Effects of Growth Irradiance Levels on the Ratio of Reaction Centers in Two Species of Marine Phytoplankton[1]

PAUL G. FALKOWSKI, THOMAS G. OWENS, ARTHUR C. LEY, AND DAVID C. MAUZERALL
Oceanographic Sciences Division, Brookhaven National Laboratory, Upton, New York 11973
(P. G. F., T. G. O.); and The Rockefeller University, 1230 York Avenue, New York, New York 10021
(A. C. L., D. C. M.)

ABSTRACT

Cells of two species of single-celled marine algae, the diatom *Skeletonema costatum* (Greve), Cleve, and the chlorophyte *Dunaliella tertiolecta* Butcher, were cultured in white light of high (500–600 microeinsteins per square meter per second) and low (30 microeinsteins per square meter per second) intensity. For both algal species, cells grown at low light levels contained more chlorophyll *a* and had a lower ratio of chlorophyll *a* to chlorophylls *b* or *c* than did cells grown at high light levels. When photosynthetic unit sizes were measured on the basis of either oxygen flash yields or P_{700} photooxidation, different results were obtained with the different species. In the chlorophyte, the cellular content of photosystem I (PSI) and photosystem II (PSII) reaction centers increased in tandem as chlorophyll *a* content increased so that photosynthetic unit sizes changed only slightly and the ratio PSI:PSII reaction centers remained constant at about 1.1. In the diatom, as the chlorophyll content of the cells increased, the number of PSI reaction centers decreased and the number of PSII reaction centers increased so that the ratio of PSI:PSII reaction centers decreased from about unity to 0.44. In neither organism did photosynthetic capacity correlate with changes in cellular content of PSI or PSII reaction centers. The results are discussed in relationship to the physical and biological significance of the photosynthetic unit concept.

Unicellular algae respond to changes in environmental light levels with changes in a number of cellular characteristics. These changes include intracellular pigment content, photosynthetic response, chemical composition, and cell volume (8, 9, 25, 29, 32). In addition, changes in the number and/or sizes of PSU[2] have been suggested to occur during light-shade adaptation (8, 9, 25, 28).

The idea of a "PSU" was first developed nearly 50 years ago as a result of the now classic experiments of Emerson and Arnold (7) and Arnold and Kohn (3, 18) and of the calculations of Gaffron and Wohl (10). These latter authors proposed the existence of a "unit" consisting of about 2,000 Chl molecules which cooperate in light absorption. Photons absorbed anywhere in the unit could be used by a single "center" for the photochemical reactions of photosynthesis. It was, of course, recognized that such units were defined in terms of the final products (O_2 production or CO_2

[2] Abbreviation: PSU, photosynthetic unit; RC, reaction center; HTE, high temperature electrode.

reduction) of a possible multi-stage reaction sequence and could be combinations of smaller assemblages. The concept of a PSU has not been greatly clarified since then, although many subcomponents have been implicated in its function. It is now generally accepted that a PSU includes RC of photosystem I (RCI) and photosystem II (RCII), accessory light-harvesting pigment molecules, enzymes, and electron transfer components (5, 8, 9, 27). The average number of Chl molecules associated with a PSU, the "PSU size" has been defined functionally from flashing light experiments as the ratio of Chl molecules to O_2 molecules evolved when the chloroplast pigments are excited with single-turnover flashes of light. Single-turnover light flashes have been operationally defined as so short that the components involved in the process will not function more than once and so strong that a further increase in flash intensity does not lead to an increase in the measured value (8, 31). PSU sizes based on O_2 flash yields are here called PSU_{O_2}. Reported PSU_{O_2} range from about 300 Chl:O_2 (31) to about 5000 Chl a:O_2, depending on the organism and conditions of measurement (7, 9, 11, 12, 16, 25, 31).

Subsequent to the introduction of the PSU concept, other methods have been developed to estimate the PSU sizes. One alternative is to estimate the molar ratio of total Chl molecules to PSI reaction centers spectrophotometrically from the changes in absorption which accompany the oxidation of reduced P700 (8, 16, 19, 27). PSU sizes based on Chl:P700 (here called PSU700) range from about 150 Chl a/P700 in some blue-green algae (16) to about 3,000 Chl a:P700 in some strongly shade-adapted diatoms (Falkowski, unpublished).

PSU_{O_2} and PSU700 can be used to count the number of reaction centers in a cell, provided that the measurement of the P700 absorption change is quantitative for RCI and that a quantum requirement for O_2 production is assumed. Usually, the minimum quantum requirement for O_2 production is taken to be four photons per RCII per O_2 evolved (based on the assumption of four light-driven one-electron oxidation steps, each with a quantum yield of unity). On this basis, the ratio RCI:RCII has been calculated to be close to unity in higher plants (4). In blue-green algae, however, the ratio has been observed to vary with the light conditions used in culturing the algae and has been reported to approach values as large as four (16). Recent measurements, relying exclusively on the measurement of spectrophotometric assays for PSI and PSII reaction centers, have demonstrated that, even for higher plants, the ratio RCI:RCII is different from unity (21).

In this study, we have estimated the intracellular content of PSI and PSII reaction centers from measurements of both P700:Chl ratios and O_2 flash yields using two species of marine phytoplankton with different responses to changes in environmental light levels. Based on Chl:P700, it was previously demonstrated that one species, *Skeletonema costatum* (Greve) Cleve, a marine dia-

tom, responds to variations in light intensity primarily with alterations in PSU700 size. The other species selected, *Dunelialla tertiolecta* Butcher, a chlorophyte, primarily alters the number of PSU700 per cell (8).

MATERIALS AND METHODS

Culture Conditions. *Skeletonema costatum* (Woods Hole clone SKEL) and *Dunaliella tertiolecta* (Woods Hole clone DUN) were axenically cultured in natural seawater enriched with f/2 nutrients as previously described (8). Each species was grown in steady-state conditions, either by periodic manual dilutions of the culture vessels (4-liter aspirator bottles) with fresh growth medium or in turbidostat culture (8). Similar results were achieved with either culture protocol. Twenty-four h continuous light was provided by "cool-white" fluorescent lamps. Various light levels were achieved either by changing the distance between the lamps and the culture vessels or by changing the number of lamps used to illuminate the cultures. Light levels inside the culture vessels were measured using a calibrated quantum detector with a spherical collector (Biospherical Instruments, Inc., Model QS-100).

Cells were adapted to each light level for at least 3 days prior to measurements of photosynthetic unit sizes and rates of photosynthesis, during which time cellular Chl content and population densities in the cultures were frequently determined. The possibility of differential self-shading was reduced by maintenance of all cultures at similar cell densities (about 3×10^5 cells/ml).

Pigment Content. Cellular Chl content was determined from acetone extracts of cells. Cells were filtered onto 2.4-cm Gelman AE glass fiber filters and were extracted by grinding in cold 90% acetone (8, 14). Glass fibers were removed by filtration and the absorbance of the extract was determined from 350 to 750 nm using an Aminco DW-2A spectrophotometer in the split-beam mode. Concentrations of Chl *a*, *b*, and *c* in the extracts were calculated using the equations of Jeffrey and Humphrey (14). Cell counts were made with a hemocytometer.

P700 Measurements. P700 concentrations were estimated from both light-induced absorbance changes and oxidized minus reduced difference spectra (8). Cells were harvested by continuous flow centrifugation at 12,000*g* with a flow rate of about 200 ml/min at 5 C. The packed cells were disrupted at 0 to 4 C in 50 mM Tris-HCl (pH 8.0), using a Polytron homogenizer (Brinkmann Instruments). Under these conditions, cell breakage was determined to be >95%. The resulting brie was centrifuged at 2000*g* for 15 min to remove large cell fragments and the supernatant suspension, containing chloroplast membranes, was kept on ice in the dark.

For the chemical determination of P700 concentrations, samples of the membrane preparation were placed in matched cuvettes. Potassium ferricyanide was added to the sample cuvette to a concentration of 1.0 mM. After 60 s, sodium ascorbate was added to the sample cuvette to a final concentration of 10 mM. Following another 60-s interval, potassium ferricyanide was added to the reference cuvette (1.0 mM) and 60 s later the difference absorbance spectrum between the sample and reference cuvettes was measured from 650 to 750 nm with an Aminco DW-2A spectrophotometer in the split beam mode. Sodium ascorbate was added to the reference cuvette to a final concentration of 10 mM and after 2 min the difference spectrum was again measured. Spectra were stored in a Midan T microprocessor and P700 concentrations were calculated from the difference in absorption at 697 nm relative to 725 nm (19).

Light-induced P700 absorption was assayed using an Aminco DW-2A spectrophotometer in the dual wavelength mode with a measuring beam at 697 nm and an isobestic reference beam at 720 nm as previously described (8). All P700 concentrations were calculated using a difference coefficient of 64 mM^{-1}cm^{-1} (13). No statistically significant differences were observed between cellular

P700 concentrations determined from chemically oxidized minus reduced difference spectra and light-induced absorbance changes. In addition, Chl:P700 ratios determined for the membrane fragments and for the centrifuged large cell fragments were essentially the same.

Oxygen Flash Yields. PSU sizes were also estimated from the rates of O_2 evolution by algae in flashing light. Repetitive, short flashes of light were provided by four synchronously-triggered flashlamps (Stroboslave, Type 1539-A) placed symmetrically about the sample chamber. The light flashes had a measured full width of 1.6 μs and 7.5 μs at one-half and one-tenth full intensity, respectively. Flashes were deemed saturating since the same rates of O_2 evolution were obtained from algae illuminated by two, three, or four (but not by one) flashlamps. Identical flash yields were obtained in the presence and absence of yellow filters (two layers of No. 195 CMS yellow cellophane, H.D. Catty Corp.) and most measurements were made without the filters. Flash yields were found to be constant for flash rates between 10 and 30 flashes/s for both species of algae. The majority of the measurements were made at a flash rate of 20 flashes/s.

Rates of O_2 production by the illuminated algae were measured using either a Clarke-type electrode (Rank Bros., Bottisham, England) or a flow-through gas system and a high-temperature zirconium oxide electrode (HTE) (Thermo-Lab Instruments, Inc., Pittsburgh, PA). For measurements using the HTE, aliquots of the same concentrated cell suspensions used for the P700 determinations were diluted with fresh f/2 growth medium to a final Chl concentration of 25 to 35 μM and benzoquinone was added in the dark to a final concentration of 1 mM to ensure open reaction centers. The diluted algal suspensions were immediately placed in the cylindrical sample chamber surrounded by the flash lamps and were rapidly bubbled in the dark with an anaerobic gas mixture (5% CO_2 in N_2, $O_2 \le 5$ μl/l). The gas mixture entered the bottom of the chamber at a constant rate through a sintered glass plate and the O_2 content of the gas leaving the chamber was monitored continuously by the HTE (11, 12). The response of the HTE was calibrated by the electrolysis of water at a known rate in a separate chamber in series in the gas line with the sample chamber. Rates of O_2 production in flashing light were measured 3 to 5 min after the addition of benzoquinone to the algal suspensions.

For measurements using the Clarke-type electrode, the concentrated algal suspensions were diluted with fresh f/2 growth medium to a final Chl concentration of 5 μM. O_2 evolution was measured at 20 C and the electrode was calibrated with air saturated distilled H_2O.

Both electrode systems were used for measurements of rates of O_2 production by *Skeletonema* with essentially the same results. Technical problems relating to excessive adhesion of *Dunaliella* cells to the glass chamber walls prevented use of the HTE system for measurements of O_2 evolution by this alga.

Photosynthetic Rates. Rates of photosynthetic O_2 evolution were measured using a polarographic O_2 electrode (Yellow Springs Instruments). Illumination was provided by a 500 w tungsten-iodide source supplying a maximum of 2,500 μEi/m$^2\cdot$s. Light attenuation was accomplished using neutral density filters and a diaphragm. Cells suspended in fresh f/2 medium were degassed to about 70% O_2 saturation with N_2 and placed in a 3-ml Lucite chamber at 15 C. Irradiance was measured with a Lambda LI 185 quantum sensor. Although only light-saturated rates of O_2 evolution are reported here, complete photosynthesis *versus* irradiance curves were measured.

RESULTS AND DISCUSSION

Characteristics of cells *S. costatum* and *D. tertiolecta* grown at high and low light levels are shown in Table I. For both species of algae, cells grown at low light levels (L cells) contain more Chl

Table I. *Characteristics of Cells of D. tertiolecta and S. costatum Grown at Various Light Levels*

Dunaliella tertiolecta

Light Intensity	Chl a/cell	Chl a:Chl b	PSU$_{O_2}$ Chl $a + b$:O$_2$ (±SD)	PSU700 Chl $a + b$:P700 (±SD)	RCII/cell	RCI/cell	RCI:RCII	P_{max}	τ
$\mu E \cdot m^{-2} \cdot s^{-1}$	$mol \times 10^{-16}$	*ratio*			$mol \times 10^{-19}$		*ratio*	$mol\ O_2 \times 10^{-16} \cdot cell^{-1} min^{-1}$	*ms*
600	11.3	5.6	2,840 ± 150	612 ± 45	19	22	1.2	45	6.2
45	33.4	2.9	3,330 ± 120	732 ± 106	54	61	1.1	42	19

Skeletonema costatum

Light Intensity	Chl a/cell	Chl a:Chl c	PSU$_{O_2}$ Chl a:O$_2$ (±SD)	PSU700 Chl a:P700 (±SD)	RCII/cell	RCI/cell	RCI:RCII	P_{max}	τ
$\mu E \cdot m^{-2} \cdot s^{-1}$	$mol \times 10^{-16}$	*ratio*			$mol \times 10^{-19}$		*ratio*	$mol\ O_2 \times 10^{-16} \cdot cell^{-1} min^{-1}$	*ms*
600	4.3	3.8	2,360 ± 190	623 ± 55	7.3	6.9	0.95	24 ·	4.5
200	5.7	3.8	2,400 ± 560	813 ± 64	9.5	7.0	0.74	21	6.7
30	6.7	3.4	2,420 ± 590	1,360 ± 145	11	4.9	0.44	21	7.9

a and have smaller ratios of Chl a to Chl b or Chl c than do cells grown at high light levels (H cells). Increased Chl a content appears to be an ubiquitous response by algae to decreased levels of incident light (8, 25, 27–30, 32). The differences are more pronounced in the chlorophyte than in the diatom. Compared to H cells, L cells of *D. tertiolecta* show a 3-fold increase in cellular Chl a content and a 2-fold decrease in Chl a:Chl b. In contrast, L cells of *S. costatum* contain only 56% more Chl a than do H cells. The Chl a to Chl c ratio in the diatom is marginally smaller in H cells than in L cells. Larger differences in Chl a:Chl c between H and L cells of *S. costatum* were described in a previous report (8). In that study, the highest levels employed in algal cultivation were lower than those used here. It seems that in *S. costatum* the maximum of Chl a:Chl c occurs at intermediate light levels.

In contrast to the large changes in cellular pigment content, for both species PSU sizes estimated from O$_2$ flash yields varied little between H and L cells. In *D. tertiolecta*, PSU$_{O_2}$ increased to a small but statistically significant extent from about 2,800 Chl ($a + b$)/O$_2$ in H cells to about 3,300 Chl ($a + b$):O$_2$ in L cells. No significant differences in PSU$_{O_2}$ were detected between H and L cells of *S. costatum*. In the diatom, the average PSU$_{O_2}$ was about 2,400 Chl a:O$_2$.

Estimates of PSU700 based on the reversible photooxidation of P700 gave considerably different results for the two algal species. In *D. tertiolecta* PSU700 changed to the same small extent (about 20%) as PSU$_{O_2}$. The average PSU700 for H cells was about 610 Chl ($a + b$)/P700 while for L cells it was about 730 Chl ($a + b$):P700. In *Skeletonema*, however, PSU700 more than doubled in L cells relative to H cells, increasing from about 620 Chl a:P700 to about 1,400 Chl a:P700.

Over the range of light intensities examined, the cellular rate of light-saturated photosynthesis (P_{max}) did not greatly vary between H and L cells of either species (Table I). This is similar to the previously reported photosynthetic characteristics of these two species (8). In the diatom, growth rates parallel the photoperiod at a given light intensity. In *D. teriolecta*, however, P_{max} decreased from about 70 to 80 mol O$_2 \times 10^{-16}$ cell^{-1} min^{-1} when cells were grown on a 14:10 light-dark cycle (8) to about 40 to 45 mol O$_2 \times 10^{-16}$ cell^{-1} min^{-1} when cells were grown under continuous illumination (Table I). Interestingly, the growth rate of the chlorophyte remained the same under the two light regimes. The growth rate seems to track the actual daily photosynthetic output.

The average cellular content of PSI and PSII reaction centers (RCI and RCII, respectively) shown in Table I were calculated from the data described above and the usual assumption that one molecule of O$_2$ is produced as a result of four light-driven, one-electron oxidation steps per PSII reaction center. For *D. tertiolecta*, the numbers of both RCI and RCII in a cell increase to the same extent as cellular Chl a levels increase. The 3-fold increase in Chl a:cell in L cells relative to H cells is accompanied by a 2.6 times greater abundance of both PSI and PSII reaction centers so that the ratio remains constant at about 1.1. The majority of the variation in Chl content of cells of *D. tertiolecta* grown at different light levels can be accounted for by proportional concomitant variations in the cellular contents of RCI and RCII with little change in the average size of their combined antennas. Of course, the absolute size of the pigment antenna serving either reaction center may vary provided there is compensatory change in the size of the antenna associated with the other reaction center. In terminology currently employed in the literature, *D. tertiolecta* adapts to variations in environmental light levels primarily with changes in the number of photosynthetic units per cell with only small changes in the size of those units.

The observed difference in Chl a:Chl b between H and L cells neither supports nor contradicts the above conclusion. Different Chl-protein complexes isolated from higher plants and green algae exhibit high and low ratios of Chl a to Chl b (1, 5, 33, 34). Variations in the relative abundances of these components would result in changes in whole cell values of Chl a:Chl b without necessarily involving changes in average PSU size or in the ratio of RCI to RCII.

In *S. costatum*, changes in RCII/cell also parallel changes in Chl a/cell: the increase in Chl a/cell of about 55% is accompanied by an approximately 50% increase in the cellular concentration of PSII reaction centers. In contrast to *Dunaliella*, however, in the diatom P700 levels decrease by about 30% as the Chl a content increases. The net result of these changes is that the calculated ratio RCI:RCII decreases by more than a factor of two; from nearly unity in H cells to about 0.4 in L cells. Similar examples of a decrease in the ratio of RCI to RCII with culture conditions have been reported for blue-green algae grown at various light levels (16) and in red or gold light fields (26). In these reports, the

minimum value of RCI:RCII was about unity. Melis and Brown (22) have recently reported the ratio of RCI to RCII to be about 0.7 and about 0.3 in chloroplasts from spinach and developing pea leaves, respectively.

Ratios of RCI to RCII which are less than unity do not necessarily imply reduced steady-state O_2 flash yields. The minimum measured reduction time for $P_{700} +$ ($\sim 10 \mu s$ [15]) is about 50 times faster than the minimum turnover time for O_2 production ($\sim 500 \mu s$ [24]). Thus, a flash which is "single-turnover" in terms of O_2 production may drive more than one electron transfer event in PSI. (Greenbaum *et al.* [12] have measured PSI activity as H_2 production by anaerobic green algae in flashing light. They found a saturating flash from a xenon flashlamp produced twice as much H_2 as a saturating submicrosecond laser flash. This observation might reflect a rapid turnover time in PSI.)

Benzoquinone can be used in intact cells to substitute for PSI as the acceptor of electrons from PSII. Greenbaum (11) used this technique to measure PSU_{O_2} of 1,700 Chl ($a + b$):O_2 in cells of the green alga *Chlorella vulgaris*. Here we find that in *S. costatum*, the PSU_{O_2} measured in the presence of benzoquinone (2,400 ± 600) is the same as that measured with CO_2 as the terminal electron acceptor (2,400 ± 200). Thus, even though we measure only half as many RCI as RCII in L cells of *S. costatum*, we find no limitation by the reduced RCI levels on the rates of O_2 production in flashing light.

Skeletonema exhibits a more complex response to changes in environmental light levels than does *Dunaliella*. In addition to changes in total cellular pigment content and the relative abundances of the various pigments, the numbers of reaction centers of PSII and PSI change in opposite directions as cells of *S. costatum* adapt to different light intensities. One effect of such changes is that PSU sizes estimated on the basis of O_2 flash yields and on P700 photooxidation give contradictory results.

The concept of the photosynthetic unit was introduced by Gaffron and Wohl (10) following the demonstration by Emerson and Arnold (7) that many molecules of Chl cooperate in photosynthetic O_2 production. Originally, a PSU was defined functionally as the ratio of Chl molecules to O_2 molecules evolved during photosynthesis in flashing light. More recently, a PSU has been described in biochemical terms as the ratio of Chl to PSI reaction centers. Since current definitions of PSU values are ratios of Chl to some other measured quantity, their interpretation in terms of the more fundamental components of the photosynthetic apparatus (*e.g.* reaction centers and pigment antennae) requires specific sets of assumptions. PSU values are usually taken to represent the average number of pigment molecules associated with the combination of one RCI and one RCII (see ref. 5 for a review and examples of such PSU values). Changes in PSU size are then interpreted to reflect changes in the number of antenna pigment molecules for RCI and/or RCII. It is clear that unless the ratio of RCI to RCII is unity, PSU_{O_2} and PSU700 will necessarily differ. Moreover, even if RCI/RCII remains constant at any value independent of conditions, measurements of "PSU sizes" will give minimal information: the number of pigment molecules associated with n_1RCI + n_2RCII. The physiologically more relevant parameters, antenna sizes for either RCI or RCII separately, are not determined. Finally, if the intracellular ratio of RCI to RCII varies, the relationship between the measured PSU and the composition of the photosynthetic apparatus is undefined.

In light of the above discussion and the results presented above and elsewhere (16, 22, 26), it seems preferable to avoid the ambiguities inherent in the PSU and to concentrate instead on the numbers of reaction centers and the size of their antennae. Relative measures of the effective antenna sizes for RCI and RCII can be obtained from the knowledge of numbers of reaction centers and measurements of the light-saturated rates of photosystem specific reactions, provided that the quantum requirements for the reac-

tions do not vary (17, 21, 22, 32). Absolute effective optical cross sections for PSII or PSI can be obtained from measurements of the light intensity dependence of such reactions in short flashes of monochromatic light (12, 20, Ley and Mauzerall, unpublished).

A strength of the PSU concept has been its provision of a theoretical basis for the development of working models of photosynthesis without a complete mechanistic understanding of the process. It has been suggested that the numbers of PSU values in a cell correspond to photosynthetic capacity and that the size of a PSU is related to light utilization efficiency. Attempts have been made, unsuccessfully, to correlate light-saturated rates of photosynthesis with the number of PSI reaction centers (2, 8). We also find no relationship between light-saturated cellular rates of O_2 evolution and the numbers of either PSI or PSII reaction centers present in the cells (Table I). For both species of algae, the light-saturated cellular photosynthetic rates remain relatively constant. This may result from adaptations by the cells which optimize photosynthetic performance rather than photosynthetic capacity (28).

The lack of correlation between maximum photosynthetic rates and the number of reaction centers implies changes in the turnover time of light-saturated photosynthesis. The final column in Table I contains turnover times calculated from data shown in Table I. For both *S. costatum* and *D. tertiolecta*, the calculated turnover time of light-saturated photosynthesis (τ) increases as the number of PSII reaction centers (and cellular Chl contents increase. Similar increases in turnover times with increased Chl contents have been reported for the green algae *Chlorella* (25) and *Scenedesmus* (32) and are commonly observed in the light-shade adaptation of higher plants (4). The lack of correspondence between photosynthetic capacities and numbers of RC values has been attributed to changes in the specific activities of concentrations of carbon fixation enzymes, electron transfer components, or pool sizes (4, 6, 23, 32). It is evident that changes in the turnover time of light-saturated photosynthesis, whatever their origin, can be as important as changes in cellular reaction center contents or PSU size in determining the possible variations of photosynthetic capacity with environmental light levels.

LITERATURE CITED

1. ANDERSON JM, JC WALDRON, SW THORNE 1978 Chlorophyll-protein complexes of spinach and barley chloroplasts. Spectral characteristics of six complexes resolved by an improved electrophoretic procedure. FEBS Lett 92: 227-233
2. ARMOND PA, HA MOONEY 1978 Correlation of photosynthetic unit size and density with photosynthetic capacity. Carnegie Inst Yrbk 1977: 234-237
3. ARNOLD W, HI KOHN 1934 The chlorophyll unit in photosynthesis. J Gen Physiol 18: 109-112
4. BOARDMAN NK 1977 Comparative photosynthesis of sun and shade plants. Annu Rev Plant Physiol 28: 355-377
5. BOARDMAN NK, JM ANDERSON, DJ GOODCHILD 1978 Chlorophyll-protein complexes and the structure of mature and developing chloroplasts. Curr Topics Bioenerg 8: 35-109
6. DINER B, D MAUZERALL 1973 The turnover time of photosynthesis and redox properties of the pool of electron carriers between the photosystems. Biochim Biophys Acta 305: 353-363
7. EMERSON R, W ARNOLD 1932 The photochemical reaction in photosynthesis. J Gen Physiol 16: 191-205
8. FALKOWSKI PG, TG OWENS 1980 Light-shade adaptation: two strategies in marine phytoplankton. Plant Physiol 66: 632-635.
9. FLEISCHHACKER PH, H SENGER 1978 Adaptation of the photosynthetic apparatus of *Scenedesmus obliquus* to strong and weak light conditions. II. Differences in photochemical reactions, the photosynthetic electron transport, and photosynthetic units. Physiol Plant 43: 43-51
10. GAFFRON H, K WOHL 1934 Zur Theorie der Assimilation. Naturwissenschaften 24: 81-92 and 103-207
11. GREENBAUM E 1977 Photosynthetic oxygen evolution under varying redox conditions: new experimental and theoretical results. Photochem Photobiol 25: 293-298
12. GREENBAUM E, AC LEY, D MAUZERALL 1979 Absolute optical reaction cross sections for Photosystem I and Photosystem II. American Society for Photo-

biology, 7th Annual Meeting. Abstract MPC-C8, June 24, Asilomar, CA

13. HIYAMA T, B KE 1972 Difference spectra and extinction coefficients of P_{700}. Biochim Biophys Acta 267: 160–171

14. JEFFREY SW, GW HUMPHREY 1975 New spectrophotometric equations for determining chlorophylls a, b, c_1 and c_2 in higher plants, algae and natural phytoplankton. Biochem Physiol Pflanz 167: 191–194

15. JUNGE W 1977 Physical aspects of light harvesting. *In* A Trebst, M Avron, eds, Encylopedia of Plant Physiology, New Series, Vol 5. Springer Verlag, Berlin, pp 61–93

16. KAWAMURA M, M MIMURO, Y FUJITA 1979 Quantitative relationship between two reaction centers in the photosynthetic system of blue-green algae. Plant Cell Physiol 20: 697–705

17. KELLEY J, K SAUER 1968 Functional photosynthetic unit sizes for each of the two light reactions in spinach chloroplasts. Biochemistry 7: 882–892

18. KOHN HI 1936 Number of chlorophyll molecules acting as an absorbing unit in photosynthesis. Nature 137: 706

19. MARKWELL JP, JP THORNBER, MP SKRDLA 1980 Effect of detergents on the reliability of a chemical assay for P_{700}. Biochim Biophys Acta 591: 391–399

20. MAUZERALL D 1978 Multiple excitations and the yield of chlorophyll a fluorescence in photosynthetic systems. Photochem Photobiol 28: 991–998

21. MELIS A, APGM THEILEN 1980 The relative absorption cross sections of Photosystem I and Photosystem II in chloroplasts from three types of *Nicotiana tabacum*. Biochim Biophys Acta 589: 275–286

22. MELIS A, JS BROWN 1980 Stoichiometry of system I and system II reaction centers and of plastoquinone in different photosynthetic membranes. Proc Natl Acad Sci USA 77: 4712–4716

23. MISHKIND M, D MAUZERALL, SI BEALE 1979 Diurnal variation *in situ* of photosynthetic capacity in *Ulva* is caused by a dark reaction. Plant Physiol 64: 896–899

24. MISHKIND M, D MAUZERALL 1980 Kinetic evidence for a common photosynthetic step in diverse seaweeds. Mar Biol 56: 261–265

25. MYERS J, J-R GRAHAM 1971 The photosynthetic unit in *Chlorella* measured by repetitive short flashes. Plant Physiol 48: 282–286

26. MYERS J, J-R GRAHAM, RT WANG 1980 Light harvesting in *Anacystis nidulans* studied in pigment mutants. Plant Physiol 66: 1144–1149

27. PREZELIN BB, RS ALBERTE 1978 Photosynthetic characteristics and organization of chlorophyll in marine dinoflagellates. Proc Natl Acad Sci USA 75: 1801–1804

28. PREZELIN BB, BM SWEENEY 1979 Photoadaptation of photosynthesis in two bloom forming dinoflagellates. *In* DL Taylor, AN Seliger, eds, Proceedings of the 2nd International Conference on Toxic Dinoflagellate Blooms, Elsevier Press, Amsterdam, pp 101–106

29. RAMUS J, SI BEALE, D MAUZERALL, KL HOWARD 1976 Changes in photosynthetic pigment concentration in seaweeds as a function of water depth. Mar Biol 37: 223–229

30. RAMUS J, F LEMONS, C ZIMMERMAN 1977 Adaptation of light-harvesting pigments to downwelling light and the consequent photosynthetic performance of the eulittoral rockweeds *Ascophyllum nodosum* and *Fucus vesiculosus*. Mar Biol 42: 293–303

31. SCHMID GH, H GAFFRON 1968 Photosynthetic units. J Gen Physiol 52: 212–239

32. SENGER H, PH FLEISCHHACKER 1978 Adaptation of the photosynthetic apparatus of *Scenedesmus obliquus* to strong and weak light. I. Differences in pigments, photosynthetic capacity, quantum yield and dark reactions. Physiol Plant 43: 35–42

33. THORNBER JP, RS ALBERTE, FA HUNTER, JA SHIOZAWA, K-S KAN 1977 The organization of chlorophyll in the plant photosynthetic unit. Brookhaven Symp Biol 28: 132–148

34. THORNBER JP, JP MARKWELL, S REIMAN 1979 Plant chlorophyll-protein complexes: recent advances. Photochem Photobiol 29: 1205–1214