

Chapter 1

Physiological and Photomorphogenic Effects of Light on Marine Macrophytes

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1.1 Introduction

The coastal zone of the marine habitat is exposed to considerable diurnal changes in solar radiation due to the position of the sun, clouding and, especially, the tides. Thus, these temporary changes in the costal environment can appear much stronger compared to terrestrial habitats. Whereas algae in air or the upper littoral zone are supplied with sufficient or even with an excess of radiation energy (Wilhelm and Selmar 2011), in deeper regions of the euphotic zone light is clearly limiting for seaweed growth. It is a reason why seaweeds generally need to grow on the continental shelf (epipelagic), down to a maximal depth where the light level is not lower as 0.05% or 0.001% of the surface irradiance in the tropics (Lüning 1990). Moreover, conditions in the coastal areas are quite different compared to the open ocean as in coastal zones generally an inflow of freshwater occurs which can be loaded with sediments. Penetration of solar radiation into the water body is largely determined by scattering and absorption of biological and inorganic material, with higher concentrations in coastal areas. Coastal waters show large temporal changes and regional differences in the concentration of dissolved and particulate matter influencing temporal penetration of solar radiation. This is the basis on which Jerlov (1976) classified marine waters into nine types of coastal and five types of oceanic waters in dependence on the respective transmittance characteristics.

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1.2 Photosynthesis Under Limiting Light Conditions

Sublittoral species growing in deep water must be adapted to chronic low light. For planktonic algae, generally a lower depth limit of 1% of the surface irradiance is regarded as defining the euphotic zone (Steemann Nielsen 1975), and this limit can be even 0.1% for picoplankton in oceanic waters. Seaweeds of the order *Laminariales* reach their lower growth limit at about 0.6–1.2% of surface light, whereas for some deep growing rhodophytes a minimum of 0.001–0.05% was determined (Lüning 1981, 1990). The photosynthetic rate of different *Laminaria* species exceeds the respiratory rate and thus the compensation point (E_c) at about 5–8 $\mu\text{mol m}^{-2} \text{s}^{-1}$, whereas in deep water red algae an irradiation of about 2 $\mu\text{mol m}^{-2} \text{s}^{-1}$ is already sufficient (Lüning 1981). Deepest crustose macroalgae seem to survive at an absolute light minimum of about 0.01 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Littler et al. 1986). These red crustose corallines show a large light absorptance and employ light-harvesting pigments with a high energy-cost in their production per unit light absorption rate in a given underwater spectrum (Raven and Geider 2003). Raven et al. (2000) outlined that it is difficult to explain growth of algae below 0.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ as there are energy-consuming reactions which use an increasing fraction of energy input when photon flux density decreases. Among these processes are redox back reactions of reaction center II, the leakage of H^+ through thylakoid membranes and the turnover of photosynthetic proteins. The first of the two processes limit the rate of linear electron transport and ADP phosphorylation, while the latter consumes ATP. Thus, it is not yet clear how crustose red algae can grow down to 274-m water depth where the average incident photon flux density for 12 h day^{-1} does not exceed 0.02 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Raven and Geider 2003).

Low light adapted species are typically characterized by high photosynthetic efficiencies and very low light compensation (E_c) and saturation points (E_k), ranging between 1 and 15 and between 14 and 52 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, respectively (Duntun and Jodwalis 1988; Wiencke et al. 1993; Weykam et al. 1996; Brouwer 1996; Eggert and Wiencke 2000).

For a certain time period net photosynthetic rates need to be high enough that seaweeds can promote growth, reproduction, as well as enough energy storage to cope with reduced light availability also during the winter season. Using data on daily changes of in situ irradiance and P–E derived parameters such as photosynthetic capacity (P_{max}), dark respiration, E_c and E_k , it is possible to calculate the daily periods over which carbon (C) assimilation exceeds C losses due to respiratory activity at different water depths. This metabolic C balance is regarded to determine the lower distribution limit of algae. Due to low E_k values, species from King George Island (Antarctica) are exposed during spring–summer for periods $\geq 12 \text{ h day}^{-1}$ at about 20 m depths to irradiances above saturation (period of saturation H_{sat}). Under these conditions, species such as *Palmaria decipiens* or *Desmarestia anceps* achieve positive C balances about 3 mg C $\text{g}^{-1} \text{FW d}^{-1}$. At 30-m depth daily light availability decreases to values between 7 and 9 h in summer, but C balance is still positive in 4 of 5 studied species (Gómez et al. 1997).

Only in the case of *Desmarestia anceps* from 30 m, a negative C balance was determined, indicating that at this depth the alga is at its lower distribution limit. In contrast, *P. decipiens*, *Gigartina skottsbergii* and *Trematocarpus antarcticus* and especially *Himantothallus grandifolius* are metabolically able to grow even in deeper waters which mean they have very modest requirements.

Under low light conditions higher pigment content within the thalli was observed as under strong light conditions (Ramus et al. 1976, 1977). The chance of photon absorption increases with increasing photosynthetic antenna size. Algae collected from or transplanted to different water depths show that the content of accessory pigments increases with lower light conditions in deep waters (Lüning 1990), e.g., in green algae the chlorophyll *a:b* ratio decreases demonstrating especially the increase of the antenna size of the photosynthetic apparatus (Yokohama and Misonou 1980). Whereas under low light conditions in deep water a larger antenna size increases the capacity of light absorption, a smaller antenna helps to avoid photoinhibition and photodamage due to over excitation under high light conditions close to the water surface or during emergence at low tide. Under low light conditions the plant invests more energy in the synthesis of light-collecting pigments and in strong light into the synthesis of photosynthetic enzymes, electron chain components as well as photo-protective structures and energy-dissipating mechanisms.

A study of Marquardt et al. (2010) showed that the saturation point E_k of all red algal species tested decreased with increasing depth concomitantly with the decreasing light availability. This may be due to the adjustment of the photosynthetic apparatus itself via changes of the reaction center ratio, changes of the relative size of the light-harvesting complex (LHC) or changes in the relative content of light protective pigments. Changes in thallus morphology are another possibility to achieve acclimation, e.g., change of thickness, branching, length, density of photosynthetic units (Küster et al. 2004). Johansson and Snoeijs (2002) demonstrated by measurements of photosynthesis versus irradiance curves (PE curves) that light-saturated net photosynthetic rates (P_{max}), respiratory rates in darkness (R_d) and the initial slope (α) were strongly related to algal morphology with generally higher values for thinner species. The compensation irradiance (E_c) and saturating irradiance (E_k) were strongly related to water depth with lower values at higher depth. One advantage of thin sheet-like and filamentous species is the capability of fast growth, which is coupled to high photosynthetic rates per unit biomass (Littler et al. 1983; Falkowski and Raven 1997), resembling rather the conditions in shallow waters. In several macroalgae the photosynthetic parameters P_{max} and α are highly dependent on thallus morphology with higher and faster O_2 production rates for thinner and filamentous species, and lower rates for coarser and thicker species when normalized to biomass (measured as dry weight) and opposite when normalized to algal surface area (Johansson and Snoeijs 2002). Similar relationships were described for five green-algal species by Arnold and Murray (1980) as well as by Littler (1980) for 45 species of marine macroalgae from field incubations. Thus, deeper growing algal species are expected to have lower E_c and

E_k as species growing higher up in the littoral. Also, within species E_c can decrease as an acclimation to ambient light with water depth (Gómez et al. 1997).

The ideal strategy for life in deep water is represented by crustose coralline algae. They are well protected against grazing and can survive in spite of slow growth. Their thallus structure represents a horizontal light receiver with none self-shading by a single cell layer which enhances light absorption (Lüning 1990). In dependence to the clarity of water and the annual sum of photosynthetic active radiation impinging at the water surface, the lower depth limit of crustose coralline algae shifts with lower latitude from several meters in cold temperate waters (e.g., 15 m on Helgoland) to several hundred meters in tropical waters (e.g., 268 m Bahamas, Lüning 1990). The annual sum of impinging irradiance must support at least the annual need of energy for maintenance metabolism, measured by the maintenance respiration rate, and guarantee a minimum of energy surplus for establishment of growth and reproduction. Compared to cold-temperate regions, Caribbean algae are able to survive in such extreme depths due to the higher solar irradiance, a 12 hour period of day light and the clear water conditions (Jerlov type I) enables these Caribbean algae to survive in such extreme depths. For algae with a more complex, even erected thallus and the presence of nonphotosynthetic tissue as typically found in kelps, the need for light energy increases and the algae have to grow in more shallow waters as the amount of respiration and self-shading areas increases.

An ideal marker for macroalgal depth distribution seems to be the respective stable carbon isotope composition. Rapid carbon assimilation under high photon fluence rates leads to ^{13}C enrichments, probably due to extracellular and/or intracellular isotopic disequilibria resulting in a trend toward more positive carbon isotope values with increasing photon fluence rates (Wiencke and Fischer 1990). The pattern of isotope composition of algae grown at different depth was found in sediment trap samples from the 2,000-m deep King George Basin off the Antarctic Peninsula. It also revealed a strong contribution of seaweeds to the total organic carbon pool of the deeper basin waters in spring and summer (Fischer and Wiencke 1992).

In conclusion, distribution of marine macrophytes to the lower light limit which accommodates biomass production depends mainly on the minimal energy input (Kirst and Wiencke 1995). This is dependent on the annual fluence or minimum light level occurring in the respective depth for the maintenance of existing plant material and a surplus for growth and reproduction. Due to seasonal changes, algae in low light habitats have to live for long periods each year at photon fluence rates which do not cover their energy needs. Then, the photosynthetic activity in high light periods of the year (e.g., summer season) needs to be high enough to produce sufficient resources to endure periods with light conditions generally below the compensation point (E_c). Light saturation of growth in seaweeds is fortunately lower than those for photosynthesis (Lüning 1990) so that algae can produce enough reserve materials under favorable light conditions. Changes in the water transparency may shift the lower light limit so that the algal distribution pattern could be affected by anthropogenic changes of the light transmittance of the water body.

1.3 Photosynthesis Under Excessive Light Conditions

In contrast to the conditions at the lower algal distribution limit, photosynthetic organisms close to the water surface are exposed to high irradiances which may even exceed their light energy requirement for photosynthetically provided anabolism. Generally, these photosynthetic organisms do not suffer from energy shortage, but instead they have to invest in proteins and cellular components which protect them from potential damage by excess supply of energy (Wilhelm and Selmar 2011). As consequence a reduction of photosynthetic activity, called photoinhibition, may occur (Powles 1984; Krause 1988; Krause and Weis 1991). As defined by Franklin et al. (2003) photoinhibition is a generic outcome of the failure of photoprotection to mitigate photoinactivation. This may result under high light conditions in which damage of reaction center proteins exceeds photorepair in the complex molecular structure of photosystem II (PSII). Photoacclimation is the adjustment in structure and function of the photosynthetic apparatus that avoid or rapidly repair damage and thus mitigate (chronic) photoinhibition. Photoprotection (also called dynamic photoinhibition) refers to processes that decrease excitation transfer to the reaction centers; these processes are mainly operative in the antenna complexes. Loss of PS II reaction center function is called photoinactivation (formerly called chronic photoinhibition), often accompanied by loss of reaction center protein D_1 , which can be repaired under dim light conditions. Under excessive light conditions a significant degradation of the reaction center protein (D_1) of PS II was found (Ohad et al. 1984; Mattoo et al. 1984). Nonfunctional photosynthetic centers are able to protect active centers against continuous damaging effects of excess absorbed light energy by harmless energy dissipation, mainly by heat dissipation (Guenther and Melis 1990; Öquist and Chow 1992; Critchley and Russell 1994). Photodamage occurs if the rate of the D_1 -protein damage exceeds the rate of its repair process, leading to a breakdown of the D_1 -protein pool (Aro et al. 1993). Photoprotection or dynamic photoinhibition is important for the regulation of quantum yield of photosynthesis, namely by the xanthophyll cycle in the chloroplasts of green and brown algae (Demmig-Adams and Adams 1992). Quantum yield of photosystem II (especially the *in vivo* fluorescence ratio F_v/F_m which represents photosynthetic efficiency after dark acclimation) is diminished reversibly by increasing thermal energy dissipation under strong light conditions. Carotenoids control this harmless dissipation of excessively absorbed light energy by, e.g., de-epoxidation of violaxanthin to zeaxanthin (Ruban et al. 2007) a process catalyzed by a thylakoid-bound deepoxidase that is activated by a low luminal pH due to a high electron transport rate (Pfündel and Dilley 1993). Zeaxanthin may dissipate excessively absorbed light energy harmlessly as heat. The process is reversed by the epoxidation of zeaxanthin to violaxanthin in dim light (Xanthophyll-cycle). The low pH induces also protonation of the photosystem II protein, PSBS, which induces a conformational change to specific chlorophyll- and carotenoid-binding LHC proteins (Peers et al. 2009). LHC may aggregate leading to, e.g., PSBS-LHC-zeaxanthin complex in some green algae. As a consequence,

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