

Chapter 7

Photoinhibition and UV Response in the Aquatic Environment

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Summary

This chapter summarizes the effects of excessive solar radiation on aquatic primary producers with an emphasis on macroalgae. The introductory paragraphs deal with the aquatic environment and the specific implications for sessile algae and their vertical distribution on the coast. Macroalgae are exposed to dramatically changing irradiances and complicated light patterns governed by the diel solar cycle, the tidal rhythm, and changing cloud cover. The following sections concentrate on the phenomenon of photoinhibition with specific reference to in situ measurements with as little disturbance of the specimens on site as possible. Despite its low percentage contribution in solar radiation, short wavelength ultraviolet is a major component in photoinhibition of algae in their natural habitat. Fast kinetics of fluorescence parameters demonstrates the rapid adaptation of the organisms to their changing photic environment. Early developmental stages are more prone to inhibitory effects of excessive solar radiation. Pigment bleaching and resynthesis are important consequences of solar exposure. Macroalgae have developed several strategies for protection against excessive light stress. UV-absorbing substances, which they share with cyanobacteria and phytoplankton, limit the amount of UV photons reaching the photosynthetic apparatus and the nucleus. They include carotenoids, mycosporine-like amino acids, as well as several chemically not yet identified substances. In addition, the fast turnover of the D1 protein in photosystem II allows rapid recovery from photoinhibition.

I. Introduction: Life in the Aquatic Environment

Macroalgae and seagrasses are major biomass producers in marine ecosystems inhabiting coastal regions and

continental shelves (Häder et al., 2003a). They are ecologically important for providing the basis of the intricate food web in coastal habitats and giving shelter to adult and larval stages of fish, crustaceans, mollusks, and other animals. In addition, they are economically

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important and are being exploited for food production, as fertilizers, and as raw materials for gelling substances such as agar and carrageenan (Jensen, 1995; Lüning, 1990).

Incident solar radiation at the surface and the depth of penetration into the water column are the decisive factors controlling photodamage to aquatic photosynthetic organisms. Aquatic ecosystems differ substantially in their transparency and thus the depth of solar penetration (Laurion et al., 2000). Especially in eutrophic freshwater systems and coastal areas of the oceans, absorbing and scattering substances limit the transparency of the water, while solar radiation penetrates to greater depths in clear oceanic waters (Conde et al., 2000a; Kuhn et al., 1999). In addition, there is a pronounced seasonal variability in the transparency (Dring et al., 2001a; Kuwahara et al., 2000). Inorganic particulate substances, dissolved and particulate organic carbon (DOC and POC), humic substances, and suspended organisms are the main absorbers of (especially short wavelength) solar radiation (Arts et al., 2000).

Phytoplankton and other pelagic organisms are free to move in the water column by active swimming or actively changing their buoyancy. E.g., several Dinophyceae have been found to undergo diel active vertical migrations of up to 30 m (Tyler et al., 1981; Yentsch et al., 1964). Diatoms and floating cyanobacteria, which do not have the capability of propelling themselves, resort to flotation by producing gas vacuoles (Walsby et al., 1992) or lipid droplets (Gosink et al., 1993). In open oceanic waters, vertical migration is superimposed by the action of waves and wind (Häder et al., 2003a). Therefore, the impact of solar radiation is modified by the depth and rate of the mixing layer (Huot et al., 2000).

In contrast to phytoplankton organisms, most marine macroalgae are confined to the coastal areas of the continental shelves. Also, while phytoplankton are motile in the water column (Häder, 1995), most macroalgae are sessile and therefore restricted to their growth site (Lüning, 1990). Macroalgae show a distinct pattern of vertical distribution in their habitat that is mainly controlled by light penetration (Dring et al., 1996; Hanelt et al., 1997; Larkum et al., 1993). The photoprotective

capabilities define the upper growth limit of a species. Some of these plants populate the supralittoral (coast above high water mark), where they are exposed only to the spray from the surf. Others inhabit the eulittoral (intertidal zone), which is characterized by the regular tidal change (Häder, 1997). Subtidal macroalgae are never exposed to air since they thrive below the tidal zone. The range in solar radiation can be substantial, from over 1000 W m^{-2} (total solar radiation) at the surface to less than 0.01% of this value, which penetrates to the understory of e.g. a kelp habitat (Markager et al., 1994).

The phenomenon of photoinhibition protects the photosynthetic apparatus by affecting photosystem II in such a way that excess absorbed energy is rendered harmless by thermal dissipation (Krause and Weis, 1991; Adams et al., this volume). This effect can be measured using pulse amplitude modulated (PAM) fluorescence. The ratio F_v/F_m (see below) is defined as the photosynthetic quantum yield. In a dark-adapted organism this is interpreted as the “optimal quantum yield” and in a light-exposed organism the “effective photosynthetic yield”. Note that this definition is in contrast to others in which the quantum yield describes the amount of oxygen released per photon or the amount of CO_2 fixed per absorbed photon. A decrease in the quantum yield is interpreted as a sign of photoinhibition (Hanelt, 1995b; see Osmond and Förster, this volume). After exposure of the plants to excessive light, several researchers found a strong degradation of the D1 protein in the reaction center of photosystem II (Critchley and Russell, 1994; Hanelt, 1998; see Edelman and Mattoo, this volume). This process is defined as chronic photoinhibition. However, D1 degradation was not determined in all experiments with aquatic photosynthetic organisms. Since the D1 levels can also be adjusted by acclimation to the prevailing light conditions (e.g. sun vs. shade), the determination of capacity is the only clear criterion for the assessment of this phenomenon.

Many algae (but also higher plants) show a typical midday depression in their photosynthetic yield between noon and the early afternoon hours. This diurnal pattern is attributed mainly to dynamic photoinhibition (Hanelt et al., 1994a, 1994b; Hanelt, 1998; Henley et al., 1992). This process is believed to be due to the xanthophyll cycle (see Yamamoto, this volume), involved in the regulation of photosynthetic quantum yield by reversibly increasing thermal dissipation of excess energy (Demmig-Adams and Adams, 1992). In marine algae this pattern is complicated by the tidal rhythm: the highest irradiance stress occurs when low tides coincide with high solar angles (Häder et al.,

Abbreviations: DOC – dissolved organic carbon; MAA – mycosporine-like amino acid; PAM – pulse amplitude modulated (fluorescence); PAR – photosynthetically active radiation, 400 – 700 nm; POC – particulate organic carbon; PS II – Photosystem II; UV – ultraviolet radiation; UV-A – ultraviolet radiation in the wavelength range 315 – 400 nm; UV-B – ultraviolet radiation in the wavelength range 280 – 315 nm