Will Stream Periphyton Respond to Increases in Light Following Forecasted Regional Hemlock Mortality?

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ABSTRACT

The hemlock woolly adelgid invasion is expected to cause widespread mortality of eastern hemlock (*Tsuga canadensis*) throughout much of New England. Light levels in streams with hemlock riparian zones are anticipated to increase as hemlock trees are replaced by deciduous trees. We sought to: (1) quantify differences in light reaching streams with hemlock and deciduous riparian zones, (2) determine if increases in light result in higher periphyton biomass, and (3) explore the role of macroinvertebrate grazing on periphyton biomass as light increases in an attempt to help predict stream ecosystem responses to hemlock mortality. Light measurements were taken along 100-800 m stream reaches with riparian zones of healthy hemlock and deciduous trees in Massachusetts and Connecticut. In addition, a 2 x 2 factorial experimental design with five replicates was executed on a deciduous reach of Egypt Brook in central Massachusetts, in which light (high light vs. low light) and grazing (high grazing vs. low grazing) were manipulated. Light measurements were significantly higher for streams with deciduous riparian zones than hemlock riparian zones. Periphyton biomass was significantly reduced by controlled shading, but was not influenced by grazer exclusion.

INTRODUCTION

The amount of light reaching the benthos of lotic ecosystems frequently limits algal primary production, with increases in irradiance leading to higher periphyton biomass (Hill 1996, Lamberti et al. 1989, Lowe et al. 1986, McIntire and Phinney 1965, Sobczak and Burton 1996). Grazing is a biotic factor that often has "top-down" effects on periphyton growth and accrual (Hart 1985, Hill and Knight 1987, Lamberti and Resh 1983). Abiotic and biotic factors in streams can limit primary production independently of each another (Borchardt 1996, Hill 1996, Steinman 1996), but in many lotic ecosystems both "bottom-up" and "top-down" effects co-influence primary production (Findlay et al. 1993, Hill et al. 2001, Rosemond 1993). In streams with high grazing pressure, the impact of increased irradiance can be concealed because biomass only increases after the removal of grazers (Feminella et al. 1989, Hill et al. 1995, Steinman 1992).

In some streams, biotic grazing can govern stream periphyton biomass and community structure (DeNicola et al. 1990). Grazing and selective consumption can control periphyton accrual and taxonomic structure by reducing filamentous forms and increasing adnate taxa (Hart 1985, Hill and Knight 1987, Rosemond 1993). Reductions in periphyton biomass result from grazing by snails and other macroinvertebrates, including caddisflies and mayflies (Hill and Knight 1987, Lamberti and Resh 1983, Wellnitz and Rader 2003). In some streams grazing pressure can override irradiance as the limiting factor controlling periphyton biomass accrual (Steinman 1992). In such cases, increases in irradiance translate into grazer biomass instead of periphyton biomass, as grazing intensifies with higher primary production (Hill et al. 1995).

Riparian vegetation can limit stream periphyton production through shading (Hill 1996). Coniferous hemlock trees (*Tsuga canadensis*) allow little light penetration through their canopies in comparison with deciduous trees (Ellison et al. 2005, Orwig et al. 2002). Currently in the eastern United States, the hemlock woolly adelgid (HWA; *Adelges*

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tsugae), an invasive insect from Japan known to cause hemlock mortality, is reducing the number and health of hemlock stands. The replacement species are birches (*Betula* spp.), oaks (*Quercus* spp.), and maples (*Acer* spp.). These species increase understory stream irradiation compared to healthy hemlock stands (Ellison et al. 2005). Ellison et al. (2005) predicted that when deciduous riparian zones replace HWA infested hemlock stands, stream periphyton biomass will increase due to irradiance increases; however, this prediction fails to consider other biotic (e.g., grazing) and abiotic (e.g., inorganic nutrient availability) factors that may influence periphyton biomass accrual. Increases in irradiance reaching streams may not result in higher periphyton biomass if grazing pressures simultaneously increase with periphyton primary production or if inorganic nutrient availability constrains periphyton growth. Currently, researchers are studying various aspects of hemlock-dominated ecosystems before regional degradation occurs (Collins et al. 2007, Ellison et al. 2005, Orwig et al. 2002), but there is a void in studies quantifying the differences in irradiance penetrating hemlock and mixed deciduous canopies, as well as the implications of hemlock mortality on periphyton communities.

The purposes of this study were (1) to quantify the amount of photosynthetically active radiation (PAR) reaching streams that flow through hemlock and deciduous riparian zones, (2) to determine if increases in PAR result in higher periphyton biomass, and (3) to explore the potential role of grazing on periphyton as PAR increases.

METHODS

Stream survey

Topographic maps and aerial photos were used to locate streams with hemlock and deciduous riparian zones in Massachusetts (MA) and Connecticut (CT). The following reaches were studied: Muddy Brook (CT), Bigelow Brook East (MA), Bigelow Brook West (MA), deciduous and hemlock segments of Egypt Brook (MA), Kenya Brook (MA), Shay's Brook (MA), Cadwell Creek (MA), and Gulf Brook (MA). All studied reaches were low order and had riparian zones dominated by either hemlock or deciduous trees. During July and August 2006 PAR measurements were made at each site every 10 m along the reach on sunny days between 1100 and 1300 with an AccuPar Linear PAR/LAI Ceptometer Model PAR 80 meter. All the measurements for each stream were averaged to find a mean value for each stream.

Shading experiment

A shading experiment was conducted on Egypt Brook in New Salem, Massachusetts. Egypt Brook is a first-order stream that flows through protected watershed land on the Prescott Peninsula. Egypt Brook starts in an upland forest and flows first through a deciduous forest and then a hemlock forest before emptying into the Quabbin Reservoir. HWA has started to infest the hemlock stands through which downstream portions of Egypt Brook flow.

A block design (five replicate blocks), with a 2 x 2 factorial design in which light (high light vs. low light) and grazing (high grazing vs. low grazing) were manipulated, was setup on the deciduous reach of Egypt Brook. Twenty plastic containers (18.0 x 18.0 x 5.5 cm) were used as the experimental units. Briefly, the inside bottoms of the containers were sanded and four unglazed ceramic tiles (4.8 x 4.8 cm) were attached with aquarium silicone sealant. Each block contained four containers with four different experimental treatments as follows: (1) high light/high grazing pressure; (2) high light/low grazing pressure; (3) low light/high grazing pressure; and (4) low light/low grazing pressure. The five blocks provided five replicates for each experimental treatment.

Prior to the attachment of the tiles, 4 x 11 cm openings were cut into opposite ends of each open-topped container. Ten of the twenty containers were set aside and used for the high-grazer pressure treatments, while the other ten were modified into the low-grazer containers. The ten low-grazer treatment containers were sanded along the edges of the two openings and the top to aid silicon adhesion. Transparent nylon mesh (1 mm^2) with no UV inhibitors was affixed to the top and to the two side openings using aquarium silicone sealant to exclude macroinvertebrates. The twenty containers where then attached to bricks to anchor them in stream.

Containers placed in-stream below unaltered deciduous canopy irradiance created the high light condition. Three layers of charcoal fiberglass screening (attached together) shaded portions of the experimental blocks to create the low light condition. The screening was attached over the stream at a 45° angle with rope to metal stakes driven vertically into the stream banks, to allow run-off of vegetative debris and rainwater. The twenty containers were placed in the five blocks in Egypt Brook, with each block containing one of each of the four treatments (four containers total). Stream substrate removal allowed the top of the bricks to be level with the surrounding substrate and the openings of the containers to be directly on the bottom of the stream bed. Blocks were visited weekly to clear leaves and debris and to monitor experimental progress. PAR was measured on cloud-free days on October 16 and October 30, 2006 at the low light shaded portion and the high light portion of each block. Experimental units were removed from the stream after 49 days.

Kick seining was conducted at seven different sites for macroinvertebrates within the deciduous reach of Egypt Brook downstream of the experimental blocks. Most macroinvertebrates were identified to family, and feeding preferences were determined (McCafferty 1998, Merritt and Cummins 1996). Dominant grazers were identified to genus (Wiggins 1996). Chlorophyll *a* (chl *a*) was used as an indicator of periphyton biomass following procedures in Sobczak (1996). Tiles were scrubbed with a toothbrush inside plastic bags, after which samples were frozen. Chl *a* was subsequently extracted with 90% acetone and measured fluorometrically.

Statistical analyses were performed with SPSS1201. A model I one-way analysis of variance (ANOVA) was conducted to test significant differences in PAR reaching streams within hemlock and deciduous riparian zones. A three-way ANOVA tested significant differences in chl *a* among three factors - light treatment (fixed), grazer treatment (fixed), and block (random). Due to finding a significant ($p < 0.05$) interaction among light treatment, grazer treatment, and block, two-way ANOVAs were conducted for each of the five blocks with light treatment and grazer treatment as fixed factors. The data were tested for homoscedasticity with Levene's tests and for normality with Kolmogorov-Smirnov tests. If normality or homoscedasticity assumptions were not met, the data underwent log transformations, followed by appropriate two-way ANOVAs. If the homoscedasticity assumption could not be met via data transformations a Scheirer-Ray test was conducted as a nonparametric substitute for a two-way ANOVA (Sokal and Rohlf, 1995). If two-way ANOVAs had significant ($p < 0.05$) interactions between light and grazing treatments, one-way ANOVAs were conducted for the light and grazing treatments.

RESULTS

The mean PAR value reaching streams with deciduous riparian zones in July and August was 67.7 ± 10.3 $\mu\mathrm{mol\ m^{-2}\ s^{-1}}$ ($n = 3$, mean ± SE) (Fig. 1), and the mean PAR value reaching streams with hemlock riparian zones was 23.3 ± 3.1 $\mu\mathrm{mol\ m^{-2}\ s^{-1}}$ ($n = 6$, mean ± SE). Streams flowing through hemlock stands received 34% of the light reaching streams in deciduous forests, and the difference was significant ($p = 0.001$).

Mean PAR in the high light condition on October 16 was 346.8 ± 130.4 $\mu\mathrm{mol\ m^{-2}\ s^{-1}}$; on October 30 it was 498.5 ± 21.8 $\mu\mathrm{mol\ m^{-2}\ s^{-1}}$. On October 16, the low light conditions received 49.8 ± 11.4 $\mu\mathrm{mol\ m^{-2}\ s^{-1}}$; on October 30, 112.4 ± 20.5 $\mu\mathrm{mol\ m^{-2}\ s^{-1}}$.

The increase in PAR values from October 16 to October 30 was due to ongoing leaf-fall. Throughout the experiment, the low light containers received 14-23% of the PAR reaching the ambient high light containers.

The only grazer collected from kick seining was the trichopteran *Glossosoma* spp. During site visits, no *Glossosoma* were found inside the low grazer pressure enclosures, while individuals were routinely observed inside the high grazer pressure containers, and grazing paths were visible on the tiles.

Overall, high light treatments had greater concentrations of benthic chl *a* than low light treatments (Fig. 2). The five blocks were statistically examined separately due to a significant three-way ANOVA interaction. Three of the five blocks had significantly more chl *a* in the high light treatments than the low light treatments (Fig. 3A). The low grazing treatment yielded more chl *a* in three of the five blocks, all being significant (Fig. 3B). Overall, periphyton responded to the light treatment; however, grazing effects varied among blocks.

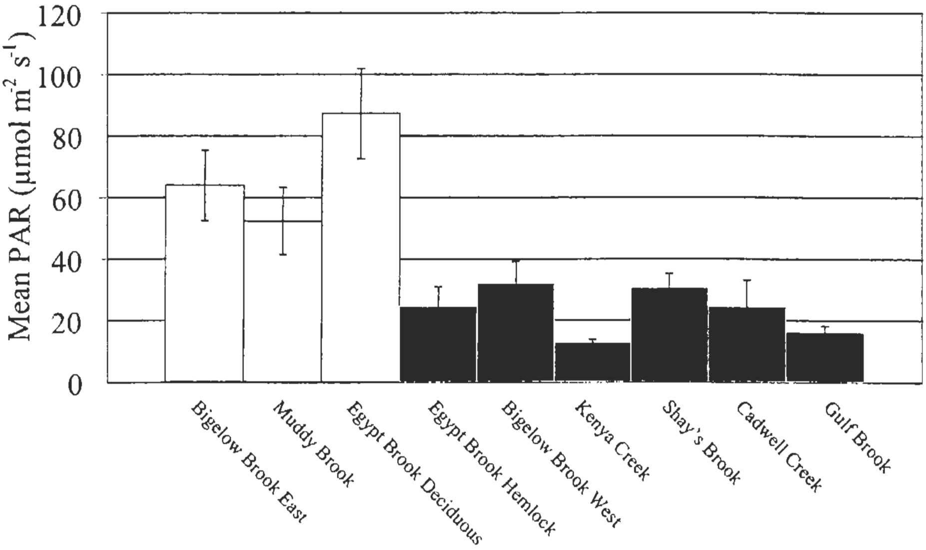

Figure 1. Mean PAR values and standard errors over streams with deciduous (white) and hemlock (black) riparian zones. Mean value for deciduous streams was significantly different from that of hemlock streams (one-way ANOVA, n = 3,6 F = 29.761, p = 0.001).

DISCUSSION

Stream ecosystem complexity often prevents a full understanding of the factors influencing in-stream primary production. Stream ecologists recognize that multiple factors including light, inorganic nutrient availability, and grazing can limit primary production. In this study of Egypt Brook, periphyton biomass was constrained by PAR reaching the substrate (bottom-up control) and not conclusively by top-down macroinvertebrate grazing. These findings were unexpected because we hypothesized that grazing and shading would both negatively impact periphyton biomass, as observed in other studies (Rosemond 1993, Steinman 1992). Instead, only shading reduced periphyton biomass in all experimental blocks, which supports the idea that irradiance limits periphyton biomass in many lotic environments (Hill 1996, Steinman and McIntire 1987). In three of the five blocks, high grazer treatments had significantly lower periphyton biomass, while in the other two blocks grazing had positive effects on periphyton biomass.

Macroinvertebrate grazing can limit periphyton biomass (Feminella et al. 1989, Steinman 1992 and 1996). Kohler (1992) found top-down effects of *Glossosoma nigrior* on periphyton biomass over a 10-month exclusion study. *Glossosoma* spp. have the ability to heavily graze (Kohler 1992, Wiggins 1996) and may have led to the reduction in periphyton in three of the five blocks. However, if the *Glossosoma* population was high and active throughout Egypt Brook, all the ambient high-grazer treatments should have yielded lower periphyton biomass than low-grazer treatments, instead of just three. It is possible that *Glossosoma* in Egypt Brook congregates to specific habitats (i.e., riffle or run) and variation in block habitats may have resulted in different *Glossosoma* numbers. Three of the blocks may have been placed in ideal conditions for *Glossosoma*, while the other two may have been located in less fit habitats. If two of the blocks were void of *Glossosoma*, other factors may have controlled biomass such as nutrient availability or sloughing.

Macroinvertebrate grazing can also induce increases in periphyton biomass. Lamberti and Resh (1983) found that a positive response of periphyton due to grazing may result from greater resource availability for viable algae as senescent algae are removed. Active grazing in the two blocks that resulted in increases in biomass with grazing may have had other ambient factors that resulted in an increase in resource availability following grazing. No two blocks were exposed exactly to the same conditions, and hydrologic and physical variations along the stream reach are undoubtedly important factors in periphyton dynamics. The results of the study indicated that periphyton accrual in Egypt Brook is likely light-limited. Shading resulted in decreased periphyton biomass in all blocks, while the effects of grazing were inconclusive.

The results from the shading experiment along with quantitative data from the deciduous and hemlock stream surveys in Massachusetts and Connecticut suggest that highly shaded hemlock riparian streams will see marked changes in light regimes and periphyton biomass as the HWA induces compositional shifts in riparian zone vegetation. During leaf-out conditions, hemlock streams are exposed to about a third of the PAR that deciduous streams receive. As hemlock trees fall victim to HWA, streams will be subjected to these higher levels of irradiance. This increase in irradiation is likely to support higher periphyton biomass as predicted by Ellison et al. 2005. The hypothesis

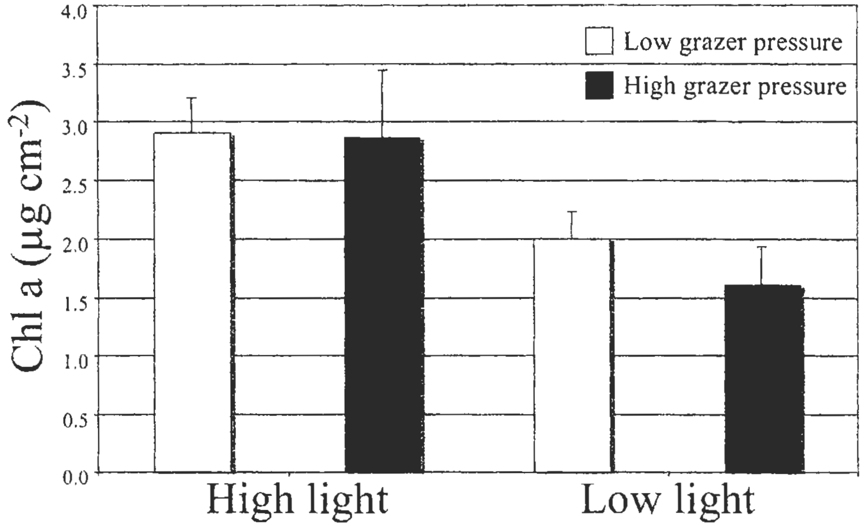

Figure 2. Mean chl *a* concentrations (biomass) on tiles in four different treatments.

that simultaneous increases in grazing pressure would keep periphyton biomass low is not supported by our study. Our study suggests that for some streams grazing may not play a significant role in limiting higher periphyton biomass as light levels change.

Importantly, our study only quantified the differences in PAR reaching streams during the summer when deciduous foliation is full. Hemlock trees are evergreen and provide year-round shade, while deciduous trees only provide high shade conditions for a portion of the year. Therefore, a shift from hemlock to deciduous riparian zones will result in even greater increases in PAR reaching streams after deciduous leaf-fall. In HWA-threatened streams like Egypt Brook, year-round increases in PAR can be expected to enhance periphyton biomass.

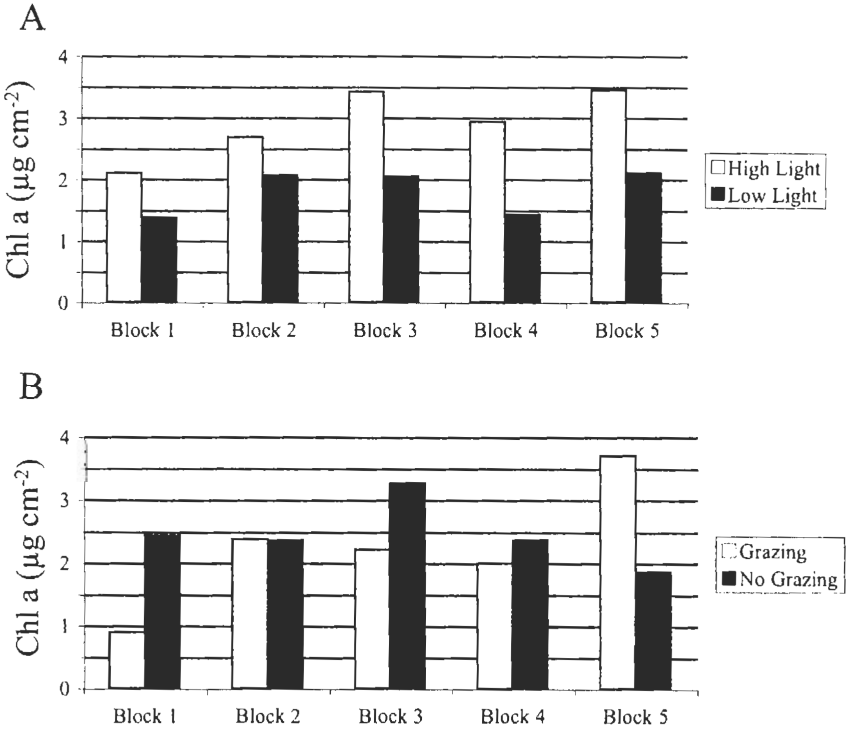

Figure 3. Mean chl *a* concentrations (biomass) on tiles in four different treatments for each block. (A) Mean chl *a* for ambient high light and low light treatments for each block. (B) Mean chl *a* for ambient high grazing and low grazing treatments for each block.

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