Plant Physiol. (1979) 63, 30–34
0032-0089/79/63/0030/05/$00.50/0

Energy Transfer from the Phycobilisomes to Photosystem II Reaction Centers in Wild Type *Cyanidium caldarium*[1]

Received for publication December 19, 1977 and in revised form August 8, 1978

BRUCE A. DINER
Institut de Biologie Physico-Chimique, 13, rue Pierre et Marie Curie, 75005 Paris, France

ABSTRACT

Nonsaturating light at 600 or 436 nanometers was used to excite specifically phycocyanin or chlorophyll *a*, respectively, both of which participate in light capture in photosystem II of *Cyanidium caldarium*. The ratio of absorption of light by phycocyanin to chlorophyll in photosystem II in this organism is >20 at 600 nanometers and ≤0.2 at 436 nanometers.

The distribution of the absorbed light energy at these two wavelengths was followed by detecting the flash yields of O_2 during each illumination. We found that light absorbed by phycocyanin was transferred to only half of the reaction centers of photosystem II. This heterogeneity of energy distribution arises because only half of the centers and their associated antennae of 40 chlorophyll *a* are attached to phycobilisomes.

Red and blue-green algae contain phycobilins as accessory photosynthetic pigments. These are aggregated in the form of phycobilisomes which are attached in most organisms to the outer surface of the thylakoid membranes. This is also the case for the organism to be considered here (14), *Cyanidium caldarium*, a Rhodophyte containing C-phycocyanin (2).

Ley and Butler (9) have reported that light energy absorbed by phycoerythrin in *Porphyridium cruentum* is transferred to the small amount of Chl (5% of the total) associated with PSII. According to these authors 50% of this energy is then transferred to PSI when PSII centers are open and 90 to 95% when the latter are closed.

The advantage of using algae containing phycobilin for energy transfer studies is that the absorption bands of the accessory pigments are well separated from those of Chl *a*. Thus, the actinic effect of light specifically exciting phycobilin can be monitored via light exciting only Chl *a* which is associated with all reaction centers of PSI and II. Using this technique, we characterized energy transfer from the phycobilisomes (containing principally C-phycocyanin) to PSII in wild type *C. caldarium*. We found that the distribution of energy was in fact extremely heterogeneous. Only one-half of the reaction centers of PSII were excited by light absorbed by the phycobilisomes.

MATERIALS AND METHODS

C. caldarium wild type and mutant III-C (lacking phycocyanin) (13) were grown as indicated in reference 3.

Action spectra were performed in a modulated light O_2 electrode built by P. Bennoun and used under the conditions described earlier (3). All other O_2 measurements were performed on an O_2 electrode similar to that described by Joliot and Joliot (6). O_2 production was measured either through modulated detection or by sampling a differentiated O_2 signal obtained a fixed time after an actinic flash. The flashes used in these measurements were Stroboslaves (General Radio type 1539A). These have a 3-μsec width at half-height and were used with the Seavom interference filters indicated in the text.

Fluorescence experiments were performed using an apparatus described by Joliot and Joliot (7). The actinic xenon flash (Verre et Quartz model VQ X CAD 22) had a 1-μsec width at half-height. The detecting flash given 15 msec after the actinic flash was a Stroboslave filtered by a 436 nm interference filter (7.5 nm bandwidth at half-height). Complementary filters, two Ulano Rubylith and one Kodak Wratten 70 (passing >680 nm), were placed before the EMI photomultiplier (model 9558).

RESULTS AND DISCUSSION

Action Spectra. The PSII antenna sizes of *Cyanidium* wild type and mutant III-C are the same when measured above 680 nm (3). Thus the Chl *a* part of the wild type PSII antenna consists of the same number of pigment molecules as the entire PSII antenna of the III-C mutant.

PSII action spectra of these algae are shown in Figure 1. These spectra were normalized to the same amplitude in the far red region (>690 nm, where there is practically no phycocyanin absorption) in order to compare the relative contributions of phycocyanin and Chl *a* in the PSII action spectrum in the wild type. C-Phycocyanin absorption overwhelmingly dominates the wild type spectrum such that by exciting these algae at 600 nm, phycocyanin excitation is favored by a factor of over 20 relative to that of Chl.

Unlike Chl *a*, phycocyanin does not show a Soret band in the blue region of the spectrum. By exciting at the Soret peak at 436 nm (not shown), Chl excitation is favored by at least a factor of 5 relative to that of phycocyanin. The carotenoids do not affect the relative excitation of Chl and phycocyanin at 436 nm as no energy transfer occurs between the carotenoids and either of these pigments in PSII in *Cyanidium*.

Profiting from this selective absorption, it was possible to use 600 nm light to induce an actinic effect upon those PSII reaction centers receiving energy from the phycobilisomes. The extent of this actinic effect could then be monitored or compared with 436 nm light which excites all PSII centers as indicated earlier.

Energy Transfer from Phycobilisomes to PSII. The O_2 yield of a single turnover flash is proportional to the fraction of O_2-evolving sites in state S_3 (three oxidizing equivalents stored [8]) just prior to the flash. In dark-adapted cells the concentration of this state is zero and the O_2-evolving sites are in states S_0 or S_1 (0 and 1 oxidizing equivalent, respectively). Upon excitation with low intensity light (continuous, modulated, or flashing) these cells show a sigmoidal increase in the rate of O_2 production as a function of time. This kinetic behavior is called the "O_2 activation curve" (5) and corresponds to the light-driven increase of the

[1] This work was supported by a grant from The Energy Research and Development Programme of the Commission of the European Communities.

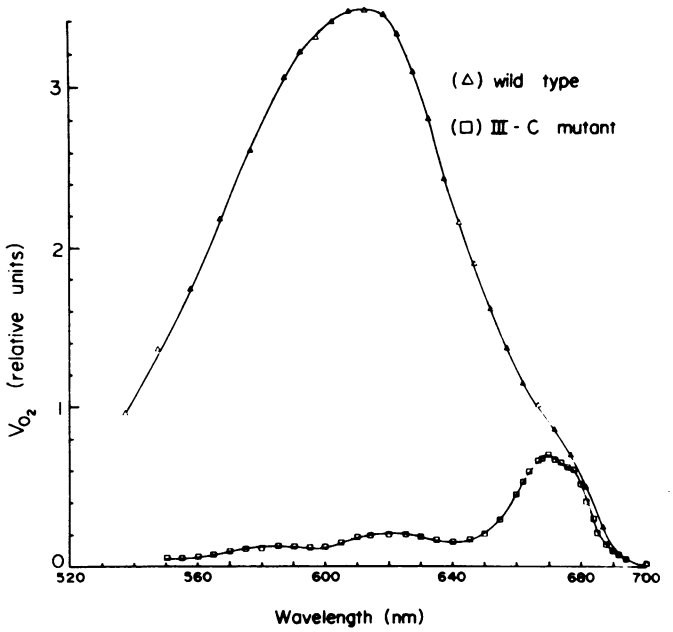

FIG. 1. PSII action spectra of *Cyanidium* wild type (△) and mutant III-C (□). Algae were illuminated with continuous far red light (>680 nm) favoring excitation of PSI relative to PSII, yet sufficient to maintain PSII activated. Weak variable wavelengh monochromatic light (3 nm bandwidth at half-height), chopped at 10 Hz, gave rise to a modulated O_2 signal which served as a measure of PSII activity. Photochemical turnover in PSI was maintained greater than 10 times that of PSII. Spectra were corrected for lamp emission. The two spectra were normalized to the same rates of O_2 production at wavelengths >690 nm.

concentration of state S_3 to its steady-state level (3, 8).

The rate of formation of state S_3 and its photoexcitation to produce O_2 are both purely light-limited phenomena provided that the illumination is not saturating. Where nonsaturating repetitive light flashes at two different wavelengths are adjusted in intensity to give the same rate of O_2 activation on the same cells, these flashes should give the same O_2 yields throughout the O_2 activation. Although this is normally true, we observed that it was not the case for previously dark-adapted *Cyanidium* wild type cells excited with 436 and 600 nm flashes (Fig. 2). The intensities of these flashes were adjusted to give the same half-rise time (14th flash, flashes given at 60-msec intervals). The O_2 yields of the 436 nm flashes were approximately 1.75 times those of the 600 nm flashes throughout the O_2 activation. The simplest interpretation of this observation is that the action spectra of all of the centers are not identical and that nearly two times more centers are excited at 436 nm (steady-state O_2 yield/flash ~10% of saturation) than at 600 nm (steady-state O_2 yield/flash ~6% of saturation).

Light at 600 nm preferentially excites the phycobilisomes which transfer their energy to PSII. Light at 436 nm preferentially excites PSI which in *Cyanidium* has a slightly larger antenna of Chl *a* than does PSII.

It might be argued that 600 nm light, in favoring excitation of PSII over PSI, would induce the reduction of the plastoquinone pool linking the two photosystems and thereby decrease the quantum yield of PSII. The pool would remain oxidized, however, in 436 nm light and would show a constant quantum yield of PSII. This hypothesis can be eliminated as it would predict that the ratio of the O_2 yields at 436 nm to those at 600 nm (Y_{436}/Y_{600}) would increase during O_2 activation which is not observed in Figure 2. It is also likely that in *Cyanidium* as in *Porphyridium* (9) light energy transferred by the phycobilisomes to PSII is subsequently transferred in part to PSI. This same argument (Y_{436}/Y_{600}) eliminates, as well, a progressive detachment of phycobilisomes from the membrane during activation at 600 nm.

It might also be argued that chromatic effects shift the distribution of light energy during the course of O_2 activation. These might result in different steady-state flash yields at 436 and 600 nm despite the similar half-rise times at these wavelengths. To test such a hypothesis, dark-adapted *Cyanidium* wild type cells were excited by 40 flashes at either 436 or 600 nm under the same conditions as in Figure 2. This series of flashes (Fig. 3) was then followed 300 msec later by a series of saturating flashes given at 300-msec intervals. The first saturating flash yield was only 63% of the subsequent steady-state yield following 600 nm preillumination. In contrast, the first saturating flash yield was within 5% of the subsequent steady-state yield after preillumination at 436 nm. There was a small oscillatory pattern of flash yields observed after 436 nm preillumination as the intermediary oxidation states of the O_2-evolving site (8) had not become fully equilibrated to their final steady-state levels. As saturating flashes, by definition, excite all centers independent of energy distribution within the antenna, this experiment indicates that the concentration of S_3

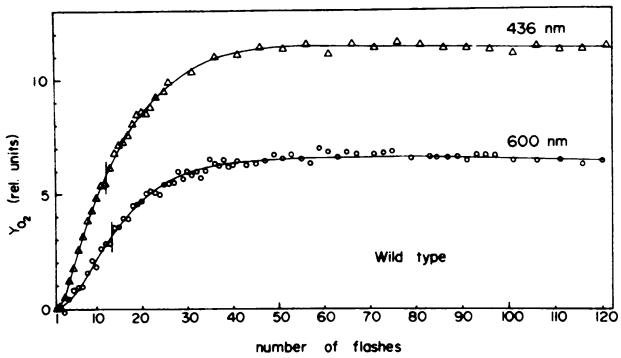

FIG. 2. Oxygen activation curves of *Cyanidium* wild type cells using 436 (△) or 600 nm (○) light flashes adjusted in intensity to give the same half-rise times (14th flash). Cells were dark-adapted for 10 min and then repetitively excited with 436 nm flashes (7.5 nm bandwidth at half-height) or 600 nm flashes (5.6 nm bandwidth at half-height) every 60 msec. Steady-state O_2 yields on plateaus following O_2 activation were ~10% of saturation for the 436 nm flashes and ~6% of saturation for the 600 nm flashes. Y_{O_2} = relative O_2 flash yields. This experiment was performed in the presence of 6 mM NaN_3.

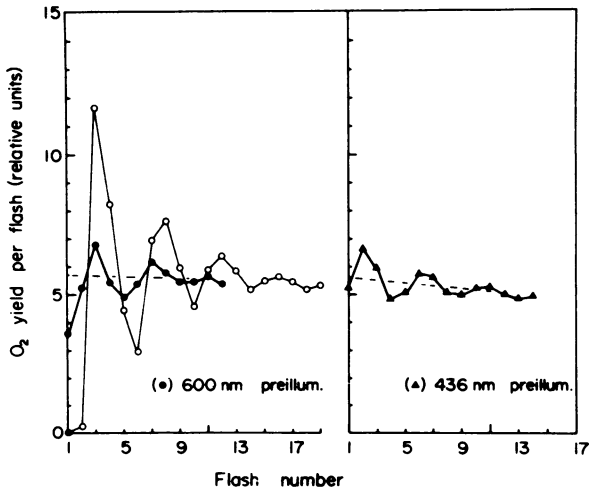

FIG. 3. O_2 yields in a sequence of saturating flashes following preillumination at either 436 (▲) or 600 (●) nm. *Cyanidium* wild type cells were dark-adapted for 10 min and then repetitively excited with 40 flashes at either 436 or 600 nm under the same conditions as in Figure 2. This preillumination was followed 300 msec later by repetitive saturating flashes given at 300-msec intervals. An O_2 flash sequence under the same conditions but without preillumination is also shown (○). These experiments were performed in the presence of 6 mM NaN_3.

after 600 nm preillumination was only 65% of that after 436 nm preillumination. We conclude that the difference in flash yields at 436 and 600 nm in Figure 2 does not arise from a shift in energy distribution during the course of O_2 activation but rather from the fact that only about 60% of the PSII centers were excited by 600 nm light at the intensities used in Figures 2 and 3. These and related experiments were performed many times and the fraction of centers insensitive to 600 nm excitation ranged from 35 to 50%. More of the remaining centers could be activated, however, by a longer or more intense 600 nm illumination.

The experiments of Figures 2 and 3 were performed in the presence of 6 mM NaN_3 which increases the quantum yield of O_2 production in *Cyanidium* (3, 12). The presence of NaN_3 did not in any way affect the distribution of light energy in PSII as similar results were obtained in its absence.

There are two possible models to explain these data (Fig. 4):

a. Half of the centers are associated with phycobilisomes and the others are not. No energy transfer occurs between the two groups of centers. No restriction is placed upon the number of centers associated with a phycobilisome as long as light energy is free to migrate among them. This last point is to satisfy requirements of energy transfer within each group of PSII centers as discussed later.

b. Two kinds of center-Chl *a* units are associated with a phycobilisome, one in direct contact with it (primary unit), the other (secondary unit) attached only to the primary unit and not touching the phycobilisome. Light energy coming from the phycobilisome is selectively trapped by the primary unit such that the secondary unit will not receive energy originating from phycocyanin as long as the primary unit is in a quenching state. Both groups of units, however, are equally accessible to light energy exciting Chl *a* directly.

It is possible to choose between these models by exciting cells with nonsaturating 600 nm light in the presence of DCMU, such that those centers receiving light energy from the phycobilisome would be closed and converted to a low quenching state. Upon continued illumination these would transfer incoming energy to secondary units in model (b) but *not* to the centers of model (a) unassociated with phycobilisomes.

Dark-adapted wild type *Cyanidium* cells were excited with 600 nm flashes having an actinic effect on PSII about 15% of that of saturating flashes (Fig. 5). Upon attaining the steady-state O_2 yield at the end of O_2 activation, the 600 nm flashes were replaced

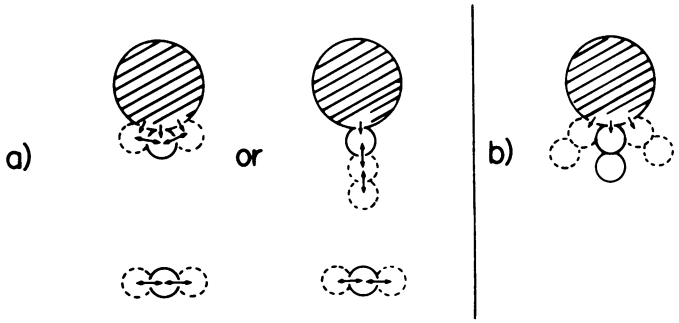

FIG. 4. Model (a): two types of center-Chl *a* antenna units—those associated with the phycobilisomes and those completely independent (not connected directly or via energy transfer to the phycobilisome). Light energy is free to circulate among the members of each group but not between the two groups.

Model (b): two types of center-Chl *a* antenna units—those attached directly to phycobilisomes (primary units) and those connected to primary units but not touching the phycobilisome (secondary units). Light energy coming from the phycobilisome is preferentially trapped in primary units. Transfer occurs to secondary units only when the primary units are closed (in a low quenching state). Light at 436 nm, directly exciting Chl *a*, is equally accessible to centers of primary and secondary units. Phycobilisomes: large hatched circles; center-Chl *a* antenna units: small open circles.

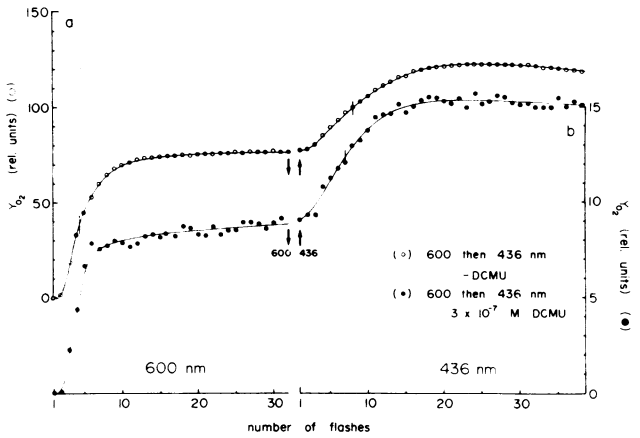

FIG. 5. a: (○) O_2 activation curves of wild type *Cyanidium* excited first with 600 nm flashes then with 436 nm flashes. Cells were dark-adapted for 10 min and then excited with 600 nm flashes (5.6 nm bandwidth at half-height) every 60 msec. After 32 flashes these were replaced 80 msec later by 436 nm flashes (7.5 nm bandwidth at half-height) given every 80 msec. Steady-state O_2 yields were about 25% of saturation for the 436 nm flashes and about 15% of saturation for the 600 nm flashes. b: (●) Same as Figure 5a but with 0.3 μM DCMU. Ordinate is expanded 10 times relative to that of Figure 5a.

by 436 nm flashes having an actinic effect of PSII about 25% of that of saturating flashes. These latter flashes induced a second activation corresponding to 40% of their final steady-state yield. Correcting for the probable 20% excitation of phycocyanin in 436 nm light, these results indicate that only 50% of the PSII centers were activated by the 600 nm illumination. The remaining centers had received no more than one photon/center and did not advance beyond state S_2 (2 oxidizing equivalents on the O_2-evolving site).

This experiment was repeated in the presence of 0.3 μM DCMU which inhibited the steady-state O_2 flash yield by a factor of 8. Were model (b) correct then one would predict that of those centers not blocked by DCMU, the fraction of these excitable by 600 nm light either directly or via energy transfer should increase relative to that fraction excitable by 600 nm light in the uninhibited case. In other words, the ratio of those centers activated by 436 nm light to those activated by 600 nm light (A_{436}/A_{600}) should have decreased in the presence of DCMU relative to this ratio in the absence of DCMU. Were the DCMU concentration increased still further, then a limiting case would be reached where all centers not blocked by DCMU should become activated by 600 nm light. All blocked centers would transfer their energy to any neighboring open centers. Figure 5 shows that the addition of DCMU did not change the ratio of A_{436}/A_{600} thus arguing against model (b) and in favor of model (a).

The only way that model (b) might still be in agreement with the above experiment would be if DCMU did not act in a random manner, preferring to block a center (primary or secondary) whose partner (secondary or primary) was blocked. Thus, both members of a pair would be inhibited or not. In this case the uninhibited centers giving rise to O_2 would show the same fraction of centers activated by 436 nm light after 600 nm preillumination.

To test this hypothesis, we performed the fluorescence analog of the experiment of Figure 5 but in the presence of 20 μM DCMU and 0.1 M NH_2OH (to assure that centers once excited remained blocked in a low quenching state [1]). Cell ere preilluminated at 577 nm (bandwidth 21 nm at half-heignt) which closed all centers connected directly to phycobilisomes or via energy transfer as shown by the plateau of the fluorescence induction curve. Nearly saturating blue actinic flashes (filtered by Schott BG 38 [2 x 1 cm]) were then given which closed the remaining centers. The fluorescence yield was determined throughout by a 436 nm detecting flash at constant intensity, which detected all centers

independent of whether or not they were associated with phycobilisomes. Figure 6 shows that the 150 flashes at 577 nm did not close all of the centers even in saturating concentrations of DCMU. The saturating flashes which followed did reach all of the centers producing a second fluorescence induction. The fluorescence induction with these actinic flashes but without 577 nm preillumination is also shown (○). Many flashes were required as the saturating flash yield was low. The dashed curve shows how the 577 nm induction curve should have evolved were 37 of the 577 nm flashes to have had the same actinic effect as one blue saturating flash. The dashed and 577 nm induction curves are initially superimposed and then diverge showing that the difference between these flashes is more than a question of intensity. Despite the same fluorescence yields after one blue saturating flash and after 37 of the 577 nm flashes, the population of closed centers was not the same. We interpret this experiment as indicating that only those centers associated with phycobilisomes were excited and closed by the 577 nm flashes, whereas any center could be excited and closed by the blue saturating flashes. Were both primary and secondary units of model (b) blocked together by DCMU then all centers should have been closed by 577 nm light. We conclude that model (b) is untenable and that there are many PSII centers which cannot be excited by light absorbed by the phycobilisomes.

The contrast between the 577 nm and blue saturating flash excitation is not as marked in this experiment as for the excitation of Figures 3 and 5. The probable reason for this is that only one excitation/center is required to close centers in the fluorescence experiment while it takes at least two excitations/center to reach state S_3 of the O_2-evolving site. During the excitation necessary to close or activate centers associated with phycobilisomes, more unassociated centers were closed in Figure 6 than were activated in Figures 3 and 5.

Harnischfeger and Codd (4) recently reported that they could vary the efficiency of energy transfer from phycocyanin to Chl in a number of blue-green algae. Increased efficiency of energy transfer was indicated by a decrease in the quantum yield of phycocyanin fluorescence relative to that of Chl. These changes were induced by pretreatment with white light or darkness, depending on the alga. Such variable efficiency would be consistent

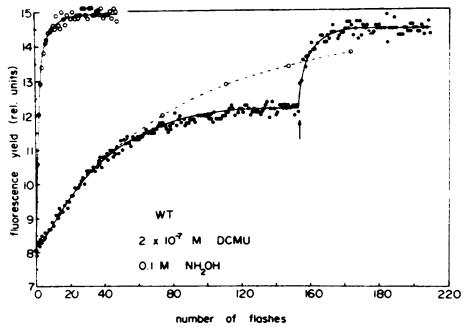

FIG. 6. Fluorescence induction of *Cyanidium* wild type cells with nearly saturating actinic blue flashes (2 cm Schott BG 38) with (●) and without (○) preillumination by low intensity 577 nm actinic flashes (21 nm bandwidth at half-height, 2 cm Schott BG 38 + Corning 3-66). Fluorescence yield was detected throughout by a 436 nm flash (bandwidth 7.5 nm at half-height) given 15 msec after each actinic flash (blue and 577 nm) and producing a negligible actinic effect. In the preillumination experiment (●) repetitive 577 nm flashes were given (5 Hz) up to the point indicated by the arrow (150 flashes) where they were replaced by the repetitive blue flashes (5 Hz). In the experiment without preillumination (○) repetitive blue flashes were given at 5 Hz. Dashed line shows the points of this latter experiment translated horizontally such that the first nearly saturating blue flash is superimposed on the 577 nm flash having attained the same fluorescence yield. In both experiments cells were dark-adapted for 5 min before the addition of 20 μM DCMU. After 5 min of dark incubation 0.1 M NH_2OH at pH 7.0 was added in the dark. The experiment was begun after at least 10 min of further dark incubation.

with attachment and detachment of phycobilisomes from the membrane. This light-dependent mechanism appears not to occur in *Cyanidium* as the quantum yield of phycocyanin fluorescence is quite low in this alga. The 655 nm phycocyanin fluorescence emission was approximately one-half that of the 695 nm chlorophyll emission at 77 K with closed PSII centers and excitation at 600 nm. As the quantum yield of Chl fluorescence is on the order of 10% under those conditions, the quantum yield of phycocyanin energy transfer to Chl must be about 95%. The concentration of free phycobilisomes must be negligible as these would be expected to show a high quantum yield of fluorescence. It should not be excluded, however, that in *Cyanidium* numerous center-Chl antenna units might be associated with each phycobilisome and that half of these might undergo reversible attachment or detachment. Phycocyanin could still transfer light energy to the remaining attached Chl containing units such that its own fluorescence quantum yield would remain low.

We do not know whether there is a control over energy transfer from the phycobilisomes to PSII. Our attempts at modifying the fraction of centers associated with phycobilisomes were unsuccessful. These included varying the intensity of illumination of culture flasks, varying the age of the cultures tested, preilluminating at different wavelengths and intensities, and fractionation based on cell maturity.

It is unclear what advantage this heterogeneity in PSII offers *Cyanidium*. There are reports using other organisms of a heterogeneity in the antenna of PSII. Melis and Homann (11) have reported that in higher plant chloroplasts two types of PSII units exist which may differ in their respective antenna sizes. Melis and Akoyunoglou (10) have reported a similar heterogeneity in greening and mature bean leaves. It remains to be seen if there is any analogy between the association of light-harvesting Chl *a/b* complex with these units in higher plants and the association of phycocyanin with the Chl *a*-containing units in *Cyanidium*.

Efficiency of Energy Transfer within PSII. Energy transfer between PSII centers occurs with lower probability in wild type *Cyanidium* than in the III-C mutant. This is shown by Figure 4 in reference 3 in which the sigmoidal shape of the fluorescence induction curve is not as marked for *Cyanidium* wild type as for the mutant and *Chlorella*.

Increasing inhibition by DCMU of *Cyanidium* mutant III-C accelerated the rate of light-driven relaxation of state S_3 to its steady-state concentration from an excess produced after two saturating flashes (3). This was done by measuring the O_2 yields (proportional to the concentration of state S_3) of the nonsaturating flashes which drove this relaxation. An acceleration of these kinetics (Fig. 6 in ref. 3) by a factor of 4 relative to the uninhibited case indicated that at least four centers were interconnected in *Cyanidium* mutant III-C. These experiments were repeated in the wild type where both 436 and 600 nm flashes of constant intensity were used to drive this relaxation. In both cases (Fig. 7) the rate of the light-driven relaxation of state S_3 was accelerated with increasing concentrations of DCMU. The factor by which the rate increases can be plotted as a function of the extent of inhibition by DCMU (Fig. 8). Extrapolation to 100% of the centers blocked gives a 2.5- to 3-fold increase in the relaxation rate with respect to uninhibited cells at both 436 and 600 nm. These results indicate that energy transfer between PSII centers associated with phycobilisomes in the wild type is less probable than between PSII centers in the III-C mutant lacking phycobilisomes. The 436 nm light detects all centers in the wild type, those associated with and those not associated with phycobilisomes. The somewhat higher probability of energy transfer in 436 nm light relative to 600 nm light (Fig. 8) may mean that the 35 to 50% of the centers not associated with phycobilisomes show the higher probability of energy transfer characteristic of the III-C mutant.

The difference in the probability of energy transfer between PSII centers in the III-C mutant and wild type is consistent with the electron micrographs of Wollman (15). In these freeze-fracture

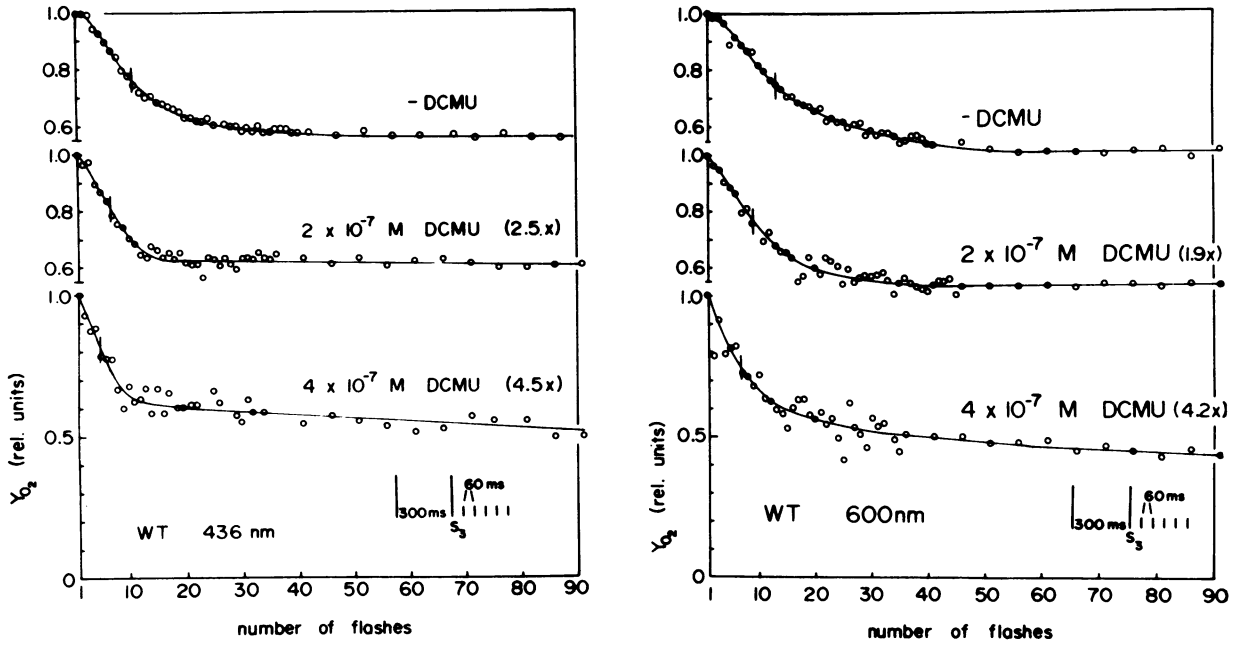

FIG. 7. Flash-driven decrease of O_2 yield (Y_{O_2}) in a series of nonsaturating 436 or 600 nm flashes following excitation by two saturating flashes in the presence of varying concentrations of DCMU. These curves correspond to the light-driven relaxation of state S_3 to the steady-state level after formation in excess by the two saturating flashes. Dark-adapted (10 min) *Cyanidium* wild type cells were excited by two saturating flashes 300 msec apart following 60 msec later by a series of repetitive nonsaturating flashes (60 msec apart) at either 436 nm (left, 7.5 nm bandwidth at half-height) or 600 nm (right, 5.6 nm bandwidth at half-height). Flash intensities were approximately the same as in Figure 2. DCMU was added at the indicated concentrations. Relaxation curves were normalized to the same initial values by multiplying by the indicated factors. NaN_3 (5 mM) was present throughout. Aside from the change in amplitude, partially inhibiting DCMU does not change the form of the oscillating pattern of O_2 yields in a sequence of saturating flashes.

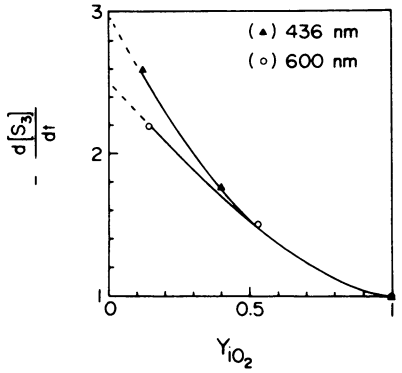

FIG. 8. Relative rate of light-driven decay ($-dS_3/dt$) of excess state S_3 to the steady-state level in weak flashes at either 436 (▲) or 600 (○) nm as a function of Y_{iO_2} (the relative nonsaturating flash yield of O_2 at various concentrations of DCMU compared to the uninhibited yield). Y_{iO_2} was measured 60 msec after two saturating flashes were given to dark-adapted cells. Data are those of Figure 7. Dashed lines show extrapolated rate $-dS_3/dt$ with 100% of the PSII centers blocked.

studies the number of particles in the EF face (attributed to PSII) in physical contact with one another was much higher for the III-C mutant than for the wild type. This observation would suggest that the more compact the organization of these particles, the more efficient is PSII energy transfer.

LITERATURE CITED

1. BENNOUN P 1971 Contribution à l'étude de la réaction photochimique II des organismes photosynthétiques. Thesis. Université de Paris
2. BOGORAD L 1975 Phycobiliproteins and complementary chromatic adaptation. Annu Rev Plant Physiol 26: 369-401
3. DINER BA, FA WOLLMAN 1979 Functional comparison of the photosystem II center-antenna complex of a phycocyanin-less mutant of *Cyanidium caldarium* with that of *Chlorella pyrenoidosa*. Plant Physiol 63: 20-25
4. HARNISCHFEGER G, GA CODD 1977 Liquid nitrogen fluorescence studies of the photosynthetic apparatus of blue-green algae. Br Phycol J 12: 225-232
5. JOLIOT P 1968 Kinetic studies of photosystem II in photosynthesis. Photochem Photobiol 8: 451-463
6. JOLIOT P, A JOLIOT 1968 A polarographic method for detection of oxygen production and reduction of Hill reagent by isolation chloroplasts. Biochim Biophys Acta 153: 625-634
7. JOLIOT P, A JOLIOT 1973 Different types of quenching involved in photosystem II centers. Biochim Biophys Acta 305: 302-316
8. KOK B, B FORBUSH, M MCGLOIN 1970 Cooperation of charges in photosynthetic O_2 evolution. I. A linear four step mechanism. Photochem Photobiol 11: 457-475
9. LEY AC, WL BUTLER 1976 Efficiency of energy transfer from photosystem II to photosystem I in *Porphyridium cruentum*. Proc Nat Acad Sci USA 73: 3957-3960
10. MELIS A, G AKOYUNOGLOU 1977 Development of the two heterogeneous photosystem II units in etiolated bean leaves. Plant Physiol 59: 1156-1160
11. MELIS A, PH HOMANN 1976 Heterogeneity of the photochemical centers in system II of chloroplasts. Photochem Photobiol 23: 343-350
12. MAISON-PETERI P, AL ETIENNE 1977 Effects of sodium azide on photosystem II of *Chlorella pyrenoidosa*. Biochim Biophys Acta 459: 10-19
13. NICHOLS KE, L BOGORAD 1960 Studies of phycobilin formation with mutants of *Cyanidium caldarium*. Nature 188: 870-872
14. SECKBACH J 1972 On the fine structure of the acidophylic hot-spring alga *Cyanidium caldarium*: a taxonomic approach. Microbios 5: 133-142
15. WOLLMAN FA 1979 Ultrastructural comparison of *Cyanidium caldarium* wild type and III-C mutant lacking phycobilisomes. Plant Physiol. In press