Vol. 191: 109–119, 1999 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published December 30

Effects of solar radiation on growth, photosynthesis and respiration of marine macroalgae from the Arctic

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ABSTRACT: The effect of artificial ultraviolet (UV) and natural solar radiation on photosynthesis, respiration and growth was investigated in 14 red, green and brown macroalgal species on Spitsbergen (Norway) during summer 1998. In June, maximum mean solar radiation at sea level was 120 W m^{-2} of visible (370 to 695 nm) and 15 W m^{-2} of UV radiation (300 to 370 nm), and decreased gradually until the end of the summer. In spite of incident irradiance, levels were low in comparison with other latitudes, and UV radiation stress on growth of Arctic macroalgae was evident. Transplantation experiments of plants from deeper to shallow waters showed, for most algae, an inhibitory effect of both UVA and UVB on growth, except in the intertidal species *Fucus distichus*. The growth rate of selected macroalgae was directly correlated to the variations in natural solar radiation during the summer. Underwater experiments both *in situ* and using UV-transparent incubators revealed a linear relationship between the depth distribution and the growth rate of the algae. In almost all species the photosynthetic oxygen production decreased after 2 h incubation in the laboratory under 38 µmol m^{-2} s^{-1} photosynthetic active radiation (PAR 400 to 700 nm) supplemented with 8 W m^{-2} UVA (320 to 400 nm) and 0.36 W m^{-2} UVB (280 to 320 nm) compared to only PAR without UV. Like in the growth experiments, the only exception was the brown alga *F. distichus*, in which photosynthesis was not affected by UV. The degree of inhibition of photosynthesis showed a relation to the depth distribution, i.e. algae from deeper waters were more inhibited than species from shallow waters. In general, no inhibitory UV effect on respiratory oxygen consumption in all macroalgae studied was detected under the artificial radiation regimes described above, with the exception of the brown alga *Desmarestia aculeata* and the green alga *Monostroma arcticum*, both showing a significant stimulation of respiration after 2 h of UV exposure. The ecological relevance of the seasonal variations in the solar radiation and the optical characteristics of the water column with respect to the vertical zonation of the macroalgae is discussed.

KEY WORDS: Arctic macroalgae · Growth · Oxygen evolution · Photosynthesis · Respiration · Ultraviolet radiation

INTRODUCTION

In recent years stratospheric ozone concentrations decreased considerably, in particular in the polar regions, and resulted in enhanced biologically harmful ultraviolet (UV) radiation at the earth's surface. Compared to values in the 1970s surface erythemal UV doses in spring increased by about 130% in the Antarctic and by approximately 22% in the Arctic (Madronich et al. 1998). The UV waveband of the solar radiation has been reported to penetrate to considerable depths in marine pelagic and benthic ecosystems (Franklin & Forster 1997, Häder et al. 1998, Boelen et al. 1999).

Many life processes of marine primary producers are affected by UV radiation from the level of molecules up to that of communities. To date, damage of biomolecules such as DNA and proteins, supression of algal physiology and metabolism, and changes in marine community structure have been reported (Jokiel 1980,

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Strid et al. 1990, Karentz et al. 1991, Smith et al. 1992, Buma et al. 1995, 1997, Davidson et al. 1996), all of which may affect cell division, mortality and consequently marine productivity (Häder et al. 1998).

Although an increasing number of studies demonstrate diverse deleterious effects of UV radiation on the photosynthetic characteristics of macroalgae (Forster & Lüning 1996, Dring et al. 1996a,b, Figueroa et al. 1997, Hanelt et al. 1997, Bischof et al. 1998a,b), no general patterns have been discerned. This situation may be due to species-specific responses, acclimation to specific habitats (Dring et al. 1996a), or simply the low number of species studied so far. In this context, the studies conducted on some selected macroalgae collected from different depths in Arctic waters indicate that the degree of inhibition of photosynthesis after exposure to UV is related to the original growth depth (Hanelt et al. 1997, Bischof et al. 1998b). The higher insensitivity of shallow-water brown algae to UV radiation compared to deep-water individuals of the same species is reflected by a smaller decline in the optimum quantum yield (F_m/F_v) which equals the degree of photoinhibition, as well as by a faster recovery after UV offset (Hanelt et al. 1997, Bischof et al. 1998a). The Arctic macroalgae studied by those authors seem to exhibit an effective physiological acclimation to increasing doses of UV radiation. The ability to resist high radiation stress may be one of the major factors controlling vertical macroalgal zonation patterns on communities (Bischof et al. 1998b, Hanelt 1998).

While at least some basic information on UV effects on macroalgal photosynthetic performance are available, only a few data exist on other physiological processes such as respiration and growth (Wood 1987, Larkum & Wood 1993, Clendennen et al. 1996, Han 1996). Therefore, this study aimed to investigate the changes in growth, photosynthetic oxygen production and respiratory oxygen consumption in Arctic macroalgae collected on Spitsbergen (Norway) and subsequently exposed to natural solar radiation or to treatments with controlled fluence rates of artifical UV radiation.

Table 1. Investigated macroalgal species from the Arctic islands of Spitsbergen (Norway) and their occurrence in the eulittoral (0 m), upper sublittoral (0 to 2 m), and lower sublittoral (2 to 20 m) zones (Svendsen 1959, Klekowski & Weslawski 1995)

Species	Habitat
Chlorophyta	
Acrosiphonia penicilliformis (Fosl.) Kjellm.	Eulittoral-upper sublittoral
Monostroma arcticum Wittrock.	Upper sublittoral-lower sublittoral
Phaeophyta	
Desmarestia aculeata (L.) Lamour.	Lower sublittoral
Fucus distichus L.	Eulittoral-upper sublittoral
Laminaria digitata (Huds.) Lamour.	Upper sublittoral-lower sublittoral
Laminaria saccharina (L.) Lamour.	Upper sublittoral-lower sublittoral
Laminaria solidungula J. Agardh	Lower sublittoral
Saccorhiza dermatodea (Pyl.) J. Agardh	Upper sublittoral-lower sublittoral
Rhodophyta	
Devaleraea ramentacea (L.) Guiry	Eulittoral-upper sublittoral
Odonthalia dentata (L.) Lyngb.	Lower sublittoral
Palmaria palmata (L.) Grev.	Upper sublittoral-lower sublittoral
Phycodrys rubens (L.) Batters	Lower sublittoral
Phyllophora truncata (Pall.) Zinova	Lower sublittoral
Ptilota plumosa (Huds.) C. Agardh	Lower sublittoral

MATERIALS AND METHODS

Algal material and study site. The macroalgal species studied and their occurrence in the littoral zone are listed in Table 1. The plants were collected in summer 1998 at the study site located in the Kongsfjord (Ny-Ålesund, Spitsbergen, Norway 78° 55.5' N, 11° 56.0' E) at the depths from 0 m down to 20 m. Algal samples were collected by SCUBA diving in black bags to avoid exposure to high irradiance during transport. After sampling, the plants were kept in the laboratory in dim light and in running seawater pumped directly from the fjord.

Measurements of solar radiation. Two different sets of radiation measurements were undertaken for this study. Continuous recording of global radiation (305 to 2800 nm) using a CM11-pyranometer (Kipp & Zonen, Delft, The Netherlands) and of UV radiation (300 to 370 nm) using a TUVR-photodiode detector (Eplab, Newport, Rhode Island, USA) was carried out with instruments of the Baseline Surface Radiation Network (BSRN) in cooperation with the Norsk Polar Institute in Ny-Ålesund, Spitsbergen (König-Langlo & Marx 1997). To calculate radiation of the UV and photosynthetic active radiation (PAR) wavelength range, measurements through a RG8 filter (cut-off at 695 nm) (Schott, Mainz, Germany) were subtracted from the global radiation data. The radiation values (W m^{-2}) through the summer were calculated 2 wk means using averaged daily irradiance values measured by the pyranometer and photodiode, respectively. The total UV (UVA+UVB) radiation was also estimated using a biological dosimeter based on a UV-sensitive bacterial spore monolayer system (VioSpor, BioSense, Bornheim, Germany). These data are expressed as

minimal erythemal dose (MED) per day (Quintern et al. 1992, Furusawa et al. 1998). The dosimeters were exposed for 1 wk at the surface and in the water column (1 and 3 m depth, respectively) close to the places where the experiments were conducted. In order to compare with the UV measurements from the photodiodes, dosimeter mesurements at the surface are represented by 2 wk means.

Underwater UVB radiation (280 to 320 nm) was measured spectrometrically using a 32 channel quanta counting radiometer equipped with a 2 π corrected detector developed at the Alfred Wegener Institute. PAR was measured by use of an underwater spectroradiometer (Kruse, Bremerhaven, Germany). From data of both radiometers, diffuse vertical attenuation coefficients of downward irradiance (K_d) were determined using following formula (after Kirk 1994):

$$K_d = \ln E_{d(z_1)}/E_{d(z_1)} \times 1/(z_1 - z_2)$$

where $E_{d(z_1)}$ and $E_{d(z_2)}$ are the respective irradiances at depths z_1 and z_2.

Growth experiments. The macroalgal species studied had to be treated differently prior to each growth experiment. Young sporophytes of 3 to 4 cm length of the *Laminaria* species and *Saccorhiza dermatodea* were marked with 2 punched holes (2 mm diameter) at a distance of 15 mm from one another in the meristematic tissue of the thallus in the longitudinal direction (Fig. 1). The length increment over time under each radiation treatment was followed by the measurement of changes in the distance between the 2 marks. Thalli of *Palmaria palmata* were cut 3 cm below the apex and their total increase in length over time was measured. In the case of *Acrosiphonia penicilliformis* and *Fucus distichus*, the growth rate was determined as the wet weight increase of young intact plants.

Fig. 1. *Laminaria saccharina*. Thalli collected from the field and exposed for 1 wk under photosynthetic active radiation (PAR) or full solar radiation. The field plant represents an untreated thallus just collected from the shore. In order to avoid self shading of the thalli in the growth chamber, they were cut in pieces of 3 to 4 cm length from the stipe. The initial size for the plants before exposure was the same as observed in thalli exposed to full solar radiation

In the first experimental set, plants were collected from the field and directly exposed to natural surface solar radiation. The subsamples were covered with cellulosetriacetate cut-off filters for UVB (cut off of wavelengths <320 nm; Ultraphan, Digefra GmbH, Munich, Germany) and polyester cut-off filters for UVA plus UVB (cut off of wavelengths <395 nm; Folex, Dreieich, Germany). The plants were then incubated outdoors in basins with running seawater. Thalli exposed to full solar radiation were rapidly and strongly affected, especially by the ultraviolet waveband as shown for the brown alga *Laminaria saccharina* (Fig. 1). After 1 wk exposure, only plants exposed to UV-filtered radiation survived, while under total solar radiation the thalli became totally photobleached. Therefore, all subsequent growth experiments were conducted after the photoacclimation period of 7 to 10 d during which the algal samples were screened with UV cut-off filters and 3 layers of neutral grey filters, each of them producing a 3-fold reduction of the incoming light intensity. One after the other the grey filters were removed every 3 d, which was then followed by the evaluation of the physiological fitness of the plants prior to the beginning of the growth experiment. This was done by the determination of the variable chlorophyll fluorescence of photosystem II (PSII) as an indicator for the optimum photosynthetic activity using a PAM-2000 device (Walz, Effeltrich, Germany) (Hanelt 1998). After acclimation all thalli showed F_v/F_m values characteristic for photosynthetically non-inhibited plants.

Parallel to the surface experiments in the basins, macroalgae were exposed to natural solar radiation in the water column at depths between 1 and 5 m using anchored floating UV-transparent plexiglass tubes (PlexiglasXT, Röhm Darmstadt, Germany, 300 × 110 mm). Each tube was wrapped with the specific filter foils to cut off UVB and UVA+UVB.

Finally, in order to assess the growth response with respect to the depth *in situ*, selected thalli of *Laminaria saccharina* and *L. digitata* growing on the harbour sea wall were labelled by a diver at 3, 6 and 9 m. Their growth was followed over 3 wk by measuring the length of each thallus using the punched-hole method described above.

The increase in the thallus length or weight after 21 d of growth was used to calculate the relative growth rate, R, expressed as the percentage increase per day (Kain 1987, Lüning 1992):

$$R = (\ln A_{21} - \ln A_0) \times 100/21$$

where A_{21} is the length or wet weight after 3 wk of treatment, and A_0 is the length or wet weight at the beginning.

Photosynthesis and respiration. Photosynthetic oxygen production was measured after 2 h (in some spe-

cies additionally after 6 h exposure) to 38 µmol m^{-2} s^{-1} PAR provided by 1 Osram daylight fluorescence tube, 8 W m^{-2} UVA (320 to 400 nm) and 0.36 W m^{-2} UVB (280 to 320 nm) provided by 2 Q-Panel UVA-340 fluorescence tubes (Q-Panel Company, Cleveland, Ohio, USA). Radiation measurements were carried out with a Li-Cor LI-190-SB cosine-corrected sensor connected to a Li-Cor LI-1000 datalogger (Lambda Instruments Ltd, Lincoln, Nebraska, USA) for PAR (400 to 700 nm) and with a RM-21 broadband UV radiometer (Dr Gröbel, Ettlingen, Germany) to determine UVA and UVB. 1 g wet weight fragments of epiphyte-free algae were incubated in UV-transparent Winkler quartz glass bottles filled with about 330 ml of 0.45 µm filtered natural seawater. 6 replicate bottles were irradiated with both types of tubes (PAR+UV treatment), and another 6 bottles were also kept covered with Ultraphan filters cutting off UVA plus UVB. After light exposure, the respiratory oxygen comsumption was estimated after following a second dark incubation period for 3 to 4 h.

The oxygen concentration in the Winkler bottles was estimated with a temperature-compensated Clark-type electrode (WTW Oxi 323, Germany). All the experiments were carried out at 1 to 2°C.

Statistics. Mean values and their standard deviations were calculated from the different replicates per treatment. Statistical significances of means were tested with a Model 1, 1-way ANOVA followed by a multirange test by Fisher's protected least significant difference (LSD) (Sokal & Rohlf 1981).

RESULTS

Radiation measurements

Sun radiation measurements on Spitsbergen showed a typical seasonal pattern, with maximum values in June followed by a decrease during July and August. By the end of the summer the radiation level at the earth's surface was only one-third of the maximum recorded in the early summer both in the UV (300 to 370 nm) and visible (370 to 695 nm) range (Fig. 2a,b). The maximum averaged irradiance did not exceed 150 W m^{-2} in the visible part of the spectrum (Fig. 2a) and the UV radiation maximum was around 15 W m^{-2} (Fig. 2b). Weighted UV radiation measured in air by the biological spore-film dosimeters showed a less clear seasonal pattern. In contrast to the gradually decreasing pyranometer measurements (Fig. 2a) the dosimeter data in July drastically decreased to 50% of those in June (Fig. 2c). The differences between the 2 sets of measurements could be explained by the fact that the photodiode detector measures mainly UVA radiation, whereas the biodosimeter measures mainly the biologically effective UVB radiation. After July, the MED in air did not change until the end of the summer. The UV radiation in the water column as measured by the dosimeter followed a different pattern as observed in air (Fig. 2d). The maximum dose of UV was measured in June due to clear optical properties of the seawater just after the break-up of the ice cover on the fjord. During that period 16% of the daily MED in air was measured at 1 m depth and 7% at 3 m depth (Fig. 2d). In contrast, in July and August the lower intensity of solar radiation reaching the earth and the gradual reduction of the transparency of the seawater due to high influx of turbid melt-water from the glaciers resulted in a strong reduction of the underwater UV radiation. The averaged vertical attenuation coefficients (K_d) from the spectroradiometer measurements were 0.66 ± 0.052 and 0.51 ± 0.25 for downward UVB irradiance and for PAR, respectively, during the period of experiments (Hanelt et al. unpubl. result). As a result, at 1 m depth UVB was attenuated to about 51% and PAR to 60%; at 3 m depth UVB was attenuated to 14% and PAR to 22%. Thus, the water was relative opaque for solar radiation, and algae growing below 1 m depth were exposed to very low doses of UV radiation.

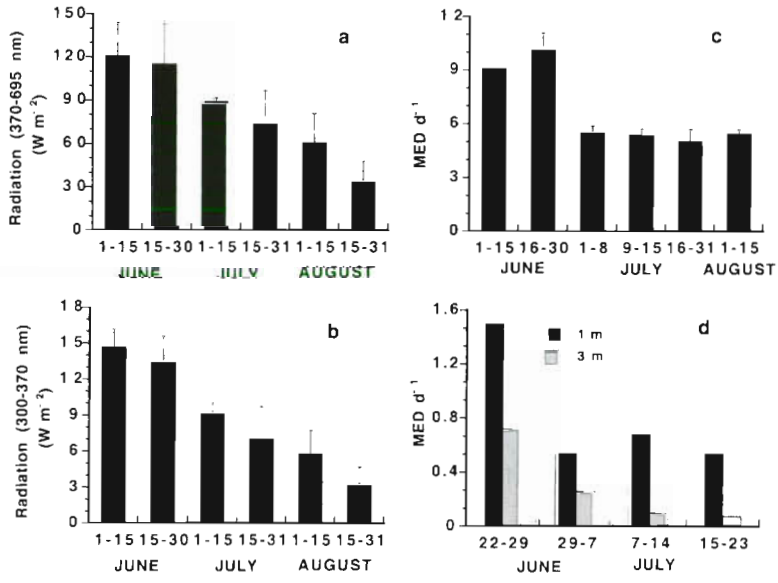

Fig. 2. Changes in solar radiation measured in air at sea level in Ny-Ålesund during summer 1998. (a) Visible (370 to 695 nm) and (b) UV in the range of 300 to 370 nm. Irradiance (W m^{-2}) during the summer was calculated in an interval of 2 wk as the average of the daily data. Total UV radiation measured with a biological dosimeter (VioSpor) (c) in air at sea level and (d) in the water column at 1 and 3 m depth. Data are expressed as minimal erythemal dose (MED) per day

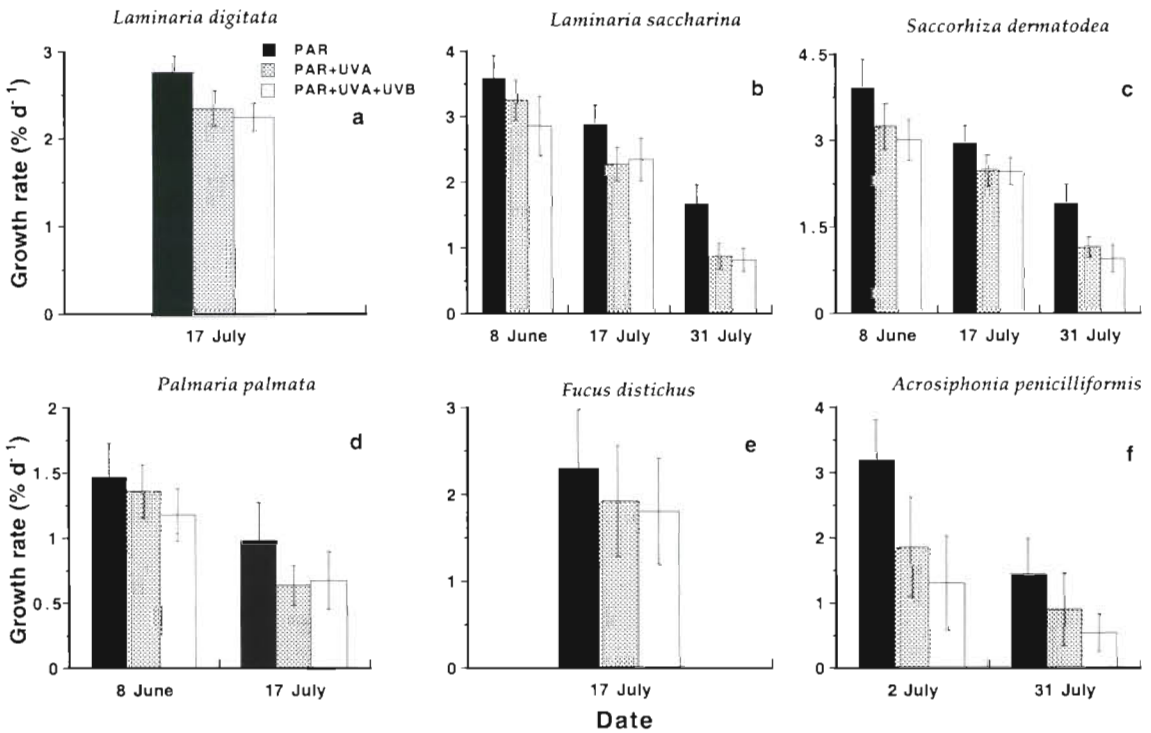

Fig. 3. Growth rate of selected macroalgal species exposed to solar radiation in basins at sea level during summer 1998. Experiments were initiated at each date given and subsequently run for 3 wk. Plants were exposed to filtered solar UV radiation (PAR >400 nm), filtered UVB radiation (PAR+UVA >320 nm) and unfiltered solar radiation (PAR+UVA+UVB). Vertical bars indicate the standard deviation of 16 replicates per treatment

Field growth measurements

Solar radiation affects the growth activity of macroalgae in surface waters in summer (Fig. 3). For all radiation conditions, the highest growth rates in all the species studied were always found in June, followed by a gradual decrease in July and August. In spite of the positive correlation between the growth activity of the algae and solar radiation reaching the earth's surface, this decrease in the growth rate may be a result of the seasonal growth pattern of the plants as discussed below. The irradiance impinging on the water surface at the end of the summer is still saturating for photosynthesis as observed in some species (data not shown).

All species were partially inhibited by UV radiation at the sea surface (Fig. 3). While *Laminaria digitata* which inhabits the upper sublittoral exhibited a small decrease in growth rate in both UV treatments, no significant difference between PAR+UVA and full solar radiation could be observed ($p > 0.05$, 1-way ANOVA) (Fig 3a). Only 1 outdoor experiment could be performed with this species due to strong ice cover near the collection site at the beginning of the summer. The growth of *L. saccharina* was significantly affected by both the PAR+UVA and the PAR+UVA+UVB treatments ($p < 0.05$, 1-way ANOVA) during June radiation maximum (Fig. 3a). However, in both experiments performed in mid- and late July no differences between the PAR+UVA and the ambient radiation solar exposure (PAR+UVA+UVB) could be estimated, while the difference in growth rate between PAR and PAR+UV was significant ($p < 0.05$, 1-way ANOVA). Growth of *Saccorhiza dermatodea* and *Palmaria palmata* was also inhibited by UV radiation compared to the PAR treatment and this could be observed throughout the summer as observed in *L. saccharina* (Fig. 3b to d). In the case of the intertidal brown alga *Fucus distichus*, exposure to full solar radiation did not significantly affect the growth rate ($p > 0.05$, 1-way ANOVA) (Fig. 3e). In contrast, the green alga *Acrosiphonia penicilliformis*, which grows very close to *F. distichus*, was strongly influenced by UV radiation (Fig. 3f). While the UVA treatment inhibited the growth rate by 40% of the PAR, UVA+UVB led to an even stronger response, resulting in a 60% reduction of the growth activity ($p < 0.05$, 1-way ANOVA).

Growth of the 3 *Laminaria* species exposed at the different water depths was affected by the radiation penetrating into the sea ($p < 0.05$, 1-way ANOVA) (Fig. 4a to c). However, at the chosen depths between 1 and 3 m no significant effect of UV radiation on this

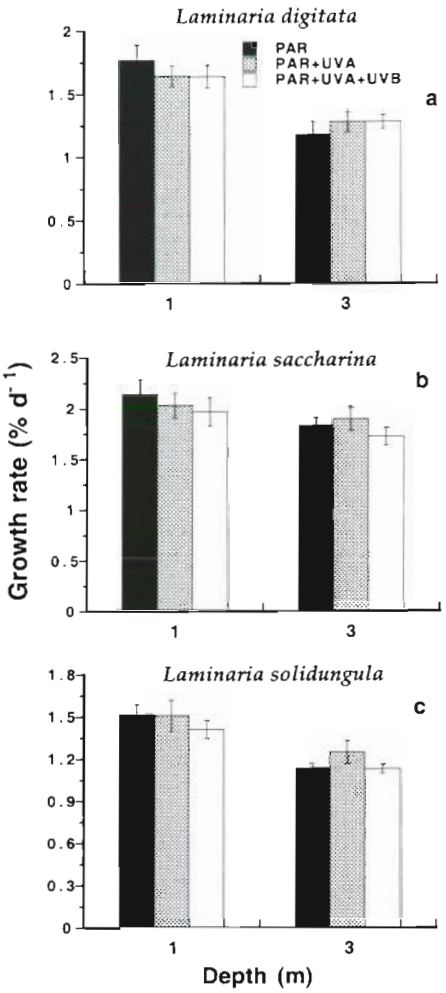

Fig. 4. Growth rate of 3 different *Laminaria* species in incubators exposed to various radiation treatments at different depths in the water column. Vertical bars indicate the standard deviation of 16 replicates per treatment. Differences were significant between the 2 depth treatments (at $p = 0.05$, $n = 16$), but not among the different radiation treatments at each depth. For radiation treatments see Fig. 3

physiological process could be determined ($p > 0.05$, 1-way ANOVA) due to the strong attenuation of underwater UVA+UVB radiation (K_d for UVB = 0.66 and for UVA = 0.62; Fig. 2d). However, there was a correlation between growth rate and depth. While the maximum growth rate of *L. digitata* decreased by 35% at 3 m compared to 1 m, the growth rates of *L. saccharina* and *L. solidungula* declined by 15 and 25%, respectively, at 5 m compared to 3 m (Fig. 4a to c).

Similar results were obtained *in situ*. Growth of *Laminaria saccharina* and *L. digitata* was studied at 3, 6 and 9 m depth (Fig. 5), and a linear correlation between growth rate and depth could be demonstrated for both species. While for *L. saccharina* a 6.8% decrease in growth rate per meter increase of depth

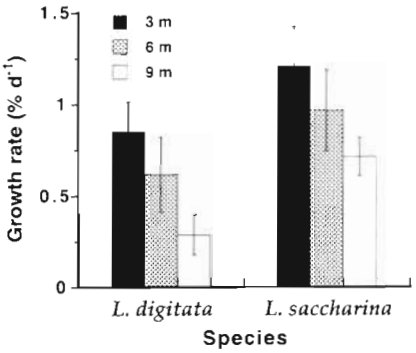

Fig. 5. *In situ* growth rates of *Laminaria digitata* and *L. saccharina* at different depths at the harbour sea wall. Vertical bars indicate the standard deviation of 7 replicates per treatment

was observed, that of *L. digitata* decreased by 11%. This corresponded with an average K_d of PAR of about 0.66 ± 0.052 in the water column.

Photosynthetic and respiratory performance

In most macroalgal species studied photosynthetic oxygen production was strongly affected after exposure to artificial PAR+UV radiation compared to the PAR treatment (Table 2). Only *Fucus distichus*, *Monostroma arcticum* and *Laminaria digitata*, all from the eulittoral and upper sublittoral zone, did not show any significant decrease in photosynthesis. As observed with growth rate, the photosynthetic activity of the other eulittoral species, *Acrosiphonia penicilliformis*, was also reduced by 40% at the UV level compared with PAR. In contrast, in most plants from the upper and lower sublittoral zone photosynthesis was strongly affected by UV, resulting in rates of 6 to 61% in respect to PAR treatments ($p < 0.05$, 1-way ANOVA). The absolute values for photosynthetic oxygen production among all macroalgal species studied ranged from 2.8 to 20.6 µmol O_2 g wet weight (fresh weight [FW]) h^{-1}

Increasing the exposure time of UV radiation in some brown algal species from 2 to 6 h was accompanied with even stronger inhibition of photosynthesis (Fig. 6). While *Fucus distichus* was again almost tolerant even in prolonged UV treatments, the 3 laminareans *Laminaria digitata*, *L. saccharina* and *L. solidungula* showed a severe decrease in photosynthesis after 6 h of exposure. In the case of *L. saccharina* and *L. solidungula* the photosynthetic oxygen production was almost completely inhibited by the end of the experiment, although the respiratiory activity was still observed (Fig. 6).

In contrast to the sensitive photosynthesis after exposure to UV, respiration was generally not inhibited

Table 2. Effect of ultraviolet radiation on the photosynthetic and respiration rates of Arctic macroalgae collected in the Kongsfjord, Spitsbergen, Norway. Plants were exposed for 2 h to a combination of artificial radiation lamps giving 30 µmol m^{-2} s^{-1} PAR and 7 W m^{-2} UVA plus 0.7 W m^{-2} UVB. The PAR treatment was conducted by filtering the total UV radiation by means of 400 nm cut-off filters. All data are given as µmol O_2 kg^{-1} fresh weight h^{-1} and represent the mean value of 6 replicates (±SD). The percentage of photosynthetic rate under PAR+UV with respect to PAR is also presented. *Significant differences between both radiation treatments (at p = 0.05, n = 6) as determined in a Model 1, 1-way ANOVA followed by a multi-range test by Fisher's protected least significant difference (LSD)

Species	Photosynthesis, 2 h PAR	Photosynthesis, 2 h PAR+UV	Difference (% of PAR treatment)	Respiration, 2 h PAR	Respiration, 2 h PAR+UV
Chlorophyta					
Acrosiphonia penicilliformis	7.31 ± 0.97	4.28 ± 0.50*	58.5	1.78 ± 0.25	1.56 ± 0.34
Monostroma arcticum	20.56 ± 8.93	16.68 ± 7.34	81.1	5.13 ± 0.66	6.72 ± 0.97*
Phaeophyta					
Desmarestia aculeata	11.63 ± 2.31	0.66 ± 0.45*	5.7	2.75 ± 0.56	3.97 ± 1.03*
Fucus distichus	4.13 ± 1.41	4.28 ± 0.88	103.6	0.88 ± 0.16	1.00 ± 0.02
Laminaria digitata	2.78 ± 0.50	2.06 ± 0.50	74.1	0.66 ± 0.09	0.78 ± 0.09
Laminaria saccharina	6.13 ± 0.88	1.53 ± 0.44*	25.0	1.00 ± 0.06	1.19 ± 0.28
Laminaria solidungula	4.84 ± 0.97	1.22 ± 0.44*	25.2	0.78 ± 0.16	0.91 ± 0.16
Saccorhiza dermatodea	3.56 ± 1.00	0.84 ± 0.47*	23.6	0.63 ± 0.19	0.72 ± 0.34
Rhodophyta					
Devaleraea ramentacea	8.13 ± 0.44	3.25 ± 0.56*	40.0	0.97 ± 0.19	0.90 ± 0.31
Odonthalia dentata	5.47 ± 1.06	1.41 ± 0.41*	25.8	2.75 ± 0.28	2.47 ± 0.22
Palmaria palmata	9.31 ± 1.19	3.38 ± 0.44*	36.3	1.28 ± 0.16	1.16 ± 0.16
Phycodrys rubens	5.78 ± 0.91	3.00 ± 1.16*	51.9	1.53 ± 0.34	1.84 ± 0.22
Phyllophora truncata	6.03 ± 1.09	4.69 ± 0.50*	77.8	0.72 ± 0.16	0.63 ± 0.16
Ptilota plumosa	5.31 ± 0.72	3.25 ± 0.75*	61.2	0.84 ± 0.22	0.75 ± 0.13

(Table 2). With the exception of *Desmarestia aculeata* and *Monostroma arcticum*, all plants showed almost unchanged respiratory rates after 2 h UV treatment. In a few species tested, an increase of the exposure time to 6 h UV radiation also did not affect this metabolic process (data not shown). However, in *D. aculeata* and *M. arcticum* a significant stimulation of respiration by 44 and 31%, respectively, was determined after 2 h UV treatment ($p < 0.05$, 1-way ANOVA) (Table 2). The absolute values for respiratory oxygen consumption among all macroalgal species studied ranged from 0.4 to 5.9 µmol O_2 g wet weight (FW) h^{-1}.

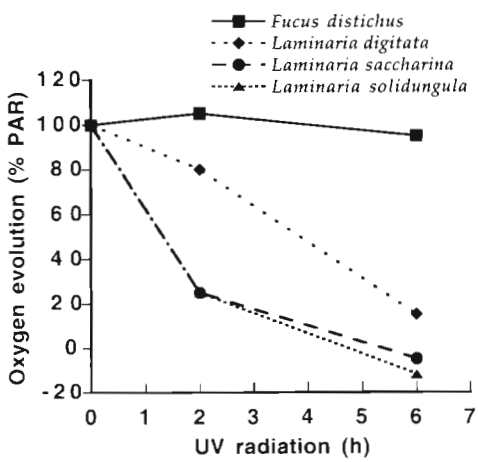

Fig. 6. Oxygen evolution (production or consumption) in Arctic brown macroalgae after 2 and 6 h exposure to artificial 30 µmol m^{-2} s^{-1} photosynthetic active radiation (PAR) and to 30 µmol m^{-2} s^{-1} PAR plus 7 W m^{-2} UVA and 0.7 W m^{-2} UVB (PAR+UV). The oxygen production under PAR of each macroalgal species was set to 100% and compared to the respective activity under PAR+UV. Standard deviation was less than 15%

DISCUSSION

Due to the latitude and the rapid changes of weather conditions during the summer season, solar radiation at the surface is relatively low and subjected to marked fluctuations. Maximum averaged radiation in the visible part of the solar spectrum (370 to 695 nm) during the experimental period was measured in June and did not exceed a daily mean value of 150 W m^{-2}, 15 W m^{-2} for UV radiation in the range of 300 to 370 nm and 0.273 W m^{-2} for solely UVB. In a recent study at the same location seasonal maximum values of 250 W m^{-2} for PAR, 19 W m^{-2} for UVA and of 1.1 W m^{-2} for UVB were reported in mid-June on a sunny day (Bischof et al. 1998a). These irradiances are still low compared with maximum radiation values at lower latitudes. While measurements with a spectroradiometer oscillate at midday in summer on Helgoland (North Sea) between 280 and 380 W m^{-2}, UVA between 30 and

40 W m^{-2}, and UVB between 1.7 and 2.2 W m^{-2} (Dring et al. 1996a), in southern Spain PAR, UVA and UVB can reach values of 450, 50 and up to 3 W m^{-2}, respectively (Figueroa et al. 1997).

The penetration of solar radiation into the water column on Spitsbergen also experiences drastic and rapid changes during the summer season. Due to a later spring in 1998, the water in the studied fjord was covered with a 1 m thick ice layer that did not disappear until 22 June. Although this month coincided with the highest water transparency for PAR and UV the ice cover reduced downwelling radiation by about 90% (Hanelt et al. unpubl. result). Usually, the ice cover disappears on Spitsbergen in late April/early May, and at this time the water in the Kongsfjord is clear and UVB radiation penetrates down to approximately 10 m (Bischof et al. 1998a). However, after the sea-ice breakup in 1998 there was a high input of turbid water due to melting of snow and calving of glaciers also causing a high influx of sediment into the water. Under these conditions the water transparency was very low and a large fraction of the impinging UV radiation was attenuated in the upper few metres of the water column (Fig. 2d).

The algal growth at the water surface confirms a general tendency toward an inhibitory effect of UV radiation. Transplantation experiments from protected to stressed environmental conditions are important to better understand the acclimation potential and the distribution patterns of these plants on the shore. Using such an experimental design, area- and weight-based growth rates in *Ulva expansa* were reported to be enhanced by excluding UV (Grobe & Murphy 1994). Growth of deep-water species was UV sensitive compared to shallow-water plants. Except for intertidal *Fucus distichus*, growth of all other studied species was affected by UVA and UVB. These growth data are in good agreement with the *in vivo* chlorophyll fluorescence measurements, which showed decreasing photosynthetic activity under UV in the same species (Hanelt et al. 1997). In the case of the other intertidal alga *Acrosiphonia penicilliformis*, growth rate was strongly inhibited under total UV, as well as under PAR+UVA. In both species, the adaptation strategy to survive under exposed and stressed conditions in the intertidal zone is different. Morphology, i.e. a thicker thallus, such as that in the kelp species *Fucus* or *Laminaria*, does better protect against high solar radiation. In such macroalgae the fluence rate of harmful radiation decreases strongly towards the inner cell layers (Dring et al. 1996b). Changes of chloroplast distribution within the cortex cell is another mechanism which decreases light absorbance especially in the outer cortex layers due to an increased sieve mechanism. The occurrence of a light-induced chloroplast displacement in seaweeds was shown by Nultsch & Pfau (1979). Later, Hanelt & Nultsch (1991) demonstrated that it is predominantly an effect due to protection from light. Growth and photosynthesis of *A. penicilliformis* was sensitive to UV radiation despite the high position of this species on the shore. This can be explained by its thallus structure with interwoven fell-like filaments at the base and slender separate filaments at the periphery of the thallus. While only the latter apical regions of the alga are exposed to strong light the basal cells are well protected due to self shading. In the field yellow-coloured tips were often observed, indicating a lack of chlorophyll as a consequence of photobleaching of the apical parts, along with dark-green pigmented healthy and non-light-stressed basal parts (data not shown).

Deep-water species transplanted to the surface showed different UV sensitivities (Fig. 3). With the exception of *Laminaria saccharina* and *Palmaria palmata* in the experiments at the beginning of the summer, the growth of all other species was already partially inhibited by UVA (320 to 400 nm). Compared to full solar radiation the inhibition was not significantly different. A reason could be the low UVB irradiance reaching the sea surface which therefore did not amply signify the inhibitory effect of UVA. Among the laminarean species, *L. digitata* grows in the upper part of the shore and showed a growth rate rather indifferent to UV compared to the strongly affected *L. saccharina* inhabiting deeper zones. These results confirm observations on the laminarean species distributed on the island of Helgoland (Dring et al. 1996b). Those authors showed that growth and photosynthesis of sporophytes of *L. saccharina* were also more sensitive to UV than higher located *L. digitata* and *L. hyperborea*. UV radiation penetrating into the water column may effectively control the upper algal distribution limit. As a consequence, *L. saccharina* shows a higher growth rate than *L. digitata* (Figs. 4 & 5) at the same depth if the UV irradiation becomes too low to be harmful. Besides UV, penetrating PAR also suppress the growth of algae (Fig. 5). Thus, on Spitsbergen, in spite of incident irradiance, levels are low in comparison with other latitudes, and when the water transparency allows good UV radiation penetration, UV radiation can be a controlling factor in communities since this is an evident stress source for most macroalgae.

Although the effect of other physical parameters on algal communities in the Kongsfjord has still to be evaluated it is obvious from the data that solar radiation is one of the key factors controlling algal growth. The decrease in the growth rate observed between June and August in almost all species was directly correlated with the changes in the total solar irradiance. Light and other abiotic factors have been described to directly affect the algal distribution in Antarctic macro-

algal communities (Drew & Hastings 1992, Klöser et al. 1993, Gómez et al. 1997). However, the seasonal growth pattern observed may not just be determined by the intensity of solar radiation. The seasonal course of daylength can also determine seasonality of growth and other physiological processes (Gómez et al. 1995, 1997, Weykam & Wiencke 1996, Gómez & Wiencke 1997). This is the case of the so-called 'season anticipators', where seasonal development is based on photoperiodism or circannual rhythms (Lüning 1986, 1988, 1991, 1994, Lüning & Dieck 1989). The annual maximum of the growth rate of *Laminaria saccharina* on the Alaska Arctic coast is between late April and late July (Dunton 1985). In contrast, *L. solidungula* from the same place completed most of its annual growth in darkness during late winter and spring (Dunton & Schell 1986, Dunton 1990). The growth strategy of both species differs in the capability for storage of carbon reserve carbohydrates and their later remobilisation (Dunton 1985, Dunton & Schell 1986, Henley & Dunton 1995, 1997). In the case of the Arctic Laminariales a drastic decrease in the growth rate after spring coincides with an increase in the photosynthetic activity during the strong light period in summer in order to accumulate new carbon reserves to produce new frond tissue during ice-cover periods (Dunton 1985, 1990).

In this study, the higher early summer growth rates of *L. saccharina*, *Saccorhiza dermatodea* and *Palmaria palmata* occur in June and the later decrease may also be a consequence of this seasonal change of physiological activities. In this respect, the higher inhibitory effect of UV on growth at the end of the summer, observed in *L. saccharina* and *S. dermatodea*, may be due to the change from high growth activity to high photosynthetic performance. Therefore, the analysis of the UV effects on photosynthesis is crucial. Most species investigated already showed strong inhibition in photosynthetic oxygen production after 2 h exposure to artificial UV radiation (Figs. 3 & 4). The UV irradiances chosen in this study were lower than those occurring in nature. However, it should be considered that under the artifical light sources PAR was much lower than under natural conditions. Nevertheless, the plants were more or less affected by the relatively low UV irradiances. Photosynthesis of macroalgae generally seems to be a major physiological target for UV radiation (Franklin & Forster 1997, Häder & Figueroa 1997, Häder et al. 1998). This was also demonstrated by the previous studies using the *in vivo* chlorophyll fluorescence of PSII (Herrmann et al. 1995, Hanelt et al. 1997, Bischof et al. 1998a,b, Häder et al. 1998). Although in macroalgal species weak correlations were sometimes demonstrated between fluorescence parameters and oxygen data (Hanelt & Nultsch 1995), the oxygen results of the present investigation are in good agreement with the earlier reports on polar macroalgae using the fluorescence technique (Hanelt et al. 1997, Bischof et al. 1998a,b). The latter authors showed that the intertidal *Fucus distichus* was generally much more resistant to UV compared to sublittoral species such as *L. saccharina*.

A decrease of photosynthetic activity under UV radiation is the result of various biomolecules such as nucleic acids, lipids and proteins being damaged due to absorption of the high energetic quanta of the UV waveband. As a consequence the ability of thylakoids to maintain their electrochemical gradient can decrease (Strid et al. 1996), and the degradation of essential molecules such as the D_1 protein (Greenberg et al. 1989), the water-splitting complex (Vass et al. 1996) or ribulose 1,5-*bis*phosphate carboxilase-oxigenase (Strid et al. 1990) can increase. However, macroalgae have developed physiological processes such as dynamic photoinhibition to regulate their photosynthetic activity to adapt to and be protected against temporary excessive radiation (Hanelt 1998). This author demonstrated that the capability of dynamic photoinhibition and especially the rate of recovery in macroalgae after offset of radiation stress is strongly related to their depth distribution on the shore. The degree of inhibition of photosynthetic oxygen production under UV treatment can be correlated to the depth zonation as well (Table 2). *Fucus distichus* was almost insensitive to prolonged periods of UV exposure, as reflected in growth response. In contrast, the 3 *Laminaria* species tested showed much less resistant photosynthesis. However, while *L. digitata*, which grows in the intertidal to higher sublittoral zone, showed a strong but incomplete decrease in photosynthetic oxygen production only after 6 h of UV exposure, *L. saccharina* and *L. solidungula*, from the deeper sublittoral zone, were fully inhibited and exhibited low respiratory activity instead (Table 2).

Exposure to UV radiation did not affect respiratory oxygen consumption in most macroalgal species studied (Table 2). This is consistent with results on various green, brown and red macroalgae from warm, temperate waters in Australia, which exhibited insensitive respiration under UV treatment as well (Larkum & Wood 1993). Similarly, UV radiation did not produce any significant change in the rate of dark respiration in the giant kelp *Macrocystis pyrifera* from Californian waters (Clendennen et al. 1996). The data available from the few publications on macroalgae and those presented here clearly indicate that respiration is much more resistant to UV stress compared to photosynthesis. In the case of *Desmarestia aculeata* photosynthesis was most severely inhibited under UV, and hence it may be speculated that a stimulation in respiration may be essential to guarantee the maintainance of basal metabolism.

Ecophysiological studies on other environmental stresses such as salinity changes and desiccation revealed that photosynthesis is strongly inhibited in macroalgae but respiration is not (Wiltens et al. 1978, Kirst 1990). In the case of osmotic stress the different response pattern between photosynthesis and respiration can be explained by ultrastructural changes in the thylakoid arrangements of the chloroplasts (Wiencke 1982), while mitochondrial fine structure is much less affected (Kirst 1990). In addition, while mitochondria in macroalgae are numerous, small and often localized in the inner parts of the cells opposite to the thallus surface, the single or few relatively large chloroplasts occupy the area adjacent to the outer cell walls. Moreover, photosynthetic tissues are always localized at the thallus surface whereas the mitochondria-rich medulla is protected within the thallus. However, the question of whether structural, physiological or biochemical features are responsible for the obvious differences in the response pattern between both organelles under UV radiation has to be investigated in future studies. In conclusion, although respiration in Arctic macroalgae is not influenced by UV radiation the conspicuous inhibition of the photosynthetic activity is finally reflected in the growth rate as the integrating process for all physiological and morphological responses in the plant.

Acknowledgements. The authors would like to thank Thomas Sawall and Kai Bischof for collecting the plant material and for logistic help, Dr Ivan Gómez for his help in the statistical analysis of the samples, and the Ny-Ålesund International Research and Monitoring Facility for their support. This project was financially supported by the European Union (Project ENV4-CT96-0188 (DG 12) - UV/marine macrophytes). J.A. is grateful to the Ministerio de Educación y Cultura of Spain and the Alexander von Humboldt Foundation for supporting his research. This is publication no. 1655 of the Alfred Wegener Institute for Polar and Marine Research, Bremerhaven.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: May 12, 1999; Accepted: August 2, 1999
Proofs received from author(s): December 14, 1999