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In Vivo Manipulation of the Xanthophyll Cycle and the Role of Zeaxanthin in the Protection against Photodamage in the Green Alga Chlorella pyrenoidosa*

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Chlorella pyrenoidosa was grown in steady-state continuous cultures in either high or low light. Samples of these cultures were incubated in darkness (violaxanthin state) or in saturating light (zeaxanthin state). These samples were kept in the respective preadapted states throughout the entire photodamage treatment. Photodamage involved exposure to single-turnover flashes fired at a low (non-actinic) frequency. The damage caused by the light stress thus applied was monitored by changes in photosynthetic properties and pigment composition. Cells preadapted in the light resisted photodamage better than those kept in darkness. The low light grown cells were more vulnerable to photodamage than the high light grown cells. Our experimental approach permitted the equilibria between the components that participate in the xanthophyll cycle to be set without addition of inhibitors. Regardless of the total amount of violaxanthin being present, its conversion to antheraxanthin and zeaxanthin is a prerequisite for protection. The protection is most effective for photosystem II. It appeared that antheraxanthin accumulates as a result of photodamaging flashes provided that these are fired in the presence of background light, i.e., with zeaxanthin present. From this, it is newly derived that the xanthophyll cycle operates in full in the light, including epoxidation of zeaxanthin. The latter conversion was also demonstrated in vitro, via nonenzymatic oxygen-dependent turnover of zeaxanthin into violoxanthin.

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1 The abbreviations used are: PS, photosystem; Chl, chlorophyll; HL, high light; HPLC, high pressure liquid chromatography; LL, low light; P/l, oxygen evolution versus irradiance determination; qP, photochemical quenching; qNP, nonphotochemical quenching.
essing of zeaxanthin. This observation reveals that the dy-
namic function of the xanthophyll cycle in vivo is larger than
would be predictable from existing data. Our approach to as-
sess photodamage in a constant background of photoprotection,
established by introducing continuous background illumina-
tion, may be useful in other areas of photosynthesis research.

MATERIALS AND METHODS

Culture—Two types of steady-state continuous cultures of Chlorella
pyrenoidosa were used, both were grown in 2-liter chemostats in BG-11
medium (Rippka et al., 1979) at 20 °C. One was grown at 30 μE·m⁻²·s⁻¹
(low light, LL) the other one at 240 μE·m⁻²·s⁻¹ (high light, HL). Circular
fluorescent tubes (Philips TLE 32W/33) were used for continuous illu-
sination. The set up of the culture system was as in Van Liere and Mur
(1978). Aeration at 60 l/min provided adequate mixing and CO₂
supply. The cultures were maintained at an A₅₇₀ of 0.18–0.20.

Preadaptation and Flash Experiments—Samples from the HL and
LL cultures were preadapted during 30 min at 20 °C in either darkness
or in the presence of actinic (background) light. The actinic light inte-
sities for the LL and HL samples were 430 and 600 μE·m⁻²·s⁻¹ respectively.
These light conditions were arrived at to be saturating from the photosynthesis
versus irradiance (P₁) curves (see Fig. 1). Preadaptation provided a basis for
comparing the experiments as described elsewhere (Dubinsky et al., 1987).
This device has been described elsewhere (Dubinsky et al., 1987). The
samples were bubbled with air to ensure a constant partial oxygen
pressure. Next, while maintaining the conditions of preadaptation (i.e.
background light or darkness), one group of samples was exposed to one
thousand supersaturating flashes (see below) in order to incite photodama-
gement. The other group was not exposed to flashes and remained in
the preincubation conditions during this time.

A delay between the flashes of 3 s was chosen in the samples without
background light. At this frequency, controls demonstrated that the
oxygen consumption rate (dark respiration) remained identical, i.e. no
oxygen production was revealed, with or without flashes. The light
preadapted samples (which receive the flashes in the continued pres-
ence of saturating background light), already perform photosynthesis at a
maximal rate. This allowed a faster flashing regime with 300–ms intervals.
A General Electric FT 230 flash tube was used at a discharge voltage
of 1.3 kV, which provided flashes of 5 μs half-width with an energy
output of 2 J/flash in the forward direction. Calculated by the
surface of the incubation chamber this amounts to the supersaturating
flux of approximately 10,000 μE·m⁻²·fl/flash. The flash tube was
connected directly to the incubation chamber (i.e. the one used for the
oxgen and fluorescence measurements, of below). During the flashes
aeration was continued. The number of flashes was selected to yield
appreciable photodamage (as judged from changes in the pigment con-
tent and physiological activity presented), while avoiding lethality. All
flash-treated samples used for the photosynthesis activity assays were
allowed recovery during 15 min in darkness to equalize the metabolic
condition of these samples. The LL samples did not show any pigment
changes during this 15-min period (especially zeaxanthin and antheraxanthin
disappear, whereas violaxanthin increases, data not shown), the overall
losses of pigment are not replenished in this short period. Samples for
pigment analysis were taken immediately after the incubation period
(with or without flashes) but before the relaxation time introduced in the
other assays.

P₁/II Curves and Fluorescence Measurements—After the preadapta-
tion, flash and recovery periods were terminated, the cuvette was
closed, and P₁/II curves were recorded according to standard procedures
(Dubinsky et al., 1987). Fluorescence measurements included two types
of measurements. A. photochemical quenching was monitored with a
pulse-amplitude-modulated chlorophyll fluorescence measuring system
(Walz, Germany) as described by Schreiber et al. (1986). During the
measurements the fiber optic light guide was directly placed against
one side of the oxygen measuring chamber. In another way, oxygen produc-
tion and photochemical quenching (qP) could be estimated simultaneously.
qP was estimated every 120 s by firing saturating pulses of 500-ms
duration (Schott KL-1500 light source, 12,000 μE·m⁻²·s⁻¹).
B. relative energy transfer efficiency from carotenoids to Chl was
measured by comparing the fluorescence yield after excitation with
blue light and orange light. The former excites both carotenoids and
chlorophyll, the latter chlorophyll only. Data were normalized on the
emission resulting from the chlorophyll excitation in the orange. These
measurements were done with a Perkin-Elmer 1000 spectrofluoromet-
er, emission wavelength 685 nm, slit width “M.” Before the measure-
ments, the samples were preadapted in darkness for 10 min at 20 °C.

RESULTS

Changes in photosynthetic activity (O₂ production) and
photochemical quenching (qP) after exposure of C. pyrenoidosa
cells to control or photodamaging conditions are shown in Fig. 1.
Control samples of LL and HL Chlorella cells behave differ-
ently. The LL cells have a lower maximal photosynthetic activity/Chl than the HL ones. The LL cells show a stronger qP
decrease than the HL cells. The rate of O₂ evolution decreases at higher irradiances of the LL cells. Using preadaptation of the
light (i.e. dark adaptation) results in HL and LL cells retain comparable activities. Following exposure to the
photodamaging flash treatment in the continued presence of actinic
background light gave rise to relatively minor losses of activity through photodamage, both in the LL and HL cells. In
contrast, clear photodamage is obvious in the samples that
were kept in darkness during preadaptation and while being exposed to the photodamaging flashes. Especially the LL cells
show an appreciable loss of oxygen evolution and qP at increasing
actinic light intensities over the course of the PⅠ curve determination.

The observed differences of the photosynthetic activities were
related to changes in the pigment composition of the samples. Table I depicts the pigment analysis of the HL and LL
cultured cells. The data reflect that in the LL cells the total Chl to
carotenoid ratio is at least twice that of the HL cells, the Chl
to summed xanthophyll cycle components ratio is lower in
the dark or light preadaptation conditions. These conditions are mainly restricted to the three xanthophyll cycle pig-
maments. The violaxanthin content decreases in the light and the
zeaxanthin content increases. This way, variable pool sizes of the
xanthophyll cycle components were established before ex-
posure to potentially photodamaging conditions.

The exposure to photodamaging flashes induced extensive

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FIG. 1. Samples of cells from the HL (left) and LL (right) cultures were monitored for oxygen production activity and photochemical quenching in a range of actinic light intensities. The two top frames (A and B) display oxygen production versus light intensity profiles (FI curves). The two lower frames show the changes in the relative photochemical quenching. Details on these measurements and preadaptation procedures are provided under "Materials and Methods." Activities are expressed as milligrams of oxygen/mg of Chl and hour or relative units for qP. Four different incubation conditions were chosen: +, control cells incubated in the presence of actinic background light; - ( ), control cells preincubated in darkness; A, light-preadapted cells exposed to flashes with background light present; B, dark preadapted cells exposed to flashes without background light (lowest line).

TABLE I
Pigment content of Chlorella cells from LL and HL cultures prior to exposure to photodamage in the presence or absence of background light

<table>
<thead>
<tr>
<th>Pigment</th>
<th>High light grown</th>
<th>Low light grown</th>
<th>Preadaptation conditions</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Darkness</td>
<td>Light</td>
<td>Darkness</td>
</tr>
<tr>
<td>Neoxanthin</td>
<td>18.2</td>
<td>17.1</td>
<td>8.4</td>
</tr>
<tr>
<td>Violasanthin</td>
<td>34.4</td>
<td>17.5</td>
<td>12.9</td>
</tr>
<tr>
<td>Antheraxanthin</td>
<td>2.6</td>
<td>4.2</td>
<td>4.0</td>
</tr>
<tr>
<td>Zeaxanthin</td>
<td>3.5</td>
<td>21.2</td>
<td>2.1</td>
</tr>
<tr>
<td>Lutein</td>
<td>37.5</td>
<td>38.1</td>
<td>23.2</td>
</tr>
<tr>
<td>Chl a</td>
<td>34.2</td>
<td>33.9</td>
<td>63.2</td>
</tr>
<tr>
<td>Chl b</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>Chl a/Chl b</td>
<td>2.92</td>
<td>2.95</td>
<td>1.58</td>
</tr>
<tr>
<td>Xanthophyll cycle</td>
<td>43.3</td>
<td>42.9</td>
<td>19.0</td>
</tr>
<tr>
<td>Calculated ratios and sums</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chl a/Chl b</td>
<td>2.92</td>
<td>2.95</td>
<td>1.58</td>
</tr>
<tr>
<td>Σ Carotenoids</td>
<td>122.1</td>
<td>120.9</td>
<td>68.2</td>
</tr>
<tr>
<td>Chl/carotenoids</td>
<td>1.10</td>
<td>1.11</td>
<td>2.39</td>
</tr>
<tr>
<td>Chl/xanthophyll cycle pigments</td>
<td>3.10</td>
<td>3.12</td>
<td>11.64</td>
</tr>
</tbody>
</table>

To define the site where the actual photodamaging process occurs and especially to locate the site at which the xanthophyll cycle provides protection against photodamage, the electron transfer capacity of the total electron transfer chain (PS II and PS I) was compared to the capacity of PS I alone (Table III).

Full chain electron transfer rates in the samples that had received the strong flashes in the presence of background light appeared to remain nearly unaltered. The samples that were exposed to the flashes in the absence of background light displayed more than 20% photodamage (both HL and LL), comparable to the data given in Fig. 1. As opposed to the full chain data, PS I capacity appeared to diminish even when the strong flashes were administered in the presence of background light. The inhibition was stronger in the LL samples. However, in the dark-flashed samples and in comparison to the full chain, the damage to PS I appeared relatively low. Compared to the full chain electron transfer rate numbers, the PS I change in the light-flashed samples is already big. The increased damage observed for the full chain rates in the dark-flashed sample does not correspond to a similar decrease in the PS I sample. The protective function of the xanthophyll cycle therefore ap-
The effect of photodamaging conditions on the electron transfer capacity of PS II plus PS I and of PS I measured separately.

Results are given in μmol of oxygen per mg of Chl a and hour. Assay conditions are given under "Materials and Methods." The control cells were preadapted in light, otherwise sample preparation and exposure to photodamaging conditions were as in Fig. 1. Experiments were performed three times with independently flushed samples, standard deviations are indicated by ±.

<table>
<thead>
<tr>
<th>Growth</th>
<th>PS I + PS II</th>
<th>PS I</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>11.6 ± 0.9</td>
<td>25.5 ± 1.9</td>
</tr>
<tr>
<td>LL</td>
<td>9.6 ± 0.7</td>
<td>20.1 ± 1.2</td>
</tr>
<tr>
<td>Light flashed</td>
<td></td>
<td></td>
</tr>
<tr>
<td>HL</td>
<td>11.5 ± 0.5 (99.2)</td>
<td>24.2 ± 0.9 (94.9)</td>
</tr>
<tr>
<td>LL</td>
<td>9.5 ± 0.5 (98.6)</td>
<td>17.7 ± 1.2 (88.1)</td>
</tr>
<tr>
<td>Dark flashed</td>
<td></td>
<td></td>
</tr>
<tr>
<td>HL</td>
<td>9.2 ± 0.5 (79.3)</td>
<td>23.1 ± 0.5 (90.6)</td>
</tr>
<tr>
<td>LL</td>
<td>7.1 ± 0.8 (73.9)</td>
<td>16.1 ± 2.6 (80.1)</td>
</tr>
</tbody>
</table>

These results suggest that the addition of carotenoids to chloroplasts can significantly enhance the light energy transfer efficiency from carotenoids to chlorophylls in the light (Table II). The observed changes in the relative abundance of carotenoids may exert effects on the light energy transfer efficiency of PS II. If so, a lower light energy conductance would give rise to a lesser fluorescence output from PS II in the presence of 3-(3,4-dichlorophenyl)-1,1-dimethyleurea. To eliminate effects of sample geometry, fluorescence excitation was done with broad blue light as well as 630-nm orange light. The latter excites chlorophylls, the former both chlorophylls and carotenoids. Normalizing on fluorescence yield in the orange by using ratio's equalizes any changes in fluorescence yield of Chl related, for example, to qNP. In HL and LL cultures, the lower fluorescence ratio observed in the dark-preadapted samples indicates that the light energy transfer efficiency from carotenoids to chloroplasts remains higher in darkness than following preadaptation in the light (Table IV). The difference in the efficiency of energy transfer carotenoids → chlorophyll between the dark and light adapted samples is more pronounced in the LL cells.

The results presented in Table II indicate that the formation of the monoepoxide antheraxanthin can only in part be accounted for by conversion of violaxanthin, in addition, the dis- appearance of zeaxanthin appears to add to antheraxanthin formation as well. The apparent two reactions by which antheraxanthin can be formed addresses the question on the nature of the molecular conversions of zeaxanthin that happen as a part of the photosynthetic reaction. In order to investigate the involvement of nonenzymatic processes, the breakdown of zeaxanthin under in vitro conditions was examined. The HPLC chromatograms shown in Fig. 2 indicate that when isolated zeaxanthin (retention time 15.4 min) was exposed to damaging conditions (10,000 μE·m⁻²·s⁻¹ white light, 50 °C, air) degradation occurred. With oxygen present, formation of violaxanthin (retention time of 8.6 min) became evident. The identity of the other "breakdown products" with retention times between 16 and 17 min has not yet been extensively determined. The cis peak in the UV region in the absorbance spectra (data not shown) indicated that these may be the different cis-isomers of zeaxanthin. A similar experiment with zeaxanthin was performed in the presence of the singlet oxygen-generating agent benzine, in just room light and at room temperature. Violaxanthin was formed, other zeaxanthin conversion products were nearly absent (data not shown). The in vitro conversion reactions of zeaxanthin support our view on the actual process of singlet oxygen quenching as part of a dynamic xanthophyll cycle in the light: zeaxanthin is recycled into violaxanthin in the light. In vivo, antheraxanthin is formed this way as well, either by monoepoxidation of zeaxanthin or by the normal viola- to anther-

**Table IV**

**Light energy transfer efficiency**

<table>
<thead>
<tr>
<th>Condition</th>
<th>High light grown</th>
<th>Low light grown</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light incubated</td>
<td>0.96 (±0.07)</td>
<td>1.06 (±0.06)</td>
</tr>
<tr>
<td>Dark incubated</td>
<td>0.62 (±0.04)</td>
<td>0.78 (±0.05)</td>
</tr>
<tr>
<td>Difference light/dark</td>
<td>34.8%</td>
<td>26.5%</td>
</tr>
</tbody>
</table>

**Fig. 2. Effects of in vitro damaging treatments on zeaxanthin.** HPLC purified and collected samples of zeaxanthin were: A, exposed to light (10,000 μE·m⁻²·s⁻¹) during 20 min at 50 °C in the presence of air; B, as A but in the presence of nitrogen gas instead of air, and C, rechromatographed after storage on ice in the dark in the presence of air. Other details are given under "Materials and Methods."

**DISCUSSION**

The two different types of cultures (i.e. LL and HL grown) allowed assays with different contents of xanthophyll cycle pigments present, i.e. relatively abundant in HL cells and low in LL cells as in Thayer and Bjorkman (1989). Applying or omitting actinic background light appeared to be a useful approach to allow or avoid the conversion of violaxanthin to zeaxanthin (Blas et al. 1959; and Yamamoto et al. 1962). In earlier studies dithiothreitol was used to study the role of zeaxanthin in the prevention of photodamage. Those experiments precluded the possibility of studies on a dynamically operating cycle. Our approach involved preadaptation of the cells in either darkness or light to install a stable pH in the thylakoid lumen. To this end, the light intensity was chosen to just reach the Pmax condition (Fig. 1), while avoiding the occurrence of appreciable photodamage (Table I). The lumen pH has been associated with the equilibria of the xanthophyll cycle (Rees et al., 1989; Pfundel and Dilley, 1953). By the preadaptation step, the ratio of the xanthophyll cycle pigments was fixed in a given status before the photodamaging flashes were given. The flashes were administered at a low frequency in order to prevent the build up of a proton gradient for the dark-adapted cells as much as possible. Obviously, if there had been a substantial acidification of the thylakoid lumen analogy with the samples prepared in the presence of actinic background light would have given a diminished breakdown of pigments through the installment of the xanthophyll cycle in the protective mode.

Regardless of the growth conditions and the preincubations, the flashed light induces general photodamage of nearly all
FIG. 3. A scheme depicting the interactions between the various singlet and triplet states of chlorophyll, oxygen, and carotenoids and the role of the xanthophyll cycle in these processes. Reactions indicated with numbers are: 1, excitation of ground state chlorophyll; 2, direct singlet ground state relaxation of excited chlorophyll by photochemistry, radiationless transfer, fluorescence, heat release or singlet quenching via zeaxanthin (Demmig-Adams, 1996; Owens et al., 1992); 3, chlorophyll triplet quenching by ground state oxygen which produces (via spin reversal) singlet excited oxygen or by ground state carotenoid which produces triplet excited carotenoid; 4, reaction of singlet excited oxygen with ground state non- or monoepoxy carotenoids resulting in the epoxidated compounds; 5, singlet energy transfer of violaxanthin-absorbed light to chlorophyll; 6 and 7, enzymatic conversions operating in the xanthophyll cycle. Further details are presented in the text.

pigments, be it to different extents. A clear exception is the increase for antheraxanthin in the samples that were flushed in the presence of actinic background light. This increase is of great interest in the understanding of the physiological function of the xanthophyll cycle. Comparison of the pigment distribution in between HL with background light only (Table I) and HL flushed with background light present (Table II), shows that the decrease of the violaxanthin content is less than the actual increase of antheraxanthin. The only feasible explanation for this observation is epoxidation of zeaxanthin. We conclude that epoxidation of zeaxanthin under photodamaging conditions in the light also contributes to antheraxanthin formation. Interestingly, earlier work (Hager, 1981; Pfendel and Dilley, 1993) established the regulatory function of the light-dependent proton gradient formation for the xanthophyll cycle. From that work can be concluded that epoxidation occurs only after relaxation of the proton gradient, i.e. in darkness. Given the conditions in our experiment, changes of the content of antheraxanthin, other than at the expense of violaxanthin, would not be expected (see above). It is concluded that in addition to the "mixed oxidase" function operating in high lumen pH, i.e. darkness (Hager, 1981), a nonenzymatic epoxidation reaction occurs in the light as well, in accordance with Fig. 2.

Control experiments in which purified zeaxanthin was treated with light plus heat in the presence of air indeed gave rise to the formation of the (di-)epoxy compound violaxanthin. This is comparable to the earlier report on the oxidative degradation of antheraxanthin for which in vitro treatment with heat and oxygen has been shown to facilitate the formation of violaxanthin (Thomas and Goodwin, 1965). A recent report describes that oxidative degradation of β-carotene yields monoo- and diepoxides (Liebler and Kennedy, 1992). This explains our observation that, regardless of the continued presence of a stable proton gradient, formation of antheraxanthin in the light is possible via a nonenzymatic epoxidation of zeaxanthin. The nonenzymatic epoxidation of zeaxanthin results from its function as a photoprotective pigment, i.e. in quenching of singlet oxygen in this particular case. Thus in the light a complete cycle is active. This includes enzymatic reutilization of nonenzymatically epoxidized zeaxanthin (i.e. recycled violaxanthin).

Our work shows that the quenching of excited oxygen by zeaxanthin involves an epoxidation reaction which effectively results in recycling to antheraxanthin and probably violaxanthin as made likely in the in vitro assay. This means that after reaction of zeaxanthin with singlet oxygen, the zeaxanthin is not lost from the cycle but is actually converted into the epoxy compounds antheraxanthin and violaxanthin, through which in the presence of the appropriate acidification of the lumen in the light zeaxanthin can be made again. Table III showed that the xanthophyll cycle was most effective in relation to PSI II, the site at which singlet oxygen generation is most likely to occur.

The position of the steady state of all the processes involved determine the actual distribution of viola-, anthera-, and zeaxanthin in a given sample. This way, the xanthophyll cycle has a real dynamic function in the photoprotective process (Fig. 3). The net decrease of xanthophyll cycle components over the course of exposure to photodamaging conditions is due to the limited number of times that zeaxanthin, in its function as quencher of excited chlorophyll triplet states, is able to withstand trans-cis-trans transitions. In this, according to Krinsky (1971), zeaxanthin has to become damaged during the quenching at a statistical rate of 1000 quenching events per degradation.

In addition to the chemical modifications associated with the operation of the xanthophyll cycle, a change in the energy transfer efficiency in the carotenoid absorbance region related to the state of the xanthophyll cycle and the amount of the xanthophyll cycle pigments as well, was observed (Table IV). The change in the molecular absorbance coefficient between zeaxanthin and violaxanthin cannot be the only reason for this appreciable change. This points to differences in the transfer efficiency between violaxanthin and zeaxanthin to Chl. An explanation for these differences is the number of conjugated double bonds: 9 in violaxanthin and 11 in zeaxanthin. With an increasing number of conjugated double bonds the energy level of the excited states becomes lower, i.e. the zeaxanthin excited states (1Ag, 1B1) lies below that of violaxanthin by which the possibility of an energy transfer to the 31 of Chl a from zeaxanthin becomes increasingly unfavorable (Owens et al., 1992). Violaxanthin has been shown to act as light-harvesting pigment (Owens et al., 1987). This implies that the energy level of the first excited state of violaxanthin is higher than the one of the final Chl acceptor.

The three ways in which the xanthophyll cycle provides protection against photodamage are qNP (singlet transfer), decrease light harvesting capacity (singlet transfer), and photosensitizer-quenching reactions (triplet related). These processes are cooperative: if a carotenoid has a protective func-

7271

\[^{2}\] A. Friedman and H. Schubert, unpublished results.
tion it also has a shadowing effect in the blue region of Chl absorbance and the possibility to quench excited chlorophylls (both singlet and triplet). This effect is important, not only with reference to the mole % numbers presented in Tables 1 and II, but more so because of the about 3.5 times higher molar absorbance coefficient of a carotenoid in comparison to Chl. In other words, in cases of excessive irradiation the shadowing effect is useful, but it should be reversed at less than optimal irradiance, which indeed occurs through the enzymatic epoxidation steps in darkness.

The advantages of the xanthophyll cycle are clear, its dynamically adjustable sun/shade function excludes the need for a constantly present shadowing pool of carotenoids, the chemical trans-cis-trans heat release involved in triplet Chl a photosensitizer quenching strongly reduces the need for de novo synthesis to replace photodamaged molecules. To this, the observation in the present study that singlet oxygen quenching provides a means for recycling of zeaxanthin to violaxanthin in the light further extends the functional role of the xanthophyll cycle. The equilibria of the system can rapidly switch from a constantly present shadowing pool of carotenoids, the chemically adjustable shade function excludes the need for protective (shadowing, chl triplet, and singlet quenching (Demmig-Adams, B. 1990)) to a light harvesting (singlet transfer from light further extends the functional role of the xanthophyll cycle. In conclusion, the xanthophyll cycle provides a dynamic tool for Chl a and b containing organisms and possibly also for brown algae with the diatoxanthin/diadinomithin conversion: tailor made photosensitizer quenching without loss of light harvesting efficiency under changing light conditions.

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