Aquat.sci.63 (2001) 294–309
1015-1621/01/030294-16 $ 1.50+0.20/0
© Birkhäuser Verlag, Basel, 2001

Aquatic Sciences

Effects of UV on carbon assimilation of phytoplankton in a mixed water column

Jan Köhler[1,*], Mechthild Schmitt[2], Hartwig Krumbeck[3], Maria Kapfer[3], Elena Litchman[4,**] and Patrick J. Neale[4]

[1] Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 301, D-12587 Berlin, Germany
[2] Centre of Environmental Research, Permoserstr. 15, D-04318 Leipzig, Germany
[3] Technical University Cottbus, Seestr. 6, D-15526 Bad Saarow, Germany
[4] Smithsonian Environmental Research Center, 647 Contees Wharf Rd, PO Box 28, Edgewater, MD 21037
** Present address EAWAG, Kastanienbaum, Switzerland

Key words: Primary production, ultraviolet radiation, light inhibition, turbulent mixing, model.

ABSTRACT

Carbon assimilation is usually measured at fairly constant light intensities. Under natural conditions, however, planktonic algae are moved through the water column and experience light of fluctuating intensity and spectral composition. They may cope with strong UV for a short residence in the upper water layer. In order to estimate the effects of UV on primary production of phytoplankton under conditions of turbulent mixing, we compared carbon assimilation and exudation of algae incubated in UV-transparent quartz and in UV-absorbing glass bottles which were moved through different water layers. Computer-controlled elevators were used to simulate mixing depths between 2 and 14 meters. Compared to the glass bottles, particulate C assimilation in the quartz bottles was reduced by 20–30% at mixing depths between 2 and 10 m. There was no significant difference between both types of incubation bottles at a mixing depth of 14 m. Exudation was enhanced by UV near the water surface (mixing depth up to 4 m) but not in the deep-mixed samples. Our results indicate serious damage of planktonic algae by UV even under conditions of vertical mixing if the euphotic zone exceeds the mixing depth. Depression was low for circulation through the whole euphotic zone and may disappear at even deeper mixing. Our results indicate lower photoinhibition per UV dosage at fluctuating than at constant light intensities. A model predicting inhibition as function of weighted irradiance spectra was adapted to describe wavelength dependent photoinhibition occurring at different mixing depths. The model results agreed very well with the inhibition rates measured under fluctuating light. These preliminary results are used to discuss the importance of UV on photosynthesis of planktonic algae in aquatic environments of different mixing depths and stabilities of stratification.

* Corresponding author, e-mail: Koehler@igb-berlin.de

Introduction

During the last decades, water quality of many alpine and pre-alpine lakes has been improved and arrived at an oligotrophic state again (e.g., Bürgi et al., 1999). As a consequence, the depth of light transmission increased and enhanced ultraviolet (UV) radiation may have greater effects on aquatic organisms.

Many studies have been done on the impact of increased UV (280–400 nm) on phytoplankton. Particular attention has focused on the UV-B (280–320 nm) which is selectively increased by stratospheric ozone depletion. Among other effects, UV radiation damages the photosynthetic apparatus as well as the DNA (e.g., Mitchell and Karentz, 1993; Buma et al., 1997; Vincent and Neale, 2000). UV inhibition is a time-dependent phenomenon. Repair mechanisms may counterbalance damage if the cell is exposed to UV for sufficiently short periods. Light of longer wavelengths may activate such repair. Therefore, effects of UV depend on duration and intensity of exposure to UV as well as on the ratio between PAR and UV radiation.

Carbon assimilation of phytoplankton is conventionally measured under constant light intensities in the laboratory or at fixed depths and thus under fairly constant light *in situ* (e.g., Gala and Giesy, 1991). Under natural conditions, planktonic algae are subjected to turbulent water movement. Vertically transported algae experience light of fluctuating intensity and spectral composition due to the exponential, wavelength-dependent decline of light intensity with depth. Under mixing conditions, planktonic algae receive strong light only for short periods and may use their stay in deeper water layers to repair any damage done near the water surface. As a consequence, the severe photoinhibition often measured during conventional incubations near the water surface may be considered an artifact rather than a process occurring under natural conditions.

Most models of phytoplankton photosynthesis do not include time dependence in the variation of photosynthetic parameters. In particular, inhibition of photosynthesis by UV has been modelled as function of biologically weighted irradiance (Cullen et al., 1992; Neale et al., 1994). This model represents the steady-state rate of photosynthesis achieved when damage is counterbalanced by repair (Lesser et al., 1994). Other modelling and measuring approaches have included time-dependent responses to UV exposure as would occur under mixing conditions. The interaction between UV inhibition and vertical mixing in the Southern Ocean was modelled using a simple relationship of inhibition to cumulative exposure (Neale et al., 1998). Complex modelling approaches could combine models of photosynthesis which incorporate known kinetics of photoinhibition and recovery (e.g., Pahl-Wostl and Imboden, 1990) with hydrodynamic models describing the vertical movement of algal cells in the mixed layer. Few attempts have been made to measure primary production under simulated light fluctuations (circulator – glass tube with pump, Jewson and Wood, 1975; laboratory, Marra, 1978; rotating wheel, Benndorf and Werner, 1980; lift, Nixdorf and Behrendt, 1991). These few studies on carbon assimilation under conditions of vertical mixing used glass incubators and thus excluded ultraviolet radiation. Even fewer attempts have been made to consider UV damage on planktonic organisms under fluctuating dose rates. Helbling et al. (1994) simulated the light regime of the mixed layer by incubating natural phytoplankton with

a rotating filter set. Zagarese et al. (1998a, 1998b) simulated light fluctuation *in situ*, using a rotating wheel, to investigate the mortality of UV on zooplankton.

This paper describes first measurements of carbon assimilation and exudation in bottles receiving high and low exposure to short wavelength ($\lambda < 350$ nm) UV which were moved through different depths by a computer-controlled lift. The lift simulated circulation cells of the Langmuir type with diameters between 2 and 14 m. We tested the hypotheses that the degree of UV damage declines with increased mixing depth and that damaging effects are negligible at sufficiently deep mixing. The experimental procedure was supplemented by a model calculation of the wavelength dependent photoinhibitory effect of UV-radiation.

Methods

Experiments were performed in Lake Lucerne on 13 and 15 September, 1999 (assessment of basic parameters described in Bossard et al., 2001, this issue). On the first day, the same water sample was used as described by Neale et al. (2001a, this issue). On 15 September, samples were drawn from 1, 3, 5, and 7 m depth, about 200 m away from the landing of EAWAG station, Kastanienbaum. The mixed water samples were subsampled into Duran and quartz bottles (about 120 ml) and inoculated with $NaH^{14}CO_3$ (final activity about 0.39 µCi ml^{-1}). A dark bottle control was wrapped into aluminium foil. Each 2–3 bottles were horizontally positioned in a special holding device and fixed at the rope of the lifts. An early version of these elevators was described by Behrendt (1989). The different lifts moved the bottles from water surface to 3.9 m and 14 m depth on 13 September and to 2.0, 3.9 and 10 m depth during the second experiment, respectively. The lifts simulated circular paths (lowest vertical speeds at the upper and lower ends) with durations of one circle of 4 min (0–2 m), 8 min (0–3.9 m) and 20 min (0–10 and 0–14 m), respectively. Exposures lasted from 12:15 h till 16:15 h at the first day and from 10:25 h till 14:25 h (CEST) at the second one. The lifts were fixed on a beam between the shadeless side of a boat and a small buoy at the sampling position of the second day. The Duran bottles used absorbed more than 95% radiation with wavelengths shorter than 315 nm and about 50% of the radiation at 340 nm. The quartz bottles absorbed about 10% of UV-B and about 50% of radiation at 200 nm (Bühlmann et al., 1987) (Figure 1A). The effect of bottle transmission on biologically effective irradiance (using the biological weighting function of Neale et al., 2001a, this issue) is shown in Figure 1B. Compared to quartz bottles, the Duran bottles absorb most of the biologically effective UV-B and a significant fraction of the biologically effective UV-A below 350 nm. At the surface, about 60% of the decrease in effective irradiance in Duran bottles is due to protection from UV-A and 40% due to protection from UV-B.

After the incubation, bottles were put into a dark box and transferred to the laboratory. Total ($TO^{14}C$), particulate ($PO^{14}C$) and dissolved ($DO^{14}C$) organic carbon were distinguished. 7 ml subsamples were filtered onto polycarbonate filters (pore size 0.2 µm), to separate particulate and dissolved organic ^{14}C. The filtrates and 7 ml of the untreated sample for $TO^{14}C$-measurements were acidified with HCl and bubbled with air for at least 30 min. Filters were placed on HCl-soaked filter paper, air dried and dissolved with Soluene (Packard). All samples were measured with stan-

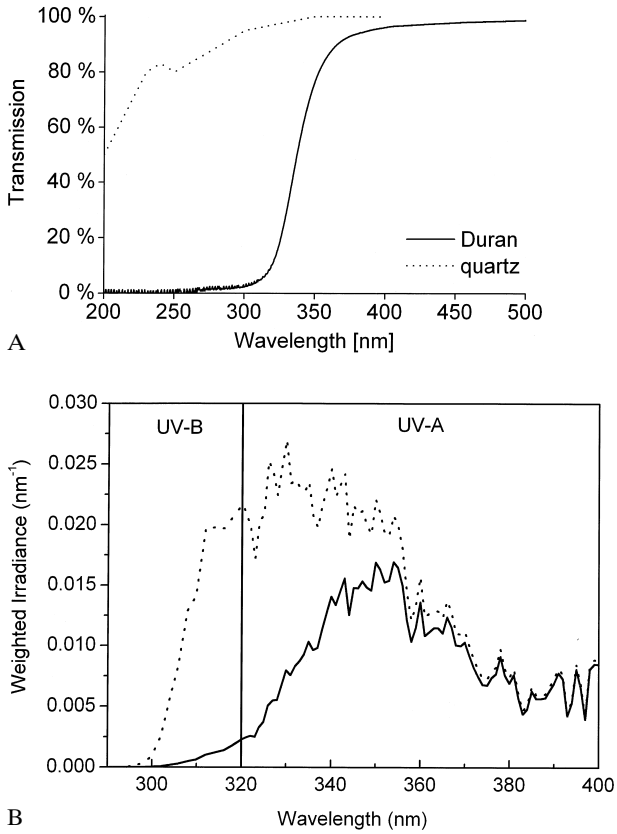

Figure 1. A Transmission properties of the Duran and quartz bottles used for incubation experiments. (Quartz bottle data are redrawn from Fig. 1 of Bühlmann et al. (1987)). B Surface spectral irradiance for local solar noon on September 13, 1999 at Lake Lucerne (see Neale et al., 2001b, this issue) as weighted with the biological weighting function for UV inhibition of photosynthesis by Lake Lucerne phytoplankton and after application of spectral transmission (Fig. 1A) of quartz (broken line) and Duran (solid line) bottles. Vertical line marks the spectral boundary between UV-B and UV-A

dard liquid scintillation techniques. At least two replicate determinations were done from each bottle.

Chlorophyll *a* analyses were performed by filtering 1–1.5 l of the mixed sample through a GF/F filter, followed by extraction of the pigments in 6 ml ethanol and HPLC measurement.

Light intensities were calculated in 10 s intervals from the incubation depth, the measured attenuation of PAR, UV-A and UV-B and the surface light intensities. Irradiance, physical water parameters and nutrients were measured by EAWAG laboratory, Kastanienbaum, using a LICOR-sensor for PAR and a MACAM-sensor for UV-A und UV-B. Broad band attenuation coefficients were calculated from a standard irradiance profile, measured on 13 September.

The wavelength dependent inhibition of photosynthesis by UV radiation was calculated according to the BWF-PI model of Cullen et al. (1992). The model represents UV effects as a function of weighted irradiance, and thus ignores dynamical effects (Cullen and Neale, 1997). Instantaneous rates were calculated in intervals of 20 s using estimated spectral irradiance. Surface spectral irradiance was measured with a SR18 UV-B spectroradiometer with 2 nm resolution (13 September) and Macam broad-band UV sensors (13, 15 September). Measurements by these sensors were used to adjust the output of a spectral radiative transfer model to obtain full spectral irradiance 290–400 nm (details in Neale et al., 2001 b, this issue). Spectral attenuation coefficients (Neale et al., 2001 a, this issue) were applied to estimate *in situ* spectral irradiance as a function of depth and time. Measurement and calculation of the biological weighting function was carried out by Neale et al. (2001 a, this issue). Application of biological weighting factors to *in situ* spectral irradiance resulted in E^*_{inh}, the biologically effective fluence rate for inhibition of photosynthesis (dimensionless). Results are expressed either as photosynthesis relative to the rate in the absence of inhibition ($1/[1 + E^*_{inh}]$) or as P/P_{max}. P is the modelled actual rate of photosynthesis depending on the intensity of the photosynthetic active radiation E_{PAR}, the inhibitory effect of UV-radiation (expressed as $1/[1 + E^*_{inh}]$) and the photosynthetic performance of the sample. P_{max} is the potential maximum rate of photosynthesis in absence of inhibition. The overall equation for P is $P/P_{max} = [1 - \exp(-E_{PAR}/E_s)] * 1/[1 + E^*_{inh}]$, where E_s is the characteristic irradiance for light saturation of photosynthesis (286 µmol photons m^{-2} s^{-1}, see Neale et al., *a* this issue). Thus, $1/[1 + E^*_{inh}]$ describes the inhibition of photosynthesis due to the effect of UV-radiation, and P/P_{max} describes the actual rate of photosynthesis depending on PAR, inhibition by UV-radiation and physiological condition of the sample. For both inhibition parameters, the relative inhibition was calculated as response in quartz bottles (with UV) as percentage of response in Duran bottles (filtered UV).

Results

1. Environmental conditions

The general limnology of Lake Lucerne as well as the conditions during our experiment have been described by Bossard et al. (2001, this issue). The vertical profiles of temperature and chlorophyll fluorescence (Fig. 2) indicate a seasonal thermocline at about 6 m with a weak temperature gradient extending to the surface. Maximum phytoplankton biomass was found in the metalimnetic zone about 6–10 m deep. Mean intensities of photosynthetically active radiation (PAR) of 1256 (13 Sept.) and 1157 µE m^{-2} s^{-1} (15 Sept.) were measured at the water surface. The attenuation coefficients of PAR, UV-A and UV-B were calculated as 0.31 m^{-1}, 0.58 m^{-1} and 1.3 m^{-1}, respectively. The euphotic zone (z_{eu}) reached about 14 m but 99% of UV radiation was attenuated at 7.9 m (UV-A) and at 3.5 m (UV-B). Intensities of radiation received by vertically moved phytoplankton samples are illustrated in Figure 3. The algae were exposed to UV-B intensities oscillating between 7.4–100% of surface intensities at the upper lift (0–2 m) and between 0.6–100% from 0–3.9 m. The

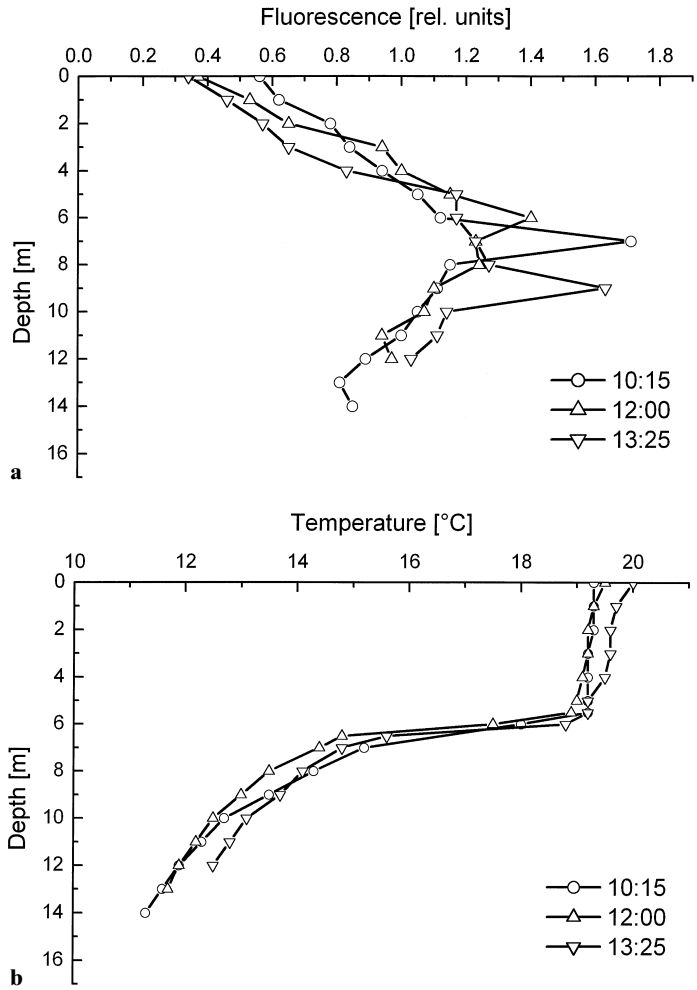

Figure 2. Vertical profiles of chlorophyll fluorescence (a) and temperature (b) at Lake Lucerne on September 15, 1999

deep-mixed samples spent more than half of each circulation period in depths with UV-B intensities below 1 μW cm^{-2} (see Table 1).

2. Carbon assimilation

The measured carbon assimilation rates are shown in Figure 4. They differed between the simulated mixing depths according to the received light intensities. Carbon assimilation was lowest at deepest mixing (0–14 m) and highest at medium mixing depths. Assimilation rates were similar in bottles moved from 0–3.9 m and

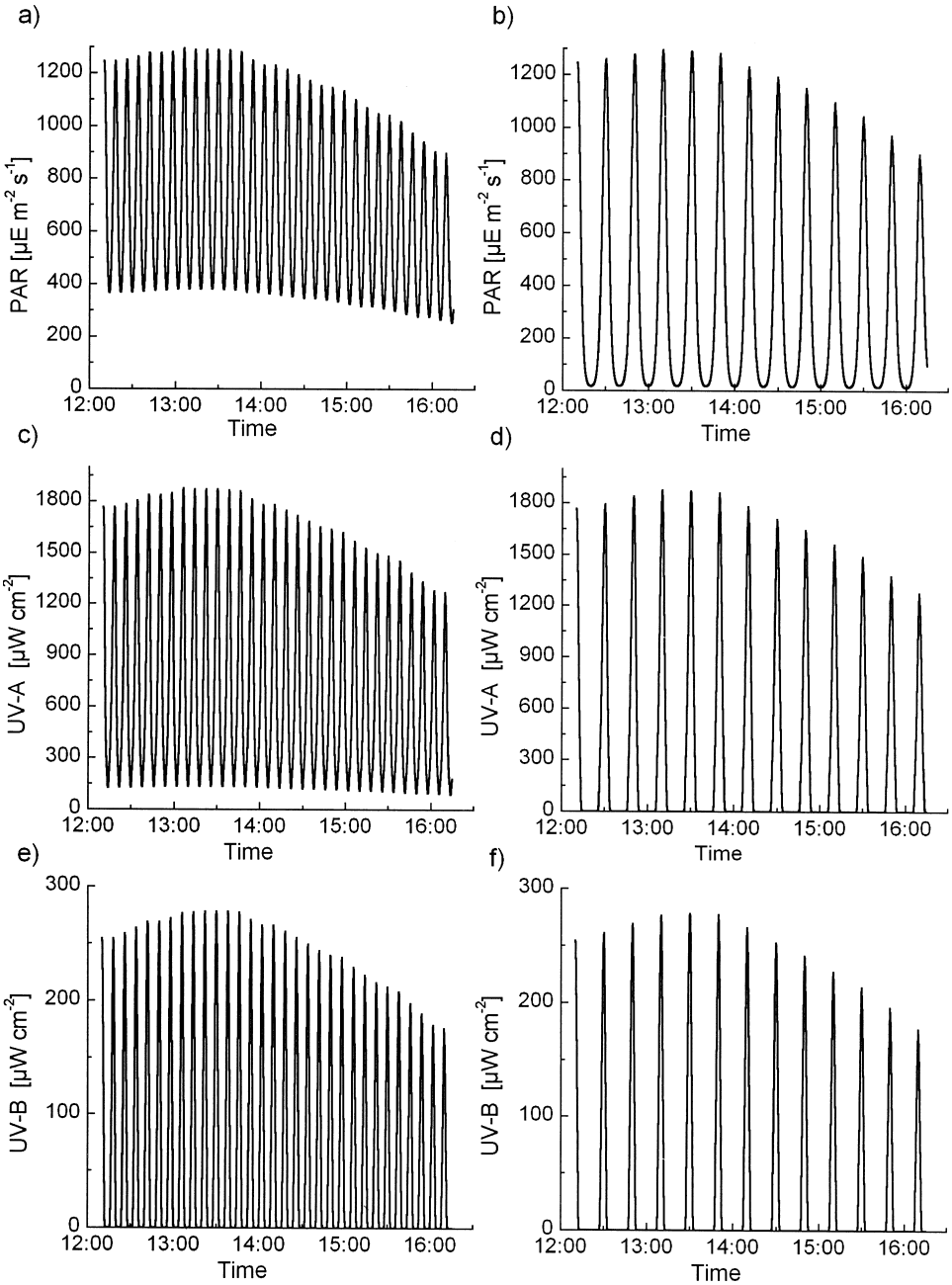

Figure 3. Time course of intensity of PAR (a, b), UV-A (c, d) and UV-B (e, f) available to phytoplankton moved from 0–3.9 m (a, c, e) and from 0–14 m (b, d, f)

Table 1. Time and depth integrated doses and intensities of photosynthetically active radiation (PAR), UV-A and UV-B received by vertically moved samples for 4:05 h (Sept. 13) and 4:00 h (Sept. 15) incubation time

	September 13		September 15		
	0–3.9 m	0–14 m	0–2 m	0–3.9 m	0–10 m
PAR [E m^{-2}]	1.02	0.51	1.16	0.93	0.56
PAR [µE m^{-2} s^{-1}]	692	345	809	643	386
UV-A [J cm^{-2}]	10.6	4.96	13.6	9.65	5.31
UV-A [µW cm^{-2}]	720	337	944	670	368
Relative time with UV-A < 1 µW cm^{-2}	0.0%	53.3%	0.0%	0.0%	42.6%
UV-B [J cm^{-2}]	1.00	0.52	1.35	0.89	0.53
UV-B [µW cm^{-2}]	68	35	94	62	37
Relative time with UV-B < 1 µW cm^{-2}	40.6%	72.0%	0.0%	40.7%	67.5%

from 0–10 m. Carbon assimilation of phytoplankton kept in the upper water layer (0–2 m) was inhibited by strong light.

Rates of carbon assimilation were lower in quartz bottles (with UV) than in Duran bottles which partially excluded UV ($\lambda < 350$ nm). The reduction varied in dependence of mixing depth. Up to a mixing depth of 10 m, UV depressed the total carbon assimilation rates by 10–30%. In the deepest mixed sample (0–14 m depth), assimilation rates in quartz bottles achieved 93% of the incubations with low UV. Particulate ^{14}C assimilation decreased by 20–25% in UV-bottles at mixing depths up to 10 m. It was not significantly reduced at deepest mixing (0–14 m). Exudation was enhanced by UV at 3.9 m mixing depth (120–134% of Duran bottles) and declined during deeper mixing by about 29% (see Fig. 5).

3. Inhibition model

The calculated relative production (P/P_{max}) was highest in both quartz and Duran bottles at depths of about 2 m (Fig. 6). Phytoplankton attained only 70% (quartz) or 75% (Duran bottle) of the maximum production even in the optimum layer. The differences between both bottle types were highest near the water surface and negligible below about 4 m.

The biological weighting function for L. Lucerne of Neale et al. (2001 a, this issue) was also used to calculate the time course of inhibition during vertical transport through the underwater light field. Figure 7 illustrates the time courses of inhibition factor E^*_{inh} and relative production P/P_{max} during circular movement between water surface and 14 m depth. The circular path of the bottles caused extended residence periods near the water surface and at depth with rapid transitions in between. For much of the cycle there was no UV, but photosynthesis was light limited. This was followed by a relatively long episode near the surface with strong inhibition. As a

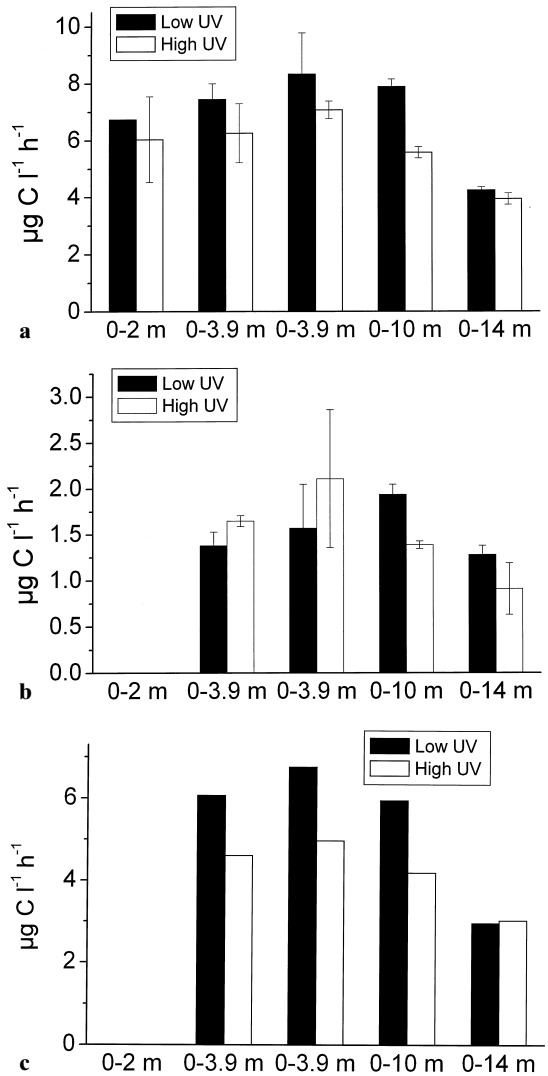

Figure 4. Average and standard deviation of total carbon assimilation (a), exudation (b) and particulate carbon assimilation (c) with high (quartz) and low (Duran) UV on Sept. 13 and 15, 1999

result, the impact of UV in the quartz bottles was stronger on P/P_{max} (which includes the effect of light limitation) than on $1/[1 + E^*_{inh}]$ when mixing depth exceeded 4 m (Table 2).

The parameters of inhibition were integrated over time to allow for comparison with measured data. The mean effective fluence rate for inhibition (E^*_{inh}) ranged from 0.10–0.31 in Duran and from 0.15–0.5 in quartz bottles. The ratio of modelled actual to potential photosynthesis (P/P_{max}) declined with increasing mixing depth

Table 2. Parameters of inhibition calculated with the BWF-PI model for phytoplankton of Lake Lucerne incubated in quartz and Duran bottles. Light conditions and mode of sample movement as on September 13 and 15, 1999

	Depth range Date	0–2 m Sept. 15	0–3.9 m Sept. 13	0–3.9 m Sept. 15	0–10 m Sept. 15	0–14 m Sept. 13
$1/(1+E^*_{Inh})$	Quartz	0.66	0.74	0.76	0.86	0.87
	Duran	0.76	0.80	0.83	0.90	0.91
	Q/D	87.5 %	91.5 %	92.1 %	95.9 %	96.3 %
P/P_{max}	Quartz	0.61	0.58	0.62	0.43	0.32
	Duran	0.70	0.64	0.68	0.47	0.35
	Q/D	87.2 %	90.3 %	91.2 %	92.6 %	91.5 %

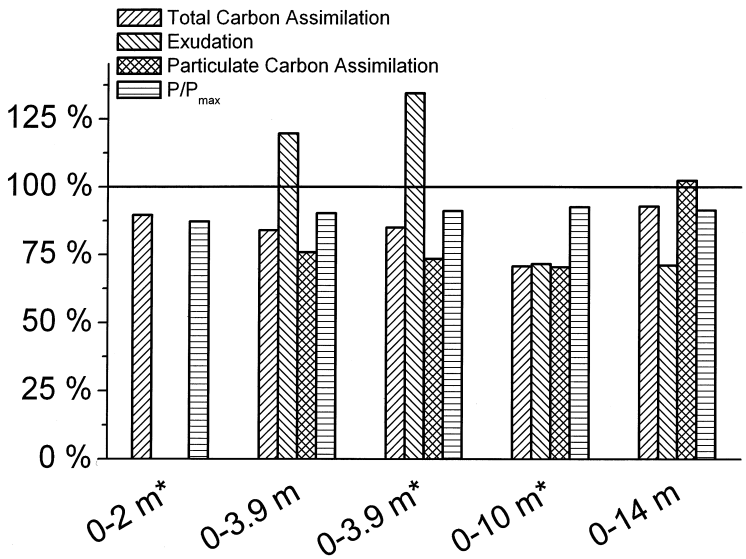

Figure 5. Effects of UV on total C assimilation, exudation and particulate C assimilation of phytoplankton moved through different mixing depths (samples with low UV = 100 %, the asterisks indicate incubation at September 15, no marker = September 13, 1999). The modelled inhibition parameter P/P_{max} is given for comparison

and was higher in Duran than in quartz bottles (Table 2). The difference between quartz and Duran bottles in computed photosynthesis ranged from 7.4–12.8 %.

Discussion

Photoinhibition by UVR was observed in the ocean (Helbling et al., 1994; Buma et al., 1996) as well as in freshwater systems (Gala and Giesy, 1991; Kinzie et al., 1998). The depth and stability of the vertical mixed layer was pointed out as an important

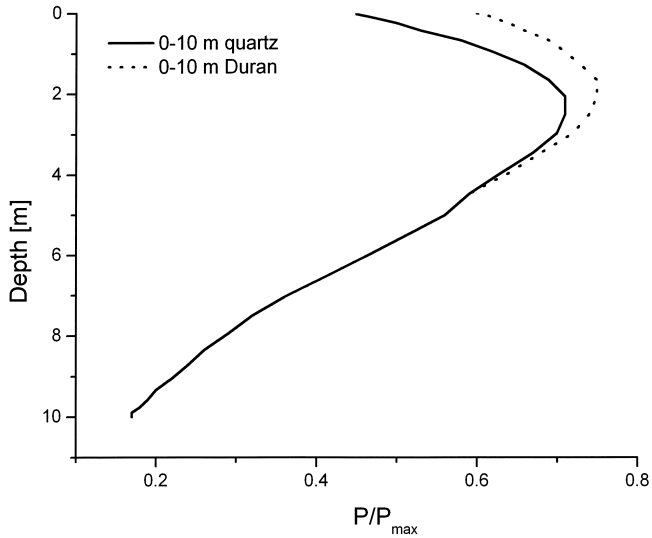

Figure 6. Vertical profile of calculated relative production (P/P_{max}) in quartz bottles with high UV (solid line) and in Duran bottles with low UV (dotted line)

regulating mechanism for photoinhibition of phytoplankton (Helbling et al., 1994; Neale et al., 1998).

In Lake Lucerne, Bossard et al. (2001, this issue) compared carbon assimilation in bottles with and without UV at fixed depths between 0 and 5 m on 13 September, 1999. In this experiment, inclusion of UV-A + B caused an average decline in C assimilation of about 25%. Depression was most severe in samples kept near the water surface. However, results can not be directly compared with circulated bottles because the fixed depth incubation used different spectral treatments (UV-A + B transparent quartz and UV opaque plastic). We therefore applied the BWF-PI model to compare production in fixed depth vs. circulated samples that are exposed to the same average weighted irradiance. According to the model, the average E^*_{Inh} was 0.46 for the mid-depth (0–3.9 m) incubations on 13 September. A fixed depth incubation at 1.2 m would have also experienced an E^*_{Inh} of 0.46 and relative inhibition ($1-1/[1+E^*_{Inh}]$) of 32% compared to 26% calculated for the 0–3.9 m circulated bottle. The 6% reduction in inhibition is not the result of a dynamic response (which is absent from the BWF-PI model) but instead from the non-linear (hyperbolic) relationship of photosynthetic response to UV (Lesser et al., 1994; Neale, 2000). Circulated bottles receive most of their UV exposure from high surface irradiance which is less efficient (per unit exposure) in inducing inhibition than moderate irradiance. Likewise, a fixed depth incubation would receive an exposure of 0.23 at 2.1 m and exhibit a 18% inhibition compared to the 13% estimated for 0–14 m circulated bottle, which received similar exposure. The actual inhibition at 1.2 m and 2.1 m during static incubation (estimated by interpolation from the standard profile presented by Bossard et al., 2001, this issue) was 40% and 24%, respectively. This is a stronger response than was estimated by the BWF-PI model under the same

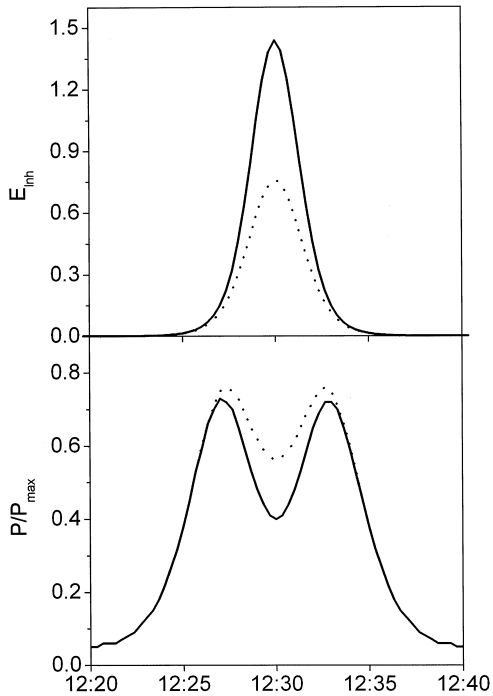

Figure 7. Time course of calculated parameters of UV-inhibition in bottles with high UV (quartz, solid line) and with low UV (Duran, dotted line) moved at a circular path between surface and 14 m depth, September 15, 1999. Top: biologically effective fluence rate for inhibition of photosynthesis E^*_{inh}, bottom: relative production P/P_{max}

irradiance conditions, but the difference between model and observed is within experiment error (Neale et al., 2001 a, this issue). However, we can not exclude the possibility that there may have been a cumulative effect of UV over 4 h static exposure, a response that is not included in the BWF-PI model.

These results indicate that several mechanisms can cause more severe damage by constant UV compared to fluctuating UV of the same dosage. The non-linear relationship between inhibition and cumulative UV exposure in the Weddell-Scotia Confluence (Neale et al., 1998) resulted in differing impacts of UV in modelled static vs. circulating water columns depending on mixing depth. Depression of integrated primary production was enhanced in shallow mixed layers but reduced in deep mixed layers. The latter result is similar to our results for Lake Lucerne. Kinzie et al. (1998) noticed a higher induction of UVR-absorbing mycosporine-like amino acids in benthic communities (which were exposed to rather constant light intensities) than in planktonic organisms (which received fluctuating light). The importance of fluctuating light pulses of PAR was also pointed out by Flameling and Kromkamp (1997). They demonstrated for cultures of *Scenedesmus protuberans* that efficiency of photosynthesis decreases during (at the short-term) constant light conditions but remained high at fluctuating light of the same dosage. Cullen and

Lesser (1991) speculated that a certain time period (in their experiments with a marine diatom ca. 30 min) is necessary to balance UV damage and repair mechanisms. They also stressed the importance of intensity and duration of UV exposure. Short exposures to high intensities of UV could cause higher damage to phytoplankton than long exposures to low intensities.

On the other hand, the BWF-PI model was based on measurements of photosynthesis made under constant polychromatic UV-PAR treatments during 1 h exposures. The model does not include the dynamics of damage and repair under fluctuating light. The nearly perfect agreement between inhibition rates measured under fluctuating light and modelled rates (Fig. 5) seems to indicate surprisingly low influence of dynamic adaptation. This could occur if the rate of dynamic adjustment (time period to attain steady-state) was much faster in the Lake Lucerne assemblage than the 30 min observed by Cullen and Lesser (1991), also if any lag in inhibition is matched by a corresponding lag in recovery.

Bottles excluding UV were not incubated at fixed depths below 5 m, so we do not know the depth limit of UV effects under constant light conditions. The model calculated similar photosynthesis in quartz and in Duran bottles at depths below 4 m (Figure 6). At this depth, about 99% of incident UV-B were attenuated. In the mixing approach, UV-B inhibition was non-negligible up to a mixing depth of 10 m. Gala and Giesy (1991) observed, that UV-inhibition of primary production was restricted to the first 6 metres of Lake Michigan, which was 1% of UV-intensity at the lake surface.

The UV dosage received by suspended algae depends on the ratio of transmission depth to mixing depth. In Lake Lucerne, the steep thermal gradient shown in Figure 2 indicated a 6–7 m mixing depth during our experiments. Most phytoplankton was concentrated below the mixed layer at a depth of 6–10 m. This metalimnetic phytoplankton received about 1–2% of the UV-A and 0.01% of the UV-B intensity of the water surface. It was much less affected by UV than the epilimnetic phytoplankton which was subjected to about 45% of the incident UV-A and 30% of the UV-B during circulation in the upper 7 m. Metalimnetic phytoplankton thus efficiently avoided UV damage as long as it was not mixed into the epilimnetic layer. Any erosion of the metalimnion by increased wind speeds would cause suddenly increased UV exposure of the re-mixed algae.

Intensity and depth of turbulent mixing of Lake Lucerne were not studied during our experiments. Our lifts simulated circular paths of planktonic algae which typically occur in Langmuir cells. Langmuir circulation is caused by wind of medium speed in the upper layer of lakes and ocean. The speed of rotation is governed by the wind speed and the mixing depth and may range from 10–60 min per turn under conditions of Lake Lucerne (see Buranathanitt et al., 1982). This roughly met the rotation frequency used in our experiments.

Low phosphorus concentrations (TP < 1 µg l^{-1}) could have further influenced the sensitivity of phytoplankton. Karentz et al. (1994) speculated that phytoplankton may be more affected by UV when cells are deficient in nutrients.

A clear influence of UVR on photosynthetic extracellular release (PER) could be detected. Especially in the upper mixed layers (0–4 m) an enhancement of 20–30% of PER in quartz bottles in comparison to Duran bottles indicates cell damage or a change of $DO^{14}C$-composition. Buma et al. (1996) noticed a change in

intracellular composition of phytoplankton during UV-exposure, especially an increase of proteins under low and moderate levels of UVR, probably associated with the biosynthesis of UV stress proteins. This might change PER too. Pausz and Herndl (1999) noticed a decrease of PER by UV in a diatom culture in the same range as total primary production is reduced, but no changes in percentage of PER to total amount of fixed carbon. They further observed a changed uptake of PER by bacteria under UV-exposure, indicating a qualitative change of PER. Kieber et al. (1989) mentioned an increased release of labile DOC as a result of UV radiation, probably stimulating bacterioplankton and shifting carbon flow in aquatic food webs.

Our preliminary results indicate serious depression of carbon assimilation of phytoplankton due to UVR even in well-mixed environments. Depression was low at circulation through the whole euphotic zone and may disappear at even deeper mixing. There was a tendency of lower photoinhibition per UV dosage at fluctuating than at constant light intensities. Response of phytoplankton to UV obviously depends not only on intensity or dosage of radiation but also on its dynamics. The latter is a function of depth, speed and type of mixing as well as of optical properties of the water. In order to understand UV effects on phytoplankton in well-mixed environments, we have to study hydrodynamical conditions as well as kinetics of photoinhibition and recovery in more detail.

ACKNOWLEDGEMENTS

This study was carried out during the 7th International GAP Workshop, held on 9–17 Sept. 1999 in Zürich, Switzerland, and supported by the Swiss National Science Foundation (SNF), the Swiss Academies of Natural and Technical Sciences (SANW and SATW), the Swiss Society of Hydrology and Limnology (SGHL), by EAWAG, Zürich Water Supply and the University of Zürich, as well as by Hoffmann-La Roche, Lonza, Novartis, Canberra Packard S.A, Millipore AG and Faust Laborbedarf AG.

We would like to thank Peter Bossard for the good working conditions at Kastanienbaum and the support of our field work. Daniel Steiner measured basic limnological parameters, global radiation and pigment concentrations. Many thanks to him for his help in the radioisotope lab and during field work.

REFERENCES

Behrendt, H., 1989. Devices for turbulence simulation during in-situ measurements of biological processes in aquatic ecosystems. II. A bottle lift for simulation of vertical movement in natural waters. Acta hydrophys. 33: 9–14.

Benndorf, J. and E. Werner, 1980. Berechnung der Wachstumsrate des Phytoplanktons in durchmischten Wasserkörpern. Limnologica (Berlin) 12: 23–31.

Bossard, P., S. Gammeter, C. Lehmann, F. Schanz, R. Bachofen, H.R. Bürgi, D. Steiner and U. Zimmermann, 2001. Limnological description of the Lakes Zürich, Lucerne, and Cadagno. Aquat. Sci. 63/3: 225–249.

Bühlmann, B., P. Bossard and U. Uehlinger, 1987. The influence of longwave ultraviolet radiation (UV-A) on the photosynthetic activity (^{14}C-assimilation) of phytoplankton. J. Plankton Res. 9: 935–943.

Buma, A.G.J., H.J. Zemmelink, K. Sjollema, W.W.C. Gieskes, 1996. UVB radiation modifies protein and photosynthetic pigment content, volume and ultrastructure of marine diatoms. Mar. Ecol. Prog. Ser. 142: 47–54.

Buranathanitt, T., D.J. Cockrell, P.H. John, 1982. Some effects of Langmuir circulation on the quality of water resource systems. Ecol. Modell. 15: 49–74.

Bürgi, H.R., C. Heller, S. Gaebel, N. Mookerji, and J.V. Ward, 1999. Strength of coupling between phyto- and zooplankton in Lake Lucerne (Switzerland) during phosphorus abatement subsequent to a weak eutrophication. J. Plankton Res. 21: 485–507.

Cullen, J.J. and M. Lesser, 1991. Inhibition of photosynthesis by ultraviolet radiation as a function of dose and dosage rate: results for a marine diatom. Marine Biology 111: 183–190.

Cullen, J.J. and P.J. Neale, 1997. Biological weighting functions for describing the effects of ultraviolet radiation on aquatic systems, pp. 97–118. In: D.-P. Häder [ed.] Effects of ozone depletion on aquatic ecosystems. R. G. Landes.

Cullen, J.J., P.J. Neale and M.P. Lesser, 1992. Biological weighting function for the inhibition of phytoplankton photosynthesis by ultraviolet radiation. Science 258: 646–650.

Flameling, I.A. and J. Kromkamp, 1997. Photoacclimation of *Scenedesmus protuberans* (Chlorophyceae) to fluctuating irradiances simulating vertical mixing. J. Plankton Res. 19: 1011–1024.

Gala, W.R. and J.P. Giesy, 1991. Effects of ultraviolet radiation on the primary production of natural phytoplankton assemblages in Lake Michigan. Ecotox. Environm. Safety 22: 345–361.

Helbling, E.W., V.E. Villafane and O. Holm-Hansen, 1994. Effects of ultraviolet radiation on Antarctic marine phytoplankton photosynthesis with particular attention to the influence of mixing. Ultraviolet radiation in Antarctica: Measurements and biological effects. Antarctic research series 62: 207–227.

Jewson, D.H. and R.B. Wood, 1975. Some effects on integral photosynthesis of artificial circulation of phytoplankton through light gradients. Verh. Intern. Verein. Limnol. 19: 1037–1044.

Karentz, D., R.B. Bothwell, A. Coffin, G.J. Hanson, G.J. Herndl, S.S. Kilham, M.P. Lesser, R.E. Moeller, D.P. Morris, P.J. Neale, R.W. Sanders, C.S. Weiler and R.G. Wetzel, 1994. Impact of UV-B radiation on pelagic freshwater ecosystems: Report of working group on bacteria and phytoplankton. Arch. Hydrobiol. Beih. 43: 31–69.

Kieber, D.J., J. McDaniel and K. Mopper, 1989. Photochemical source of biological substrates in seawater: implications for carbon cycling. Nature 341: 637–639.

Kinzie, R., A.T. Banaszak and M. Lesser, 1998. Effects of UV-radiation on primary productivity in a high altitude tropical lake. Hydrobiologia 385: 23–32.

Lesser, M.P., J.J. Cullen and P.J. Neale, 1994. Carbon uptake in a marine diatom during acute exposure to ultraviolet B radiation: relative importance of damage and repair. J. Phycol. 30: 183–192.

Marra, J., 1978. Phytoplankton photosynthetic response to vertical movement in a mixed layer. Marine Biology 46: 203–208.

Mitchell, D.L. and D. Karentz, 1993. The induction and repair of DNA photodamage in the environment. In: Young, A.R., L. Björn, J. Moan and W. Nultsch (ed): Plenum Press: Environmental UV photobiology. 245–377.

Neale, P.J., E. Litchman, C. Sobrino, C. Callieri, G. Morabito, V. Montecino, Y. Huot, P. Bossard, C. Lehmann and D. Steiner, 2001a. Quantifying the response of phytoplankton photosynthesis to ultraviolet radiation: Biological weighting functions versus *in situ* measurements in two Swiss lakes. Aquat. Sci. 63/3: 265–285.

Neale, P.J., P. Bossard and Y. Huot, 2001b. Incident and *in situ* irradiance in Lakes Cadagno and Lucerne: A comparison of methods and models. Aquat. Sci. 63/3: 250–264.

Neale, P.J., 2000. Spectral weighting functions for quantifying the effects of ultraviolet radiation in marine ecosystems, pp. 73–100. In: S.J. de Mora, S. Demers and M. Vernet [eds.], The effects of UV radiation on marine ecosystems. Cambridge Univ. Press.

Neale, P.J., M.P. Lesser and J.J. Cullen, 1994. Effects of ultraviolet radiation on the photosynthesis of phytoplankton in the vicinity of McMurdo Station (78°S), pp. 125–142. In: C.S. Weiler and P.A. Penhale [eds.], Ultraviolet Radiation in Antarctica: Measurements and Biological Effects. Am. Geophysical Union.

Neale, P.J., R.F. Davis and J.J. Cullen, 1998. Interactive effects of ozone depletion and vertical mixing on photosynthesis of Antarctic phytoplankton. Nature 392: 585–589.

Nixdorf, B. and H. Behrendt, 1991. Discrepancies between O_2- and ^{14}C-method resulting from measurements of primary production under consideration of vertical mixing in a shallow eutrophic lake. Verh. Intern. Verein. Limnol. 24: 1268–1271.

Pahl-Wostl, C. and D.M. Imboden, 1990. DYPHORA – a dynamic model for the rate of photosynthesis of algae. J. Plankton Res. 12: 1207–1221.

Pausz, C. and G.J. Herndl, 1999. Role of ultraviolet radiation on phytoplankton extracellular release and its subsequent utilization by marine bacterioplankton. Aquat. Microb. Ecol. 18: 85–93.

Vincent, W.F. and P.J. Neale, 2000. Mechanisms of UV damage in aquatic organisms, pp. 149–176. In: S.J. de Mora, S. Demers and M. Vernet [eds.], The effects of UV radiation on marine ecosystems. Cambridge Univ. Press.

Zagarese, H., W. Cravero, P. Gonzalez and F. Pedrozo, 1998a. Copepod mortality induced by fluctuating levels of natural ultraviolet radiation simulating vertical water mixing. Limnol. Oceanogr. 43: 169–174.

Zagarese, H., B. Tartarotti, W. Cravero and P. Gonzalez, 1998b. UV damage in shallow lakes: the implications of water mixing. J. Plankton Res. 20: 1423–1433.

Received 3 March 2000;
revised manuscript accepted 22 September 2000.


To access this journal online:
http://www.birkhauser.ch