9

The Xanthophyll Cycle in Aquatic Phototrophs and Its Role in the Mitigation of Photoinhibition and Photodynamic Damage

Miriam Zigman[1], Zvy Dubinsky[1] and David Iluz[1,2]
[1]*The Mina and Everard Goodman Faculty of Life Sciences, Bar-Ilan University, Ramat-Gan*
[2]*The Department of Geography and Environment, Bar-Ilan University, Ramat-Gan*
Israel

1. Introduction

Solar energy is the initial power of photosynthesis. Plants and algae cannot proceed in the absence of light, and limited light conditions will limit photosynthesis. However, the conversion of solar energy into chemical energy is a potentially hazardous business that photosynthetic organisms expertly master. Whenever sunlight can actually be converted to chemical energy, there is minimal potential for problems. However, no leaf or algal cell can utilize all the light absorbed by the antenna system during exposure to full sunlight. Excessive light may be potentially dangerous to phototrophic organisms because it has the potential to be transferred to the formation of reactive oxygen species (ROS), which can result in cell damage (Ledford &Niyogi, 2005). It can also inhibit photosynthesis and lead to photooxidative destruction of the photosynthetic apparatus - photoinhibition (Demmig-Adams &Adams, 2006; Lu &Vonshak, 1999). It is known that photosynthesis is the basis of crop yield in plants and primary production in algae, and photoinhibition has an obvious adverse effect on photosynthesis and the accumulation of dry weight, which could lead to a decrease of carbon assimilation by about 10%. Thus, the ability of plants and algae to dissipate excessive light energy in order to resist photoinhibition, would significantly affect plant and alga yield and primary production.

In the first step of the photosynthetic process, light is intercepted by a variety of light-absorbing substances, the photosynthetic pigments. These pigments are associated with proteins forming light-harvesting 'antennae' that have a large optical cross-section for absorbing photons whose energy is efficiently transmitted to reaction centers (Dubinsky, 1992; Emerson &Arnold, 1932; Kirk, 1994).

The light energy absorbed by the chlorophyll of photosynthetic organisms drives photosynthesis and is also dissipated as heat and fluorescence.

To avoid massive ROS accumulation, phytoplankton and plants employ a host of protective mechanisms (Kanervo et al., 2005; Lavaud et al., 2002) – including various alternative energy-dissipation pathways (Adams et al., 2006) and multiple antioxidant systems

(Mullineaux & Rausch, 2005; Noctor & Foyer, 1998). Furthermore, both short- and long-term changes in positioning, stoichiometry, and/or activity of the components of photosystem cores and light-harvesting antennae can occur (Adir et al., 2003; Durnford et al., 2003; Kanervo et al., 2005; Matsubara et al., 2002).

The focus of the present review is photoprotection by the xanthophyll cycle, whereby excess light energy is safely dissipated as heat rather than being transferred to oxygen and, thus, result in ROS production. In this key photoprotective process, potentially damaging energy absorbed by chlorophyll and other light harvesting pigments is dissipated by the carotenoids violaxanthin or diadinoxanthin via the xanthophyll cycle.

In 1962, Yamamoto demonstrated a reversible epoxidation of hydrophilic carotenoids in higher plant leaves (Yamamoto et al., 1962). This class of reactions was subsequently demonstrated in all non-phycobilisomes containing oxygenic photoautotrophs, including algae.

In 1988, Demmig-Adams showed a remarkable correlation between the de-epoxidation reaction and chlorophyll fluorescence quenching. Exposure to high irradiance causes the photosynthetic rates to drop since the harvested light energy cannot be utilized fast enough and has to be dissipated to avoid photodynamic damage due to the formation of free radicals. A significant part of this excess energy turns to heat. This process, which appears to be wasteful, acts as a protective mechanism (Demmig et al., 1988; Krause & Weis, 1991).

2. The evolutionary inheritance of algal pigments in the oceans

The apparatus responsible for the photochemical production of oxygen in photosynthetic organisms is contained within distinct organelles called plastids. Based on small subunit ribosomal RNA sequences, it would appear that all plastids are derived from a single common ancestor that was closely related to extant cyanobacteria (Bhattacharya & Medlin, 1995; Palmer, 2003); however, early in the evolution of eukaryotic photoautotrophs, major schisms occurred that gave rise to two major clades, a 'green lineage' and a 'red lineage', from which all eukaryotic photoautotrophs descended (Delwiche, 1999) (Fig. 1). While all eukaryotic photoautotrophs contain chlorophyll *a* as a primary photosynthetic pigment, one group utilizes chlorophyll *c* and the other appropriated chlorophyll *b* as primary accessory pigments. No extant chloroplast contains all three pigments (Falkowski et al., 2004a, 2004b).

The chlorophyll *c*-containing plastid lineage, which is widely distributed among at least six major groups (i.e., phyla or divisions) of aquatic photoautotrophs, with the exception of some soil-dwelling diatoms and xanthophytes, is not present in any extent terrestrial photoautotroph. In contrast, the chlorophyll *b*-containing plastid lineage is in three groups of eukaryotic aquatic photoautotrophs and in all terrestrial plants. Because additional accessory pigments (carotenoids) found in the chlorophyll *c*-containing group have yellow, red, and orange reflectance spectra (i.e., they absorb blue and green light), the ensemble of organisms in this group are referred to, in the vernacular, as the 'red lineage'. The chlorophyll *b*-containing group contains a much more limited set of carotenoids in the chloroplast, and members of this group generally have a green color. Thus, in effect, the ensemble of organisms responsible for primary production on land is green, while the ecologically dominant groups of eukaryotic photoautotrophs in the contemporary oceans are red.

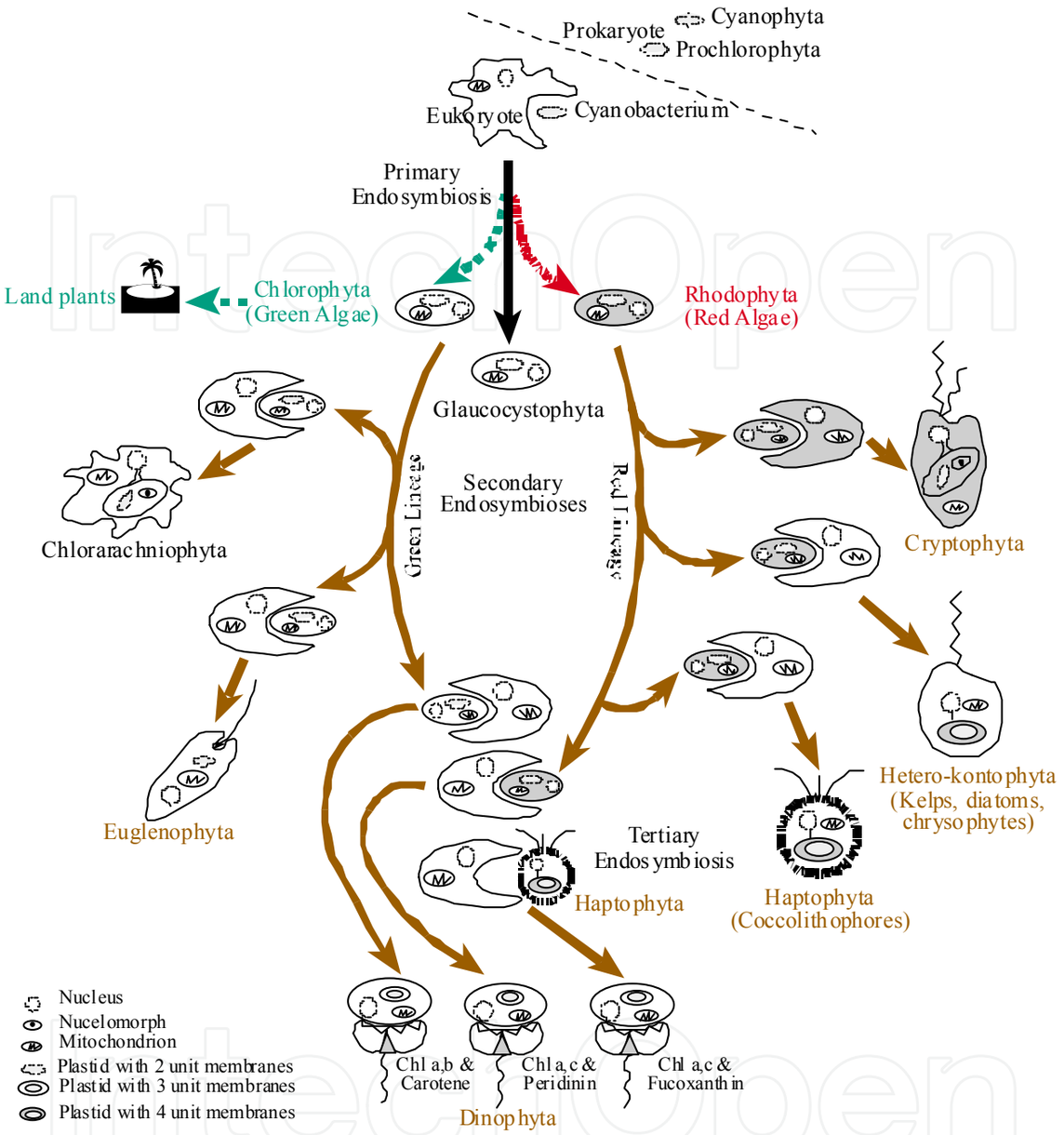


Fig. 1. The evolutionary inheritance of red and green plastids in eukaryotic algae. The ancestral eukaryotic host cell appropriated a cyanobacterium to form a primary photosynthetic symbiont. Two main groups split from this primary association: one formed a 'green' line ▪▪▪▶ and one a 'red' line ➡ (after Falkowski, 2004b).

One potential selection mechanism for red and green plastids is spectral irradiance. Compared to land plants, the majority of the phytoplankton biomass in the ocean is light-limited for growth and photosynthesis. On land, competition for light within a canopy is based on total irradiance, not primarily on the spectral distribution of irradiance. On the average, 85-90% of total incident photosynthetically available radiation on a leaf is absorbed. In contrast, in the oceans, absorption of light by seawater itself is critical to the spectral

distribution of irradiance. The spectral irradiance is further modified by dissolved organic matter, sediments, and the spectral properties of the phytoplankton themselves. Hence, it is not surprising that phytoplankton have evolved an extensive array of accessory pigments, including carotenoids and chlorophylls, that permit light absorption throughout a wide range of the visible spectrum (Falkowski et al., 2004a; Jeffrey et al., 1997).

The 'red' and 'green' algal lineages differ, in addition to several cellular and life-cycle characteristics, in the evolution of their photosynthetic pigments, hence, it is not surprising that they also differ in the carotenoids of which their xanthophyll cycle consists. In accordance with their evolutionary linkeage, no xanthophyll cycle was found in cyanophyceae and rhodophyceae (Fig. 2).

From the investigation of fossil evidence regarding the evolution of the eukaryotic phytoplankton taxa, we can consider and develop some hypothesis that may account for the origin and ecological success of the red line in the oceans, while the green line maintained genetic hegemony on land.

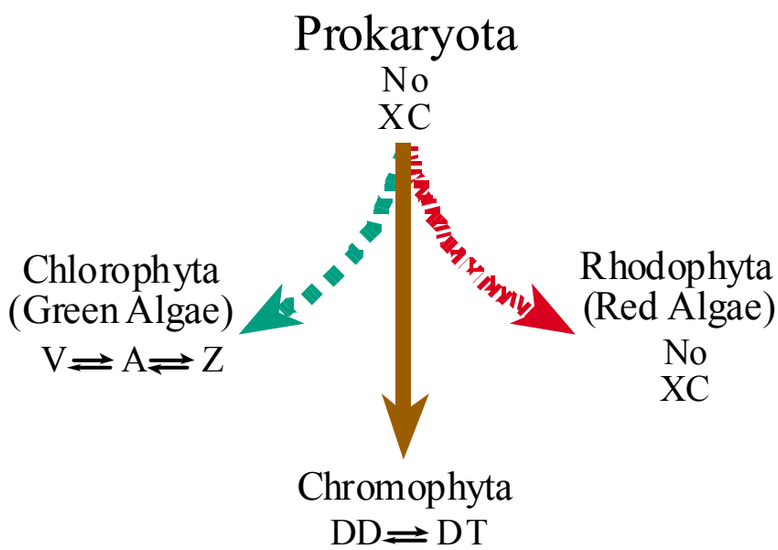


Fig. 2. The three major groups split from the primary prokaryotic prototroph and secondary endosymbiosis. This is characteristic of their xanthophyll cycle. Green line ▪▪▪▶ and red line ▬▶.

3. Carotenoids in the xanthophyll cycle

Carotenoids containing one or more oxygen atoms have a number of functions in photosynthetic systems. They act as: (i) accessory light-harvesting pigments, such as peridinin and fucoxanthin; (ii) photoprotective pigments, such as carotene and astaxanthin quenchers of triplet-state chlorophyll (chl); and (iii) xanthophyll cycle components, quenchers of singlet oxygen (O_2). Studies on plastid biogenesis and *in vitro* reconstitution have also identified a key role for carotenoids in the structure/organization of the photosynthetic apparatus. Xanthophylls are yellow pigments from the carotenoid group. Some xanthophylls have further been implicated in the non-photochemical quenching of chlorophyll fluorescence in plants and some algae, an important photoprotective process. The role of xanthophylls in this process, resulting in dissipation of excess excitation energy

via quenching of chlorophyll fluorescence, is a feature of the interconversion of carotenoids due to the xanthophyll cycle. The xanthophyll cycle involves only 5 carotenoids out of many hundreds of carotenoids found in all phyla of algae and land plants (Tables 1, 2).

Pigment	Solvent	Spectra	Ref.
Diadinoxanthin	acetone	426, 447.5, 478	Johnsen et al. (1974)
Diatoxanthin	Acetone	429, 454, 482	Berger et al. (1977)
Zeaxanthin	acetone	425, 450, 478	Withers et al. (1981)
Antheraxanthin	ethanol	422, 444, 472	Stransky & Hager (1970)
Violaxanthin	acetone	417, 440, 470	Renstrom et al. (1981)

Table 1. Absorbance peaks of xanthophyll-cycle pigment

The xanthophyll cycle involves the enzymatic removal of epoxy groups from xanthophylls (violaxanthin, antheraxanthin, diadinoxanthin) to create so-called de-epoxidized xanthophylls (diatoxanthin, zeaxanthin).The interconversion of violaxanthin to zeaxanthin and of diadinoxanthin to diatoxanthin alters the extent of the conjugated double-bond system as a result of the epoxidation and de-epoxidation reactions (Figs. 3, 4).

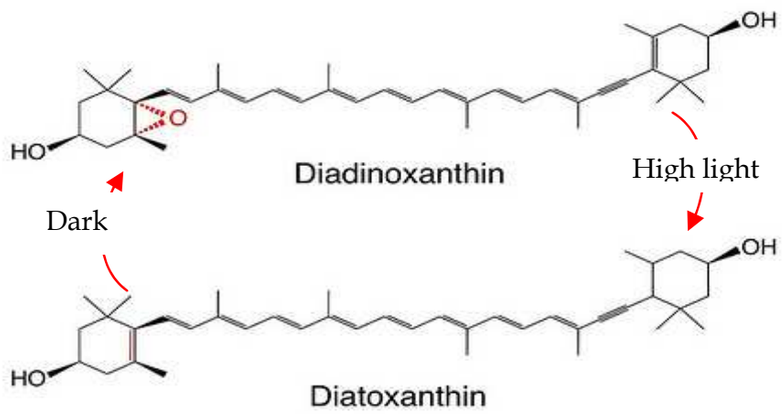


Fig. 3. The xanthophyll biosynthetic pathway in chromophyta algae. Under high light, diadinoxanthin converts to diatoxanthin reverting to diadinoxanthin under dim light or darkness

In chlorophyll *b*-containing organisms (higher plants and green algae), the carotenoid pigment structures that are active in the xanthophyll cycle are: violaxanthin ((3S, 5R, 6S, 3'S, 5'R, 6'S)-5,6;5',6'-diepoxy-5,6,5',6'-tetrahydro-l3,!3-carotene-3,3'-diol), antheraxanthin ((3S, 5R, 6S, 3'R)-5,6-epoxy-5,6-dihydro-B,I3-carotene-3,3'-diol), and zeaxanthin ((3R, 3'R)-l3,Rcarotene-3,3'-diol) (Fig. 4) During light stress, violaxanthin is converted to zeaxanthin via the intermediate antheraxanthin, which plays a direct photoprotective role acting as a lipid-protective antioxidant and by stimulating non-photochemical quenching within light-

harvesting proteins. This conversion of violaxanthin to zeaxanthin is done by the enzyme violaxanthin de-epoxidase, while the reverse reaction is performed by zeaxanthin epoxidase. In chlorophyll *c*-containing organisms (some algae groups), the xanthophyll cycle consists of the pigment diadinoxanthin ((3S,5R, *6S,*3 'R)-5,6-epoxy-7',8'-didehydro-5,6-dihydroS,R-carotene-3,3'-diaonld), which is transformed into diatoxanthin ((3R, 3'R)-7,8- didehydro-l3,l3-carotene-3,3'-diol)) (Fig. 3). Some of chlorophyll *c* algae groups use both cycles (Lohr & Wilhelm, 2001).

The implications of this are**:** (i) the extent of the conjugated system in carotenoids affects both the energies and lifetimes of their excited states, from 9 to 11 C-C double bonds in violaxanthin and zeaxanthin, respectively; (ii) for carotenoids in which the end-groups are in conjugation with the main polyene chain, a coplanar conformation is energetically favored. In zeaxanthin, steric hindrance prevents it from being fully coplanar and a near-planar conformation is adopted. In contrast, in carotenoids such as violaxanthin, in which the conjugation is removed (by the presence of epoxide groups in the C5,6 position) the end-group occupies a perpendicular position relative to the main chain. Such conformational changes in the carotenoid molecule may, in turn, affect the organization of the light-harvesting complex (LHC).

4. Operation and characteristics of the xanthophyll cycle

The xanthophyll cycle is one of the main processes regulating excessive photon flux in the light-harvesting complexes of photosystems since it is responsible for most of the non-photochemical quenching of chlorophyll fluorescence (NPQ) (Demmig-Adams & Adams, 2006; Goss & Jakob, 2010; Lavaud, 2007).

This photoprotective cycle in its generally recognized form occurs in most eukaryotic algae and in higher plants. While much work has been carried out on higher plants and green algae such as *Chlamydomonas* (Baroli & Melis, 1996; Demmig-Adams & Adams, 1993), much less has been carried out on the other algal taxa. In microalgae, two main groups can be distinguished with regard to pigments involved in the xanthophyll cycle. The first group is characterized by the two-step de-epoxidation of violaxanthin into zeaxanthin via antheraxanthin at high light, which is reversed in the dark (Fig. 3). One molecule of oxygen is released (de-epoxidation) or taken up (epoxidation) for a complete transition. A truncated vilaxanthin-to-antheraxanthin version also occurs in some primitive green algae. The second group exhibits a simpler conversion, with the single step de-epoxidation of diadinoxanthin to diatoxanthin (Fig. 4). Many specificities of the diadinoxanthin cycle relative to the violaxanthin (Goss & Jakob, 2010; Wilhelm et al., 2006) might explain the rapid and effective synthesis of diadinoxanthin in large amounts (Lavaud et al., 2004; Lavaud et al., 2002). Lohr and Wilhelm (Lohr & Wilhelm, 1999) showed that some algae display the diadinoxanthin type of xanthophyll cycle, as well as features of the violaxanthin-based cycle.

In other groups of phytoplankton, there is no (cyanobacteria) or a questionable (red algae) xanthophyll cycle (Goss & Jakob, 2010) but the involvement of various de-epoxidized forms of xanthophylls (including zeaxanthin) in NPQ (Table 3) occurs by reaction center (RC) down-regulation (Kirilovsky, 2007; Stransky & Hager, 1970).

In general, as light intensity increases, the level of violaxanthin/diadinoxanthin decreases, reaching a steady state and, conversely, the level of zeaxanthin/diatoxanthin increases to asymptote (Demmig-Adams & Adams, 1993; Yamamoto, 1979).

Algal Division/Class													
Pigment	Cyanophyta	Prochlorophyta	Rhodophyta	Cryptophyta	Chlorophyceae	Prasinophyceae	Euglenophyta	Eustigmatophyta	Bacillariophyta	Dinophyta	Prymnesiophyceae	Chrysophyceae	Raphidophyceae
Chlorophyll *a*	+		+	+	+	+	+	+	+	+	+	+	+
b					+	+	+						
c_1									+		+		+
c_2				+					+	+	+	+	+
c_3											+	+	
Carotenes- β,ε		+	+	+	+	+					+		
β,β	+	+			+	+	+	+	+	+	+	+	+
β,ψ					+								
ε,ε				+								+	
ψ, ψ				+									
Xanthophylls Alloxanthin				+									
Antheraxanthin					+	+	+						
Diadinoxanthin							+		+	+	+	+	+
Diatoxanthin							+		+	+	+	+	+
Zeaxanthin	+	+	+		+			+					
Violaxanthin					+	+		+					
Astaxanthin											+	+	
Dinoxanthin										+			
Fucoxanthin									+		+	+	+
Lutein					+	+							
Monadoxanthin				+									
Neoxanthin					+	+	+						
Peridinin										+			
Peridininol										+			

Algal Division/Class													
Pigment	Cyanophyta	Prochlorophyta	Rhodophyta	Cryptophyta	Chlorophyceae	Prasinophyceae	Euglenophyta	Eustigmatophyta	Bacillariophyta	Dinophyta	Prymnesiophyceae	Chrysophyceae	Raphidophyceae
Prasinoxanthin						+							
Pyrrhoxanthin										+			
Biliproteins Allophycocyanin	+		+										
Phycocyanin	+		+	+									
Phycoerythrin	+		+	+									

Table 2. Distribution of major and taxonomically significant pigments in algal divisions/classes

Group 1	**Group 2**	**Group 3**
Zeaxanthin *No xanthophyll cycle*	*Zeaxanthin* *Violaxanthin*	*Diadinoxanthin* *Diatoxanthin*
Cyanobacteria Rodophyceae Cryptophyceae ? Glaueystophyceae	Phacophyceae Chlorophyceae Chrysophyceae Xanthophyceae Mosses Ferns Gymnosperms Angiosperms	Diatoms Chrysophyceae Xanthophycea Chloromonads Dinoflagellates Euglenophyceae

Table 3. The three groups of algal phyla according to their xanthophylls. Group 1 does not show a reversible epoxidation reaction.

The photoprotective NPQ process takes place in the light-harvesting complex of PSII. When irradiance exceeds the photosynthetic capacity of the cell, NPQ dissipates part of the excessively absorbed light energy, thus decreasing the excitation pressure on PSII (Li et al., 2009). NPQ is composed of three components – qE, qT, and qI, whose respective importance varies among photosynthetic lineages, qE being essential for most of them. qE is the energy-dependent quenching that is regulated by the build-up of a transthylakoid ΔpH and the operation of the xanthophyll cycle. The qT refers to the part of the quenching resulting from state transitions, while qI is due to photoinhibition. qT is relevant in phycobilisome-containing organisms (cyanobacteria and red algae) and green microalgae, but it is not really significant in high light (Ruban & Johnson, 2009). The origin of qI is not clearly defined except for some higher plants, and it requires special conditions (Demmig-Adams & Adams, 2006). Although the relationship between qE and the accumulation of de-epoxidized

xanthophylls has been reported in many algal groups (Lavaud et al., 2007), there is still no clear picture of the functioning of qE in microalgae, although models have been proposed (Goss & Jakob, 2010; Lavaud, 2007), with the exception of *Chlamydomonas* (Peers et al., 2009). Regarding cyanobacteria and red algae, although there is a qE quenching that is supported by the presence of xanthophylls and a ΔpH, the composition and organization of the antenna obviously support another type of qE mechanism (Bailey & Grossman, 2008; Kirilovsky, 2007). Nevertheless, qE in cyanobacteria is not as powerful as in other phytoplankton taxa (Lavaud, 2007), possibly because of the lack of a finely regulated xanthophyll cycle. When necessary, cyanobacteria favor other photoprotective processes such as qT (described above) and the rapid repair of the D1 protein of the PS II reaction center (Six et al., 2007; Wilson et al., 2006).

The influence of the size and shape of cells on the capacity for regulation of photosynthesis and, in particular, via the xanthophyll-cycle operation, merits more attention (Key et al., 2010). Cell size could significantly affect xanthophyll-cycle functioning (Dimier et al., 2007b, 2009b; Lavaud et al., 2004). Indeed, physiological acclimation to light changes is a costly process. Cell size determines the structure of the PS II antenna and, therefore, pigment content, which constrains the use of the light resource, hence limiting the energy available for physiological responses to light fluctuations (Key et al., 2010; Litchman & Klausmeier, 2008; Raven & Kübler, 2002) . The influence of cell size/shape on metabolism, coupled with the metabolic theory of ecology (Brown et al., 2004) applied to the fast regulation of photosynthesis versus light, would bring interesting insights for studying photoadaptative strategies versus niche properties in microalgae. This would provide a background to understand how the environmental conditions affect photoregulatory capacity and efficiency and what their impact is on cell metabolism. Picoeukaryotes turned out to be interesting models to further explore this hypothesis (Dimier et al., 2007a, 2009a; Six et al., 2008, 2009). Dimier (2009a) suggested that the energy cost of enhanced photoregulation due to high-light fluctuation could be responsible for the decrease of growth rate in the shade-adapted picoeukaryote *Pelagomonas*. Additionally, *in situ* studies showed, in agreement with laboratory experiments, that picoeukaryotes have high plasticity of PS II photoregulatory responses. This is probably related to the fact that the main limiting resource for these organisms is light (Timmermans et al., 2005), since nutrient availability does not seem to significantly determine their rate of primary productivity.

Recently, a specific role for the chlorophyll-binding, 22 kDa protein, psbS, has been shown (Goss & Jakob, 2010). This protein might be located in an intermediate position between LHCII and the inner antenna of RCII (Nield et al., 2000). The evidence suggests that energy-dependent quenching qE (which is defined as that component of the total non-photochemical quenching qN' directly attributable to the energization of the thylakoid membrane and, therefore, the rapidly entrained composition of qN) occurs when: i) there is ΔpH across the thylakoid membrane; and ii) zeaxanthin/diadinoxanthin is at high concentration (and violaxanthin/diadinoxanthin at low concentration) as a result of de-epoxidation of violaxanthin/diatoxanthin. Horton and Ruban (1994) suggested that there is a pocket extending from the intrathylakoid lumen into the membrane, by which low pH in the thylakoid lumen can influence a critical site in the thylakoid membrane. Since psbS is essential for qE to occur, it may be the protein which senses the low pH and binds zeaxanthin or it may play a crucial structural role in energy transfer/dissipation (Li et al., 2000; Raven & Beardall, 2003).

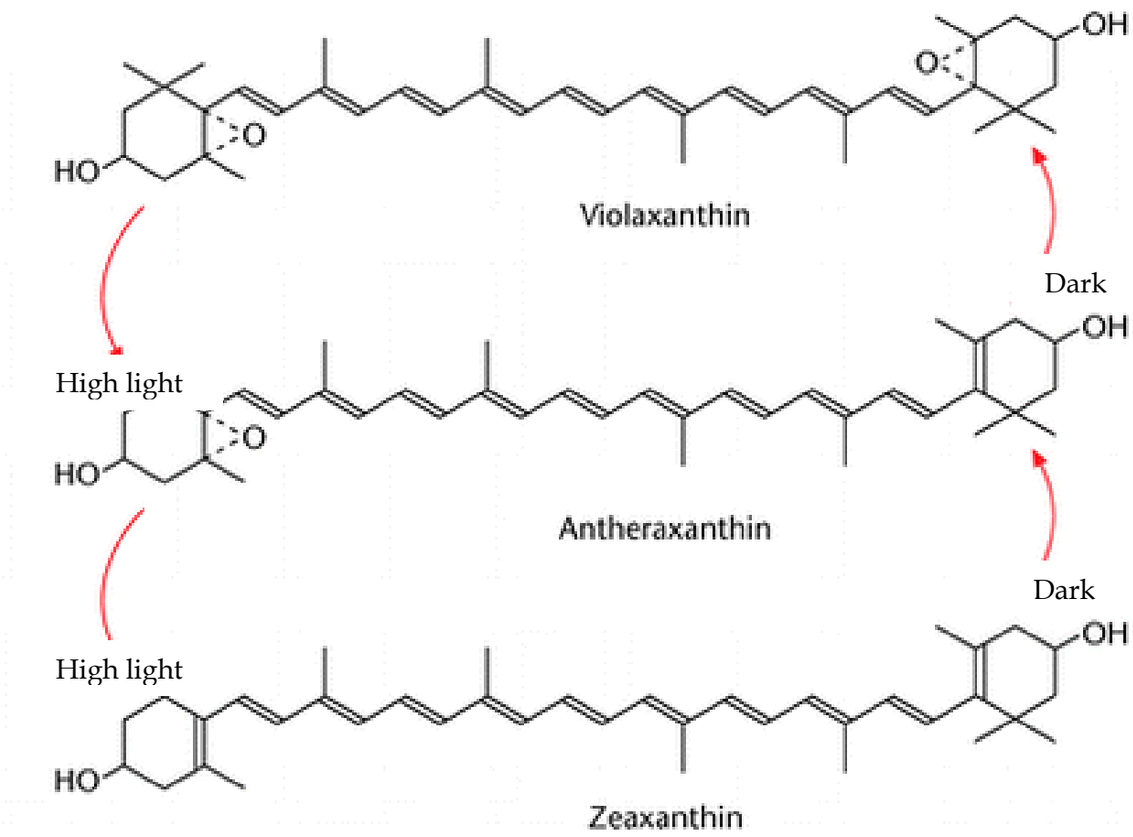


Fig. 4. The xanthophyll biosynthetic pathway in green algae and plants. When exposed to high light, violaxanthin converts to zeaxanthin, turning back into violaxanthin under low light or darkness

5. Xanthophyll cycle in higher plants and algae

Photosynthetic organisms have developed strategies to optimize light harvesting at low intensities while minimizing photoinhibitory damage due to excess energy at high-light intensity. They regulate the quantity and composition of the light-harvesting complexes (LHCs) and a number of other components of their photosynthetic machinery (Anderson et al., 1995; Falkowski & LaRoche, 1991). On shorter time scales, they react to an imbalance between light intensity and photosynthetic capacity (e.g., due to a change in light intensity, temperature, or nutrient supply) by rapid structural modification within the LHC of PSII (Bassi & Caffarri, 2000; Horton et al., 1996). These modifications lead to a decrease in NPQ. The partitioning of absorbed energy between transfer to the reaction center and photoprotective non-radiative dissipation is controlled by the trans-thylakoid pH gradient (Müller et al., 2001) and by the xanthophyll cycle. The molecular mechanisms of photoprotection have been mostly studied in higher plants (Demmig-Adams & Adams, 2006).

In comparison to higher plants, phytoplankton are well known to flourish in turbulent waters (Harris, 1986), where the amount of light available to phytoplankton unicellular organisms is highly unpredictable. The deep vertical mixing continuously sweeps them up

and down, exposing the cell to very large short-term changes in light intensity on a time scale of minutes to hours. Higher plants, even though they are attached to the ground, are also exposed to light fluctuations due to a flicker effect caused by leaf movement in forests (Leakey et al., 2002, 2005).

The organization of the photosynthetic apparatus in diatoms differs in many respects from that of green algae and higher plants. The thylakoid membranes are loosely appressed and organized in extended layers of three without grana stacking, and the PSI and PSII are not segregated in different domains. The LHCs, which contain Chl *a*, Chl *b*, fucoxanthin, and the xanthophyll-cycle pigment diadinoxanthin, are equally distributed among appressed and nonappressed regions (Pyszniak & Gibbs, 1992) and there is no evidence of any state 1 to state 2 transitions (Owens, 1986). The xanthophyll concentration relative to chl can be two to four times more than in a higher plant.

The LHC subunits are made of several highly homologous proteins encoded by a multigene family (Bhaya & Grossman, 1993). The CP26 and CP29 subunits present in higher plants are not found in diatoms (Müller et al., 2001). When the cells are suddenly exposed to high-light intensity, an NPQ is rapidly developed. NPQ is associated with a xanthophyll cycle, the diadinoxanthin cycle, which differs from that of higher plants. The diadinoxanthin cycle converts the mono-epoxide carotenoid diadinoxanthin into the de-epoxide form diatoxanthin under high light, and diatoxanthin back into diadinoxanthin under low light or darkness (Arsalane et al., 1994).

In a diatom, the diadinoxanthin content can be modulated by the light regime to which culture is exposed (Willemoes & Monas, 1991). In higher plants, the xanthophyll cycle converts zeaxanthin through asteroxanthin to violaxanthin.

The microalgal xanthophyll-cycle activity shows striking peculiarities with respect to higher plants. This includes a high degree of variation in that cycle's regulation among the different taxa/species (Goss & Jakob, 2010; Lavaud et al., 2004; van de Poll et al., 2010), together with the growth phase (Arsalane et al., 1994; Dimier et al., 2009b; Lavaud et al., 2002, 2003;), the nutrient state (Staehr et al., 2002; Van de Poll et al., 2005), and the light history with both visible and UV radiation (Laurion & Roy, 2009; Lavaud, 2007; van de Poll & Buma, 2009). Also, recent reports demonstrated how xanthophyll-cycle activity and efficiency might be influenced by niche adaptation, and vice versa, in both pelagic (Dimier et al., 2007b, 2009a; Lavaud et al., 2004, 2007; Meyer et al., 2000) and benthic {Serodio, 2005 #3081;van Leeuwe, 2008 #3082} species, and how this could influence species succession {Meyer, 2000 #3080;Serodio, 2005 #3081;van Leeuwe, 2008 #3082}. This functional trait is part of the overall adaptive photophysiological properties of PS II, as shown for the diatoms (Wagner et al., 2006; Wilhelm et al., 2006). It highlights the narrow functional relationship between the niche adaptation and the capacity for photo-regulation/-acclimation, thus elucidating that the fast regulation of photosynthesis might be a crucial functional trait for microalgal ecology. In this respect, diatoms are currently the most studied group, probably because they appear to be the best xanthophyll cycle/NPQ performers among microalgae (Lavaud, 2007). Nevertheless, diatoms show a large interspecies xanthophyll cycle/NPQ diversity (Dimier et al., 2007b; Lavaud et al., 2004, 2007), which might take its source in the special evolution of this group (Armbrust, 2009), leading to its successful adaptation to all aquatic habitats driven by a change from a benthic to a pelagic way of life (Kooistra et al., 2007).The decrease in accessory-pigment diversity in diatoms compared with other microalgal groups would especially be an advantage for an opportunistic strategy (Dimier et al., 2009b) that

might be related to the high plasticity of their PS II antenna function, including the xanthophyll cycle (Lavaud, 2007).

6. PSII protection by NPQ against photoinhibition

In higher plants and algae, the capacity for photosynthesis tends to saturate at high light intensities while the absorption of light remains linear. Therefore, the potential exists for the absorption of excess light energy by photosynthetic light-harvesting systems. This excess excitation energy leads to an increase in the lifetime of singlet excited chlorophyll, increasing the chances of the formation of long-lived chlorophyll triplet states by inter-system crossing. Triplet chlorophyll is a potent photosensitizer of molecular oxygen forming singlet oxygen, which can cause oxidative damage to the pigments, lipids, and proteins of the photosynthetic thylakoid membrane. One photoprotective mechanism that exists to counter this problem is the so-called non-photochemical quenching of chlorophyll fluorescence (NPQ), which relies upon the conversion and dissipation of the excess excitation energy into heat (Fig. 5). Excitation energy is, thereby, diverted away from the photosynthetic reaction centers and is no longer available for photochemistry. Although this increase in the rate of radiationless dissipation is associated with a reduction in the

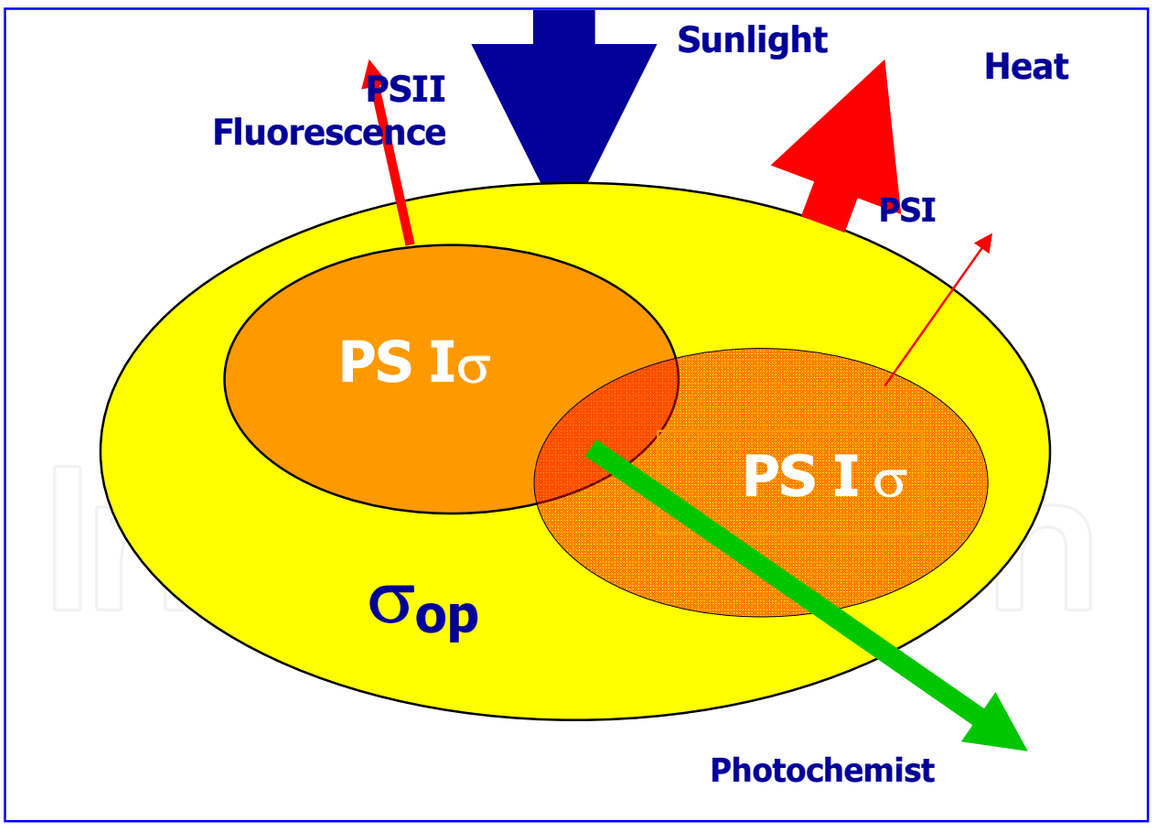


Fig. 5. The paths of energy dissipation and the use of harvested light energy in phototrophs. The σ symbol represents the different optical and functional cross sections of photosynthesis (for definitions, see Dubinsky (1980, 1992). Light energy diverted by the xanthophyll cycle is dissipated as heat, also included in the term NPQ.

efficiency of photosynthesis at low light, this disadvantage is most likely outweighed by the benefits of preventing the accumulation of excess excitation energy at high light, whereby damage to the reaction centers is avoided. In higher plants, the quenching could be as high as 80% and was induced by exposure to high irradiance (Demmig et al., 1988), and from one half to nearly all of the absorbed energy in algae. NPQ involves conformational changes within the light-harvesting proteins of photosystem II that bring about a change in pigment interactions, causing the formation of energy traps. The conformational changes are stimulated by a combination of transmembrane proton gradient, the PsbS subunit of photosystem II, and the enzymatic conversion of the carotenoid violaxanthin to zeaxanthin or diadinoxanthin to diatoxanthin (the xanthophyll cycle).

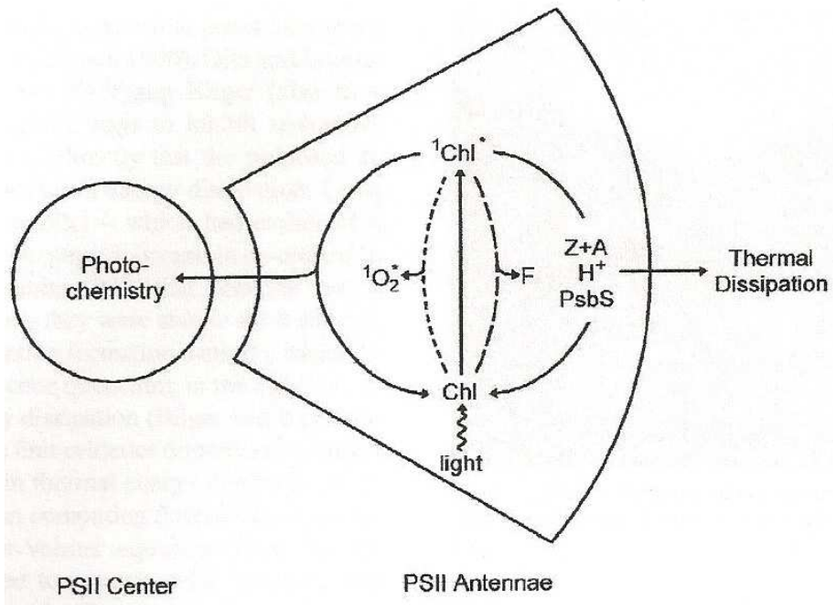


Fig. 6. Four routes of excitation energy in photosystem II light–collecting antennae. After moving chlorophyll electron by light to the (singlet) excited state, this energy can be used either for photochemistry or, alternatively, be dissipated thermally (as heat) in a process facilitated by xanthophylls (via the xanthophyll cycle), an acidic thylakoid, and the PsbS protein. A very small fraction of excitation energy is re-emitted as chlorophyll fluorescence, and can be used to monitor the excitation energy. If excited singlet chlorophyll were allowed to accumulate transiently, energy could also be transformed to oxygen, forming destructive singlet excited oxygen (after Demmig-Adams (2003)).

The xanthophyll cycle allows the fine tuning of the photosynthetic apparatus to ambient light by switching between two or three states of pigment couples constituting the xanthophyll cycle. When exposed to low light, most of its energy is used in the photochemical photolysis of water and the subsequent reduction of CO_2 to high-energy photosynthate. Under high light, the xanthophyll-cycle pigments undergo epoxidation and now divert light energy to harmless heat rather than damaging excess light (Adams et al., 1999; Demmig-Adams, 1998).

The NPQ mechanism depends on the size of the diadinoxanthin pool and can reach much larger values in algae than in higher plants (Lavaud et al., 2002; Li et al., 2002). NPQ and

diatoxanthin are directly linearly related and if diatoxanthin is not present, NPQ cannot be formed. A fast diadinoxanthin de-epoxidation and concomitant formation of NPQ occurs within seconds (Lavaud et al., 2004). A linear relationship between zeaxanthin formation and NPQ has also been frequently observed in higher plants (Demmig-Adams & Adams, 1996). On the other hand, a number of reports show poor correlation between the light-induced zeaxanthin accumulation and the quenching of variable chlorophyll fluorescence in higher plants (Lichtenthaler et al., 1992; Schindler & Lichtenthaler, 1994; Schindler & Lichtenthaler, 1996), as well as in green algae (Masojidek et al., 1999). Poor correlation has been also found in green algae *Dunaliella*, which has similar light-harvesting and xanthophyll-cycle pigments to that of higher plants (Casper-Lindley & Bjorkman, 1998).

7. The biophysical mechanism of NPQ

There is a lack of knowledge concerning the exact nature and organization of light-harvesting complex containing fucoxanthin (LHCF) subunits in diatoms, and especially the location of diadinoxanthin and diatoxanthin in the antenna complex. In diatoms, the size of the diadinoxanthin pool increases under intermittent light and a larger fraction of the pool is susceptible to de-epoxidation (diatoxanthin). The diatoxanthin molecules produced under high light were shown to enhance the dissipation of excess energy and were, therefore, likely to be bound to the antenna subunits responsible for the NPQ. One hypothesis about diadinoxanthin enrichment under intermittent light is pigment-pigment 'replacement'. Under such conditions, the LHCF subunit would bind two diadinoxanthin molecules at the same time in continuous light. This is supported by the observation that the diadinoxanthin enrichment is correlated with a stoichiometrically parallel decrease in fucoxanthin content (Lavaud et al., 2003). In higher plants, the possibility that a given site of a LHC protein can bind different xanthophylls has been demonstrated.

The existence of LHCF subunits with different pigment content is very likely. Since, in parallel to the increase in diadinoxanthin content, Chl *c* decreases to the same extent as fucoxanthin, some subunits could be specifically rich in diadinoxanthin while others could mainly bind fucoxanthin and Chl *c* (Lavaud et al., 2003).

Under excess light, a higher degree of de-epoxidation occurs in diadinoxanthin- enriched cells. To be de-epoxidized, xanthophylls have to be accessible to the de-epoxidase localized in the lipid matrix. The fraction of diadinoxanthin that can be transformed to diatoxanthin is thus likely located at the periphery of pigment-protein complexes.

The exact biophysical mechanism by which fluorescence is quenched via the xanthophyll cycle is unclear. One possibility is that physical aggregation of chlorophyll molecules induced by the de-epoxidation of the xanthophylls leads to a reduction in the optical absorption cross section (i.e., a*) of the entire antenna system, and associated quenching of the fluorescence (Horton et al., 1996). The quenching mechanism in this scenario is unclear, however, if this scenario is valid, it should lead to change in both the optical and effective cross sections. An alternative hypothesis is based on direct competition for excitation energy within the LHC between the reaction center and the xanthophylls, upon de-epoxidation from a singlet state that can be populated with excitations emanating from the lowest singlet excited state of chlorophyll *a* (Frank & Cogdell, 1996; Owens, 1994). In effect, this hypothesis suggests that xanthophylls become reversibly activated quenchers within the pigment bed. Upon activation, they increase the probability that absorbed photons will be dissipated as heat through nonradioactive energy transfer to carotenoids. The process should lead to a

change in the effective cross section of one or both reaction centers (depending upon which antenna system the xanthophyll cycle is associated with), but not a change in the optical absorption cross section (Falkowski & Chen, 2003).

8. Microalgal response to variable light environments

Phytoplankton species must cope with a highly variable environment that continuously requires energy for maintenance of photosynthetic productivity and growth. This is relevant in such aquatic ecosystems in which biodiversity is high and competition for resources is strong. Indeed, in a few cubic millimeters of water, many phytoplankton species can grow together, sharing and competing for the same energy resources, especially light and nutrients (Liess et al., 2009). To be competitive, phytoplankton must be able to respond quickly to any kind of changes occurring in their habitat. The main abiotic driving forces are temperature, nutrients, and light, the latter showing the highest variations in amplitude and frequency (Dubinsky & Schofield, 2010; MacIntyre et al., 2000; Raven & Geider, 2003). Hence, the response of phytoplankton might be supported by at least one irradiance-dependent physiological process that must be fast, flexible, and efficient (Dubinsky & Schofield, 2010; Li et al., 2009). Huisman et al. (2001) proposed that the diversity of life history and physiological abilities might promote the high biodiversity of phytoplankton. It has been proposed that the variability of physiological responses to light fluctuations would allow competitive exclusion and thus the spatial co-existence and/or the temporal succession of a multitude of species in both pelagic (Dimier et al., 2007b, 2009b; Lavaud et al., 2007) and benthic {van Leeuwe, 2008 #3082} ecosystems. Indeed, growth rate responds to fluctuating light in different ways as a function of groups/species of phytoplankton (Flöder et al., 2002; Litchman, 2000; Mitrovic et al., 2003; Wagner et al., 2006) and of the photoacclimation ability and light history of the cells (Laurion & Roy, 2009; Litchman & Klausmeier, 2001; van de Poll et al., 2007; van Leeuwe et al., 2005; Wagner et al., 2006). The photoresponse ultimately leading to a change in growth rate is thus a matter of both genomic plasticity and time scale (Dubinsky & Schofield, 2010; Grobbelaar, 2006). In the short term (a few seconds/minutes), the light fluctuations are mainly due to cloud movement, surface sunflecks, ripples on water surface, and vertical mixing generating unpredictable changes. These fluctuations, and especially their extremes (darkness and excess light), are generated by a lensing effect that simultaneously focuses and diffuses sunlight in the upper few meters of the water column, producing a constantly moving pattern of interspersed light and shadows on the substrate (Fig. 6). Due to the lensing effect, light intensity in shallow water environments sometimes reaches more than 9,000 µmol quanta m^{-2} s^{-1}, corresponding to 300-500% of the surface light intensity. For review of the "flicker effect" see Alexandrovich et al. (this volume).

These fluctuations in light can be harmful for the photosynthetic productivity of microalgae by promoting an imbalance between the harvesting of light energy and its use for photochemical processes and carbon fixation (Dubinsky & Schofield, 2010; Long et al., 1994; Raven & Geider, 2003). In order to regulate photosynthesis versus rapid light fluctuations, phytoplankton have evolved a number of physiological photoprotective mechanisms such as the photosystem II (PS II) and PS I electron cycles, the state-transitions, the fast repair of the D1 protein of the PS II reaction center, and the scavenging of reactive oxygen species (see (Falkowski & Raven, 1997; Lavaud, 2007; Ruban & Johnson, 2009)). Among these processes, the xanthophyll cycle and the dependent thermal dissipation of the excess light

energy (NPQ for non-photochemical fluorescence quenching) play a central role. At longer time scales (hours to seasons), acclimation processes are supported by gene regulation, which modifies the architecture of the photosynthetic apparatus as well as enzymatic reactions involved in photochemistry and metabolism (Dubinsky & Schofield, 2010; Grobbelaar, 2006). These two types of responses, regulative and acclimative, are not mutually exclusive (Lavaud et al., 2007). For instance, long-term acclimation to a prolonged light regime (low or high intensity, or intermittent light) modifies the amount of pigments involved in the xanthophyll cycle, leading to a modulation of the high light response via the kinetics and amplitude of NPQ (Dimier et al., 2009b; Gundermann & Büchel, 2008; Lavaud et al., 2003; van de Poll et al., 2007).

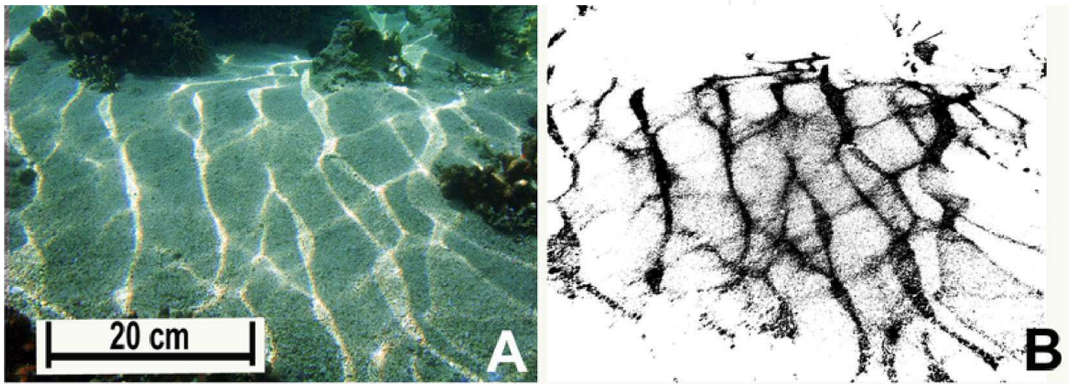


Fig. 7. Flicker light: (A) on a sandy bottom substrate; (B) digital processing of the original photo to enhance the high light regimes. Photos were taken at Bise, Okinawa, Japan (Yamasaki & Nakamura, 2008).

9. Conclusions

1. Phytoplankton evolution results in a taxonomic linkage between microalgae groups and xanthophyll-cycle development. In the ancestral cyanobacteria and the red algae, no xanthophyll-cycle mechanism is found. In the chlorophyta and land plants, the violaxanthin cycle evolved, whereas in the chromophyta, the diadinoxanthin variant has become the rule.
2. In two of the phototrophic phytoplankton groups (cyanobacteria and red algae), the composition of the antennae does not support a xanthophyll-cycle mechanism. In these taxa, there is another type of photoprotective process, a quenching mechanism that is supported by the xanthophylls and a pH gradient.

10. Acknowledgments

This study was supported by NATO SfP 981883. We thank Sharon Victor for the English editing.

11. References

Adams, W.W., Demmig-Adams, B., Logan, B.A., Barker, D.H. & Osmond, C.B. (1999). Rapid changes in xanthophyll cycle-dependent energy dissipation and photosystem II

efficiency in two vines, Stephania japonica and Smilax australis, growing in the understory of an open Eucalyptus forest. *Plant Cell and Environment,* Vol.22, No.2, pp. 125-136, ISSN 0140-7791

Adams, W.W. III, Zarter, C.R., Mueh, K.E., Amiard, V. & Demmig-Adams, B. (2006). Energy dissipation and photoinhibition: a continuum of photoprotection. In: *Photoprotection, photoinhibition, gene regulation, and environment. Advances in photosynthesis and respiration*,Vol. 21, W.W. Demmig-Adams III & A.K. Mattoo (Eds.), 49-64, Springer, Dordrecht, The Netherlands

Adir, N., Zer, H., Shochat, S. & Ohad, I. (2003). Photoinhibition - a historical perspective. *Photosynthesis Research*, Vol.76, No.1-3, pp. 343-370, ISSN 0166-8595

Anderson, J.M., Chow, W.S. & Park, Y.I. (1995). The grand design of photosynthesis: Acclimation of the photosynthetic apparatus to environmental cues. *Photosynthesis Research*, Vol.46, No.1-2, pp. 129-139, ISSN 0166-8595

Armbrust, E.V. (2009). The life of diatoms in the world's oceans. *Nature*, Vol.459, No.7244, pp. 185-192, ISSN 0028-0836

Arsalane, W., Rousseau, B. & Duval, J.C. (1994). Influence of the pool size of the xanthophyll cycle on the effects of light stress in a diatom - Competition between photoprotection and photoinhibition. *Photochemistry and Photobiology*, Vol.60, No.3, pp. 237-243, ISSN 0031-8655

Bailey, S. & Grossman, A. (2008). Photoprotection in cyanobacteria: Regulation of light harvesting. *Photochemistry and Photobiology*, Vol.84, No.6, pp. 1410-1420, ISSN 0031-8655

Baroli, I. and Melis, A. (1996). Photoinhibition and repair in *Dunaliella salina* acclimated to different growth irradiances. *Planta*, Vol.198, No.4, pp. 640-646, ISSN 0032-0935

Bassi, R. & Caffarri, S. (2000). LHC proteins and the regulation of photosynthetic light harvesting function by xanthophylls. *Photosynthesis Research*, Vol.64, No.2-3, pp. 243-256, ISSN 0166-8595

Berger, R., Liaaen-Jensen, S., McAlister, V. & Guillard, R.R.L. (1977). Carotenoids of the Prymneiophyceae (Haptophyceae). *Biochemical Systematicas and Ecology*, Vol.5, pp. 71-75

Bhattacharya, D. & Medlin ,L. (1995). The phylogeny of plastids - a review based on comparisons of small-subunit ribosomal-RNA coding regions. *Journal of Phycology*, Vol.31, No.4, pp. 489-498, ISSN 0022-3646

Bhaya, D. & Grossman, A.R. (1993). Characterization of gene clusters encoding the fucoxanthin chlorophyll proteins of the diatom *Phaeodactylum tricornutum*. *Nucleic Acids Research*, Vol.21, No.19, pp. 4458-4466, ISSN 0305-1048

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology*, Vol.85, No.7, pp. 1771-1789, ISSN 0012-9658

Casper-Lindley, C. & Bjorkman, O. (1998). Fluorescence quenching in four unicellular algae with different light-harvesting and xanthophyll-cycle pigments. *Photosynthesis Research*, Vol.56, No.3, pp. 277-289, ISSN 0166-8595

Delwiche, C.F. (1999). Tracing the thread of plastid diversity through the tapestry of life. *American Naturalist*, Vol.154, pp. S164-S177, ISSN 0003-0147

Demmig-Adams, B. (1998). Survey of thermal energy dissipation and pigment composition in sun and shade leaves. *Plant and Cell Physiology*, Vol.39, No.5, pp. 474-482, ISSN 0032-0781

Demmig-Adams, B. (2003). Linking the xanthophyll cycle with thermal energy dissipation. *Photosynthesis Research*, Vol.76, No.1-3, pp. 73-80, ISSN 0166-8595

Demmig-Adams, B. & Adams, W.W. (1993). The xanthophyll cycle, protein turnover, and the high light tolerance of sun-acclimated leaves. *Plant Physiology*, Vol.103, No.4, pp. 1413-1420, ISSN 0032-0889

Demmig-Adams, B. & Adams, W.W. (1996). The role of xanthophyll cycle carotenoids in the protection of photosynthesis. *Trends in Plant Science*, Vol.1, No.1, pp. 21-26, ISSN 1360-1385

Demmig-Adams, B. & Adams, W.W. (2006). Photoprotection in an ecological context: the remarkable complexity of thermal energy dissipation. *New Phytologist*, Vol.172, No.1, pp. 11-21, ISSN 0028-646X

Demmig, B., Winter, K., Kruger, A. & Czygan, F.C. (1988). Zeaxanthin and the heat dissipation of excess light energy in *Nerium oleander* exposed to a combination of high light and water stress. *Plant Physiology*, Vol.87, No.1, pp. 17-24, ISSN 0032-0889

Dimier, C., Corato, F., Saviello, G. & Brunet, C. (2007a). Photophysiological properties of the marine picoeukaryote Picochlorum RCC 237 (Trebouxiophyceae, Chlorophyta). *Journal of Phycology*, Vol.43, No.2, pp. 275-283, ISSN 0022-3646

Dimier, C., Corato, F., Tramontano, F. & Brunet, C. (2007b). Photoprotection and xanthophyll-cycle activity in three marine diatoms. *Journal of Phycology*, Vol.43, pp. 937-947, ISSN 0022-3646

Dimier, C., Brunet, C., Geider, R. & Raven, J. (2009a). Growth and photoregulation dynamics of the picoeukaryote Pelagomonas calceolata in fluctuating light. *Limnology and Oceanography*, Vol.54, No.3, pp. 823-836, ISSN 0024-3590

Dimier, C., Saviello, G. & Tramontano, F. (2009b). Comparative ecophysiology of the xanthophyll cycle in six marine phytoplanktonic species. *Protist*, Vol.160, pp. 397-411

Dubinsky, Z. (1980). Light utilization efficiency in natural phytoplankton communities. In: *Primary Productivity in the Sea*, P.G. Falkowski (Ed.), 83-97, Plenum Press, New York

Dubinsky, Z. (1992). The optical and functional cross-sections of phytoplankton photosynthesis. In: *Primary Productivity and Biogeochemical Cycles in the Sea*, P.G. Falkowski & A.D. Woodhead (Eds.), 31-45, Plenum Press, New York

Dubinsky, Z. & Schofield, O. (2010). From the light to the darkness: thriving at the light extremes in the oceans. *Hydrobiologia* ,Vol.639, No.1, pp. 153-171, ISSN 0018-8158

Durnford, D.G., Price, J.A., McKim, S.M. & Sarchfield, M.L. (2003). Light-harvesting complex gene expression is controlled by both transcriptional and post-transcriptional mechanisms during photoacclimation in Chlamydomonas reinhardtii. *Physiologia Plantarum*, Vol.118, No.2, pp. 193-205, ISSN 0031-9317

Emerson, R. & Arnold, W. (1932). The photochemical reaction in photosynthesis. *Journal of General Physiology*, Vol.16, pp. 191-205

Falkowski, P.G. & LaRoche, J. (1991). Acclimation to spectral irradiance in algae. *Journal of Phycology*, Vol.27, pp. 8-14

Falkowski, P.G. & Raven, J.A., (1997). *Aquatic Photosynthesis.* Blackwell Science Inc., Malden, USA.

Falkowski, P.G. & Chen, Y.B. (2003). Photoacclimation of light harvesting systems in eukaryotic algae. In: *Light-harvesting Antennas in Photosynthesis*, B.R. Green and W.W. Parson (Eds.), Kluwer Academic Publishers, Dordrecht, Boston

Falkowski, P.G., Katz, M., van Schootenbrugge, B., Schofield, O. & Knoll, A.H. (2004a). Why is the land green and the ocean red? In: *Coccolithophores: From Molecular Processes to Global Impact*, H.R. Thierstein & J. Young (Eds.), Springer-Verlag, Berlin

Falkowski, P.G., Katz, M.E., Knoll, A.H., Quigg, A., Raven, J.A., Schofield, O. & Taylor, F.J. (2004b). The evolution of modern eukaryotic phytoplankton. *Science*, Vol.305, pp. 354-360

Flöder, S., Urabe, J. & Kawabata, Z. (2002). The influence of fluctuating light intensities on species composition and diversity of natural phytoplankton communities. *Oecologia*, Vol.133, No.3, pp. 395-401, ISSN 0029-8549

Frank, H.A. & Cogdell, R.J. (1996). Carotenoids in photosynthesis. *Photochemistry and Photobiology*, Vol.63, No.3, pp. 257-264, ISSN 0031-8655

Goss, R. & Jakob, T. (2010). Regulation and function of xanthophyll cycle-dependent photoprotection in algae. *Photosynthesis Research*, Vol.106, No.1-2, pp. 103-122, ISSN 0166-8595

Grobbelaar, J.U. (2006). Photosynthetic response and acclimation of microalgae to light fluctuations In: *Algal Cultures Analogues of Blooms and Applications*, D.V. Subba Rao (Ed.), 671-683, Science Publishers, Enfield (NH), USA, Plymouth, UK

Gundermann, K. & Büchel, C. (2008). The fluorescence yield of the trimeric fucoxanthin-chlorophyll-protein FCPa in the diatom Cyclotella meneghiniana is dependent on the amount of bound diatoxanthin. *Photosynthesis Research*, Vol.95, No.2-3, pp. 229-235, ISSN 0166-8595

Harris, G.P. (1986). *Phytoplankton Ecology: Structure, Function and Fluctuation*. Chapman & Hall, London.

Horton, P. and Ruban, A.V. (1994). The role of LHCII in energy quenching. In: *Photoinhibition of photosynthesis - from molecular mechanisms to the field (monograph)*, N.R. Baker & J.R.G. Bowyer (Eds.), 111-128, Bios Scientific Publishers, Oxford

Horton, P., Ruban, A.V. & Walters, R.G. (1996). Regulation of light harvesting in green plants. *Annual Review of Plant Physiology and Plant Molecular Biology*, Vol.47, pp. 655-684, ISSN 0066-4294

Huisman, J., Johansson, A.M., Folmer, E.O. & Weissing, F.J. (2001). Towards a solution of the plankton paradox: the importance of physiology and life history. *Ecology Letters*, Vol.4, No.5, pp. 408-411, ISSN 1461-023X

Jeffrey, S.W., Mantoura, R.F.C. & Wright, S.W. (1997). *Phytoplankton Pigments in Oceanography*. UNESCO Publishing, Paris

Johansen, J.E., Svec, W.A., Liaaenje. S & Haxo, F.T. (1974). Algal carotenoids. 10. Carotenoids of Dinophyceae. Phytochemistry, Vol.13, No.10, pp. 2261-2271, ISSN 0031-9422

Kanervo, E., Suorsa, M. & Aro, E.M. (2005). Functional flexibility and acclimation of the thylakoid membrane. *Photochemical & Photobiological Sciences*, Vol.4, No.12, pp. 1072-1080, ISSN 1474-905X

Key, T., McCarthy, A., Campbell, D.A., Six, C., Roy, S. & Finkel, Z.V. (2010). Cell size trade-offs govern light exploitation strategies in marine phytoplankton. *Environmental Microbiology*, Vol.12, No.1, pp. 95-104, ISSN 1462-2912

Kirilovsky, P. (2007). Photoprotection in cyanobacteria, the orange carotenoid protein (OCP)-related non-photochemical quenching mechanism. *Photosynthesis Research*, Vol.93, pp. 7-16

Kirk, J.T.O. (1994). *Light and Photosynthesis in Aquatic Ecosystems*, 2nd ed. Cambridge University Press, London, New York

Kooistra, W.H.C.F., Gersonde, R., Medlin, L.K. & Mann, D.G. (2007). The origin and evolution of the diatoms: their adaptation to a planktonic existence. In: *Evolution of planktonic photoautotrophs*, P.G. Falkowski & A.H. Knoll (Eds.), 207-249, Academic Press, Inc., Burlington, MA

Krause, G.H. & Weis, E. (1991). Chlorophyll fluorescence and photosynthesis - the basics. *Annual Review of Plant Physiology and Plant Molecular Biology*, Vol.42, pp. 313-349

Laurion, I. & Roy, S. (2009). Growth and photoprotection in three dinoflagellates (including two strains of Alexandrium tamarense) and one diatom exposed to four weeks of natural and enhanced ultraviolet-B radiation. *Journal of Phycology*, Vol.45, No.1, pp. 16-33, ISSN 0022-3646

Lavaud, J. (2007). Fast regulation of photosynthesis in diatoms: mechanisms, evolution and ecophysiology. *Plant Science and Biotechnology*, Vol.1, pp. 267-287

Lavaud, J., Rousseau, B., van Gorkom, H.J. & Etienne, A.L. (2002). Influence of the diadinoxanthin pool size on photoprotection in the marine planktonic diatom *Phaeodactylum tricornutum*. *Plant Physiology*, Vol.129, No.3, pp. 1398-1406, ISSN 0032-0889

Lavaud, J., Rousseau, B. & Etienne, A.L. (2003). Enrichment of the light-harvesting complex in diadinoxanthin and implications for the nonphotochemical fluorescence quenching in diatoms. *Biochemistry*, Vol.42, pp. 5802-5808

Lavaud, J., Rousseau, B. & Etienne, A.L. (2004). General features of photoprotection by energy dissipation in planktonic diatoms (Bacillariophyceae). *Journal of Phycology*, Vol.40, No.1, pp. 130-137, ISSN 0022-3646

Lavaud, J., Strzepek, R.F. & Kroth, P.G. (2007). Photoprotection capacity differs among diatoms: Possible consequences on the spatial distribution of diatoms related to fluctuations in the underwater light climate. *Limnology and Oceanography*, Vol.52, No.3, pp. 1188-1194, ISSN 0024-3590

Leakey, A.D.B., Press, M.C., Scholes, J.D. & Watling, J.R. (2002). Relative enhancement of photosynthesis and growth at elevated CO_2 is greater under sunflecks than uniform irradiance in a tropical rain forest tree seedling. *Plant Cell and Environment*, Vol.25, No.12, pp. 1701-1714, ISSN 0140-7791

Leakey, A.D.B., Scholes, J.D. & Press, M.C. (2005). Physiological and ecological significance of sunflecks for dipterocarp seedlings. *Journal of Experimental Botany*, Vol.56, No.411, pp. 469-482, ISSN 0022-0957

Ledford, H.K. & Niyogi, K.K. (2005). Singlet oxygen and photo-oxidative stress management in plants and algae. *Plant Cell and Environment*, Vol.28, No.8, pp. 1037-1045, ISSN 0140-7791

Li, X.P., Bjorkman, O., Shih, C., Grossman, A.R., Rosenquist, M., Jansson, S. & Niyogi, K.K. (2000). A pigment-binding protein essential for regulation of photosynthetic light harvesting. *Nature*, Vol.403, No.6768, pp. 391-395, ISSN 0028-0836

Li, X.P., Gilmore, A.M. & Niyogi, K.K. (2002). Molecular and global time-resolved analysis of a psbS gene dosage effect on pH- and xanthophyll cycle-dependent nonphotochemical quenching in photosystem II. *Journal of Biological Chemistry*, Vol.277, No.37, pp. 33590-33597, ISSN 0021-9258

Li, Z.R., Wakao, S., Fischer, B.B. & Niyogi, K.K. (2009). Sensing and responding to excess light. *Annual Review of Plant Biology*, Vol.60, pp. 239-260, ISSN 1543-5008

Lichtenthaler, H.K., Burkart, S., Schindler, C. & Stober, F. (1992). Changes in photosynthetic pigments and *in-vivo* chlorophyll fluorescence parameters under photoinhibitory growth conditions *Photosynthetica*, Vol.27, No.3, pp. 343-353, ISSN 0300-3604

Liess, A., Lange, K., Schulz, F., Piggott, J.J., Matthaei, C.D. & Townsend, C.R. (2009). Light, nutrients and grazing interact to determine diatom species richness via changes to productivity, nutrient state and grazer activity. *Journal of Ecology*, Vol.97, No.2, pp. 326-336, ISSN 0022-0477

Litchman, E. (2000). Growth rates of phytoplankton under fluctuating light. *Freshwater Biology*, Vol.44, No.2, pp. 223-235, ISSN 0046-5070

Litchman, E. & Klausmeier, C.A. (2001). Competition of phytoplankton under fluctuating light. *American Naturalist*, Vol.157, No.2, pp. 170-187, ISSN 0003-0147

Litchman, E. & Klausmeier, C.A. (2008). Trait-based community ecology of phytoplankton. *Annual Review of Ecology Evolution and Systematics*, Vol.39 , pp. 615-639, ISSN 1543-592X

Lohr, M. & Wilhelm, C. (1999). Algae displaying the diadinoxanthin cycle also possess the violaxanthin cycle. *Proceedings of the National Academy of Sciences of the United States of America*, Vol.96, No.15, pp. 8784-8789, ISSN 0027-8424

Lohr, M. & Wilhelm, C. (2001). Xanthophyll synthesis in diatoms: quantification of putative intermediates and comparison of pigment conversion kinetics with rate constants derived from a model. *Planta*, Vol.212, No.3, pp. 382-391, ISSN 0032-0935-

Long, S.P., Humphries, S. & Falkowski, P.G. (1994). Photoinhibition of photosynthesis in nature. *Annual Review of Plant Physiology and Plant Molecular Biology*, Vol.45, pp. 633-662

Lu, C. & Vonshak, A. (1999). Photoinhibition in outdoor *Spirulina platensis* cultures assessed by polyphasic chlorophyll fluorescence transients. *Journal of Applied Phycology*, Vol.11, No.4, pp.355-359, ISSN 0921-8971

MacIntyre, H.L., Kana, T.M. & Geider, J.R. (2000). The effect of water motion on the short-term rates of photosynthesis by marine phytoplankton. *Trends in Plant Science*, Vol.5, pp. 12-17

Masojidek, J., Torzillo, G., Koblizek, M., Kopecky, J., Bernardini, P., Sacchi, A. & Komenda, J. (1999). Photoadaptation of two members of the Chlorophyta (Scenedesmus and Chlorella) in laboratory and outdoor cultures: changes in chlorophyll fluorescence quenching and the xanthophyll cycle. *Planta*, Vol.209, pp. 126-135

Matsubara, S., Gilmore, A.M., Ball, M.C., Anderson, J.M. & Osmond, C.B. (2002). Sustained downregulation of photosystem II in mistletoes during winter depression of photosynthesis. F*unctional Plant Biology*, Vol.29, No.10, pp. 1157-1169, ISSN 1445-4408

Meyer, A.A., Tackx, M. & Daro, N. (2000). Xanthophyll cycling in *Phaeocystis globosa* and *Thalassiosira* sp.: a possible mechanism for species succession. *Journal of Sea Research*, Vol.43, No.3-4, pp. 373-384, ISSN 1385-1101

Mitrovic, S.M., Howden, C.G., Bowling, L.C. & Buckney, R.T. (2003). Unusual allometry between in situ growth of freshwater phytoplankton under static and fluctuating light environments: possible implications for dominance. *Journal of Plankton Research*, Vol.25, No.5, pp. 517-526, ISSN 0142-7873

Müller, P., Li, X.P. & Niyogi, K.K. (2001). Non-photochemical quenching. A response to excess light energy. *Plant Physiology*, Vol.125, No.4, pp.1558-1566, ISSN 0032-0889

Mullineaux, P.M. & Rausch, T. (2005). Glutathione, photosynthesis and the redox regulation of stress-responsive gene expression. *Photosynthesis Research*, Vol.86, No.3, pp. 459-474, ISSN 0166-8595

Nield, J., Orlova, E.V., Morris, E. P., Gowen, B., van Heel, M. & Barber, J. (2000). 3D map of the plant photosystem II supercomplex obtained by cryoelectron microscopy and single particle analysis. *Nature Structural Biology*, Vol.7, No.1, pp. 44-47, ISSN 1072-8368

Noctor, G. & Foyer, C.H. (1998). Ascorbate and glutathione: Keeping active oxygen under control. *Annual Review of Plant Physiology and Plant Molecular Biology*, Vol.49, pp. 249-279, ISSN 1040-2519

Owens, T.G. (1986). Light-harvesting function in the diatom *Phaeodactylum tricornutum*. 2. Distribution of excitation-energy between the photosystems. *Plant Physiology*, Vol.80, No.3, pp. 739-746, ISSN 0032-0889

Owens, T.G. (1994). In vivo chlorophyll fluorescence as a probe of photosynthetic physiology. In: *Plant Responses to the Gaseous Environment*, R.G. Alscher & A.R. Wellburn (Eds.), 195-217, Chapman & Hall, London

Palmer, J.D. (2003). The symbiotic birth and spread of plastids: How many times and whodunit? *Journal of Phycology*, Vol.39, No.1, pp. 4-11, ISSN 0022-3646

Peers, G., Truong, T.B., Ostendorf, E., Busch, A., Elrad, D., Grossman, A.R., Hippler, M. & Niyogi, K.K. (2009). An ancient light-harvesting protein is critical for the regulation of algal photosynthesis. *Nature*, Vol.462, No.7272, pp. 518-U215, ISSN 0028-0836

Pyszniak, A.M. & Gibbs, S.P. (1992). Immunocytochemical localization of photosystem-I and the fucoxanthin-chlorophyll-a/c light-harvesting complex in the diatom *Phaeodactylum tricornutum*. *Protoplasma*, Vol.166, No.3-4, pp. 208-217, ISSN 0033-183X

Raven, J.A. & Kübler, J.E. (2002). New light on the scaling of metabolic rate with the size of algae. *Journal of Phycology*, Vol.38, pp. 11-16

Raven, J.A. & Beardall, J. (2003). CO_2 acquisition mechanisms in algae: Carbon dioxide diffusion and carbon dioxide concentrating mechanisms. In: *Photosynthesis in the algae*, A. Larkum, J.A. Raven & S. Douglas (Eds.), 225-244, Kluwer

Raven, J.A. & Geider, J.R. (2003). Adaptation, acclimation and regulation in algal photosynthesis. In: *Photosynthesis in Algae*, W.D. Larkum, S.E. Douglas & J.A. Raven (Eds.), 385-412, Kluweer Academic Publishers, Dordrecht, The Netherlands

Renstrom, B., Borch, G., Skulberg, O.M. & Liaaenjensen, S. (1981). Natural occurrence of enantiometric and meso-astaxanthin. 3. Optical purity of (3s,3's)-astaxanthin from *Haematococcus pluvialis*. *Phytochemistry*, Vol.20, No.11, pp. 2561-2564, ISSN 0031-9422

Ruban, A.V. & Johnson, M.P. (2009). Dynamics of higher plant photosystem cross-section associated with state transitions. *Photosynthesis Research*, Vol.99, No.3, pp. 173-183, ISSN 0166-8595

Schindler, C. & Lichtenthaler, H.K. (1994). Is there a correlation between light-induced zeaxanthin accumulation and quenching of variable chlorophyll a fluorescence. *Plant Physiology and Biochemistry*, Vol.32, No.6, pp. 813-823, ISSN 0981-9428

Schindler, C. & Lichtenthaler, H.K. (1996). Photosynthetic CO_2 assimilation, chlorophyll fluorescence and zeaxanthin accumulation in field grown maple trees in the course of a sunny and a cloudy day. *Journal of Plant Physiology*, Vol.148, No.3-4, pp. 399-412, ISSN 0176-1617

Serodio, J., Cruz, S ,.Vieira, S. & Brotas, V. (2005). Non-photochemical quenching of chlorophyll fluorescence and operation of the xanthophyll cycle in estuarine microphytobenthos. *Journal of Experimental Marine Biology and Ecology*, Vol.326, No.2, pp. 157-169, ISSN 0022-0981

Six, C., Finkel, Z.V., Irwin, A.J. & Campbell, D.A. (2007). Light variability illuminates niche-partitioning among marine picocyanobacteria. *PLoS One*, Vol.2, No.12, pp. e1341, ISSN 1932-6203

Six, C., Finkel, Z.V., Rodriguez, F., Marie, D., Partensky, F. & Campbell, D.A. (2008). Contrasting photoacclimation costs in ecotypes of the marine eukaryotic picoplankter Ostreococcus. *Limnology and Oceanography*, Vol.53, No.1, pp. 255-265, ISSN 0024-3590

Six, C., Sherrard, R., Lionard, M., Roy, S. & Campbell, D.A. (2009). Photosystem II and pigment dynamics among ecotypes of the Green Alga Ostreococcus. *Plant Physiology*, Vol.151, No.1, pp. 379-390, ISSN 0032-0889

Staehr, P.A., Henriksen, P. & Markager, S. (2002). Photoacclimation of four marine phytoplankton species to irradiance and nutrient availability. *Marine Ecology Progress Series*, Vol.238, pp. 47-59

Stransky, H. & Hager, A. (1970). Carotenoid pattern and occurrence of light induced xanthophyll cycle in various classes of algae. 2. Xanthophyceae. *Archiv Fur Mikrobiologie*, Vol.71, No.2, pp. 164-190, ISSN 0003-9276

Timmermans, K.R., van der Wagt, B., Veldhuis, M.J.W., Maatman, A. & de Baar, H.J.W. (2005). Physiological responses of three species of marine pico-phytoplankton to ammonium, phosphate, iron and light limitation. *Journal of Sea Research*, Vol.53, pp. 109-120

Van de Poll, W.H., Van Leeuwe, M.A., Roggeveld, J. & Buma, A.G.J. (2005). Nutrient limitation and high irradiance acclimation reduce PAR and UV-induced viability loss in the Antarctic diatom Chaetoceros brevis (Bacillariophyceae). *Journal of Phycology*, Vol.41, pp. 840-850

van de Poll, W.H., Visser, R.J.W. & Buma, A.G.J. (2007). Acclimation to a dynamic irradiance regime changes excessive irradiance sensitivity of *Emiliania huxleyi* and *Thalassiosira weissflogii*. *Limnology and Oceanography*, Vol.52, No.4, pp. 1430-1438, ISSN 0024-3590

van de Poll, W.H. & Buma, A.G.J. (2009). Does ultraviolet radiation affect the xanthophyll cycle in marine phytoplankton? *Photochemical & Photobiological Sciences*, Vol.8, No.9, pp. 1295-1301, ISSN 1474-905X

van de Poll, W.H., Buma, A.G.J., Visser, R.J.W., Janknegt, P.J., Villafane, V.E. & Helbling, E.W. (2010). Xanthophyll cycle activity and photosynthesis of *Dunaliella tertiolecta* (Chlorophyceae) and *Thalassiosira weissflogii* (Bacillariophyceae) during fluctuating solar radiation. *Phycologia*, Vol.49, No.3, pp. 249-259, ISSN 0031-8884

van Leeuwe, M.A., van Sikkelerus, B., Gieskes, W.W.C. & Stefels, J. (2005). Taxon-specific differences in photoacclimation to fluctuating irradiance in an Antarctic diatom and a green flagellate. *Marine Ecology-Progress Series*, Vol.288, pp. 9-19, ISSN 0171-8630

van Leeuwe, M.A., Brotas, V., Consalvey, M., Forster, R.M., Gillespie, D., Jesus, B., Roggeveld, J. & Gieskes, W.W.C. (2008). Photoacclimation in microphytobenthos and the role of xanthophyll pigments. *European Journal of Phycology*, Vol.43, No.2, pp. 123-132, ISSN 0967-0262

Wagner, H., Jakob, T. & Wilhelm, C. (2006). Balancing the energy flow from captured light to biomass under fluctuating light conditions. *New Phytologist*, Vol.169, No.1, pp. 95-108, ISSN 0028-646X

Wilhelm, C., Büchel, C., Fisahn, J. Goss, R., Jakob, T., LaRoche, J., Lavaud, J., Lohr, M., Riebesell, U., Stehfest, K., Valentin, K. & Kroth, P.G. (2006). The regulation of carbon and nutrient assimilation in diatoms is significantly different from green algae. *Protist*, Vol.157, No.2, pp. 91-124, ISSN 1434-4610

Willemoes, M. & Monas, E. (1991). Relationship between growth irradiance and the xanthophyll cycle pool in the diatom *Nitzschia palea*. *Physiologia Plantarum*, Vol.83, No.3, pp. 449-456, ISSN 0031-9317

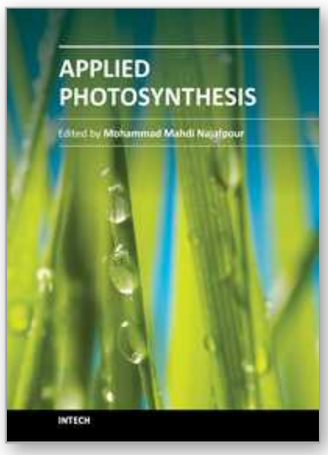
Wilson, A., Ajlani, G., Verbavatz, J.M., Vass, I., Kerfeld, C.A. & Kirilovsky, D. (2006). A soluble carotenoid protein involved in phycobilisome-related energy dissipation in cyanobacteria. *Plant Cell*, Vol.18, No.4, pp. 992-1007, ISSN 1040-4651

Withers, N.W., Fiksdahl, A., Tuttle, R.C. & Liaaenjensen, S. (1981). Carotenoids of the Chrysophyceae. *Comparative Biochemistry and Physiology B-Biochemistry & Molecular Biology*, Vol.68, No.2, pp. 345-349, ISSN 0305-0491

Yamamoto, H.Y. (1979). Biochemistry of the violaxanthin cycle in higher plants. *Pure and Applied Chemistry*, Vol.51, pp. 639-648

Yamamoto, H.Y., Nakayama, T.O.M. & Chichester, C.O. (1962). Studies on the light and dark interconversion of leaf xanthophylls. *Archives of Biochemistry*, Vol.97, pp. 168-173

Yamasaki, H. & Nakamura, T. (2008). Flicker light effects on photosynthesis of symbiotic algae in the reef-building coral *Acropora digitifera* (Cnidaria: Anthozoa: Scleractinia). *Pacific Science*, Vol.62, No.3, pp. 341-350, ISSN 0030-8870



Applied Photosynthesis

Edited by Dr Mohammad Najafpour

ISBN 978-953-51-0061-4
Hard cover, 422 pages
Publisher InTech
Published online 02, March, 2012
Published in print edition March, 2012

Photosynthesis is one of the most important reactions on Earth, and it is a scientific field that is intrinsically interdisciplinary, with many research groups examining it. This book is aimed at providing applied aspects of photosynthesis. Different research groups have collected their valuable results from the study of this interesting process. In this book, there are two sections: Fundamental and Applied aspects. All sections have been written by experts in their fields. The book chapters present different and new subjects, from photosynthetic inhibitors, to interaction between flowering initiation and photosynthesis.

How to reference

In order to correctly reference this scholarly work, feel free to copy and paste the following:

Miriam Zigman, Zvy Dubinsky and David Iluz (2012). The Xanthophyll Cycle in Aquatic Phototrophs and Its Role in the Mitigation of Photoinhibition and Photodynamic Damage, Applied Photosynthesis, Dr Mohammad Najafpour (Ed.), ISBN: 978-953-51-0061-4, InTech, Available from: http://www.intechopen.com/books/applied-photosynthesis/the-xanthophyll-cycle-in-aquatic-phototrophs-and-its-role-in-the-mitigation-of-photoinhibition-and-p

INTECH
open science | open minds

InTech Europe
University Campus STeP Ri
Slavka Krautzeka 83/A
51000 Rijeka, Croatia
Phone: +385 (51) 770 447
Fax: +385 (51) 686 166
www.intechopen.com

InTech China
Unit 405, Office Block, Hotel Equatorial Shanghai
No.65, Yan An Road (West), Shanghai, 200040, China
中国上海市延安西路65号上海国际贵都大饭店办公楼405单元
Phone: +86-21-62489820
Fax: +86-21-62489821

IntechOpen