

EFFECTS OF SOLAR ULTRAVIOLET RADIATION ON STREAM BENTHIC COMMUNITIES: AN INTERSITE COMPARISON

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Abstract. The effects of solar ultraviolet radiation (UVR), both mid-ultraviolet (UVB; 280–320 nm) and near-ultraviolet (UVA; 320–400 nm), on benthic algal and invertebrate communities were compared in three reaches of a British Columbia coastal stream that differed in the degree of shading by riparian canopy (a full canopy, a partial canopy, and no canopy). At each of the three sites benthic communities were exposed to three different radiation treatments: photosynthetically active radiation alone (PAR; 400–700 nm), PAR+UVA, and PAR+UVA+UVB. Relative to the site with no canopy, UVR was 88% and 66% lower, and PAR was 83% and 49% lower at sites with full and partial canopy, respectively. Late summer increases in UVR to the streambed caused by declines in water level and dissolved organic carbon (DOC) were also lower at sites with high canopy.

Sites with less canopy shading had greater algal accrual, decreased biomass of total invertebrates, mayflies, and stoneflies, and reduced invertebrate community diversity compared to the heavily shaded reach of the stream. UVR produced taxon-specific community responses that varied across sites and increased with increasing UVR as summer progressed. At the full canopy site UVR had no impact, and the final (day 91) biomass and diversity of invertebrates was highest, and algal biomass lowest. Higher UVA radiation under reduced canopies inhibited algal accrual but had little effect on algal community composition. The biomass of several invertebrate taxa (e.g., *Dicosmoecus* spp., Limnephilidae) and community diversity were reduced by both UVA and UVB. Less sensitive taxa (e.g., *Paraleptophlebia* spp., Paraleptophlebiidae) were inhibited only by the highest UVB levels in late summer when water transparency to UVR was greatest. Inhibition of grazers by UVR appeared to indirectly increase algal accrual, particularly at the partial canopy site.

Our results indicate that riparian shading may moderate UVR effects on benthic communities, mainly through impacts on invertebrates with indirect effects on algae. By reducing UVR exposure of streambeds, riparian canopies may be important for ameliorating UVR effects on shallow lotic systems, especially during late-summer, low-flow periods when DOC concentrations are reduced.

Key words: epilithon; lotic system; photoinhibition; riparian canopy; stream benthic invertebrates; stream shading; trophic interactions; ultraviolet radiation.

INTRODUCTION

Riparian canopies affect the functioning of aquatic ecosystems by controlling inputs of solar energy and contributing allochthonous materials to water bodies (Hynes 1975, Vannote et al. 1980, Gregory et al. 1991, Naiman and Decamps 1997). These canopies also protect the aquatic biota from exposure to ultraviolet radiation (UVR, 280–400 nm, expressed as moles of quanta), now recognized to be an important factor shaping freshwater communities (reviewed by Williamson 1995, Hader et al. 1998). The management of riparian zones has been the subject of extensive research, due in part to the impacts of land-use practices along ri-

parian corridors on freshwater systems (Osbourne and Koviak 1993, Allan et al. 1997, Naiman et al. 2000). Alteration of the riparian canopy through land-use activities, such as logging and urban development, or through natural disturbances such as fires, wind, and floods, can result in large increases in water body exposure to sunlight. Canopy removal also can alter the concentration of dissolved organic carbon (DOC) (Hobbie and Likens 1973, Meyer and Tate 1983, Hill 2000), the principal factor controlling UVR attenuation in oligotrophic freshwaters (Scully and Lean 1994). We studied the effects of the riparian canopy on stream exposure to UVR and, in turn, UVR effects on benthic communities in a clear coastal stream located on Vancouver Island, British Columbia.

Natural fluxes of UVR have been shown to be potentially harmful to benthic algae and invertebrates, and can alter the composition of benthic communities (Bothwell et al. 1993, 1994, Kiffney et al. 1997a, b, Donahue and Schindler 1998, Vinebrooke and Leavitt

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1999, McNamara and Hill 2000, Kelly et al. 2001, Watkins et al. 2001). Increases in UVR exposure can cause significant changes in benthic communities because of large variation in the sensitivity of different organisms to UVR (Karentz et al. 1991, Bothwell et al. 1993, McNamara and Hill 1999, Leech and Williamson 2000, Sommaruga and Buma 2000). Photoinhibitory effects of UVR are wavelength dependent, and can affect components of riverine food webs differently, thereby influencing herbivory and predation (Bothwell et al. 1994, Hessen et al. 1997, Kelly et al. 2001, Kelly and Bothwell 2002a). Changes in the intensities of UVB and UVA relative to photosynthetically active radiation (PAR, 400–700 nm) resulting from alteration of the riparian canopy complicate the ability to predict which species might be affected.

Removal of the riparian canopy along streams has been shown to result in large changes to benthic communities (Shortreed and Stockner 1983, Robinson and Rushforth 1987, Garman and Moring 1991, Hetrick et al. 1998a, b). Increased light levels usually result in higher autotrophic production (Shortreed and Stockner 1983, Robinson and Rushforth 1987). However, effects on invertebrate biomass have been variable, either decreasing in response to the reduced inputs of coarse particulate organic matter (CPOM) or increasing because of greater algal production (Newbold et al. 1980, Murphy and Hall 1981, Hetrick et al. 1998b, Garman and Moring 1991). The magnitude of benthic community response is strongly influenced by the extent of canopy removal, type of catchment vegetation, and discharge of the stream (Murphy and Hall 1981). Riparian buffer strips have been adopted to mitigate the effects of the removal of catchment vegetation. However, the width and composition of prescribed buffer strips vary considerably, and so provide variable protection to streams from UVR exposure (Gregory et al. 1991, Osborne and Kovacic 1993). Although several studies have examined the effects of increased sunlight intensity on stream communities following canopy removal (Shortreed and Stockner 1983, Robinson and Rushforth 1987, DeNicola et al. 1992) only one has looked specifically at the effects of increased UVR (Clare 2000).

We compared the effects of UVA and UVB radiation on benthic communities at three study sites with differing degrees of riparian shading along a fourth-order stream (Little Qualicum River) on Vancouver Island, British Columbia. We quantified how shading influenced the intensity and spectral composition of UVR reaching streambeds and how UVR exposure affected the development of benthic communities. We hypothesized that under a fully developed canopy, the effects of UVR on benthic community development would be negligible, but in stream reaches with less canopy cover UVR would have measurable impacts.

MATERIALS AND METHODS

Study site

Experiments were conducted during the summer of 1996 along a 3-km section of the Little Qualicum River

TABLE 1. Water chemistry parameters for Little Qualicum River during the 1996 experimental trial ($n = 4$).

Parameter	Mean \pm 1 SD
pH	7.8 \pm 0.3
Conductivity ($\mu\text{S}/\text{cm}$)	91 \pm 0.5
Alkalinity (mg CaCO_3/L)	45.9 \pm 0.2
Hardness (Ca+Mg [mg/L])	42.7 \pm 1.1
Nitrate ($\mu\text{g}/\text{L}$)	11.4 \pm 6.7
Total nitrogen ($\mu\text{g}/\text{L}$)	63.3 \pm 10.8
SRP ($\mu\text{g}/\text{L}$)	2.2 \pm 1.2
Total phosphorus ($\mu\text{g}/\text{L}$)	6.3 \pm 1.1
Silica (mg/L)	7.2 \pm 0.5
DOC (mg/L)	1.3 \pm 0.5

(49°17' N, 124°35' W). The Little Qualicum River catchment (135 km²) is located in the Nanaimo lowlands on the east coast of Vancouver Island, British Columbia. Forests in this Pacific Coastal Ecoregion watershed are predominantly mature second growth, although clearings from logging, residential development, and farming occur along the stream. There are also some areas of intact old-growth forest. The heterogeneity in the canopy along this section of the stream results in widely varying amounts of cover to the stream. Riparian forests are dominated by western red cedar (*Thuja plicata*), Douglas fir (*Pseudotsuga menziesii*), red alder (*Alnus rubra*), and bigleaf maple (*Acer macrophyllum*). Substrata in the stream is composed mainly of cobble (5–15 cm) and gravel (2 mm–5 cm), with some sand (64 μm –2 mm), and silt (<64 μm). Peak flows occur in November ($\sim 15 \text{ m}^3/\text{s}$), declining to summer base-flows ($\approx 2 \text{ m}^3/\text{s}$) by July through September. During base-flow, the stream in the vicinity of the study area has a mean width of 22 m and a mean depth of 0.47 m. During the summer of 1996, stream water had a mean pH of 7.8 (6.9–8.0), a conductivity of 92 $\mu\text{S}/\text{cm}$, an alkalinity of 43 mg CaCO_3/L , and low nutrient concentrations ($\leq 20 \mu\text{g}/\text{L}$ NO_3^- , $\leq 10 \mu\text{g}/\text{L}$ total phosphorus) (Table 1). Water transparency to UVR was high, with a mean DOC concentration of 1.3 mg/L.

Experimental approach

The effects of UVR on stream communities were assessed using a 91-d experiment conducted in the mainstem of the Little Qualicum River (18 May and 17 August 1996). We used a two-way, repeated measures, nested analysis of variance (RM-ANOVA) design to compare three radiation treatments (PAR+UVA+UVB [control], PAR+UVA, and PAR) at each of three reaches. The reaches were selected because of their different degrees of shading by riparian vegetation (no canopy, partial canopy, and full canopy). Because there was only one site of each canopy type, site effects could have been the result of several other site-specific factors. In subsequent discussion we assume that site effects are the result of differences in canopy because of its obvious

differences between sites and its clear relationship to solar radiation.

Overhead canopy cover at the three sites was quantified along a 50-m reach of the stream using a spherical canopy densitometer (Lemmon 1957). Mean canopy covers were 0% (no canopy), 33% (partial canopy), and 90% (full canopy) cover. The open canopy site was bordered on both sides by cleared farmland that left the stream channel completely unshaded for ~100 m. At the partial canopy site the channel passed through a tall heterogeneous riparian corridor of ~20 m width on either stream bank, but large openings above the stream channel allowed variable shading at different times of the day. The full canopy site was bordered on both sides by thick, mature second-growth forest that nearly overhung the entire wetted width of the stream channel and provided complete shade for most of the day. The upstream-downstream sequence of canopy reaches was: full canopy site, open canopy site, and partial canopy site. Each study reach was ~50 m in length and the study sites were separated by 1–2 km of stream run.

Radiation treatments were established within each reach by suspending large (~1.5 m²) plastic filters immediately (~3 cm) above the water surface, with ~1 m distance between the filters. Three filters of each type (total of nine) were randomly placed in the stream channel to control for small-scale variation in water depth and current velocity. The filters used were: for PAR, UF4 Plexiglas (Rohm and Hass West Hill, Ontario, Canada; 6.4 mm thick; 50% transmission at 398 nm); for PAR+UVA, Mylar-D (Du Pont, Wilmington, Delaware, USA; 0.1 mm thick, 50% transmission at 318 nm); and for PAR+UVA+UVB, OP4 acrylic sheets (CYRO, Toronto, Ontario, Canada; 4.7 mm thick; 70–90% transmittance throughout the UVB and UVA) (Fig. 1). Filters were placed over shallow riffle zones of approximately equal depth (0.39 ± 0.03 m) and water velocity (0.38 ± 0.05 m/s).

A mixture of air-dried gravel and cobble was placed in screen-bottomed colonization trays (30.3 cm length \times 30.3 cm width \times 3.0 cm height) that served as substrata for colonization by the benthic community under the solar filters. A total of four trays were placed under each screen, and a single tray was collected from underneath each solar filter, starting on day 28 at 3-week intervals (i.e., day 28, 49, 70, and 91) until all the trays were removed. Trays were dug into the channel substrata to allow for uninterrupted flow over the stream bottom. Trays were placed >30 cm in from the edge of the UVR filters to ensure exposure to the intended radiation treatment.

Physical variables

PAR (400–700 nm) was integrated over hourly intervals at the noncanopied site with a Licor (Lincoln, Nebraska, USA) LI100 data logger and a LI190SA quantum cosine sensor. Ambient UVB radiation was

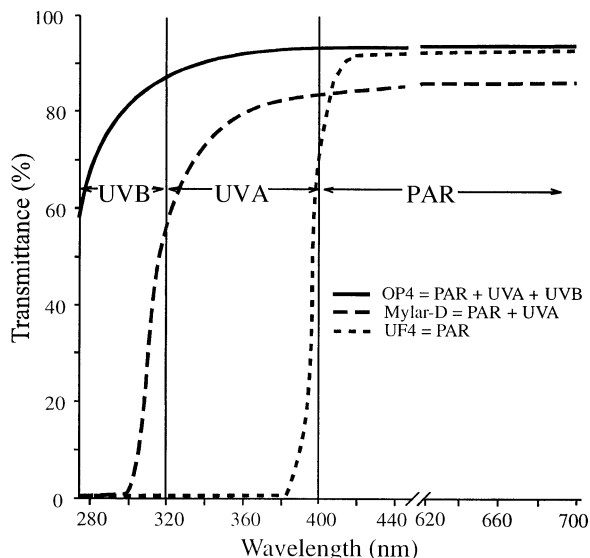


FIG. 1. Transmittance properties of the three plastic filters used in the experimental trials, OP4 acrylic, Mylar-D, and UF4 Plexiglas, through the UVB (280–320 nm), UVA (320–400 nm), and PAR (400–700 nm) spectral ranges.

estimated from UVB measurements at Environment Canada's meteorological station on Saturna Island (32 km southwest of the study location). UVB flux at Saturna Island was recorded with a Brewer Ozone Spectrophotometer (Kipp and Zonen, Saskatoon, Saskatchewan, Canada) at hourly intervals during daylight periods. Readings made at 0.5-nm intervals between 280 and 320 nm were integrated over the UVB spectral range to determine hourly UVB flux. Total daily PAR flux with no canopy shading ranged between 12.3 and 57.1 mol·m⁻²·d⁻¹, with a mean of 40.4 mol·m⁻²·d⁻¹ (Fig. 2). Mean total daily UVB flux, estimated from

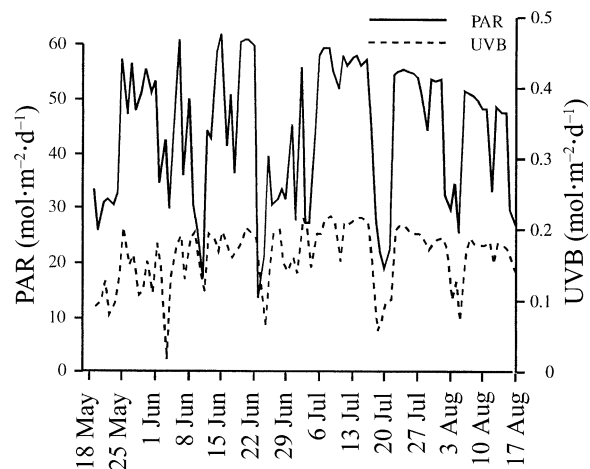


FIG. 2. Above-canopy daily PAR irradiance at the study site during the 1996 experimental trial, and daily UVB irradiance measured at Saturna Island meteorological station, located ~35 km from the site.

Saturna Island, ranged between 0.007 and 0.21 mol·m⁻²·d⁻¹, with a mean daily flux of 0.15 mol·m⁻²·d⁻¹. Total daily PAR at the site was highly correlated with UVB at Saturna Island over a two-year period (1995–1996, $R^2 = 0.55$, $P < 0.001$).

Solar radiation at each site (full canopy, partial canopy, and no canopy) was quantified during a two-week period in August 1997 with an Optronics OL-754 scanning spectroradiometer (Optronics Laboratories, Orlando, Florida, USA). Hourly scans of irradiance at 2-nm intervals between 290 and 700 nm were recorded (in watts per square meter per nanometer) during daylight hours over three days at each site. It was assumed that the site with no riparian canopy received 100% of the above-canopy irradiance. The proportion of ambient irradiance transmitted through the canopy at the canopied sites was calculated from the mean total daily irradiance (at each wavelength) measured at each site over the three days.

Light attenuation by stream water during the experiment was quantified by measurements of absorbance of water samples collected at the same times as biological samples. Absorbance of stream water was measured between 280 and 700 nm (at 0.5-nm intervals) using a Cary 50 (Varian Instruments, Walnut Creek, California, USA) scanning spectrophotometer equipped with a 2-cm quartz cuvette. Total daily irradiance between 280 and 700 nm reaching the streambed was calculated by multiplying water column transmittance (over the mean site water depth) by the mean total daily irradiance at the site.

Water temperature was measured at hourly intervals at each site with either Licor thermistors or Hobotemp temperature loggers. Mean daily water temperature ranged between 12.9° and 20.1°C during the four-month trial. No significant differences in water temperature were found between sites (RM-ANOVA, $P = 0.842$). Water velocities measured with a Marsh-McBirney (Frederick, Maryland, USA) electromagnetic flow meter decreased during the experiment as discharge fell. Stream velocity averaged 0.27 m/s (range 0.14–0.44 m/s), with no significant differences in velocity between the stream sites (RM-ANOVA, $P = 0.08$).

Epilithic community

On each sampling date samples were collected for chlorophyll *a* concentration and algal elemental composition (C and N) by scraping (with a hard bristle brush) 4.92 cm² of biofilm from randomly selected rocks. Chlorophyll *a* samples were collected in triplicate, filtered onto Whatman GFC filters (Maidstone, UK), and stored frozen until analysis. Chlorophyll *a* was later extracted with 90% ethanol in the dark at 78°C for five minutes and analyzed fluorometrically (Turner Designs Model 10au, Sunnyvale, California, USA) (Nusch 1980). Single 4.92-cm² scrapings for epilithic carbon and nitrogen determination were stored frozen in vials until analysis with a CHN elemental

analyzer (Control Equipment Corporation Model 440, Cazenovia, New York, USA). Frozen algal samples were filtered onto precombusted, preweighed Whatman GFF filter papers, and dried overnight at 60°C in a drying oven.

Benthic invertebrate community

Benthic invertebrates were collected from the remaining substrata washed through a 125- μ m mesh sieve. All organisms retained on the sieve were preserved in 70% ethanol until analysis. Invertebrates were enumerated with keys by Merritt and Cummins (1996) and Clifford (1991). Insects were identified to genus, except Diptera, which were identified to family. Noninsect taxa (e.g., Hydrozoa, Hydracarina, Crustacea, Oligochaeta, and Hirudinea) were identified to order. All invertebrates retained by a 2-mm sieve were enumerated, but smaller invertebrates were subsampled. Those passing through the sieve (taxa $\geq 125 \mu\text{m}$ and $\leq 2 \text{ mm}$) were diluted to 1 L in an Imhoff cone, and five 50-mL subsamples collected while air was bubbled through the cone to homogenize the sample (Wrona et al. 1982). Invertebrates were counted in a minimum of three subsamples, or until at least 100 individuals of the most abundant taxa were counted. The biomasses of invertebrate taxa were calculated from the mean dry masses of at least 5–20 individuals from both the coarse ($>2 \text{ mm}$) and fine ($125 \mu\text{m} \leq 2 \text{ mm}$) fractions at each site for each sampling time. Specimens were dried overnight at 60°C and weighed using a Cahn electrobalance (Madison, Wisconsin, USA). The mean mass of each taxon was multiplied by abundance to determine the total biomass.

Statistical analyses

Effects of solar treatments on the response variables were assessed using nested design two-way repeated measures analysis of variance (RM-ANOVA). Solar treatments were nested within canopy types in a split-plot design. Where there was a significant interaction between the two independent variables (i.e., between spectral quality and degree of stream-side shading) the effects of the solar exclusions were reanalyzed for each site independently. We interpret the interaction term in this design as a measure of how stream-side shading influenced the impact of solar UVR on the benthic communities.

A two-way nested (split-plot) repeated measures multivariate analysis of variance (RM-MANOVA) was used to test for the effect of UVR treatment on the biomass of the major benthic invertebrate groups: mayflies, stoneflies, caddisflies, dipterans, and other taxa. Invertebrate taxa not comprising at least 2% of the total invertebrate biomass (Coleoptera, Hydrozoa, Hydrachnidia, Crustacea, Oligochaeta, and Hirudinea) were grouped into the “other” category because there were insufficient degrees of freedom to allow for all taxa to be analyzed separately in the model. Statistical

analysis of the data was completed on $\log(n + 1)$ transformed data when necessary to meet homogeneity of variance (Cochran's *C* test) or normality assumptions. For RM-MANOVAs, both multivariate and univariate test results are reported. Fisher's least-squares difference post hoc tests were performed on univariate RM-ANOVAs. All analyses were conducted using the SPSS (1995) or SuperANOVA (Abacus Concepts 1991) statistical packages.

RESULTS

Solar irradiance

Interception of light by the riparian canopy varied over daylight hours (Fig. 3). At the partial canopy site, the stream was shaded predominantly in the hour before solar noon (1300 hours in August), and in the two hours following solar noon. The full canopy site was shaded throughout most of the day, except for 2–3 hours around solar noon when $\sim 95\%$ of the total daily solar energy reaching the stream surface occurred. The spectral characteristics of solar energy transmitted to the two sites within canopies also differed (Fig. 4). The proportion of total daily irradiance penetrating at the partial canopy site increased with decreasing wavelength, whereas the proportion of energy penetrating at the full canopy site increased with increasing wavelength. During daylight hours, the partial canopy transmitted $\sim 51\%$ PAR (mean $4960 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), 62% UVA (mean $533 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), and 70% UVB (mean $28.4 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), whereas the full canopy transmitted 17% PAR (mean $2650 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), 13% UVA (mean $154 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), and 11% UVB (mean $7.1 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) (Fig. 4).

Exposure of the streambed to solar radiation increased during the summer due to simultaneous decreases in water depth and DOC concentration (Table 2). Water depth declined on average by 46% (0.18 m) over the 91-d trial and DOC concentration decreased from 1.87 mg/L to 0.87 mg/L . As a result, transmission of PAR to the streambed increased 46% (from 24 to $35 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) at the site without canopy cover over the course of the experiment. The increase in UVB exposure over the same time period was even greater because of higher attenuation of shorter wavelengths by colored DOC. Mean UVB flux increased 10-fold (from 4.1 to $44 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) at the site without canopy cover. The absolute magnitude of this increase was buffered by canopy shading, although it remained proportionally the same. UVB increased from 2.0 to $23 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ under the partial canopy, and from 0.5 to $5.4 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ under the full canopy.

Epilithic algal biomass

UVR exposure had a significant effect on epilithic biomass (chlorophyll *a*, UVR effect, $P < 0.05$), and the effect differed between sites (Site \times UVR, $P < 0.0001$) (Fig. 5, Table 3). At the full canopy site, there

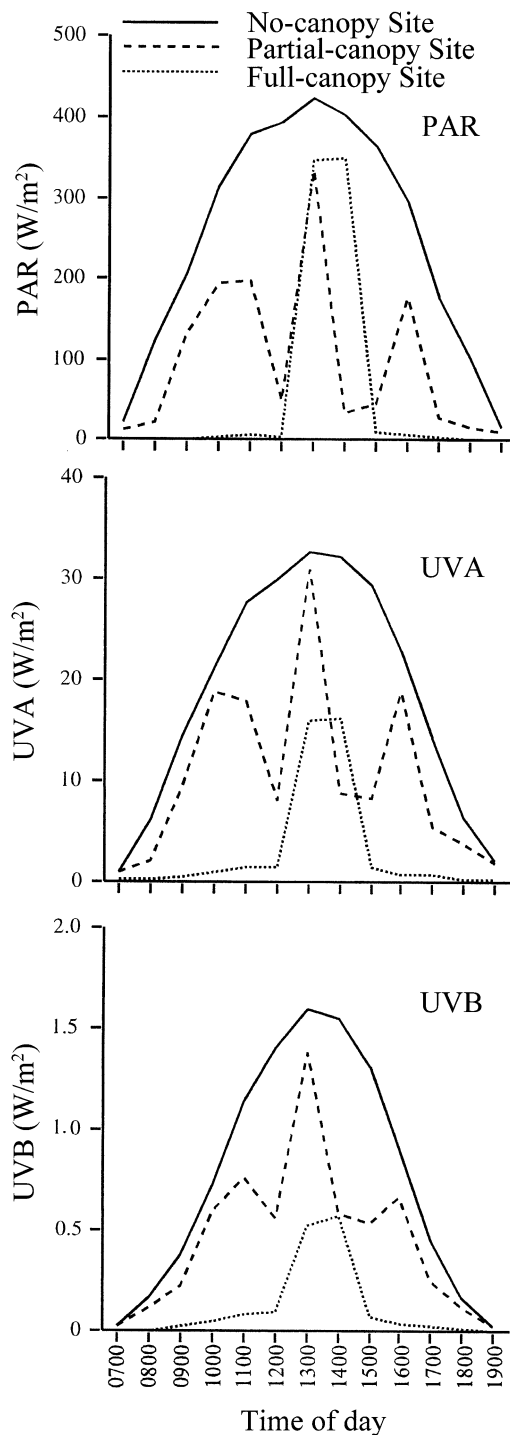


FIG. 3. Daytime downwelling PAR, UVA, and UVB irradiance at three sites with different amounts of riparian canopy cover on the Little Qualicum River.

were no effects of UVR on either chlorophyll *a* or epilithic C accrual (Table 3). At the partial canopy site, chlorophyll *a* was 82% higher under PAR+UVA and PAR+UVA+UVB (Fisher LSD, $P < 0.05$) than under

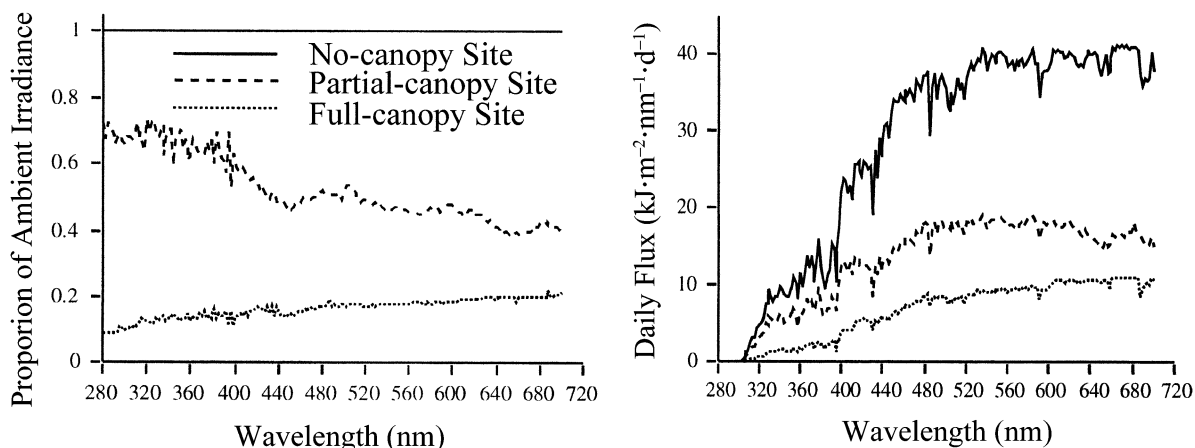


FIG. 4. The total daily proportion of above-canopy irradiance, and total daily energy of downwelling irradiance to the stream surface at three sites on the Little Qualicum River with different amounts of riparian canopy cover.

PAR alone by day 91. Conversely, at the fully exposed site, both chlorophyll *a* and epilithic C were >20% higher under PAR alone (Fisher's LSD, $P < 0.05$) than under both PAR+UVA and PAR+UVA+UVB on day 91. As expected, time was a significant factor under all treatments and at all sites due to the accrual process (Time, $P < 0.001$). However, there were some significant interaction effects of time with UVR (Table 3). There was no significant effect of either site (canopy type) or UVR exposure on epilithon stoichiometric C:N ratios, which were all close to 10:1.

Invertebrate community

There were significant differences in the biomass of colonizing invertebrates (e.g., mayflies, stoneflies) between the different canopied sites, although these effects varied during the experiment (Table 4; Figs. 6 and 7). At the full and partial canopy sites, total invertebrate biomass generally increased over time, with peak biomass observed on day 91 (Fig. 6). In contrast, at the no canopy site, invertebrate biomass was highest on day 49 and declined thereafter. Under full-spectrum sunlight, final invertebrate biomass at the full canopied

TABLE 2. Stream parameters including mean daily light exposure to the streambed ($[\pm 1 \text{ SD}]$, $n = 7$) over the 13-week experimental trial in 1996 at three sites on the Little Qualicum River that varied in riparian canopy cover.

Stream parameters	Week 1 (15–21 May)	Week 7 (1–7 July)	Week 10 (22–28 July)	Week 13 (9–15 August)
DOC (mg/L)	1.87	1.63	0.93	0.87
Full-canopy site (90% cover)				
Mean depth (m)	0.36	0.34	0.26	0.20
Current velocity (m/s)	0.34	0.32	0.23	0.18
Mean daily temperature (°C)	...	14.9	18.3	16.2
Streambed PAR ($\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)	4.3 $[\pm 1.2]$	6.4 $[\pm 2.3]$	8.0 $[\pm 0.6]$	6.3 $[\pm 1.5]$
Streambed UVA ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)	77 $[\pm 22]$	153 $[\pm 54]$	201 $[\pm 16]$	240 $[\pm 58]$
Streambed UVB ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)	0.5 $[\pm 0.2]$	1.9 $[\pm 0.3]$	3.4 $[\pm 0.2]$	5.4 $[\pm 0.6]$
Partial-canopy site (33% cover)				
Mean depth (m)	0.42	0.38	0.30	0.24
Current velocity (m/s)	0.44	0.35	0.21	0.14
Mean daily temperature (°C)	...	15.0	19.2	16.3
Streambed PAR ($\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)	11 $[\pm 3]$	17 $[\pm 6]$	21 $[\pm 2]$	17 $[\pm 4]$
Streambed UVA ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)	284 $[\pm 83]$	595 $[\pm 212]$	753 $[\pm 57]$	970 $[\pm 236]$
Streambed UVB ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)	2.0 $[\pm 0.7]$	7.6 $[\pm 1.3]$	14 $[\pm 0.8]$	23 $[\pm 2.7]$
No-canopy site (0% cover)				
Mean depth (m)	0.38	0.32	0.24	0.18
Current velocity (m/s)	0.37	0.33	0.19	0.17
Mean daily temperature (°C)	...	15.2	19.4	16.4
Streambed PAR ($\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)	24 $[\pm 7]$	35 $[\pm 12]$	44 $[\pm 3]$	35 $[\pm 9]$
Streambed UVA ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)	511 $[\pm 151]$	1034 $[\pm 367]$	1344 $[\pm 102]$	1646 $[\pm 401]$
Streambed UVB ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)	4.1 $[\pm 1.5]$	15 $[\pm 2.6]$	27 $[\pm 1.7]$	44 $[\pm 5.1]$

Note: Light exposure measured as moles of quanta.

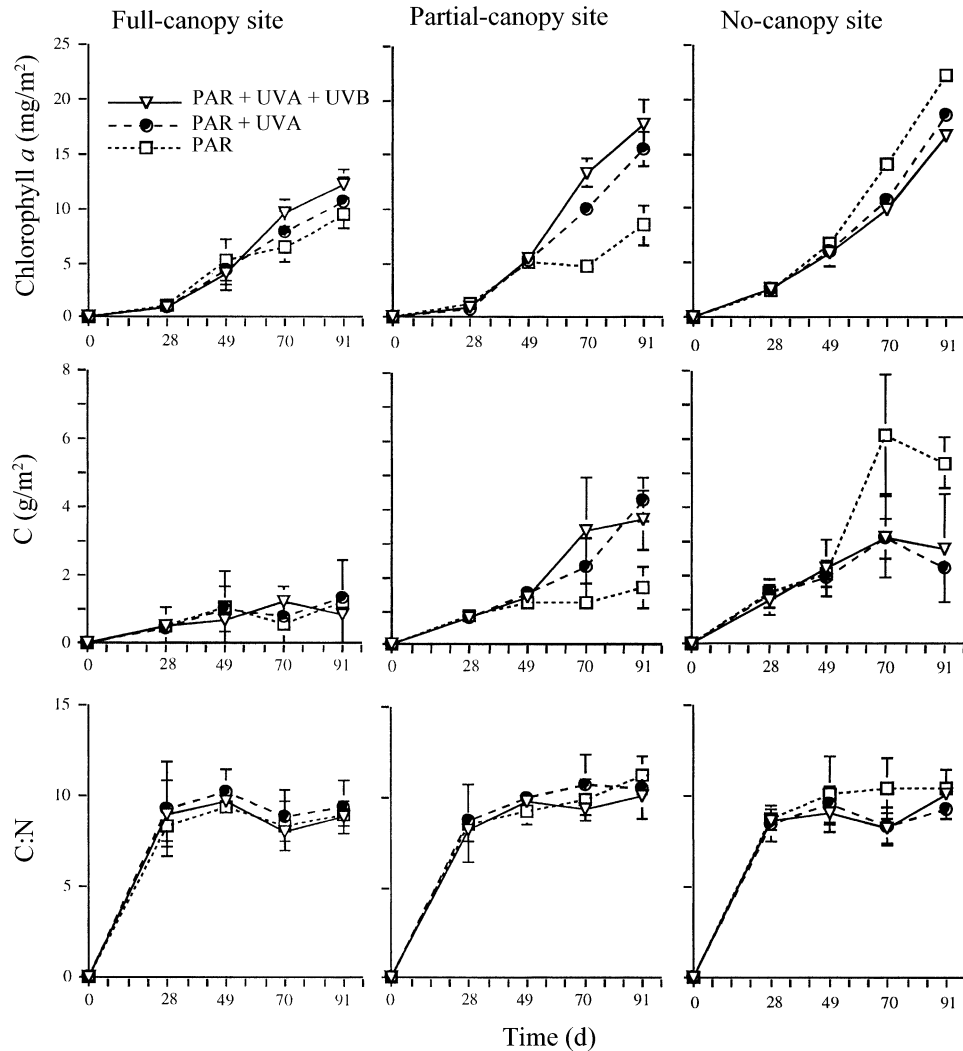


FIG. 5. Epilithic chlorophyll *a*, C biomass, and the C:N ratio for epilithon communities under different UVR exposures at three sites on the Little Qualicum River with different amounts of riparian shade. Values represent means \pm 1 SE ($n = 3$).

site was 235% and 277% greater than those found at the partial and open canopied sites, respectively.

There were also differences in the composition of invertebrate communities between the sites (Fig. 7, Table 4). Mayflies, initially abundant at all sites, decreased over time under both the partial and open canopy sites (Fig. 7). However, at the full canopy site mayfly abundance increased progressively with time, and by day 91 total mayfly numbers were twice those found at the more exposed sites (Fisher's LSD, $P < 0.05$). Enhanced mayfly abundance at the most heavily shaded site was most pronounced for *Cinygmula* spp. (Heptageniidae) and *Baetis* spp. (Baetidae), both of which were approximately fourfold higher under the full canopy than at the other two sites by the end of the experiment (Table 5). Stonefly biomass was also higher ($\sim 150\%$) at the fully shaded site compared to the other two canopy types by day 91 (Fisher's LSD,

$P < 0.05$). In contrast, dipteran biomass was greatest at the sites exposed to higher sunlight (Table 4). Dipterans were twice as abundant at the site without any riparian canopy than under a full canopy (Fisher LSD, $P < 0.05$).

A small number of noninsect taxa were also encountered. Of these, only Oligochaeta and Hydracarina were present at $\geq 1\%$ of the total biomass, and there were no significant differences in these two taxa among the three sites (Tables 4 and 5).

The response of benthic invertebrates to UVR depended on the site (Table 4, Figs. 6 and 7). At the fully canopied reach, UVR had no impact on total invertebrate biomass, community diversity, or abundance of any invertebrate group (Table 4). The most pronounced inhibitory effect of UVR on benthic invertebrates was found at the partially canopied site (Table 4). At that site differences in insect abundance between PAR alone

TABLE 3. Results of the repeated-measures multivariate analysis of variance (RM-MANOVA) of the effects of ultraviolet radiation (UVR) on algal biomass (chlorophyll *a* and epilithic C) at three sites on the Little Qualicum River that varied in riparian canopy cover.

Source	df	Univariate tests				MANOVA <i>H</i>
		Chlorophyll <i>a</i>		Epilithic C		
		MS	<i>F</i>	MS	<i>F</i>	
All sites						
UVR	2	11.1	3.52*	0.33	0.87	2.14
Site	2	141	3.56	32.0	5.05	1.71
Site × UVR	4	39.5	12.53***	6.33	16.59***	11.51***
Error	18	3.15	...	0.38
Time	3	846	243***	17.6	38.82***	104.0***
Time × site	6	26.7	2.14	3.54	1.63	4.56**
Time × UVR	6	7.02	2.02	0.29	0.63	1.31
Time × site × UVR	12	12.4	3.57***	2.17	4.80***	3.63***
Time × error	54	3.48	...	0.45
Independent sites						
Full-canopy site						
UVR	2	6.92	1.64	0.03	0.17	1.01
Error	6	4.23	...	0.16
Time	3	149	25.06***	0.62	7.39***	12.32***
Time × UVR	6	4.90	0.82	0.22	2.67	2.13*
Time × error	18	5.94	...	0.08
Partial-canopy site						
UVR	2	61.3	25.32**	4.11	7.00*	5.94*
Error	6	2.42	...	0.59
Time	3	280	70.23***	10.11	28.38***	38.71***
Time × UVR	6	21.5	5.41**	1.62	4.54**	3.91**
Time × error	18	3.98	...	0.36
No-canopy site						
UVR	2	21.9	7.79*	8.86	22.14**	28.51***
Error	6	2.80	...	0.40
Time	3	470	895.6***	13.98	15.2***	434.4***
Time × UVR	6	5.48	10.42***	2.80	3.04*	7.01***
Time × error	18	0.53	...	0.92

Notes: Reported are the results from the two-way split-plot design analysis RM-MANOVA testing for UVR effects among all sites, and separate RM-MANOVAs testing the effects of UVR under each canopy type ("Independent sites"). Data are mean-square (MS) and *F* values ($n = 3$) for univariate tests and Hotelling's (*H*) statistic for the multivariate test. Significance of *F* values is indicated by asterisks (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

and PAR+UVA+UVB environments increased through the summer coincident with higher exposure of the streambed to UVR (Table 4), and by day 91 total invertebrate biomass was fivefold greater under PAR alone than under any other canopy-treatment combination (Fig. 6). Caddisflies were the group most responsive to UVR ($P = 0.029$). Final biomass of *Dicosmoecus* spp. (Limnephillidae) under PAR alone was ~5000 mg/m² (Table 5), 15 times higher than under PAR+UVA and more than 40 times higher than the caddisfly biomass under PAR+UVA+UVB at the partially canopied site. The numbers of stoneflies at this site also averaged 51% higher under PAR than full-spectrum treatments (Fisher LSD, $P < 0.05$), although their overall biomass was still low in comparison to the fully canopied site (Table 4). In contrast, dipterans at the partially shaded site were higher under UVR-exposed treatments than under PAR alone (Fisher's LSD, $P < 0.05$).

Surprisingly, in the absence of any riparian shade there were no overall effects of UVR on invertebrate biomass (Table 4, Figs. 6 and 7). However, toward the end of the experiment when stream bottom UVR exposure was highest, there was a tendency for insect biomass to be greater in the environments shaded from UVR. Although these differences were not statistically significant when all sampling days were considered, restricting the analysis to data from day 91 only (i.e., MANOVA of the invertebrate groupings), several of these comparisons were significant. For example, final invertebrate biomass under PAR (820 mg/m²) was significantly higher than under PAR+UVA (602 mg/m²) or PAR+UVA+UVB (388 mg/m²) (Fisher LSD, $P < 0.05$, Table 5). Likewise, day 91 biomasses of mayflies, stoneflies, and caddisflies under PAR and PAR+UVA treatments were significantly greater (Fisher LSD, $P < 0.05$) than under the full-spectrum sunlight. In contrast, the biomass of dipterans and other invertebrate taxa

TABLE 4. Results of the repeated-measures multivariate analysis of variance (RM-MANOVA) of the effects of ultraviolet radiation (UVR) on the biomass of the major invertebrate groupings (i.e., mayflies, stoneflies, caddisflies, dipterans, and others) at three sites on the Little Qualicum River that varied in riparian canopy cover.

Source	df	Univariate tests							Diversity MANOVA
		Mayflies	Stoneflies	Caddisflies	Dipterans	Others	Total		
All sites									
UVR	2	0.064	0.244*	3.20**	0.011	0.204	0.711***	0.129***	6.1***
Site	2	0.904**	3.17**	5.56	1.50**	0.287	0.190	0.593	...
UVR × site	4	0.049	0.058	1.20*	0.054*	0.106	0.351***	0.176***	1.72*
Error	18	0.027	0.060	0.324	0.015	0.066	0.016	0.011	...
Time	2	0.720***	0.727***	0.292	0.207***	0.082	0.101**	0.166***	11.2***
Time × UVR	4	0.065***	0.053	0.304	0.038	0.106	0.034	0.049***	1.90*
Time × site	4	0.548**	0.156	0.849	0.153*	0.176	0.284	0.085	2.23
Time × UVR × site	8	0.047*	0.081	0.380	0.030	0.070	0.101***	0.052***	1.59*
Time × error	36	0.017	0.072	0.203	0.017	0.054	0.014	0.005	...
Independent sites									
Full-canopy site									
UVR	2	0.001	0.072	0.727	0.023	0.002	0.027	0.078	1.23
Error	6	0.008	0.078	0.318	0.035	0.043	0.019	0.023	...
Time	2	0.177***	0.844***	0.865	0.269***	0.003	0.325**	0.009	6.65***
Time × UVR	4	0.011	0.122	0.041	0.027	0.013	0.031	0.009	0.73
Time × error	12	0.012	0.076	0.288	0.025	0.028	0.027	0.011	...
Partial-canopy site									
UVR	2	0.158*	0.217	4.46**	0.092**	0.046	1.37***	0.036*	5.79*
Error	6	0.035	0.081	0.246	0.008	0.037	0.021	0.007	...
Time	2	0.634***	0.140	0.259	0.169**	0.004	0.162***	0.015	3.17*
Time × UVR	4	0.019	0.034	0.522	0.029	0.006	0.179***	0.004	1.23
Time × error	12	0.020	0.060	0.162	0.013	0.008	0.009	0.005	...
No-canopy site									
UVR	2	0.005	0.051	0.410	0.004	0.096	0.020	0.011	0.83
Error	6	0.037	0.021	0.408	0.003	0.048	0.007	0.005	...
Time	2	0.946***	0.055	0.866*	0.076*	0.708**	0.182***	0.029	34.3***
Time × UVR	4	0.129**	0.058	0.501	0.040	0.090	0.026*	0.010	3.58*
Time × error	12	0.018	0.082	0.157	0.013	0.038	0.006	0.009	...

Notes: Reported are the results from the two-way split-plot design analysis RM-MANOVA testing for the effects of UVR on major invertebrate groups among all sites, and separate RM-MANOVAs testing the effects of UVR under each canopy type ("Independent sites"). All data are $\log(x + 1)$ transformed. Tests for total invertebrate biomass (Total) and invertebrate taxonomic diversity (Diversity) were conducted separately. Data are mean-square values ($n = 3$) for univariate tests and Hotelling's (H) statistic for the multivariate test (MANOVA), with significance indicated by asterisks (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

showed no response at any time to the UVR treatments at the open canopy site.

Shannon-Weiner diversity of invertebrate communities was also affected by UVR (Fig. 6). Overall, diversity was significantly higher under PAR alone than under UVR-exposed treatments (Fisher LSD, $P < 0.05$) (Table 4). These effects were most pronounced at the partially canopied site (RM-ANOVA, $P = 0.048$) and were not significant at either the open or fully canopied sites.

DISCUSSION

Effects of riparian canopy on solar irradiance reaching streambeds

Riparian canopy density influenced the intensity, the spectral composition, and the total amount of solar energy reaching the stream surface. The partial canopy allowed 51% and 66% of above-canopy PAR and UVR daily flux, respectively, to reach the water surface. The full riparian canopy not only reduced solar exposure

to a much greater extent, it also blocked a larger percentage of ambient UVR compared to visible light (PAR). At the heavily canopied site, PAR and UVR daily fluxes were reduced to 17% and 12% of above-canopy levels, respectively. The spectral composition of sunlight reaching a stream depends in part upon the relative amounts of direct vs. diffuse sunlight it receives. Diffuse solar irradiance at the earth's surface is enriched in UVR because of preferential molecular (Rayleigh) scattering of shorter wavelength radiation in the atmosphere (Dahlback 2002). Riparian shading that blocks more diffuse than direct irradiance will therefore result in lower UVR:PAR ratios. Under dense canopies, a significant proportion of total daily irradiance takes the form of intermittent sunflecks moving across the forest floor (Reifsnnyder et al. 1971, Chazdon 1988). However, openings in riparian canopies over stream channels can allow direct sunlight to reach streams for at least some portion of daylight hours, in addition to the penetration of diffuse irradiance over

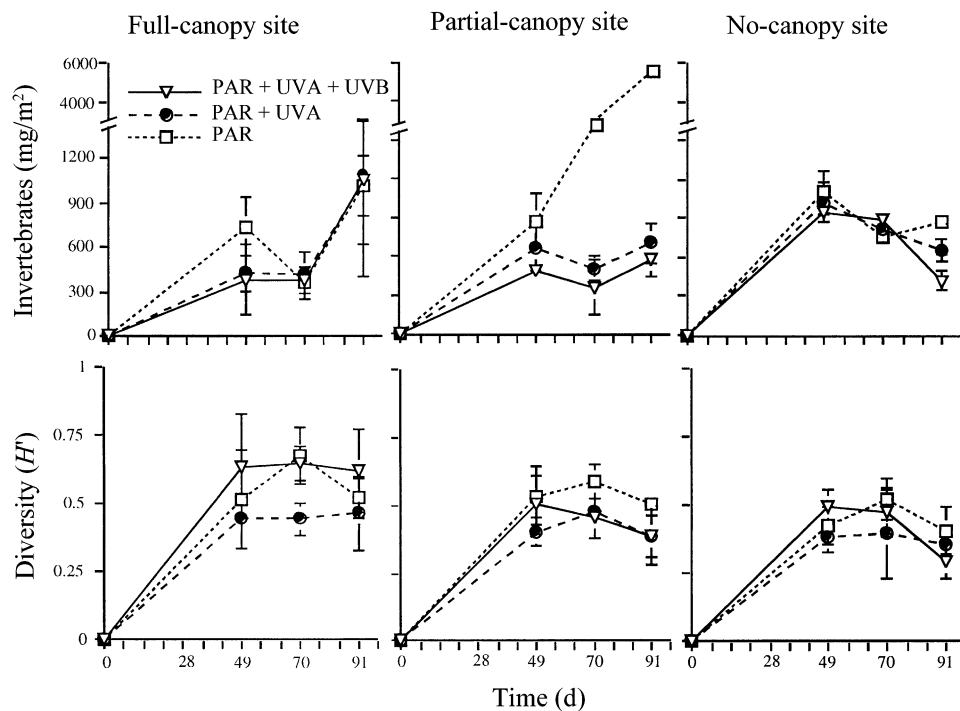


FIG. 6. Total invertebrate biomass and Shannon-Wiener diversity (H') of benthic invertebrates under variable UVR exposures at three sites on the Little Qualicum River with variable amounts of riparian canopy cover. Values represent mean biomass \pm 1 SD ($n = 3$).

most of the day (DeNicola et al. 1992, Davies-Colley and Payne 1998). At the heavily canopied site, 95% of the total irradiance on a sunny day occurred in a three-hour period around solar noon, while most diffuse skylight was blocked, producing a reduction in UVR relative to PAR on a daily basis. In contrast, the larger openings above the partially canopied reach allowed a higher proportion of diffuse skylight to reach the stream surface during periods of shade, thereby enriching the spectrum in UVR relative to PAR on a daily basis. Although the partial canopy transmitted a higher ratio of UVR to PAR than the fully shaded site, UVR was still 30% lower than at the site with no canopy.

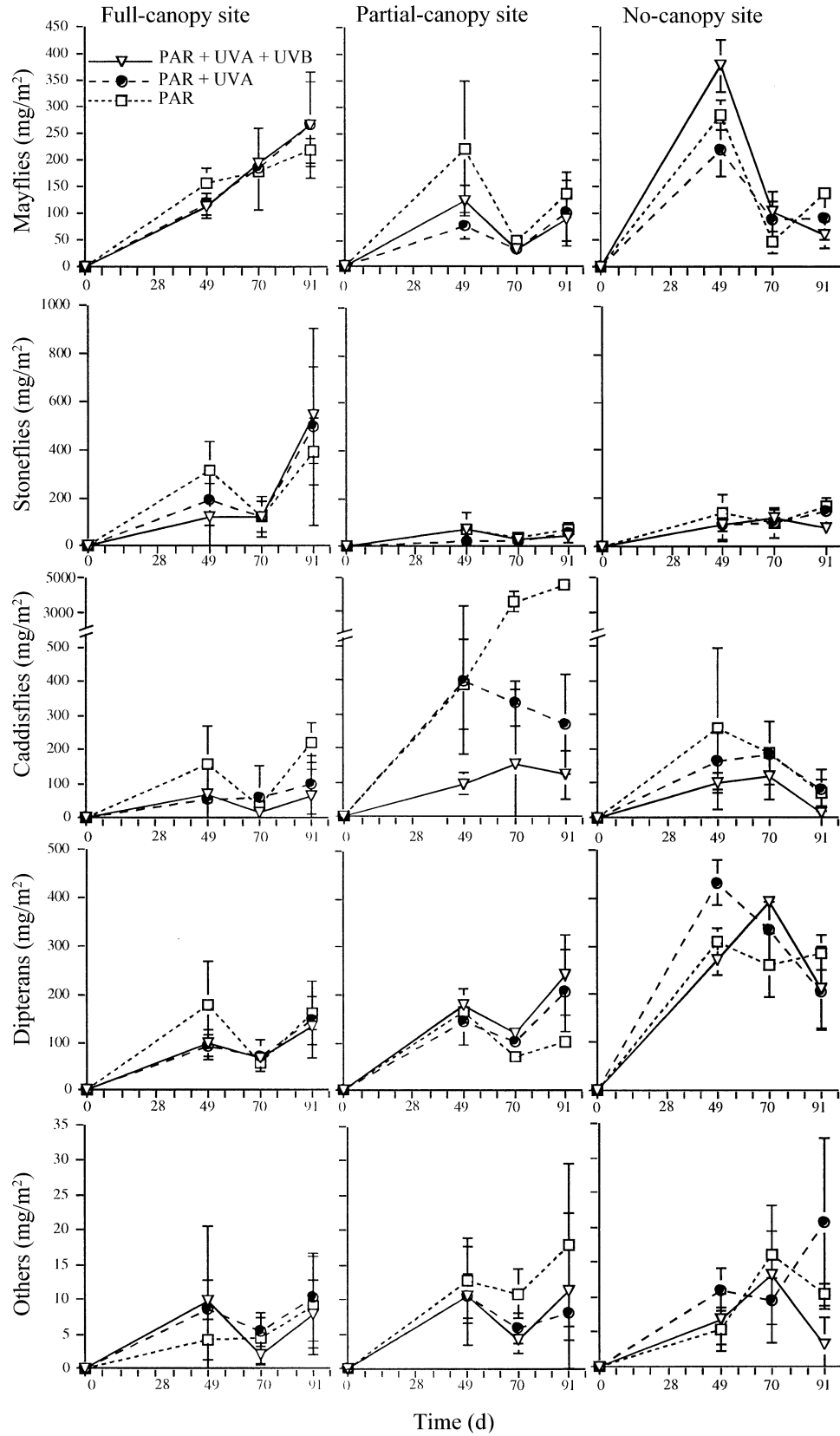
Most importantly, riparian vegetation can block UVR from reaching streams at critical times of the year. Midsummer increases in UVR flux to streambeds occur when water levels decline and DOC concentrations concurrently reach their lowest values. At the site without riparian cover, such synergistic declines in water level and DOC resulted in 6.6-fold and 1.9-fold increases in UVB and UVA, respectively, reaching the streambed by the end of the summer. A full riparian canopy can greatly reduce the absolute magnitude of this elevated exposure to UVR. UVB reaching the streambed at the fully shaded site only increased from 0.7% to 4.5% of the above-canopy levels over the course of the summer, while at the open site UVB increased from 3.7% to 28.0% over the same period. Therefore, riparian canopy protection of streams from

UVR exposure was most important during late-summer, low-flow conditions, when absorption of UVR by the water column was minimal.

Effects of solar irradiance on benthic communities

Under full-spectrum sunlight, stream reaches exposed to higher light intensities had greater algal accrual rates, decreased overall invertebrate biomass, altered composition of benthic invertebrate communities, and decreased invertebrate diversity. These effects increased in magnitude over the course of the summer coincident with elevated UVR exposure of the streambed.

Effects of solar energy and UVR on algal accrual.—The two sites with no canopy and with partial canopy cover had significantly higher levels of chlorophyll *a* (30–39%) and epilithic C over 91 d compared to the fully canopied reach. Epilithic primary productivity in small, forested streams is often light limited (Hill and Knight 1988, DeNicola et al. 1992, Hill et al. 1995). In agreement with these studies, we found that chlorophyll *a*, which was lowest under full-canopy shading, was significantly higher at the two more open sites. Smaller differences in chlorophyll *a* than in epilithic C between sites with different light levels could result from photoadaptation, i.e., increased chlorophyll *a* content in algal cells under more shaded conditions (Falkowski and LaRoche 1991). At the full-canopy site,



mean chlorophyll *a*:C was approximately double those of the other two sites.

There were also significant differences in the abundance of algal grazers between sites, which likely influenced algal biomass. Top-down grazer control of algal standing crop in streams has been shown to mask positive effects on algae of elevated light and nutrient levels (Feminella et al. 1989, Steinman 1992). Although we did not quantify grazing rates, algal biomass was usually inversely proportional to the biomass of grazers. For instance, under full-spectrum sunlight, chlorophyll *a* and epilithic C were greater at the partial-canopy site than at the open-canopy site, with the opposite occurring in total invertebrate biomass. Similarly, the lowest algal accrual and the greatest invertebrate biomass was usually present at the most shaded site. Hence, algal biomass in the stream reaches with less riparian canopy cover may have been higher both because of elevated amounts of photosynthetically active radiation and because of reduced levels of overall invertebrate abundance.

The response of algal accrual to the presence or absence of UVR differed between sites. At the fully shaded site, UVR had no effect on algal chlorophyll *a* or epilithic C, and overall epilithic biomass was the lowest of the three stream reaches. However, at the completely open site, UVR suppressed algal abundance, while at the partial-canopy site UVR promoted algal accumulation. The direct inhibitory effects of UVR on benthic algal photosynthesis and growth are well known (Bothwell et al. 1993, McNamara and Hill 2000, Watkins et al. 2001). It has also been shown that under normal daylight spectral regimes, much of the direct inhibitory effect of UVR on algae is associated with UVA wavelengths (Bühlmann et al. 1987, Bothwell et al. 1994, Milot-Roy and Vincent 1994). We also found algal accrual to be primarily inhibited by UVA at the unshaded site. Removal of UVB from the spectrum did not elevate chlorophyll *a* biomass, while removal of UVA+UVB resulted in 19% greater chlorophyll *a* accrual over 91 days compared to full-spectrum sunlight. The predominance of UVA inhibition of algal accrual on the streambed at the unshaded site would be accentuated by selective attenuation of shorter wavelength UVR (i.e., UVB) by DOC in the water column (Kelly et al. 2001).

Despite inhibitory effects of UVR on algae, longer term (3–6 weeks) studies have shown counterintuitive increases in algal biomass as a result of UVR-inhibited grazer activity (Bothwell et al. 1994, Kelly et al. 2001). Food-web feedback impacts of UVR on algal com-

munities are not only in the opposite direction, but can also be of greater magnitude than direct inhibitory effects (Bothwell et al. 1994). The pattern of algal accrual seen at the partial canopy site resembles such a counterintuitive response. At that site, screening of UVA+UVB increased invertebrate biomass 10-fold and suppressed both chlorophyll *a* and epilithic C accrual by $\approx 53\%$ over 91 days compared to full-spectrum sunlight.

Effects of solar energy and UVR on invertebrate communities.—The biomass and community composition of colonizing invertebrates were different at each of the three sites studied. Mayflies and stoneflies were significantly higher at the most shaded site ($P < 0.006$), while dipterans (chironomids) were negatively associated ($P = 0.001$) with canopy cover. Increases in total invertebrate biomass in streams following canopy removal have been attributed to increased autotrophic production (Newbold et al. 1980, Murphy and Hall 1981, Hetrick et al. 1998b). While we also observed greater invertebrate densities early in the season at the more exposed sites, this trend did not persist. Later in summer, invertebrate numbers either remained static (partial canopy) or declined (open canopy). In contrast, at the most heavily shaded site, invertebrate biomass continued to increase throughout the summer, eventually surpassing the other two sites. Higher invertebrate biomass at the more open sites occurred when differences in streambed PAR exposure between sites were high but differences in UVR were relatively low due to attenuation of UVR by stream water. The reversal in insect abundance between sites later in the summer, particularly for mayflies and caddisflies, coincided with large increases in UVR penetrating to the streambed at the open-canopy site. Shaded stream reaches may act as refugia for invertebrate taxa that emigrate (drift) from exposed reaches during periods of high streambed UVR exposure. Insect drift in response to UVR has been reported (Donahue and Schindler 1998, Kelly and Bothwell 2002b), and several taxa, notably *Paraleptophlebia* spp. and *Cinygmula* spp., that were abundant at the shaded site during late summer were also present at the open-canopy sites when UVR was blocked. If lower total invertebrate biomass at sites with less canopy cover is related to higher UVR exposure, then UVR impacts on stream invertebrate communities would be most pronounced under low-flow conditions and/or in streams with very low DOC concentrations (Newbold et al. 1980, Murphy and Hall 1981).

←

FIG. 7. Biomass (mean ± 1 SD, $n = 3$) of the dominant invertebrate orders under variable UVR at three sites on the Little Qualicum River differing in the amount of riparian canopy cover. "Others" represent all groups (orders or classes) comprising $<1\%$ of the total biomass of the community and included Coleoptera, Hydracarina, Oligochaeta, Ostracoda, and Hydrazoa.

TABLE 5. Mean final biomass (mg/m² [± 1 SD]; $n = 3$) of benthic invertebrate taxa under different UVR exposures at three sites on the Little Qualicum River that varied in riparian canopy cover.

Taxon	Feeding guild	Full-canopy site		
		PAR+UVA+UVB	PAR+UVA	PAR
Ephemeroptera				
<i>Baetis</i> sp.	CG	76 [± 42]	87 [± 26]	78 [± 7]
<i>Caudatella</i> sp.	CG	30 [± 8]	33 [± 17]	24 [± 5]
<i>Cinygmula</i> sp.	SC	97 [± 25]	49 [± 13]	37 [± 7]
<i>Rithrogena</i> sp.	SC	11 [± 5]	19 [± 14]	8 [± 1]
<i>Paraleptophlebia</i> sp.	CG	50 [± 36]	76 [± 19]	72 [± 8]
Plecoptera				
<i>Amphinemura</i> sp.	SH	54 [± 47]	29 [± 17]	27 [± 4]
<i>Calineuria</i> sp.	PR	39 [± 67]	73 [± 134]	39 [± 68]
<i>Isoptera</i> sp.	PR	22 [± 14]	20 [± 13]	29 [± 3]
<i>Sweltsa</i> sp.	PR	431 [± 188]	372 [± 254]	300 [± 193]
Tricoptera				
<i>Dicosmoecus</i> sp.	SC	42 [± 72]	84 [± 73]	210 [± 72]
<i>Hydroptila</i> sp.	CG	2 [± 0.4]	4 [± 5]	2 [± 1]
<i>Rhyacophila</i> sp.	PR	22 [± 3]	8 [± 13]	7 [± 13]
Coleoptera				
<i>Zaitzevia</i> sp.	SC	2 [± 4]	4.2 [± 5]	3 [± 4]
Diptera				
<i>Hexatoma</i> sp.	PR	26 [± 10]	26 [± 19]	27 [± 25]
Chironomidae	CG	107 [± 38]	121 [± 62]	133 [± 14]
Oligochaeta				
<i>Hydracarina</i> sp.	PR	23 [± 17]	22 [± 19]	21 [± 8]
Total invertebrates		1046 [± 266]	1096 [± 631]	1029 [± 224]

Notes: The reported taxa represent >1% of the total invertebrate biomass for at least one of the treatment/canopy combinations (np = not present). Feeding guilds are classified according to Merritt and Cummins (1996) and Thorp and Covich (1991) and include collector gatherers (CG), scrapers (SC), shredders (SH), and predators (PR).

At least three factors other than direct effects of solar UVR could have contributed to lower invertebrate numbers over longer periods of time at the more exposed sites. First, the shift from diatom communities to less edible filamentous green algal communities (*Spirogyra* spp. and *Odegonium* spp.) that occurred under the open and partial canopies (D. Kelly, unpublished data) might have reduced food availability to grazers and contributed to overall declines in consumers (Lowe et al. 1986). In contrast, algal communities in the fully shaded stream reach remained diatom dominated throughout the summer. Second, greater inputs of terrestrial particulate organic carbon at the more heavily canopied sites could positively affect invertebrate densities, particularly collector-gatherer and shredder taxa (Vannote et al. 1980, Garman and Moring 1991). However, this would not explain the higher invertebrate numbers present at the more open sites earlier in the experiment. A third factor potentially influencing invertebrate abundance is temperature. Temperature is paramount in controlling growth and development of stream invertebrates (Sweeney and Vannote 1978, Benke 1993). We minimized temperature differential between sites by selecting stream reaches with different degrees of canopy cover that were short (~100 m) and separated by 1–2 km lengths of stream that were shaded. The difference in mean

daily temperature between sites was <0.6°C over the 90-d trial.

In spite of the overall inverse relationship between insect biomass and light exposure, dipterans (largely chironomids) were consistently more abundant at the more exposed sites. Higher chironomid abundance has been associated with canopy removal in previous studies and tied to increased algal productivity (Newbold et al. 1980, Clare 2000). Our results agree with this. Chironomid biomass was proportional to algal density at all sites. However, not all grazers or algal scrapers responded this way. *Cinygmula* spp. and *Dicosmoecus* spp. were not proportional to algal biomass. Similarly, *Baetis* spp., previously reported to increase in abundance following canopy removal (Behmer and Hawkins 1986), were 350% greater at the intact canopy reach than at either the partial- or open-canopy sites by mid-August. Therefore it is unclear to what extent chironomids were responding positively to increased algal abundance at the open sites, or were being excluded by more abundant predators or herbivorous competitors at the heavily shaded site (Wootton et al. 1996), or perhaps both.

The impact of UVR on benthic invertebrate colonization differed at each of the three sites. At the fully canopied site where water surface irradiances of UVA and UVB were reduced to <13% of ambient levels, no

TABLE 5. Extended.

Partial-canopy site			No-canopy site		
PAR+UVA+UVB	PAR+UVA	PAR	PAR+UVA+UVB	PAR+UVA	PAR
22 [±12]	14 [±4]	20 [±3]	22 [±12]	28 [±9]	51 [±4]
10 [±1]	2 [±1]	4 [±5]	21 [±11]	31 [±17]	57 [±13]
8 [±8]	1 [±0.2]	21 [±4]	8 [±3]	7 [±7]	10 [±9]
1 [±3]	1 [±0.1]	5 [±4]	0.1 [±0.1]	3 [±2]	2 [±3]
48 [±19]	82 [±57]	83 [±32]	4 [±2]	16 [±11]	12 [±2]
7 [±4]	10 [±7]	12 [±3]	24 [±4]	26 [±16]	39 [±4]
np	np	np	np	39 [±67]	np
11 [±8]	4 [±3]	7 [±3]	22 [±10]	23 [±5]	50 [±9]
27 [±10]	45 [±36]	57 [±4]	33 [±21]	61 [±31]	81 [±16]
94 [±81]	236 [±163]	4906 [±342]	np	46 [±80]	np
10 [±4]	8 [±4]	1 [±2]	2 [±1]	5 [±1]	11 [±3]
15 [±13]	22 [±22]	np	9 [±14]	26 [±26]	60 [±39]
5 [±8]	1 [±1]	4 [±1]	2 [±3]	4 [±3]	6 [±3]
27 [±14]	10 [±4]	4 [±4]	7 [±6]	5 [±4]	4 [±4]
214 [±89]	199 [±87]	98 [±9]	207 [±91]	202 [±82]	282 [±39]
15 [±6]	12 [±2]	8 [±4]	14 [±1]	14 [±3]	22 [±7]
37 [±21]	27 [±3]	18 [±7]	7 [±1]	22 [±6]	28 [±10]
564 [±118]	685 [±168]	5266 [±353]	388 [±130]	602 [±127]	820 [±59]

discernible effects of UVR were seen on insect colonization. In contrast, at the partial canopy site, UVR had pronounced impacts on insect communities. Most of these effects resulted from exposure to UVA. We observed a 10-fold increase in total invertebrate biomass (primarily *Dicosmoecus* spp.) under PAR only compared to PAR+UVA and PAR+UVA+UVB. High UVR sensitivity of *Dicosmoecus* spp. was unexpected because the gravel-matrix case of this caddisfly should largely shield its body from UVR. With a protruding head, the absence of *Dicosmoecus* spp. in UVR-exposed environments supports the visual-cue, behavioral avoidance of UVR found in other groups of insects (Bothwell et al. 1994, Kiffney et al. 1997b, Donahue and Schindler 1998, Kelly and Bothwell 2002b). Some have suggested that encased or highly pigmented invertebrates might be less sensitive to UVR (Ringelberg et al. 1984, Hill et al. 1997). The strong UVR avoidance we observed in *Dicosmoecus* spp. is contrary to this generalization.

Previous studies reported that invertebrate taxa were predominantly inhibited by UVB (Bothwell et al. 1994, Kiffney et al. 1997a, b). Although some mayfly (e.g., *Paraleptophlebia* spp.) and stonefly taxa (e.g., *Amphinemura* spp. and *Sweltsa* spp.) colonized PAR+UVA treatments at greater densities than PAR+UVA+UVB, the differences were not significant (e.g., mayflies $P = 0.072$, stoneflies $P = 0.14$), probably because they appeared only at the end of the experiment. In contrast, *Dicosmoecus* spp. responded strongly and significantly

to UVA. Differential responses of invertebrate taxa to UVA and UVB might be expected if behavioral avoidance, driven by visual detection of UVA, and physiological damage resulting from UVB wavelengths were operating with different effectiveness on various species (McNamara and Hill 1999).

Surprisingly, we found nonsignificant overall effects of UVR on insects at the most open site where irradiance on the stream surface was not attenuated by canopy cover. The lack of response by invertebrates at the noncanopied site seems to have resulted from *previously established large-scale differences* in the invertebrate communities among the stream reaches. At the open site the taxa that declined with UVR at the partial-canopy site (e.g., *Dicosmoecus* spp. and *Paraleptophlebia* spp.) were rare. Furthermore, the invertebrate community at the open site was dominated by chironomids, particularly in the latter portion of the experiment. Although chironomids are sensitive to UVB (Bothwell et al. 1994, Kelly et al. 2001), they are known to utilize filamentous algae (the dominant growth form at the open sites) as a protective refugia from UVR (Clare 2000). When adequate algal refugia are present, UVR tends not to reduce chironomids (Clare 2000). For these reasons, light environments of whole-stream reaches apparently had a significant influence on the invertebrates that colonized the experimental treatments and therefore limited our ability to detect UVR effects using smaller scale (1 m²) manipulations.

In spite of this shortcoming, certain taxa appeared to be inhibited by UVR at the noncanopied site, but only during late summer when exposure of the streambed to UVR was highest. Most notable was the response of *Baetis* spp., *Caudaetella* spp., *Isoperla* spp., and *Rhyancophila* spp. Invertebrate sensitivity to UVR is taxon specific, and some evidence suggests a threshold mechanism may be operating (McNamara and Hill 1999, Kelly et al. 2001). The appearance of UVR effects on invertebrates at the most exposed site between days 70 and 91 occurred when UVA levels exceeded $1500 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, or $\approx 55\%$ of unattenuated midsummer sunlight. In another British Columbia river system, Kelly et al. (2001) found significant UVR inhibition of invertebrate assemblages (chironomids and black flies) when UVR was greater than $\sim 50\%$ of ambient. Similarly, Kiffney et al. (1997a) only found UVR inhibition of invertebrate colonization in an alpine stream during late-summer, low-flow periods when water depth had decreased from 50 to 15 cm and stream water UVR absorbance had decreased by 30%. The findings of Kiffney et al. (1997a) and our own results indicate that effects of UVR on invertebrate communities are sensitive to fluctuations in water depth and/or DOC, and that impacts of UVR on stream communities are most pronounced during periods of low flow in late summer.

Taxonomic diversity can also be negatively impacted by the stress of UVR. Declines in the diversity of benthic diatom communities under the influence of UVR have been previously documented (Bothwell et al. 1993). Likewise, we found the taxonomic diversity of benthic invertebrate communities to be negatively affected by higher levels of UVR exposure. The number of invertebrate taxa declined through time at unshaded sites exposed to higher levels of UVR, while at the fully shaded site, Shannon-Wiener diversities remained highest and were unaffected by UVR. By limiting the magnitude of seasonal increases in UVR to streambeds, shading by riparian vegetation appears to be an important factor maintaining the diversity of benthic invertebrate communities.

Effects of UVR on trophic interactions.—The potential for UVR to indirectly mediate algal standing crop through effects on grazers is now well known (Bothwell et al. 1994). Our study highlights some of the difficulties in experimentally determining interactive UVR impacts in natural settings. We found strikingly different UVR-impacted algal/grazer interactions at sites with different amounts of streamside shading. These differences appeared to be related to established differences in the composition of insect communities colonizing experimental substrata at the different reaches. At the partially canopied site inhibition of invertebrate colonization by UVA+UVB allowed a $>100\%$ increase in chlorophyll *a* accrual by the end of the experiment, compared to UVA+UVB blocked treatments. In this instance, the release of algal biomass from grazer control was associated with caddisflies (*Di-*

cosmoecus spp.), which strongly avoided UVA. Other studies have also shown *Dicosmoecus gilvipes* to be an effective controller of algal biomass (Feminella et al. 1989, DeNicola et al. 1990, Wootton et al. 1996). UVR-sensitive grazers may be more likely to colonize partially shaded reaches of streams because they provide some temporal and spatial shading from high UVR exposure, while still maintaining a higher abundance of algal food resources than heavily shaded reaches. Riparian vegetation associated with partially shaded reaches may also provide a greater diversity of food resources for invertebrates, including particulate terrestrial organic matter, than would be present in completely open reaches. The greater diversity and abundance of colonizing insects at the partially shaded site allowed both avoidance of UVR by insects and subsequent feedback effects of UVR on algal communities to be seen on the experimental scale (1 m^2) of our study.

At the completely open site the UVR-sensitive caddisflies did not colonize in abundance, with or without UVR shielding. In the absence of negative feedback effects on algal communities, the direct inhibition of UVR on algal growth at that site became apparent. Although a diverse and abundant insect fauna was present at the heavily shaded site, the UVR intensity was so low that neither inhibitory effects on algae nor insects were present.

Some workers have suggested that UVR can negatively affect invertebrates by altering the nutritional quality of algae by impairing nutrient uptake and reducing cellular fatty acid and protein content (Wang and Chai 1994, Van Donk and Hessen 1995, Hessen et al. 1997, Arts and Rai 1997). In our study we found no differences in C:N ratios of epilithon between any of our treatments, suggesting that the nutritional quality of algae was unaffected by UVR. Furthermore, in an earlier study on this river system we found no significant effect of UVR on algal community composition under full solar exposure (D. J. Kelly, *unpublished data*), indicating that the algal composition had not shifted to larger, less-edible species under the influence of UVR. For these reasons we believe that the effects of UVR on insect communities that we document in this study represent direct inhibition by UVR and are not the consequence of UVR alteration of algal food quality.

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