

COMMENT

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Effects of ultraviolet radiation on trophic interactions not detected?¹

In contrast to earlier studies (Bothwell et al. 1993, 1994; DeNicola and Hoagland 1996; Kiffney et al. 1997b), Hill et al. (1997) recently concluded that there was no effect of ambient solar ultraviolet (UV) radiation on periphyton and grazers in a small Tennessee stream. These conclusions were based on the appearance that grazing pressure by pleurocerid snails (*Elimia clavaeformis*) controlled algal biomass and primary production in three in situ stream experiments designed to test the role of UV radiation in trophic interactions. We assert that Hill et al.'s experimental design, site selection, and assumptions about the organisms within the system minimized biotic response to any UV radiation treatment and thus, preclude them from making general claims about lack of sensitivity of stream systems to UV radiation.

UV effects on periphyton communities were investigated by Hill et al. in White Oak Creek, a small, north-south-oriented, clear-water stream with high densities of *Elimia*. Plexiglas sheets (40 × 40 cm) impermeable to UV radiation (50% cut-off @ 375 nm) were suspended 5–10 cm above the water surface approximately 1 m apart in an upstream-downstream orientation (Hill pers. comm.), and each of these sheets was paired with a directly adjacent sheet of UV-permeable plastic of the same size. In each of three experiments performed between June and November, ten 1-in. square ceramic tiles were placed under each sheet; chlorophyll *a* (Chl *a*), ash-free dry mass, and photosynthetic rates were measured from these. During these experiments, tiles were 10–25 cm below the surface of the water and were preconditioned in full-spectrum sunlight for at least 1 yr prior to the experiment. During all three experiments, experimental substrates were exposed to sunlight for at least 6 h during the day (varying according to season).

We suggest that a fundamental error in Hill et al.'s experimental design resulted from the small size of the Plexiglas sheets. As a result of varying solar angles, both elevational and rotational, during the day as well as over seasonal scales, the actual area under the screens that was shielded or exposed to solar UV changed position with time. Using solar elevation and azimuth angles, the site longitude and latitude, and the experimental dates, we demonstrate that, during the experiments performed by Hill et al., there would have been times when area thought to be shielded from UV would have been exposed to UV. A corollary of this is that the "UV-exposed" substrate, directly under the adjacent UV-transparent plastic, would have been shielded from UV during parts of the day when the shadow of the UV-opaque Plexiglas passed over it.

We have calculated best- and worst-case scenarios for each of Hill et al.'s three experiments, based on 15- and 35-cm height, respectively, of Plexiglas above the artificial substrate (range of heights above water plus range of depths of water). We have also assumed that the minimum 6-h exposure bracketed solar noon (approximately 1330 h Eastern Standard Time), the time of day when both photosynthetically active radiation (PAR) and UV fluxes are greatest. For the sake of argument, we are limiting our discussion to this time period because the plastic sheets would be most effective when the sun is highest in the sky during these hours, thus potentially providing the greatest degree of protection from UV. Outside this period, shadow "movement" would be even more extreme as a result of low elevational angles of the sun.

Figure 1 represents shadow progression below a 40- × 40-cm shield at two different heights on 24 June, when the elevation angle of the sun was greater than at any other time of year. The higher the Plexiglas from the substrate (Fig. 1A; 35 cm), the more the shadow moved relative to the overhead shield. No area under the UV shield was shielded for the full 6 h when the Plexiglas was 35 cm above the algal substrate. Figure 1B demonstrates the effect of having the Plexiglas closer to the substrate. Displacement of the UV shadow was decreased on a north-south axis; however, there was still movement of the shadow in an east-west direction as the day progressed. In both cases, the adjacent experimental area that was assumed to be exposed to UV would be much smaller than 40 × 40 cm during either the morning or the afternoon as a result of being shielded by the UV-opaque Plexiglas next to it. Early in the morning or late in the afternoon, the shadows would have been displaced even more than shown, and the mixture of treatments would have increased.

In November (Fig. 2), the displacement of the Plexiglas shadows was much more dramatic than in June. At 35 cm, the area shielded from UV did not fall under the Plexiglas at any time of day! Even in the best-case scenario, with the Plexiglas 15 cm above the substrate, just under half of the substrate below was exposed to full-spectrum solar radiation throughout the 6 h. Again, the adjacent area assumed to be exposed to UV would be partially shielded during the morning or afternoon.

During the summer solstice, when the sun was highest in the sky, only 32% of the "shielded" substrate below would have been actually shielded for 6 h when the Plexiglas was 15 cm above the substrate. While only a small percentage of the 40- × 40-cm area below would have been exposed to full-spectrum solar radiation for the entire day, little more than 50% of the substrate would have been shielded for a

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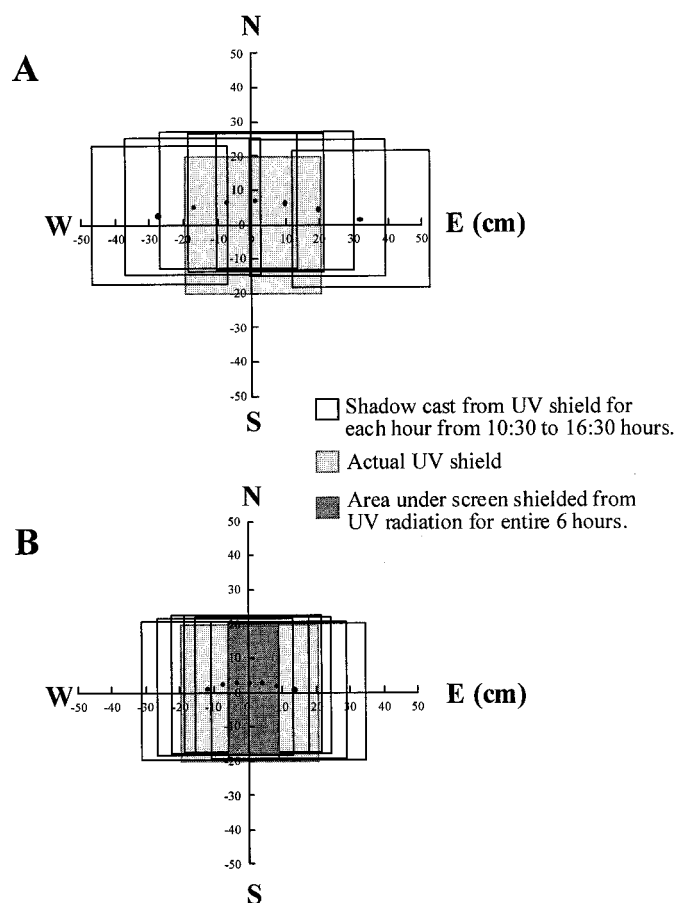


Fig. 1. Hourly progression of the shield shadow on 24 June for the (A) 35-cm and (B) 15-cm shield height above streambed.

total of 5 h (Table 1). None of the substrate 35 cm below a 40- × 40-cm sheet of Plexiglas, would have been shielded for 6 h during any of the experiments. At most, 50% of the substrate would have been covered for only 4–5 h. During the two experiments performed in the autumn, UV-shielded treatment areas would have been much less, reduced to 0% by 11 November. This lack of complete coverage of the substrate during the day is important when one considers the potential of UV to affect invertebrate behavior in the short term. For example, black fly larval densities decreased by more than 60% in experimental streams exposed to solar UV

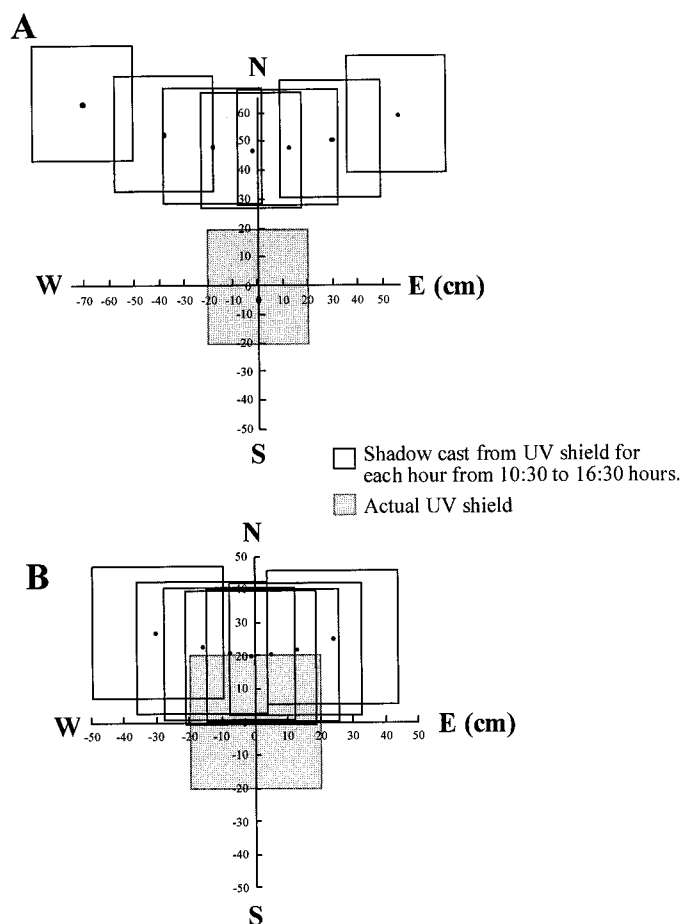


Fig. 2. Hourly progression of the shield shadow on 11 November for the (A) 35-cm and (B) 15-cm shield height above streambed.

radiation between sunrise and 1030 h (Donahue and Schindler 1998). In other experiments, black fly drift response to UV exposure was also rapid (Kiffney et al. 1997b; Bothwell pers. comm.). This indicates that invertebrates have the capacity to sense and react to UV radiation and that periods outside the hours of most intense exposure can still be important in causing community changes.

Beyond the problems associated with experimental design, Hill et al. did not consider several other critical factors in testing the effects of UV radiation on trophic interactions in

Table 1. Percent area under a 40- × 40-cm. UV screen that would actually be screened during the 6-h period from 1030 to 1650 h (peak solar intensities bracketing solar noon).

Date	% area under UV screen protected at 15- and 35-cm depths													
	0 h		1 h		2 h		3 h		4 h		5 h		6 h	
	15 cm	35 cm	15 cm	35 cm	15 cm	35 cm	15 cm	35 cm	15 cm	35 cm	15 cm	35 cm	15 cm	35 cm
24 Jun	2	9	98	91	97	88	95	83	92	80	55	13	32	0
21 Jul	7	12	93	88	91	84	86	74	79	69	54	6	30	0
18 Sep	27	67	73	33	72	33	71	32	53	10	34	0	8	0
5 Oct	29	78	71	22	70	21	63	19	54	8	27	0	0	0
8 Oct	36	79	64	21	63	19	58	17	44	1	24	0	0	0
11 Nov	48	100	52	0	46	0	44	0	36	0	20	0	0	0

streams. First, the study site chosen was on a reach of the stream lacking riparian cover, allowing full solar exposure in the streambed for at least 6 h on clear days in spring and late fall. Hill et al. hypothesized that these high light levels, coupled with "the tight interaction between periphyton and snails," maximized the potential propagation of indirect effects. However, the observance of any "solar cascade" (Williamson 1995) depends entirely on whether *Elimia* spp. and the algal communities are particularly sensitive to UV radiation. It seems reasonable to assume that the natural biological community, including both invertebrates and algae, in a shallow stream exposed to high levels of sunlight might have evolved or be adapted to a high light, and thus high UV, environment. Otherwise, one would expect significant temporal changes in the community coincident with high UV exposure. The community that developed on the ceramic tiles in Hill et al.'s experiments under natural solar radiation during the year-long conditioning period was likely well-adapted to a high light and high UV environment. As a result, even if the treatments had been effective in shielding or exposing the substrates to UV, the communities may not have responded to shielding of UV. If the goal of the experiment was to investigate the sensitivity of the system to UV, it might have been better to precondition the substrate in the absence of UV and look at effects of subsequent UV exposure. Alternatively, one could monitor complete colonization and development of the community in the absence of UV, compared to a UV control, as Bothwell et al. (1993, 1994) have done, rather than employing a before-after, control-impact (BACI) design.

Second, in discussing community changes and interactions, Hill et al. neglected to consider potential changes in the algal communities themselves and chose a system dominated by an herbivore that is known to be an inhabitant of high light sections of streams. Snails are key grazers in many streams in the southern and northwestern U.S. and often reduce algal biomass (Lamberti et al. 1987; Johnson and Brown 1997). Grazing by snails also increases rates of primary production in the algal mats upon which they feed, changes the taxonomic assemblage of the periphyton, and affects nutrient cycling (Lamberti et al. 1987; Steinman et al. 1987). Johnson and Brown (1997) showed that *Elimia semicarinata* (Say), another dominant grazer in streams, preferred sites with high light levels. In focusing on a grazer that may prefer high light environments, Hill et al. have selected an organism likely unaffected by normal solar UV fluxes. *Elimia* is also darkly pigmented, possibly indicating a physiological mechanism protecting the snail from sunlight and UV radiation (Karentz 1994; Siebeck et al. 1994).

In addition, Hill et al. did not report if the taxonomic structure of the algal community changed in response to UV radiation. Successional changes in algae have the capacity to alter physiological responses of the overall community and to affect food quality and availability for grazers. Also, affected organisms may be replaced by other, less sensitive ones if the opportunity for immigration or replacement exists. Measuring the response of the algal community to UV radiation in terms of changes in biomass and photosynthetic parameters (e.g., Chl *a*) is not adequate for examining this potentially important community response. Measures like

ash-free dry mass only give the mass of combustible carbon within an algal mat, including invertebrates, algae (alive and senescent cells), and detritus; this is not the same as algal biomass, as is often implied (Lamberti et al. 1987; Steinman et al. 1987; Steinman and Parker 1990; Hill et al. 1997). At best, this gives a gross measure by which to compare periphyton communities. Chl *a* concentrations, often used as a proxy for algal biomass (Kiffney et al. 1997a), can also be misleading because of differences in chlorophyll concentrations within cells of different algal taxa; in a mixed community, chlorophyte biovolume can correspond well to Chl *a*, but diatom biovolume does not necessarily correspond. Not measuring algal taxonomy and biovolume gives only the simplest view of what is actually happening in the algal community. One is thus limited in ability to draw inferences related to any differences and unable to comment on changes in the makeup of the community.

In addition, taking sample algal communities from in situ UV and no-UV treatments to the laboratory to do photosynthetic rate incubations under homogeneous artificial light conditions could be misleading. If algae dedicate more energy to cellular mechanisms for dealing with UV in situ, it is possible by energetic limitation that photosynthesis:respiration relationships might change in the presence of UV. As a result, net primary production could be reduced in the presence of UV radiation. Hill et al.'s laboratory measurements of ^{14}C -uptake would not account for this, and perhaps controls for short-term physiological adaptation to changed light spectra should have been performed on similar communities, including ^{14}C -uptake in the presence and absence of UV radiation.

In general, designing experiments to test the effects of environmental factors like UV radiation must consider which systems are likely to be sensitive, if the aim of the research is to identify sensitivities. One must avoid applying broad assumptions to all systems. In UV research, it might be more advisable to try to identify systems in which increases in exposure over relatively short time periods have occurred or are expected to occur, either by chemical or physical alteration of the systems. In this way, one stands a better chance of identifying mechanistic relationships between changes in aquatic systems and biological responses to them. When investigating the linkages between biological, physical, and chemical components of aquatic systems, one must give considerable forethought to each of them and to their interactions. Our fear is that because of the growing popularity of UV research, undue haste in the design and completion of experiments is becoming common. Care must be taken to avoid this.

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