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Effects of solar ultraviolet radiation on the periphyton community in lotic systems: comparison of attached algae and bacteria during their development

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Abstract

The effects of solar ultraviolet radiation (UVR) on the development of a periphyton community were studied in an outdoor artificial stream apparatus. Algal biomass, species composition, and bacterial cell density were measured under full sunlight and non-UVR (photosynthetically active radiation [PAR]-only) conditions. Attachment of algae was detected on days 6–9. Although the chlorophyll-*a* concentration under non-UVR conditions was 2–4 times that under full sunlight (PAR + UVR) throughout the experiment, neither net algal growth rate nor species composition differed significantly between the two light conditions. The relative carotenoid pigment contents of attached algae in the PAR + UVR condition were 1.1–1.3 times those in the non-UVR condition. Rates of increase of bacterial cell densities under the PAR + UVR condition were depressed by solar UVR for the first few days, although there were no apparent differences in the rates of increase between the light conditions later in the experiment. The small effect of UVR on the development of this periphyton community may be attributable to low UV flux at this study site and to the experimental conditions under which the algae were kept: a high physiological state with high nutrient conditions. Attached bacteria and algae that colonize substrata first are likely to be sensitive to solar UVR, and the negative effects of UVR are mitigated by the development of a periphyton community.

Introduction

The amount of mid-range ultraviolet radiation (UVR, known as 'UVB,' 280–320 nm) reaching the Earth's surface has increased owing to stratospheric ozone depletion (Kerr & McElroy, 1993). This has drawn attention to the potential effects of solar UVR (280–400 nm) on aquatic ecosystems. Recent studies of attached algal communities have shown that solar UVR affects algal growth, production, and community structure (Bothwell et al., 1993; Vinebrooke & Leavitt, 1996; Kiffney et al., 1997; Francoeur & Lowe, 1998). Indirect effects of solar UVR are also important in aquatic systems. Bothwell et al. (1994) showed that the development of a periphyton community in the first 2 weeks was inhibited by direct effects of UVA (320–400 nm). However, later, the attached algal biomass under ambient solar conditions was higher than that under non-UVR conditions, because UVB reduced alga grazers. Therefore, solar UVR does not always have detrimental effects on net algal growth and production, which highlights the need to evaluate the effects of various environmental factors on a target organism.

In contrast, DeNicola & Hoagland (1996) found little effect of UVR on algae or grazers in their *in situ* experiment; they concluded that the

effects of light quality (including UVR) on periphyton are less apparent than the effects of other environmental factors such as nutrients, disturbance, current, and grazing. Hill et al. (1997) and Hill & McNamara (1999) also found no significant UVR effects on periphyton biomass, photosynthetic rate, or species composition, and cautioned that the effects of UVR cannot be generalized.

The responses of periphyton to solar UVR are thus not fully understood, mainly due to the geographical and environmental differences among study sites, including differences in UVR flux. The degree of UVR flux varies with weather, season, and location (e.g., latitude, altitude, and degree of canopy development). Other environmental factors (e.g., temperature and nutrient conditions) also vary greatly among aquatic systems and may influence organisms' sensitivity to UVR. The indirect effects of UVR such as decreases in grazers also make it difficult to evaluate the direct effects of solar UVR on attached algae.

Moreover, few studies of solar UVR have dealt with other organisms (bacteria, fungi, and protozoa) that comprise periphyton communities. These organisms depend closely on each other for nutrient supply and community structure (Hoagland et al., 1982). In particular, attached bacteria are important decomposers of both algal products and organic matter input (leaf litter and dissolved organic matter; Findlay & Howe, 1993).

In the present study, my objective was to evaluate the direct effects of solar UVR on attached algae and bacteria in a lotic system. The experiments were performed in an experimental stream apparatus to eliminate the effects of grazers and to control other environmental factors. Biomass, growth rate, pigment composition, and species composition of the attached algal community and attached bacterial abundance were compared between ambient UVR and non-UVR conditions.

Methods

Experiments were conducted in outdoor artificial streams at Hachioji, Tokyo, Japan (35° 37′ N, 139° 22′ E) in summer (13 August–4 September 1998) and winter (15 December 1998–25 February 1999). River water (120 l) was circulated in eight straight stainless steel flumes (1.2 m long, 10 cm wide). The flow through each flume was 8–9 l min^{-1}, which resulted in a water velocity and depth of approximately 30 cm s^{-1} and 2 cm, respectively. The experimental water was kept at a constant temperature (22 ± 3 °C in summer, 10 ± 3 °C in winter) with coolers and heaters.

Water used for the experiments was collected from the Tama River at Hamura (35° 43′ N, 139° 20′ E) in southwestern Tokyo. The Tama River flows across the urban area of the Kanto region, and thus the concentrations of dissolved inorganic phosphorus (DIP), dissolved inorganic nitrogen (DIN), and chlorophyll-*a* (chl-*a*) during the experiments were high: 19–50, 400–1200, and 0.8–3 μg l^{-1}, respectively. The river water was filtered through a plankton net (100-μm mesh) to eliminate large animals and protozoa. Nutrient concentrations (DIP and DIN) during the experiment were measured every day. Potassium nitrate and potassium phosphate were added to maintain ranges of 200–2000 and 5–200 μg l^{-1}, respectively. The water in the flumes was replaced every 5–10 days. To prevent reattachment of algae that had sloughed from the substrata, the water was filtered through a plankton net (20–100-μm mesh) every day. The chl-*a* concentration of the water was kept below 10 μg l^{-1}.

To determine the effects of solar UVR on the development of periphyton, the experimental flumes were covered with two different films. Polytetrafluoroethene film (PTFE film, 0.06 mm thick, CI Kasei Co.), which transmits the entire solar spectrum, was used for the photosynthetically active radiation (PAR) + UVR condition (Fig. 1). Polyvinylchloride (PVC-400) film (0.1 mm thick, CI Kasei Co.), which completely blocks UVB (280–320 nm) and UVA (320–400 nm), was used for the non-UVR condition (Fig. 1). In the summer experiment, each treatment (PAR + UVR and non-UVR) had two replications (total, four flumes). In the winter experiment, each treatment had four replications (eight flumes). During the experimental periods, solar PAR (400–700 nm) was measured with a Li-Cor quantum sensor (Q11109, Li-Cor, Inc.), UVA (315–400 nm) with a broadband UVA radiometer (MS 330A, EKO Instruments Co. Ltd.), and UVB (280–315 nm) with a broadband UVB radiometer

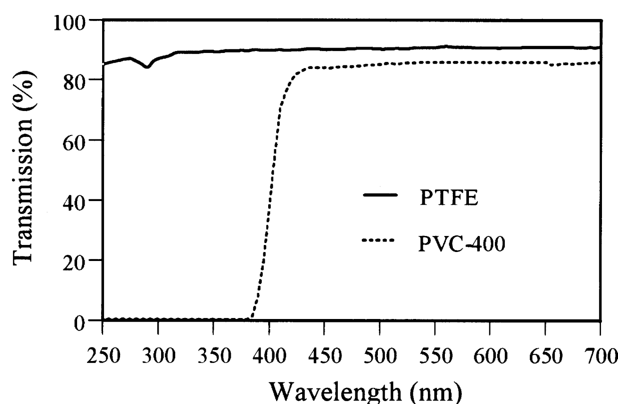

Figure 1. Light transmission characteristics of polytetrafluoroethene (PTFE) film and PVC-400 film in ultraviolet (UV) and photosynthetically active radiation (PAR) regions.

(MS 210W, EKO Instruments Co. Ltd.). Sensors were set on the side of the artificial streams and adjusted to the same height as the water surface. Mean irradiances of PAR, UVA, and UVB were recorded every 10 min in a data logger (LI-1000, Li-Cor, Inc.).

One hundred precombusted (420 °C, 3 h), frosted glass tiles (3 cm × 3 cm) were placed on the bottom of each flume as substrata for periphyton, and 3–10 randomly selected tiles were removed on each sampling date. Samples were taken on days 1, 2, 3, 4, 6, 8, 10, 12, 14, 16, 18, 20, and 22 in the summer experiment, and on days 1, 3, 6, 9, 15, 21, 27, 33, 40, 47, 54, 61, and 72 in the winter experiment. Only periphyton on the top side of each tile were evaluated. Those on the back and sides were wiped away with Kimwipes (Kimberly-Clark Co.), and the tile was rinsed with Milli-Q water. Tiles were transferred to 100 ml Milli-Q water, and periphyton were removed by gentle sonication (20 kHz, 50 W, 3–4 min) according to the methods of Claret (1998). Half (50 ml) of the suspension was fixed with glutaraldehyde (final concentration, 1%) for enumeration of algae and bacteria. The remaining suspension was filtered through precombusted Whatman GF/F filters, and the filters were used for analysis of chl-*a*, pigment spectrum, and attached organic matter. Chl-*a* concentrations were determined with a fluorometer (TD-700, Turner Designs) after extraction in 100% methanol for 24 h. The absorption spectrum of the extract was measured at 300–700 nm with a spectrophotometer (UV-160A, Shimadzu Co.), and relative carotenoid pigment contents were evaluated by normalizing the carotenoid pigment peak at 465–485 nm to the chl-*a* maximum peak at 665 nm. Total organic carbon (TOC) and total nitrogen (TON) on the tiles were analyzed with a CHN analyzer (MT-5, Yanaco Co.). Total phosphorus was analyzed by the ascorbic acid method after oxidation with potassium peroxodisulfate. In the present study, detection limits of chl-*a* and TOC were 0.03 ng cm^{-2} and 1.5 μg cm^{-2}, respectively (values of upper 95% confidence limit obtained by measuring washed and sterilized grass tiles). Data below these values were not used in the later analysis.

Attached algae were counted at 400× magnification with a Fuchs–Rosenthal hemocytometer. At least 500 cells were counted. Species of diatoms were identified according to Watanabe et al. (1986). Identifications were aided by reference slides of permanent mounts. Green algae and cyanobacteria were identified according to Hirose (1977).

Bacteria were stained with 4′6-diamidino-2-phenylindole (DAPI, final concentration of 10 μg ml^{-1}) for 10 min at room temperature and filtered on a black Nuclepore filter (pore size, 0.2 μm). The filter was washed with Milli-Q water and mounted on a glass slide in non-fluorescent immersion oil (Olympus Co.). Bacterial cells were counted at 1500× magnification under an epifluorescence microscope (Olympus, model IMT-2 RFM) equipped with a mercury lamp (100 W). The excitation was fixed at UV wavelengths (IMT2-DMU, DM400). At least 300 cells were counted in each of eight optical fields.

Net growth rates of attached algae and bacteria and TOC accumulation rates were calculated for every sampling interval as:

$$\mu = (\ln N_2 - \ln N_1)/(t_2 - t_1), \quad (1)$$

where N_1 and N_2 are the amounts of chl-*a*, bacteria, or TOC at times t_1 and t_2, respectively. Two-way repeated-measures ANOVA (RM-ANOVA, Milliken & Johnson, 1984) was used to test for the effects of UVR on the growth of attached algae and bacteria, TOC accumulation rate, and variation in carotenoid pigment content. Differences between the light conditions were regarded as differential effects of solar UVR to which the cells were exposed throughout the experimental periods. Differences among days were regarded as daily changes within each condition. A difference in interaction (conditions × days) was regarded as a difference in the temporal variations in growth rate (or carotenoid content) between the two light conditions. The species compositions of algal communities were compared by using the similarity index (SIMI, Pianka, 1973). Bias adjustment and estimation of the 95% confidence interval for SIMI were performed by using the jackknife method (Smith et al., 1986). Temporal variations in SIMI were analyzed to fit a simple linear regression, and the differences in the regression coefficient (β) and intercept were tested by *t*-test (Sokal & Rohlf, 1997), defining the null hypotheses as $H_0 = 0$ and $H_0 = 1$, respectively.

Results

Ambient solar radiation varied greatly in the summer experiment because of the unstable weather (Fig. 2A, C and E). The mean PAR, UVA, and UVB values at noon were 846.6 μmol m^{-2} s^{-1}, 23.7 W m^{-2}, and 1.01 W m^{-2}, respectively. In the winter experiment, the weather was more stable (Fig. 2B, D and F). The mean PAR, UVA and UVB values were 827.9 μmol m^{-2} s^{-1}, 14.4 W m^{-2}, and 0.48 W m^{-2}, respectively.

In both experiments, the C:N and C:P ratios of attached organic matter were always low (molar ratios, mean ± SD; summer C:N = 7.7 ± 1.2, C:P = 102 ± 22; winter C:N = 8.4 ± 1.5, C:P = 112 ± 33), and there was no difference between PAR + UVR and non-UVR conditions.

Chl-*a* was detected on day 6 in the summer experiment and on day 9 in the winter experiment (Fig. 3). Chl-*a* concentrations in the non-UVR condition were 2–4 times those in the PAR + UVR condition until the late logarithmic growth phase (day 22 in summer and day 47 in winter). In the winter experiment, the differences in chl-*a* concentrations between the PAR + UVR and

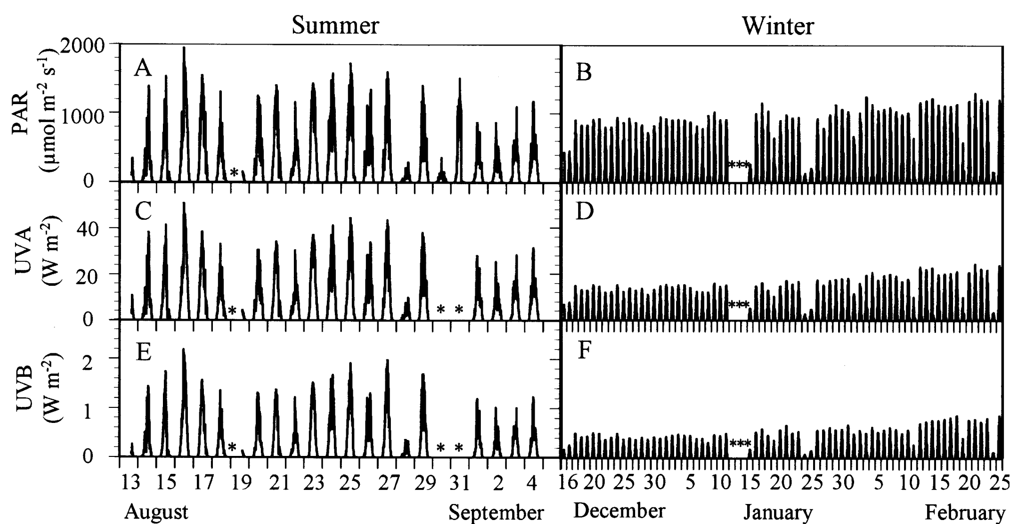

Figure 2. Variations in the irradiances of photosynthetically active radiation (PAR; A, B), UVA (C, D), and UVB (E, F) during the summer and winter experiments. Asterisks indicate the days when no measurements were made.

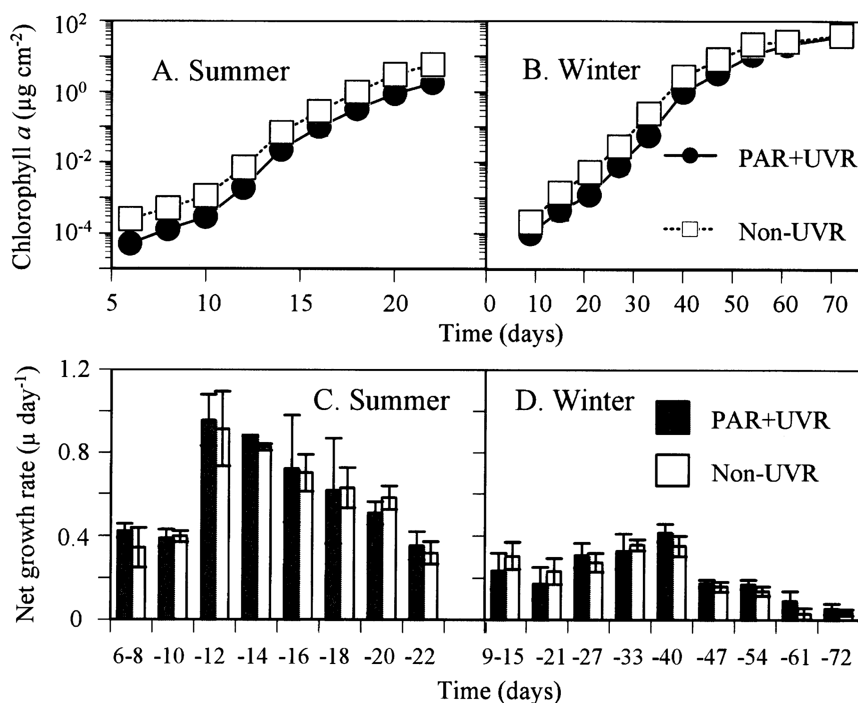

Figure 3. Chlorophyll-*a* accrual (A, B) and algal net growth rate (C, D). Bars indicate means ± 1 SD.

non-UVR conditions gradually became smaller in the late logarithmic growth phase and were negligible by day 72. Figure 3C and D shows the temporal variations in the net growth rates calculated for every sampling interval. In both seasons, differences in the net growth rates between the two light conditions were not obvious at any sampling interval. RM-ANOVA for net algal growth rates showed significant differences between the days in both seasons (Table 1). However, UVR conditions and interactions (conditions × days) were not significantly different in either season.

In both seasons, TOC was detected before chl-*a* (Fig. 4A and B) and increased during the first 2 weeks. The increases stopped from days 8 to 12 in the summer experiment and from days 15 to 21 in the winter experiment (Fig. 4A and B), however, and then increased again. Differences in TOC accumulation rate were observed during the initial periods (until day 6 in summer and day 15 in winter, Fig. 4C and D). RM-ANOVA for the summer experiment showed significant differences between the light conditions and among the days (Table 1). The accumulation rate in the non-UVR condition was higher than that in the PAR + UVR condition during days 4–6 (Fig. 4C). In the winter experiment, the difference between the light conditions was not significant, although differences among other sources of variation were significant (Table 1).

In both seasons, algal communities were always dominated by the genera *Nitzschia* and *Stigeoclonium* (Table 2). Other species occasionally appeared during the experiments. SIMIs of attached algal communities were high at all sampling times (Fig. 5A and B). Regression coefficients (H_0, $\beta = 0$) and intercepts (H_0, intercept = 1) of SIMI data were not significantly different in either experiment (summer slope: df = 4, $t = 0.20$, $p > 0.5$; intercept: df = 4, $t = 0.01$, $p > 0.5$; winter slope, df = 5, $t = 0.19$, $p > 0.5$; intercept: df = 5, $t = 0.01$, $p > 0.5$).

Although absorption spectra of methanol extracts in both light conditions showed similar patterns and did not have any peaks that suggested the existence of UV-absorbing compounds (300–400 nm) such as mycosporine-like amino acids and scytonemin, absorbances of carotenoid pigment regions (400–500 nm) differed from each other; the relative absorbance of carotenoid pigments ([465–

Table 1. The results of two-way repeated measures ANOVA of algal net growth rates, TOC accumulation rates, relative carotenoid pigments contents and bacterial net growth rates

Analysis	Source of variation	Summer expeiment				Winter expeiment			
		df	MS	*F*	*p*	df	MS	*F*	*p*
Algal net growth rate	Light conditions	1	0.0030	7.5	n.s.	1	0.0001	0.3	n.s.
	Within groups	2	0.0004			6	0.0003		
	Days	7	0.3561	22.5	**<0.001**	6	0.0616	18.7	**<0.001**
	Conditions × days	7	0.0026	0.2	n.s.	6	0.0051	1.6	n.s.
	Within groups	14	0.0158			36	0.0033		
TOC accumulation rate	Light conditions	1	0.0250	444.0	**<0.01**	1	0.0002	1.2	n.s.
	Within groups	2	0.0001			6	0.0001		
	Days	8	0.1170	5.7	**<0.01**	9	0.0640	42.4	**<0.001**
	Conditions × days	8	0.0190	0.9	n.s.	9	0.0040	2.5	**<0.05**
	Within groups	16	0.0210			54	0.0020		
Relative caronetoid contents	Light conditions	1	0.0330	33.0	**<0.05**	1	0.1840	56.8	**<0.001**
	Within groups	2	0.0010			6	0.0030		
	Days	4	0.1190	58.0	**<0.001**	5	0.0680	20.5	**<0.001**
	Conditions × days	4	0.0020	0.8	n.s.	5	0.0180	5.3	**<0.01**
	Within groups	8	0.0025			30	0.0035		
Bacterial net growth rate	Light conditions	1	0.0460	61.8	**<0.05**	1	0.0070	24.3	**<0.01**
	Within groups	2	0.0010			6	0.0003		
	Days	7	1.9250	39.7	**<0.001**	11	0.5220	290.4	**<0.001**
	Conditions × days	7	0.0380	0.8	n.s.	11	0.0130	7.1	**<0.001**
	Within groups	14	0.0480			66	0.0020		

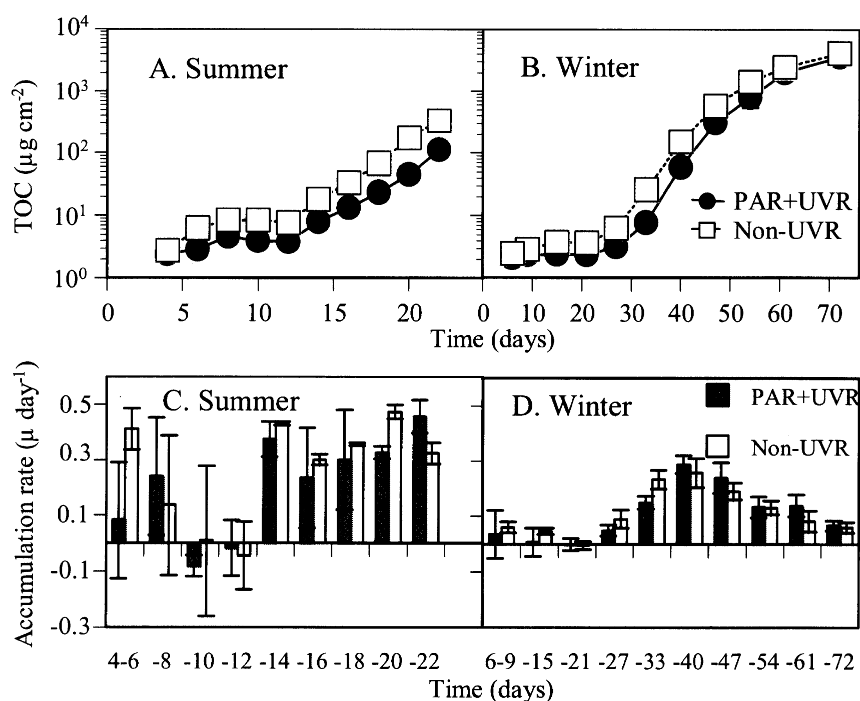

Figure 4. Temporal variations in total organic carbon (TOC) concentrations (A, B) and TOC accumulation rates (C, D). Bars indicate means ± 1 SD.

485 nm]/[665 nm chl-*a* maximum]) was slightly higher in the PAR + UVR than in the non-UVR condition (Fig. 6A and B). The relative abundance in the PAR + UVR conditions was 1.1–1.3 times that in the non-UVR conditions at any sampling time, and significant differences between the light conditions and among days were found in both seasons (Table 1).

In the summer experiment, attached bacterial cell densities increased rapidly in the early experimental phase in both light conditions and gradually diverged. On day 4, the bacterial cell density in the non-UVR condition was three times that in the PAR + UVR (PAR + UVR, 1.2×10^6 cells cm^{-2}; non-UVR, 3.7×10^6 cells cm^{-2}; Fig. 7A). Net growth rates of attached bacteria in the PAR + UVR condition were 1.3 times those in the non-UVR condition until day 3 (Fig. 7C). After day 6, no obvious differences in the increase rates were observed between the conditions, although bacterial cell densities increased slowly in both conditions. In the winter experiment, after rapid increases during the first 2 weeks (day 15: PAR + UVR, 3.7×10^6 cells cm^{-2}; non-UVR, 7.6×10^6 cells cm^{-2}), bacterial cell densities decreased slightly in both light conditions (Fig. 7B). Attached bacterial cell densities in the non-UVR condition were always higher than those in the PAR + UVR condition until the end of the logarithmic growth phase (day 61). Although net growth rates of attached bacteria in the PAR + UVR condition were higher than those in the non-UVR condition until day 3, no obvious difference was detected between conditions thereafter (Fig. 7D). Significant differences between light conditions and between days were observed in both seasons (Table 1).

Discussion

Weak effects of UVR on algal communities have been reported in some studies dealing with both phytoplankton and periphyton (Karentz, 1994; DeNicola & Hoagland, 1996; Halac et al., 1997; Hill et al., 1997). Some authors suggested that weak effects on algae indicate UVR resistance mechanisms. UV-absorbing compounds

Table 2. Dominant species in the attached algal communities. Only taxa more than 1% of the total cell number are presented

Experiment		% Cell no. (SD)	
Days	Species	PAR + UVR	Non − UVR
Summer			
8	*Nitzschia palea* (Kutzing) W. Smith	34.9 (0.1)	33.6 (6.7)
	Navicula seminulum (Grunow)	11.8 (4.5)	12.3 (3.7)
	Achnanthes subhudsonis (Hustedt)	6.8 (2.6)	10.0 (2.1)
	Gomphonema parvulum (Kutzing)	7.2 (4.0)	7.1 (1.9)
	Asterionella formosa (Hassall)	4.7 (0.5)	4.1 (0.3)
	Stigeoclonium sp.	32.4 (3.4)	29.9 (12.2)
14	*Nitzschia palea*	77.9 (5.3)	52.2 (3.8)
	Navicula seminulum	9.7 (0.8)	4.0 (1.4)
	Stigeoclonium sp.	10.6 (3.3)	40.6 (6.4)
22	*Nitzschia palea*	88.2 (15.2)	79.6 (0.7)
	Navicula seminulum	9.7 (3.8)	4.6 (0.6)
	Scenedesmus spp.	6.7 (0.4)	5.7 (0.4)
	Stigeoclonium sp.	4.1 (1.2)	8.2 (1.2)
Winter			
8	*Nitzschia palea var. debilis* (Kutzing)	27.0 (11.0)	29.8 (9.1)
	Nitzschia palea	8.0 (3.4)	8.0 (3.3)
	Achnanthes minutissima (Kutzing)	5.9 (2.0)	6.4 (1.0)
	Merosilla varians (Agardh)	6.1 (5.0)	5.8 (9.4)
	Achnanthes lanceolata (Breb. Ex. Kutz.)	3.4 (2.0)	2.8 (1.8)
	Cymbella sinuata (Gregory)	2.5 (1.4)	2.7 (1.6)
	Navicula elginensis (W. Greg.)	1.2 (0.9)	2.6 (1.6)
	Stigeoclonium sp.	25.5 (10.6)	20.3 (6.6)
	Chloococcus sp.	16.4 (4.9)	15.7 (4.9)
33	*Nitzschia palea var. debilis*	17.0 (2.5)	13.4 (5.9)
	Achnanthes minutissima	6.6 (1.9)	3.2 (2.6)
	Nitzschia palea	3.7 (1.6)	3.3 (2.0)
	Nitzschia linearis (Agardh) W. Smith	3.5 (1.6)	2.4 (1.1)
	Stigeoclonium sp.	18.7 (22.8)	6.1 (1.6)
	Ulothrix zonata (Weber et Mohr) Kutzing	1.9 (1.5)	8.2 (5.6)
	Chloococcus sp.	45.3 (22.7)	60.5 (15.7)
60	*Nitzschia palea var. debilis*	24.3 (3.0)	32.0 (3.2)
	Nitzschia palea	18.9 (3.2)	16.2 (2.6)
	Nitzschia linearis	3.8 (1.3)	3.2 (1.2)
	Nitzschia frustulum	1.8 (0.5)	1.3 (0.4)
	Achnanthes lanceolata	1.8 (0.8)	1.6 (1.0)
	Navicula saprophila	2.2 (1.1)	2.7 (1.1)
	Stigeoclonium sp.	7.0 (1.8)	7.6 (2.9)
	Ulothrix zonata	4.5 (2.1)	3.8 (0.8)
	Chloococcus sp.	35.0 (6.3)	31.1 (7.0)

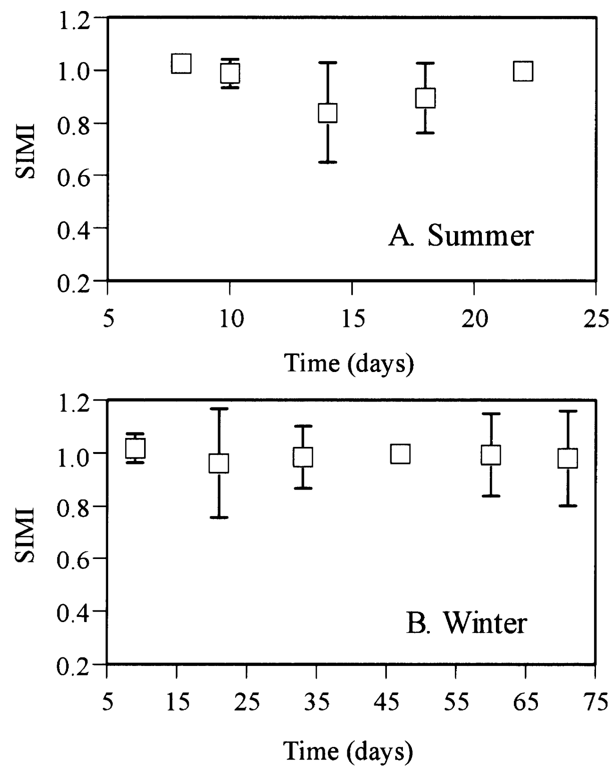

Figure 5. Time courses of similarity indices (SIMI) of attached algal species composition. Bars indicate 95% confidence intervals.

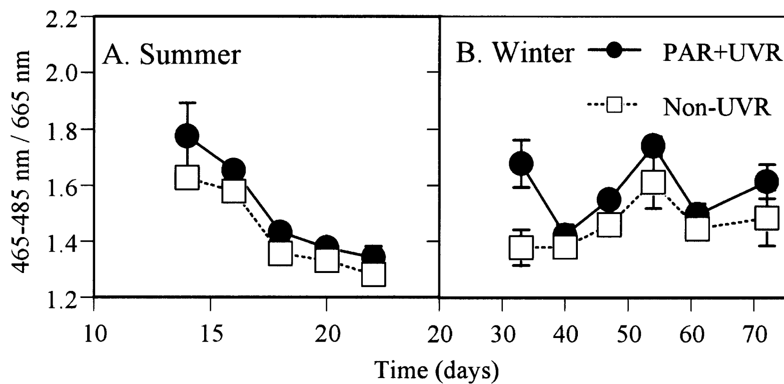

Figure 6. Temporal variations in relative carotenoid pigment contents. Bars indicate means ± 1 SD.

(mycosporine-like amino acids and scytonemin), carotenoids, and DNA repair enzymes mitigate UV damage (Vincent & Roy, 1993; Karentz, 1994; Quesada et al., 1995; Quesada & Vincent, 1997). In the present study, although there were no statistical differences in algal growth (Table 1) or species composition (Fig. 5) during the experiments, the relative carotenoid contents of attached algae in the PAR + UVR condition were higher than those in the non-UVR condition (Fig. 6, Table 1). Thus, the attached algae did respond to solar UVR, and mechanisms protecting against solar UVR undoubtedly functioned in the PAR + UVR condition, although the UVR effects were weak enough not to decrease algal growth or alter algal species composition.

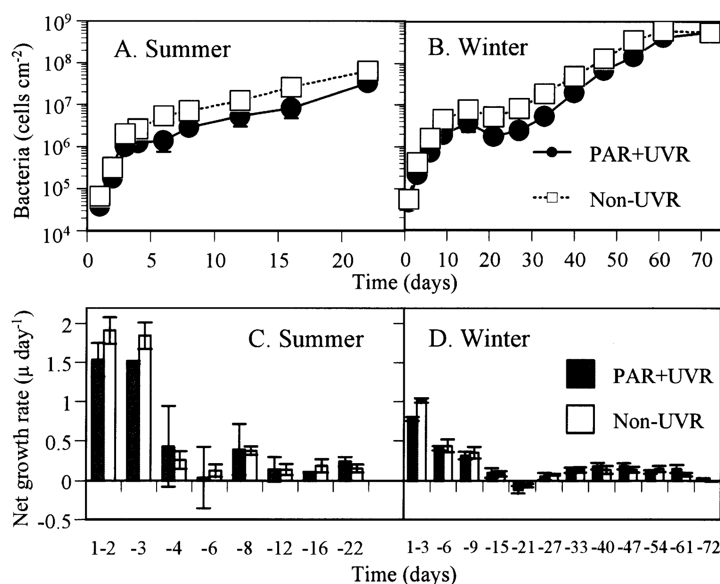

Figure 7. Temporal variations in attached bacterial densities (A, B) and in net growth rate of attached bacteria (C, D). Bars indicate means ± 1 SD.

Lesser et al. (1994) showed that UV inhibition of photosynthesis simply represents the balance between damage and repair. The net UV effect is thought to worsen either by increasing the rate of damages (e.g., increased UVR dosage rate) or by decreasing the rate of repairs (Roos & Vincent, 1998). According to this concept, the main cause of the small effect of UVR in this study is low solar UVR flux. Vinebrook & Leavitt (1996) reported that maximum UVB flux during their experiment was 3.0 W m^{-2}, which is 1.5–3 times higher flux density than those in the present study (Fig. 2). The low UVB fluxes in the present study are probably due not to underestimation of UVB, but to the geographical and seasonal characteristics of the study site. Sasaki et al. (1994) reported temporal variations in solar UVR from October 1990 to September 1992 in Kanagawa, Japan (35° 21′ N, 139° 16′ E), and showed that the mean daily integrated UVB from August to September and from December to February were very similar to those in the present study. Therefore, the potential effects of UVR in this region were much smaller than those in the regions previously studied.

The secondary cause is the environmental factors that mitigated the effects of UVR. UV inhibition of growth increases linearly with decreasing temperature under a constant UVR flux (Roos & Vincent, 1998). Nutrient limitations also increase the susceptibility of algae to UVR (Cullen & Lesser, 1991; Bothwell et al., 1993). Since both temperature and nutrient conditions directly influence algal physiological states and biosynthesis rates, the rate of repair to UV damage should also be affected by these environmental factors. In the present study, nutrients (N and P) were continuously added in each experimental flume, resulting in the low C:N and C:P ratios of attached organic matter. Therefore, small UVR effects in this study may have been caused not only by low UV flux but also by high nutrient concentrations.

In addition, self-shading of attached algae should be noted. McNamara & Hill (2000) compared the effects of UVR on photosynthesis by attached algae between low (4.2 μg chl-*a* cm^{-2}) and high biomass (24.1 μg chl-*a* cm^{-2}). They found no deleterious effect of UVR in the high-biomass community even under artificially UVB-enhanced conditions (4× the ambient UVB intensity); but photosynthesis was significantly depressed in the low-biomass community when UVB was twice the ambient intensity. Although the effectiveness of self-shading in mitigating the effects of UV on an attached algal community needs further study, it is plausible that, since attached algae greatly change their vertical structure

and community composition during succession (Hoagland et al., 1982), degrees of UVR exposure probably differ among upper, middle, and lower layers in the periphyton community.

Although effects of solar UVR on attached bacteria are not well studied, much information on the effects on bacterioplankton in lakes and marine ecosystems has been reported. Solar UVB has harmful effects on bacterial physiology, such as inducing DNA damage, destroying extracellular enzymes, and decreasing organic matter uptake (Jeffery et al., 1996; Lindell & Edling, 1996; Sommaruga et al., 1997). In the present study, the effects of solar UVR on the growth of attached bacteria were detected in the initial period of the experiments, but differences in growth rates between light conditions were obscure in the later periods (Fig. 7). Indirect positive effects such as photochemical production of labile organic matter from refractory dissolved organic matter (Lindell et al., 1995; Wetzel et al., 1995) and depression of bacterivory of heterotrophic nanoflagellates (Sommaruga et al., 1996) might compensate for the negative effects of solar UVR on the growth of attached bacteria. However, these effects seem to be minor in my experimental system. Since the same river water was circulated in all flumes, if photochemical alterations of dissolved organic matter occurred, these would affect both light conditions equally. Likewise, if bacterivorous organisms were significantly inhibited by solar UVR, this effect could be detected by differences in net growth rate of attached bacteria throughout the experimental period.

Attached bacteria at different developmental stages showed different responses to UVR, possibly because shading by attached algae may effectively mitigate the damage by solar UVR. Many studies have reported that attached bacteria are usually primary colonizers and form a thick biofilm on the substrate within a few days (e.g., Hoagland et al., 1982; Liu et al., 1993). In the later periods of development, however, attached bacteria generally exist beneath the algal cells or are embedded in the exopolysaccharide matrix (Blenkinsopp & Lock, 1994). In the present study, temporal variations of TOC accumulation rates and net growth rates of attached bacteria clearly showed two periods (Figs. 4 and 7). The earlier peak of TOC accumulation rate can be explained by bacterial growth and excreted matter; the later peak may have been caused mainly by attached algal growth, because the TOC increased again after the appearance and increase of the attached algae in both seasons. This implies that the sensitivity of attached bacteria to solar UVR changes according to the development of attached algal biomass. This assumes that shading by algal cells and their excreted matter mitigates UVR damage to attached bacteria as well as to the attached algae themselves.

Experiments in the present study clearly demonstrated that the periphyton community during early development, especially when bacteria first colonize and grow on substrata, is the most sensitive period to solar UVR level. In contrast, the solar UVR hardly affected either growth or species composition of the attached algae during their logarithmic growth phase. Although there still may be unknown functions that mitigate UVR damage in the logarithmic growth phase, the findings of this study may describe the present status of periphyton communities in mid-latitude urban rivers with low UVR intensity and high inorganic nutrient concentrations.

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