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Effects of Hemlock Mortality on Streams in the Southern Appalachian Mountains

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ABSTRACT.—The death of eastern hemlock (*Tsuga canadensis*) trees in response to infestation by the introduced hemlock woolly adelgid (*Adelges tsugae*) may affect ecosystem processes and structure of streams. Prior to hemlock mortality, we documented the conditions of eight small streams and their associated riparian forests within the Appalachian Mountains of North Carolina, U.S.A. Hemlock was the dominant tree species on all riparian sites and was always associated with rhododendron (*Rhododendron maximum*). Significant trends of increasing canopy openness, increasing light to the streams and increasing annual temperature range were observed. Contributions of hemlock to litterfall, in-stream wood, and benthic organic matter were important at the beginning of the study, suggesting that the loss of hemlock may significantly modify the trophic dynamics and physical structure of southern Appalachian streams. Increased growth of rhododendron in response to hemlock mortality may compensate for the trophic influences of hemlock loss. However, because of rhododendron's negative effect on growth of seedlings of other tree species, the greatest ecosystem impact of hemlock woolly adelgid may be more extensive rhododendron thickets within the riparian corridors of southern Appalachian streams.

INTRODUCTION

Historically, eastern hemlock (*Tsuga canadensis* (L.) Carr.) has been considered a foundation species throughout much of eastern North America (Ellison *et al.*, 2005). But stands of eastern hemlock and Carolina hemlock (*T. caroliniana* Engelm) are currently declining rapidly due to infestation by the hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) and little regeneration is expected (Orwig and Foster, 1998; Preisser *et al.*, 2011). While in the Northeast, hemlock typically occurs along ridge tops, on steep slopes, and in narrow valleys (Orwig *et al.*, 2002), in the southern Appalachians, eastern hemlock is the only conifer abundant along streams and may play an important role as a riparian species. These regional differences in distribution could influence the consequences of hemlock mortality. Ehrenfeld (2010) contrasted the structure of terrestrial and aquatic ecosystems and concluded that structural differences do not produce fundamental differences in the mechanisms by which invasive exotic organisms alter ecosystem function. But, in the case of the adelgid, differential effects on forests and streams of the southern Appalachians may produce such fundamental differences. In forests, the adelgid causes death of a single tree species, which, on a regional basis, may be relatively unimportant (Albani *et al.*, 2010). But, because hemlock is one of the dominant riparian species along small mountain streams, its

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loss may have larger effects on stream organisms and in-stream processes (Siderhurst *et al.*, 2010).

In addition, while hemlocks killed by the adelgid are typically replaced by hardwoods in the Northeast (Battles *et al.*, 2000; Orwig and Foster, 1998; Jenkins *et al.*, 1999; Kizlinski *et al.*, 2002; Small *et al.*, 2005), riparian forest regrowth in the Southeast may be very much influenced by the presence of rhododendron, especially *Rhododendron maximum* L. (Kincaid, 2007; Kincaid and Parker, 2008; Nuckolls *et al.*, 2009; Roberts *et al.*, 2009; Spaulding and Rieske, 2010; Krapfl *et al.*, 2011; Ford *et al.*, 2012). The co-occurrence of hemlock and rhododendron in riparian areas was noted in the earliest studies of southern Appalachian vegetation (*e.g.*, Pinchot and Ashe, 1897). Rhododendron is known to inhibit seed germination and seedling growth of many trees (Beckage *et al.*, 2000; Nilsen *et al.*, 2001; Beier *et al.*, 2005; Lei *et al.*, 2006). Hemlock is one of the few tree species that can propagate under a dense rhododendron canopy (Phillips and Murdy, 1985; Van Lear *et al.*, 2002). Consequently, we might expect hemlock death to be followed by expansion of dense thickets of rhododendron along low-order streams (Roberts *et al.*, 2009).

This study was conducted at Coweeta Hydrologic Laboratory, Macon Co., North Carolina, U.S.A., where eastern hemlock has been an abundant and important streamside species. Both the distribution and abundance of hemlock at Coweeta increased in the 20th Century. Between 1934, shortly after the catchment was logged, and the 1990s, hemlock basal area in Coweeta's permanent vegetation plots increased 400% (Elliott *et al.*, 1999; Elliott and Swank, 2008). Hemlock occurred in only 16% of the plots in 1934, but by the 1990s it was found in 50% of the plots (Elliott *et al.*, 1999; Elliott and Swank, 2008), indicating that hemlock became increasingly important. Measurements made in the permanent vegetation plots in 1970 indicated that hemlock then contributed only about 3% of the catchment basal area. However, those hemlock made up as much as 50% of the basal area in locations along streams (K. J. Elliott, pers. obs.). Narayanaraj *et al.* (2010) found that hemlock abundance at Coweeta was strongly negatively correlated with distance from streams and that most hemlocks occurred within 50 m of a stream.

It is not clear if the extensive riparian distribution of hemlock in 2003 was similar to the conditions of the ancestral Appalachian forest or if it was a response to either logging or the loss of American chestnut (*Castanea dentata* (Marsh.) Borkh.) due to chestnut blight (*Cryphonectria parasitica* (Murr.) Barr). However, various sources suggest that hemlock was an important riparian species in the pre-logging cove hardwood forests of the southern Appalachians (Cain, 1943; Braun, 1950). Braun (1950) noted that hemlock was more abundant in stream bottoms and riparian areas than in uplands and that where hemlock was dominant, rhododendron was usually present in the understory. Harshberger (1903) described hemlock growing with *Rhododendron maximum* in locations "along mountain streams." In an examination of an unlogged tract in western North Carolina near Linville, Reed (1905) identified a forest type as "hemlock bottom" in which hemlock represented 37% of stem density. Finally, Pinchot and Ashe (1897) noted that hemlock was common in the mountains in cool ravines along streams and that it was typically associated with birches (*Betula lenta* L. and *Betula alleghaniensis* Britton) and rhododendron.

Loss of riparian hemlock could be expected to affect streams in several ways. The heavy shade of tree and shrub canopies limits stream primary production, but trees provide energy to the streams during autumn leaf fall. Hemlocks provide especially dense year-round shade, maintaining cool summer temperatures in headwater streams (Snyder *et al.*, 2002; Siderhurst *et al.*, 2010). Fish and macroinvertebrates in streams draining hemlock stands are distinct from those in streams with adjacent hardwoods, suggesting that changes in

density or species distribution will occur with hemlock death (Snyder *et al.*, 2002; Ross *et al.*, 2003; Willacker *et al.*, 2009). Hemlock mortality could alter the hydrologic regime of streams because, unlike hardwoods, hemlocks transpire at a low rate in the summer, continue to transpire through the winter, and transpire heavily in the early spring before deciduous leaf-out (Ford and Vose, 2007). Elimination of hemlocks from watersheds may make streams more prone to summer droughts and spring floods. Since an increase in summer droughts in the southern Appalachians is also a prediction of climate change models (*e.g.*, Bates *et al.*, 2008), organisms adapted to these normally perennial streams may experience the compounding effects of hemlock loss and climate change.

The objective of this study was to measure stream conditions prior to hemlock mortality and to follow some of the early changes in stream temperature and light regime as hemlock mortality progressed. Over the course of this study, from 2003 through 2011, adelgid infestation spread from none at most sites to 100% infestation with nearly 100% hemlock death at all sites.

METHODS

STUDY SITES

This study was conducted at Coweeta Hydrologic Laboratory (35°03'35"N, 83°25'51"W), a 2185-ha research area operated by the USDA Forest Service located in the Nantahala Mountains of the Blue Ridge physiographic province. Summers are cool (mean 21.6 C), winters are mild (mean 11.7 C), and average precipitation varies with altitude from 180 to 230 cm/y (Swift *et al.*, 1988; Riedel, 2006). Underlying bedrock consists of gneiss, schist and metasandstone units (Hatcher, 1979, 1988). Deeply weathered regolith averages about 7 m deep (Swank and Crossley, 1988).

HWA was first noted at Coweeta in 2003, and in less than 3 y all hemlock trees were infested and had an average of 81% crown loss (Elliott and Vose, 2011). By 2008, 33% of hemlock trees were dead, and the most recent survey (2011) showed almost complete loss of remaining trees (K. J. Elliott, pers. obs.). Most of the data reported in this study (riparian vegetation, litterfall, benthic organic matter) were collected before any crown loss had occurred at the study sites (2003–2005). Measurement of large wood was completed in 2008 but before any input of newly dead hemlock wood. Measurements of water temperature, light, and canopy openness began before any crown loss had occurred and continued through near 100% crown loss at all sites.

In 2003, we chose nine locations (Table 1) for vegetation measurements and eight of these sites were selected for stream measurements. All sites were located in areas that have not been logged since the area became National Forest in the late 1920s and where streams passed through or were adjacent to permanent vegetation plots in which trees were measured in 1934–1935, 1969–1973, and 1988–1993 (Elliott and Swank, 2008). Six stream sites were located on 1st–2nd order streams and two were located on 4th order streams (Ball Creek and Shope Fork). We attempted to find small streams in reference forests without riparian hemlock. However, we found that hemlock was ubiquitous near streams at Coweeta.

RIPARIAN VEGETATION

In 2004, all trees and two evergreen shrubs (*Kalmia latifolia* L. and *Rhododendron maximum*) (≥ 2.5 cm diameter at 1.37 m height (dbh)) were measured to the nearest 0.1 cm dbh in one 20 × 40 m riparian plot at each of the nine sites following methods described by Elliott and Swank (2008). We calculated frequency, density, basal area, foliage mass, leaf area, branch mass, bole mass, total tree mass, and total wood mass for all species. We used the allometric

TABLE 1.—Study sites at Coweeta Hydrologic Laboratory and parameters measured. xx indicates measurements made in previous studies

Stream Names	Watershed number	Approximate stream order	Average channel width (m)	Elevation (m)	Riparian Vegetation	Stream Water Temp	Light	Canopy Openness	Litterfall	Large Wood	Benthic Organic Matter
Larger Streams:											
Ball Creek		4th	4.1	846	x				x	x	
Shope Fork		4th	3.8	709	x				x	x	
Smaller Streams:											
Hugh White Creek, upper site	WS 14	1st	3.5	793	x	x	x	x	x	x	x
Hugh White Creek, lower site	WS 14	2nd	3.3	716	x	x	x	x	x	x	x
Mill Branch	Downstream of WS 31	2nd	3.3	862	x	x	x	x	x	x	x
Reynolds Branch		1st	3.0	930	x	x	x	x	x	x	x
Cunningham Creek	WS 32	2nd	2.3	907	x	x	x	x		x	x
Wykle Branch		2nd	3.4	991	x	x		x	x	x	x
Upper Ball Creek	WS 27	2nd	7.7	1070	x				xx		xx

equations of Santee and Monk (1981) to estimate mass and the equation of Ford and Vose (2007) to estimate leaf area for hemlock, those of Day and Monk (1974) for *Kalmia* and *Rhododendron* and those of Martin *et al.* (1998) for mass and leaf area for all other species.

TEMPERATURE, LIGHT, AND CANOPY OPENNESS

Beginning in Aug. 2004, one temperature recorder (Thermochron iButton, Dallas Semiconductor/Maxim, Sunnyvale, CA, U.S.A., or HOBO Pendant temperature/light data logger, Onset Computer Corp., Bourne, MA, U.S.A.) was submerged at the downstream end of each of six small stream sites (Table 1). Temperature was recorded every 4 h. Trends in mean monthly temperatures were analyzed with the Seasonal Kendall test for trend (Hirsch and Slack, 1984; Helsel *et al.*, 2006). For attributes with yearly observations (annual minimum and maximum temperature and annual range in temperature), trends over time were examined with the Regional Kendall test (Helsel and Frans, 2006).

Beginning in Jun. 2005, relative light intensity at five stream sites (Table 1) was monitored every 5 min with HOBO Pendant temperature/light data loggers. These loggers record light intensity between 150 and 1200 nm wavelength and provide a measure of relative rather than absolute light intensity. The data are approximately lumens m^{-2} . At each site, five light meters were fastened to 1-m high posts spaced at intervals of 10 m immediately adjacent to the streams. Monthly means of integrated daily intensity were calculated. Trends in relative light intensity were analyzed with the Seasonal Kendall test for trend. The same technique was used to look for trends in solar radiation data from the same time period from Coweeta Climate Station 1, which is not influenced by canopy (data provided by USDA Forest Service, Coweeta Hydrologic Laboratory). Although units for light measurements at this station are different ($w m^{-2}$) presence or absence of trends over time are comparable.

Starting in 2006, we took hemispherical photographs in late Mar. or early Apr. of each year before deciduous leaf-out at six locations along six streams (Table 1). Pictures were taken at 10-m intervals at permanently marked mid-stream points. A Nikon Coolpix 950 digital camera with a Nikon FC E8 0.21X Fisheye Converter was mounted 1.5 m above the stream on a monopod and leveled with bubble indicators. Automatic settings for aperture width and shutter speed were used. Images were enhanced using Adobe Photoshop Elements 6.0 to ameliorate low light levels near the horizon, then analyzed for canopy openness using Gap Light Analyzer (GLA), Version 2.0 image processing software (Frazer *et al.*, 1999). The blue color plane provided the best contrast between sky and canopy and was used for calculations. We looked for trends in canopy openness over time in streams using linear regression (PROC AUTOREG, SAS v 9.2, SAS Institute) and over all streams using the Regional Kendall test (Helsel and Frans, 2006).

LITTERFALL

Litterfall was measured at eight sites between Sep. 2003 and Dec. 2004. Litter was collected in buckets (each 0.066 m^2 in cross-section area) located over or immediately adjacent to the streams. Ten buckets were placed at intervals (5 m in small streams and 10 m in large streams) along each stream. Leaves in the buckets were collected approximately monthly in autumn and every 2 mo through the rest of the year. They were sorted by species, dried (55 C) and weighed, samples were composited by species for each plot and one subsample was ashed (550 C) to determine ash free dry mass (AFDM) inputs to the streams.

LARGE WOOD

Large wood was measured in summer 2008 in eight of the stream sites (Table 1) using the line-intersect method (Warren and Olsen, 1964; Wallace and Benke, 1984). We laid out a

line of at least 100 m along the thalweg of each stream and then measured the diameter and length of each piece of wood with a diameter greater than 5 cm that intersected the line. When possible we identified the species of log in the field, but when in doubt, we sampled the log and used microscopic examination in the laboratory to identify the sample as hemlock or non-hemlock.

BENTHIC ORGANIC MATTER

Benthic organic matter was measured quarterly beginning in Nov. 2004. All large organic material (leaves, leaf particles larger than 1 mm, sticks less than 5 cm in diameter, fruits, etc.) was collected with a 30 cm-diameter core sampler (*e.g.*, Golladay *et al.*, 1989). Samples were taken at points located 5 m apart along each stream. At each point, organic matter was collected at $\frac{1}{4}$, $\frac{1}{2}$, and $\frac{3}{4}$ of the distance across the stream width for a total of 15 samples per stream each quarter. The starting point for sampling was moved 1 m upstream each quarter to avoid repeatedly sampling the same points. Samples were dried (55 C) and sorted into five categories: leaves, hemlock needles, wood, hemlock wood, and other. The samples were weighed and composited within category, then one subsample per category was ashed (550 C) to determine AFDM.

RESULTS

RIPARIAN VEGETATION

Hemlock occurred in all sites and accounted for an average of 19% of the stem density and 35% of the basal area (Tables 2 and 3). In all but one site, hemlock was the species with the highest basal area (Table 2). Rhododendron, yellow poplar (*Liriodendron tulipifera* L.), sweet birch (*Betula lenta* L.), and red maple (*Acer rubrum* L.) also occurred in all nine plots. Rhododendron had low basal area in only one site (2% of the basal area) but was more abundant in the other sites, ranging from 8% to 19% of the total basal area (Table 2).

TEMPERATURE, LIGHT AND CANOPY OPENNESS

We calculated monthly mean temperatures from daily averages. Despite occasional recorder failures, these data were relatively complete (407/462 possible stream months), and the nonparametric Kendall tests are particularly robust in dealing with missing data (Hirsch and Slack, 1984). We found no significant long-term trend in mean monthly temperatures over the 6 y period (Seasonal Kendall trend tests, $P > 0.05$, P values adjusted for serial correlation). However, no trends would be detected if the direction of change in temperature is opposite in different seasons. When we looked at seasonally specific responses (Fig. 1), we did observe a significant decrease in the annual minimum daily mean [Regional Kendall test, $P = 0.0002$, τ (analogous to the parametric Pearson correlation coefficient) = -0.556 , β (slope) = -0.441], a significant increase in the annual maximum daily mean (Regional Kendall test, $P = 0.0174$, $\tau = 0.356$, $\beta = 0.304$), and a significant increase in the annual temperature range (Regional Kendall test, $P = 0.0009$, $\tau = 0.543$, $\beta = 0.826$). Based on hemlock foliage measurements made in 2004, Apr. 2005, and Aug. 2004 mean stream water temperatures were significantly and negatively related to foliage mass (Fig. 2).

Light intensity showed a typical annual pattern with a small peak in autumn after leaf fall, low intensity during winter, and a larger peak in spring followed by an abrupt decline with leaf emergence (Fig. 3). Seasonal Kendall trend tests indicated that relative light intensity increased through time for all five streams whereas there was no trend in the light data from the reference site (Fig. 3). The trend across all five streams was highly significant ($P <$

TABLE 2.—Basal area ($m^2 ha^{-1}$) of trees in vegetation plots adjacent to the nine stream sites (P = present but less than $0.05 m^2 ha^{-1}$)

Species	Hugh White Cr.,		Shohe Fork	Mill Br.	Ball Cr.	Reynolds Br.	Cunningham Cr.	Wykle Br.	Upper Ball Cr.	Average	
	upper	lower								basal area	Frequency (%)
<i>Tsuga canadensis</i> (L.) Carr.	13.5	11.2	9.3	14.2	21.3	16.9	13.0	21.8	14.4	15.1	100
<i>Rhododendron maximum</i> L.	7.0	6.1	4.3	4.9	0.7	3.9	14.3	4.1	8.9	6.0	100
<i>Liriodendron tulipifera</i> L.	4.6	2.1	1.7	0.1	4.5	15.1	0.5	10.0	1.5	4.4	100
<i>Quercus rubra</i> L.		3.1	9.1	2.1	10.1	2.1			5.9	3.6	67
<i>Betula lenta</i> L.	5.7	3.7	4.2	2.2	1.7	7.3		1.9	1.8	3.2	89
<i>Acer rubrum</i> L.	3.8	5.5	0.1	4.4	p	0.8	6.7	1.6	0.7	2.6	100
<i>Quercus alba</i> L.			2.5	5.4	4.2				1.2	1.7	44
<i>Magnolia fraseri</i> Walt.		1.1		0.1	0.2	3.4			3.9	1.0	55
<i>Nyssa sylvatica</i> Marsh.			0.6				4.1		3.1	0.9	33
<i>Quercus montana</i> L.	2.0	1.7			0.3			6.3	3.3	0.8	44
<i>Tilia americana</i> L.							0.6			0.8	22
<i>Oxydendrum arboreum</i> (L.) DC.					0.6		1.9			0.5	44
<i>Quercus velutina</i> Lam.		1.6	2.2	p	2.0					0.4	22
<i>Acer saccharum</i> Marsh.								3.6		0.4	11
<i>Carya Nutt.</i> spp				0.5	0.1					0.4	33
<i>Quercus coccinea</i> Muenchh.			2.2							0.3	11
<i>Prunus serotina</i> Ehrh.			2.8					2.7		0.3	11
<i>Magnolia acuminata</i> L.	2.5									0.3	11
<i>Fraxinus americana</i> L.	0.4								0.9	0.2	22
<i>Kalmia latifolia</i> L.			p	0.2	p		1.3		0.8	0.2	44
<i>Robinia pseudoacacia</i> L.										0.1	11
<i>Aesculus flava</i> Ait.	0.5	0.1								0.1	25
<i>Fagus grandifolia</i> Ehrh.		0.3	0.4				0.1			0.1	33
<i>Acer pensylvanicum</i> L.							0.7		0.1	0.1	22
<i>Sassafras albidum</i> (Nutt.) Nees							0.7			0.1	11
<i>Hamamelis virginiana</i> L.			0.1		p				0.2	p	33
<i>Cornus florida</i> L.							0.3			p	11
<i>Clethra acuminata</i> Michx.							0.1			p	11
<i>Pyrolarica pubera</i> Michx.			p							p	11
<i>Amelanchier arborea</i> Michx.				p	0.1					p	33
<i>Betula alleghaniensis</i> Brit.								0.1		p	11
Total	37.2	39.3	39.6	34.2	45.8	49.5	44.3	52.1	46.7	43.2	

TABLE 3.—Characteristics of hemlock in the nine riparian plots. Numbers in parentheses are proportion of hemlock contribution to the total of that characteristic within the plot

	Density (stems/ha)	Basal area (m ² ha ⁻¹)	Foliage mass (kg ha ⁻¹)	Leaf area (m ² ha ⁻¹)	Branch mass (kg ha ⁻¹)	Bole mass (kg ha ⁻¹)	Total wood (kg ha ⁻¹)	Total biomass (kg ha ⁻¹)
Hugh White Cr., upper	200 (8.2)	13.5 (36.2)	1919 (27.5)	16,755 (32.5)	21,736 (33.8)	55,634 (38.2)	77,370 (40.9)	79,288 (36.6)
Hugh White Cr., lower	113 (4.3)	11.2 (28.4)	1705 (22.2)	14,803 (23.9)	17,679 (26.4)	42,309 (26.8)	59,988 (29.2)	61,693 (26.5)
Shope Fork	1125 (37.2)	9.3 (23.6)	2133 (29.3)	16,021 (25.0)	14,513 (21.1)	34,395 (18.4)	48,908 (20.2)	51,041 (19.4)
Mill Br.	250 (9.0)	14.2 (41.6)	2163 (32.8)	18,584 (35.7)	22,764 (37.3)	56,775 (37.2)	79,539 (40.1)	81,702 (37.1)
Ball Cr.	1038 (65.4)	21.3 (46.5)	4787 (58.8)	37,470 (47.5)	32,390 (45.9)	68,191 (32.3)	100,581 (36.0)	105,368 (36.4)
Reynolds Br.	588 (23.2)	16.9 (34.2)	3267 (41.0)	26,433 (37.4)	26,266 (38.7)	59,587 (28.4)	85,853 (32.3)	89,120 (31.2)
Cunningham Cr.	325 (6.7)	13.0 (29.4)	2107 (19.7)	17,780 (27.4)	20,712 (23.2)	50,618 (35.6)	71,330 (38.2)	73,438 (30.3)
Wykle Br.	413 (16.4)	21.8 (41.9)	3002 (38.1)	26,397 (36.7)	35,424 (41.4)	91,918 (34.4)	127,342 (37.3)	130,344 (36.1)
Upper Ball Cr.	75 (1.9)	14.4 (30.9)	1439 (16.6)	13,811 (20.9)	24,318 (27.6)	70,744 (33.5)	95,062 (34.8)	96,501 (31.3)
Average [Standard error] (proportion)	458 [129] (19.1)	15.1 [1.42] (34.7)	2502 [345] (31.8)	20,895 [2579] (31.9)	23,978 [2216] (32.8)	58,908 [5623] (31.6)	82,886 [7728] (34.3)	85,388 [7899] (31.7)

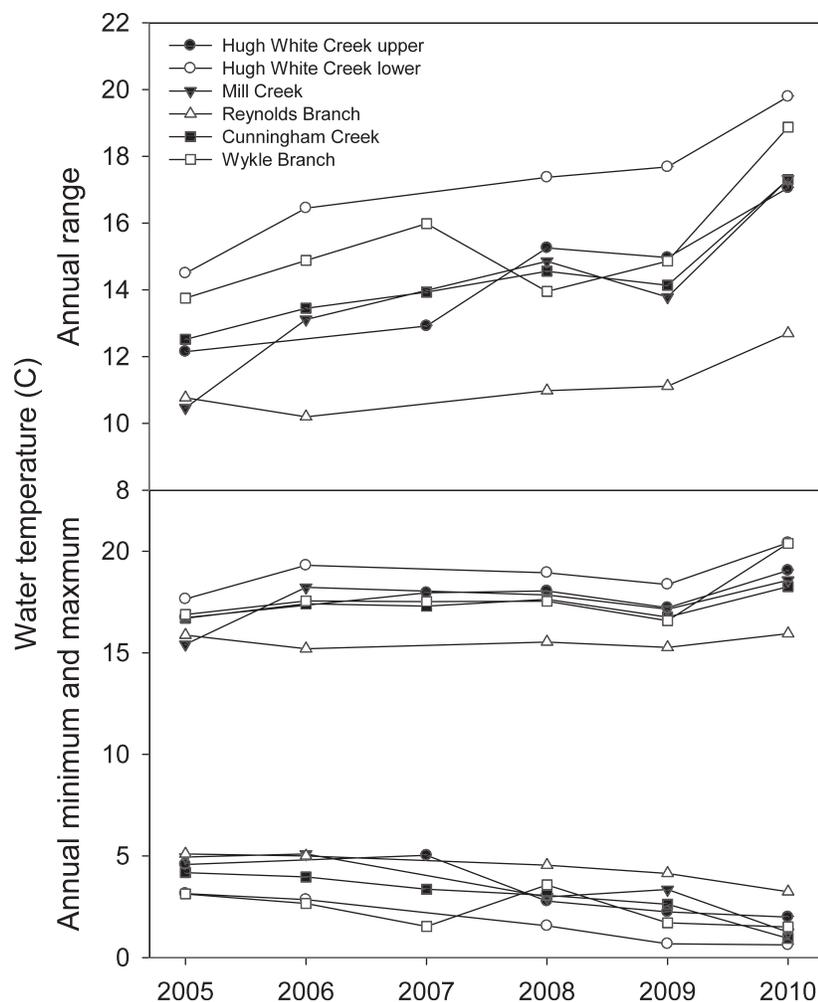


FIG. 1.—Upper panel: Trends over time in annual range in stream water temperature in small streams affected by hemlock death. Lower panel: Trends over time in annual minimum and maximum stream water temperatures

0.0001, $\tau = 0.535$, $\beta = 72.5$). There was a significant linear regression of light during the Apr. spring maxima on canopy openness ($P < 0.0001$, $r^2 = 0.622$, $\beta = 294.79$).

A trend of increased canopy openness over time was evident for Hugh White Creek lower, Hugh White Creek upper and Reynolds Branch, and trends in Cunningham Creek and Mill Branch approached but did not reach statistical significance (Fig. 4). No trend was found in Wykle Branch. Over all streams, there was a significant increase in canopy openness over time (Regional Kendall test, $P = 0.0006$, $\tau = 0.511$, $\beta = 0.951$).

LITTERFALL

Litterfall to the streams was dominated by yellow poplar and rhododendron leaves (Table 4). Litterfall was lowest for the two larger streams, Shope Fork and Ball Creek, but litterfall to the small streams was very similar to previously reported values. Annual leaf input to Hugh White Creek has been previously measured as 415 g AFDM m^{-2} (Webster *et al.*, 1990), 327 g AFDM m^{-2} (Webster *et al.*, 2001) and 300 g AFDM m^{-2} (Hagen, 2004). Hemlock needles averaged 21% of total leaf fall across all streams and 12% of total litterfall. The percent of litterfall contributed by hemlock ranged from 36% at the Shope Fork site to 6% at the Hugh White Creek upper site. Like deciduous leaf fall, hemlock needle fall peaked in Oct.–Nov.

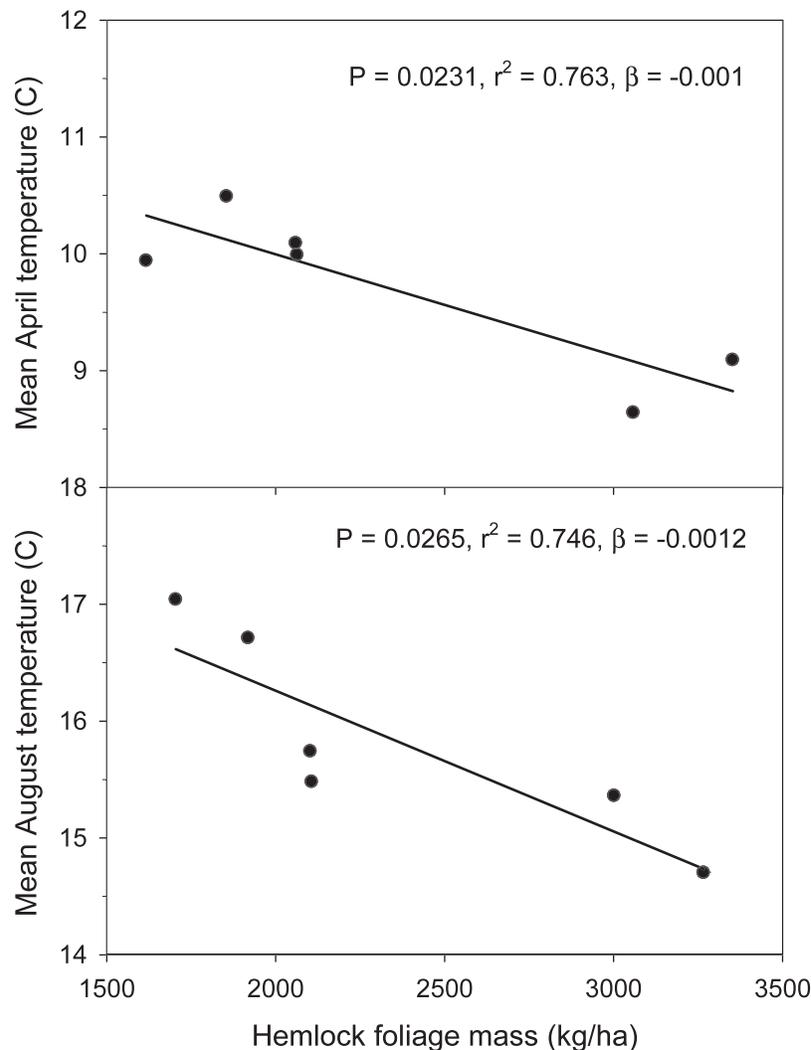


FIG. 2.—Linear regression of mean Apr. 2005 (upper panel) and Aug. 2004 (lower panel) stream water temperature on hemlock foliage mass in plots adjacent to each stream (β is slope of relationship)

LARGE WOOD

The volume of large (>5 cm diameter) wood in the streams was highly variable, ranging from $400 \text{ cm}^3 \text{ m}^{-2}$ in Shope Fork to $38,000 \text{ cm}^3 \text{ m}^{-2}$ in Reynolds Branch (Fig. 5). We observed generally less wood in larger streams (Ball Creek and Shope Fork) and generally more wood in streams in steep sided valleys. Wood biomass in Hugh White Creek (4.8 kg m^{-2} , average of upper and lower sites; based on a density of $0.4 \text{ g AFDM cm}^{-3}$) was very similar to previous measurements: 5.1 kg m^{-2} (Golladay *et al.*, 1989), 4.4 kg m^{-2} and 6.3 kg m^{-2} (J. R. Webster and S. W. Golladay, pers. obs.). The hemlock component of large wood ranged from absent in Shope Fork to 56% in Reynolds Branch where two large hemlock logs (75 and 99 cm diameter) were located in the reach.

BENTHIC ORGANIC MATTER

Benthic organic matter ranged from 58 g AFDM m^{-2} (Hugh White Creek lower site) to $154 \text{ g AFDM m}^{-2}$ at the upper Hugh White Creek site (Fig. 5). Hugh White Creek values were similar to previously reported measurements: 33 g AFDM m^{-2} (Gurtz and Wallace, 1984; lower reaches only), $213 \text{ g AFDM m}^{-2}$ (Golladay *et al.*, 1989), $102 \text{ g AFDM m}^{-2}$ (Stout

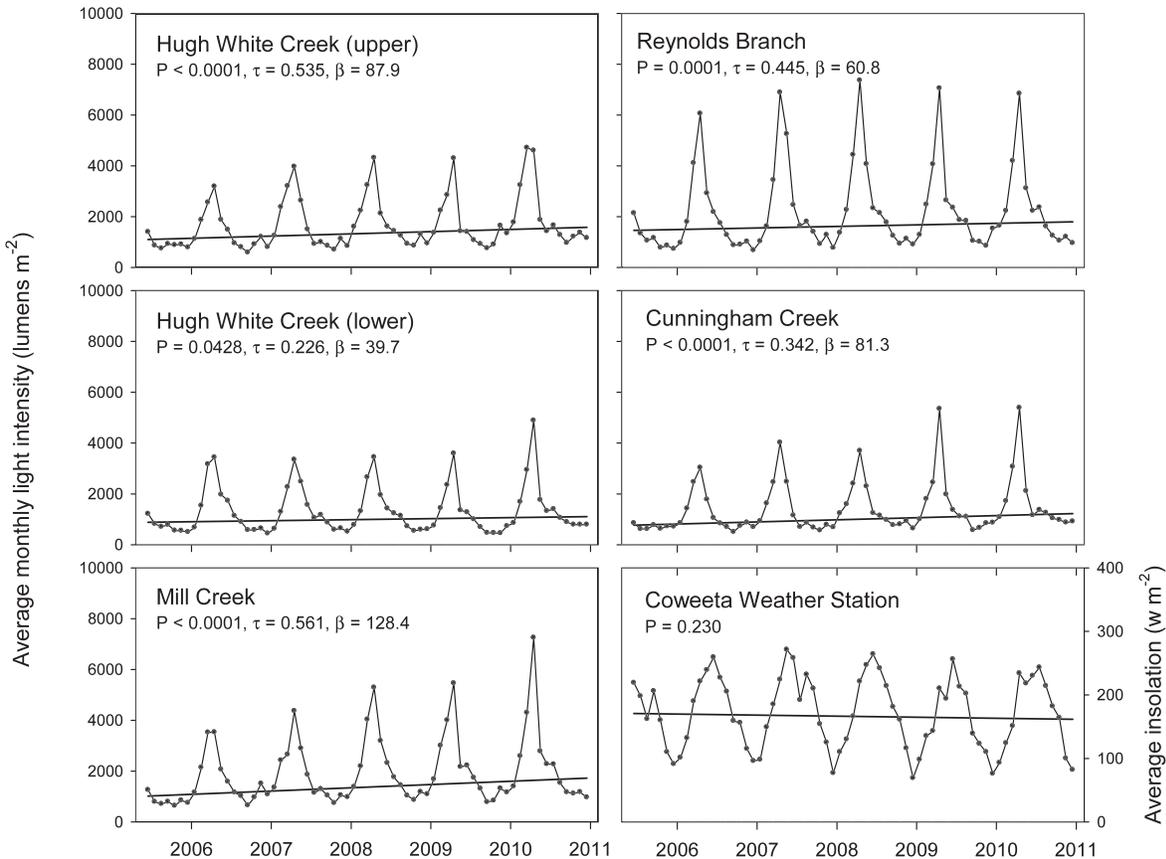


FIG. 3.—Trends over time in monthly average relative light intensity at five of the streams. Connected circles are measured data, and the lines are the linear trends after removing seasonal variation (τ is the nonparametric correlation coefficient, and β is slope of relationship)

et al., 1993) and 120 g AFDM m⁻² (Webster *et al.*, 2001). Hemlock material was not a large component of benthic organic matter at any site (Fig. 5) during any collection period. Hemlock needles averaged less than 1% of the leaf material in the six streams, but the small quantity of hemlock needles may be an artifact of our sampling technique. When collecting material from the benthic samples, we probably missed many of the hemlock needles. Hemlock twigs were abundant in many of the samples, especially in Mar. and Jun. On average, hemlock twigs made up 16% of the small wood in the streams.

DISCUSSION

The results of our study confirm that eastern hemlock has been an abundant and important streamside species in the southern Appalachian Mountains. Prior to infestation by the hemlock wooly adelgid, eastern hemlock made a greater contribution to basal area than any other riparian tree or shrub at Coweeta and has been a significant component of stream organic matter budgets (Table 4). This study also confirms that riparian hemlock is typically associated with rhododendron (Table 2). As noted in the studies cited above, hemlock and rhododendron were associated before widespread logging and chestnut blight. Analysis of long-term data from Coweeta shows that both species subsequently increased in their importance in streamside areas (Dobbs and Parker, 2004; Elliott and Swank, 2008). Ten years ago, a comparison of sites spread broadly across a region would likely have shown a positive association between hemlock and rhododendron because their

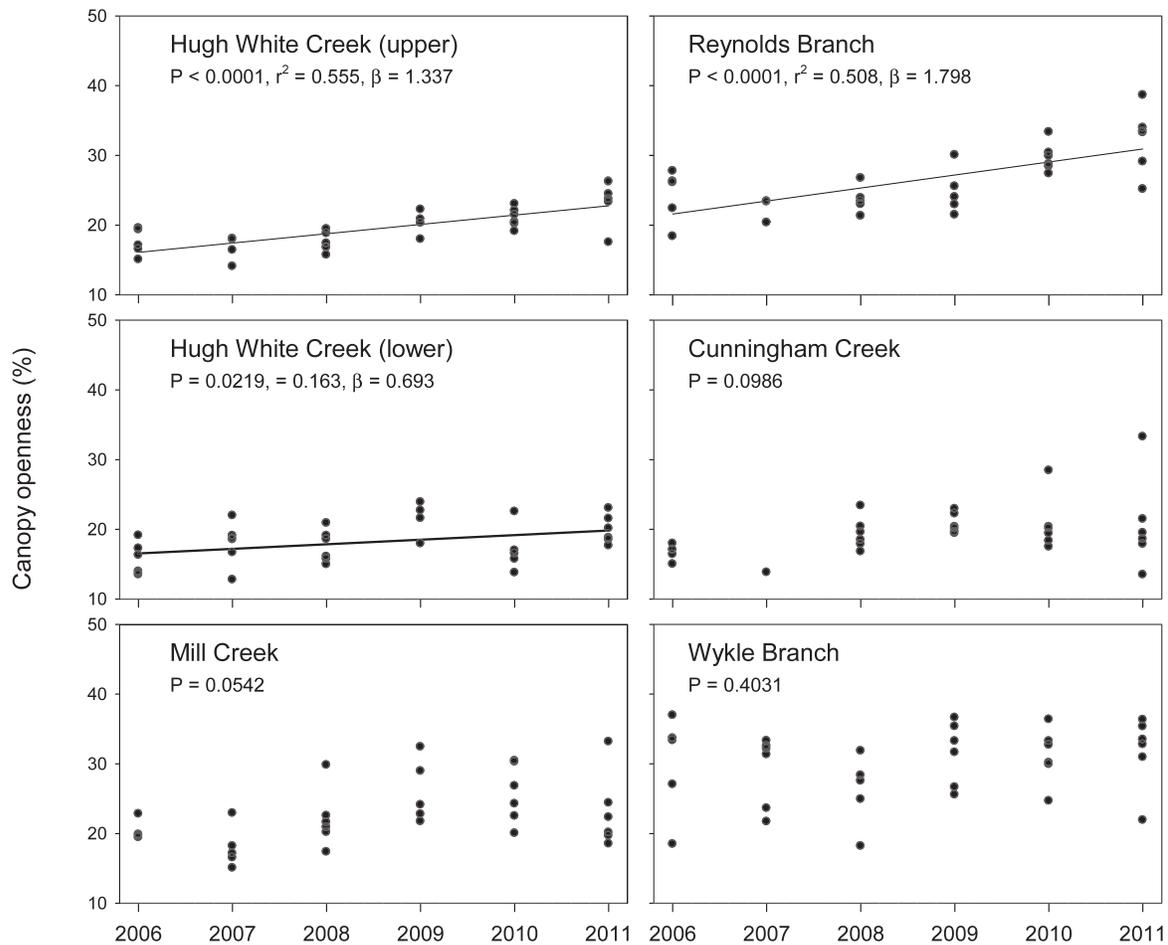


FIG. 4.—Linear regression of canopy openness over time for small streams affected by hemlock mortality. Each point is from a single photograph (β is slope of relationship)

habitat requirements are similar (*i.e.*, riparian areas). However, at a more local scale, we compared density of these two species among our nine riparian sites and found a negative relationship ($r = -0.68$, $P = 0.045$, Fig. 6). Preliminary results of a more extensive analysis of 55 plots at Coweeta, all located within 50 m of streams, showed a significant negative correlation between hemlock and rhododendron foliage mass ($r = -0.31$, $P = 0.033$, K. J. Elliott, pers. obs.). This suggests the possibility of some competitive interaction between these two non-deciduous species. As noted above, rhododendron is known to inhibit seed sprouting and seedling growth of many tree species, though hemlock is one of the species least affected by rhododendron. It is also known that rhododendron responds with increased growth following canopy removal (Roberts *et al.*, 2009). Ford *et al.* (2012) observed a 2.6 fold increase in rhododendron growth in stands where hemlock was infested with hemlock wooly adelgid. From these observations and the results of our study, we propose that the effect of the loss of hemlock on streams in the Southeast may be ameliorated in the short term by shade provided by increased rhododendron growth. In the longer term, expansion of rhododendron thickets may result in decreases in the quality of litter and amounts of large wood inputs to the stream.

Temperature.—Shading by hemlock appears to have been a major factor in the cool stream temperatures of this area (Fig. 2). The increased range in water temperature following

TABLE 4.—Annual (18 Oct. 2003–16 Oct. 2004) litterfall (g AFDM m⁻² y⁻¹) to each of the streams

	Hugh White Cr. upper	Hugh White Cr. lower	Shope Fork	Mill Br.	Ball Cr.	Reynolds Br.	Wykle Br.	Upper Ball Cr. ¹	Average
Beech	0	4	0	0	0	0	0	0	1
White oaks ²	1	1	0	1	1	4	0	36	6
Hemlock	20	63	88	62	87	70	38	62	61
Hickory	8	0	3	4	8	3	4	5	4
Misc. leaves	80	58	50	67	53	63	126	70	71
Misc. OM	13	18	18	19	41	18	9	12	19
Red maple	17	1	9	11	8	39	13	60	20
Red oaks ³	13	8	9	48	8	3	6	22	15
Rhododendron	73	58	57	47	46	29	71	31	51
Seeds and fruit	19	31	22	77	31	31	47	19	35
Sweet birch	57	50	18	30	28	15	8	54	33
Yellow poplar	59	40	10	25	12	61	106	58	46
Wood	137	53	276	89	248	99	71	39	126
Total leaves	328	284	244	295	252	287	371	398	307
Total non-wood	360	333	284	391	324	337	427	429	361
Total litter	497	386	560	480	572	436	497	468	487

¹ Data from 1992–1993 (J. R. Webster and E. F. Benfield, pers. obs., and Benfield *et al.*, 2000)

² Includes white oak and chestnut oak

³ Includes red oak, scarlet oak and black oak

hemlock mortality (Fig. 1) is consistent with a decrease in winter insulation allowing for greater winter heat loss and greater summer insolation creating higher daily maxima. However, these water temperature trends also need to be considered within the broader context of climate change. Within the last 6 y, average and maximum air temperatures at Coweeta have been fairly steady, while the winter minimum temperature has dropped (Laseter *et al.*, *in press*). But, over the last 30 y, there has been a significant increase in average, maximum and minimum annual air temperatures (Laseter *et al.*, *in press*). Thus our observed changes in stream water temperature over 6 y may be only a reflection of a series of rather cold winters within an overall warming climate. Siderhurst *et al.* (2010) found no increases in water temperature in a small southern Appalachian stream coinciding with hemlock decline and suggested that groundwater influenced water temperature more than light at that site.

Light and canopy openness.—There was a significant increase in light in all streams (Fig. 3) and a general increase in canopy openness (Fig. 4). Siderhurst *et al.* (2010) also found increases in light in a small southern Appalachian stream coinciding with hemlock decline. With the increase in light reaching streams, particularly in the spring when water temperature rises, algal production could be stimulated (Rowell and Sobczak, 2008). A pattern of peak algal primary production in spring has been observed in Walker Branch, Tennessee, where no evergreen trees or shrubs shade the stream (Hill *et al.*, 2001). Grady *et al.* (2007) suggested that gypsy moth defoliation stimulated algal production in western Virginia streams. Increased primary production could promote growth of algae-scraping macroinvertebrates.

Litterfall.—If hemlock litter inputs to streams are replaced by deciduous, broad-leaved species, there would be a significant change in the overall quality of allochthonous inputs to

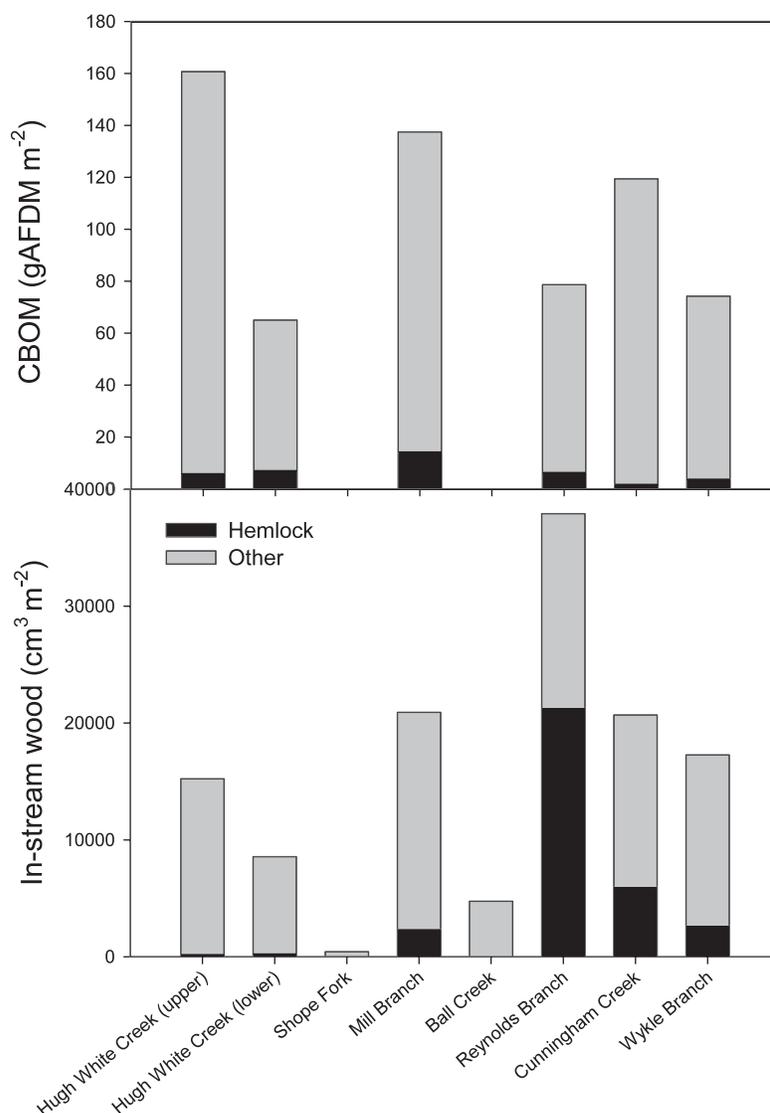


FIG. 5.—Upper panel: coarse benthic organic matter (CBOM) standing stocks at six sites. Black portions of bars represent hemlock needles and sticks, and gray portions represent particulate organic matter from other species. Data are means of quarterly samples taken from Nov. 2004 through Aug. 2005. Lower panel: large (>5 cm diameter) wood in Coweeta streams. The black portion of each bar is hemlock and the gray portion represents all other species of large wood

streams. Because hemlock needles have a thick, waxy cuticle, and high secondary compound content, they break down slowly compared to hardwood leaves (Webster and Benfield, 1986; Malony and Lamberti, 1995; Richardson *et al.*, 2004). The poor quality of hemlock needles is evidenced by the low level of microbial activity supported by needle leachate (McArthur and Richardson, 2002) and the disparity between assemblages of macroinvertebrates found on needles and those on other leaves (Malony and Lamberti, 1995; Richardson *et al.*, 2004). Replacement of hemlock needles with higher-quality leaf material could encourage the growth of shredders. Macroinvertebrate assemblages in hemlock-dominated streams in the Delaware Water Gap had more predators, fewer grazers, higher species richness but lower overall density than hardwood-dominated streams (Snyder *et al.*, 2002). However, if hemlock is replaced by rhododendron and there is a further expansion of rhododendron thickets

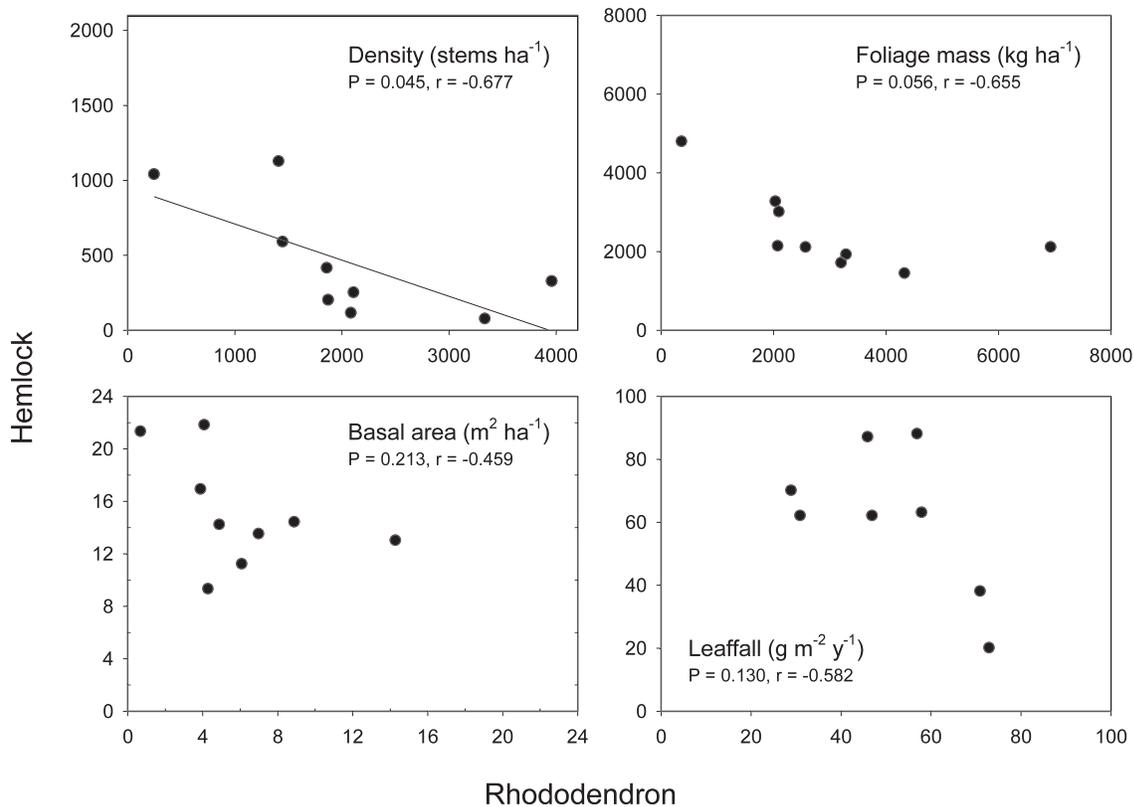


FIG. 6.—Correlation of measures of hemlock and rhododendron importance at the stream sites

along streams, the effect on stream macroinvertebrate assemblages could be quite different. Like hemlock needles, rhododendron leaves are low quality and decompose very slowly in streams (*e.g.*, Webster and Benfield, 1986). Wallace *et al.* (1970) found that rhododendron leaves were the least preferred of 15 different leaf species offered to leaf-eating stonefly nymphs. On the other hand, because they decompose slowly, rhododendron leaves are one of the few sources of organic matter to stream organisms during summer. Many stream macroinvertebrates with annual life cycles are not actively feeding during this time of year (Cummins *et al.*, 1989), but for longer-lived organisms, such as crayfish and some of the stoneflies, rhododendron leaves may fill an important gap in food availability (Huryn and Wallace, 1987).

Large wood.—We found the current contribution of hemlock to large wood in streams to be highly variable, a result that is in part a product of the patchy distribution of large logs of any species. Whatever the volume of wood now in a stream, we expect that the proportion contributed by hemlock and the total volume of wood will increase substantially in the coming decades. Wood in streams slows and diversifies the flow of water, causing the accumulation of sediment and organic matter and modifying stream geomorphology (Bilby and Likens, 1980; Bilby, 1981). These processes in turn provide favorable conditions for the biotic processing of leaves, wood, and dissolved nutrients (Bilby and Likens, 1980; Hedin, 1990; Valett *et al.*, 2002). Hemlock trees were large and numerous, and, because they have a high tannin content, they will decay very slowly in streams (Harmon *et al.*, 1986). Hedman *et al.* (1996) predicted that hemlock wood in southern Appalachian streams will last for about 200 y. A large input of hemlock wood is likely to increase the retentiveness of streams and lead to the formation of step-pool sequences. But, in the longer term, highly resistant

hemlock wood will eventually be absent from streams, with consequences for organic matter and sediment retention and geomorphology.

Insight on potential repercussions of hemlock loss to streams might be gained by examining the consequences of a previous forest pest invasion. American chestnut made up as much as 50% of the canopy in some areas at Coweeta (Elliott and Swank, 2008). In the early 1930s, chestnut blight killed all American chestnuts in Coweeta, which were replaced primarily by red maple and oaks. The replacement of chestnut leaves by more slowly decaying maple and oak leaves has modified the quality and temporal availability of leaves in forest streams, where many benthic insect life cycles are closely adapted to the availability of decaying leaves (Smock and MacGregor, 1988).

American chestnut death has had substantial and long-term impacts on stream wood dynamics. Blight-killed chestnut logs, which were large and resistant to breakdown, fell into streams between the early 1930s and the early 1950s. Investigations on large wood in one Coweeta stream in 1998 showed that nearly a quarter of the mass of wood was still chestnut (Wallace *et al.*, 2001). The species distribution of wood in this stream more closely reflected forest composition recorded in 1934 than in the 1970s and 1990s, indicating that relatively sudden changes in the quality and timing of wood inputs to streams can have long-term effects (Wallace *et al.*, 2001). Chestnut logs probably provided important streambed stabilization in streams where logging reduced the natural inputs of wood (Webster *et al.*, 1992). The effects of hemlock mortality on streams may be similar to those of the chestnut blight. On a watershed scale, hemlock was not as abundant as chestnut was, but hemlock occurred primarily in valleys along streams, and conifer logs such as hemlock are more resistant to decay than logs of broadleaved species such as chestnut (Harmon *et al.*, 1986).

Simberloff (2011) noted that most introduced species do not become invasive and probably the great majority do not have ecosystem impacts. The hemlock woolly adelgid is clearly invasive in eastern North America, and there are indications of clear ecosystem impacts to streams. These include changes to the timing and quality of allochthonous energy sources, possibly elevated autochthonous inputs and structural changes associated with the short-term input of small and large wood and the long-term loss of decay-resistant large wood. However, increased growth of rhododendron in response to hemlock mortality may compensate for the trophic influences of hemlock by replacing stream shading and refractory leaf litter. Because of rhododendron's negative effect on growth of seedlings of other tree species, the greatest ecosystem impact of hemlock woolly adelgid may be more extensive rhododendron thickets within the riparian corridors of southern Appalachian streams.

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