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

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ABSTRACT

Cells of two species of single-celled marine algae, the diatom Skeletonema costatum (Grev.) Cleve, and the chlorophyte Dunaliella tertiolecta Butcher, were cultured in white light of high (500–600 microEinsteins per 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 chlorophyll 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 P700 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, 26, 32). In addition, changes in the number and/or sizes of PSU2 have been suggested to occur during light-shade adaptation (8, 9, 25, 26).

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 (O2 production or CO2 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 O2 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 O2 flash yields are here called PSUO2. Reported PSUO2 range from about 300 ChlO2 (31) to about 5000 Chl aO2, 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).

PSUO2 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 O2 production is assumed. Usually, the minimum quantum requirement for O2 production is taken to be four photons per RCII per O2 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 cultivating 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 O2 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 (Grev.) Cleve, a marine dia-
tom, responds to variations in light intensity primarily with alterations in PSU700 size. The other species selected, Dunaliella 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 DU7) 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 Q5-100).

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 x 10⁶ 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-2-A spectrophotometer in the split-beam mode. Concentrations of Chl a, b, and c in the extracts were calculated using the equations of Jeffrey and Humphreyy (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 12,000g 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 bire was centrifuged at 2000g 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⁻¹cm⁻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 O₂ evolution by algae in flashing light. Repetitive, short flashes of light were provided by four synchronously-triggered flashlamps (Stroboslove, 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. Flash rates were determined by the same rates of O₂ 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 flashes 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 O₂ 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% CO₂ in N₂, O₂ ≤ 5 μl/l). The gas mixture entered the bottom of the chamber at a constant rate through a sintered glass plate and the O₂ 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 with the sample chamber. Rates of O₂ 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. O₂ evolution was measured at 20 C and the electrode was calibrated with air saturated distilled H₂O.

Both electrode systems were used for measurements of rates of O₂ 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 O₂ evolution by this alga.

**Photosynthetic Rates.** Rates of photosynthetic O₂ evolution were measured using a polarographic O₂ electrode (Yellow Springs Instruments). Illumination was provided by a 500 w tungsten-iodide source supplying a maximum of 2,300 μE/m²·s. Light attenuation was accomplished using neutral density filters and a diaphragm. Cells suspended in fresh f/2 medium were degassed to about 70% O₂ saturation with N₂ 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 O₂ 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 1. Characteristics of Cells of D. tertiolecta and S. costatum Grown at Various Light Levels

<table>
<thead>
<tr>
<th>Light Intensity</th>
<th>Chl a/cell</th>
<th>Chl a:Chl b</th>
<th>PSU700 Chl a + b:O₂ (±SD)</th>
<th>PSU700 Chl a + b:P700 (±SD)</th>
<th>RCII/cell</th>
<th>RCI/cell</th>
<th>RCI:RCII</th>
<th>P_max</th>
<th>τ</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>mol × 10⁻¹⁶</td>
<td>ratio</td>
<td>mol × 10⁻¹⁹</td>
<td>ratio</td>
<td>mol O₂ × 10⁻¹⁶ min⁻¹</td>
<td>ms</td>
<td></td>
</tr>
<tr>
<td>600</td>
<td>11.3</td>
<td>5.6</td>
<td>2,840 ± 150</td>
<td>612 ± 45</td>
<td>19</td>
<td>22</td>
<td>1.2</td>
<td>45</td>
<td>6.2</td>
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<tr>
<td>45</td>
<td>33.4</td>
<td>2.9</td>
<td>3,330 ± 120</td>
<td>732 ± 106</td>
<td>54</td>
<td>61</td>
<td>1.1</td>
<td>42</td>
<td>19</td>
</tr>
</tbody>
</table>

Dunaliella tertiolecta

<table>
<thead>
<tr>
<th>Light Intensity</th>
<th>Chl a/cell</th>
<th>Chl a:Chl c</th>
<th>PSU700 Chl a:O₂ (±SD)</th>
<th>PSU700 Chl a:P700 (±SD)</th>
<th>RCII/cell</th>
<th>RCI/cell</th>
<th>RCI:RCII</th>
<th>P_max</th>
<th>τ</th>
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<td></td>
<td></td>
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<td>mol × 10⁻¹⁶,</td>
<td>ratio</td>
<td>mol O₂ × 10⁻¹⁶ min⁻¹</td>
<td>ms</td>
<td></td>
</tr>
<tr>
<td>600</td>
<td>4.3</td>
<td>3.8</td>
<td>2,360 ± 190</td>
<td>623 ± 55</td>
<td>7.3</td>
<td>6.9</td>
<td>0.95</td>
<td>24</td>
<td>4.5</td>
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<tr>
<td>200</td>
<td>5.7</td>
<td>3.8</td>
<td>2,400 ± 560</td>
<td>813 ± 64</td>
<td>9.5</td>
<td>7.0</td>
<td>0.74</td>
<td>21</td>
<td>6.7</td>
</tr>
<tr>
<td>30</td>
<td>6.7</td>
<td>3.4</td>
<td>2,420 ± 590</td>
<td>1,360 ± 145</td>
<td>11</td>
<td>4.9</td>
<td>0.44</td>
<td>21</td>
<td>7.9</td>
</tr>
</tbody>
</table>

Skeletonema costatum

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 O₂ flash yields varied little between H and L cells. In D. tertiolecta, PSU₀₈ increased to a small but statistically significant extent from about 2,800 Chl (a + b)/O₂ in H cells to about 3,300 Chl (a + b)/O₂ in L cells. No significant differences in PSU₀ were detected between H and L cells of S. costatum. In the diatom, the average PSU₀ was about 2,400 Chl a:O₂.

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 PSU₀. 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 1). 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. tertiolecta, however, P_max decreased from about 70 to 80 mol O₂ × 10⁻¹⁶ cell⁻¹ min⁻¹ when cells were grown on a 14:10 light-dark cycle (8) to about 40 to 45 mol O₂ × 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 O₂ is produced as a result of four light-driven, one-electron oxidation steps per PSI 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 RCI/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 $R_{CI}/R_{CII}$ was about unity. Melis and Brown (22) have recently reported the ratio of $R_{CI}$ to $R_{CII}$ to be about 0.7 and about 0.3 in chloroplasts from spinach and developing pea leaves, respectively.

Ratios of $R_{CI}$ to $R_{CII}$ which are less than unity do not necessarily imply reduced steady-state $O_2$ flash yields. The minimum measured reduction time for $P_{PSII}$ ($\pm 10 \mu s$ [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 PSI. 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 ($2,400 \pm 600$) is the same as that measured with $O_2$ as the terminal electron acceptor ($2,400 \pm 200$). Thus, even though we measured only half as many $R_{CI}$ as $R_{CII}$ in L cells of S. costatum, we find no limitation by the reduced $R_{CI}$ 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 number 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 $P_{700}$ 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 $R_{CI}$ and one $R_{CII}$ (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 $R_{CI}$ and/or $R_{CII}$. It is clear that unless the ratio of $R_{CI}$ to $R_{CII}$ is unity, PSU$_{O_2}$ and PSU$_{700}$ will necessarily differ. Moreover, even if $R_{CI}/R_{CII}$ remains constant at any value independent of conditions, measurements of "PSU sizes" will give minimal information: the number of pigment molecules associated with $n_{R_{CI}} + n_{R_{CII}}$. The physiologically more relevant parameters, antenna sizes for either $R_{CI}$ or $R_{CII}$ separately, are not determined. Finally, if the intracellular ratio of $R_{CI}$ to $R_{CII}$ 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 $R_{CI}$ and $R_{CII}$ 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 reactions 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 (26).

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 ($\tau$) 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.

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