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O_2 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 O_2 uptake occurring in the light under saturating CO_2 concentration in *Chlamydomonas reinhardii* has been investigated. For this purpose, a mass spectrometer with a membrane inlet system was used to measure O_2 uptake and evolution in the algal suspension. First, we observed that the O_2 uptake rate was constant (about 0.5 micromoles of O_2 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 O_2 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 O_2 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 O_2 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 CO_2 concentration or at the CO_2 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 O_2 uptake processes might be present in these two algal species.

Mass isotope studies using $^{18}O_2$ provided evidence that O_2 uptake was occurring during photosynthesis both in algae (6, 15, 18, 26) and in higher plants (7, 13). This O_2 uptake process was recognized to be of a different nature from that taking place in dark respiration (18, 19). Oxygenase activity of Rubisco[1] and the associated metabolism of glycolate were shown to be involved in this light O_2 consumption (1, 4, 9). The effects of CO_2 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 O_2 uptake which is sensitive to CO_2 concentration (7, 13, 25). In the light, under saturating CO_2 concentration, conditions where the oxygenase activity of Rubisco should be completely inhibited and the glycolate pathway stopped, residual O_2 uptake still occurs (7, 14, 25). The nature of this remaining O_2 uptake is at present unknown.

Mitochondrial dark respiration could be responsible for this CO_2-insensitive O_2 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 CO_2 compensation point and CO_2 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 O_2 photoreduction (*i.e.* Mehler reactions) can be involved in O_2 uptake processes in the light (22). Such reactions could play an important role in green cells in supplying sufficient ATP for CO_2 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 O_2 uptake in the light are presently not elucidated. The aim of this work was to determine, in the green alga *Chlamydomonas reinhardii*, the nature of the O_2 uptake processes present in the light under CO_2 saturation when no photorespiration occurs. For this purpose, we studied the effects on O_2 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 CO_2 fixation.

MATERIALS AND METHODS

Chlamydomonas reinhardii (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 $l \cdot h^{-1}$. Cells were harvested by centrifugation and then resuspended in the culture medium lacking NH_4^+. The pH of the medium was 6.0. Chl concentration was between 25 and 40 $\mu g\ Chl \cdot ml^{-1}$. Algal suspension was bubbled with air in a thermostated (25°C) flask, under a light intensity of 1000 $\mu E \cdot m^{-2} \cdot s^{-1}$ (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 $\mu E \cdot m^{-2} \cdot s^{-1}$ (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 CH_4). After bubbling the algal suspension with N_2 in the light, $^{18}O_2$ (98.1% ^{18}O from CEA Saclay, France) was injected to obtain an initial O_2 concentration of about 20% O_2. Then, the reaction

[1] Abbreviations: CCCP, carbonyl cyanide *m*-chlorophenylhydrazone; Rubisco, ribulose-1,5 bisphosphate 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 $^{16}O_2$ (m/e = 32) and $^{18}O_2$ (m/e = 36). Each cycle lasted about 30 s. O_2 uptake rate (*Uo*) and gross O_2 evolution rate (*Eo*) were calculated from the expressions:

$$Uo = \left(\frac{\Delta[^{18}O_2]}{\Delta t} - k[^{18}O_2]\right)\left(\frac{[^{18}O_2] + [^{16}O_2]}{[^{18}O_2]}\right)$$

$$Eo = \left(\frac{\Delta[^{16}O_2]}{\Delta t} - k[^{16}O_2]\right) + Uo\left(\frac{[^{16}O_2]}{[^{16}O_2] + [^{18}O_2]}\right)$$

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 μM at 25°C). $[^{16}O_2]$ and $[^{18}O_2]$ represent, respectively, the amounts of each molecular species expressed in μmol $O_2 \cdot mg^{-1}$ 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 $^{16}O_2$ (m/e = 32) and were calculated from the expression:

$$R = \frac{\Delta[^{16}O_2]}{\Delta t} - k[^{16}O_2]$$

In one experiment carried out to determine the optimal CCCP[1] 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 μmol $O_2 \cdot mg^{-1}$ Chl $\cdot min^{-1}$ 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 (*Uo*) and gross evolution rates (*Eo*) in the light and in the following dark period. Stationary O_2 evolution rate was about 2 μmol $O_2 \cdot mg^{-1}$ Chl $\cdot min^{-1}$. O_2 uptake rate in the light was 0.5 μmol $O_2 \cdot mg^{-1}$ Chl $\cdot min^{-1}$ and no significant change was observed after switching off the light. Addition of DCMU (50 μM 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 μmol $O_2 \cdot mg^{-1}$ Chl $\cdot min^{-1}$.

In the light (Fig. 3), addition of cyanide first stimulated O_2 uptake rate to a value of about 0.9 μmol $O_2 \cdot mg^{-1}$ Chl $\cdot min^{-1}$, and then O_2 uptake decreased and stabilized at a level of about 0.6 μmol $O_2 \cdot mg^{-1}$ Chl $\cdot min^{-1}$. 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 μmol $O_2 \cdot mg^{-1}$ Chl $\cdot min^{-1}$. 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 μmol $O_2 \cdot mg^{-1}$ Chl $\cdot min^{-1}$; Fig. 2), whereas in the light (Fig. 3) it remained at a relatively high value (about 0.3 μmol $O_2 \cdot mg^{-1}$ Chl $\cdot min^{-1}$). This remaining O_2 uptake was completely suppressed by addition of 50 μM 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 μmol $O_2 \cdot mg^{-1}$ Chl $\cdot min^{-1}$) 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 μM and was maximum at 2 μM, corresponding to an increase of the dark respiration rate of about 0.33 μmol $O_2 \cdot mg^{-1}$ Chl $\cdot min^{-1}$ (Fig. 6). CCCP concentrations higher than 2 μM strongly decreased the respiration rate. Inhibitory effect of CCCP on net O_2 evolution was first observed at a concentration of 1 μM. We, therefore, chose a CCCP concentration of 1 μM 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 μmol $O_2 \cdot mg^{-1}$ Chl $\cdot min^{-1}$ without effect on gross O_2 evolution. The stimulation (0.26 μmol $O_2 \cdot mg^{-1}$ Chl $\cdot min^{-1}$) 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

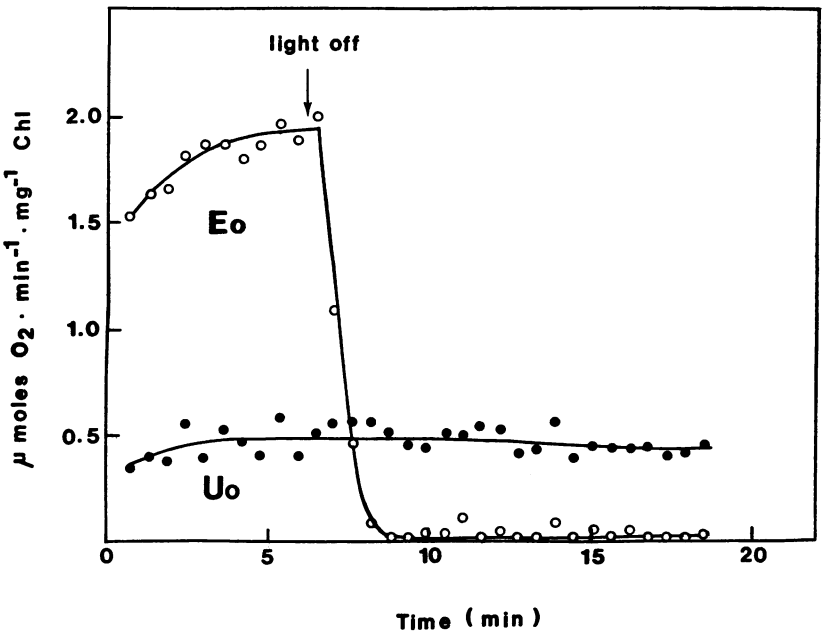

FIG. 1. O_2 exchanges at saturating CO_2 concentration during a light to dark transition. *Eo*: gross O_2 evolution rate; *Uo*: O_2 uptake rate. Initial O_2 concentration was 22% O_2; initial $NaHCO_3$ concentration was 10 mM; Chl concentration was 23.7 $\mu g \cdot ml^{-1}$. Similar results were obtained when DCMU (50 μM final concentration) was added instead of switching off the light.

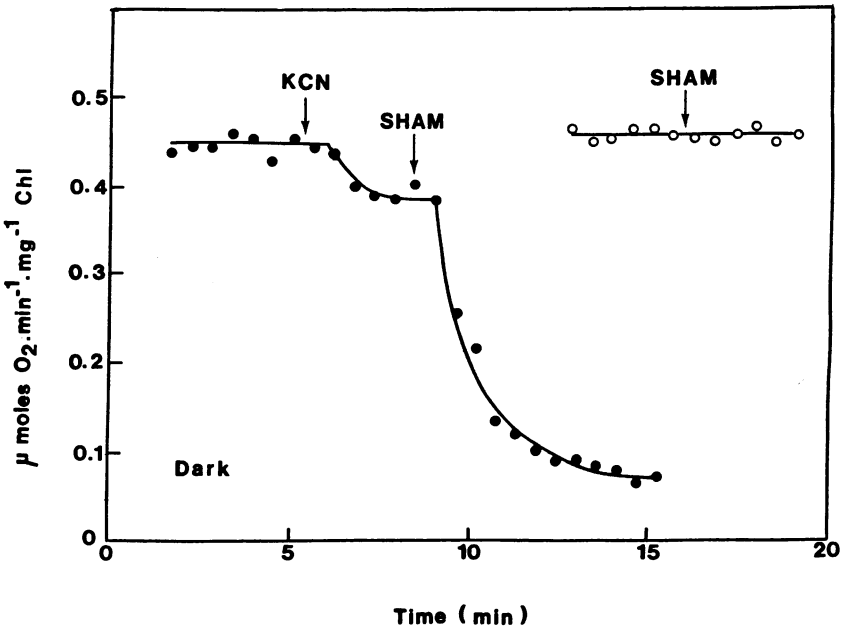

FIG. 2. Effects of cyanide and SHAM on dark O_2 uptake. Final concentrations of cyanide and SHAM were 1 mM. Initial O_2 concentration was 21% O_2; Chl concentration was 31.5 $\mu g \cdot ml^{-1}$.

the O_2 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, O_2-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 O_2 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 fo 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 O_2 evolution was probably the consequence of Rubisco inhibition by cyanide (20). If Calvin cycle is stopped, reducing power which continues to be produced cannot be used to fix CO_2 and can be diverted to O_2. This explains the cyanide-O_2 uptake stimulation observed at the onset of illumination. Such a competition between CO_2 and O_2 towards utilization of the reducing power generated by the photosystems has been reported earlier to occur in the green alga *Scenedesmus* (26). However, O_2 was unable to maintain the electron transport at the same rate as CO_2, as shown by an eventual decrease in the O_2 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 O_2 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 O_2 evolution in the same extent as O_2 uptake in cyanide-treated algae. Because SHAM had no effect on O_2 exchanges (Fig. 4), when added to untreated algae, we can

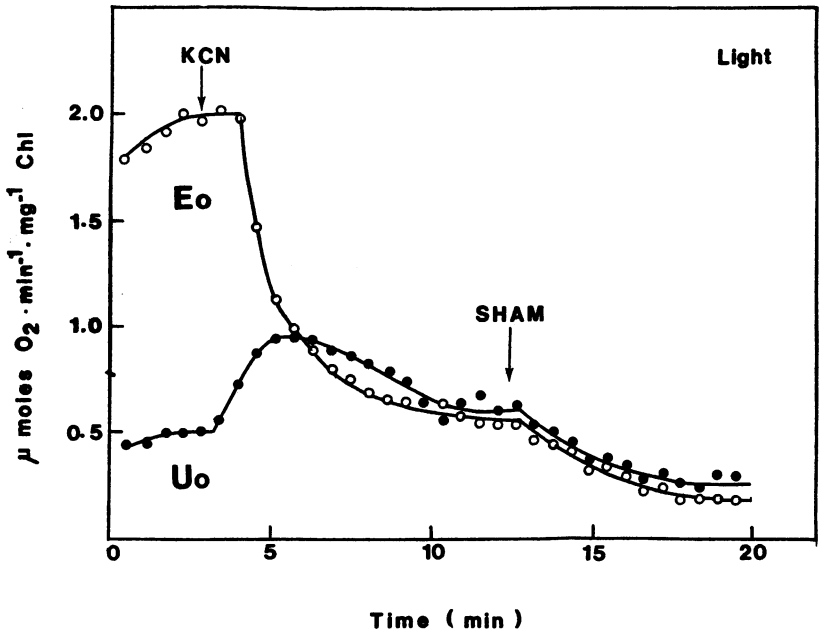

FIG. 3. Effects of cyanide and SHAM on O_2 exchanges in the light at saturating CO_2 concentration. *Eo*: gross O_2 evolution rate; *Uo*: O_2 uptake rate. Final concentration of cyanide and SHAM were 1 mM. Initial O_2 concentration was 22% O_2; initial $NaHCO_3$ concentration was 10 mM; Chl concentration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

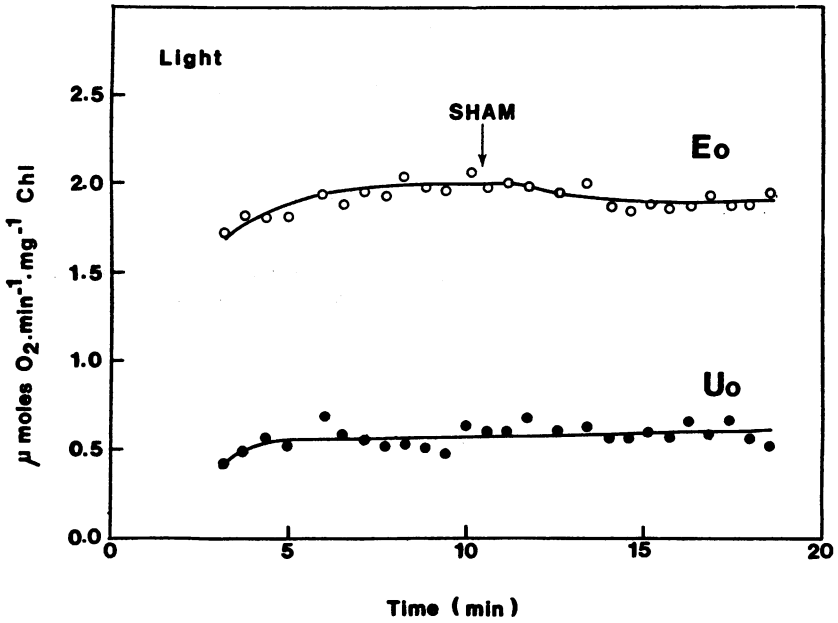

FIG. 4. Effect of SHAM (1 mM) on O_2 exchanges in the light at saturating CO_2 concentration. *Eo*: gross O_2 evolution rate; *Uo*: O_2 uptake rate. Initial O_2 concentration was 18% O_2; initial $NaHCO_3$ concentration was 10 mM; Chl concentration was 32.1 $\mu g \cdot ml^{-1}$.

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

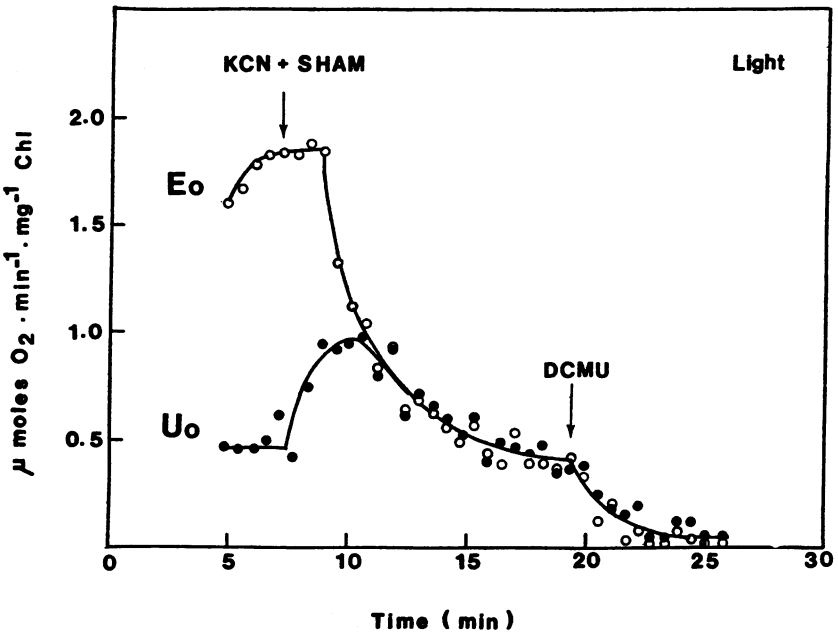

FIG. 5. Effect of DCMU (50 μM) on residual O_2 uptake observed in the presence of cyanide and SHAM. *Eo*: gross O_2 evolution rate; *Uo*: O_2 uptake rate. Final concentrations of cyanide and SHAM were 1 mM. Initial O_2 concentration was 17% O_2; initial $NaHCO_3$ concentration was 10 mM; Chl concentration was 34.3 $\mu g \cdot ml^{-1}$.

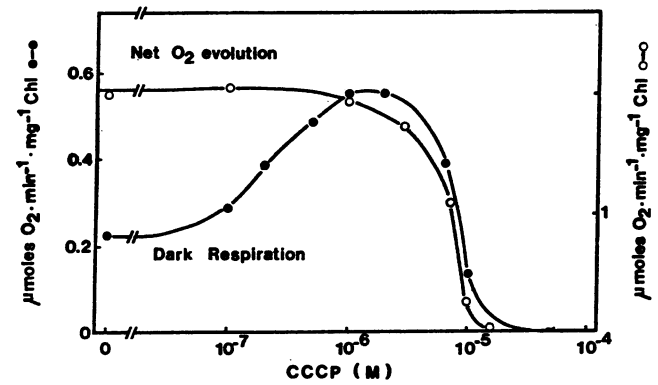

FIG. 6. Effect of CCCP on dark respiration and net O_2 evolution. O_2 concentrations were measured using an O_2-electrode chamber; algae were darkened at least 1 h prior to the measurements; initial $NaHCO_3$ concentration was 10 mM; initial O_2 concentration was 21% O_2; Chl concentration was 24 $\mu g \cdot ml^{-1}$.

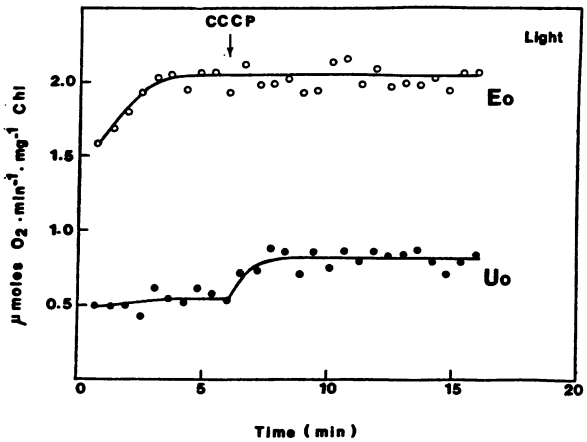

FIG. 7. Effect of CCCP on O_2 exchanges in the light at saturating CO_2 concentration. *Eo*: gross O_2 evolution rate; *Uo*: O_2 uptake rate. Final concentration of CCCP was 1 μM; initial O_2 concentration was 20% O_2; initial $NaHCO_3$ concentration was 10 mM; Chl concentration was 28.9 $\mu g \cdot ml^{-1}$.

results are in conflict with this interpretation. Rather, we confirm the pioneering isotope studies of Brown (5) who observed no light inhibition of O_2 uptake in *Chlorella*, in conditions where photorespiration was absent (8% O_2 and 0.8% CO_2).

Another conclusion which can be drawn from these experiments is that in *Chlamydomonas* no other O_2 uptake process like Mehler reactions are present in the light under saturating CO_2 concentrations. Moreover, even at the CO_2 compensation point, such reactions are very unlikely. This comes from the fact that the overall CO_2-sensitive O_2 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 O_2 and CO_2 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 *Chlamydomonas*, the competition is not complete (12, 25): only about 15% of the maximum electron flow (measured as gross O_2 evolution) occurring at CO_2 saturation can be diverted to O_2 at the CO_2 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 O_2 uptake processes and the regulation of the electron flow under different CO_2 levels in these two algal species remains to be elucidated.

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