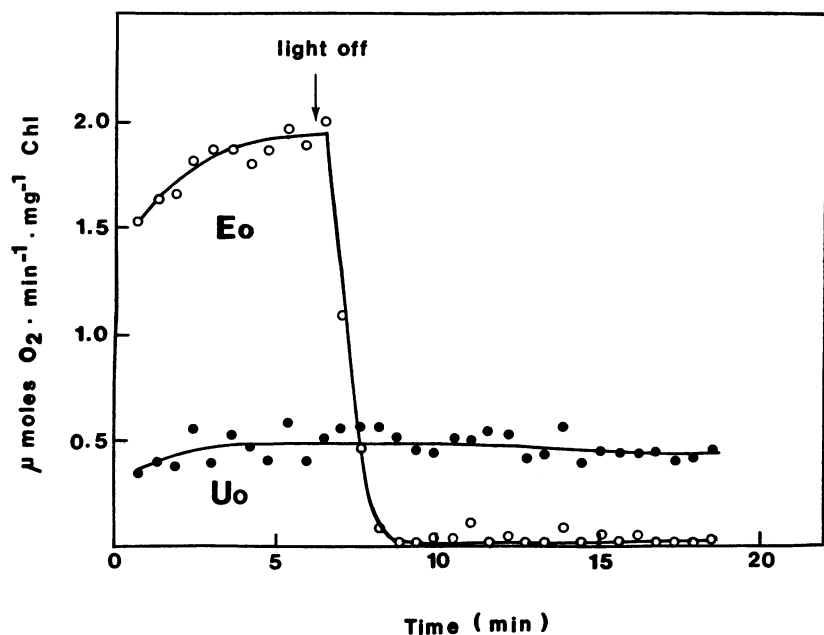


FIG. 1. O₂ exchanges at saturating CO₂ concentration during a light to dark transition. *E_o*: gross O₂ evolution rate; *U_o*: O₂ uptake rate. Initial O₂ concentration was 22% O₂; initial NaHCO₃ concentration was 10 mM; Chl concentration was 23.7 μg·ml⁻¹. Similar results were obtained when DCMU (50 μM final concentration) was added instead of switching off the light.

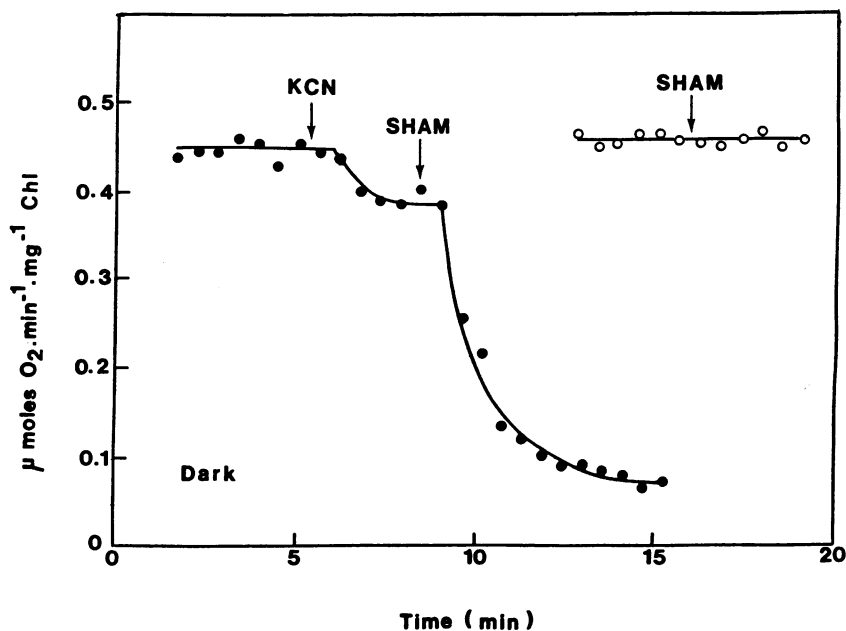


FIG. 2. Effects of cyanide and SHAM on dark O₂ uptake. Final concentrations of cyanide and SHAM were 1 mM. Initial O₂ concentration was 21% O₂; Chl concentration was 31.5 μg·ml⁻¹.

the O₂ uptake rate measured in light-pretreated *Chlamydomonas* was the same in the light, in the dark, or in the presence of DCMU. This suggests that in conditions where photorespiration does not take place, O₂-consuming processes involved in the light are only due to mitochondrial respiration.

This assumption was tested by studying the effects of mitochondrial oxidase inhibitors on O₂ exchanges. Cyanide was found to act differently in the light than in the dark. In the dark, the treatment of algae by cyanide gives a measurement of the maximum capacity for the alternative pathway (8), which was about 80% of the total respiration rate in our conditions. Because SHAM alone had no effect on the respiration rate (Fig. 2), we can conclude that the maximum rate of the Cyt path is at least the measured respiration rate. Thus, the effects of cyanide and SHAM in the dark can be easily interpreted in terms of the Cyt and alternative pathways.

In the light, the effect of cyanide appears to be more complex. Complete inhibition of net O₂ evolution was probably the con-

sequence of Rubisco inhibition by cyanide (20). If Calvin cycle is stopped, reducing power which continues to be produced cannot be used to fix CO₂ and can be diverted to O₂. This explains the cyanide-O₂ uptake stimulation observed at the onset of illumination. Such a competition between CO₂ and O₂ towards utilization of the reducing power generated by the photosystems has been reported earlier to occur in the green alga *Scenedesmus* (26). However, O₂ was unable to maintain the electron transport at the same rate as CO₂, as shown by an eventual decrease in the O₂ uptake rate. The reason for this regulation is unknown.

In spite of this complex effect of cyanide, SHAM, when added to cyanide-treated algae was shown to have the same inhibitory effect on O₂ uptake rate in the light and in the dark. This observation supports the proposal that mitochondrial respiration is probably present in *Chlamydomonas* in the light. Surprisingly, SHAM was found to inhibit O₂ evolution in the same extent as O₂ uptake in cyanide-treated algae. Because SHAM had no effect on O₂ exchanges (Fig. 4), when added to untreated algae, we can

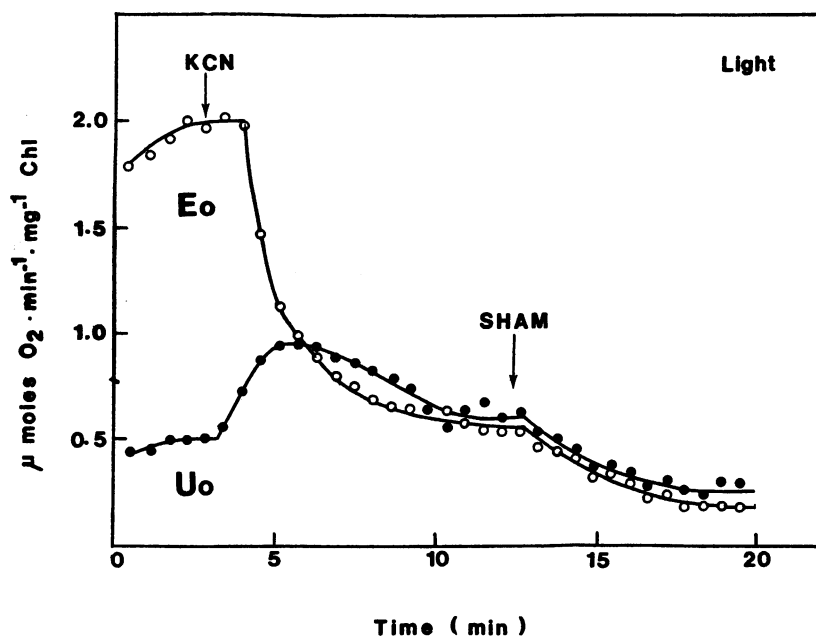


FIG. 3. Effects of cyanide and SHAM on O_2 exchanges in the light at saturating CO_2 concentration. E_o : gross O_2 evolution rate; U_o : O_2 uptake rate. Final concentration of cyanide and SHAM were 1 mM. Initial O_2 concentration was 22% O_2 ; initial $NaHCO_3$ concentration was 10 mM; Chl concentration was $41.4 \mu g \cdot ml^{-1}$.

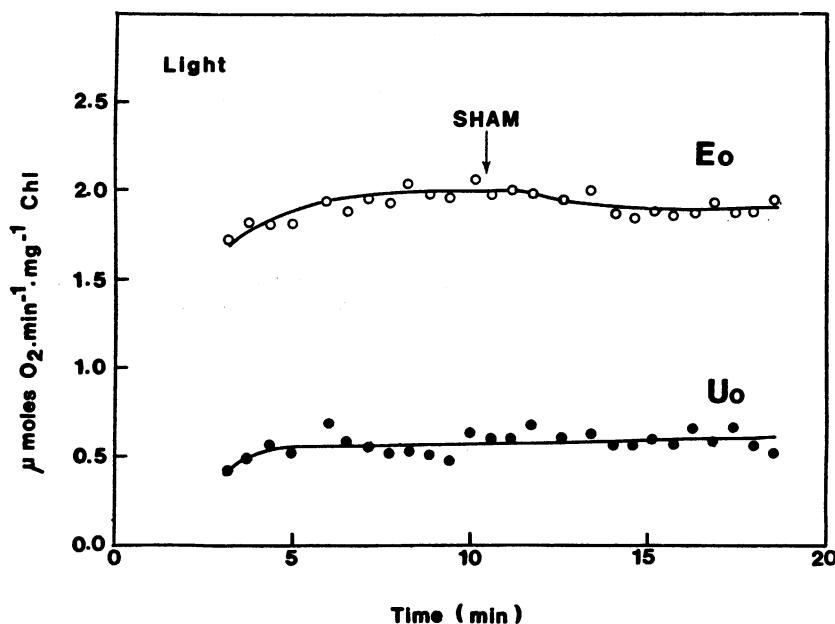


FIG. 4. Effect of SHAM (1 mM) on O_2 exchanges in the light at saturating CO_2 concentration. E_o : gross O_2 evolution rate; U_o : O_2 uptake rate. Initial O_2 concentration was 18% O_2 ; initial $NaHCO_3$ concentration was 10 mM; Chl concentration was $32.1 \mu g \cdot ml^{-1}$.

conclude that this product does not directly inhibit photosynthetic electron transport. A possible explanation for these coupled inhibitions would be to consider that in these conditions the reducing power used by mitochondrial respiration originates from the chloroplast via the metabolic shuttles. In such conditions, the inhibition of the mitochondrial oxidations would lead to an accumulation of the reducing power within the chloroplast and therefore to an inhibition of O_2 evolution because no more electron acceptors are available. On the other hand, the occurrence, in the light, after cyanide and SHAM additions of a DCMU-sensitive O_2 uptake confirms that cyanide can induce a different type of O_2 uptake process which was absent in untreated algae. This is supported by the fact that DCMU had no effect on O_2 uptake in untreated algae (Fig. 1). Thus, the DCMU-sensitive O_2 uptake process, which requires the photosynthetic electron transfer could be due to Mehler reactions induced by cyanide addition.

The uncoupler CCCP was shown to induce about the same increase in the O_2 uptake rate measured in the dark (increase of

$0.33 \mu mol O_2 \cdot mg^{-1} Chl \cdot min^{-1}$) and in the light (increase of $0.26 \mu mol O_2 \cdot mg^{-1} Chl \cdot min^{-1}$). This similar effect of CCCP provides a further argument that mitochondrial respiration continues in the light and therefore is not inhibited by high levels of ATP generated by the chloroplast.

The conclusion that in *Chlamydomonas* cells, mitochondrial respiration is not inhibited by light, apparently disagrees with the interpretation of Hoch *et al.* (18). However, if inhibition was observed in the cyanobacteria *Anacystis*, these authors failed to show it in the green alga *Scenedesmus*. Moreover, it is now considered that inhibition of dark respiration by light in cyanobacteria (27) as well as in photosynthetic bacteria (29) is due to the interaction between the respiratory and the photosynthetic chains present in the same membrane. In green algae, respiration is sequestered in the mitochondria. The only interactions between chloroplasts and mitochondria must be through metabolic shuttles (11). On the basis of ATP measurements, some authors have concluded that mitochondrial respiration should be inhibited by ATP production within the chloroplast (21, 28). Our

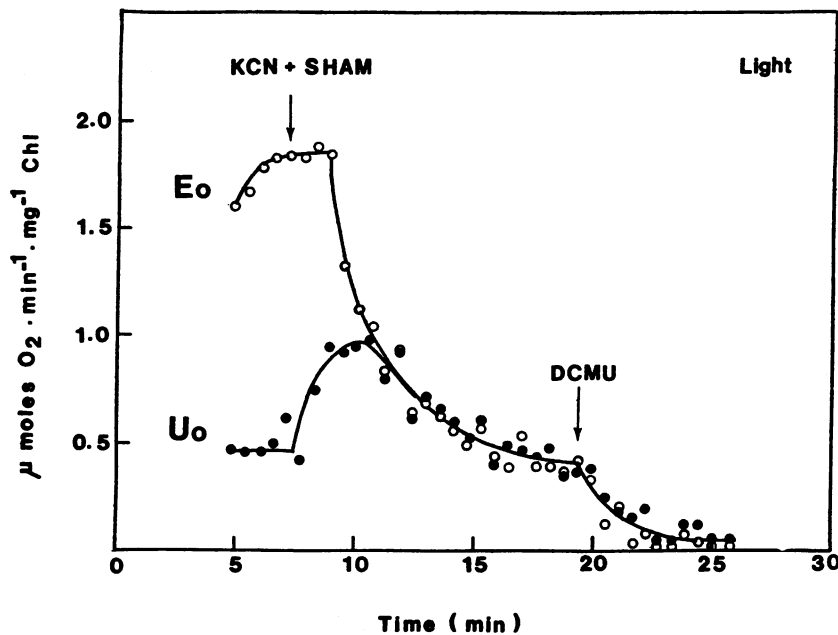


FIG. 5. Effect of DCMU (50 μM) on residual O₂ uptake observed in the presence of cyanide and SHAM. *Eo*: gross O₂ evolution rate; *Uo*: O₂ uptake rate. Final concentrations of cyanide and SHAM were 1 mM. Initial O₂ concentration was 17% O₂; initial NaHCO₃ concentration was 10 mM; Chl concentration was 34.3 $\mu\text{g}\cdot\text{ml}^{-1}$.

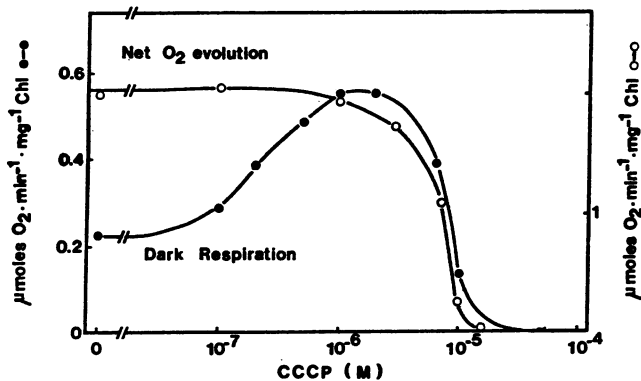


FIG. 6. Effect of CCCP on dark respiration and net O₂ evolution. O₂ concentrations were measured using an O₂-electrode chamber; algae were darkened at least 1 h prior to the measurements; initial NaHCO₃ concentration was 10 mM; initial O₂ concentration was 21% O₂; Chl concentration was 24 $\mu\text{g}\cdot\text{ml}^{-1}$.

results are in conflict with this interpretation. Rather, we confirm the pioneering isotope studies of Brown (5) who observed no light inhibition of O₂ uptake in *Chlorella*, in conditions where photorespiration was absent (8% O₂ and 0.8% CO₂).

Another conclusion which can be drawn from these experiments is that in *Chlamydomonas* no other O₂ uptake process like Mehler reactions are present in the light under saturating CO₂ concentrations. Moreover, even at the CO₂ compensation point, such reactions are very unlikely. This comes from the fact that the overall CO₂-sensitive O₂ uptake measured in *Chlamydomonas* was previously reported to be entirely due to the glycolate pathway (25). Therefore, if Mehler reactions are present in *Chlamydomonas*, their existence is probably limited to conditions where both photosynthetic carbon reduction and oxidation cycles are inhibited (as in cyanide-treated algae).

This situation appears to be quite different in the green alga *Scenedesmus*. In this species, Radmer and Kok (26) reported a direct and complete competition between O₂ and CO₂ towards the utilization of the photosynthetically generated reducing power. The use of inhibitors allowed the authors to conclude that a high capacity oxidase (possibly involving ferredoxin) distinct from Rubisco was responsible for this process. In *Chlamy-*

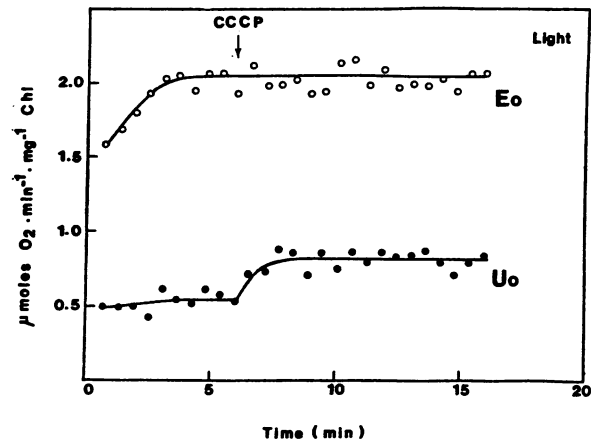


FIG. 7. Effect of CCCP on O₂ exchanges in the light at saturating CO₂ concentration. *Eo*: gross O₂ evolution rate; *Uo*: O₂ uptake rate. Final concentration of CCCP was 1 μM ; initial O₂ concentration was 20% O₂; initial NaHCO₃ concentration was 10 mM; Chl concentration was 28.9 $\mu\text{g}\cdot\text{ml}^{-1}$.

domonas, the competition is not complete (12, 25): only about 15% of the maximum electron flow (measured as gross O₂ evolution) occurring at CO₂ saturation can be diverted to O₂ at the CO₂ compensation point (see Table I in reference 25), and is entirely due to the photosynthetic carbon oxidation cycle. The significance of such differences concerning the O₂ uptake processes and the regulation of the electron flow under different CO₂ levels in these two algal species remains to be elucidated.

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