EFFECTS OF EASTERN HEMLOCK MORTALITY ON FOREST MICROCLIMATE AND SPECIES COMPOSITION

ANDREA MARTIN AND SANDY SKOLOCHENKO

Abstract. Extirpation of eastern hemlock (*Tsuga canadensis*) throughout its natural range is occurring due to attack from the exotic hemlock woolly adelgid (*Adelges tsugae* Annand). Death of the eastern hemlock, a foundation species, will affect many ecosystem characteristics. Both aboveground and belowground processes will be altered, likely resulting in microclimatic changes in temperature, moisture, and solar radiation. However, the empty niche created by its death will provide opportunities for other species. This study investigates the changes in these microclimatic and species compositional factors due to hemlock mortality in the southern Appalachians through the use of experimental plots that simulate current and future hemlock conditions, from the onset of infestation to complete hemlock absence. We found that light penetration through the canopy increased as hemlock trees died, although there was high interception from the subcanopy evergreen shrub *Rhododendron maximum*, potentially limiting available resources for new species establishment. Soil moisture increased in hemlock plots, especially in the winter months when hemlock is the only transpiring canopy species. Average soil temperature did not increase over time in experimental hemlock plots, although the temperature was consistently higher in plots without hemlock present. Variation in soil temperature was not affected by hemlock mortality or absence. Hemlock basal area and wood biomass

increment decreased due to the adelgid-induced mortality, and *Betula lenta* and *Liriodendron tulipifera* growth suggests that these species may take its place, although the long-term changes are unclear. With the loss of the eastern hemlock foundation species, it seems that its accompanying biota and climatic factors will be altered and perhaps lost, replaced by a distinctly different forest type.

Key words: Adelges tsugae*; Eastern hemlock; hemlock woolly adelgid; microclimate; riparian zones;* Tsuga canadensis

INTRODUCTION

Preserving forest diversity is of utmost importance ecologically, economically, and aesthetically. Within a forest there are typically several ecosystems present that are shaped by the geography and microclimate of a particular area. Foundation tree species shape their own ecological communities, controlling the biota present and the functions of that ecosystem (Ellison et al. 2005). The southern Appalachians support a diversity of forest community types. High elevation forests along mountaintops and ridges are often dominated by oaks (*Quercus* spp.), northern hardwoods, or spruce (*Picea*) and fir (*Abies*). Exposure at high elevations can create rock outcrop communities or balds that lack canopy species but support grasses and ericaceous shrubs. Lower elevation forests are typically comprised of mixed hardwoods that make up the oak-hickory (formerly oak-chestnut) forest type. In protected coves, riparian corridors, or along mesic ridges, hemlock dominates with a heavy rhododendron understory (Schafale and Weakley 1990). This high diversity of community types offers a variety of habitats that support a wide array of plant and animal life, many endemic to the area. Apart from

its ecological richness, the southern Appalachian landscape has been important economically through agriculture, mining, forestry, tourism, and recreation (Kilpatrick et al. 2004).

Due to globalization and industrialization, humans have developed the capacity to threaten and destroy the high biodiversity in these forests. Through the accidental (and sometimes intentional) introduction of exotic species (*i.e.*, plants, insects, and diseases), many economically and ecologically important native species are facing extirpation or even extinction. Over the last century exotic species-induced losses have caused the decline of dominant canopy species such as chestnut, elm, fir, and beech. Such species loss due to exotic species introduction alters forest structure, composition, function, and productivity, commonly resulting in a loss of biodiversity.

The landscape of the southern Appalachians has been significantly altered by the introduction of the chestnut blight (*Cryphonectria parasitica*) (Anagnostakis and Hillman 1992). In the early 20th century, the chestnut blight effectively eliminated overstory American chestnut (*Castanea dentata*) trees in deciduous forests across the eastern United States. The species that replaced the chestnut vary with location, as there was no co-dominant species that spanned the entirety of the native chestnut range. For example, in southwestern Virginia, *Quercus rubra* is now the dominant species, *Quercus alba* has declined, and other species (*Acer saccharum, Amelanchier arborea, Betula lenta, Prunus serotina* and *Robinia pseudoacacia*) that were previously understory species are now found in the canopy (Stephenson 1986). These compositional changes were temporary, as McCormick and Platt (1980) found that, with time, a chestnut-oak forest transformed to an oak-hickory. In addition to these vegetational changes induced by chestnut mortality, wildlife was also impacted: squirrel populations crashed, woodpeckers increased (due to an increase in dead tree habitat), and seven moth species that fed on chestnut are now extinct (Opler 1978). These structural and compositional changes brought

on chestnut are now extinct (Opler 1978). These structural and compositional changes brought about by extensive chestnut mortality are well understood; however, very little is known concerning the *specific* ecosystem responses to such a drastic and sudden alteration of the landscape since many ecosystem parameters were not measured prior to the death of chestnut.

In addition to the chestnut blight, many other exotic species have altered natural forest ecosystems of the Unites States and significantly decreased the rich biodiversity of the impacted areas. The presence of the beech bark disease (*Nectria coccinea* var. *fraginata*) in hemlock sites increased the abundance of hemlock, decreased the abundance of American beech and yellow birch, and presumably decreased the production of mast, thus lowering the diversity of wildlife species (Runkle 1990, Castello et al. 1995). Likewise, Dutch elm disease (*Ophiostoma ulmi*) resulted in a 60% increase in sugar maple (*Acer saccharum*) basal area and a significant increase in shrub density in Illinois and Wisconsin, respectively (Boggess and Bailey 1964, Dunn 1986). The selective mortality caused by these aforementioned pathogens act indirectly to alter their inhabited ecosystems compositionally, structurally, functionally, and microclimatically. These ecosystem changes carry implications for the future forest biodiversity and, thus, long-term viability of these ecosystems.

Eastern hemlock (*Tsuga canadensis*), a foundation canopy tree, is a species whose loss could bring about many ecosystem responses. Hemlocks often grow in pure stands in the northeastern United States, but in the southern Appalachians they often dominate riparian and cove sites in mixed high elevation hardwood forests. In forests in which hemlocks dominate the canopy they create a shaded environment, deposit acidic litter, and mediate soil moisture. Hemlocks contribute greatly to transpiration rates throughout the year, especially in the winter and spring when deciduous trees are leafless (Ellison et al. 2005). Their presence therefore

creates a fairly stable environment with low variation in soil moisture, slow rates of nitrogen cycling, low light availability, and low seasonal variation of light (Eschtruth et al. 2006). This type of environment stabilizes stream flow and supports a number of salamanders, fish, and aquatic invertebrates, along with terrestrial dwellers such as birds, mammals, and forest carnivores that depend on hemlock stands for habitat and cover (Orwig et al. 2002, Ellison et al. 2005). Hemlock trees typically have a shallow rooting system, thin bark, and are slow-growing, making them vulnerable to disturbance. Wind, fire, drought, exotic pests, or anthropogenic disturbance can severely impact hemlock populations. For this reason, most hemlock forests today are found in protected coves and ravines, or on historically protected sites (Orwig and Foster 1998).

Since European settlement, eastern hemlock has played an important role economically as well as ecologically. Hemlock was logged heavily in the 1800s throughout the mid-Atlantic. Although hemlock was considered a low-value softwood, it was a preferred source of tannins and was used extensively in leather processing (Brown 2000). Consequentially, loggers often felled hemlock trees, stripped them of their bark, and left the log to rot. Parts of the bark have also been used historically in ointments to treat rheumatism and colds, and such ointments were even applied on the skin to stop bleeding wounds (Brown 2000). In the past century, logging of hemlock has decreased significantly and much of the previously cleared farmland has been abandoned, allowing for hemlock recovery and reforestation throughout its native range (Weckel et al. 2006).

The entire range of the eastern (*Tsuga canadensis*) and Carolina (*Tsuga caroliniana*) hemlock is currently under threat of extirpation by the introduced hemlock woolly adelgid (HWA). This insect, native to Japan and first observed in the United States in the 1950s, has quickly dispersed throughout the natural range of hemlock by wind, animal, and human vectors

quickly dispersed throughout the natural range of hemlock by wind, animal, and human vectors and can cause tree mortality within 4-10 years of infestation (McClure 1990, 1991; Souto et al. 1996). The HWA feeds on the ray parenchyma cells of young hemlock twigs and in doing so injects a toxic saliva that causes needle loss and mortality of the buds and branches (Young et al. 1995). The fate of hemlocks from these pests seems dim, as the trees show no sign of resistance. Additionally, HWA is parthenogenetic, reproduces rapidly with two generations per year, can kill hemlocks of all sizes and age classes, and seems to have no native predators within its range (McClure 1989, 1990, 1991; Kizlinski et al. 2002).

The current decline of hemlock provides a unique opportunity to examine the effect of selective tree loss on forest structure, composition, function, and microclimate as it occurs, as opposed to past pathogen and pest-induced tree mortality that could only be studied after mortality had already occurred (Orwig 2002). The loss of hemlock, a foundation species that regulates and influences understory environment and composition, will most likely alter its accompanying microenvironment to an extent not seen in other less influential tree species. Also, unlike the pathogens of other past tree species, the ability of the HWA to eliminate all ages of hemlock gives it the potential to completely eliminate hemlock from an area in a short period of time, as opposed to other exotic pathogens and pests that have only targeted a certain age group (Castello et al. 1995).

Ecosystem responses to hemlock decline have been examined extensively in the northeastern United States. Numerous studies have monitored hemlock stands infested with HWA, have simulated HWA impact by girdling hemlocks, and have simulated hemlock loss with canopy gaps in hemlock-dominated forests (Rankin and Tramer 2002, Yorks et al. 2003). These studies have found that the loss of hemlock causes an increase in understory species

richness, light availability, and abundance of birch and maple (Battles et al. 1995, Orwig and Foster 1998, Eschtruth et al. 2006). Although these studies have examined ecosystem responses to hemlock mortality, these responses have not been observed and quantified in the southern Appalachians, a region with a unique climatic regime, unusually high biodiversity, and the presence of a *Rhododendron maximum* subcanopy and mixed-deciduous canopy.

In this study, we examined the effects of natural, artificially accelerated, and complete hemlock mortality due to the HWA on soil temperature, soil moisture, light availability, and species composition. We hypothesized that dying hemlock trees will result in forests that begin to show microclimate and compositional similarities to the southern hardwood deciduous forests, by 1) increased light availability, soil moisture, average soil temperature, and diurnal soil temperature variation; 2) a shift in species composition to hardwood species, such as black birch (*Betula lenta*) and yellow poplar (*Liriodendron tulipifera*); and 3) an increased growth of the dominate subcanopy species, *Rhododendron maximum*.

MATERIALS AND METHODS

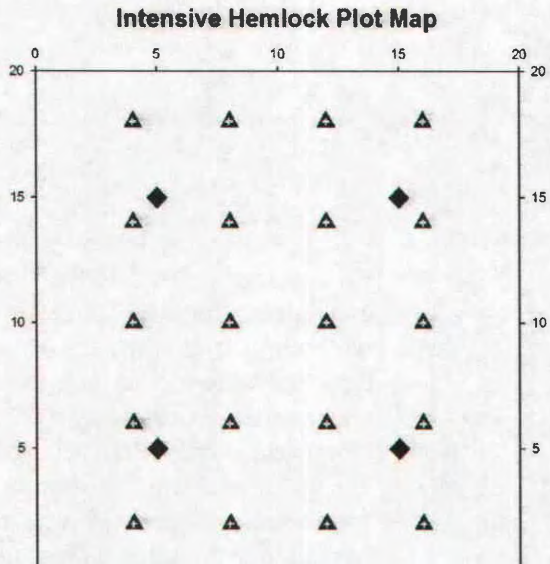
This study was conducted at Coweeta Hydrologic Laboratory (35°03'N, 83°27'W) located on the east side of the Nantahala mountain range in western North Carolina. The 2100 ha basin spans in elevation from 700 to 1600m. The regional climate has cool summers, mild winters, and abundant precipitation. Mean annual precipitation varies from 1780 mm at lower elevation and up to 2500 mm at high elevations (Swank and Crossley 1988). Average monthly temperatures range from 3°C in January to 19°C in July. Soils are primarily inceptisols and ultisols (Swank and Crossley 1988). The forest is predominantly mixed oak with oak-pine

forests along drier slopes and cove hardwoods in riparian corridors. Dominant canopy species include *Quercus alba, Q. rubra, Acer rubrum, Oxydendrum arboreum, Liriodendron tulipifera, Nyssa sylvatica, Betula lenta, Carya* spp., and *Tsuga canadensis* (Swank and Crossley 1988). There is an abundant evergreen understory up to 8m above the forest floor that is predominantly occupied by *Rhododendron maximum* (Clinton 2003).

Twelve 20m x 20m plots were established in 2004 (Fig. 1). Plots were located in riparian areas with and without hemlock present. Four plots were selected with no hemlocks. These were predominantly comprised of hardwoods, with some evergreen understory present. The remaining eight sites contain hemlock trees infested with HWA. In four of these plots the hemlock trees were girdled in August 2004 to accelerate their death and predict and analyze future ecosystem changes.

To measure the effects of hemlock loss on light levels and soil moisture, six of the twelve plots were selected for measurement, two from each treatment. Twenty light level measurements were taken at equal intervals throughout the plot and three soil moisture probes were placed randomly within each plot (Fig. 1). Networks of multiplexers and CR10X programmable dataloggers (Campbell Scientific, Logan, Utah) were connected to the sensors in each of the six plots, allowing for multiple measurements of light levels and soil moisture to be recorded simultaneously. Within each plot, dataloggers were located at the edge and data were downloaded monthly from each site.

Photosynthetically active radiation (PAR; μmols $m^{-2}s^{-1}$) was measured in each plot using twenty Gallium Arsenide Photodiodes (Hamamatsu Corporation, Tokyo, Japan). PAR refers to the visible spectral range of light (400-700 nm) available for photosynthesis by terrestrial plants. PAR light energy was measured in millivolts every 60 seconds and logged as hourly means between the hours of 0500 and 2300 from June 2005 to August 2007. Each sensor was individually calibrated to a known quantum sensor using simple linear regression. Regression coefficients were used to convert recorded millivolt signals to μmols m^{-2} s^{-1}. Twenty sensors were installed on each plot on a 2m x 2m grid alternating in height between 1m and 5m above the forest floor in order to separate the effects of the rhododendron subcanopy on changes in light levels due to loss of hemlock.



Soil moisture was measured in each plot using time domain reflectometry (TDR) with CS616 probes (Campbell Scientific, Logan, Utah). Three reflectometers were installed randomly on each plot. Each reflectometer is comprised of a pair of 30cm stainless steel rods inserted vertically into the soil to measure volumetric soil water content (%) integrated across the 30cm depth. TDR

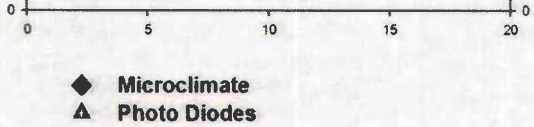


FIG. 1. Layout of experiment plot (20m x 20m). Microclimate stations measured soil temperature. Alternating high (5m) and low (1m) photo diodes measured light intensity. Three soil moisture probes were randomly placed in each plot as well (not pictured).

integrated across the 50cm depth. TDR probes were calibrated for the soils found in the plots. Probes were scanned hourly and data were stored in an automated data logger.

Soil temperature was monitored in each plot at 5cm mineral soil depth using I-button dataloggers (Maxim Integrated Products, Sunnyvale, CA). Four temperature sensors were installed on a 5m x 5m grid in each plot. Measurements were collected hourly over the study period.

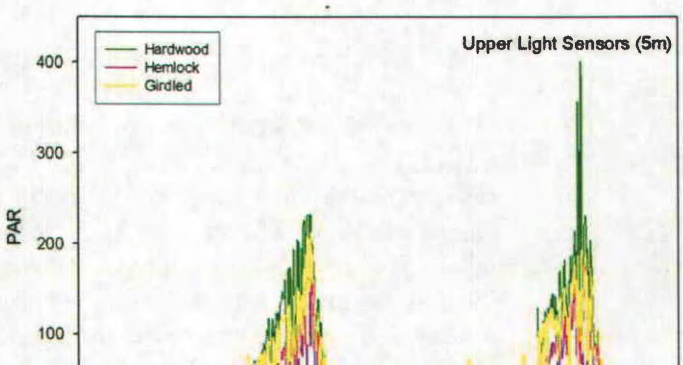
The diameter at breast height (1.37 m, DBH) of woody vegetation in each plot was measured annually each winter using dendrometer bands and a DBH tape from 2004 to 2007. Dendrometer bands were placed on all trees greater than 15 cm DBH in October 2004 to allow the bands to settle into the bark prior to the initial measurement in December 2004. These DBH values were used with species-specific allometric equations (Martin et al. 1998) to calculate woody biomass for each tree. The following trees were not well represented in the plots and were thus placed in the "other" category: *Acer pensylvanicum, A. rubrum, A. saccarum, Amelanchier arborea, Carpinus caroliniana, Cornus florida, Fagus grandifolia, Fraxinus* spp., *Hamamelis virginiana, Pinus rigida, P. strobus, Quercus coccinea, Q. prinus, Robinia pseudoacacia,* and *Sassafras albidum.*

Data Analysis

For this study we analyzed the collected data using SAS version 9.1 (SAS Institute Inc., Cary, NC). This program was used to process all data and perform statistical analyses including analysis of variance. We used least significant difference (LSD) mean separation tests to delineate treatment effects among multiple means. We evaluated statistical differences at the $\alpha = 0.05$ level using PROC GLM (SAS Institute Inc., Cary, NC). We used SigmaPlot® version 9.0 (Systat Software, Inc., San Jose, CA) to create figures.

RESULTS

Light Levels (PAR)



Light level trends from the upper and lower sensors varied among plots. In the winter and spring months, light levels were higher in the hardwood treatment due to the lack of leaf cover in deciduous trees. Comparing daily PAR values at the upper and lower sensors, the lower sensors received less light overall due to interception from

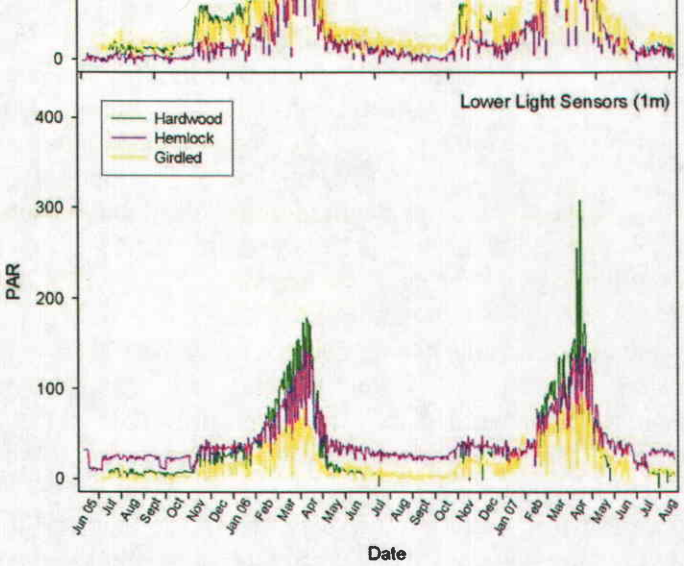
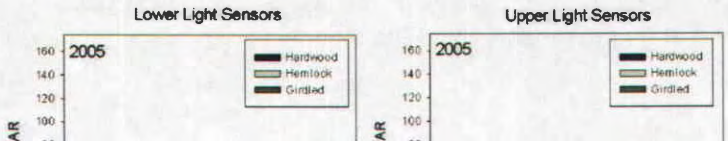


FIG. 2. Daily mean photosynthetically active radiation (PAR; μmol $m^{-2} s^{-1}$) averaged by treatment. Treatments include plots with hardwood only, natural hemlock forest, and girdled hemlock ($N = 2$ plots per treatment).

low leaf cover and understory evergreen shrubs, principally *Rhododendron maximum* (Fig. 2). At the upper level, the girdled treatment exhibited higher PAR values than the hemlock treatments throughout the study. This would be expected as a result of the girdling. The girdling in August 2004 would presumably speed mortality of these trees, leading to greater and earlier needle loss and allowing more light penetration. However, in the lower sensors, the opposite occurred and the girdled treatment exhibited lower PAR than the hemlock treatment, again due to the distribution of *Rhododendron maximum*.

PAR values were averaged seasonally and compared among treatments (Fig. 3). There was no significant difference in PAR among treatments in winter or spring. At the 5m level, no difference was observed in the fall either. In summer 2005, all three treatments had significantly different (P = 0.0002) seasonal PAR. In the summer of 2006, light levels in the hemlock and girdled treatments differed from one another (P = 0.06), but neither differed significantly from the hardwood treatment. During the summer of 2007, PAR in the girdled treatment was significantly higher (P = 0.01) than both the hardwood and hemlock treatments. Comparing the summer data across years, the girdled treatment exhibited the highest PAR values for all three summers. As the summer hardwood PAR value remained fairly constant for the three years, the girdled treatment value increased slightly and the hemlock treatment PAR value increased significantly between the summers of 2005 and 2006.

At the 1m level, summer 2005 data showed a significantly higher PAR (P = 0.0009) in the hemlock plots than either the girdled or hardwood plots. In 2006, the hemlock treatment was significantly higher (P = 0.0004) in the summer and in the fall the girdled and hemlock treatments were significantly different (P = 0.06). PAR in the hemlock treatment was also significantly higher (P = 0.008) than the girdled or hardwood treatments in the summer of 2007. The summer data exhibited a similar trend to the upper level. The hardwood treatment again maintained stable light levels across the three years while the girdled treatment PAR increased slightly with time and the hemlock PAR increased between 2005 and 2006.



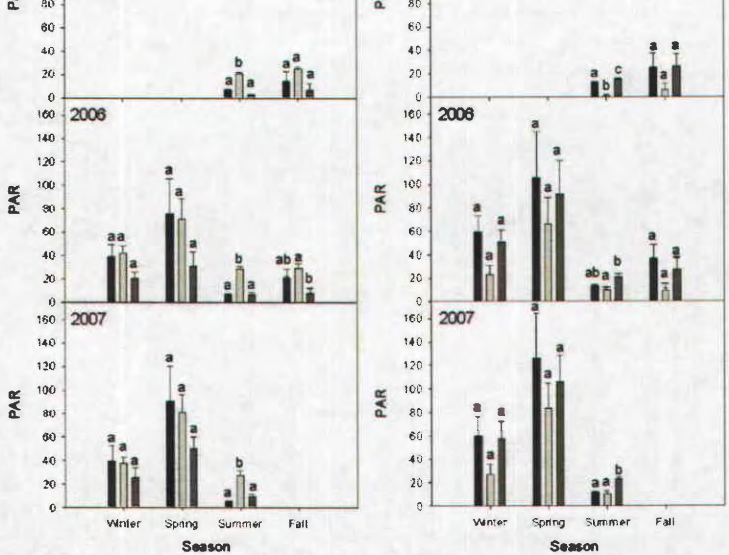


FIG. 3. Seasonal PAR variation among treatment plots. Treatments include plots with hardwood only, natural hemlock forest, and girdled hemlock ($N = 2$ plots per treatment). Error bars represent one standard error. Treatment values with the same letter were not significantly different using the LSD mean separation test at the $\alpha < 0.05$ level.

Soil Moisture

Soil moisture in all plots was heavily dependent on precipitation. Daily soil moisture values averaged by plot type were graphed with daily precipitation data (Fig. 4). Soil moisture correlated very closely with precipitation events and showed effects of seasonal variability. During the majority of the year, soil moisture in both hemlock treatments was higher than that of the hardwood treatment. In the late spring of both 2006 and 2007, all treatments experienced a decline in soil moisture as hardwood species began producing new leaves. The water content in the hardwood treatment decreased at a faster rate than either hemlock treatment, experiencing the driest soils as hardwood species approached their maximum transpiration levels in early summer. The hemlock treatment exhibited the slowest rate of soil moisture dry-down following precipitation events and had the highest soil moisture content their by early summer compared with the other treatments.

Another drying event occurred in the fall that was prominent in 2005 and 2007, but not as obvious in 2006 due to missing hardwood data. This can be partially explained by the gradual loss of leaf area as the fall season progress and the consequent increase in insolation at the forest floor, resulting in higher soil evaporation rates. Again, this effect was most dramatic in the hardwood treatment and least dramatic in the hemlock treatments.

For all three treatments, highest seasonal soil moisture occurred during the winter. During this period the hardwood treatment was driest, the hemlock treatment was slightly moister, and the girdled treatment contained the highest moisture content.

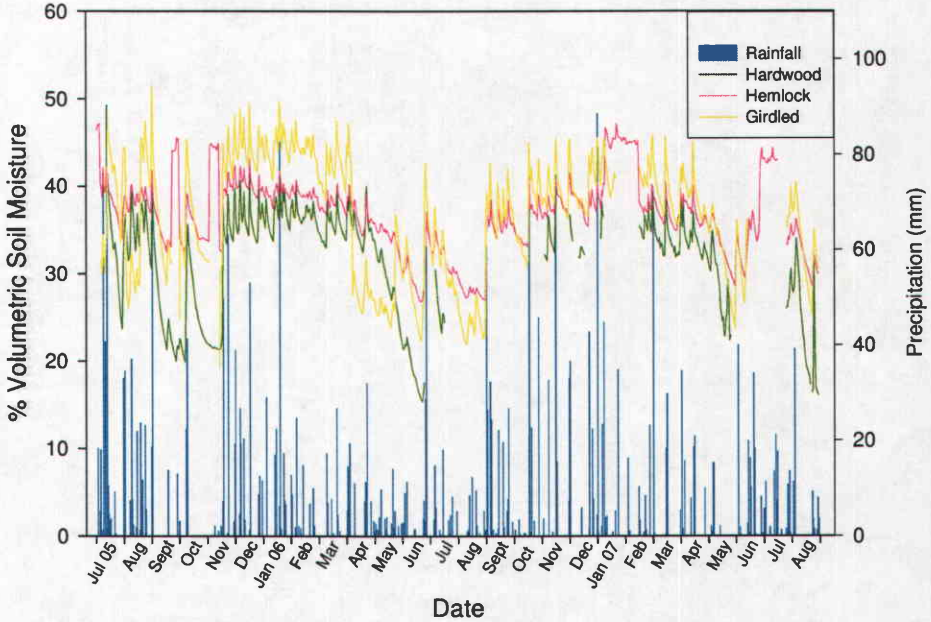
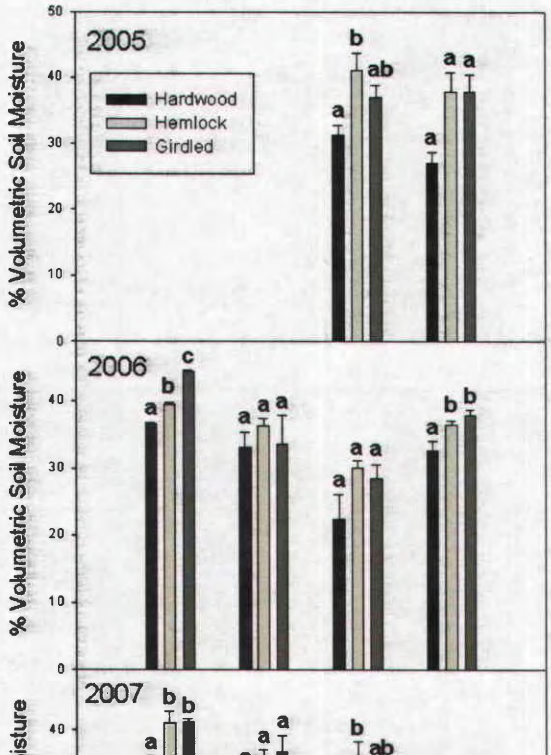


FIG. 4. Daily soil moisture (% volumetric water content) averaged by treatment with daily precipitation (mm).

Soil moisture was also averaged seasonally (Fig. 5). In the spring of 2006 and 2007, none of the treatments exhibited significantly different seasonal means. This is due to high



productivity from hardwoods in all treatments. In the summers of 2005 and 2007, differences between hemlock and hardwood treatments were marginally significant (P = 0.09 and P = 0.06, respectively) with the highest moisture content occurring in the hemlock treatment. In fall 2005, none of the plots were significantly different, but in fall 2006, the hardwood treatment had a significantly lower soil moisture than either hemlock or girdled treatments (P = 0.03). As mentioned, this is due to reduced transpiration during the fall and higher soil water evaporation rates. Winter data supported the trend seen in Fig. 3. In winter 2006, all three treatments had significantly different soil moisture values ($P < 0.0001$). The girdled treatment had the highest soil water content, followed by the hemlock and hardwood treatments. However, in winter 2007, the hardwood soil moisture was still significantly lower (P = 0.01)

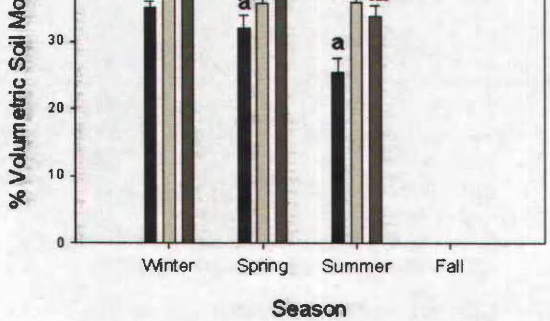
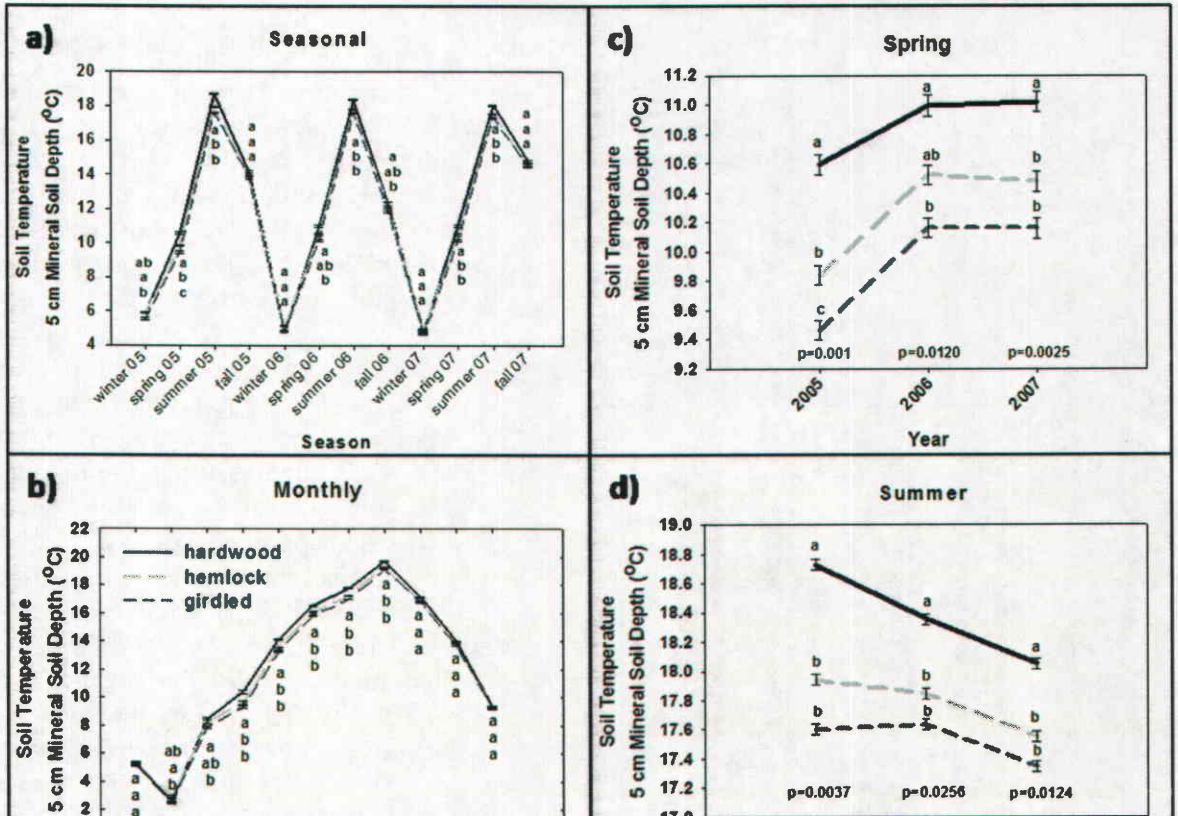


FIG. 5. Seasonal soil moisture by treatment. Treatments include plots with hardwood only, natural hemlock forest, and girdled hemlock (N = 2 plots per treatment). Error bars represent one standard error. Treatment values with the same letter were not significantly different using the LSD mean separation test at the $\alpha = 0.05$ level.

was still significantly lower ($P = 0.01$), but the hemlock and girdled treatments were not significantly different from one another.

Soil Temperature

Because hemlock presence is associated with cooler temperatures, the effect of hemlock mortality on soil temperature was examined. For all years, there was higher variation in average daily soil temperature among treatment groups during the spring (March-May) and summer (June-August) months than during the winter (December-February) or fall months (September-November) (Fig. 6). In spring and summer, the hardwood treatment had significantly higher average daily soil temperature than the hemlock and girdled treatments. The average daily soil temperature was consistently lower in the girdled than the natural hemlock treatment.


a)
Seasonal
Soil Temperature
5 cm Mineral Soil Depth (°C)
winter 05
spring 05
summer 05
fall 05
winter 06
spring 06
summer 06
fall 06
winter 07
spring 07
summer 07
fall 07
Season
c)
Spring
p=0.001
p=0.0120
p=0.0025
2005
2006
2007
Year
b)
Monthly
hardwood
hemlock
girdled
d)
Summer
p=0.0037
p=0.0256
p=0.0124

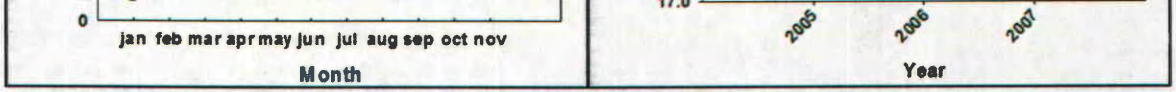


FIG. 6. (a) Seasonal variation in average daily soil temperature (measured at 5-cm mineral soil depth) among treatment groups. Treatments include plots with hardwood only, natural hemlock forest, and girdled hemlock. Individual points represent means of treatments ($N = 4$ for each treatment). Error bars represent one standard error. (b) Monthly variation in average daily soil temperature among treatment groups for 2007. (c) Spring and (d) summer variation in average daily soil temperature among treatment groups across years. Treatment values with the same letter for a time period were not significantly different using the LSD mean separation test at the $\alpha < 0.05$ level.

Because hemlocks play a role in moderating diurnal temperature variation, the effect of hemlock mortality on the maximum daily soil temperature was also examined. Fig. 7 shows the seasonal variation in the maximum daily soil temperature among treatment groups. Like the average soil temperature, the maximum daily soil temperature was markedly higher in the hardwood treatment than in the natural and girdled hemlock treatments.

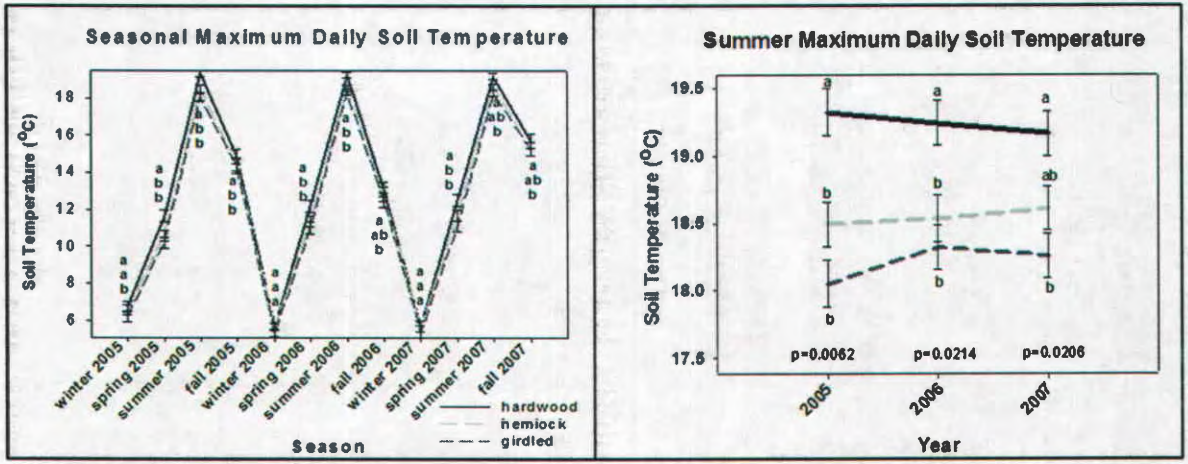


FIG. 7. Seasonal variation in maximum daily soil temperature (measured at 5-cm mineral soil depth). Treatments include plots with hardwood only, natural hemlock forest, and girdled hemlock trees. Individual points represent means within treatment types ($N = 4$ for each treatment). Error bars represent one standard error. Treatment values with the same letter were not significantly different for that time period using the LSD mean separation test at the $\alpha < 0.05$ level.

When comparing girdled and natural hemlock treatments, no significant difference was observed for any season or year, except for the first soil temperature measurement in spring 2005.

Species Composition

In 2004, the hardwood treatment plots were primarily comprised of *Quercus alba* (basal area 28.42 m^2 ha^{-1}), *Liriodendron tulipifera* (ba 7.58 m^2 ha^{-1}), and *Oxydendrum arboreum* (ba 5.20 m^2 ha^{-1}) (Fig. 8). The control hemlock treatment plots were primarily comprised of *Tsuga canadensis* (ba 32.74 m^2 ha^{-1}), *Rhododendron maximum* (ba 4.56 m^2 ha^{-1}), and *Betula lenta* (ba 3.72 m^2 ha^{-1}). The girdled hemlock treatment plots were also primarily comprised of *Tsuga canadensis* (ba 22.25 m^2ha^{-1}), *Rhododendron maximum* (ba 5.22 m^2 ha^{-1}), and *Betula lenta* (ba 3.29 m^2 ha^{-1}). The total mean live basal area was similar between control and hemlock treatments, but higher than that of the girdled plots. The girdled treatment groups exhibited a significantly lower total mean plot basal area than the natural hemlock or hardwood treatments during the last two years (2006 and 2007) (P = 0.0148 and P = 0.0126, respectively). This difference in the last two years may be attributed to the effects of girdling, also shown in Figure 8, where hemlock mean plot basal area significantly decreased from 22.25 m^2 ha^{-1} in 2004 to 0.07 m^2ha^{-1} in 2007 (P = 0.003). The hemlock basal area in the natural hemlock and hardwood treatments did not show a significant change with time (P = 1.00 and P = 0.9991, respectively).

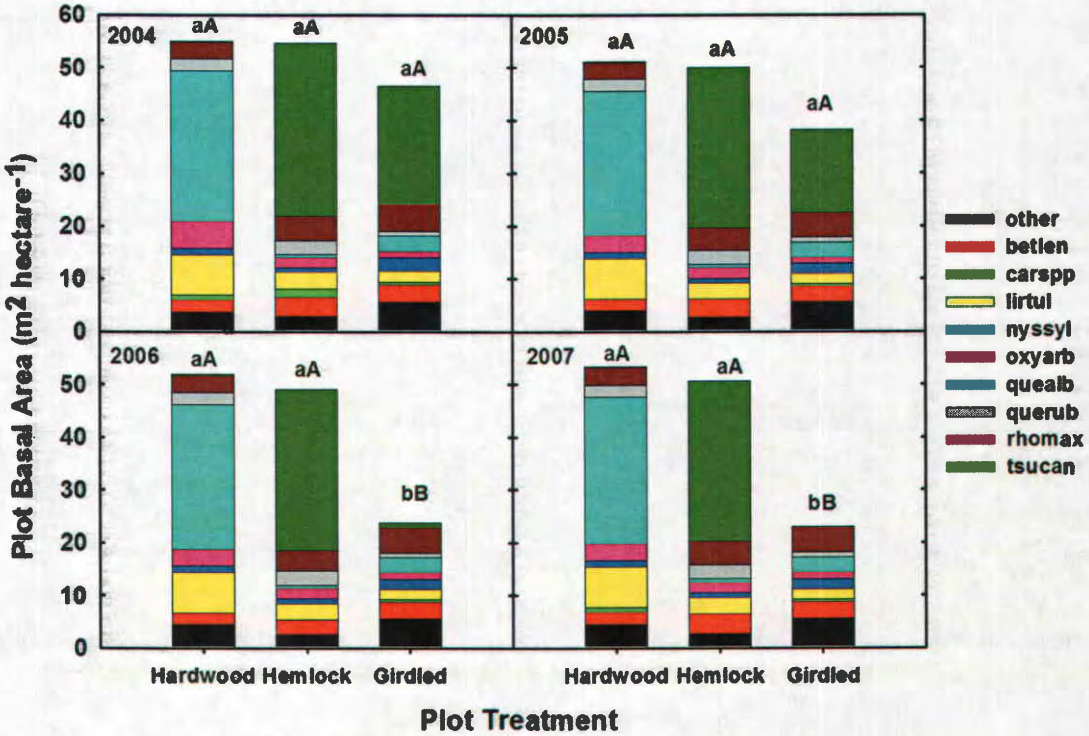


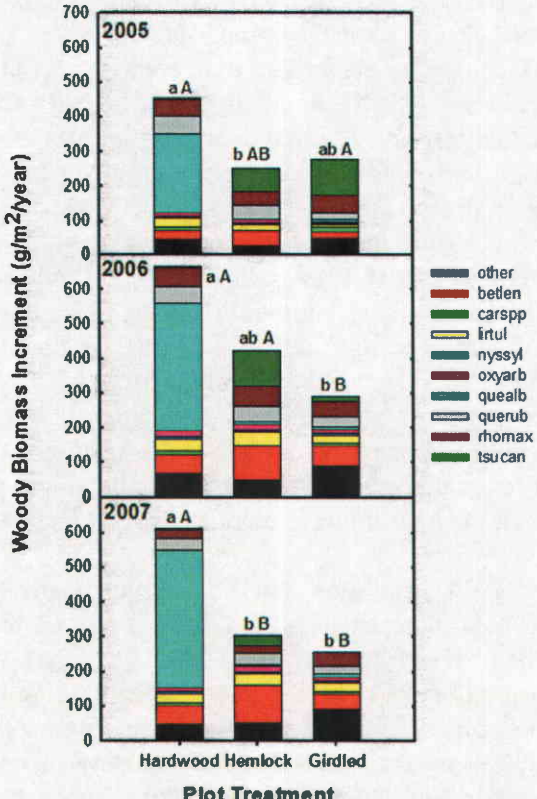
FIG. 8. Mean live basal area by species by year. Treatments include plots with hardwood only, natural

FIG. 8. Mean live basal area by species by year. Treatments include plots with hardwood only, natural hemlock forest, and girdled hemlock (N = 4 for each treatment). The figure legend indicates each woody species by the first three letters of the genus and species, except for "other" which includes species listed in the methods section. Total treatment values with the same lowercase letter (within a year) were not significantly different using the LSD mean separation test at the $\alpha < 0.05$ level. Hemlock basal areas with the same uppercase letter (within a treatment) were not significantly different across years using the LSD mean separation test at the $\alpha < 0.05$ level.

TABLE 1. Mean aboveground woody biomass by treatment by year. Treatments include plots with hardwood only, natural hemlock forest, and girdled hemlock (N = 4 plots per treatment).

		Mean Plot Biomass (grams/m^2)			
Year	Treatment	Live	Dead	Dead Fallen	Total
	Hemlock	28167	2620	0	30787
2004	Girdled	25680	1082	0	26762
	Hardwood	39954	1712	0	41665
	Hemlock	28381	2658	0	31039
2005	Girdled	22705	4321	31	27057
	Hardwood	40389	1730	0	42120
	Hemlock	28721	2717	27	31465
2006	Girdled	15273	11908	152	27334
	Hardwood	41027	1752	22	42801
	Hemlock	28968	2772	30	31770
2007	Girdled	15078	12361	152	27591
	Hardwood	41602	1790	22	43414

The treatment effects on the aboveground woody biomass are shown in Table 1. The total and live biomass is consistently higher in the hardwood treatment than in the girdled or natural hemlock treatments. By 2007, the girdled plots had much higher dead and dead fallen biomass than the natural hemlock or hardwood plots.



The treatment effects on the annual aboveground wood increment for 2005, 2006, and 2007 are shown in Figure 9. The wood increment was higher in the hardwood treatment than in the hemlock treatments for all three years, although this trend was only statistically significant in 2007. Wood increments of all non-hemlock species were generally higher in 2006, across all treatments. The girdled treatment had a higher wood increment than the hemlock treatments in 2005, but showed a progressive decrease in 2006 and 2007.

DISCUSSION

Light Levels

When a dominant tree

FIG. 9. Annual aboveground woody biomass increment over three years. Treatments include plots with hardwood only, natural hemlock forest, and girdled hemlock (N = 4 for each treatment). The figure legend indicates each woody species by the first three letters of the genus and species, except for "other" which includes species listed in the methods section. Total treatment values with the same lowercase letter (within a year) were not significantly different using the LSD mean separation test at the $\alpha < 0.05$ level. Hemlock values with the same uppercase letter (within a treatment) were not significantly different across years using the LSD mean separation test at the $\alpha < 0.05$ level.

species begins to decline, more light is able to penetrate the canopy as leaves fall, gradually changing the microclimate of the forest floor. In the southern Appalachians the effects of HWA on needle loss and light penetration are not always predictable since hemlock occurs in mixed forests in the presence of other hardwoods and a dense rhododendron understory. The results from light intensity at the lower sensor illustrate a trend opposite from what was expected (Fig. 2). Considering that PAR in the girdled treatment was higher than hemlock at the upper canopy level, the switch in this trend at the lower lever is probably due to light interception from rhododendron between 1m and 5m. In a study of light responses to experimental canopy gaps, Beckage et al. (2000) found that light levels reaching the understory increased twofold when rhododendron was absent, but did not change when rhododendron was present. Therefore, the light levels recorded at the 1m level are sometimes more dependent upon the presence of rhododendron than the decline in tree health and needle loss (Beckage et al. 2000).

Light levels among treatments may vary due to aspect and sun angle as well. The sun is never directly overhead in the southern Appalachians and throughout the year the angle of the

sun is changing. This affects the area that receives the most light when there is penetration through the canopy and Canham et al. (1990) found that in some cases the light was never able to reach understory levels due to the high ratio of canopy height to gap diameter. Aspect always plays a role in light dynamics and since hemlocks are usually found in coves or mesic north-facing slopes, light levels are affected by hillshade dynamics. Although an attempt was made to minimize these effects by placing hemlock and girdled plots adjacent to one another, there will always be slight variation, which could also explain the unexpected result in 1m PAR levels.

Monitoring light levels at the understory level gives insight to the conditions available for seed regeneration. Many case studies have proven that availability of light induced by experimental canopy gaps leads to a high density of seedling recruitment (Barden 1979, Beckage et al. 2000, Clinton 2003) but in the case of HWA effects, light levels will increase much less, especially when rhododendron is present, leading to different responses. In New England, declining hemlock stands are typically replaced by hardwoods such as *Betula lenta* and *Acer rubrum* (Battles et al. 1995, Orwig and Foster 1998, Eschtruth et al. 2006). As hemlocks of the southern Appalachians continue to die and light resources gradually become available it is likely that rhododendron will benefit most from hemlock decline, limiting recruitment of other canopy species (Ford and Vose unpublished).

Eventually, hemlocks that cannot survive HWA infestation will die completely and create a canopy gap with their fall. In a situation like this, other species may have a chance to take advantage of the immediate resources. In a nearby old growth forest with advanced HWA infestation, PAR measurements show a peak in light levels after a tree fall (Fig. 10). With the available light, canopy species may be able to establish seedlings, but growth and development of those seedlings have been shown to be inhibited by rhododendron for a variety of reasons including surface soil acidification due to its acidic litter (Nilsen et al. 1986). Those that do

including surface soil acidification due to its acidic litter (Nilsen et al. 1986). Those that do survive are typically hardwood species; very rarely is a hemlock gap filled by other hemlocks (Barden 1979, Jenkins et al. 1999, Eschtruth et al. 2006).

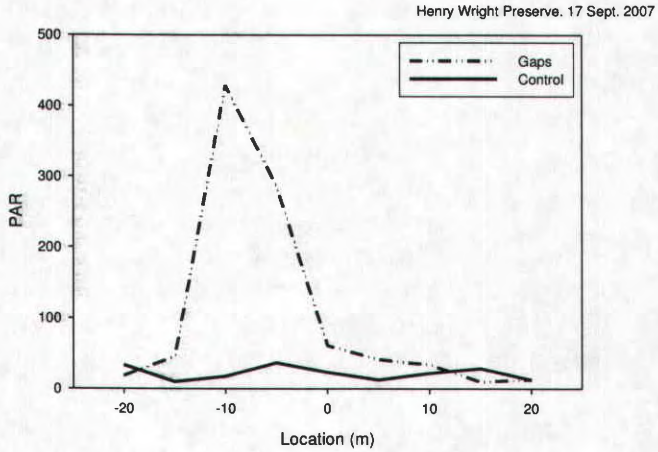


FIG. 10. Average PAR along a 40m transect through the center of treefall gaps (N=2) for each condition.

Soil Moisture

In the southern Appalachians, eastern hemlocks are typically found in riparian and mesic areas where soil moisture is high. This explains why both the hemlock and girdled treatments had slightly higher volumetric water content throughout the study period. As hemlock plays an important role in maintaining moisture levels, its decline will have a great impact on soils and hydrologic processes (Ellison et al. 2005). In winter 2006 (Fig. 5), we see that girdled treatment soil moisture is significantly higher than hemlock treatment soil moisture. Hemlock account for 30% percent of winter and

early spring evapotranspiration (Ford and Vose unpublished). As death of the girdled trees progresses, their transpiration rates decrease due to less and less annual leaf area development to maintain normal rates of transpiration (Ford pers. comm.). This has the greatest impact on total evapotranspiration in the winter months when we see significantly higher soil moisture in the girdled treatment. From winter 2006 to winter 2007, soil moisture values from the hemlock and girdled plots became much closer, indicating that the effects of natural HWA infestation were producing soil moisture conditions very similar to those experienced from accelerated hemlock death through girdling.

Furthermore, as hemlocks lose biomass through needle-fall and woody debris, less precipitation will be intercepted, leading to even higher soil water content (Ford and Vose unpublished). As the death of both HWA-infested hemlocks and girdled hemlocks progress, soil moisture is expected to continue to increase, specifically in winter months. Apart from an increase in soil moisture, the excess leaf and branch litter may result in higher infiltration of the forest floor and a rise of the water table (Ford pers. comm.).

Since hemlock populations are concentrated in riparian sites and influence hydrologic processes, future loss of the species will have serious implications for these environments. As shown in Fig. 4, the presence of hemlock slows the rate of soil moisture loss in the spring and early summer when hardwoods are producing new leaves, leading to less dramatic drying events. Similarly, with a significant precipitation event, soil moisture in the hemlock treatment does not increase as dramatically as moisture in the girdled treatment. The storage of soil moisture helps to stabilize stream flow through hemlock forests, supporting a wide and unique diversity of aquatic creatures (Ellison et al. 2005). With hemlock decline, we may see more extreme drying and soaking events which will cause more pronounced fluctuations in runoff and stream flow, potentially harming the aquatic life (Ford and Vose unpublished).

potentially harming the aquatic life (Ford and Vose unpublished).

In the future, it is unlikely that these changes would be alleviated naturally since hemlock gaps will probably be filled by rhododendron or hardwood tree species (Battles et al. 1995, Orwig and Foster 1998, Eschtruth et al. 2006). If some type of evergreen restoration were applied, perhaps a species such as *Pinus strobus* could assume some of the ecohydrological processes currently maintained by hemlock by providing winter and spring evapotranspiration.

Soil Temperature

Apart from spring of 2004, the soil temperature at 5-cm depth did not significantly differ between the natural hemlock and girdled hemlock treatments. Because the girdled hemlock treatment presumably simulates the effects of continued HWA infestation, these data suggest that soil temperature will not significantly change within the next few years of infestation in natural stands of hemlock.

Despite the absence of any girdled effect on soil temperature, the hardwood treatment had higher soil temperatures than the girdled and the hemlock treatments during the spring and summer months (April—August) for every year evaluated. These results are expected for any comparison of hardwood and hemlock-dominated forests since hemlocks are known to maintain lower temperatures. It is possible, however, that these soil temperature differences between treatments are not due to the absence of hemlock in the hardwood treatment, but rather the absence of another accompanying species, *Rhododendron maximum*. This supposition seems likely, as Clinton (2003) found mean spring and summer soil temperatures to be lower in plots with rhododendron as well. Because it is unknown whether *Rhododendron maximum* will be

impacted as hemlocks die due to HWA, it is not certain that the hardwood-only plots represent with any accuracy a post-hemlock forest. Therefore, although the results suggest that the complete elimination of hemlock will increase average soil temperature, this conclusion cannot be certain until the girdled and/or natural hemlock plots are completely devoid of living and/or dead standing hemlock trees.

Although girdling accelerates the eventual decline of hemlocks to the adelgid, such a decline was not evident through examination of soil temperature. The results show neither divergence of girdled plots from the natural hemlock stands or convergence of girdled plots with the hardwood-only treatment. Through random sampling, the girdled treatment has an average initial soil temperature that was lower than that of the natural hemlock treatment. This initial difference is most likely due to the topographic positions of the plots in regards to the slope aspect, as well as the random, close proximity of the girdled plots to streams. This initial pattern of temperature difference continues throughout the study, showing no indication of a treatment-induced increase or decrease of temperature.

The trends in the diurnal variation of soil temperature were similar across all treatments, as shown by both the maximum diurnal soil temperature and the standard error of the average temperatures (Figs. 6 and 7). Because daily temperature fluctuations are typically smaller in the understories of hemlock forests, it is expected that the diurnal variation of the hemlock stands would be lower than that of the hardwood-only plots. This inconsistency with expected conditions could be due to the depth of the soil temperature readings, where temperature ranges are typically more buffered from air temperature and solar fluctuations at deeper soil depths.

Species Composition

The effects of girdling can be clearly seen by a significant decrease in mean live basal area for the girdled treatment. The significant decrease in total basal area in the girdled treatment in 2006 and 2007 can be attributed to hemlock mortality, where the mean hemlock basal area significantly decreased from the onset of experimentation in 2004 (20 ± 10 m^2ha^{-1}) to 2007 (0.10 ± 0.05 m^2ha^{-1}; $P = 0.003$) . Such a drastic decrease in hemlock basal area was also reported in New England, in which the hemlock basal area decreased 70% over a 20 year period in a Connecticut forest (Small et al. 2005).

The annual aboveground wood increment was higher in the hardwood treatment than in hemlock treatments for all years, although this difference was not statistically significant until 2007. Although the natural hemlock treatment wood increment did not appear to significantly differ from the hardwood stands until 2007, the effects of girdling can be seen as early as 2006, when the girdled hemlock treatment had a significantly lower wood increment than the hardwood treatment. The decrease in woody biomass increment in the girdled treatment as compared to the hardwood treatment can be attributed to hemlock mortality, as wood increment from hemlock declined in the girdled treatment dramatically from 2005 to 2007. Despite the significantly lower wood increment in the girdled as compared to the hardwood treatment, these effects of girdling were not statistically significant when compared to the natural hemlock treatment, suggesting that HWA may be affecting woody production at a rate comparable to girdling.

The species that seem to be benefiting the most from hemlock mortality in the girdled and natural hemlock plots are black birch (*Betula lenta*) and tulip poplar (*Liriodendron tulipifera*), whose woody biomass increments have increased more in the natural and girdled

hemlock treatments than the hardwood treatment. The accelerated mortality by girdling does not seem to affect this response, however, as a sizeable increase in woody increment for these species was seen in both the natural and girdled hemlock treatments. These results suggest that the compositional response to hemlock mortality in the southern Appalachians may be similar to that of the northeastern United States, where Orwig and Foster (1998) found *Betula lenta* seedlings and saplings to be the predominant species that grew beneath the dying hemlock canopy in New England.

Betula lenta replacement has also been observed in areas of the southern Appalachians that lack rhododendron (Ellison et al. 2005), although all of the plots in this study contain a rhododendron subcanopy. It has been predicted that the subcanopy would inhibit seedling recruitment of any species, although this study shows that a subcanopy will not inhibit the increased growth of already-established canopy species. With a subcanopy, it has also been predicted that rhododendron biomass will increase in response to the increased resource availability that accompanies hemlock mortality (Ford and Vose unpublished). An increase in rhododendron biomass has not been observed in this study. To the contrary, *R. maximum* wood increment has actually decreased to a relatively equal extent in all treatment groups. This result could be attributed to an increase in belowground or leaf biomass for *R. maximum*, or perhaps the response of *R. maximum* will be observed with future, increased hemlock mortality. Further examination of species composition trends with hemlock mortality may provide a more apparent trend in these opportunistic replacement species.

Conclusion

Eastern hemlock (*Tsuga canadensis*) is an economically important foundation species

Eastern hemlock (*Tsuga canadensis*) is an economically important foundation species that plays the unique and critical role of moderating and maintaining a specific microclimate in the ecosystem that it inhabits. Because of HWA, mortality of this important tree species is inevitable across the entirety of its range. Although the effects of hemlock mortality have been speculated and studied extensively in the pure hemlock stands of New England, the ecosystem responses to hemlock mortality in hemlock forests of the southern Appalachians are not as well understood. The presence of a thick rhododendron subcanopy and the mixed deciduous nature of these hemlock forests create a potential for unique ecosystem responses that may differ from those seen in New England. Through examination of forests that simulate current and future HWA damage, we have found that hemlock mortality will result in a variety of microclimatic changes. As expected, the loss of this dominant species will result in an increase in light levels reaching the forest floor, elevated soil moisture levels, and an increase in average soil temperature. However, the diurnal and annual variation in soil temperature did not respond to hemlock mortality as expected, with no change in diurnal variation observed between the hemlock and hardwood treatments.

As hemlock mortality progresses, the species composition of HWA-infected southern forests shows a general trend towards resemblance to the composition of a hardwood-deciduous forest, although this trend cannot be accurately assessed this early in the study. While the hemlocks show signs of mortality through decreased live basal area and aboveground wood biomass production, established hardwood species such as *Betula lenta* and *Liriodendron tulipifera* seem to be responding to the accompanying ecosystem responses with increased growth. With the loss of this foundation species, it seems that its accompanying biota and

climatic factors will be lost and replaced by a distinctly different forest type, the dynamics and consequential ecosystem alterations of which we can only speculate.

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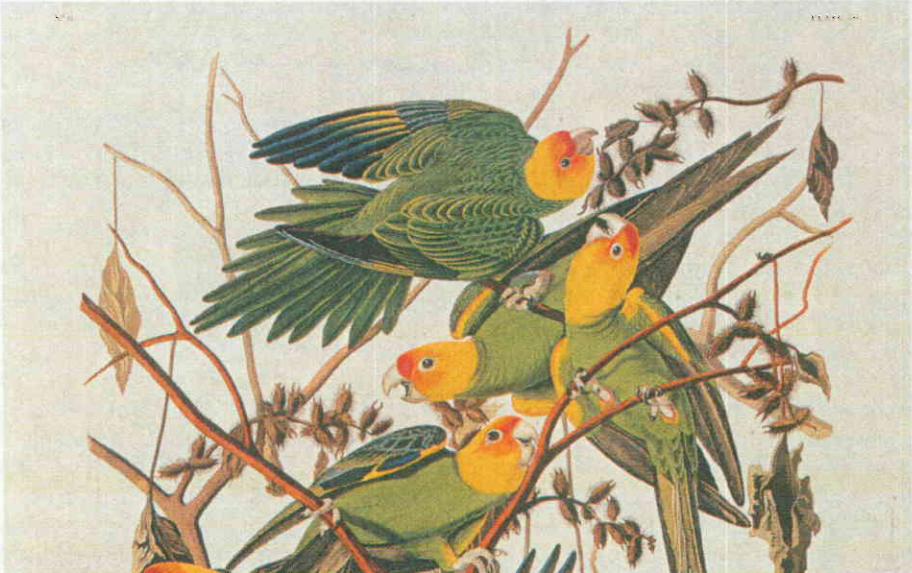


Highlands Biological Station

Highlands, North Carolina

Illustrations

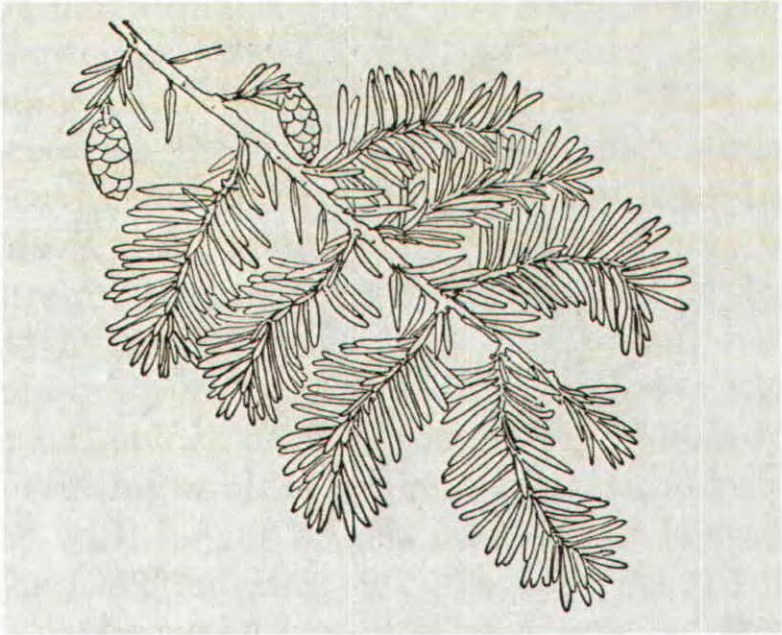
Front cover: John James Audubon "Carolina Parakeet (*Conuropsis carolinensis* L.)" reproduced in Magee, J. (2007) The art and science of William Bartram. Pennsylvania State University Press. University Park, PA, USA. Introduction page: "Hemlock (*Tsuga canadensis* L.): twig with mature seed cones." Page 37 in Coker, W. C, and H. R. Totten (1934) Trees of the Southeastern states. University of North Carolina Press, Chapel Hill, NC, USA. Acknowledgements page: Laura Louse Foster "Boott's Fern (*Dryopteris Boottii* [Tudkerm.]Underw.)—A hybrid between *D. spinulosa* var. *intermedia* and *D. cristata*." Page 79 in Cobb, B (1956) A field guide to the ferns. Houghton Mifflin Company. Boston, MA, USA. Back cover: William Bartram. "Franklinia (*Franklinia altamaha* W. Bartram ex Marshall)" reproduced in Magee, J. (2007) The art and science of William Bartram. Pennsylvania State University Press. University Park, PA, USA.

INTRODUCTION

This volume represents the culmination of the semester-long internship research component of the Institute for the Environment at Highlands Field Site during fall 2007. The Institute for the Environment (IE) sponsors off-campus programs for students of the University of North Carolina, Chapel Hill, and the Highlands Biological Station has served as one of its Field Sites since 2001. Located on the Blue Ridge Escarpment of the southern Appalachian Mountains, the Highlands Biological Station affords IE students abundant opportunities to study aspects of the ecology and evolution of the region's rich biota, its complex history of land use, and increasing threats to southern Appalachian natural systems. Aside from the coursework that students complete, a central component of the IE program at the Highlands Field Site is an internship experience in which students identify areas of personal interest and are paired with mentors in matching fields. This year's mentors come from research institutions, government agencies, non-profit organizations, and innovative "green" business groups. Mentors from each organization work directly with each student to design and help them to implement hands-on projects in such diverse areas as ecology, conservation, land use planning, and policy. The students spend two days per week on their projects collecting and analyzing data, ultimately presenting their results in scientific paper format.

This year's projects not only highlight the environmental problems facing the Highlands Plateau and environs; they also reflect innovative solutions to pressing conservation concerns. Some students explored unique and threatened plant and animal communities, while others contributed directly to private and public efforts to conserve them. The fruits of their labors – from maps and data tables to policy recommendations and interpretive material – are presented here as contributions toward an improved understanding of the complex nature of natural

here as contributions toward an improved understanding of the complex nature of natural biological systems and the ways in which humans impact them.



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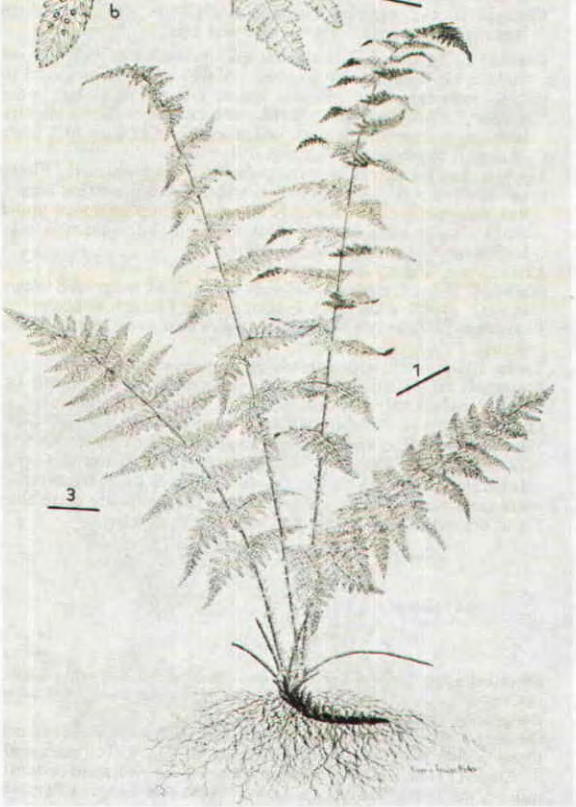
Jim Costa, Site Director
Anya Hinkle, Associate Site Director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