James Madison University

From the SelectedWorks of Heather P. Griscom

2010

Changes in light levels with loss of eastern hemlock (Tsuga canadensis) at a southern Appalachian headwater stream: implications for brook trout (Salvelinus fontinalis)

L. A Siderhurst Heather P. Griscom, *James Madison University* M. Hudy Z. J Bortolot



ELSEVIER

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Changes in light levels and stream temperatures with loss of eastern hemlock (*Tsuga canadensis*) at a southern Appalachian stream: Implications for brook trout

Leigh A. Siderhurst^a, Heather P. Griscom^{a,*}, Mark Hudy^{a,b}, Zachary J. Bortolot^c

- ^a Department of Biology, James Madison University, Harrisonburg, VA, United States
- ^b Fish and Aquatic Biology Unit, East USDA Forest Service, United States
- ^c Department of Integrated Science and Technology, James Madison University, Harrisonburg, VA, United States

ARTICLE INFO

Article history: Received 4 May 2010 Received in revised form 16 July 2010 Accepted 5 August 2010

Keywords: Tsuga canadensis Eastern hemlock mortality Hemlock woolly adelgid Light levels Stream temperature Southern Appalachians Brook trout

ABSTRACT

The exotic invasive insect, hemlock woolly adelgid (Adelges tsugae Annand), is causing mortality in eastern hemlocks (Tsuga canadensis [L.] Carr.) throughout the eastern U.S. Because hemlocks produce dense shade, and are being replaced by hardwood species that produce less shade, their loss may increase understory light levels. In the southern Appalachians, increases in light could increase stream temperatures, threatening species such as brook trout (Salvelinus fontinalis). We studied changes in light and stream temperature with eastern hemlock decline at a headwater southern Appalachian brook trout stream. Our results indicate that stream light levels have increased significantly with adelgid infestation. Leaf-on light levels are currently significantly higher (P < 0.02) in plots containing high basal areas of hemlock (mean global site factor (GSF)(SE) = 0.267(0.01)) compared with plots containing no hemlock (mean GSF(SE) = 0.261(0.01)), suggesting that increases in light have occurred with hemlock decline. The Normalized Difference Vegetation Index (NDVI), a remotely sensed metric of vegetation density, decreased with hemlock decline from 2001 to 2008. In 2001, NDVI showed no relationship ($R^2 = 0.003$; F = 0.14; P = 0.71) with hemlock basal area, but by 2008, there was a significant negative relationship ($R^2 = 0.352$; F=19.55; P<0.001) between NDVI and hemlock basal area. A gap experiment showed that light levels may increase by up to 64.7% more (mean increase in GSF = 27.5%) as hemlocks fall, creating gaps in the canopy. However, stream temperatures did not increase with hemlock decline during the study period, and we found that ground water inputs have a stronger influence on water temperature than light levels at this site. Linear regression showed a significant negative relationship between water temperature and proximity to ground water sources ($R^2 = 0.451$; F = 13.14; P = 0.002), but no relationship between water temperature and light levels ($R^2 < 0.02$; P > 0.05). In addition, by comparing light levels between plots containing hemlock and those containing only hardwoods, we found that if hemlocks are replaced by hardwoods, light levels under an all-hardwood canopy (mean GSF(SE) = 0.240(0.005)) are unlikely to be higher than they are under the current forest (mean GSF(SE) = 0.254(0.007)). These results suggest that loss of hemlock along southern Appalachian headwater streams could have short-term impacts on light levels, but that long-term changes in light levels, increases in water temperature, and adverse effects on brook trout may be unlikely.

© 2010 Elsevier B.V. All rights reserved.

1. Introduction

The hemlock woolly adelgid (Adelges tsugae Annand) is an exotic insect pest of eastern hemlock (Tsuga canadensis [L.] Carr.) and Carolina hemlock (Tsuga caroliniana Engelm) that was accidentally introduced from Asia to the eastern U.S. in the 1950s. Since then it has spread to 18 states, causing the widespread decline and mortality of eastern hemlock (hereafter referred to simply as hemlock)

(McClure and Cheah, 1999; Morin et al., 2009; Trotter and Shields, 2009). Once infested, hemlocks can die within 4–15 years and so far no controls for hemlock woolly adelgid that are both economical and practical for use on a large scale have been found (Orwig et al., 2002; Trotter and Shields, 2009). Loss of hemlock is predicted to have major impacts on forest ecosystems throughout the eastern U.S. because hemlock is considered to be a foundation species – one that strongly influences the structure and function of ecosystems in which it is found (Ellison et al., 2005; Rohr et al., 2009).

Hemlocks influence the forest environment through a unique combination of species traits. They are long-lived, extremely shadetolerant evergreens that form self-regenerating late-successional forests. They cast deep shade year-round, creating cool damp

^{*} Corresponding author at: Department of Biology, MSC 7801, James Madison University, Harrisonburg, VA 22807, United States. Tel.: +1 540 568 5525. E-mail address: griscohp@jmu.edu (H.P. Griscom).

microclimates, produce acidic litter that is slow to decompose, and are associated with low rates of nitrogen cycling (Hadley, 2000; Orwig, 2002; Lovett et al., 2006). In addition, hemlock stands often occur along streams, where they help to maintain cooler water temperatures in summer, warmer temperatures in winter, and more stable flow regimes year round compared with hardwood streams (Snyder et al., 2002; Hadley et al., 2008). Because of their unique combination of species traits, hemlock forests also provide habitat for unique communities of insect, bird, and fish species (Snyder et al., 2002; Ross et al., 2003, 2004; Dilling et al., 2007; Allen et al., 2009; Rohr et al., 2009).

Following adelgid-induced mortality, hemlock will most likely be replaced by various hardwood species (Sullivan and Ellison, 2006; Spaulding and Rieske, 2010). Studies in New England show that hemlocks are being replaced by less shade-tolerant species such as black birch (*Betula lenta*), oaks (*Quercus* spp.), and maples (*Acer* spp.) (Orwig and Foster, 1998; Orwig et al., 2002; Stadler et al., 2005). Hardwood species, however, cannot fill the structural and functional role of hemlocks in forest ecosystems, so changes in microclimate, nutrient cycling, hydrology, and species composition are likely to occur (Jenkins et al., 1999; Ellison et al., 2005; Stadler et al., 2005; Ford and Vose, 2007; Nuckolls et al., 2009).

Because hemlock is often found along streams, loss of this species and its replacement by hardwoods could cause particularly pronounced changes in stream ecosystems. Studies have shown that hemlock streams differ from hardwood streams in the amount of solar radiation they receive (Rowell and Sobczak, 2008) and in invertebrate community composition (Snyder et al., 2002; Willacker et al., 2009). In addition, brook trout (Salvelinus fontinalis) have been shown to occur more frequently in hemlock streams than in hardwood streams (Ross et al., 2003). Therefore, loss of hemlock could cause major shifts in stream communities accompanied by regional losses in diversity as hemlock streams become more like nearby hardwood streams.

One of the most important changes governing the influence that loss of hemlock will have on stream communities is the potential for increases in light levels. As hemlocks are defoliated by hemlock woolly adelgid and die, they create gaps in the riparian canopy that could increase the amount of solar radiation reaching the stream. In addition, if hemlocks are eventually replaced by hardwood species in the riparian canopy, light levels in the understory could remain higher because hemlock canopies, and those of evergreen species in general, allow less light to penetrate into the understory than hardwood canopies (Gower and Norman, 1991; Canham et al., 1994; Catovsky et al., 2002). Increases in light levels could in turn cause increases in stream water temperatures, because solar radiation tends to be the primary controlling factor for stream temperature in small streams (Danehy et al., 2005; Caissie, 2006), and riparian forests in general have a strong influence on water temperature (Johnson, 2004; Moore et al., 2005; Malcolm et al., 2008; Kreutzweiser et al., 2009; Pollock et al., 2009).

The potential for increases in stream water temperatures caused by increased solar input following loss of hemlock is of particular concern in the southern Appalachian region where riparian hemlock forests are thought to play an important role in keeping stream temperatures cool enough for the survival of brook trout (Ross et al., 2003; Johnson, 2004; Ward et al., 2004; Whitledge et al., 2006). Brook trout, an important ecological indicator species whose populations have already been greatly reduced, is in the southernmost part of its range in this area (Hudy et al., 2008). The optimal stream temperature for brook trout is about 18.9 °C, and the maximum temperature is approximately 23.9 °C (Eaton et al., 1995). In the southeastern U.S., where summer maximum water temperatures are already near these thermal limits, any increases in water temperature due to increases in light level could adversely affect brook trout populations (Eaton et al., 1995). In addition, the effects of

climate change might exacerbate adelgid-induced changes, posing a significant threat to already reduced populations (Caissie, 2006; Webb et al., 2008). Natural resource managers in the southeastern U.S. need to be able to predict changes in light levels and stream temperatures at adelgid-impacted sites in order to evaluate the potential effects on stream ecosystems and make appropriate management decisions.

Predicting the degree to which loss of hemlock will change stream conditions, however, is challenging. This is because the degree to which solar input to streams increases, and in turn the level of impact on stream temperatures, depends heavily on local site-related factors such as latitude, topography, and riparian vegetation. Light levels increase with decreasing latitude, from north to south (Canham, 1988; Canham et al., 1990), and topography (slope and aspect of banks) has also been shown to influence the amount of light reaching streams (Barnes et al., 1998; Moore et al., 2005). In addition, riparian vegetation shades streams to different degrees depending not only upon the species involved (e.g., hemlock vs. hardwood), but also on the height of the vegetation (Kelley and Krueger, 2005), its density, and its volume (Drever and Lertzman, 2003). Therefore, changes in solar input to streams in adelgid-impacted hemlock forests will be strongly influenced not only by latitude but also by riparian topography and the percentage of hemlock in the riparian canopy, all of which are highly site-specific factors.

Nearly all research to date on changes in light levels due to hemlock decline and mortality has been carried out in the northeastern U.S. These studies have noted dramatic increases in light levels in declining hemlock stands (Orwig and Foster, 1998; Jenkins et al., 1999; Eschtruth et al., 2006; Cleavitt et al., 2008). In addition, Rowell and Sobczak (2008) found that hemlock streams in Massachusetts and Connecticut received significantly less light (34% less) than hardwood streams. However, few studies have examined the impacts of hemlock mortality on understory light or stream temperatures in southeastern forests.

Southern riparian hemlock forests tend to differ from those in the northeast in that they tend to occur as mixed hemlock-hardwood stands, often with a rhododendron understory, while in northeastern forests, hemlocks tend to form very dense, almost pure stands with little or no understory (Ellison et al., 2005; Kincaid, 2007; Roberts et al., 2009). Because of these differences in hemlock forest composition and structure, changes in light levels observed in northeastern forests may not be applicable to hemlock forests of the southern Appalachians (Kincaid and Parker, 2008). If hemlock plays a primary role in influencing solar input to southern streams, its loss could cause even more dramatic changes in light levels than those seen in the northeast due to the effects of latitude on solar radiation. Alternatively, other factors such as slope and aspect of stream banks, the mixed hemlock-hardwood nature of the canopy, and/or understory vegetation may be more important than hemlock in regulating stream light levels in this region. If this is the case, changes in light levels may be less dramatic in the southeastern U.S. than those that have been observed in the northeast.

We studied changes in light level and stream temperature with hemlock decline and mortality at the headwaters of a southern Appalachian mixed hemlock-hardwood brook trout stream using hemispherical photography, remote sensing techniques, and water temperature loggers. In addition to measuring current light levels using hemispherical photography, we used remote sensing techniques to obtain data prior to hemlock decline because the study was initiated after hemlock decline had already begun and onthe-ground light data were not available from prior to adelgid infestation. Remote sensing techniques have become important tools for monitoring forest health, especially where on-the-ground data are not available (Maingi and Luhn, 2005; Quiñonez-Piñón et

al., 2007; Gross et al., 2009) and they have been used in previous studies to monitor damage to hemlock forests caused by hemlock woolly adelgid (Royle and Lathrop, 1997, 2002; Bonneau et al., 1999). We used the Normalized Difference Vegetation Index (NDVI) derived from satellite images (ASTER: NASA Land Processes Distributed Active Archive Center) to examine hemlock decline. The NDVI is a measure of the density of green leaves and tends to show a direct linear correlation with the amount of photosynthetically active radiation (PAR) absorbed by the canopy (Nagler et al., 2004; Glenn et al., 2008). Higher NDVI values mean that more light is being absorbed and reflected by leaves in the canopy and therefore that less light is being transmitted to the understory. NDVI has been widely used in studies monitoring changes in vegetation and forest health because it can detect declines in canopy cover (Pettorelli et al., 2005) and, more specifically, it has been useful in monitoring insect defoliation in forests over time (de Beurs and Townsend, 2008; Dennison et al., 2009; Eklundh et al., 2009).

The objectives of this study were (1) to determine whether light levels have increased with hemlock decline and mortality at the headwaters of a southern Appalachian brook trout stream in Virginia, (2) to predict how solar input to this stream is likely to change in the future as more hemlocks die, and (3) to assess the potential for changes in light level to cause increases in water temperature. We hypothesized that: (1) despite adelgid infestation and the current state of hemlock decline at this stream, light levels would currently still be lower in areas containing greater basal areas of hemlock than those containing less hemlock or only hardwood species (i.e., areas with more hemlock would be shadier), but that (2) adelgid infestation has caused stream light levels to increase from what they were prior to infestation in areas containing hemlock, (3) light levels are likely to continue to increase in the near future as more hemlocks die and fall, (4) light levels will remain higher in the long-run if hemlocks are completely replaced by hardwood species, and (5) increases in light level are likely to cause increases in stream temperature. In testing these hypotheses, we predicted that: (1) plots with higher basal areas of hemlock would currently have lower light levels under both leaf-on and leaf-off conditions, (2) canopy cover, measured using NDVI, has declined from 2001 to 2008 because of adelgid infestation, (3) removing up to 70% of the riparian basal area by felling dying hemlocks would increase understory light levels, (4) light levels in a simulated future all-hardwood forest would be higher than those in the mixed hemlock-hardwood forest, and (5) there would be a positive relationship between light levels and stream temperatures.

2. Materials and methods

2.1. Site description

This study was conducted at Fridley Run, which is located at Fridley Gap (38.49°N; 78.70°W) in George Washington National Forest, near Harrisonburg, VA (Fig. 1). Hemlocks occur in the riparian area in a mixed hemlock-hardwood forest along approximately 1.7 km of the stream. Fridley Run is also the headwaters for the Smith Creek watershed, which is part of the Eastern Brook Trout Joint Venture's program to restore and protect brook trout habitat (Hudy et al., 2008; Eastern Brook Trout Joint Venture, 2010) (Fig. 1). The stream was limed in 1993 to counteract the effects of years of acid deposition that had decimated brook trout populations (Hudy et al., 2000). Following liming, a population of brook trout was successfully restored at Fridley Run and the population has been subsequently monitored. Forest restoration efforts are also underway downstream at Smith Creek to encourage the brook trout population to extend its range and increase in numbers. However, riparian hemlock trees at Fridley Gap were found to be infested with hemlock woolly adelgid as of 2000–2001, so the loss of hemlocks along the stream poses a potential new threat to this already small population of brook trout.

2.2. Detecting changes in light levels and stream temperatures from early adelgid infestation to the present

2.2.1. Monitoring hemlock defoliation and changes in stream temperature

We monitored hemlock defoliation at Fridley Gap in 2002, 2004, 2006, and 2007 by measuring the crown densities of all hemlock trees in the riparian area that were over 10 cm in diameter at breast height (DBH). Crown density was measured using the U.S. Department of Agriculture (USDA), Forest Service crown density classification method as described in Schomaker et al. (2007).

In 2008, we established 38 study plots (20 m in radius) at 50 m intervals along the stream, starting at a randomly selected point in the hardwood forest portion of the stream, downstream from the section containing hemlocks (Fig. 2). GPS coordinates were recorded in the field for each plot center using a Trimble® GeoXMTM handheld GPS unit, and all data were post-processed using differential correction in GPS Pathfinder® software version 3.1 (Trimble Navigation Ltd.) to an accuracy level of approximately 1–5 m. We then imported GPS plot coordinates into ArcMap (Arc GIS 9.2 ESRI 2006) for use in mapping and data analysis.

We placed HOBO® water temperature data loggers (Onset: HOBO® Pro v2) in the center of the stream at every other plot (Fig. 2). Loggers were set to record temperatures at half hour intervals. Water temperatures had also been monitored from 2002 to 2006 at a location about 300 m downstream of plot 1 (Fig. 2), so we were able to look for changes in mean daily maximum stream temperatures (for the July–September critical period for brook trout) from 2002 to 2009 using these data and data from plot 1 (for 2008–2009). We used the paired samples Wilcoxon Signed-Ranks test to compare mean daily maximum temperatures between years.

2.2.2. Forest composition and hemlock basal area

In 2008, we inventoried the riparian forest in 38 inventory plots located at 50 m intervals along the stream in order to characterize the composition of the riparian forest at Fridley Gap. Inventory plot centers were located in the riparian forest 15 m from the stream plot centers on either the left or right bank. Left and right bank plots were chosen randomly. GPS coordinates were recorded for each plot center. All trees over 10 cm DBH within a 20-m radius of each plot center were included in the inventory. We identified each tree to species and measured its DBH. We calculated the basal area of each species and determined the relative basal area of hemlock (as percentage of the total basal area) in each plot and at the study site as a whole.

2.2.3. Current light levels

To determine current stream light levels, we measured leaf-off (late February 2008) and leaf-on (early October 2008) light levels in the study plots using hemispherical photography. Leaf-on data was collected in October instead of during the summer because of scheduling conflicts and weather conditions. We measured light levels in odd numbered stream plots for leaf-off data, and in all 38-stream plots for leaf-on data. Photographs were taken at 1 m above stream center under uniform cloud cover conditions in which no shadows were being cast (with a NIKON FC-E8 fish-eye converter lens fitted to a Nikon Coolpix 950 digital camera) and subsequently analyzed using HemiView 2.1 SR1 software (Delta T Devices Ltd., 2000). Hemispherical photographs create 360° horizon-to-horizon images. When taken in a forest, the area of the canopy included in the photograph is approximately 20 m in radius, with the center being the point from which the photograph is taken (our

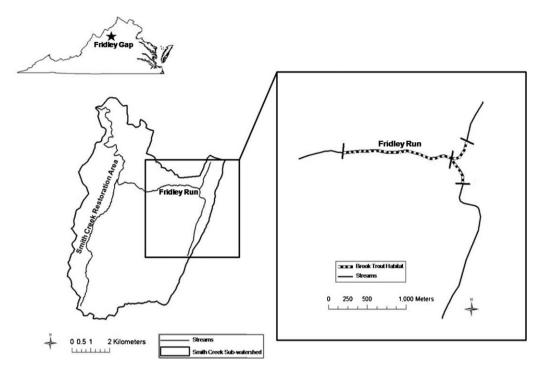


Fig. 1. The location of the study site at Fridley Gap in Rockingham County, Virginia. The headwater study site, Fridley Run, is shown in relation to the Eastern Brook Trout Joint Venture's restoration site downstream at Smith Creek.

stream plot centers). After taking photographs in each plot, we used HemiView software to calculate the global site factor (GSF) for each plot. The GSF is the total amount of diffuse and direct light penetrating the canopy relative to the amount that would be received given no canopy interception (values range from zero to one) (Anderson, 1964). Topography, altitude and geographic location are taken into account by the software in the calculation of the GSF.

To assess the relationship between hemlock basal area and current light levels at the site, we examined the relationship between hemlock basal area (as % of the total basal area) and GSF in the

study plots using linear regression analyses. We also looked for differences in mean light level among plots grouped by the percentage of the total basal area composed of hemlock (0% hemlock, <20% hemlock, and >20% hemlock). We used the non-parametric Mann–Whitney U test to compare means between basal area groups.

2.2.4. Changes in NDVI

No data on stream light levels had been collected at the study site prior to adelgid infestation. Therefore, in order to assess the possi-

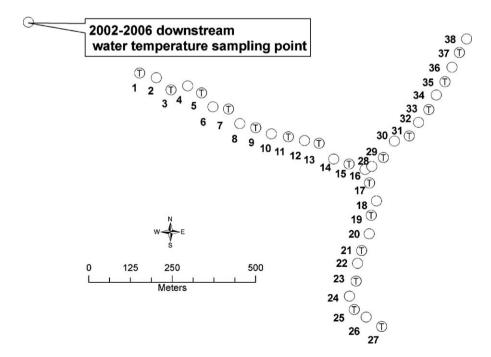


Fig. 2. Locations of 38 study plots established at Fridley Run in 2008. Plots containing water temperature loggers are marked with a 'T'. The location of the earlier 2002–2006 water temperature sampling point is also shown.

bility that increases in light levels have occurred due to decreases in canopy cover since hemlock woolly adelgid was first noticed at the site (around 2001), we conducted a remote sensing analysis using satellite images acquired by the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER). ASTER is a multispectral sensor that records data from different spectral ranges using three sensors. For this study, we used data from bands 2 and 3, red and near infrared (NIR) respectively, acquired by ASTER's VNIR sensor, which has a 15-m resolution. ASTER images of the study site for August 9, 2001 and August 12, 2008 were ordered from the NASA Land Processes Distributed Active Archive Center (LPDAAC) as expedited L1A reconstructed unprocessed instrument data. Both images were acquired on clear days with no cloud cover over the study site.

From the ASTER images, we calculated the Normalized Difference Vegetation Index (NDVI) for each of our study plots. NDVI was calculated as follows from the digital number (DN) values in the red and NIR extracted from the ASTER images using plot GPS coordinates:

$$NDVI = \frac{DN_{NIR} - DN_{red}}{DN_{NIR} + DN_{red}}$$

The plot coordinates we used to extract DN data from the ASTER images were those recorded at stream plot centers and had an accuracy of approximately 1–5 m. Our study plots were each 20 m in radius and each ASTER image pixel covered an area of 15 m \times 15 m, so it is likely that the ASTER image pixels selected for data extraction using GSP point coordinates fell within our on-the-ground study plots.

Because of differences in raw NDVI values from the 2001 and 2008 images created by atmospheric and illumination differences, we could not directly examine absolute differences in NDVI values between 2001 and 2008. Instead, we looked at the relationship between hemlock basal area and NDVI for both 2001 and 2008 using linear regression analyses. This allowed us to assess the relative impact of hemlock on NDVI for each year and to look for any changes in the relationship between NDVI and hemlock basal area between 2001, around the beginning of adelgid infestation, and 2008 when the current study was conducted. For example, we expected to see a more negative relationship between NDVI and hemlock basal area in 2008 compared with 2001 if there had been a decrease in hemlock canopy cover over that time period. In addition, we used linear regression to examine the relationship between hemlock basal area and the difference in NDVI (NDVI 2008-NDVI 2001) for each plot to see whether NDVI decreased more from 2001 to 2008 (indicating greater decreases in canopy cover) for plots that contained more hemlock compared with plots containing little or no hemlock.

2.2.5. Effects of topography on light level

To examine any effects that riparian topography might have on light levels at Fridley Run, we calculated the potential solar radiation for each of our 38-stream plots using ArcGIS Spatial Analyst extension's area solar radiation tool (ArcGIS 9.2, ESRI 2006). ArcGIS's potential solar radiation model calculates the total radiation (sum of direct and diffuse radiation) in watt hours per square meter (Wh/m²) based on a digital elevation model (DEM). The solar radiation model takes into account the effects of topography, atmosphere, elevation, daily and seasonal changes in sun angle, and latitude in its calculations (Ruiz-Arias et al., 2009; Gastli and Charabi, 2010). It does not take vegetative cover into account and therefore measures only the amount of light a given location would receive in the absence of any vegetation. Such models have been shown to provide reliable estimates of daily solar radiation for DEMs with resolutions of 100 m or less (Pons and Ninyerola, 2008; Ruiz-Arias et al., 2009). For our analysis, we used a U.S. Geological Survey (USGS) 30 m resolution DEM (National Elevation Dataset: Gesch, 2007) of the study area acquired from the University of Virginia library (Geospatial and Statistical Data, Alderman Library) and calculated the total potential solar radiation from March to September for the study area. In ArcGIS, we created a 20-m radius buffer around each plot center and then used ArcGIS's zonal statistics tool to calculate the mean potential solar radiation for each of our study plots from the potential solar radiation model. We then examined the relationship between potential solar radiation (i.e., the degree of shading due to effects of topography) and hemlock basal area at the study site using linear regression, and we compared mean potential solar radiation between hardwood and hemlock plots using the Mann–Whitney *U* test.

2.3. Predicting future light level changes and potential for changes in stream temperature

2.3.1. Gap experiment

Because most of the live and dead hemlocks at Fridley Gap are still standing, though heavily defoliated, we conducted a gap experiment to determine how much light levels are likely to change in the near future as hemlocks continue to die and fall, creating gaps in the canopy. For this experiment, we divided our study plots into two groups: those with low hemlock basal area (<15% hemlock by basal area) and those with high hemlock basal area (>20% hemlock by basal area). These groupings allowed for a clear distinction between basal area groups and an approximately equal number of plots in each basal area group from which to sample. Four nonadjacent plots were randomly chosen from each group and, in each selected plot, all hemlocks over 20 cm DBH within a 20 m radius of the stream center were cut in March 2009 (Fig. 3). This study employed a paired sampling design in that we measured light levels in the same plots both before and after selective removal of hemlocks. This allowed us to examine the influence of hemlock on light levels apart from other potentially confounding variables, such as topography, since no major changes other than the loss of hemlocks over 20 cm in DBH occurred in these plots between sampling dates. We measured light levels in the gap experiment plots using hemispherical photography in early October of 2008, prior to selective removal, and again in early October of 2009, after selective removal. Since light level (GSF) data for gap experiment plots showed some deviation from normality, we analyzed changes in light level using the paired samples Wilcoxon Signed-Ranks test. We also looked for a difference in mean change in light level between high and low basal area experimental groups using the Mann-Whitney U test for independent samples.

2.3.2. Light levels in a simulated future all-hardwood forest

We matched hemlock plots with non-hemlock plots based on their potential solar radiation values in order to predict what stream light levels might be like in a future all-hardwood riparian forest. Each hemlock plot was then assigned the 2008 leaf-on light level (GSF) of the hardwood plot most closely matching it in potential solar radiation (potential solar radiation values ranged from 869,007.31 to 981,937.25 Wh/m² and the difference in potential solar radiation for each pair of matched plots was no greater than 26,000.00 Wh/m²). This allowed us to account for the effects of topography on light level while simulating leaf-on light levels under a potential future all-hardwood riparian forest. We then compared the mean light level for the simulated all-hardwood forest with the mean light level of the current forest using the paired Wilcoxon Signed-Ranks test.

2.3.3. Relationship between hemlock basal area, light levels, and stream temperature

Finally, to assess the impact that observed and predicted changes in light levels might have on the brook trout popula-

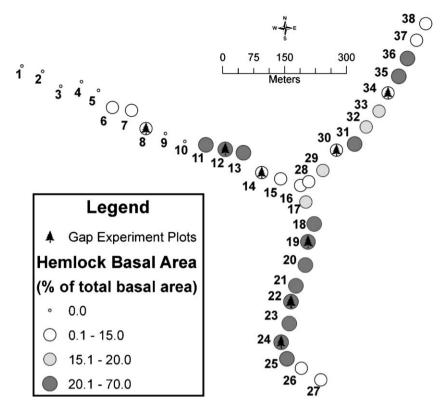


Fig. 3. Hemlock basal area (% of the total basal area) in each study plot at Fridley Run. Plots randomly selected for the gap experiment are identified by an evergreen tree symbol

tion at Fridley Gap, we looked at the relationship between mean daily maximum stream temperatures, recorded between July and September of 2008 and 2009, and hemlock basal area for all study plots using linear regression analyses. We also used regression analyses to examine the relationships between stream temperatures and GSF, between stream temperature and potential solar radiation, and between stream temperature and relative distance from primary ground water inputs (located just upstream of plots 27 and 38).

All statistical analyses in this study were conducted using either SPSS 15.0 or PASW Statistics 17.0, and all determinations of significance were made at the α < 0.05 level.

3. Results

3.1. Current status of the forest and changes in light levels and stream temperatures from early adelgid infestation to the present

3.1.1. Forest composition, hemlock defoliation, and changes in stream temperature

Forest inventory results showed that at Fridley Gap hemlock is co-dominant with chestnut oak (*Quercus prinus*) in a mixed hemlock-hardwood riparian forest. We observed extensive patches of mountain laurel (*Kalmia latifolia*) in the understory, but unlike some other southeastern hemlock forests, Fridley Gap does not possess a dense rhododendron understory. We found that hemlocks make up 18% of the total basal area at the study site with the hemlock component of the basal area ranging from 0 to 70% in individual plots (Fig. 3). Other species that make up a significant proportion of the riparian forest are chestnut oak (*Q. prinus*) at 19.1% of basal area, red oak (*Quercus rubra*) at 11.2% of basal area, tulip-poplar (*Liriodendron tulipifera*) at 10.3% of basal area, red maple (*Acer rubrum*) at 8.0% of basal area, birch (*Betula* spp.) at 7.3% of basal area, and basswood (*Tilia americana*) at 5.7% of basal area.

Hemlocks at the site have become heavily defoliated since the adelgid infestation began, but most trees are still standing. Average crown density declined from 42.1% in early 2002 to 8.2% by the end of 2007, but there was no increase in mean daily maximum water temperature at the downstream sampling points (plot 1 and earlier 2002–2006 sampling points; Fig. 2), which had the warmest temperatures out of all the plots across all years (Fig. 4).

3.1.2. Current light levels

Leaf-off light levels (GSF) measured in 2008 showed a significant negative relationship (R^2 = 0.40; F = 10.80; P = 0.005) with hemlock basal area (Fig. 5a). In addition, plots containing no hemlock had significantly higher light levels (mean GSF(SE) = 0.600(0.032)) than

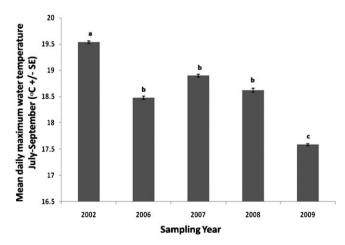


Fig. 4. Mean daily maximum water temperatures (${}^{\circ}C \pm SE$) recorded at the downstream sampling point (years 2002–2007) and plot 1 (2008 and 2009). Bars with different letters indicate significant differences in mean daily maximum water temperature among years (Wilcoxon *Z* test: P < 0.05).

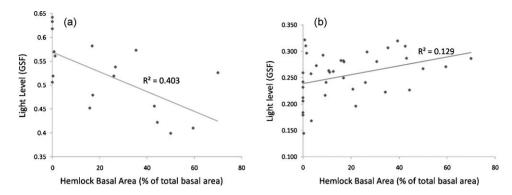


Fig. 5. (a) The relationship between hemlock basal area (% of the total basal area in each plot) and light level (measured as the global site factor (GSF)) under leaf-off (winter) conditions in 2008 ($R^2 = 0.403$; F = 10.80; P = 0.005) and (b) the relationship between hemlock basal area (% of total basal area) and light level (measured as the global site factor (GSF)) under leaf-on (summer) conditions in 2008 ($R^2 = 0.129$; F = 5.355; P = 0.026).

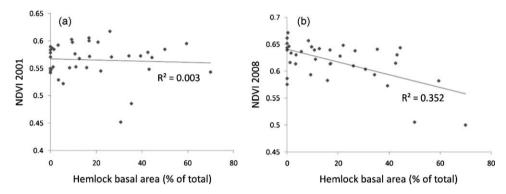


Fig. 6. (a) The relationship between hemlock basal area (% of the total basal area in each plot) and NDVI in 2001 (prior to hemlock decline) ($R^2 = 0.003$; F = 0.14; P = 0.71) and (b) the relationship between hemlock basal area (% of total basal area) and NDVI in 2008 (post-hemlock decline) ($R^2 = 0.352$; F = 19.55; P < 0.001).

plots with high hemlock basal area (mean GSF(SE) = 0.480(0.023)) (Mann-Whitney U, Z = -2.04; P = 0.042). Light levels in plots with low hemlock basal area had intermediate light levels (mean GSF(SE) = 0.527(0.022)) which were not significantly different from plots with no hemlock (Mann-Whitney U, Z = -1.71; P = 0.088) or plots with high hemlock basal area (Mann–Whitney U, Z = -1.23; P = 0.220). These results are not unexpected considering that hemlocks are known to produce more shade than hardwood species, especially in winter when hardwood species have lost their leaves. In contrast however, leaf-on light levels showed a significant positive relationship ($R^2 = 0.13$; F = 5.355; P = 0.026) with hemlock basal area (Fig. 5b), though less strongly so due to substantial variation in light level among plots containing little or no hemlock. These results were supported by comparison of mean light levels among hemlock basal area groups, which showed that during the summer, plots containing no hemlock had significantly lower light levels (mean GSF(SE) = 0.216(0.011)) than either plots with low hemlock basal area (mean GSF(SE) = 0.254(0.014)) (Mann-Whitney U, Z=-2.45; P=0.013) or plots with high hemlock basal area (mean GSF(SE) = 0.267(0.010) (Mann-Whitney *U*, Z = -2.46; P = 0.012). Light levels in plots with low hemlock basal area did not show significantly different light levels from plots with high hemlock basal area (Mann-Whitney U, Z = -0.44; P = 0.681).

3.1.3. Changes in NDVI

On-the-ground light level data were supported by the results of our remote sensing analysis. In 2001 (prior to hemlock decline), there was no significant relationship (R^2 = 0.003; F = 0.14; P = 0.71) between the Normalized Difference Vegetation Index (NDVI) and hemlock basal area in the study plots (Fig. 6a); however, by 2008 (post-hemlock decline), there was a significant negative relationship (R^2 = 0.352; F = 19.55; P < 0.001) (Fig. 6b). Similarly, there was

a significant negative relationship (R^2 = 0.15; F = 6.35; P = 0.016) between the difference in NDVI between 2008 and 2001 and hemlock basal area (Fig. 7). This indicates that NDVI decreased more from 2001 to 2008 in plots containing more hemlock and therefore that canopy cover decreased more in those plots.

3.1.4. Effects of topography on light level

Regression analysis showed a significant negative relationship (R^2 = 0.30; F = 15.09; P < 0.001) between hemlock basal area

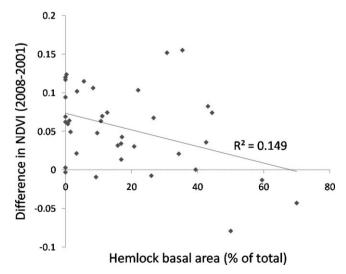


Fig. 7. The relationship between hemlock basal area (% of the total basal area in each plot) and the difference in NDVI between 2008 and 2001 (R^2 = 0.149; F = 6.35; P = 0.016).

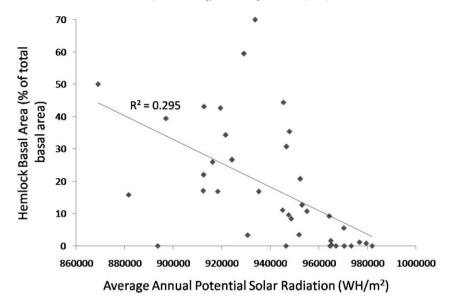


Fig. 8. The relationship between average annual potential solar radiation (Wh/ m^2) and hemlock basal area (% of the total basal area in each plot) (R^2 = 0.295; F = 15.09; P < 0.001).

and potential solar radiation at the study site (Fig. 8). Plots that have shadier topography also tend to have more hemlock. In addition, plots containing hemlock had significantly lower (Mann–Whitney U, Z=-2.02, P=0.044) potential solar radiation values (mean = 936,400.4 Wh/m²) than plots containing no hemlock (mean = 956,786.4 Wh/m²). That is, the stream receives less sunlight in plots containing hemlock because of the slope and aspect of banks alone, regardless of canopy cover.

3.2. Future light level changes and the potential for increases in stream temperature

3.2.1. Gap experiment

Gap experiment results showed significant increases (Wilcoxon Z=-2.52, P=0.012) in light levels (GSF) with hemlock loss across all experimental plots. Increases in light level ranged from 6.1 to 64.7% in individual plots and the mean increase in GSF was 27.5% (Fig. 9). There was no significant difference (Mann–Whitney U, Z=0.000, P=1.000) in mean change in light level between high hemlock

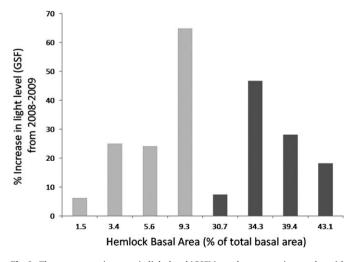


Fig. 9. The percentage increase in light level (GSF) in each gap experiment plot with original hemlock basal area (% of total) in each plot shown on the y-axis. Low basal area treatment group plots are represented by light grey bars and high basal area treatment plots by dark grey bars.

basal area (mean increase in GSF = 25%) and low hemlock basal area (mean increase in GSF = 30%) treatment groups.

3.2.2. Light levels in a simulated future all-hardwood forest

By matching current leaf-on GSF data from hardwood plots to hemlock plots paired based on topographic similarity, we found that the predicted future all-hardwood forest would have significantly lower (Wilcoxon Z=-2.31, P=0.021) light levels (mean GSF(SE)=0.240(0.005)) than the current mixed hemlock-hardwood forest (mean GSF(SE)=0.254(0.007)) (Fig. 10).

3.2.3. Relationship between hemlock basal area, light levels, and stream temperature

Mean daily maximum water temperatures downstream of the hemlock riparian area appear to have generally decreased since adelgid infestation began (Fig. 4). We did find a negative relationship (for 2008: R^2 = 0.23; F = 4.8; P = 0.04 (data not shown), and for 2009: R^2 = 0.25; F = 5.4; P = 0.03) between hemlock basal area and current summer mean daily maximum water temperatures at the site (Fig. 11a), suggesting that hemlocks might be influencing stream temperatures to some degree. However, plots with greater hemlock basal area also currently have higher summer light levels

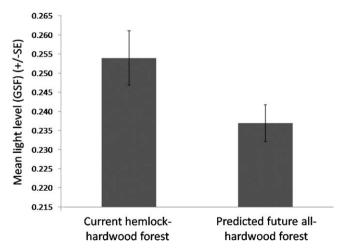
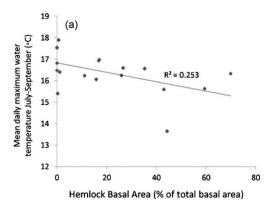


Fig. 10. Mean summer light level (GSF \pm SE) for all plots (n=38) for the current mixed hemlock–hardwood forest and a potential future all-hardwood forest.



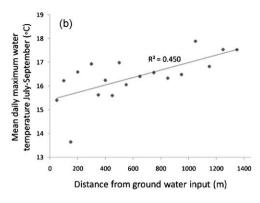


Fig. 11. (a) Hemlock basal area (% of total basal area) versus mean daily maximum water temperature from July to September (in $^{\circ}$ C) at Fridley Run for 2009 (R^2 = 0.253; F = 5.40; P = 0.03) and (b) distance from primary ground water input versus mean daily maximum water temperature from July to September (in $^{\circ}$ C) for 2009 (R^2 = 0.450; F = 13.14; P = 0.002).

and we found no relationship between water temperature and light levels. Linear regression analysis showed no significant relationship ($R^2 < 0.02$; P > 0.05) between either stream temperature and potential solar radiation or stream temperature and GSF. In addition we found that mean daily maximum temperatures showed a negative relationship (for 2008: $R^2 = 0.315$; F = 7.36; P = 0.015 (data not shown), and for 2009: $R^2 = 0.451$; F = 13.14; P = 0.002) with proximity to the stream's primary ground water input points located just upstream of plots 38 and 27 (Fig. 11b).

4. Discussion

Natural resource managers need to be able to predict changes in light levels and stream temperatures at adelgid-impacted sites in order to assess potential impacts to stream ecosystems. In the southern Appalachians in particular, managers need to know whether the loss of hemlock is likely to increase solar input to streams sufficiently to increase stream temperatures such that brook trout populations would be adversely affected (Ross et al., 2003; Ward et al., 2004; Whitledge et al., 2006; Roberts et al., 2009). Understanding the influence that loss of hemlock along southern Appalachian streams is having on understory light levels and stream temperatures will help to inform management decisions.

The results of our study suggest that, in the short-term, stream light levels could increase with hemlock decline and mortality in the southern Appalachians, even where hemlocks occur at low densities in mixed hemlock-hardwood forests. At our study site (Fridley Gap), where hemlocks have become severely defoliated by woolly adelgid, we found that plots containing hemlock had significantly higher (P < 0.02) light levels in summer than plots with no hemlock and that there was a positive relationship ($R^2 = 0.13$; P = 0.026) between hemlock basal area (ranging from 0 to 70% of the total basal area in individual plots) and stream light level. Because this is the opposite of what we would expect under healthy hemlock conditions, in which hemlocks produce more shade than hardwood species (Canham et al., 1994; Catovsky et al., 2002), these data suggest that light levels have already increased at this site with adelgid-induced hemlock decline. In addition, there was no significant relationship ($R^2 < 0.05$; P > 0.05) between total plot basal area and light levels under either leaf-off or leaf-on conditions so the observed patterns could not have been due merely to differences in total basal area among plots.

These results were supported by results obtained from ASTER satellite images, which showed that, while there was no relationship (R^2 = 0.003; P = 0.71) between the Normalized Difference Vegetation Index (NDVI) and hemlock basal area in 2001, by 2008 there was a significant negative relationship (R^2 = 0.352; P<0.001) between NDVI and hemlock basal area, where plots with more

hemlock had lower NDVI values. Similarly, there was a significant negative relationship (R^2 = 0.15; P = 0.016) between hemlock basal area and the difference in NDVI between years indicating that NDVI decreased more between 2001 and 2008 in plots that contained more hemlock. These results clearly show that canopy cover has been reduced more in areas with greater hemlock abundance at Fridley Gap since the beginnings of woolly adelgid infestation. These decreases in canopy cover were most likely due to hemlock decline because we did not observe signs of other types of damage to trees at the site. Plots containing hemlock did not contain large numbers of snags or downed trees and, according to USDA Forest Service maps, there has been no gypsy moth damage recorded in the area since 1995 (U.S. Department of Agriculture, Forest Service, 2008).

In addition, the results of our gap experiment showed that as dying hemlocks continue to fall, light levels will increase even more. We found that when hemlocks were removed from the canopy in both low basal area (0-15% of the total basal area) and high basal area (20-70% of the total basal area) treatments, stream light levels increased significantly (P = 0.012). There was no significant difference (P=1.000) in increase in light level between high and low hemlock basal area treatments, but this may have been due to a combination of small sample size and the fact that we saw an exceptionally high increase in light level in one of the low basal area plots (original hemlock basal area of 9.3% of the total basal area) and a surprisingly small increase in light level in one of the high basal area plots (original hemlock basal area of 30.7% of the total basal area). The high increase in light level in the low basal area plot might have been due to a large amount of understory vegetation that had been shading the stream but was removed by cut hemlocks that fell on top of it. The relatively small increase in light observed in the high basal area plot was probably due to the steep, high nature of the stream banks at this location, which allows for extra shading of the stream regardless of canopy cover. However, these results show that in the near future, as dying hemlocks fall, solar input to the stream at Fridley Gap will increase significantly regardless of the proportion of hemlock in the canopy.

Overall, we observed a mean increase in light level (GSF) of 27.5% in gap experiment plots. With this degree of increase in light level, extended to the entire study site as the hemlocks in non-gap experiment areas also fall, it is possible that stream temperatures could increase at some point in the future. Previous studies have found stream temperatures to increase anywhere from 0.5 to 6 °C with increases in light resulting from the removal of canopy cover ranging from 15% to completely clear-cut (Bourque and Pomeroy, 2001; Johnson, 2004; Gravelle and Link, 2007). At Fridley Gap, hemlock makes up approximately 18% of the total basal area (ranging from 0 to 70% in any given plot) over 1.7 km of the stream. According to a water temperature model developed downstream of Fridley Run at

Smith Creek, a mean increase of 25–30% in light level over 1.7 km of stream is predicted to increase mean daily maximum water temperatures by approximately 2 $^{\circ}$ C (Fink, 2008). This would put mean daily maximum water temperatures at Fridley Run near the maximum (23.9 $^{\circ}$ C) that brook trout can withstand (Eaton et al., 1995) and would likely place considerable stress on the population.

However, at Fridley Run this level of increase in water temperature appears to be unlikely. Our data suggest that the cooling effects of ground water inputs, due to Fridley Run's status as a headwater stream fed by ground water, and shady topography would be likely to mitigate potential increases in temperature caused by increases in solar radiation. We found that water temperature has not increased so far with increasing light levels accompanying hemlock decline from 2002 to 2009. Instead mean daily maximum temperatures actually decreased overall and therefore appear to vary from year to year due to variation in factors unrelated to canopy cover, such as air temperature or precipitation. In addition, we found a significant negative relationship (for 2008: R^2 = 0.315; P = 0.015, and for 2009: $R^2 = 0.451$; P = 0.002) between water temperatures and proximity to primary ground water input locations, but no relationship ($R^2 < 0.02$; P > 0.05) between water temperatures and light levels. We also found that at Fridley Run, hemlock tends to occur in areas that are already shadier due to topography (slope and aspect of banks) alone. Plots with hemlock had significantly lower potential solar radiation values than plots with no hemlock (Mann–Whitney U, Z = -2.02, P = 0.044). These results suggest that ground water inputs and shady topography may be more important than hemlock in maintaining cool temperatures at southeastern headwater streams such as this one. However, where hemlock occurs farther downstream, at sites that are less influenced by the cooling effects of ground water inputs or shady topography, the effects of loss of hemlock on water temperatures

Though our study indicates that increases in light levels may occur in the short-term with hemlock decline and mortality at southern Appalachian streams, our results also suggest that in the long-run, if hemlocks are replaced by hardwood species in the riparian canopy, light levels and therefore stream temperatures are unlikely to be higher. When we matched plots currently containing no hemlock with plots containing hemlock based on similarities in potential solar radiation (i.e., topography), mean light level in the predicted future all-hardwood riparian forest at Fridley Gap was actually significantly lower (P = 0.021) than current light levels. Although this is only a rough estimate of how light levels may change if hemlocks are completely replaced by hardwood species at this site, it is more likely to be an overestimate of predicted light levels than an underestimate because the plots that currently contain hemlock tend to be shadier than plots currently containing only hardwoods based on topography alone. Our finding that mean light level is likely to be lower in a future all-hardwood forest than in the current mixed hemlock-hardwood forest is probably due to the current state of hemlock decline at Fridley Gap. Hemlocks at this site have already become heavily defoliated by hemlock woolly adelgid and are therefore allowing more light to pass through the canopy into the understory than are the hardwood species. We found that plots currently containing only hardwood species tend to have lower light levels, in spite of having sunnier topographies, than plots currently containing hemlock, which have shadier topographies. This is a strong indication that light levels have increased in areas of the forest where hemlock is present such that the hardwood species are now producing more shade than the declining hemlocks. Therefore, replacement of these declining hemlocks by hardwoods would in effect lower light levels relative to current conditions.

In addition, NDVI results from ASTER images indicate that in 2001, before hemlocks were severely damaged by adelgid, there

was no relationship between canopy cover and percentage of the basal area composed of hemlock at this site. Prior to adelgid infestation, all-hardwood portions of the study site did not differ in density of canopy cover from portions composed of mixed hemlock-hardwood forest. Therefore, even if hemlocks are completely replaced by hardwood species, light levels are unlikely to be higher than they were under the original healthy mixed hemlock-hardwood canopy. These results concur with those of Roberts et al. (2009), who found that southern Appalachian mixed hemlock-hardwood riparian forests in Great Smoky Mountains National Park (Tennessee and North Carolina) do not necessarily have lower understory light levels than hardwood riparian forests. If percentages of hemlock in the canopy are similar at other southeastern streams, our results and those of Roberts et al. (2009) suggest that, unlike the effects of hemlock mortality observed at northeastern streams, solar input to southeastern streams may be unlikely to be higher in the long-term if hemlocks are completely replaced by hardwood species.

Because stream temperatures at Fridley Run are not currently higher than they were at the beginnings of adelgid infestation, it is also unlikely that stream temperatures would be too warm to support brook trout under a possible future all-hardwood riparian canopy. Daily maximum summer water temperatures currently do not exceed the thermal limits for brook trout, and our results suggest that after hardwoods have replaced hemlocks in the canopy, solar input to the stream will be lower than it is currently. Therefore, water temperatures should not be any higher under a future all-hardwood canopy than they are currently. These results are similar to those of the Roberts et al. (2009) study on light levels and stream temperatures in southern Appalachian hemlock forests. Roberts et al. (2009) compared light levels and stream temperatures at hemlock-dominated streams paired topographically with hardwood-dominated streams in Great Smoky Mountains National Park. They found that hemlock riparian forests generally had lower light levels than hardwood forests, but that light levels were strongly influenced by Rhododendron species in the understory (i.e., hardwood forests with rhododendron had lower light levels than hemlock forests with no rhododendron). In addition, Roberts et al. (2009) found no significant differences in stream temperatures between hemlock and hardwood sites in Great Smoky Mountains National Park. Their study, like ours, suggests that longterm changes in light levels and stream temperatures resulting from loss of hemlock in southern riparian forests may not be as great as those observed in the northeastern U.S. At southeastern hemlock streams, other factors such as topography, ground water inputs, understory vegetation, and the degree of hardwood canopy cover may contribute more to keeping light levels and/or stream temperatures low than does the presence of hemlock.

However, the lag time that will occur between loss of hemlock and regeneration of an all-hardwood canopy could be of concern at streams where temperatures are less influenced by ground water inputs or topography. Given the degree of increase in light levels predicted by our gap experiment, it is possible that water temperatures in some streams, with less ground water input and/or less shady topography, could increase during this lag time. In addition, regeneration of hardwood seedlings could be slowed by factors such as deer herbivory (Eschtruth and Battles, 2008) or, in the southern Appalachians in particular, by competition with *Rhododendron* species or mountain laurel (*K. latifolia*) in the understory (Beier et al., 2005), especially during the initial stages of regeneration (Waterman et al., 1995).

Though more studies of southern Appalachian riparian hemlock forests are needed, this study suggests that loss of hemlock at streams in the southeastern U.S. may not have as much influence on light levels as those observed in northeastern hemlock forests and may have little impact on stream temperatures. Although light levels could increase significantly in the short-term with hemlock mortality, substantial hardwood cover mixed with hemlock at these sites, the fact that hemlock tend to occur in areas that are already shadier due to topography, and the influence of ground water, particularly at headwater streams such as Fridley Run, may minimize long-term effects on light levels and both short and long-term effects on water temperatures.

Acknowledgements

We would like to thank Dr. Bruce Wiggins for assistance with GIS-related aspects of this project as well as helpful comments on study design and earlier drafts of the manuscript. We also gratefully acknowledge the James Madison University undergraduate research assistants who helped with some of the field work; in particular, Hunter Bedard and Andrew Buijs for their assistance with the forest inventory. This study was funded by U.S. Department of Agriculture, Forest Service, Southern Research Station grant No. 07-CA-11330139-131.

References

- Allen, M.C., Sheehan Jr., J., Master, T.L., Mulvihill, R.S., 2009. Responses of acadian flycatchers (*Empidonax virescens*) to hemlock woolly adelgid (*Adelges tsugae*) infestation in appalachian riparian forests. Auk 3, 543–553.
- Anderson, M.C., 1964. Studies of the woodland light climate. I. The photographic computation of light conditions. Journal of Ecology, 27–41.
- Barnes, B.V., Zak, D.R., Denton, S.R., Spurr, S.H., 1998. Forest Ecology. John Wiley & Sons Inc.. New York.
- Beier, C.M., Horton, J.L., Walker, J.F., Clinton, B.D., Nilsen, E.T., 2005. Carbon limitation leads to suppression of first year oak seedlings beneath evergreen understory shrubs in Southern Appalachian hardwood forests. Plant Ecology 1, 131–142.
- Bonneau, L.R., Shields, K.S., Civco, D.L., 1999. Using satellite images to classify and analyze the health of hemlock forests infested by the hemlock woolly adelgid. Biological Invasions 2–3, 255–267.
- Bourque, C.P., Pomeroy, J.H., 2001. Effects of forest harvesting on summer stream temperatures in New Brunswick, Canada: an inter-catchment, multiple-year comparison. Hydrology and Earth System Sciences 4, 599–613.
- Caissie, D., 2006. The thermal regime of rivers: a review. Freshwater Biology 8, 1389–1406.
- Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research 5, 620–631.
- Canham, C.D., Finzi, A.C., Pacala, S.W., Burbank, D.H., 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Canadian Journal of Forest Research 2, 337–349.
- Canham, C.D., 1988. An index for understory light levels in and around canopy gaps. Ecology 5, 1634–1638.
- Catovsky, S., Holbrook, N.M., Bazzaz, F.A., 2002. Coupling whole-tree transpiration and canopy photosynthesis in coniferous and broad-leaved tree species. Canadian Journal of Forest Research 2, 295–309.
- Cleavitt, N.L., Eschtruth, A.K., Battles, J.J., Fahey, T.J., 2008. Bryophyte response to eastern hemlock decline caused by hemlock woolly adelgid infestation. Journal of the Torrey Botanical Society 1, 12–25.
- Danehy, R.J., Colson, C.G., Parrett, K.B., Duke, S.D., 2005. Patterns and sources of thermal heterogeneity in small mountain streams within a forested setting. Forest Ecology and Management 1–3, 287–302.
- de Beurs, K.M., Townsend, P.A., 2008. Estimating the effect of gypsy moth defoliation using MODIS. Remote Sensing of Environment 10, 3983–3990.
- Dennison, P.E., Nagler, P.L., Hultine, K.R., Glenn, E.P., Ehleringer, J.R., 2009. Remote monitoring of tamarisk defoliation and evapotranspiration following saltcedar leaf beetle attack. Remote Sensing of Environment 7, 1462–1472.
- Dilling, C., Lambdin, P., Grant, J., Buck, L., 2007. Insect guild structure associated with eastern hemlock in the southern Appalachians. Environmental Entomology 6, 1408–1414.
- Drever, C.R., Lertzman, K.P., 2003. Effects of a wide gradient of retained tree structure on understory light in coastal Douglas-fir forests. Canadian Journal of Forest Research 1, 137–146.
- Eastern Brook Trout Joint Venture, 2010. Eastern Brook Trout Joint Venture Homepage. http://easternbrooktrout.org (accessed January 2010) (online).
- Eaton, J.G., McCormick, J.H., Stefan, H.G., Hondzo, M., 1995. Extreme value analysis of a fish/temperature field database. Ecological Engineering 4, 289–305.
- Eklundh, L., Johansson, T., Solberg, S., 2009. Mapping insect defoliation in Scots pine with MODIS time-series data. Remote Sensing of Environment 7, 1566–1573.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 9, 479–486.

- Eschtruth, A.K., Battles, J.J., 2008. Deer herbivory alters forest response to canopy decline caused by an exotic insect pest. Ecological Applications 2, 360–376.
- Eschtruth, A.K., Cleavitt, N.L., Battles, J.J., Evans, R.A., Fahey, T.J., 2006. Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation. Canadian Journal of Forest Research 6, 1435–1450.
- Fink, D.B., 2008. Artificial shading and stream temperature modeling for watershed restoration and brook trout (*Salvelinus fontinalis*) management. M.S. Thesis, James Madison University, Virginia.
- Ford, C.R., Vose, J.M., 2007. Tsuga canadensis (L.) Carr. mortality will impact hydrologic processes in southern Appalachian forest ecosystems. Ecological Applications 4, 1156–1167.
- Gastli, A., Charabi, Y., 2010. Solar electricity prospects in Oman using GIS-based solar radiation maps. Renewable and Sustainable Energy Reviews 2, 790–797.
- Gesch, D.B., 2007. The national elevation dataset. In: Maune, D. (Ed.), Digital Elevation Model Technologies and Applications: The DEM Users Manual, 2nd edition. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland, pp. 99–118.
- Glenn, E.P., Huete, A.R., Nagler, P.L., Nelson, S.G., 2008. Relationship between remotely-sensed vegetation indices, canopy attributes and plant physiological processes: what vegetation indices can and cannot tell us about the landscape. Sensors 4, 2136–2160.
- Gower, S.T., Norman, J.M., 1991. Rapid estimation of leaf area index in conifer and broad-leaf plantations. Ecology 5, 1896–1900.
- Gravelle, J.A., Link, T.E., 2007. Influence of timber harvesting on headwater peak stream temperatures in a northern Idaho Watershed. Forest Science 2, 189–205
- Gross, J.E., Goetz, S.J., Cihlar, J., 2009. Application of remote sensing to parks and protected area monitoring: introduction to the special issue. Remote Sensing of Environment 7, 1343–1345.
- Hadley, J.L., 2000. Understory microclimate and photosynthetic response of saplings in an old-growth eastern hemlock (*Tsuga canadensis* L.) forest. Ecoscience 1, 66–72
- Hadley, J.L., Kuzeja, P.S., Daley, M.J., Phillips, N.G., Mulcahy, T., Singh, S., 2008. Water use and carbon exchange of red oak- and eastern hemlock-dominated forests in the northeastern USA: implications for ecosystem-level effects of hemlock woolly adelgid. Tree Physiology 4, 615–627.
- Hudy, M., Downey, D.M., Bowman, D.W., 2000. Successful restoration of an acidified native brook trout stream through mitigation with limestone sand. North American Journal of Fisheries Management 2, 453–466.
- Hudy, M., Thieling, T.M., Gillespie, N., Smith, E.P., 2008. Distribution, status, and land use characteristics of subwatersheds within the native range of brook trout in the Eastern United States. North American Journal of Fisheries Management 28, 1069–1085.
- Jenkins, J.C., Aber, J.D., Canham, C.D., 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. Canadian Journal of Forest Research 5, 630–645.
- Johnson, S.L., 2004. Factors influencing stream temperatures in small streams: substrate effects and a shading experiment. Canadian Journal of Fisheries and Aquatic Sciences 6, 913–923.
- Kelley, C.E., Krueger, W.C., 2005. Canopy cover and shade determinations in riparian zones. Journal of the American Water Resources Association 1, 37–46.
- Kincaid, J.A., 2007. Compositional and environmental characteristics of *Tsuga canadensis* (L.) Carr. forests in the southern Appalachian Mountains, USA. Journal of the Torrey Botanical Society 4, 479–488.
- Kincaid, J.A., Parker, A.J., 2008. Structural characteristics and canopy dynamics of *Tsuga canadensis* in forests of the southern Appalachian Mountains, USA. Plant Ecology, 1–16.
- Kreutzweiser, D.P., Capell, S.S., Holmes, S.B., 2009. Stream temperature responses to partial-harvest logging in riparian buffers of boreal mixedwood forest watersheds. Canadian Journal of Forest Research 3, 497–506.
- Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., Fitzhugh, R.D., 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. BioScience 5, 395–405.
- Maingi, J.K., Luhn, W.M., 2005. Mapping insect-induced pine mortality in the Daniel Boone National Forest, Kentucky using Landsat TM and ETM+ data. GlScience and Remote Sensing 3, 224–250.
- Malcolm, I.A., Soulsby, C., Hannah, D.M., Bacon, P.J., Youngson, A.F., Tetzlaff, D., 2008. The influence of riparian woodland on stream temperatures: Implications for the performance of juvenile salmonids. Hydrological Processes 7, 968–979.
- McClure, M.S., Cheah, C.A.S., 1999. Reshaping the ecology of invading populations of hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae), in eastern North America. Biological Invasions 2–3, 247–254.
- Moore, R.D., Spittlehouse, D.L., Story, A., 2005. Riparian microclimate and stream temperature response to forest harvesting: a review. Journal of the American Water Resources Association 4, 813–834.
- Morin, R.S., Liebhold, A.M., Gottschalk, K.W., 2009. Anisotropic spread of hemlock woolly adelgid in the eastern United States. Biological Invasions, 1–10.
- Nagler, P., Glenn, E., Thompson, T., Huete, A., 2004. Leaf area index and Normalized Difference Vegetation Index as predictors of canopy characteristics and light interception by riparian species on the Lower Colorado River. Agricultural and Forest Meteorology, 103–112.
- Nuckolls, A.E., Wurzburger, N., Ford, C.R., Hendrick, R.L., Vose, J.M., Kloeppel, B.D., 2009. Hemlock declines rapidly with hemlock woolly adelgid infestation: Impacts on the carbon cycle of southern Appalachian forests. Ecosystems 2, 179–190.

- Orwig, D.A., 2002. Ecosystem to regional impacts of introduced pests and pathogens: historical context, questions and issues. Journal of Biogeography 10–11, 1471–1474.
- Orwig, D.A., Foster, D.R., 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. Journal of the Torrey Botanical Society 1, 60–73.
- Orwig, D.A., Foster, D.R., Mausel, D.L., 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. Journal of Biogeography 10–11, 1475–1487.
- Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J., Tucker, C.J., Stenseth, N.C., 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology and Evolution 9, 503–510.
- Pollock, M.M., Beechie, T.J., Liermann, M., Bigley, R.E., 2009. Stream temperature relationships to forest harvest in Western Washington. Journal of the American Water Resources Association 1, 141–156.
- Pons, X., Ninyerola, M., 2008. Mapping a topographic global solar radiation model implemented in a GIS and refined with ground data. International Journal of Climatology 13, 1821–1834.
- Quiñonez-Piñón, R., Mendoza-Durán, A., Valeo, C., 2007. Design of an environmental monitoring program using NDVI and cumulative effects assessment. International Journal of Remote Sensing 7, 1643–1664.
- Roberts, S.W., Tankersley Jr., R., Orvis, K.H., 2009. Assessing the potential impacts to riparian ecosystems resulting from hemlock mortality in Great Smoky Mountains National Park. Environmental Management 44, 335–345.
- Rohr, J.R., Mahan, C.G., Kim, K.C., 2009. Response of arthropod biodiversity to foundation species declines: the case of the eastern hemlock. Forest Ecology and Management 7, 1503–1510.
- Ross, R.M., Bennett, R.M., Snyder, C.D., Young, J.A., Smith, D.R., Lemarie, D.P., 2003. Influence of eastern hemlock (*Tsuga canadensis* L.) on fish community structure and function in headwater streams of the Delaware River basin. Ecology of Freshwater Fish 1, 60–65.
- Ross, R.M., Redell, L.A., Bennett, R.M., Young, J.A., 2004. Mesohabitat use of threatened hemlock forests by breeding birds of the Delaware River basin in northeastern United States. Natural Areas Journal 4, 307–315.
- Rowell, T.J., Sobczak, W.V., 2008. Will stream periphyton respond to increases in light following forecasted regional hemlock mortality? Journal of Freshwater Ecology 1, 33–40.
- Royle, D.D., Lathrop, R.G., 1997. Monitoring hemlock forest health in New Jersey using Landsat TM data and change detection techniques. Forest Science 3, 327–335
- Royle, D.D., Lathrop, R.G., 2002. Discriminating Tsuga canadensis hemlock forest defoliation using remotely sensed change detection. Journal of Nematology 3, 213-221

- Ruiz-Arias, J.A., Tovar-Pescador, J., Pozo-Vázquez, D., Alsamamra, H., 2009. A comparative analysis of DEM-based models to estimate the solar radiation in mountainous terrain. International Journal of Geographical Information Science 8, 1049–1076.
- Schomaker, M.E., Zarnoch, S.J., Bechtold, W.A., Latelle, D.J., Burkman, W.G., Cox, S.M., 2007. Crown-condition Classification: A Guide to Data Collection and Analysis. Gen. Tech. Rep. SRS-102. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, 78 p.
- Snyder, C.D., Young, J.A., Lemarieĭ, D.P., Smith, D.R., 2002. Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. Canadian Journal of Fisheries and Aquatic Sciences 2, 262– 275.
- Spaulding, H.L., Rieske, L.K., 2010. The aftermath of an invasion: structure and composition of Central Appalachian hemlock forests following the establishment of hemlock woolly adelgid, *Adelges tsugae*. Biological Invasions, doi:10.1007/s10530-010-9704-0.
- Stadler, B., Müller, T., Orwig, D., Cobb, R., 2005. Hemlock woolly adelgid in New England forests: canopy impacts transforming ecosystem processes and landscapes. Ecosystems 3, 233–247.
- Sullivan, K.A., Ellison, A.M., 2006. The seed bank of hemlock forests: implications for forest regeneration following hemlock decline. Journal of the Torrey Botanical Society 3, 393–402.
- Trotter, R.T., Shields, K.S., 2009. Variation in winter survival of the invasive hemlock woolly adelgid (Hemiptera: Adelgidae) across the eastern United States. Environmental Entomology 3, 577–587.
- U.S. Department of Agriculture, Forest Service, 2008. Gypsy moth in North America: gypsy moth defoliation maps. http://www.fs.fed.us/ne/morgantown/4557/gmoth/atlas/ (accessed January 2010) (online).
- Ward, J., Montgomery, M., Cheah, C., Onken, B., Cowles, R., 2004. Eastern Hemlock Forests: Guidelines to Minimize the Impacts of Hemlock Woolly Adelgid. U.S. Department of Agriculture, Forest Service, Northeastern Area State and Private Forestry, Morgantown, WV, 32 p.
- Waterman, J.R., Gillespie, A.R., Vose, J.M., Swank, W.T., 1995. The influence of mountain laurel on regeneration in pitch pine canopy gaps of the Coweeta Basin, North Carolina, USA. Canadian Journal of Forest Research 11, 1756–1762.
- Webb, B.W., Hannah, D.M., Moore, R.D., Brown, L.E., Nobilis, F., 2008. Recent advances in stream and river temperature research. Hydrological Processes 7, 902–918.
- Whitledge, G.W., Rabeni, C.F., Annis, G., Sowa, S.P., 2006. Riparian shading and groundwater enhance growth potential for smallmouth bass in Ozark streams. Ecological Applications 4, 1461–1473.
- Willacker Jr., J.J., Sobczak, W.V., Colburn, E.A., 2009. Stream macroinvertebrate communities in paired hemlock and deciduous watersheds. Northeastern Naturalist 16, 101–112.