Quantifying the response of phytoplankton photosynthesis to ultraviolet radiation: Biological weighting functions versus *in situ* measurements in two Swiss lakes

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ABSTRACT

The sensitivity of photosynthesis to ultraviolet radiation (UV) was assessed for phytoplankton assemblages in two Swiss lakes, pre-alpine Lake Lucerne (Vierwaldstättersee) and alpine Lake Cadagno, using both *in situ* and laboratory incubations. Biological weighting functions for UV inhibition of photosynthesis (BWFs) were determined in the laboratory using polychromatic exposures in a Xe-lamp based incubator. Samples were concurrently incubated *in situ* under UV exposed and protected bottles (profiles 0–5 m), while additional spectral treatments were carried out at the 50% UV-B penetration depth: full spectrum, UV-A only (Mylar protected) and UV protected quartz tubes. Both particulate (> 0.2 µm) and total organic carbon incorporation were measured. Measured attenuation coefficients and incident UV spectral irradiance data was used to evaluate a BWF/photosynthesis-irradiance model (BWF/P-I) for *in situ* exposure conditions and compared with measurements. The BWFs showed sensitivity across the UV spectrum at similar, though somewhat lower, levels than an average BWF for marine assemblages. Relative photosynthesis *in situ* (UV exposed/UV excluded) was about 40% at the surface and about 60% at the 50% UV-B penetration depth. Similar inhibition was predicted by the BWF/P-I model. Generally, full spectrum (UV-B and UV-A) exposure had little additional effect compared to UV-A only exposure. Reciprocal transfer of samples between lakes showed enhancement of UV effects in L. Cadagno compared to incubation of the same sample in L. Lucerne, consistent with increased UV sensitivity due to the 5°C cooler water temperature in L. Cadagno. Similarly, BWF prediction of *in situ* response in L. Cadagno was improved by increasing UV sensitivity according to a Q_{10} of 2.

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Full profile calculations using the BWF/P-I model suggest stronger effects of UV on L. Lucerne compared to L. Cadagno phytoplankton due to greater sensitivity of the assemblage combined with higher overall transparency to UV relative to PAR in L. Lucerne. The BWF/P-I model was a good overall predictor of UV-dependent photosynthetic performance in these lakes.

Introduction

The inhibition of aquatic primary production by solar ultraviolet radiation (UV) has been established in a wide range of freshwater and marine planktonic environments (Karentz et al., 1994; de Mora et al., 2000). Though the significance of UV as factor affecting productivity has been known for some time (Lorenzen, 1979), only recently has work focused on developing predictive models that can account for UV effects within the overall context of aquatic productivity models (review, Neale, 2000). These models are useful tools for predicting the possible effects of environmental changes that may increase UV, such as decreases in stratospheric ozone (Herman and McKenzie, 1999) and decreases in chromophoric dissolved organic carbon (Schindler et al., 1996). To this date, however, most models have been defined for marine systems, and little is known about their applicability to freshwater phytoplankton production (Smith et al., 1998).

Experimental exposures to determine the spectral dependence of UV effects are commonly made with either solar radiation or a lamp (e.g. xenon arc). The solar *in situ* incubations have the advantage of a more accurate reproduction of natural UV exposure, whereas lamp exposures in a laboratory can be more precisely controlled (Neale, 2000). There are numerous investigations of UV inhibition of photosynthesis using either approach (Smith and Cullen, 1995), but there are only a few cases where the two approaches have been compared (Lesser et al. 1996). A basic approach is to use responses to lamp exposures to fit a biological weighting function/photosynthesis-irradiance (BWF/P-I) model, which is then applied to spectral irradiance to predict *in situ* photosynthesis of the same sample. Similarly, Huot et al. (2000) developed models to predict *in situ* DNA damage based on laboratory-determined weighting functions for DNA damage and repair, and compared the model results to net DNA damage measured during *in situ* incubation of marine bacterioplankton. Since the duration of the *in situ* incubation may differ from the lamp exposure, the model must also define the relationship between exposure and response (Cullen and Neale, 1997). In many marine phytoplankton assemblages and cultures of temperate marine phytoplankton inhibition is a function of biologically effective irradiance (e.g. Cullen et al., 1992; Lesser et al., 1994; Neale et al., 1998a; Banaszak and Neale, 2001), though dependence on cumulative exposure has also been reported (Neale et al., 1998b). The irradiance-dependent response does not obey reciprocity and is consistent with an equilibrium between damage and repair processes for exposure time scales of 0.5 to 4 h. Lesser et al. (1996) found good agreement between the predictions of an irradiance-dependent BWF/P-I model and observed inhibition by solar UV in Antarctic diatoms.

In the investigation reported here, the UV sensitivity of photosynthesis by natural phytoplankton assemblages from two lakes in Switzerland was assessed during September 1999. Both *in situ* and laboratory incubations were performed, with

measurements of ^{14}C incorporation into both particulate (> 0.2 µm) and total organic carbon. Separate measurements were also made of photosynthetic activity in the nano- (> 2 µm) and pico- (< 2 µm) phytoplankton fractions, these will be reported elsewhere (Callieri et al., 2001; and Teubner et al., 2001, this issue). Inhibition potential as a function of UV wavelength was quantified using biological weighting functions (BWFs) which are associated with a photosynthesis model (BWF/P-I model). The BWF/P-I model was used to predict *in situ* inhibition by UV radiation in the two lakes using *in situ* spectral irradiance. The predictions of the model are compared with *in situ* incubations conducted during the same period.

Site Description

All experiments were conducted as part of the International Association of Theoretical and Applied Limnology (SIL) working group on Aquatic Primary Productivity (GAP) workshop at the Swiss Federal Institute for Environmental Science and Technology (EAWAG), Limnological Research Center in Kastanienbaum, Switzerland, during the period September 8–15, 1999. Natural phytoplankton assemblages in two lakes were the focus of the experiments conducted by the Ultraviolet Radiation experimental group. Lake Lucerne (Vierwaldstättersee) is an oligotrophic pre-alpine lake (434 m a.s.l., 113 km^2 surface area, 104 m mean depth) in Central Switzerland. During the GAP Workshop (September 7, 1999) the phytoplankton assemblage consisted of chrysophytes (3.0 g m^{-2}), and centric (2.3 g m^{-2}) and pennate (1.1 g m^{-2}) diatoms. Lake Cadagno is a mesotrophic alpine lake (1923 m a.s.l., 0.26 km^2 surface area, 9 m mean depth) in the southern part of Central Switzerland, maximum depth is about 20 m but the bottom 10 m is a meromictic monimolimnion (Peduzzi et al., 1998). UV transparency of both lakes is modest, with significant (>10% of surface UV-B) UV exposures to a near-surface layer extending to about 1 m in L. Cadagno and to about 3 m in L. Lucerne (Neale et al., 2001a, and Bossard et al., 2001, this issue). On 13 September (see Camacho et al., 2001) the phytoplankton community of the euphotic zone was dominated by the green algae *Echinocoleum elegans* and *Elakatothrix* sp., followed by the diatom *Cyclotella radiosa*, other chlorophytes, diatoms, and autotrophic picocyanobacteria. Total phytoplankton fresh weight from 0–10 m depth was 43 g FW m^{-2} (calculated from data obtained by Camacho et al., 2001). For additional information on conditions in both lakes during the GAP workshop see paper by Bossard et al. (2001, this issue).

Materials and Methods

Laboratory incubations

All laboratory measurements were conducted at the EAWAG laboratory in Kastanienbaum, Switzerland. Samples were taken near sunrise at 1 m (Lucerne) and 0.5 m (Cadagno), transported to the EAWAG lab, and maintained at ambient temperature and low light until use around local solar noon (13:00 h). The dependence of photosynthesis on PAR and inhibition by UV radiation was measured as the rate

of uptake of $H^{14}CO_3^-$ in a special incubator (the "photoinhibitron") which provided 72 spectral treatments (8 UV cutoff filters each with 9 irradiances, maximum 2000 µmol m^{-2} s^{-1}) during a 1-hour exposure to a Xe lamp (cf. Neale et al., 1998a). Sample aliquots were 2 ml for each treatment contained in quartz cuvettes positioned in a temperature-regulated block (18 °C). Effective sample temperature is about 2 °C higher than block temperature. The spectral irradiance for each treatment was measured with a scanning monochromator system as described (Neale et al., 2001 b) calibrated using a NIST-traceable 1000 W standard lamp. BWFs were determined from the measured rates of photosynthesis and spectral irradiance using a principal component analysis as previously described (Cullen et al., 1992). The data were fit to the following equation:

$$P^B = P_S^B (1 - e^{-E_{PAR}/E_S}) \frac{1}{1 + E_{inh}^*} \qquad (1)$$

where P^B (mg C mg Chl^{-1} h^{-1}) is the rate of photosynthesis normalized to chlorophyll a (Chl) content, P_s^B is a saturated rate of photosynthesis in the absence of photoinhibition, and E_s is a saturation parameter for PAR (400–700 nm) irradiance (E_{PAR}, W m^{-2}). E_{inh}^* is a dimensionless inhibition index defined as follows:

$$E_{inh}^* = \sum_{\lambda = 280}^{400} \varepsilon(\lambda) \, E(\lambda) \, \Delta\lambda \qquad (2)$$

where $\varepsilon(\lambda)$ is a biological weight (mW m^{-2})$^{-1}$ at wavelength λ (nm) and $E(\lambda)$ is spectral irradiance at λ (mW m^{-2} nm^{-1}). Treatment E_{PAR} and fitted E_s are given in units of µmol m^{-2} s^{-1} for comparison with *in situ* irradiance, using the conversion factor (for the Xe lamp) of 4.3 µmol J^{-1}.

A second set of photosynthesis-irradiance incubations was conducted to obtain better estimates of photosynthetic dependence on PAR. The incubator is a modification of the small volume "photosynthetron" design (Lewis and Smith, 1983), in which irradiance is provided by two 250 W and two 400 W high intensity discharge lamps (Osram HQI-D). Samples are incubated in 20 ml scintillation vials that are mounted in metal racks plumbed with water flow to maintain temperature. Samples are shaken during the incubation. The output of these lamps includes UV as is typical for metal halide lamps. The spectral distribution of the lamp irradiance was estimated from the relative lamp energy distribution (as provided by the manufacturer) scaled by the UV-A irradiance as measured by the Macam SD/104 meter. Scaling took into account the spectral response of the Macam sensor as provided by the manufacturer (see companion paper by Neale et al. 2001a, this issue) and the spectral transmission of the borosilicate glass of the scintillation vial. The estimated spectral irradiance was used to evaluate E_{inh}^* and P^B determined from the photoinhibitron incubations.

In situ incubations

In situ inhibition of photosynthesis by UV was measured in profiles of photosynthesis exposed and protected from UV, and in single depth incubations employing

multiple spectral treatments and measuring carbon incorporation into particulate and total organic carbon. Productivity profiles were measured on September 13 (L. Lucerne) and September 14 (L. Cadagno), samples were incubated in quartz (surface only), UV transparent (to 300 nm) Duran, and UV protected (acrylic sleeves) bottles of the same shape and volume (120 ml) at depths of 0.5, 1, 1.5, 2.5, 3.75 and 5 m. A complete description of the protocols and irradiance data for these profiles is given by Bossard et al. (2001, this issue).

Sampling for the single depth incubations was performed at 06:00 h on two days, September 12 and 14, 1999 in both lakes. On September 14, the incubations included a reciprocal exchange of samples between L. Lucerne and L. Cadagno. Samples were maintained at near ambient temperature during transport between lakes in thermally insulated containers. *In situ* carbon assimilation was measured in quartz tubes suspended at the approx. 50% UV-B penetration depth (0.3 m in L. Cadagno, 1.0 m in L. Lucerne). The incubation in L. Cadagno was 4 h duration (11:00–15:00 h Central European Summer Time [CEST = GMT + 2 h]). On September 12, samples were taken from L. Cadagno and incubated between 12:00 and 16:00 h (CEST) in L. Cadagno. Spectral treatments were uncovered quartz tubes (PAB: includes PAR, UV-B and UV-A), quartz tubes wrapped with Mylar D (PA: includes PAR, UV-A), quartz tubes wrapped with Ultraphan (P: PAR only), each in duplicate. The Mylar D film had <1% transmittance below 310 nm, <10% transmittance below 315 nm (the CIE upper wavelength limit for UV-B), <50% transmittance below 320 nm (an alternate upper limit for UV-B), and a transmittance of 90% for PAR and UV-A above 340 nm. The Ultraphan film had < 1% transmittance below 370 nm, < 50% transmittance below 395 nm and 90% transmittance for PAR. The tube volume was 150 ml to which 12.5 µCi NaH^{14}CO$_3$ was added. Total organic carbon assimilated (TOC) was determined using the acid bubbling technique (Gächter and Mares, 1979). The particulate organic carbon (POC) fixation was determined by post incubation differential filtration (Fahnenstiel et al., 1994) using 2 and 0.2 µm Nuclepore™ polycarbonate filters. Total POC fixation is reported as the sum of the two fractions (fractionation results are reported separately Callieri et al., 2001, this issue). Total inorganic carbon was estimated by pH and alkalinity measurements. Carbon-specific growth rate was also measured by the incorporation of NaH^{14}CO$_3$ into chlorophyll *a*, applying the equations of Welschmeyer and Lorenzen (1984) and Redalje (1993) to the chlorophyll concentration at the beginning of the incubation, the chlorophyll specific activity at the end of the incubation, and the activity of inorganic carbon. Chlorophyll *a* (mg Chl m^{-3}) was measured by HPLC on pico- and nano fraction at the beginning of the incubation (Bossard et al., 2001, this issue); we report the sum of the fractions. *In situ* incubations for the reciprocal transfer experiment in L. Lucerne used basically the same experimental design as for L. Cadagno except that the volume of the tubes was about 80 ml. Usable results were only obtained for POC incorporation.

In Situ Irradiance and Productivity Modeling

Attenuation coefficients were estimated from radiometer profiles (Neale et al., 2001a, this issue) and interpolated/extrapolated as necessary to obtain spectral attenuation

290–400 nm (1 nm resolution). Spectral irradiance 290–400 nm ($E(\lambda)$, mW m^{-2} nm^{-1}, 1 nm resolution) as a function of depth and time was then calculated from surface spectral irradiance (Neale et al., 2001a, this issue). In the event of cloud cover that sometimes occurred at L. Cadagno, a proportionality factor (constant with wavelength) was used to obtain agreement with the output of the Macam UV-B sensor at its effective center wavelength, 320 nm (see details in Neale et al., 2001a, this issue). Surface albedo was estimated by Fresnel formula (evaluated at solar zenith angle) since calm, clear conditions prevailed during the experimental period. Weighted irradiance (E_{inh}^*, Equation 2) was then obtained by application of the appropriate BWF and photosynthesis (relative to maximum photosynthesis in absence of inhibition) estimated as $1/(1 + E_{inh}^*)$. Rate estimates were made at the interval of irradiance measurement, i.e., 1 min during operation of the SR18 and 10 min otherwise (Neale et al., 2001a, this issue). Rates were averaged over the incubation period for comparison with observed rates. The UV-A predictions were based on the transmittance of the Mylar D used in the *in situ* incubations.

Biologically weighted UV transparency (m) was calculated as described by Pienitz and Vincent (2000) as:

$$\sum_{\lambda=290}^{400} \frac{1}{K(\lambda)}\, \varepsilon_{300}(\lambda)\, E_{0\,rel}(\lambda)\, \Delta\lambda \tag{3}$$

Where $K(\lambda)$ is attenuation coefficient (m^{-1}), $E_{0\,rel}(\lambda)$ (unitless) is noon incident irradiance spectrum normalized to 400 nm, and $\varepsilon_{300}(\lambda)$ (unitless) is the BWF normalized at 300 nm for inhibition of photosynthesis in each lake.

Results

Laboratory Measurements

Photosynthesis measured in the photoinhibitron is shown in Fig. 1 (example data set for L. Cadagno, September 13, 1999). UV exposure had a very strong effect on phytoplankton photosynthesis in both lakes, with almost 90% inhibition at the highest exposure level and generally a several-fold range between treatments with the most vs. least UV (Fig. 1A). The scatter in the overall photosynthesis vs. E_{PAR} relationship produced by the different UV treatments is almost completely removed by application of the BWF to the treatment spectra (Fig. 1B). The fitted BWF produces a single hyperbolic relationship between photosynthesis and weighted UV (overall $R^2 = 0.97$).
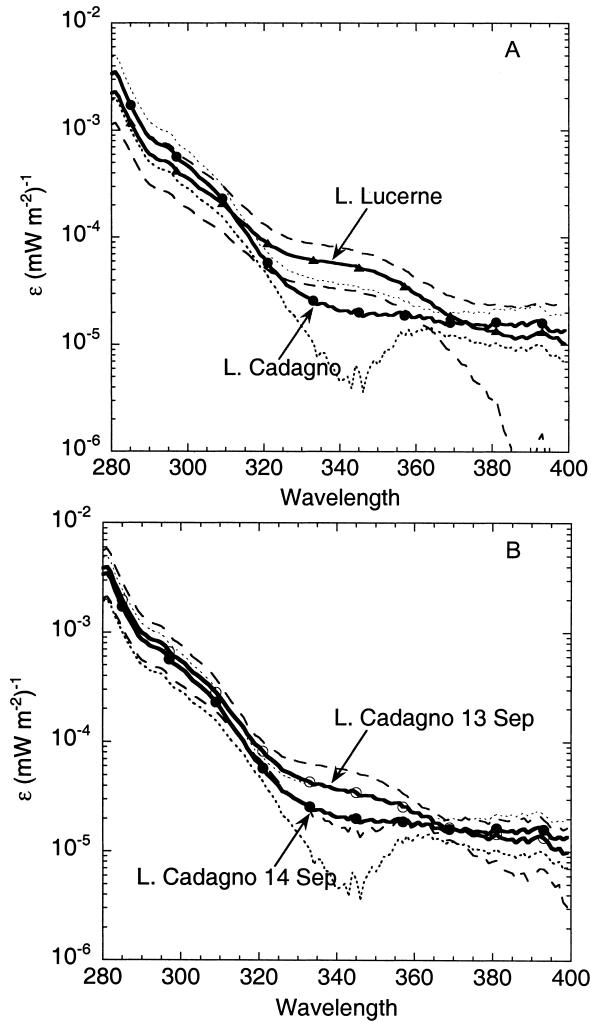
Fitting of the biological weighting functions for inhibition of photosynthesis required using two or three principal (spectral) components as determined by application of a sequential *F*-test ($p < 0.05$) for measurement variance explained by the model (R^2, Table 1). The fitted BWF/P-I model was successful in explaining the UV-dependent variation in photosynthesis, accounting for 97% of the variation for L. Cadagno and 90% of the variation for L. Lucerne. Maximum rate of photosynthesis (P_s^B) ranged between 1.7 and 9 mg C mg Chl^{-1} h^{-1}, and the saturation parameter was in the range of 200 to 300 µmol m^{-2} s^{-1} indicating acclimation to high irradiance in both lakes.
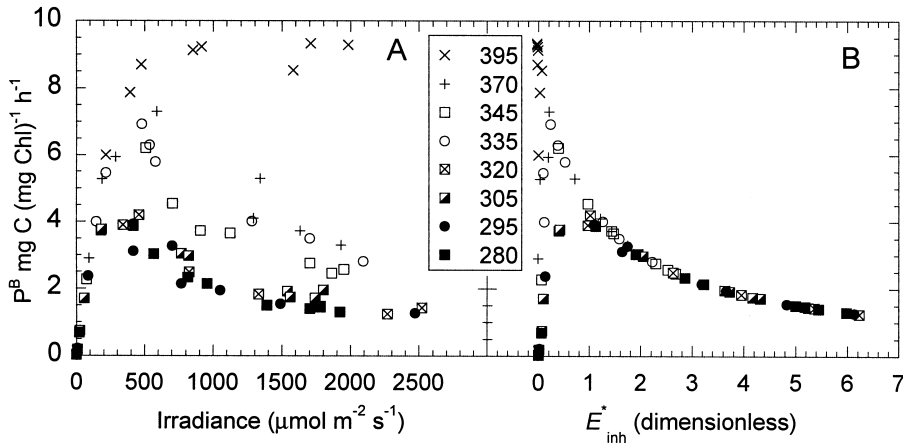
Figure 1. Photosynthesis as measured in the photoinhibitron, example for sample from L. Cadagno, September 13, 1999. (A) Observed rates as a function of E_{PAR}, each symbol denotes a distinct spectral treatment (Xe lamp+long-pass filter), labeled according to the nominal wavelength of 50% transmission, irradiance is further varied by addition of screens. (B) Observed rates as a function of weighted UV irradiance (E^*_{inh}) using the biological weighting function (BWF) fitted for this sample (Fig. 2B). The estimation procedure produces the BWF which best explains inhibition as a hyperbolic function of weighted UV ($1/[1+E^*_{inh}]$), the proportion of variance accounted for by the model (R^2) is 0.97

The BWFs indicated high sensitivity to UV over the full spectral range with the highest weighting coefficients for inhibition of photosynthesis ($\varepsilon(\lambda)$, $[mW\ m^{-2}]^{-1}$) in the UV-B region (Fig. 2). There was no significant inhibitory effect of PAR only exposure (cf. Fig. 1). For the shortest and longest wavelengths of UV, sensitivity of photosynthesis to UV was similar between the lakes, i.e. the weighting coefficients for each lake differed by less than the estimated 95% confidence interval for either BWF. Nevertheless, the L. Lucerne phytoplankton were more sensitive to UV in the 320–360 nm region than phytoplankton from L. Cadagno (Fig. 2A). While there was a significant decrease in P^B_s between the 13th and 14th of September in L. Cadagno, there were only small and not significant differences in the BWFs (Fig. 2B). This suggests that the UV sensitivity of the L. Cadagno phytoplankton remained fairly constant during the GAP period.

Despite our finding of no inhibitory effects of PAR in the BWF incubations, photosynthesis measured in the photosynthetron also exhibited inhibition at high light intensities (examples, Fig. 3). We hypothesized that this inhibition was due to UV emitted by the metal-halide HID lamps used in this incubator. To test this possibility, we applied the BWF/P-I model defined using the photoinhibitron to spectral irradiance in the photosynthetron estimated as described in methods. The BWF/P-I model reproduced observed relative inhibition (scaled by P^B_s) for all the photosynthetron measurements. However, the model was not always a good predictor of absolute rates normalized to chlorophyll (P^B). Measured P^B agreed well with the predictions of the BWF/P-I model for L. Cadagno samples (Fig. 3, circles), though the model overestimated P^B for irradiance > 400 µmol m^{-2} s^{-1}. On the other

Figure 2. Comparisons of biological weighting functions (ε, $[\text{mW m}^{-2}]^{-1}$) for (A) UV inhibition of photosynthesis for L. Cadagno (solid line, circles) and L. Lucerne (solid line, triangles) on September 14, 1999 and for (B) September 13 (open circle) and September 14, 1999 (closed circle) in L. Cadagno. Broken lines show the upper and lower bounds of the estimated 95 % confidence interval for individual weights (ε) for each BWF

hand, P^B for L. Lucerne samples was consistently higher than BWF/P-I predictions (data not shown). Using non-linear regression on the photosynthetron measurements, we estimated that the effective P_s^B for the photosynthetron sample was 1.5 times higher than the P_s^B estimated from the photoinhibitron data and the BWF/P-I model (Table 1). This calculation included only photosynthetron measurements where $E_{PAR} > E_s$ from the BWF/P-I fit, so that photosynthesis would be a simple hyperbolic function of weighted irradiance ($P^B = P_s^B/[1 + E_{inh}^*]$) (Fig. 3). After
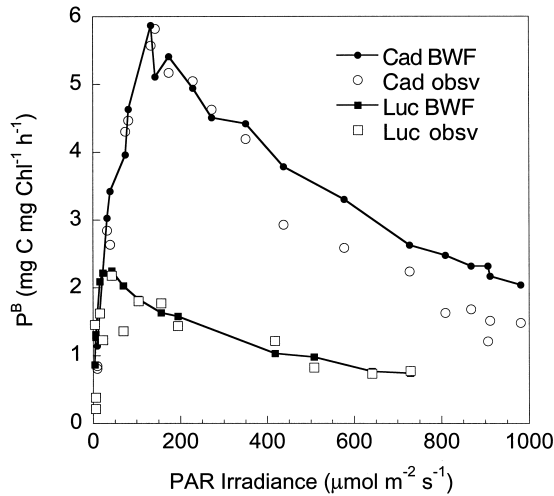
Figure 3. Comparison of photosynthesis measured in the photosynthetron (metal-halide irradiance source) (open symbols) with photosynthesis predicted by the BWF/P-I model (line, filled symbols) defined for the same sample given estimated spectral irradiance in the photosynthetron. For L. Cadagno, prediction was made with the BWF/P-I estimates of P_s^B and E_{inh}^*. For the L. Lucerne samples, $1/(1 + E_{inh}^*)$ was defined using the BWF but P_s^B was estimated by nonlinear regression on $P_s^B/(1 + E_{inh}^*)$. The P_s^B so estimated was 2.6 mg C mg Chl^{-1} h^{-1} compared to 1.7 estimated for the BWF/P-I model. See text for additional details

Table 1. Results of statistical fitting of the BWF/P-I model to photoinhibitron results for L. Cadagno and L. Lucerne samples on September 13 and 14, 1999. PCA components-the number of spectral components which significantly increased the proportion of variance explained by the model (R^2) as determined by the sequential F-test ($p < 0.05$), P_s^B-light saturated rate of photosynthesis (mg C mg Chl^{-1} h^{-1}), E_s -a saturation parameter, ± estimated standard error. The fitted E_s (W m^{-2}) was converted to µmol m^{-2} s^{-1} using a factor of 4.3 µmol J^{-1}

Date	Sample	PCA Components	$P_s^B \pm$ se	$E_s \pm$ se	R^2
13	L. Cadagno	3	9.10 ± 0.62	212 ± 24.5	0.97
14	L. Cadagno	3	3.02 ± 0.25	254 ± 33.0	0.97
14	L. Lucerne	2	1.67 ± 0.37	271 ± 77.0	0.90

accounting for this difference in P_s^B, the BWF/P-I model also reproduced P^B observed for the L. Lucerne samples (Fig. 3). A similar proportion between photosynthetron and BWF/P-I values was seen for a test set of experiments conducted on September 12 (data not shown). It is not clear why such a systematic difference would occur in the measurements for L. Lucerne assemblages but not the L. Cadagno assemblages. Apart from the difference in spectral composition of the light source, the main difference in the incubator designs was the presence of vigorous agitation in the photosynthetron. It is possible that the chrysophyte/diatom-dominated assemblage in L. Lucerne was more sensitive to limitations on the flux of inorganic carbon to the cell in the unagitated state than the mixed flagellate/cyanobacterial assemblage in L. Cadagno (Kiørboe, 1993).

In situ incubations

Photosynthesis of samples from the L. Cadagno and L. Lucerne assemblages was measured during *in situ* incubation at the 50 % UV-B depth in each lake, i.e. both the "native" lake that was source of the sample as well as the other "transfer" lake. Detailed information on the solar surface radiation (PAR, UV-A, UV-B) during *in situ* incubations are described in a companion paper (Neale et al., 2001 a, this issue). The average PAR irradiance at depth of incubation estimated from this data was 795 µmol $m^{-2} s^{-1}$ for L. Lucerne and 710 µmol $m^{-2} s^{-1}$ for L. Cadagno. When incubated in their native lake, both assemblages showed strong inhibition by full spectrum UV (PAB) as well as in the Mylar protected, UV-A only, (PA) treatments relative to the no UV (P) tubes (Fig. 4). However, reciprocal transfer had contrasting effects on the two assemblages. The L. Cadagno assemblage was less sensitive to UV exposure when transferred to L. Lucerne (Fig. 4 upper panel, POC-Cad vs. POC-Luc), and the L. Lucerne assemblage was more sensitive to UV exposure when transferred to L. Cadagno (Fig. 4 lower panel). The transfer also affected the overall rate of photosynthesis (higher in L. Lucerne, lower in L. Cadagno). Rates of TOC incorporation were generally higher than POC incorporation.
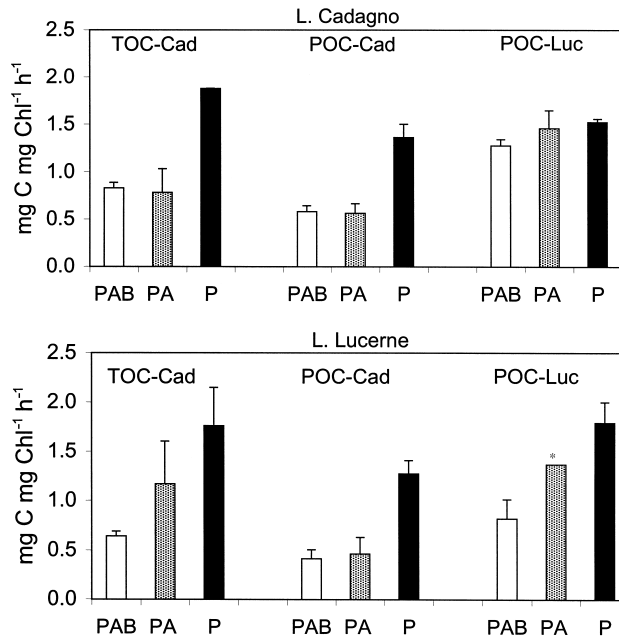
Figure 4. Chorophyll specific carbon incorporation into particulate organic carbon (POC) and total organic carbon (TOC) (mg C mg $Chl^{-1} h^{-1}$), during *in situ* incubation under the three different UV treatments (PAB: quartz, PA: Mylar D, P: Ultraphan), for samples from L. Cadagno (upper panel) and L. Lucerne (lower panel). Labels over the bars indicate measurement type and incubation in either L. Cadagno (TOC-Cad, POC-Cad) or L. Lucerne (POC-Luc). Error bars correspond to the standard deviation of replicate treatments, * denotes a PA treatment with only one measurement

For incubations in L. Cadagno (POC-Cad, TOC-Cad), the carbon assimilation (data not shown) and the chlorophyll specific photosynthesis (Fig. 4) were both significantly lower in UV exposed tubes compared to the tubes with PAR only. Two-way ANOVAs were significant for both L. Lucerne (F = 15.67, DFn = 2, DFd = 9, P = 0.0012) and L. Cadagno (F = 69.59, DFn = 2, DFd = 9, P = 0.0001) assemblages, if tested for all the treatments together. Nevertheless, PAB and PA were not significantly different for both assemblages, while PA and P were different (L. Cadagno: P = 0.0001 and L. Lucerne: P = 0.0189). UV exposure also slowed carbon incorporation into chlorophyll (Fig. 5). This suggests that the reduction in photosynthesis translates into a reduction in the growth rate of the phytoplankton, though direct effects of UV on chlorophyll turnover are also possible.

For incubations conducted in Lake Lucerne (POC-Luc), differences between treatments were not significant by ANOVA (P > 0.05) because of greater variance between replicates compared to inhibition especially for the L. Cadagno sample. For the L. Lucerne sample, one replicate PA treatment was omitted from the analysis because the rate was unusually high (by about 10-fold) compared to other measurements.

Comparison of Laboratory and In Situ Incubation Results

In comparing the results from the several different experimental approaches, we consider two issues separately: 1) maximum photosynthetic rates in the absence of UV (P_s^B in our notation), 2) relative photosynthesis in the presence and absence of UV. The first issue addresses how well different methods compare in the determination of absolute rates of primary production (one of the general objectives of the GAP workshop) while the second focuses directly on the effect of UV on photosynthesis.

Maximum photosynthetic rates: The *in situ* methods measured carbon incorporation into particulate organic carbon as well as total incorporation (dissolved and particulate), whereas the laboratory incubations measured only total incorporation. As already mentioned, samples incubated in L. Cadagno had generally lower productivity than the same samples incubated in L. Lucerne for all Ultraphan incubations (quartz tubes) (Table 2). For P_s^B, the rates are 15–30% lower in L. Cadagno. This
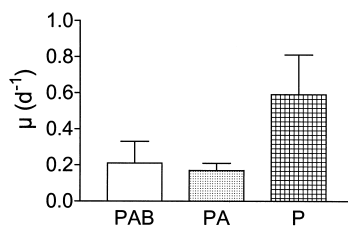
Figure 5. Carbon-specific growth rate of the total phytoplanktonic fraction in L. Cadagno as inferred from ^{14}C incorporation into chlorophyll a during *in situ* incubations. On the x axis the treatments are indicated (PAB: quartz, PA: mylar D, P: Ultraphan). Error bars represent the standard error of the mean

Table 2. Comparison of light-saturated assimilation numbers in absence of UV measured in both *in situ* and laboratory incubations. Samples were taken at 1 m and incubated *in situ* shielded from UV by Ultraphan film (Uph) or during the standard profile at 0, 1 and 1.5 m protected by UV opaque acrylic sheet (Pro). The upper part of the table shows rates for incorporation into particulate organic carbon (POC) collected on filters (> 0.2 μm) and the lower part shows rates of incorporation into total organic carbon (TOC). The statistical estimate of maximum photosynthetic rate (P_s^B) is from the photoinhibitron (BWF/P-I) and photosynthetron (P-tron) laboratory incubations. *In situ* rates are the averages (±standard deviation) of replicate bottles or over the replicate bottles at three depths of the standard profile. Second column shows the chlorophyll concentration used in the calculation of assimilation number. All incubations conducted mid-day on 14 September, except (*) was conducted on 13 September. Standard deviation of the chlorophyll a determinations is about 0.3 mg Chl m^{-3}

Sample	Incubation	POC mg C mg Chl^{-1} h^{-1}	Chl mg m^{-3}
Luc	Luc-Uph	1.79 ± 0.21	2.31
Luc	Cad-Uph	1.27 ± 0.20	2.31
Cad	Cad-Uph	1.36 ± 0.14	2.66
Cad	Luc-Uph	1.52 ± 0.30	2.66
		TOC mg C mg Chl^{-1} h^{-1}	Chl mg m^{-3}
Luc	Luc-Pro*	6.50 ± 2.20	1.00
Luc	Cad-Uph	1.76 ± 0.39	2.31
Luc	BWF/P-I	1.67 ± 0.37	2.31
Luc	P-tron	2.60 ± 0.40	2.31
Cad	Cad-Pro	3.26 ± 1.00	3.03
Cad	Cad-Uph	1.90 ± 0.004	2.66
Cad	BWF/P-I P-Tron	3.02 ± 0.25	2.61

may be partly a systematic difference between two groups working in two different facilities, but a more important factor could be the lower temperature (15 °C) in L. Cadagno compared to L. Lucerne (20 °C) (Davison, 1991). For example, given a typical temperature coefficient (Q_{10}) of 2.0, photosynthesis at 15 °C would be expected to be 71 % of the rate at 20 °C.

For incubations in L. Lucerne, the Ultraphan (POC), profile (TOC), BWF/P-I and photosynthetron assimilation numbers are generally in the range of 1.7–2.6 mg C mg Chl^{-1} h^{-1} which is similar to the long term average of around 3 for the lake (Bloesch et al., 1995). The assimilation number was much higher (6.5) in the 0–1.5 m depth range of the profile, but this was associated with a much lower Chl estimate suggesting that the difference may be caused by variation in the Chl determination. The minimum was estimated for the BWF/P-I which may have been due to the lack of agitation in the photoinhibitron, as already discussed. There is good overall agreement in profile, BWF/P-I, and photosynthetron P_s^B for L. Cadagno, but the TOC incorporation in the Ultraphan *in situ* incubation in L. Cadagno is low.

Relative Inhibition by UV: Relative differences in productivity as a function of *in situ* UV exposure were measured in the upper 5 m of the standard profile in L. Lucerne

and Lake Cadagno by comparing assimilation in UV transparent Duran bottles vs. bottles covered with UV opaque acrylic sheet. For the standard profile on September 13 in L. Lucerne, photosynthesis was measured during a 4-hour incubation between 1240 and 1640 h (CEST). Absolute rates for these profiles are presented by Bossard et al. (2001, this issue). Inhibition by UV was observed over the upper 3 m, with photosynthesis in the presence of UV only 40 % of UV-protected rates at the surface (Fig. 6A). For comparison, E_{inh}^* (Equation 2) was calculated as a function of depth and time based on surface spectral irradiance (1 minute resolution) and attenuation coefficients. The predicted rate of relative photosynthesis ($1/[1 + E_{inh}^*]$) was averaged over the incubation period. The observed and predicted profiles are similar (Fig. 6A): Average E_{inh}^* exceeded 0.1 (ca. 10 % inhibition) only in the upper 3 m and rates at the surface were predicted to be 45 % of rates in the absence of UV. In general, the predicted and observed inhibition differed by less than 10 % of P_s^B, which is about the level of error on these measurements (errors are considered in more detail below). While the discrepancy was usually small, the model rates did tend to be higher than observed rates.

The standard profile in L. Cadagno had a similar pattern as for L. Lucerne after taking into account the lower UV transparency of L. Cadagno, which limits effects to the upper 1.5-m (Fig. 6B, Note different depth scale). However, relative photosynthesis predicted by the model considerably overestimated observed relative photosynthesis, by more than 20 % of P_s^B at the surface. The main difference compared to the application of the BWF/P-I model to L. Lucerne is that *in situ* incubations in L. Cadagno were at a colder temperature (15 °C) than during the laboratory measurements (ca. 20 °C). This suggests that UV effects may be enhanced by lower temperature, a possibility that is supported by the results from the reciprocal transfer experiment. Increased sensitivity at lower temperature could be caused, for example, by slower rates of repair of UV damage (Lesser et al., 1994). The lower rate of photosynthesis at low temperature may also limit energy available for repair (Markager et al., 1999). If the increase in sensitivity is assumed to follow a conservative Q_{10} of 2 (Davison, 1991), the stronger photoinhibition brings modeled and observed relative photosynthesis within 10 % (Fig. 6C), as found for L. Lucerne. Average relative photosynthesis predicted using the temperature corrected BWF for L. Cadagno 13 September also agreed well with the standard profile measured in L. Cadagno on 12 September (results not shown).

Results for the *in situ* reciprocal transfer experiment were also in agreement with the predictions of the temperature-corrected BWF model (Fig. 7). Predictions of relative photosynthesis were made for both Mylar-protected (PA) and full spectrum (PAB) tubes relative to Ultraphan protected (P) tubes. A temperature correction factor of 1.4 was applied to both the L. Cadagno and L. Lucerne BWFs for prediction of *in situ* incubation in L. Cadagno. The pattern of observed and predicted responses was similar, i.e. few differences exceeded measurement error/model uncertainty (Fig. 7). There was some apparent difference in relative effect of full spectrum UV compared to UV-A only as measured by POC vs. TOC (POC-Cad vs. TOC-Cad for L. Lucerne sample) though the difference is not statistically significant. Error assessments (error bars, Fig. 7) were based on the replicate differences for the incubations and the sensitivity of the BWF/P-I prediction to an increase or decrease in the BWF by one standard error. Inhibition (predicted and observed)
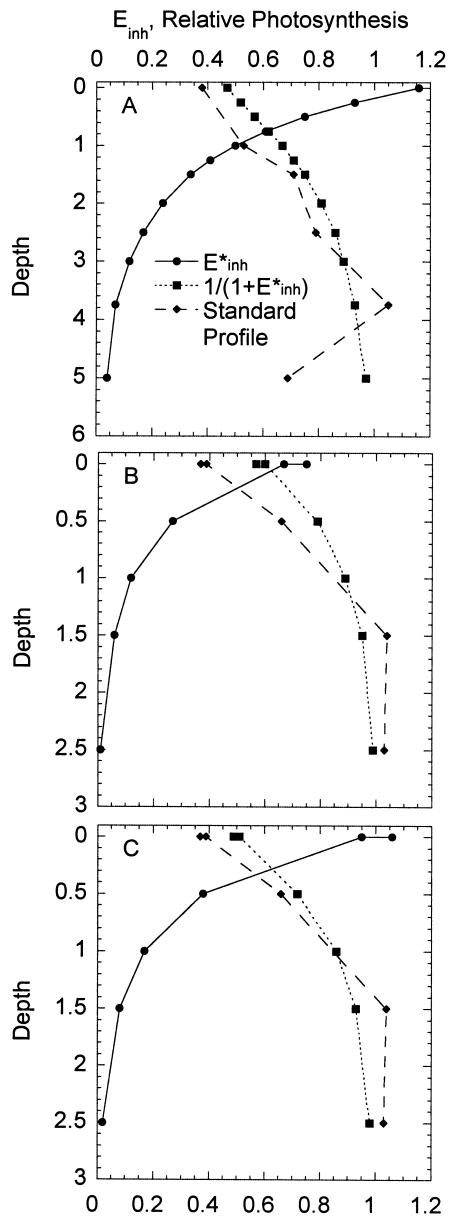
Figure 6. Profiles of relative photosynthesis for standard profiles and as estimated by the BWF/P-I model for incubations conducted on September 13, 1999 at L. Lucerne (A) and September 14 at L. Cadagno (B, C). The profile of estimated average weighted irradiance (E^*_{inh}, circles), estimated average relative photosynthesis ($1/[1 + E^*_{inh}]$, squares) and the proportion between UV exposed and UV protected bottles in the standard profile (diamonds, broken line) are shown for each lake. For L. Cadagno, there are two sets of points for the surface corresponding to both quartz (more inhibition) and Duran (less inhibition) bottles. In panel C, the predictions for L. Cadagno were generated from BWFs that were temperature corrected by a factor of 1.4
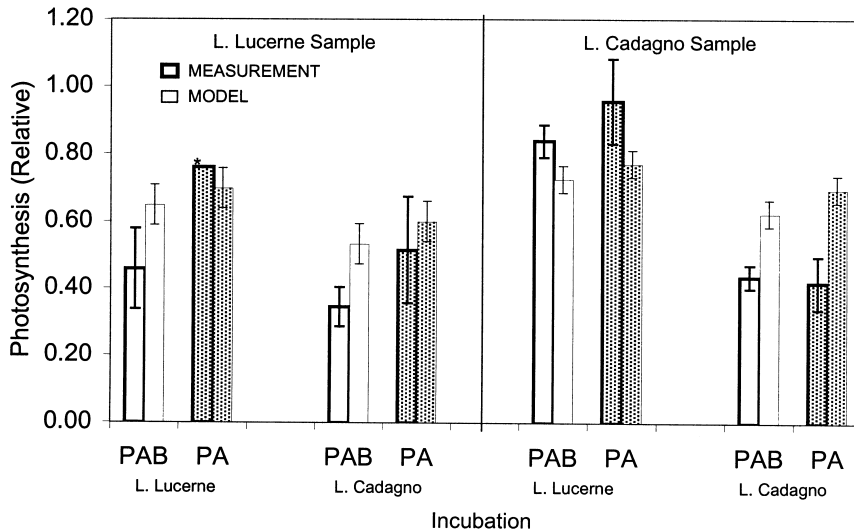
Figure 7. Relative effect of UV exposure on photosynthesis by L. Cadagno and L. Lucerne phytoplankton as measured during incubations on 14 September and predicted using the BWF/P-I model. For each lake incorporation (cf. Fig. 4) in quartz tubes (PAB, open bars) and tubes covered with Mylar (PA, shade bars) was normalized to rates measured in tubes covered with UV opaque Ultraphan (P). The L. Cadagno averages include incorporation both TOC and POC, whereas L. Lucerne includes only POC (cf. Fig. 4). Relative rates are compared with average relative photosynthesis ($1/[1 + E^*_{inh}]$) estimated for the incubation period using the laboratory determined BWFs (Fig. 2). For L. Cadagno E^*_{inh} was temperature corrected by a factor of 1.4. Measurements (thick line, bars) are paired with BWF/P-I predictions (thin line bars). Labels at the top indicate sample source and labels on the bottom indicate location of incubation. Error bars indicate standard error of measured photosynthesis (propagation of standard deviations of measurements in the ratio, * denotes a PA treatment with only one measurement) and an uncertainty range for the BWF/P-I prediction corresponding to a ±one standard error shift in the estimated $\varepsilon(\lambda)$

was about the same for both assemblages in their native environments (40–50% of P). Sensitivity of the L. Cadagno assemblage was moderated by transfer to L. Lucerne whereas the L. Lucerne assemblage was more severely inhibited in L. Cadagno, consistent with a temperature dependence of UV sensitivity. Addition of Mylar resulted in only small increases in photosynthesis, both measured and predicted. This confirms that effects of UV-A dominate *in situ* responses which is primarily due to low penetration of UV-B into these waters as opposed to low sensitivity to UV-B (cf. Fig. 2). At 0.3 m, UV between 290 and 315 nm accounts for <15% of total weighted irradiance (<22% for 290 to 320), depending on the BWF.

Comparison Between Lakes

Several factors come into play in determining phytoplankton responses to UV in a lake. As discussed previously, incident irradiance, assemblage sensitivity, size distribution and temperature can all significantly affect UV responses. Nevertheless,

inhibition of production by UV was similar in both lakes, resulting in about 60 % reduction of photosynthesis close to the surface. We further examined how factors affecting UV responses trade-off in these two environments by using the BWF/P-I model to predict noontime profiles of production under various conditions. We performed a simulated reciprocal transfer by evaluating profiles in each lake using the BWFs for both L. Lucerne and L. Cadagno assemblages (Fig. 8). In L. Cadagno the lower depth for the integration was 10 m, below which the assemblage is affected by proximity to an anoxic monimolimnion (Peduzzi et al., 1998), note the different depth scale for L. Cadagno in Fig. 8. This analysis showed that even though surface effects are similar for the native assemblage in each lake (inhibited is about 0.4 of uninhibited), the predicted overall impact of UV on integrated primary production is higher in L. Lucerne (15.0 % as compared with 9.9 % in L. Cadagno). Two factors, higher inherent sensitivity of the assemblage and higher transparency of the water column in Lake Lucerne, appear to outweigh the moderating influences of lower altitude and higher water temperature of L. Lucerne. The model results indicate that the two factors (transparency and sensitivity) contribute about equally to the overall effect. The L. Lucerne assemblage, transferred to L. Cadagno, had relatively more simulated inhibition than the native L. Cadagno assemblage because of the higher inherent sensitivity of L. Lucerne phytoplankton (Fig. 8). Moreover, the sensitivity of the L. Lucerne assemblage is apparently enhanced upon transfer in the colder L. Cadagno. However, inhibition of integral primary production in the simulated transfer of the L. Lucerne assemblage to L. Cadagno (12 % at solar noon) is
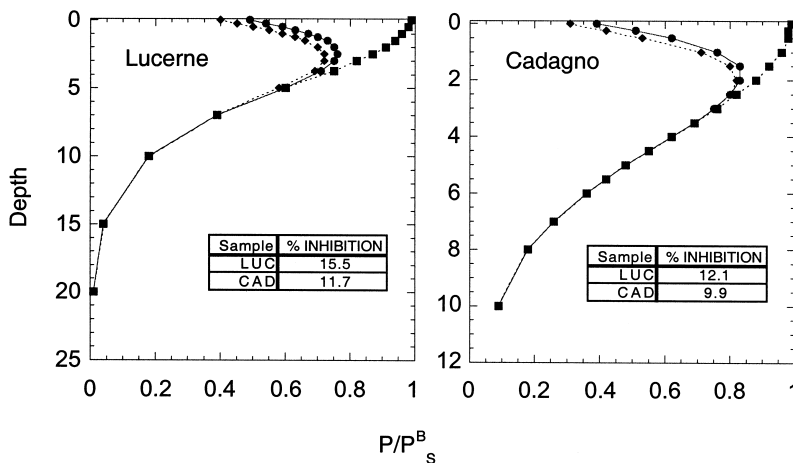

Figure 8. Profiles of relative inhibition of photosynthesis by UV (as proportion of photosynthesis under PAR only) under surface solar irradiance (clear sky, solar noon) for September 13, 1999 at L. Lucerne (left panel) and September 14 at L. Cadagno (right panel). Predictions are made using the BWF/P-I model with the BWFs estimated for L. Lucerne phytoplankton (Luc, diamonds, broken line) and L. Cadagno phytoplankton (Cad, circles solid line) (i.e. Fig. 2). Squares show the predicted profile in absence of UV effects. The predictions for L. Cadagno were generated from BWFs that were temperature corrected by a factor of 1.4. Inset boxes show predicted per cent loss of primary productivity integrated over the profile [integral of (PAB-P)/P] depending on which BWF is used for prediction

still less than the inhibition simulated for L. Lucerne assemblage in its native environment (15.5 % at solar noon). The factor dominating the difference in UV effects between the lakes is UV transparency. Biologically weighted UV transparency (Pienitz and Vincent, 2000) is much higher in L. Lucerne (5.8 m) compared to L. Cadagno (1.4 m). Also the UV/PAR ratio is higher in the euphotic zone of L. Lucerne. PAR penetrates to about 4 times greater depth than UV-B in L. Lucerne (ratio of k_{320} to k_{PAR}), in comparison, PAR penetrates much farther than UV in L. Cadagno (6.4 times greater depth than UV-B). In other words, about twice as much of the euphotic zone is exposed to UV in L. Lucerne as in L. Cadagno. Despite the greater sensitivity to UV, the L. Lucerne assemblage is more productive on a chlorophyll specific basis. Scaled to a 1 mg Chl m^{-3} concentration, integral noontime production in L. Lucerne was 5.7 mg C m^{-2} h^{-1} compared to 4.7 mg C m^{-2} h^{-1} in L. Cadagno.

Discussion

The impact of UV on primary productivity in two lakes was quantified using both laboratory and *in situ* approaches. The two approaches were compared using biological weighting functions (BWFs), and this study is one of the first to estimate BWFs for freshwater phytoplankton. The BWFs for UV inhibition of photosynthesis indicate sensitivity to the full spectrum of UV. The spectral dependence (i.e. relative importance of UV-A and UV-B) is similar to marine assemblages (Fig. 9, cf.
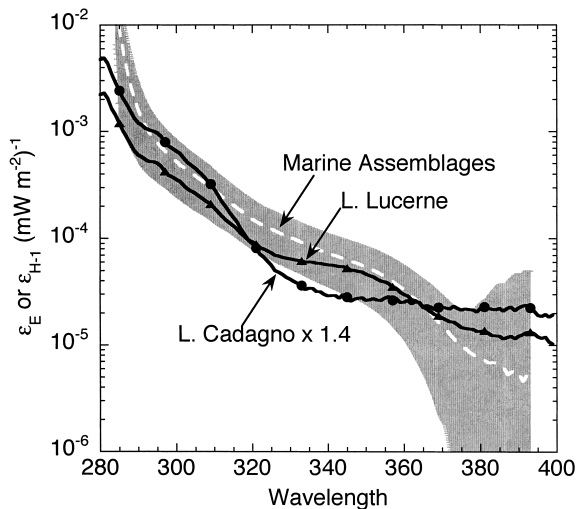
Figure 9. Biological weighting functions (ε, [mW m^{-2}]$^{-1}$) for L. Cadagno and L. Lucerne for September 14, 1999 (solid lines) compared to the average ($\pm$ standard deviation) BWF for UV inhibition of photosynthesis in marine assemblages of phytoplankton (cf. Neale and Kieber 2000). The marine average combines both irradiance and cumulative exposure dependent BWFs, the latter scaled to reflect effects over a 1 h exposure (Neale and Kieber 2000). The L. Cadagno BWF has been scaled by the temperature correction factor of 1.4

Neale and Kieber, 2000). Absolute sensitivity to UV is generally less compared to the average BWF for marine assemblages, but the BWFs are within one standard deviation of the marine average BWF. The L. Cadagno BWF had to be multiplied by 1.4 for this comparison to agree better with *in situ* sensitivity. Presently, there are no other published BWFs for freshwater assemblages but more BWFs should be available soon since this is an active area of investigation.

The *in situ* incubations showed strong effects by UV-A with limited additional effect of UV-B on photosynthesis, similar to *in situ* measurements in other lakes (Bühlmann et al., 1987; Moeller, 1994; Villafañe et al., 1999). These results are consistent with the BWF/P-I model that also predicted little additional inhibition by UV-B despite high sensitivity because of significantly lower penetration of UV-B compared to UV-A. These results indicate that phytoplankton productivity in these lakes could be more affected by changes in UV-A, e.g. due to variations in CDOM, as opposed to changes in UV-B, e.g. due to ozone depletion (Pienitz and Vincent, 1999). Indeed, the strong direct effects of UV on these lake assemblages may be important in suppressing phytoplankton growth and maintaining near-surface transparency.

The laboratory determined BWF/P-I model was a good predictor of both the pattern and magnitude of UV effects in these lakes, supporting the use of the model as a tool in understanding UV impacts on the productivity of limnetic ecosystems. The most direct test of the model is the comparison with the standard profile and transfer experiment in L. Lucerne. In these cases, predictions and observations were within error tolerances. However, there was a tendency for *in situ* inhibition to exceed predictions for the L. Lucerne assemblage. Similarly, the average relative photosynthesis during UV exposure over all experiments (Fig. 7) was 59 % of the PAR-only rate, while the average BWF/P-I value was 7 % higher, at 66 % of the PAR-only rate. The BWF/P-I model used in the analysis assumes that photosynthesis responds to weighted UV irradiance consistent with an ongoing balance between UV damage and repair processes (Neale, 2000). Some deviation from this assumption may have occurred during the 4 h *in situ* incubations. Inhibition may have intensified during the incubation, also productivity levels may not have recovered as quickly as predicted by the model as UV decreased towards the latter part of the incubation period. A test of the irradiance-dependence assumption by measuring time courses of photosynthesis was not possible during this study. However, preliminary time-course measurements using a PAM fluorometer showed rapid attainment of steady-state in quantum yield of photosynthesis upon shifts in UV (Roettgers Rüdiger, pers. comm.). The validity of an irradiance-based model was also supported by the results of a simulated mixing experiment performed in L. Lucerne. Relative photosynthesis by samples exposed to time-varying UV due to simulated mixing was similar to the BWF/P-I-based prediction given the time sequence of UV exposure (Köhler et al., 2001, this issue). This suggests that UV damage and recovery tracked the variation in UV, as expected for an irradiance-dependent response.

Photosynthesis was lower, and UV effects on photosynthesis were stronger, for incubations in L. Cadagno vs. in L. Lucerne. These shifts are consistent with the physiological effects of temperature, both directly on photosynthesis as well as indirectly through the enzymes involved in repair of UV damage (Davison, 1991; Markager et al., 1999). This indicates that acute changes in temperature can have strong

effects on UV sensitivity, and again point out the importance of repair processes in determining UV sensitivity. The somewhat lower sensitivity of these freshwater assemblages (compared to the marine average) is interesting considering that available phosphorus was probably limiting phytoplankton growth. Nitrogen limitation increases the sensitivity of phytoplankton to UV (Cullen and Lesser, 1991; Litchman et al., unpubl.), but little is known about the effects of phosphorus limitation which is more common in freshwater environments. In any case, these BWFs are still substantially higher than the average BWF of diatoms and dinoflagellates grown in nutrient replete cultures (Neale and Kieber, 2000). One mechanism that decreases sensitivity in the 320–360 nm region is photoprotection by UV screening compounds (e.g. Mycosporine-like Amino Acids, MAAs, Neale et al., 1998a). In the case of the L. Cadagno assemblage, however, MAAs could not be detected either because they were absent or there was insufficient sample (Ruben Sommaruga, pers. comm.). Nevertheless, absorption spectra of particulates from both lakes showed significant UV absorption (Rodney Forster, pers. comm.), though the absorption was lower than that associated with significant screening (Neale et al., 1998a).

In summary, our comparative study showed that laboratory-determined BWF/P-I models are useful predictors of *in situ* photosynthetic response to UV in these freshwater environments. Additional work is obviously necessary to show whether the model is equally applicable under the wide variety of conditions found in limnetic environments. However, such environments do present a valuable opportunity for comparison of *in situ* and laboratory work that is usually much more difficult to do for marine systems. It is expected that application of laboratory approaches and the BWF/P-I model will be a useful tool complementing *in situ* experiments in understanding the interaction of UV sensitivity and environmental factors such as temperature and nutrient availability in freshwater environments.

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