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Attenuation of ultraviolet radiation in streams of northern Michigan

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Abstract. We measured the attenuation of ultraviolet B (UVB) and ultraviolet A (UVA) radiation in 32 streams located within the Ontonagon River watershed on the Upper Peninsula of Michigan, USA. Attenuation coefficients (K_d) of UVB and UVA ranged widely among these streams, but generally translated into relatively shallow 1% transmission depths into the water column (2–45 cm for UVB and 6–103 cm for UVA). Both $K_{d\ \mathrm{UVB}}$ and $K_{d\ \mathrm{UVA}}$ were positively correlated with stream dissolved organic C concentration (DOC, range 2–35 mg C/L). Absorbance coefficients of dissolved matter (a_d) of UVB and UVA also were strongly correlated with DOC. $K_{d\ \mathrm{UVA}}$ (but not $K_{d\ \mathrm{UVB}}$) was weakly related to the concentration of particulate organic C and DOC molar absorptivity. DOC-specific $K_{d\ \mathrm{UVB}}$ was, on average, higher in streams of our study compared to previously published values from lakes and wetlands. We developed a statistical model that predicts UVB flux to benthic organisms. The model incorporates information on water depth, DOC concentration, surface reflectance, and forest canopy cover. This stream-UVB model (SUM) predicts very low UVB flux to the benthic areas of most wetland and forested streams of this region during cloudless, midsummer days. Overall, our results suggest a low likelihood that stream organisms in this region are normally exposed to high levels of ultraviolet radiation because shading is provided by both stream DOC and forest canopy.

Key words: UV radiation, dissolved organic matter, forest canopy, river, benthos.

The depth of ultraviolet radiation (UVR) penetration is negatively correlated with the concentration of dissolved organic C (DOC) in many freshwater ecosystems (reviewed by Xenopoulos and Schindler 2001). This correlation between UVR attenuation and DOC concentration has been documented in lakes of the boreal forest (Huovinen et al. 2003), the north-temperate forest (Scully and Lean 1994, Williamson et al. 1996), the montane forest (Palen et al. 2002), the alpine (Laurion et al. 2000), and in wetlands (Peterson et al. 2002). The absorptivity of DOC (i.e., amount of UV absorbance per unit of C) also can affect UVR penetration among aquatic systems (Williamson et al. 1996, Crump et al. 1999). DOC concentration and chemistry largely control the spectral depth distribution of solar radiation in many lakes, but much less is known about the factors that control UVR exposure of benthic organisms in streams and rivers.

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In relatively flat terrain, the flux of solar radiation into a particular water body is controlled by atmospheric conditions, riparian vegetation, surface reflectivity, and water quality (Diamond et al. 2005). Riparian vegetation is an important filter of UVR to small streams. A full forested canopy can block >90% and a partial canopy can block >66% of mid-day solar radiation (Grant et al. 2002, Kelly et al. 2003). In contrast, attenuation of UVR by riparian vegetation is less prevalent in lakes and large rivers because of the greater extent of unshaded surface area in these systems. Given its importance in lakes (Xenopoulos and Schindler 2001), DOC is likely to play a key role in attenuating UVR in streams and rivers. Suspended particles also affect the penetration of UVR into some water bodies through absorption and scattering of light energy (Belzile et al. 2002). The depth of the water column is another physical factor that controls the amount of UVR reaching the benthos in streams. Greater depth increases the distance that photons must travel through DOC in the water column and reduces the amount of UVR reaching the stream bed.

We quantified the attenuation of UVR and as-

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sessed its environmental control in streams of the Upper Great Lakes region. We examined the relationships between attenuation coefficients (K_d) of UVR and their potential controllers, including DOC concentration, the concentrations of suspended particulate organic C (POC) and chlorophyll *a* (chl), and DOC molar absorptivity. We also measured the absorbance coefficients of dissolved organic matter (a_d) in water from these streams. We used our data to model the interactive effects of DOC concentration, stream depth, and forest canopy on ultraviolet B (UVB) flux to the stream bed. Given the wide range of DOC concentrations (2–35 mg C/L) found in streams surveyed in our study, we predicted that UVR attenuation would be strongly correlated with DOC concentration, but we also expected stream depth, DOC absorptivity, and forest canopy to be important moderators of UVR flux to benthic organisms in streams.

Methods

Site description

We measured the attenuation of UVR on multiple occasions in 32 streams (for a total of 51 measurements) in the Ontonagon River watershed during the midsummers of 2003 and 2004 (20 June–20 August and 14–19 July, respectively). The Ontonagon River watershed is in northern Wisconsin (Vilas County) and the Upper Peninsula of Michigan (Gogebic, Houghton, Iron, and Ontonagon Counties) and is largely covered by mixed deciduous and coniferous forest. Significant areas of lakes and wetlands also are found in the southern half of the watershed. Our sites were mostly headwater streams (1^{st}- and 2^{nd}-order streams) but also included some larger streams (3^{rd}- and 4^{th}-order). Most of the 1^{st}- and 2^{nd}-order streams were relatively shallow with maximum depths ≤0.5 m during midsummer flows. Larger streams (3^{rd}- and 4^{th}-order) were deeper and had maximum depths ≥1 m. Streams in this region are characterized by mixed substrates, with rock and cobble being most prevalent. Soft sediments and fine sand also are found in some streams of the Ontonagon River watershed.

Underwater measurements of UV radiation

We measured UVR in slow-moving, flat-water, canopy-free reaches of each stream during mid-day (1000–1500 h) on cloud-free days. We measured ambient UVR in the air and at increasing depth within the water column using a fiber-optics spectrometer (USB2000, Ocean Optics, Dunedin, Florida) connected by a 10-m fiber-optic cable to a submersible cosine corrector (Peterson et al. 2002). Because of the rapid attenuation of UVR within these streams, we measured UVR at standard depth intervals close to the water surface (e.g., 1, 3, 5, 10, and 15 cm). The spectrometer instantaneously measured flux at wavelengths every ~0.33 nm between 290 nm and 400 nm and transferred the data to a streamside laptop computer. We used these data to calculate integrated values of UVB (290–320 nm) and ultraviolet A (UVA) (320–400 nm) for each depth. Following Morris et al. (1995), we estimated K_d values for UVB and UVA as the slope of the regression between natural log-transformed irradiance and stream depth. Given the highly turbulent nature and strong vertical mixing common in streams, we assumed constant optical properties throughout the water column. We did not retain K_d values derived from regressions with $r^2 < 0.95$ in our dataset, and we dropped them from subsequent analyses. In total, we excluded 12 $K_{d\ \mathrm{UVB}}$ and 0 $K_{d\ \mathrm{UVA}}$ estimates from the analysis based on this criterion.

Analyses of streamwater chemistry

We assessed the relationships between K_d and streamwater chemistry using water samples collected from each stream. Specifically, we analyzed the DOC concentration and a_d of stream water in both years (2003 and 2004). During summer 2003, we also measured the concentration of suspended POC and suspended chl. In all cases, water was transported back to the laboratory and filtered within 6 h of collection. DOC samples were passed sequentially through a pre-ashed GF/F filter and a 0.2-μm polycarbonate filter (pre-rinsed to remove potential contaminants; Yoro et al. 1999) and refrigerated until analysis. DOC was analyzed on a Shimadzu TOC 5000 analyzer (Columbia, Maryland) after acidification and purging of CO_2 (Sharp et al. 1993). UVR absorbance was measured in 1-cm quartz cuvettes for individual wavelengths between 280 and 400 with an Ocean Optics S2000 spectrometer (Dunedin, Florida) connected to a cuvette holder with a fiber-optics cable.

These absorbance values were converted to a_d by multiplying by 2.303 and dividing by the path length (Crump et al. 1999). After conversion, $a_{d\ UVB}$ and $a_{d\ UVA}$ were calculated as average values across these individual wavebands. DOC molar absorptivity was calculated as the ratio of raw absorbance at 280 nm to the molar concentration of DOC. Suspended POC was collected on pre-ashed GF/F filters, dried at 60°C, and frozen until analysis on a Costech elemental analyzer (ECS 4010, Valencia, California). Chl samples were also collected onto GF/F filters and immediately frozen. Chl was estimated, without phaeophytin correction, fluorometrically after cold, dark extraction of thawed samples for 24 h in methanol (Marker et al. 1980).

Statistical analysis

We assessed the relationship between K_d values (UVB and UVA) and DOC concentrations using simple linear regressions. Given the nonlinear relationship between 1% transmission depths (UVB and UVA) and DOC concentrations, we transformed the 1% transmission depths (for both UVB and UVA) and the DOC (for only UVB) before fitting a linear regression. For the data from 2003, we completed multiple linear regressions between stream K_d and DOC concentration, suspended POC, suspended chl, and molar absorptivity using SAS (version 8, SAS Institute, Cary, North Carolina). In this analysis, we selected the best model fit from all possible model combinations as the one that had the smallest ΔAIC (Akaike's information criterion) and greatest AIC w_i, where w_i is the Akaike weight and approximates the probability that a particular regression model is the best fit among all alternatives (Westphal et al. 2003).

Stream-UVB model (SUM)

To estimate the flux of UVB to the stream benthos, we created a numerical model that incorporated canopy cover, DOC concentration, and stream depth. We calculated UVB flux as:

$$E_b = E_o C_r (1 - R_s) e^{(-K_d z)} \qquad [1]$$

where E_b is the irradiance reaching the benthos, E_o is the irradiance above the canopy, C_r is fraction of irradiance penetrating through the canopy, R_s is the fraction of irradiance reflected from the surface of the stream, K_d is the attenuation coefficient within the water column, and z is the water column depth. We set E_o at 222 μW/cm², which represents an average mid-day UVB value for cloudless days in this region (Diamond et al. 2002). We estimated C_r using a regression equation in Grant et al. (2002):

$$C_i = -0.431 + 1.5787e^{(-m)} - 0.0435 \ln(\theta) \qquad [2]$$

where m is the proportion of canopy cover and θ is the solar zenith angle. For simplicity, we held θ constant at 45°, a normal midsummer value for this geographic region. We used a range of values for m from no shade ($m = 0$) to nearly full cover ($m = 0.90$). We used a value of 0.05 for R_s, which would be a maximum mid-day reflectance of UVB from many water surfaces (Kirk 1994). We estimated $K_{d\ UVB}$ using the stream DOC–$K_{d\ UVB}$ regression equation parameterized by our study. We restricted SUM to 3 stream depths (1, 7, and 20 cm) for simplicity and because most UVB was predicted to be removed by 20 cm. We restricted our model to UVB because, to our knowledge, a model of C_r has not been determined for UVA.

Results

We found a wide range of attenuation coefficients of UVB and UVA radiation among the streams within the Ontonagon River watershed (Table 1). The ranges of both $K_{d\ UVB}$ and $K_{d\ UVA}$ were similar to those found in other aquatic systems (Table 1). Given the K_d values estimated from our study, 1% transmission depths of UVB and UVA penetration for these streams would range from 2 to 45 cm and from 6 to 103 cm, respectively. Both $K_{d\ UVB}$ and $K_{d\ UVA}$ were significantly related to stream DOC concentration, which ranged from 2 to ~35 mg C/L (Fig. 1A, B). DOC explained 67% and 88% of among-stream variation in $K_{d\ UVB}$ and $K_{d\ UVA}$, respectively. One percent transmission depths of both UVB and UVA also were strongly correlated with DOC (Fig. 1C, D), as was a_d for UVB and UVA. Slopes from the DOC–a_d regressions (Fig. 2A, B) were very similar to those found between K_d and DOC for both UVB and UVA. Multiple regression analysis of the 2003 data showed the best model fit for $K_{d\ UVB}$ had DOC (from among DOC, suspended POC, suspended chl, and molar absorptivity) as the only significant predictor variable ($r^2 = 0.67$). The best model fit for $K_{d\ UVA}$

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TABLE 1. Comparison of our values with ranges of values from previous studies from dissolved organic C (DOC), attenuation coefficients for ultraviolet B ($K_{D\ \mathrm{UVB}}$), and the 1% transmission depth (1% depth) of UVB and ultraviolet A (UVA) radiation. Unless otherwise noted, $K_{d\ \mathrm{UVB}}$ are for integrated values. 1% transmission depth was calculated using Beer's Law and the given K_d values. n = number of measurements.

Geographic location	Type	n	DOC (mg/L)	$K_{d\ \mathrm{UVB}}$ (/m)	UVB 1% depth (m)	$K_{d\ \mathrm{UVA}}$ (/m)	UVA 1% depth (m)	Literature source
Finland	Lakes	5	4.9–8.7	8.1–40	0.11–0.56	4.5–39.8	0.12–1.0	Huovinen et al. 2003[a]
Wisconsin and Minnesota (USA)	Wetlands	43	5.3–36.7	5.6–136	0.03–0.82	3.5–125	0.04–1.31	Peterson et al. 2002
Europe	Alpine lakes	26	0.2–3.5	0.2–5.7	0.81–27.1	0.1–4.2	1.1–46.1	Laurion et al. 2000[b]
Northeastern USA	Lakes	12	1.2–23.5	0.4–133	0.03–11.5	0.2–55.7	0.08–23.0	Morris et al. 1995[c]
Colorado (USA)	Lakes	16	0.8–10.1	0.4–43.1	0.01–12.4	2.2–30.1	0.15–2.1	Morris et al. 1995[c]
Argentina	Lakes	17	0.2–2.7	0.2–8.9	0.52–27.1	0.1–5.8	0.79–46.1	Morris et al. 1995[c]
Alaska (USA)	Lakes	12	4.5–11.1	7.10–48.0	0.10–0.65	5.4–38.2	0.12–0.85	Morris et al. 1995[b]
Saskatchewan (Canada)	Freshwater lakes	25	4.1–80.1	5.2–165.4	0.03–0.89	2.2–54.7	0.08–2.1	Arts et al. 2000
Northern Michigan	Streams	51	2.0–34.5	10.3–225[d]	0.02–0.45[d]	4.44–77.6	0.06–1.03	Our study

[a] $K_{d\ \mathrm{UVB}}$ = mean of K_d at 305, 310, 320 mm; $K_{d\ \mathrm{UVA}}$ = mean of K_d at 340, 360, 380 nm
[b] $K_{d\ \mathrm{UVB}}$ = mean of K_d at 320 nm; $K_{d\ \mathrm{UVA}}$ = mean of K_d at 345–370 nm
[c] $K_{d\ \mathrm{UVB}}$ = mean of K_d at 305 nm; $K_{d\ \mathrm{UVA}}$ = mean of K_d at 340 nm
[d] n = 39

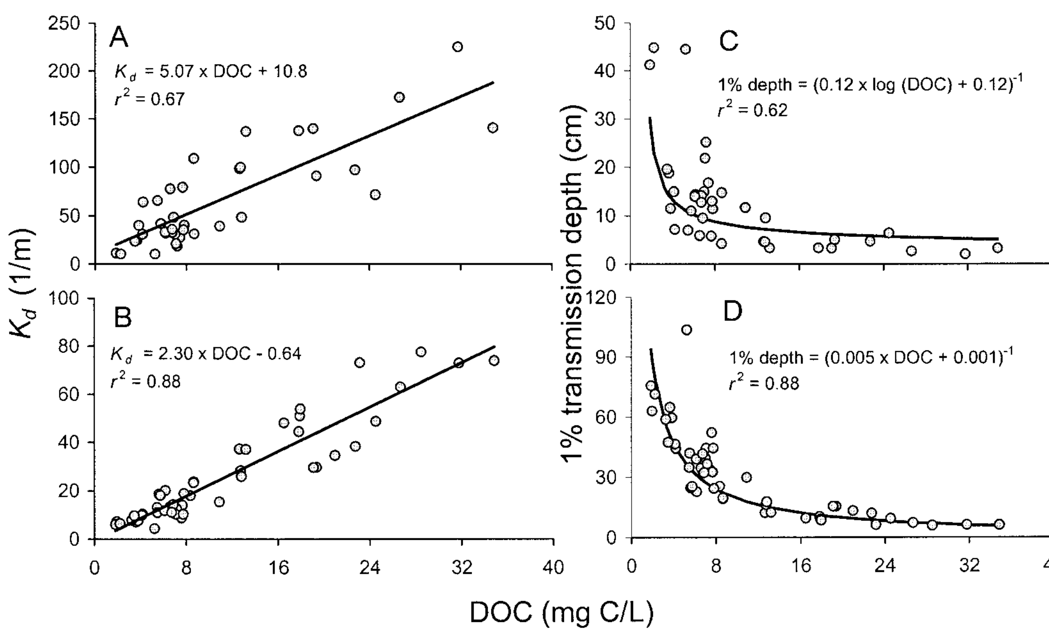

FIG. 1. Relationships between attenuation coefficients for ultraviolet B ($K_{d\ \mathrm{UVB}}$) (A), ultraviolet A ($K_{d\ \mathrm{UVA}}$) (B), 1% transmission depth for UVB (C), and 1% transmission depth for UVA (D) and dissolved organic C (DOC) concentrations in streams in the Ontonagon River watershed in northern Michigan.

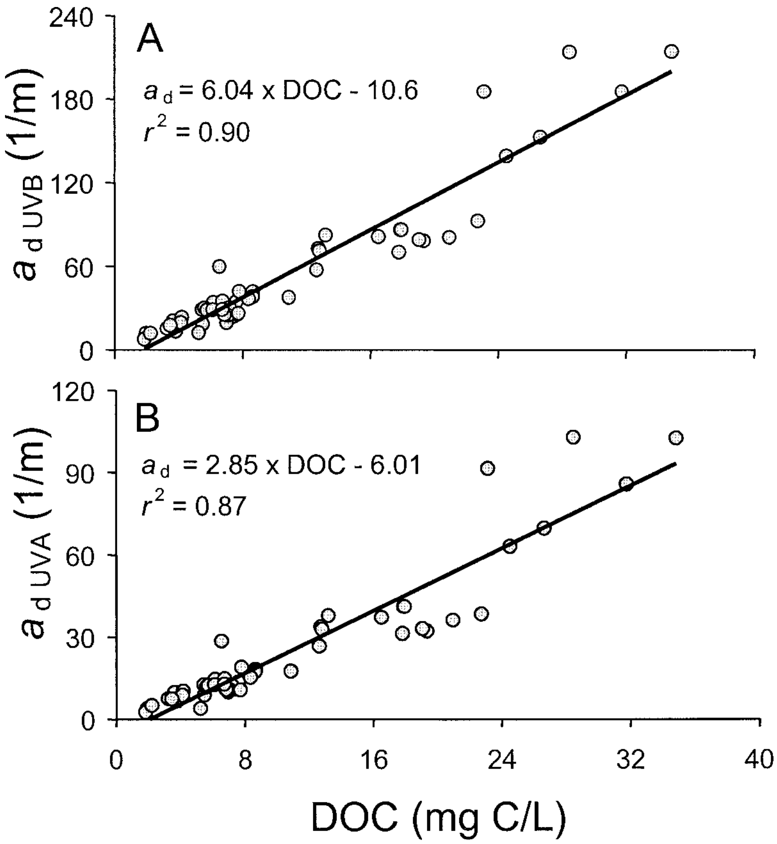

FIG. 2. Relationships between absorbance coefficients (a_d) of dissolved organic C (DOC) for ultraviolet B ($a_{d\ UVB}$) (A) and ultraviolet A ($a_{d\ UVA}$) (B) and DOC concentrations in streams from the Ontonagon River watershed. $a_{d\ UVB}$ and $a_{d\ UVA}$ represent the absorbance values averaged across all UVB and UVA wavelengths (280–320 nm and 320–400 nm, respectively).

included DOC, suspended POC, and molar absorptivity (r^2 = 0.91).

UVB flux to the stream benthos was modeled with our stream-UVB model (SUM) as a function of 3 environmental variables: forest cover, DOC concentration, and water depth. The greatest UVB flux was predicted for very shallow streams (1 cm) having low DOC (<3 mg C/L) and no canopy cover (0%) (Fig. 3A). Increases in any 1 of the 3 factors (depth, DOC, or canopy cover) led to dramatic reductions in mid-day UVB flux to the stream benthos (Fig. 3A, B, C). For example, almost no UVB would be expected to reach the benthos at a stream depth of 20 cm even in moderately clear streams (DOC < 5 mg C/L) having little or no canopy cover (Fig. 3C). Similarly, high canopy cover (m = 0.90) would remove a large proportion of UVB flux to the benthos (Fig. 3A, B, C). DOC also dramatically reduced UVB reaching the benthos in all but the shallowest streams (1 cm, Fig. 3A). The greatest exclusion of UVB is predicted by SUM to occur in streams having high values of ≥2 of these variables.

Discussion

We observed rapid attenuation of UVB and UVA in the wetland and forested streams of northern Michigan. Across a wide range of DOC concentrations (2 to ~35 mg C/L), 1% transmission depths for UVB ranged from 2 to 45 cm. This rapid attenuation of UVB in the water column suggests that the biological importance of this physical factor is restricted to only the shallowest portions of streams of the Upper Great Lakes region. As previously shown for lakes (reviewed by Xenopoulos and Schindler

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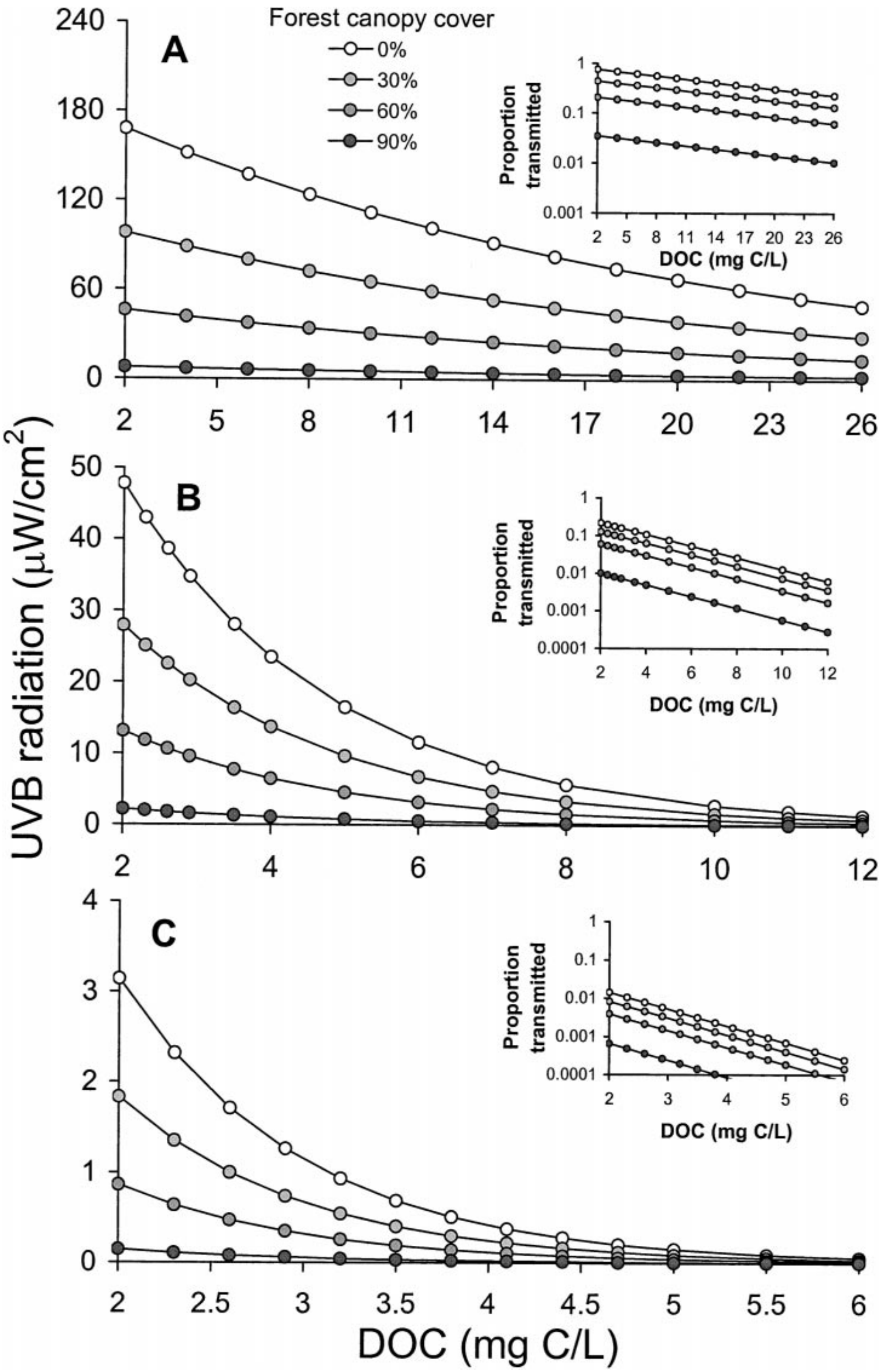

FIG. 3. Modeled ultraviolet B (UVB) flux in streams as a function of water depth, DOC, and forest canopy cover as determined by the stream-UVB model (SUM) for 1-cm depth (A), 7-cm depth (B), and 20-cm depth (C). Proportion transmitted (insets) was calculated as the ratio of irradiance at the benthos (E_b) to the irradiance above the canopy (E_o). E_o was set at 222 μW/cm², an average mid-day value for cloudless days in this region (Diamond et al. 2002).

2001), we observed less attenuation and greater penetration of UVA than UVB in the water column of these streams; the 1% transmission depths for UVA ranged between 6 and 103 cm. Greater depths of UVA penetration would translate into relatively higher doses and, perhaps, a relatively greater impact of UVA on the benthos of small streams in this region.

DOC is the primary attenuator of UVR in freshwater ecosystems (Xenopoulos and Schindler 2001, Peterson et al. 2002). We found that $K_{d\ \mathrm{UVB}}$ and $K_{d\ \mathrm{UVA}}$ were significantly correlated with DOC concentration in our streams. We also found strong positive relationships between a_{d} and DOC concentrations for UVB and UVA. These relationships were similar to those found between K_d and DOC, which suggests that our in situ method provided reasonable estimates of K_d. However, we found that relatively less variation (67%) in $K_{d\ \mathrm{UVB}}$ was explained by DOC concentration compared with previous studies in lakes (97%, Scully and Lean 1994; 87%, Morris et al. 1995; 95%, Huovinen et al. 2003). Similarly low proportions (~43% and 63%, respectively) of variation in $K_{d\ \mathrm{UVB}}$ were explained by DOC in studies of UVR attenuation in wetlands (Peterson et al. 2002) and ponds (Crump et al. 1999). We found no evidence to suggest that the molar absorptivity of DOC could account for the residual variation in $K_{d\ \mathrm{UVB}}$. One potential reason for the limited effect of molar absorptivity would be little among-stream variation in DOC-specific absorptivity, but this explanation does not appear supported as molar absorptivity ranged from 200 to 650 L mol C^{-1} cm^{-1} among streams in our survey. An alternative explanation for the modest amount of variation in $K_{d\ \mathrm{UVB}}$ explained by DOC is that sampling error in measuring depth or changing sunlight intensity during the depth profile altered our K_d estimates. However, such events presumably would have lowered the goodness-of-fit in our original depth–light regressions, and we retained only K_d values derived from UVR–depth profiles with $r^2 > 0.95$ (see Methods).

The low variation in $K_{d\ \mathrm{UVB}}$ explained by DOC could have also resulted from the effects of other aspects of stream chemistry (e.g., dissolved solids). For example, flowing waters can have high levels of suspended organic and inorganic material (e.g., Lamberti and Resh 1987), which potentially affect the attenuation of UVR through absorption and scattering. Previous work in lakes showed a very limited role of absorption by suspended solids, except in systems having little DOC (Smith et al. 1999, Belzile et al. 2002). Similarly, we found no relationship between the attenuation of UVB and suspended chl or POC. This absence of a relationship may have been a consequence, in part, of the relatively small range in chl (~0.3–10 μg/L) and suspended POC (~0.2–2.0 mg C/L) observed in these streams during midsummer flows. $K_{d\ \mathrm{UVB}}$ values also could have been affected by particle scattering (not quantified in our study), which often is assumed to be relatively unimportant compared to absorption. In aquatic ecosystems with high DOC absorption, the effects of particle scattering may be amplified and, thereby, contribute significantly to variation in K_d values, especially at shorter wavelengths (Kirk 1991, Belzile et al. 2002). Scattering and its effects on UVB attenuation in streams with high DOC concentrations should be examined in the future, especially during periods (e.g., spring and autumn) when suspended materials may be found at elevated concentrations in streams.

We found a strong relationship between $K_{d\ \mathrm{UVA}}$ and stream DOC concentration, but UVA attenuation also was significantly related to suspended POC and molar absorptivity in our multiple regression analysis. It is not clear why these 2 variables (POC and molar absorptivity) were significant predictors of $K_{d\ \mathrm{UVA}}$ but not of $K_{d\ \mathrm{UVB}}$, especially as less residual variation in $K_{d\ \mathrm{UVA}}$ remained unexplained by DOC concentration. One potential reason for this result is that UVA has a longer path length than UVB in the water column, a fact that allowed us to capture the relatively subtle effects of suspended materials and DOC absorptivity on $K_{d\ \mathrm{UVA}}$. UVA attenuation also is measured more easily than UVB in surface waters because of its higher total energy; this ease of measurement may have resulted in lower sampling error when measuring $K_{d\ \mathrm{UVA}}$ (but see above), allowing us to detect the relatively minor effects of POC and molar absorptivity. In any case, additional empirical and theoretical work is needed to better understand how dissolved and suspended materials affect the absorption and scattering of UV radiation and, thereby, contribute to its attenuation in streams of contrasting DOC concentrations.

The underwater attenuation of UVB was, on average, higher in the Michigan streams in our study than in lakes having comparable DOC

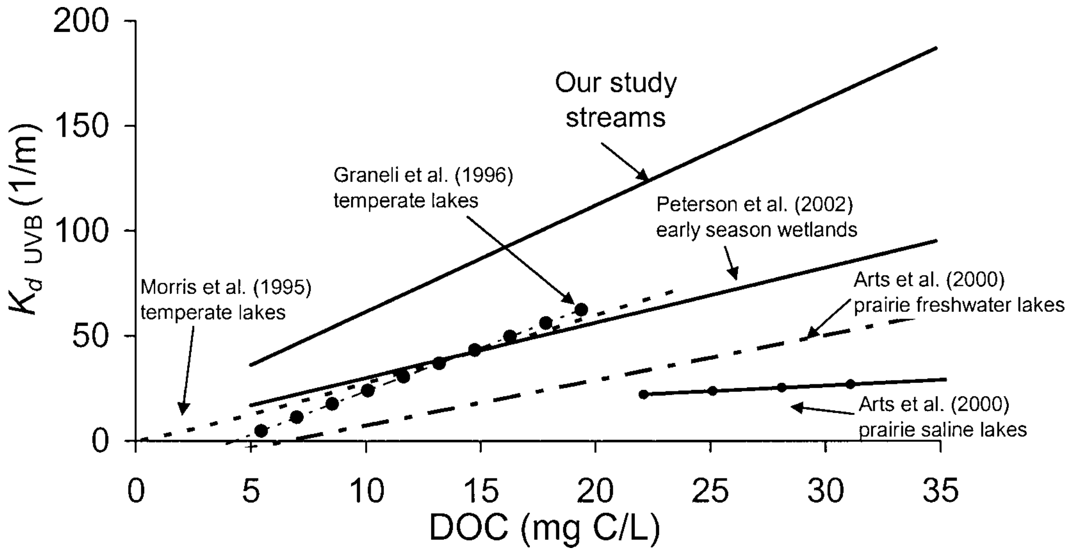

FIG. 4. Comparison of regressions for dissolved organic C (DOC) and attenuation coefficients for ultraviolet B ($K_{d\ \mathrm{UVB}}$) from our study of northern Michigan streams and regressions derived from lake systems having a wide range of DOC concentrations.

concentrations (Fig. 4). Previous studies of lakes also have shown regional variation in DOC-specific $K_{d\ \mathrm{UVB}}$ (Arts et al. 2000, Peterson et al. 2002). In particular, saline and freshwater lakes on the Canadian prairie have much greater UVR penetration than other lakes with comparable DOC concentrations (Arts et al. 2000). The reduced UVR attenuation by DOC in these lakes is probably a consequence of long water-residence times that allow extensive photochemical and biological processing of the DOC. Our result of higher DOC-specific $K_{d\ \mathrm{UVB}}$ suggests that DOC in these forested streams is relatively new and has not undergone extensive photochemical or biological transformation. Another factor that may account, in part, for differences in the attenuation of UVR is whether the DOC is derived from terrestrial or instream sources. Terrestrial DOC is more humic and absorptive of UVR than DOC produced by algae and bacteria (McKnight et al. 1994). Small headwater streams in forested regions such as northern Michigan may have a higher % of their DOC recently derived from terrestrial sources. However, the lack of a significant correlation between DOC absorptivity and $K_{d\ \mathrm{UVB}}$ suggests that the effects of DOC chemistry in UVR attenuation is not straightforward, at least in streams within this region. More work comparing the type and extent of degradation of DOC to the attenuation coefficients in streams and lakes will be needed to fully test these alternative explanations for the higher UVB absorptivity of stream water documented here.

Our stream-UVB model (SUM) is the first to generate mid-day estimates of UVB flux to the stream benthos using information on forest cover, DOC concentration, and stream depth. SUM predicts that appreciable quantities of UVB will be found only in the shallowest areas of unshaded streams (i.e., shallow riffles or barely submerged rocks) with low DOC concentrations. However, more work is needed to determine how UVB flux to the stream surface is affected by a host of other factors not incorporated into SUM: stream width and geophysical orientation, slope of the surrounding landscape, riparian vegetation, cloud cover, solar angle, and the diffuse nature of UVR radiation (Brown et al. 1994, Xenopoulos and Schindler 2001, Diamond et al. 2005). Other factors that potentially alter UVR attenuation in streams include stream surface smoothness, foaming, and bubbling. In addition, a similar model estimating UVA flux to the benthos would be useful but will require knowledge of canopy effects on these longer wavelengths. Nonetheless, it appears that stream DOC and forest canopy prevent a significant proportion of UVB from reaching the benthos of most streams in this region.

Given the strong attenuation of UVR in the forested reaches of these streams, benthic organisms probably receive small doses of these energetic wavelengths compared to planktonic organisms found in relatively transparent lakes. It remains unclear how sensitive stream taxa will be to future increases in UVR. For example, morphological protection (e.g., shells on snails) and behavioral avoidance (e.g., negative phototaxis by mayflies) could place limits on the potential effects of increased UVR exposure on many important stream consumers (McNamara and Hill 1999). Less mobility and a physiological requirement for solar radiation would probably increase the likelihood that benthic algae experience negative effects of increasing UVR exposure. However, many algal taxa can be largely insensitive to UVR exposure (Bothwell et al. 1994, Xenopoulos and Frost 2003) because of the protection afforded by pigments and physiological repair mechanisms (Garcia-Pichel 1994). Given these complexities, research is needed to examine how current levels and potential increases in UVR affect benthic communities, especially in forested streams such as those documented here where UVR is currently found at exceedingly low levels.

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