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Environmental Controls of UV-B Radiation in Forested Streams of Northern Michigan

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ABSTRACT

We examined UV-B radiation flux and its environmental control within and among streams of northern Michigan. UV-B flux was estimated in streams by plastic dosimetry strips, which allow for the simultaneous and repeated *in situ* measurement of solar radiation. During the summer of 2004, UV-B flux was measured across depth gradients and along longitudinal transects in seven streams, which were chosen to encompass a range of dissolved organic carbon (DOC) concentrations and canopy cover. Attenuation coefficients of UV-B ($K_{d\ UV\text{-}B}$) were estimated using plastic dosimeters placed along a depth gradient. $K_{d\ UV\text{-}B}$ were positively correlated with DOC concentration and similar to values obtained with laboratory and *in situ* spectrometry. Along 100 m longitudinal transects, UV-B flux varied along all streams regardless of their canopy cover and DOC concentration. Within-stream fluxes of UV-B were correlated to canopy cover in the only two streams that both had relatively low DOC concentration and variable canopy cover. Large differences were found among streams in the average UV-B flux (corrected for incident solar flux) reaching the dosimeters at 5 cm depth. These among-stream differences were largely accounted for by the stream width, canopy cover, and DOC concentration. Our results illustrate an inherent variability in UV-B flux within and among streams of northern Michigan that is strongly tied to the interactions of DOC concentration, stream size and riparian vegetation.

INTRODUCTION

The depletion of the stratospheric ozone layer at high latitudes and the resulting increases in ultraviolet-B radiation (UV-B, 280–320 nm) reaching the earth's surface has received considerable attention over the past 20 years. This concern about ozone depletion has been accompanied by efforts to understand UV-B effects on populations, community interactions and ecosystem processes in lakes and oceans (1–3). UV-B can reduce the growth and survivorship of aquatic organisms (4,5), modify trophic interactions between producers and consumers (6) and alter the biogeochemical cycling of carbon and other nutrients in aquatic ecosystems (7). A full understanding of UV-B effects on aquatic ecosystems requires coupling information on its ecological effects to estimates of its flux into these environments (8). However, the flux of UV-B radiation and its relationships with the nonatmospheric, physico-chemical environment remains poorly understand in many ecosystems.

The attenuation of UV-B radiation within freshwater ecosystems is primarily controlled by dissolved organic carbon (DOC) concentration (9,10). The wide range of DOC concentrations found among lakes results in considerable variation in the UV-B flux at depth into these systems. UV-B penetration into lakes and ponds can also be affected by the absorption of solar radiation by suspended particles (11) and by differences in DOC molar absorptivity (12). UV-B attenuation has been shown to vary considerably among small forested streams, largely because of differences in their DOC concentration (10). Although the importance of DOC concentration in controlling UV-B attenuation in freshwaters is well established, the effects of other environmental factors of its flux remain largely unstudied.

Riparian vegetation is an important environmental filter of UV-B in both aquatic and terrestrial environments (13–15). Forest canopies are known to strongly attenuate visible and UV-B radiation before it reaches ground level (14,16). For example, in a mixed deciduous forest in Maryland, 40–70% of incident UV-B radiation (280–320 nm) was absorbed by the top 25% of the canopy and only 1–2% of this radiation reached the forest floor under a closed canopy (14). Consequently, heavy canopy can strongly affect UV-B flux reaching the surface of forested streams (15). In streams, UV-B flux may also relate to channel width, which can alter solar flux into streams by partly determining the density of overhanging vegetation (17). Although the presence of forest canopy is acknowledged to have strong effects on solar flux (i.e., 15), the relationship among canopy cover, stream width and UV-B flux within and among streams has not received previous study.

In this study, we examine the relationship between UV-B flux and physical shading factors in seven streams of northern Michigan. Our primary objective was to measure UV-B flux within and among streams as it relates to stream shade and DOC concentration. We measured UV-B flux across depth gradients in streams to estimate attenuation coefficients in streams of contrasting DOC concentrations. We also measured UV-B flux along longitudinal transects (at fixed depths) within streams of contrasting canopy covers, stream widths and DOC concentrations. We expected an interactive effect of stream shade and DOC on UV-B flux such that (1) UV-B flux in low-DOC streams would be directly related to the extent of stream shade and (2) UV-B flux in

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Table 1. Location of and UV flux into streams on the dates examined in this study

Stream	Date	Latitude and longitude	UV-B flux (kJ m^{-2})*
Banner†	**9 July 2004**	**46°21′N 89°35′W**	**56.62‡**
Brown†	**21 June 2004**	**46°12′N 89°29′W**	**60.77‡**
Cisco Branch	29 July 2004	46°5′N 89°27′W	30.38‡
Marshall	15 July 2004	46°24′N 89°34′W	31.90
Nelson	03 July 2004	46°23′N 89°37′W	25.37
Tenderfoot 1	19 June 2004	46°15′N 89°32′W	34.31
Tenderfoot 2	29 July 2004	46°15′N 89°32′W	27.47
Trout Brook†	**22 July 2004**	**46°26′N 89°31′W**	**45.58‡**

*UV-B flux is the nonshaded incident radiation reaching the study location over the duration of the dosimeter deployment.
†Bold type indicates that exposure at these stream sites lasted for 2 days; other locations had 1 day exposures.
‡Exposure at these streams was corrected as outlined in the Methods to account for streamside shading.

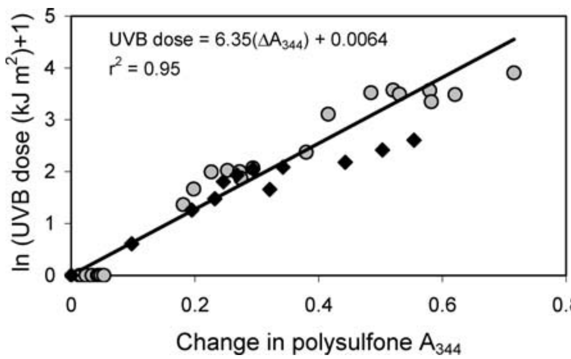

Figure 1. *In situ* calibration (gray circles) used to convert the absorption change at 344 nm (A_{344}) of polysulfone plastics into UV-B dose. Also shown is the laboratory verification (black diamonds) of *in situ* calibration of UV-B response of polysulfone plastics. The regression line and statistics do not include the laboratory data. See Methods for details on the generation of both calibration curves.

high-DOC streams would be low regardless of canopy cover and stream width.

MATERIALS AND METHODS

Overview. The flux of UV-B was measured with the use of plastic dosimeters (described below) in seven streams located in northern Wisconsin and the upper peninsula of Michigan (Table 1). At each stream, UV-B was measured along a longitudinal gradient to determine the amount of within-stream variability. To do so, dosimeters were placed in the center of the stream at a depth of 5 cm every 10 m along a haphazardly chosen 100 m longitudinal transect. At one nonshaded location in each stream, UV-B attenuation coefficients (K_d) were estimated using data from dosimeters placed along a water depth gradient (1, 3, 5, 10 and 20 cm). All dosimeters were deployed during daybreak (before 8:00 A.M.), left for 1 or 2 days (Table 1) and retrieved after sunset. One stream (Tenderfoot Creek) was measured on two occasions.

Dosimeter description. We used polysulfone plastic to measure UV-B flux in the study streams. This plastic has previously been used to estimate UV-B doses in wetlands (18) and has been widely used to measure UV-B in terrestrial studies (see 19). The absorbance properties of polysulfone in the lower UV-A wavelengths (330–340 nm) change predictably with increasing UV-B exposure and thus provide a reliable index of UV-B flux (20). This absorption change in the polysulfone primarily results from exposure to UV-B radiation (290–320 nm; 20) and, as such, we refer to measurements in this study as UV-B flux. We constructed dosimeters by attaching strips (1.2 cm × 1.8 cm) of polysulfone plastic to the tops of small vials. One layer of Teflon plastic (10 mm) was placed directly over the polysulfone to diffuse sunlight. A layer of black plastic was placed under the polysulfone strips to ensure that all solar radiation absorbed by the polysulfone originated from above. Dosimeter vials were filled with water to diminish their buoyancy and taped into groups of three for placement at each location along the depth and longitudinal gradients. Wooden dowels driven into the stream bottom held the dosimeters at a constant location, depth and angle in the streams. Three dark-control dosimeters (black plastic on both sides of the polysulfone strip) were also placed in the stream at a depth of 5 cm and adjacent to one set of *in situ* dosimeters. After the exposure period, dosimeter plastic was stored in the dark until its absorbance (A_{344}) of the wavelengths of 343.98 to 344.34 nm was measured with an Ocean Optics Inc. S2000 spectrometer (Dunedin, FL). This wavelength band was chosen because it was the one where a measurable change was produced by UV-B exposure for the polysulfone plastic used in this study.

Solar radiation measurements. The flux of solar radiation at a relatively canopy-free location on the stream bank was measured every 5 min with a silicon pyranometer (spectral range: 300 to 1100 nm) connected to a Hobo® microstation data logger (Onset Computer, Bourne, MA). The total flux of solar radiation (J m^{-2}) for the period of exposure was estimated by integrating the logged data over each 5 min interval and summing the flux for the total exposure period. This measured solar flux was converted into UV-B flux using the energy ratio of total solar radiation to these spectral wavelengths. The energy ratio was determined by taking simultaneous measurements of midday solar radiation with the silicon pyranometer and a fiber optics spectrometer (USB2000, Ocean Optics Inc.) connected to a cosine corrector. The UV spectroradiometer was calibrated by the manufacturer (Ocean Optics Inc.) using a NIST traceable D2 lamp prior to its use in the field. Given the forested nature of the region, we were unable to find an entirely canopy-free location for the pyranometer at several of the streams. To ensure that the total flux that we measured was indicative of above-canopy flux, we compared our measured solar radiation to data obtained by a CM3 pyranometer (Kipp & Zonen, Delft, Netherlands) that continuously logs solar data at the University of Notre Dame Environmental Research Center (UNDERC). This UNDERC solar logger is located in the same general area as all of our study streams. On four of our sampling dates, we found a lower flux at the stream site than that recorded at UNDERC. On these dates (see Table 1), we increased our measured flux to be proportional to that measured at the completely unshaded location at the field station.

Dosimeter calibration. To generate a calibration curve relating UV-B dose to dosimeter polysulfone absorption change, we deployed three sets of three dosimeters adjacent to the pyranometer during each sampling period. These dosimeters were exposed to full sunlight, partial shade (exposed to 20% of incident radiation) or complete shade (0% incident radiation). Dosimeters were partially shaded by placing one layer of neutral-density shade cloth above the polysulfone plastic. To generate a calibration curve, data from the all of the sampling days were pooled and a single regression line was fit after natural-log transformation of the estimated UV-B flux (Fig. 1). This calibration curve was applied to the average polysulfone A_{344} for in-stream dosimetry strips to estimate the *in situ* UV-B flux. We also independently verified our field dosimeter calibration by exposing the plastic dosimeters (in the configuration as described above) to increasing UV-B doses produced by a Philips TL20W/12 fluorescent lamp in a laboratory setting (Fig. 1).

Assessment of stream shade. At each transect location a hand-held, spherical densitometer was used to estimate the percentage of vegetative cover above the stream (21). In addition, we measured the stream channel width (m) at each of 10 locations within each stream transect. We defined a stream shading index (SSI) that incorporated measurements of canopy cover (% canopy) and stream width (m) as follows:

$$SSI = \%\ canopy \times (1/stream\ width) \quad (1)$$

Larger values of SSI, produced by relatively small streams with greater canopy cover, should be indicative of greater canopy density and, consequently, increased stream shade.

Water analysis. Coincident to the placement of dosimeters in each respective stream, water was collected from the site for analysis of DOC concentration and UV-B absorbance. Water samples were filtered through prerinsed 0.22 μm polycarbonate filters and stored in a refrigerator until analyzed. DOC concentration was measured with a Shimadzu TOC 5000 analyzer (Columbia, MD) after acidification and purging of CO_2 (22). UV-B (290–320 nm) absorbance of the stream water was measured with an Ocean Optics S2000 spectrometer. The average dissolved attenuation

Table 2. Comparison of UV-B attenuation coefficients for seven streams in northern Michigan as determined by plastic dosimetry (D–$K_{d\ UV\text{-}B}$), UVR absorbance spectrometry ($A_{d\ UV\text{-}B}$), and an underwater spectrometer (Sp–$K_{d\ UV\text{-}B}$). See (10) for details of estimates derived by the underwater spectrometry. Also provided is the concentration of the dissolved organic carbon ([DOC], mg C L^{-1}) measured for each stream on the sampling day

Stream	D–$K_{d\ UV\text{-}B}$ (m^{-1})	$A_{d\ UV\text{-}B}$ (m^{-1})	Sp–$K_{d\ UV\text{-}B}$ (m^{-1})	[DOC]
Banner	244.8	237.8	213.7	42.67
Brown	58.83	55.13	79.53	11.51
Cisco Branch	10.53	18.84	10.34	5.23
Marshall	45.16	36.91	38.15	7.88
Nelson	178.8	213.1	140.8	38.15
Tenderfoot 1	47.20	34.80	45.52	9.05
Tenderfoot 2	22.92	26.22	36.03	6.72
Trout Brook	20.90	29.17	48.24	12.81

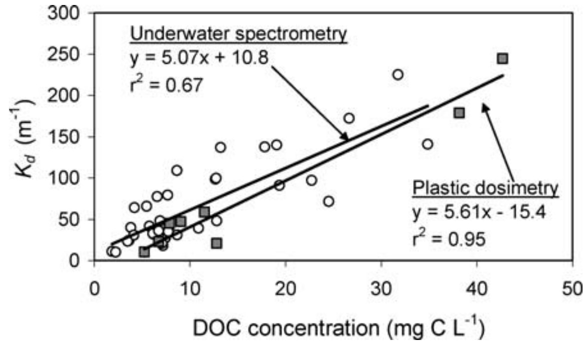

Figure 2. Relationship between $K_{d\ UV\text{-}B}$ and DOC concentrations based on estimates with dosimetry (solid squares) and underwater UV radiation spectrometry (open circles). UV-B spectrometry data was obtained from a dataset of a larger stream sampling in the same geographic region as previously presented (10).

($A_{d\ UV\text{-}B}$) was estimated for each stream by averaging across the wavelength-specific raw absorbances, multiplying this product by 2.303 and then dividing by the cell path length (12). In addition, DOC molar absorptivity (UV-B) was calculated as the ratio of average raw UV-B absorbance by the molar concentration of DOC.

Data analysis. Using the depth gradient dosimeters, K_d values for UV-B were estimated as the regression slope between natural-log transformed irradiance and stream depth (23). Dosimetry-based estimates of UV-B flux (after natural-log transformation) were analyzed either with all data (point estimates) or averaged along stream transects (reach estimates). Point estimates along transects within each stream were related to the percentage of canopy cover with simple linear regressions using JMP® software (version 4.04; SAS Institute, Cary, NC). In addition, UV-B flux (natural-log transformed) was related to stream width, canopy cover and the SSI using point estimate data from all streams with simple linear regression. Average UV-B flux into stream reaches was related to stream DOC concentration, stream DOC molar absorptivity, stream width (natural log transformed), canopy cover and the SSI with simple linear regressions. Average UV-B flux into stream reaches was also related to stream DOC concentration, stream DOC molar absorptivity, canopy cover and the SSI with a forward stepwise, multiple-factor linear regression also using the JMP® software.

RESULTS AND DISCUSSION

Depth profiles and K_d estimates

$K_{d\ UV\text{-}B}$ values derived from the dosimeters placed along the depth gradient ranged widely among streams in this study (Table 2) and were strongly and linearly correlated to $A_{d\ UV\text{-}B}$ ($r = 0.987$). Stream $K_{d\ UV\text{-}B}$ was also strongly correlated to DOC concentration (Fig. 2). This relationship is remarkably similar to one produced with data from *in situ* spectrometry of UV radiation attenuation derived from a larger sampling of streams within this same area (10). Additional data, especially at higher DOC concentrations, would be needed to more fully describe the relationship between dosimetry-derived K_d and DOC in streams from this region. Regardless, our results demonstrate that rates of UV radiation attenuation in streams estimated by polysulfone dosimetry can be largely equivalent to other commonly used laboratory and *in situ* spectrometric methods (Table 2).

Variable UV-B doses within streams

The dose of UV-B at a 5 cm depth also ranged widely among streams in this study. Three of the streams showed relatively high UV-B flux at 5 cm (Fig. 3), which corresponded to the transmission of about 10–20% of above-canopy incident UV-B radiation (Fig. 3). The four other streams in our study were characterized by much lower UV-B flux (Fig. 3), with between 0.5% and 2.5% of incident UV-B radiation found at a depth of 5 cm. In some streams, UV-B flux varied considerably along the 100 m transect. For example, in Trout Brook, UV-B flux varied between 1.0% and 9.3% of incident irradiance within only 20 m of stream length (Fig. 3). Other streams showed less range in UV-B transmission along the 100 m transect. For example, in Banner Creek, UV-B flux at 5 cm depth was at or less than 1.1% of incident irradiance for the entire 100 m transect (Fig. 3).

Relationship of UV-B flux with stream canopy, shading and DOC

Variability in percentage of UV-B transmission to 5 cm depth within individual streams along the transects did not, as expected, correlate to canopy cover for all streams (Table 3). In several streams, little or no variation in canopy cover provided no explanation for the longitudinal variation that was measured. For example, Tenderfoot Creek had no canopy cover for its entire 100 m transect and, hence, no longitudinal variation was explained by canopy cover (Table 3). In other streams (*e.g.* Banner Creek), high DOC concentrations reduced the UV-B flux to levels where differences in UV-B flux potentially produced by changing canopy were not detectable at the depth (5 cm) that dosimeters were placed in the stream. However, in two streams with relatively low DOC concentrations and large differences in canopy (Marshall Creek and Trout Brook), UV-B flux transmitted to 5 cm varied considerably along the 100 m transect and correlated strongly with the percentage of canopy cover. This result matches our prediction that spatial variability in UV-B flux into streams would be greatest in low DOC streams with intermediate amounts of stream shading.

Although point estimates of the percentage of UV-B transmission were not strongly correlated with canopy along the 100 m transect within most of these streams, transmission percentage was negatively related to increasing canopy cover when point estimates from all streams were pooled (Fig. 4). This negative correlation was not a consequence of canopy cover being correlated with DOC (results not shown) and indicates that, regardless of DOC concentration, streams with greater canopy cover generally have less UV-B flux at a given depth. This reduction in UV-B flux with increasing forest shading among streams is consistent with previous work showing a strong effect of vegetation on UV radiation

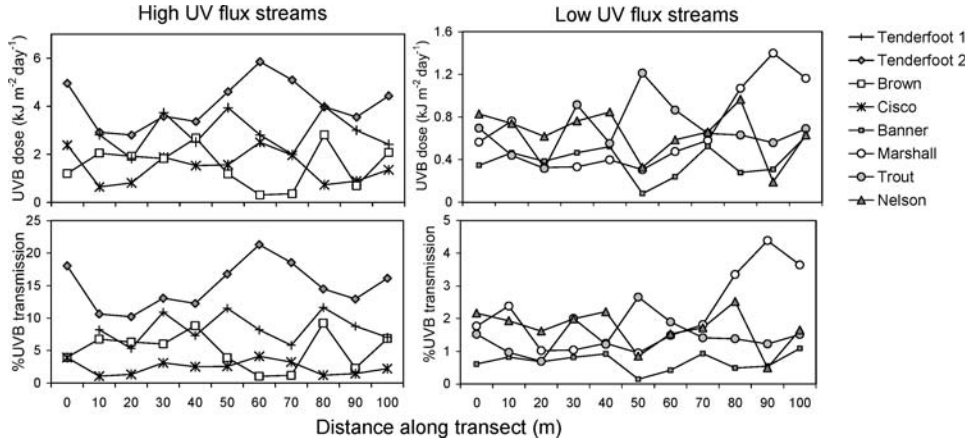

Figure 3. Point estimates of daily UV-B doses and percentage of transmission (at 5 cm depth) along stream transects in seven northern Michigan streams. For visual clarity, streams were split into two groups: high UV-B flux and transmission percentage, and low UV-B flux and transmission percentage. Note that although point estimates of UV-B fluxes are presented on a daily basis, the total unshaded UV-B flux for each particular day was different and accounts for some of the among-stream differences in dose.

flux to the forest floor (5,14) and on light penetration to stream surfaces (13,24). We also found that wider streams have greater UV-B flux than narrower streams (Fig. 4). This difference is undoubtedly because, in part, of less canopy cover over wider streams. Smaller streams generally had a greater amount of and variation in canopy cover, which should produce greater variability in UV-B flux. Narrow streams, even without a full canopy, may also have less diffuse UV-B radiation reaching their surfaces because of absorbance by bank-side vegetation (25). The SSI, which weighted the percentage of canopy cover in a stream by its channel width explained marginally more UV-B variation than did canopy cover and less than stream width (Fig. 3). The greater variation of UV-B flux explained by stream width compared to canopy cover and the SSI indicates that another physical shading factor covaries with width but not with canopy cover. Stream DOC was strongly and negatively correlated to stream width ($R = -0.77$) but only weakly correlated to canopy cover ($R = 0.28$). The positive relationship between UV-B flux and stream width thus appears to be a consequence of less canopy and lower DOC in the wider streams. Future work would need to increase the number of streams to include all pair-wise combinations of stream sizes, percentage of canopy cover and DOC concentrations to be able to fully understand this significance of stream width on UV-B flux. Additional measurements of UV-B flux at the stream surface would also be useful to separate out the effects of DOC concentration and canopy cover in streams of increasing size.

Table 3. Linear regressions between point estimates of % UV-B transmission (natural log transformed) at 5 cm depth and canopy cover in the seven streams of this study. Given is the slope of regression, its *P*-value, the regression y-intercept, and the *r*-square

Stream	Range in canopy cover	Slope	*P*-value	Intercept	r^2
Banner	68–100	0.0004	0.96	0.46	<0.01
Brown	1–49	−0.016	0.09	1.04	0.28
Cisco	7–63	−0.012	0.38	1.76	0.08
Marshall	20–94	−0.015	0.03	1.51	0.41
Nelson	0–28	0.007	0.74	0.40	0.01
Tenderfoot 1	no canopy	0	1.00	2.10	0
Tenderfoot 2	no canopy	0	1.00	2.67	0
Trout Brook	48–100	−0.012	0.02	1.31	0.47

The relationship between UV-B flux and canopy cover was generally weaker within individual stream transects (Table 3) than when all streams were considered together (Fig. 4). This could be the result of the much greater variation in canopy cover among

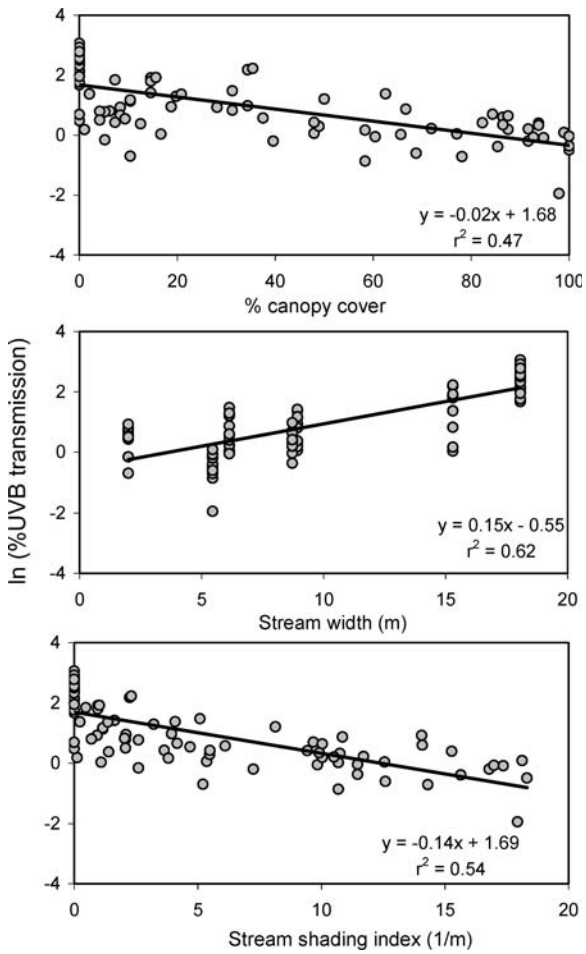

Figure 4. Relationships between percentage of UV-B transmission to 5 cm depth and canopy cover percentage, stream width and SSI using all point estimates from streams in this study. Note that the *P*-value for each slope estimate was <0.05.

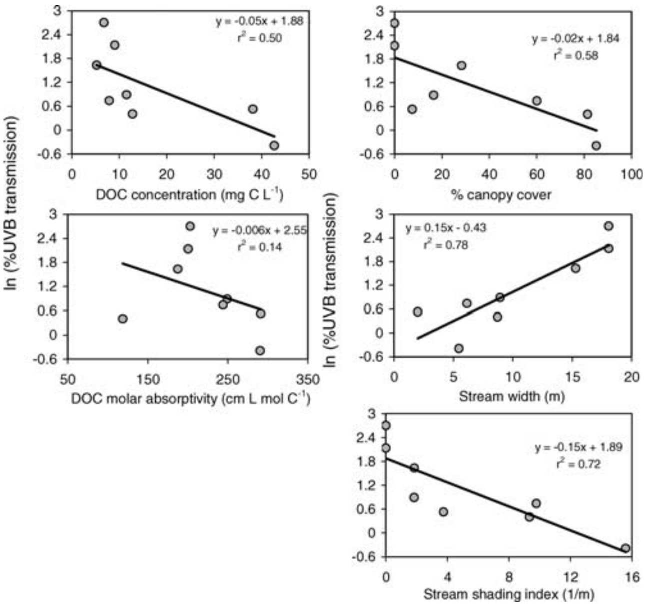

Figure 5. Relationships between percentage of UV-B transmission to 5 cm depth and DOC concentration, DOC molar absorptivity (UV-B), canopy cover percentage, stream width and SSI using average reach estimates from streams of this study.

streams than within streams. Measurements over much longer stream reaches may improve the predictive power of canopy cover on UV-B flux within particular streams. The relatively coarse canopy cover measurements given by the hand-held densitometers (26) may have also limited our ability to distinguish smaller-scale variation in canopy cover within the 100 m stream transects. A more accurate method for determining canopy cover (*e.g.* fish-eye–lens photography or above-canopy measurements; 26) may improve the correlations between percentage of canopy cover and UV-B flux within stream reaches. Also, canopy cover is only one aspect of the streamside vegetation that affects stream shading. For example, sun flecks and the orientation of the stream channel to the solar path can alter the flux of sunlight through the vegetative canopy (13,27,28). In addition, vegetation type, height and density can affect the solar flux through the forest canopy (27) and should be measured in future studies.

Interstream variability in UV-B flux was significantly related to DOC concentration but not to its UV-B molar absorptivity (Fig. 5). The concentration of DOC, in turn, explained less variation in UV-B transmission percentage than did canopy cover, stream width or SSI (Fig. 5). This suggests that knowledge of DOC concentration alone is insufficient to predict the UV environment at reach scales within forested streams. In a multiple-factor regression, average UV-B flux (natural-log transformed) into stream reaches was largely explained by a model that included the canopy cover and DOC concentration ($R^2 = 0.83$, $P < 0.001$). This result indicates that the underwater UV-B environment in streams from this region can be reliably predicted with knowledge of stream shading and DOC concentration. Such regression models, with better parameterization, could be coupled with spatial information on canopy cover and DOC concentration (or perhaps with stream width on its own) to predict the UV-B exposure of the stream benthos across broad spatial scales (*i.e.* within and among river watersheds). Dosimeters would be useful in future efforts to parameterize and verify models of solar flux into river systems at these broad spatial scales.

Summary and conclusions. We measured UV-B flux and attenuation with plastic dosimeters in seven northern Michigan streams. Rates of attenuation derived from dosimetry measurements were comparable to those estimated by other spectrometric methods. UV-B flux into streams was high only in relatively low DOC streams that had little or no canopy cover. Uniform canopy cover (either high or low) and/or high DOC concentrations created a relatively constant UV-B flux along stream transects. UV-B flux correlated best with channel width when all point estimates from all streams were pooled, which likely reflects a combined influence of canopy cover and DOC concentrations. Among-stream reach-scale variability in UV-B flux was almost entirely explained by the stream width alone or by canopy cover and DOC concentrations together.

Stream ecosystems are characterized by high heterogeneity in flow velocity, turbulence, depth, substrate size and shape and light environment (29). We found considerable variation in the UV-B environment of small forested streams both within specific streams and among streams. This variation was linked with both the amount of stream canopy and to stream DOC concentration. The consequences of this variable UV-B flux and transmission to benthic communities should be examined in the future. For example, are benthic algae from constantly low–UV-B environments more sensitive to increased UV-B flux than algae from streams with higher or more variable UV-B flux? *In situ* UV-B flux estimates will be an important component of future studies examining the magnitude and extent of UV-B effects on the biota of stream ecosystems.

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REFERENCES

1. Hader, D.-P. (1997) *The Effects of Ozone Depletion on Aquatic Ecosystems.* R. G. Landes Company, Austin, TX.
2. de Mora, S., S. Demers and M. Vernet (2000) *The Effects of UV Radiation in the Marine Environment*. Cambridge University Press, New York.
3. Hessen, D. O. (2002) *UV Radiation and Arctic Ecosystems.* Springer: Berlin.
4. Hader, D.-P., H. D. Kumar, R. C. Smith and R. C. Worrest (1998) Effects on aquatic ecosystems. *J. Photochem. Photobiol. B–Biology* **46**, 53–68.
5. Flint, S. D., R. J. Ryel and M. M. Caldwell (2003) Ecosystem UV-B experiments in terrestrial communities: a review of recent findings and methodologies. *Ag. For. Meterorol.* **120**, 177–189.
6. Bothwell, M. L., D. M. J. Sherbot and C. M. Pollock (1994) Ecosystem response to solar ultraviolet-B radiation—influence of trophic-level interactions. *Science* **265**, 97–100.
7. Zepp, R. G., T. V. Callaghan and D. J. Erickson (1998) Effects of enhanced solar ultraviolet radiation on biogeochemical cycles. *J. Photochem. Photobiol. B–Biology* **46**, 69–82.
8. Diamond, S. A., P. C. Trenham, M. J. Adams, B. R. Hossack, R. A. Knapp, S. L. Stark, D. Bradford, P. S. Corn, K. Czarnowski, P. D. Brooks, D. Fagre, B. Breen, N. E. Detenbeck and K. Tonnessen (2005) Estimated ultraviolet radiation doses in wetlands in six national parks. *Ecosystems* **8**, 462–477.

9. Xenopoulos, M. A. and D. W. Schindler (2001) Physical factors determining ultraviolet flux into ecosystems. In *Ecosystems, Evolution and UV Radiation* (Edited by C. S. Cockell and A. R. Blaustein), pp. 36–62. Springer, New York.
10. Frost, P. C., J. H. Larson, L. E. Kinsman, G. A. Lamberti and S. D. Bridgham (2005) Attenuation of ultraviolet radiation in streams of northern Michigan. *J. North Am. Benthol. Soc.* **24**, 246–255.
11. Laurion, I., M. Venture, J. Catalan, R. Psenner and R. Sommaruga (2000) Attenuation of ultraviolet radiation in mountain lakes: factors controlling the among- and within-lake variability. *Limnol. Oceanogr.* **45**, 1274–1288.
12. Crump, D., D. Lean, M. Berrill, D. Coulson and L. Toy (1999) Spectral irradiance in pond water: influence of water chemistry. *Photochem. Photobiol.* **70**, 893–901.
13. DeNicola, D. M., K. D. Hoagland and S. C. Roemer (1992) Influences of canopy cover on spectral irradiance and periphyton assemblages in a prairie stream. *J. North Am. Benthol. Soc.* **11**, 391–404.
14. Brown, M. J., G. G. Parker and N. E. Posner (1994) A survey of ultraviolet-B radiation in forests. *J. Ecol.* **82**, 843–854.
15. Kelly, D. J., M. L. Bothwell and D. W. Schindler (2003) Effects of solar ultraviolet radiation on stream benthic communities: an intersite comparison. *Ecology* **84**, 2724–2740.
16. Flint, S. D. and M. M. Caldwell (1998) Solar UV-B and visible radiation in tropical forest gaps: measurements partitioning direct and diffuse radiation. *Glob. Change Biol.* **4**, 863–870.
17. Davies-Colley, R. J. and J. M. Quinn (1998) Stream lighting in five regions of North Island, New Zealand: control by channel size and riparian vegetation. *New Zealand J. Mar. Freshwater Res.* **32**, 591–605.
18. Peterson, G. S., L. B. Johnson, R. P. Axler and S. A. Diamond (2002) Assessment of the risk of solar ultraviolet radiation to amphibians. II. *In situ* characterization of exposure in amphibian habitats. *Environ. Sci. Technol.* **36**, 2859–2865.
19. Krins, A., B. Dorschel, P. Knuschke, H. K. Seidlitz and S. Thiel (2001) Determination of the calibration factor of polysulphone film UV dosemeters for terrestrial solar radiation. *Radiation Protection Dosimetry* **95**, 345–352.
20. Kollias, N., A. Baqer, I. Sadiq, R. Gillies and H. Ou-Yang (2003) Measurement of solar UV-B variations by polysulphone film. *Photochem. Photobiol.* **78**, 220–224.
21. Feminella, J. W., M. E. Power and V. H. Resh (1989) Periphyton responses to invertebrate grazing and riparian canopy in 3 northern California coastal streams. *Freshwater Biol.* **22**, 445–457.
22. Sharp, J. H., R. Benner, L. Bennett, C. A. Carlson, R. Dow and S. E. Fitzwater (1993) Reevaluation of high-temperature combustion and chemical oxidation measurements of dissolved organic carbon in seawater. *Limnol. Oceanogr.* **38**, 1774–1782.
23. Morris, D. P., H. Zagarese, C. E. Williamson, E. G. Balseiro, B. R. Hargreaves, B. Modenutti, R. Moeller and C. Queimalinos (1995). The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnol. Oceanogr.* **40**, 1381–1391.
24. Ringold, P. L., J. Van Sickle, K. Rasar and J. Schacher (2003) Use of hemispheric imagery for estimating stream solar exposure. *J. Am. Water Res. Ass.* **39**, 1373–1384.
25. Parisi, A. V., M. G. Kimlin, J. C. F. Wong and M. Wilson (2001) Solar ultraviolet exposures at ground level in tree shade during summer in south east Queensland. *Int. J. Env. Health Res.* **11**, 117–127.
26. Hauer, F. R. and W. R. Hill (1996) Temperature, light and oxygen. In *Methods in Stream Ecology* (Edited by F. R. Hauer and G. A. Lamberti), pp. 93–106. Academic Press, New York.
27. Lieffers, V. J., C. Messier, K. J. Stadt, F. Gendron and P. G. Comeau (1999) Predicting and managing light in the understory of the boreal forest. *Can. J. For. Res.* **29**, 769–811.
28. Rutherford, J. C., N. A. Marsh, P. M. Davies and S. E. Bunn (2004) Effects of patchy shade on stream water temperature: how quickly do small streams heat and cool? *Mar. Freshwater Res.* **55**, 737–748.
29. Allan, J. D. (1995) *Stream Ecology: Structure and Function of Running Waters*. Chapman and Hall, London.