

**Riparian Ecosystem Response to Hemlock Woolly Adelgid (*Adelges tsugae*)
Induced Eastern Hemlock (*Tsuga canadensis*) Mortality in the Great Smoky
Mountains National Park, USA**

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Misty Dawn Huddleston

December 2011

Copyright © 2011 by Misty D. Huddleston
All rights reserved.

ACKNOWLEDGEMENTS

I am indebted to Dr. Wayne Clatterbuck for giving me the opportunity to pursue an advanced degree in natural resources and forest entomology and for providing the guidance needed to complete this study. Special thanks are extended to the rest of my committee, Dr. David A. Etnier, Dr. Paris Lambdin, and Dr. J. Larry Wilson, for their assistance and support throughout the duration of my doctoral program. Great appreciation is expressed to Dr. Becky Nichols and Dr. Kristine Johnson at the Great Smoky Mountains National Park for the guidance and support they offered throughout this effort. Their assistance and advice were vital to the completion of this study.

I also thank my fellow graduate student, Eric Miller, who served as my field assistant during the duration of this project; his work ethic and contributions were invaluable. I would also like to thank my other fellow graduate students and departmental staff that contributed their time and enthusiasm to this project: Rebecca Stratton, Melinda Wilson, and Joyce Coombs. I am very grateful for the funding from the Department of Forestry, Wildlife and Fisheries; which was provided in the form of tuition waivers during the course of this program. Special thanks are extended to the owners and fellow co-workers at my new employer, AquAeTer, Inc., for their support and patience during the final weeks of my dissertation program.

ABSTRACT

An invasive insect, hemlock woolly adelgid (HWA), has initiated widespread hemlock decline and mortality in the Great Smoky Mountains National Park (GSMNP). Riparian hemlock mortality impacts on vegetative and aquatic systems of first-order, headwater streams were evaluated. Reference sites for this study were representative of the best available conditions within the GSMNP, with initial stages of HWA presence. Impacted sites were defined as areas with over 90 percent hemlock mortality. Impacted streams had decreased canopy coverage and increased light availability. Residual red maple, yellow birch, and sweet birch capitalized on the loss of hemlock, with increases in relative basal area and species importance values. Rosebay rhododendron responded with increased density and height at impacted sites, thereby preventing woody regeneration. Since long-term regeneration and post-mortality canopy recruitment are limited, alterations of vegetative composition and structure in the stream riparian zone are expected. A seasonal assessment (Sept. 2009 – March 2010) of aquatic impacts revealed increased diurnal variation in stream temperature and exhibited cooler temperatures during the colder months than reference streams. Impacted streams exhibited greater amounts and larger size classes of large woody debris (LWD). Higher concentrations for several nutrients, including silicon, sodium, potassium, magnesium, chlorine, and copper were detected in impacted streams than detected in reference streams. Impacted streams were characterized by higher pH and increased acid neutralization capacity, while reference streams exhibited nitrate concentrations three times higher than impacted stream concentrations. Reference streams were experiencing the initial stage of HWA-induced defoliations, increasing stream nitrate concentrations, while impacted sites had levels suggesting nitrate concentrations have returned to pre-infestation

levels. A seasonal assessment of macroinvertebrates found species diversity, abundance, and taxa richness were not affected by hemlock mortality. Impacted streams had a lower density of Chironomidae and Ephemeroptera when compared to reference streams, while Pleuroceridae snails were virtually eliminated at impacted stream sites. Reference streams were dominated by the collector/filter functional feeding group (FFG), while impacted streams were dominated by the scraper FFG. Hemlock mortality induced by the presence of HWA has resulted in short-term impacts to vegetative and aquatic dynamics in stream riparian areas of the Great Smoky Mountain National Park.

TABLE OF CONTENTS

CHAPTER	PAGE
I. INTRODUCTION	1
II. LITERATURE REVIEW	6
a. Invasive species	6
b. Eastern hemlock and rosebay rhododendron	8
c. Hemlock woolly adelgid biology and impacts.....	13
d. Study design justification (reference vs. impaired)	16
III. DESCRIPTION OF STUDY AREA	17
IV. METHODS	23
a. Research site selection	23
b. Data collection and analysis methodology	27
1. Vegetation sampling and analyses	27
2. Canopy and light measurements	31
3. Large woody debris	33
4. Water quality and temperature monitoring	34
5. Macroinvertebrate sampling and analyses	38
V. RESULTS AND DISCUSSION	41
a. Vegetation sampling and analyses	41
b. Canopy and light measurements	49
c. Large woody debris	55
d. Water quality and temperature monitoring	58
e. Macroinvertebrate sampling and analyses	76
VI. SUMMARY AND RECOMMENDATIONS	85
LITERATURE CITED	91
APPENDICES	106
VITA	122

LIST OF TABLES

TABLE	PAGE
Table 1. Disturbance history illustrating stand condition for forests within selected stream basins located in the eastern portion of the Great Smoky Mountains National Park, USA. This information was used to ensure that selected research streams were not located in heavily disturbed areas of the park, such as areas that historically endured heavy logging.....	21
Table 2. Stream measurement data by stand condition for stream length, gradient, drainage area, stream flow, and dissolved oxygen for study streams used in the evaluation of aquatic and vegetative ecosystem impacts from HWA-induced hemlock mortality in the Great Smoky Mountains National Park, USA.	26
Table 3. Methodology and definitions for the calculation of species importance values (Curtis and McIntosh 1951).	32
Table 4. Benthic macroinvertebrate community metric categories and explanations of significance used in the evaluation of aquatic ecosystem impacts from HWA-induced hemlock mortality in the Great Smoky Mountains National Park, USA.....	40
Table 5. Relative density, relative frequency, relative dominance, and importance values for tree species located within vegetation plots at reference and impacted stream sites in the Great Smoky Mountains National Park, USA. Reference conditions refer to stands with little to moderate levels of HWA infestation, while impacted sites refer to those sites with near complete HWA-induced hemlock mortality.	42
Table 6. Mean canopy cover percentage and mean fraction of photosynthetically active radiation (FiPAR) percentage for reference and impacted stream sites across two measurement seasons, leaf on and leaf off, for research conducted in the Great Smoky Mountains National Park, USA.	50
Table 7. Chemical parameters found to be significantly different between reference and impacted streams as a result of HWA-induced eastern hemlock mortality in the Great Smoky Mountains National Park, USA. Reference streams represented a mild to moderate level of HWA impact, while impacted streams represented complete hemlock mortality.....	59
Table 8. Measures of community richness from data pooled across habitat types (qualitative and quantitative) for reference and impacted streams used in the assessment of HWA-induced impacts to ecosystem health in the Great Smoky Mountains National Park, USA.	77

Table 9. Measures of community richness, community composition, tolerance, and feeding guild composition from quantitative data collected from reference and impacted streams used in the assessment of HWA-induced impacts to ecosystem health in the Great Smoky Mountains National Park, USA.	80
---	----

Table 10. ANOVA output for quantitative data collected from reference and impacted streams used in the assessment of HWA-induced impacts to aquatic system health in the Great Smoky Mountains National Park, USA.	81
---	----

TABLE OF FIGURES

FIGURE	PAGE
Figure 1. Boundaries of the Great Smoky Mountains National Park, USA, and the location of the state line between Tennessee and North Carolina.	18
Figure 2. Disturbance history of the Great Smoky Mountains National Park, USA. This map layer was used to ensure that study streams were not located within areas that had a history of heavy logging (Pyle 1985).	20
Figure 3. Elevation zones, stream locations, and topography of the Great Smoky Mountains National Park, USA. Research streams were selected from these data utilizing landscape characteristics including slope, elevation, aspect, and dominant vegetation.	22
Figure 4. Reference and impacted streams used in the evaluation of aquatic ecosystem impacts from HWA-induced hemlock mortality in the Great Smoky Mountains National Park, USA. Streams were selected <i>a priori</i> based on a landscape-scale site selection design modified from Young et al. (2002).	25
Figure 5. Plot layout design used in the evaluation of aquatic and terrestrial ecosystem impacts from HWA-induced hemlock mortality in the Great Smoky Mountains National Park, USA. Upper half of illustration depicts the vegetation plot layout and illustrates which strata were measured within each concentric circle. The lower half of the illustration depicts the stream sampling scheme including the temperature logger, PAR measurement, canopy cover measurement, and benthic macroinvertebrate sample locations.	28
Figure 6. Illustration of <i>Rhododendron maximum</i> density classes used in the assessment of ecosystem response to HWA-induced eastern hemlock mortality in the Great Smoky Mountains National Park, USA. Density classes were used because of the tendency of this species to sprout and layer, creating densely tangled thickets that are often difficult to accurately count individual stems.	30
Figure 8. Schematic diagram illustrating the location of measurements taken to calculate stream cross-sectional area, a value used in the calculation of stream flow, which is often useful in determining habitat potential for aquatic biota.	37
Figure 9. Mean riparian basal area at reference and impacted streams in the Great Smoky Mountains National Park, USA. Data for impacted streams is shown including hemlock snags and without snags and is intended to illustrate the impact of hemlock mortality on stand basal area. These data showed a significantly lower range of values for impacted streams when compared to the basal area values observed in reference streams.	44

Figure 10. Mean density class and mean height class for <i>Rhododendron maximum</i> for reference and impacted streams in the Great Smoky Mountains National Park, USA. Impacted sites exhibited density and height classes twice that of reference sites, illustrating the success of <i>R. maximum</i> at capitalizing on the increase in available resources due to HWA-induced hemlock mortality. (Classes are 1=zero, 2=very light, 3=light, 4=medium, and 5=heavy).	47
Figure 11. Boxplot of mean canopy cover percentage for reference and impacted stream sites across two measurement seasons, leaf on and leaf off, for research conducted in the Great Smoky Mountains National Park, USA	52
Figure 12. Boxplot of mean percentage of photosynthetically active radiation (FiPAR) differences between reference and impacted sites for two measurement seasons, leaf on and leaf off, for research conducted in the Great Smoky Mountains National Park, USA. Mean FiPAR percentage is the fraction of photosynthetically active radiation available for productivity in aquatic and vegetative ecosystems.	54
Figure 13. Large woody debris (LWD) density by distribution class, length class, and diameter class for reference (n=5) and impacted streams (n=5) in response to HWA-induced hemlock mortality in the Great Smoky Mountains National Park, USA.	56
Figure 14. Boxplot comparison of mean nitrate concentrations of reference and impacted streams and across seasons. This analysis was conducted to assess changes in water quality in response to HWA-induced eastern hemlock mortality in the Great Smoky Mountains National Park, USA.	64
Figure 15. Mean weekly water temperature for reference and impacted stream conditions in the Great Smoky Mountains National Park, USA. Reference streams represented a mild level of HWA presence, while impacted streams represented complete hemlock mortality.....	72
Figure 16. Mean monthly water temperature for reference and impacted stream conditions in the Great Smoky Mountains National Park, USA. Reference streams represented a mild level of HWA presence, while impacted streams represented complete hemlock mortality.....	73
Figure 17. Mean diurnal water temperature variation for reference streams compared to impacted streams in response to HWA-induced eastern hemlock mortality in the Great Smoky Mountains National Park, USA. Reference streams represented a mild level of HWA presence, while impacted streams represented complete hemlock mortality.	75

CHAPTER I

INTRODUCTION

The presence of the eastern hemlock (*Tsuga canadensis*, L., Carriere) conifer, a “foundation” species in eastern hardwood forests, creates a unique set of stand and environmental conditions. Foundation species are those that, by their presence alone, have the ability to “define much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes” (Dayton 1972). Eastern hemlock (EH), a late successional shade-tolerant species, eventually reaches a climax stage resulting in towering large trees that dominate the forests. Under these conditions, the forest floor receives very little light which results in minimal understory plant growth. The soil environment of hemlock stands includes slowly decomposing litter, a decreased rate of nitrogen cycling, and nutrient poor, acidic soils (Jenkins et al. 1999, Yorks et al. 2003). Hemlock canopies exhibit a higher leaf area index and lower transpiration rates than canopies of deciduous trees. Shady crowns and cooler sites moderate soil temperature and moisture levels, stabilize stream base-flows, and decrease diurnal variation in stream temperatures (Catovsky et al. 2002).

These unique forest conditions are currently in danger of being lost due to the invasive insect pest, hemlock woolly adelgid (HWA), *Adelges tsugae* Annand (Hemiptera: Adelgidae). Both eastern and Carolina hemlock (*Tsuga caroliniana* Engelman) are suitable host trees for this pest. Upon arriving on the host tree, HWA will make its way to the base of the hemlock needles, insert its stylet, and begin to feed on the parenchyma, the vital food storage cells. This feeding activity creates a disruption in the flow of nutrients within the tree and eventually results in tree mortality due to water and nutrient deprivation (Young et al. 1995). Trees gradually

succumb to these effects with complete mortality occurring between four and ten years post-infestation (McClure 1991). All age classes of eastern and Carolina hemlock trees are susceptible to this pest regardless of geographical location.

Exotic pests, such as hemlock woolly adelgid, in forest ecosystems have the potential to significantly alter species composition, stand structure, and ecosystem functions (Jenkins et al. 1999). Researchers have studied this pest extensively and more recently have begun to evaluate the potential impacts of HWA infestation of eastern hemlock trees. The majority of the existing knowledge covering hemlock woolly adelgid and its impacts has been acquired through research conducted in the northeast portion of the range of eastern hemlock. However, the ecosystem response in the southern portion of the range of EH may be different due to differences in climate and existing vegetative composition.

Eastern hemlock in the southern Appalachian Mountains is exposed to warmer temperatures, shorter winters, and direct impacts of understory shrub species such as rosebay rhododendron (*Rhododendron maximum* L.) and mountain laurel (*Kalmia latifolia* L.). These conditions increase the susceptibility of EH to hemlock woolly adelgid (Rivers et al. 1999). Several studies have been conducted to evaluate the potential impacts of this pest in hemlock-dominated systems in the southern Appalachian Mountains. Research conducted in western North Carolina indicated that reductions in evergreen riparian canopy due to hemlock mortality resulted in decreases in forest transpiration from 10 to 30 percent (Ford and Vose 2006), which has the potential for increasing stream discharge and decreasing diurnal stream flow fluctuations (Ford and Vose 2007). Another study comparing girdled hemlock trees to hemlock in decline from HWA found that fine root mass production for both conditions decreased from 20 to 40 percent, indicating that hemlock response to HWA infestation was fairly rapid and similar to the

effects of girdling (Nuckolls et al. 2009). This study also indicated that increased detritus inputs made available to the ecosystem from hemlock mortality impacted carbon and nutrient levels, which could play a significant role in future vegetative regeneration in hemlock-dominated ecosystems. The majority of HWA research has been focused on the physiological impacts to the tree and on biological and chemical control methods for the pest. Relatively little information exists regarding the aquatic and vegetative ecosystem responses created by this invasive insect pest. Management information on the vegetative and aquatic system impacts from the loss of hemlock is needed by resource managers. This study was initiated to address those needs by assessing key components of the aquatic and vegetative ecosystem responses to the loss of hemlock from HWA-induced mortality.

According to Johnson et al. (2005), the hemlock woolly adelgid was first detected within the boundary of the Great Smoky Mountains National Park (GSMNP) in 2002 in the Cataloochee Valley. Now, more than eight years later, varying degrees of HWA infestation are represented within the hemlock forests of the park. At this time, comparisons are possible between stands with varying levels of HWA infestation, from minimally infested stands to those with complete mortality. The National Park Service has used a variety of treatments across the park, including chemical, mechanical, and biological control agents, in an attempt to protect and maintain as many trees as possible (Johnson et al. 2008). Unfortunately, large-scale hemlock mortality is inevitable with this insect pest. However, researchers and biologists are trying to develop a solution to control HWA. This research provides an opportunity to assess the impacts of hemlock mortality on stream biotic and environmental conditions and riparian vegetative response. In an attempt to understand these impacts, the following subject hypotheses were investigated.

Objective 1: Examine the influence of HWA-induced mortality in hemlock-dominated riparian forests on water quality conditions.

Hypothesis 1: Hemlock woolly adelgid-induced mortality in hemlock-dominated riparian forests will alter stream temperatures.

Sub-hypotheses:

- a. Impacted streams will exhibit increased daily temperature extremes (colder in winter and warmer in spring).
- b. Impacted streams will exhibit increased diurnal variation.
- c. Impacted streams will exhibit altered mean temperature parameters (daily, weekly, monthly, seasonally).

Hypothesis 2: Hemlock woolly adelgid-induced hemlock mortality will alter woody debris inputs (source of allochthonous material) into impacted streams.

Sub-hypotheses:

- a. Impacted stream reaches will exhibit an increased density of large woody debris (LWD).
- b. Impacted stream reaches will exhibit differences in large woody debris size class and distribution.

Hypothesis 3: Hemlock woolly adelgid-induced hemlock mortality will alter water chemistry parameters.

Sub-hypotheses:

- a. Impacted streams will exhibit decreased pH (more acidic) and lower acid neutralizing capacity (ANC) values.
- b. Impacted streams will exhibit changes in values for major ions, conductivity, and trace metals.

Objective 2: Examine the influence of HWA-induced hemlock mortality on aquatic macroinvertebrate community.

Hypothesis 1: The aquatic macroinvertebrate community will respond to HWA-induced hemlock mortality with changes in species interactions and population parameters.

Sub-hypotheses:

- a. Macroinvertebrate communities will exhibit altered trophic structure due to changing conditions.
- b. Macroinvertebrate communities will exhibit changes in diversity, abundance, or richness.
- c. Macroinvertebrate communities will shift in abundance of functional feeding groups in response to altered resource availability.

Objective 3: Examine the forest riparian vegetative response to HWA-induced hemlock mortality.

Hypothesis 1: Hemlock woolly adelgid-induced hemlock mortality will result in changing forest conditions.

Sub-hypotheses:

- a. Impacted streams will exhibit decreased canopy cover and increased photosynthetically active radiation (PAR) values in the riparian zone.
- b. Rhododendron presence will inhibit understory regeneration when present.
- c. Understory regeneration will be dominated by non-hemlock species.

CHAPTER II

LITERATURE REVIEW

Invasive Species

Invasive exotic pests have become one of the most immediate threats to conservation of ecosystems. According to Liebhold et al. (1995), biological invasions have become the most significant environmental threat to the world's forested ecosystems. The Ecological Society of America lists the top five major threats to biodiversity as habitat loss and destruction, over-exploitation, global climate change, pollution and contamination, and introduction of exotic species (ESA 2003). An estimated 7,000 exotic species are established in the United States, and less than 600 of those species actually damage crops, forest systems, or do some form of ecological harm (Dajoz 2000). Many of these pests pose a serious threat to biological diversity, ecosystem function, economies, aesthetics, and human health (White and Harrod 1997).

Our society has an intimate knowledge of invasive pests and our history has shown the widespread damage and associated economic and environmental costs associated with these pests. One example, the Irish potato famine, destroyed potato crops, resulting in large scale starvation and eventually prompted a mass migration to North America between 1845 and 1852. The famine was attributed to an oomycete [*Phytophthora infestans* (Mont.) de Barry], commonly known as blight, that was brought to Ireland from the United States (Paddock 1992). The forests of the eastern United States have been permanently altered due to another invasive species, chestnut blight. This non-native, invasive pathogen [*Cryphonectria parasitica* (Murrill) Barr] is responsible for the decimation of American chestnut trees and the subsequent altered forest landscapes of North America (Burnham et al. 1986). At present, the United States (US) is battling multiple invasions on multiple fronts, including the emerald ash borer (*Agilus*

plannipennis Fairmaire), gypsy moth (*Lymantria dispar* Linnaeus), and cogon grass (*Imperata cylindrical* Linnaeus) in the eastern US, and leafy spurge (*Euphorbia esula* Linnaeus) and the Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky) in the western US, just to mention a few.

Human health and economies can also be dramatically affected by invasive pests. The Asian tiger mosquito (*Aedes albopictus* Skuse) is an example of a non-native, insect pest capable of creating tremendous impacts to human health. This mosquito can serve as a vector for a long list of insect-borne diseases such as malaria, dengue fever, filarial nematodes, West Nile virus, chikungunya, and several types of encephalitis. Governments spend billions of dollars each year on research, prevention, and eradication programs for current and anticipated infestations of invasive and exotic pests like the Asian tiger mosquito, which target human or animal populations, agricultural crops, or forested environments (Estrada-Franco and Craig 1995, Global Invasive Species Database 2011).

Invasive, insect pests in forested ecosystems have the potential for widespread impacts to ecological processes that may include altered stand dynamics, succession, and nutrient cycling (Orwig et al. 2002). For example, repeated defoliations by the invasive insect pest, gypsy moth, result in a one-story (single age class) condition, often altering stand structure and function (Campbell and Sloan 1977). Invasive species can disrupt ecological relationships and processes in aquatic environments as well. These impacts can be harmful by altering or destroying habitat, creating shifts in feeding niches, altering water quality, and impacting nutrient cycling and overall system productivity (Lovett et al. 2006). The zebra mussel (*Dreissena polymorpha* Pallas) is a highly invasive, exotic species that has created alterations to aquatic habitat and water quality by bio-fouling streams and rivers and through the reduction of phytoplankton populations

(Benson and Raikow 2011). Another aquatic pest is the invasive freshwater alga didymo [*Didymosphenia germinata* (Lyngbye) M. Schmidt]. This pest, if grown unchecked, can result in large algal blooms capable of preventing sunlight penetration in aquatic systems and subsequently disrupting ecological processes (Spaulding and Elwell 2007).

Hemlock woolly adelgid has now joined the ranks of gypsy moth, Dutch elm disease, and other exotic invasive species that are having a severe impact on the forests of the eastern US. However, HWA is unique in being a terrestrial invasive insect capable of directly impacting the forested environment and indirectly creating significant impacts to aquatic systems. Hemlock woolly adelgid was first discovered in North America in the western US during the 1920s (Stoetzel 2002). It was later found in the eastern US in the 1950s in Richmond, Virginia (Paddock 1992). Hemlock woolly adelgid likely traveled to the eastern US through the movement of nursery stock of EH trees (Cheah et al. 2004).

The spread of HWA throughout eastern North America has been facilitated by wind, birds, and mammals, including humans. Since its original detection in eastern North America, this tiny adelgid has been infesting native eastern hemlock and Carolina hemlock, leaving millions of dead hemlock trees in its path. In some areas, such as Shenandoah National Park in Virginia, the mortality rate for hemlock has risen to greater than 90 percent (Evans 2002). Hemlock woolly adelgid is currently considered a threat to hemlock forests in 17 states ranging from New Hampshire to Georgia, including the Great Smoky Mountains National Park (USDA Forest Service 1989).

Eastern hemlock and rosebay rhododendron

Eastern hemlock is a slow growing, shade-tolerant coniferous tree that is found in eastern

North America, from Canada to Georgia (Hough 1960, Little et al. 1980). This species occurs throughout a wide range of topographic positions, except in the southern Appalachians where it is restricted to moist cool coves, rocky outcrops, and north-facing slopes. Eastern hemlock trees can also occupy a wide range of elevations, from sea level to 730 m throughout its northern range and between 300 m and 910 m in the southern portion of its range. In the Great Smoky Mountains National Park (GSMNP), eastern hemlock occurs from 610 m to 1,520 m (Hough 1960, Little et al. 1980). Eastern hemlock usually occupies sites in areas with cool, humid climates and where annual precipitation ranges from 740 mm to 1,520 mm. In areas of the southern extent of its range, the average January temperature is about 6 C (42 F) with as many as 200 frost-free days and in the northern extent of its range the average January temperature is about -12 C (10 F) with a frost-free period of about 80 days (Rogers 1980).

Since EH is a slow growing species, it can attain lengthy life spans with some exceptional specimens found to live up to 800 years. They can also reach heights greater than 44-m (175 feet) with diameters of 1.8 m (Hough 1960, Ward et al. 2004). At present, the GSMNP is home to the national champion hemlock (a towering tree measuring over 50 meters in height). The park also has a few areas of virgin hemlock that exceed 400 years in age (Johnson et al. 1999). Historically, hemlock trees have been used for a variety of purposes including the construction of boxes and crates, and for pulpwood, timber, railway ties, and general construction. This species was heavily used by early homebuilders prior to the turn of the century, when depletion of the large, old growth EH trees forced a shift to other timber species (Lancaster 1985). Hemlocks were once felled in large numbers just for the bark, which was valuable for its tannin component. Tannins are now imported from other regions of the world (Hough 1960). Hemlock trees and their material have also been used to make poultice and liniments for wounds, and have been

heavily hybridized to create many varieties that are now widely planted as ornamental trees by the horticulture industry.

In addition to human uses, eastern hemlock is also ecologically important. This species is used for food and shelter for a variety of organisms including birds, fish, mammals, herpetofauna, and macroinvertebrates (Snyder et al. 2002). Between 415 and 550 species of canopy arthropods have been associated with eastern hemlock (Buck et al. 2005), with unique guilds being associated with specific EH age classes (Dilling et al. 2007). Several bird species are dependent on hemlock for feeding and nesting habitat including the blackburnian warbler (*Dendroica fusca* Miller), Acadian flycatcher (*Empidonax virens* Brewster), blue-headed vireo (*Vireo solitarius* Bonap), and black-throated green warbler (*Dendroica virens* Gmelin) (Tingley et al. 2002). Squirrels, mice, and chipmunks are known to eat hemlock seed (Hough 1960). Several species utilize hemlock for cover including ruffed grouse (*Bonasa umbellus* L.), turkey (*Meleagris gallopavo* L.), and white-tailed deer (*Odocoileus virginianus* Zimmerman) (Jordan and Sharp 1967, Quimby 1996). The eastern redback salamander (*Plethodon cinereus* Green) is another species that prefers hemlock-dominated habitats. In a Connecticut study, simulated hemlock mortality resulted in short-term population impacts with numbers exhibiting a recovery within a few years (Brooks 2001). The brook trout (*Salvelinus fontinalis* Mitchill) is also heavily dependent on this species due to its ability to moderate stream temperatures and stream flow (Snyder et al. 2002, Ford and Vose 2007). According to Evans et al. (1996), streams that drain hemlock-dominated forests are 3-4 C cooler than areas that drain hardwood-dominated forests. During the hot summer months this difference in temperature keeps stream temperatures at levels that can be tolerated by temperature sensitive species of fish and macroinvertebrates. Aquatic macroinvertebrate abundance can be as much as 37 percent greater in streams that drain hemlock

stands than in streams that drain hardwood stands (Evans 2002).

The Society of American Foresters (SAF) publication, “Forest Cover Types of the United States and Canada”, defines forest cover type as “a category of forest defined by its vegetation (particularly its composition) and/or locality (environmental) factors” (Eyre 1980). The Great Smoky Mountains unique geology and topography, coupled with the temperature climate of the region helps to support a diversity of communities. Eastern hemlock is the main component of four of the SAF defined forest communities or types: eastern hemlock, white pine (*Pinus strobus* Linnaeus)-hemlock, tulip-poplar (*Liriodendron tulipifera* Linnaeus)-eastern hemlock, and hemlock-yellow birch (*Betula allegheniensis* Britton). Eastern hemlock occurs with seven other forest types and is listed as a minor species in 18 other forest types (Eyre 1980). In the southern extent of its range, hemlock grows in mixed stands, often in riparian areas and moist coves on north and/or east facing slopes, and is found to co-occur with dense understories of rosebay rhododendron.

Rosebay rhododendron (RR) is an important component in forests of the southern Appalachian Mountains (Rivers et al. 1999), occupying approximately 30-million ha (Nilsen et al. 1999). Rhododendron historically and naturally occurs within the same riparian habitats as eastern hemlock due to moisture requirements and a preference for the dense shade provided by hemlock trees (Plocher and Carvell 1987). In areas where these two species co-occur, RR has the ability to vigorously sprout and layer, thus allowing this species to fill the gaps created by disturbances such as the wide-spread mortality of hemlock from HWA (Plocher and Carvell 1987). Rosebay rhododendron structure and tendency to layer provides deep shade and influences tree seedling survival and persistence of other species (Lei et al. 2006). The rapid spread of RR into those environments where EH is dead or declining has the potential to severely

limit woody regeneration (Whittaker 1979). The potential for long-term ecological changes, both vegetative and aquatic, warrant further investigation.

Results from vegetative studies so far have been variable, with most observations indicating birch (*Betula* spp.), maple (*Acer* spp.), oak (*Quercus* spp.), and shrubs will be the primary species to take advantage of the open canopy and increased sunlight available after hemlock mortality (Orwig and Foster 1998, Orwig and Kizlinski 2002, Kizlinski et al. 2002, Ford and Vose 2007). Researchers in New York indicated that in the northern portion of the EH range, yellow birch was the dominant tree species found in the understory after hemlock mortality (Yorks et al. 2003). In another study in the northeastern United States, black birch (*Betula lenta* L.) was the dominant tree species utilizing the newly available habitat, with red maple (*Acer rubrum* L.) also present in large quantities (Stadler et al. 2005). Research by Jenkins et al., (1999) simulated hemlock death to predict post-hemlock mortality regeneration and indicated that successional dynamics were highly dependent upon the initial density of hemlock in the stand. Predicting exactly which species will dominate in the absence of eastern hemlock is difficult considering the wide range of the EH. However, understanding how the vegetative community will respond to the loss of EH is crucial for predicting short-term and long-term responses of the forest ecosystem in the wake of HWA infestations.

Long-term impacts to aquatic systems will likely depend upon the vegetation that regenerates within riparian, hemlock-dominated stands. There are no tree species in eastern North America that are capable of performing the same vital functions as eastern hemlock (Ford and Vose 2007). Research conducted at Delaware Water Gap National Recreation Area (DEWA) explored and predicted the long-term, aquatic impacts from hemlock mortality in a comparative study of hemlock-dominated stands versus hardwood-dominated stands. Their findings suggested

that forest type did play an important role in aquatic biota diversity and that hemlock mortality could result in forest conversion to all hardwood species and subsequently result in decreased diversity within-streams and at a park-wide level (Snyder et al. 2002).

Hemlock Woolly Adelgid Biology and Impacts

Hemlock woolly adelgid is a species native to Japan. Scientists originally believed the pest to have originated in China; however, Havill et al (2006), using mitochondrial DNA, was able to identify the origin of the HWA as being the southern region of Japan. In its native range, HWA is a non-destructive inhabitant of Northern Japanese hemlock (*Tsuga diversifolia* Masters) and Southern Japanese hemlock (*T. sieboldii* Carrieré) (McClure 1995). The adelgid is also found in China, where it occurs on Chinese hemlock (*T. chinensis* Pritzels ex Diels), Himalayan hemlock [*T. dumos* (D. Don) Eichler], and Forrest's hemlock (*T. forrestii* Downie) (Annand 1924, Yu et al. 1977, Montgomery et al. 1998). In the United States, HWA can be found on western hemlock (*T. heterophylla* Sargent) and mountain hemlock (*T. mertensiana* Carriere), where it is considered to be relatively harmless, due to the existence of natural predators and host resistance (Annand 1924). In eastern North America, widespread range expansion of HWA has been achieved in the absence of natural predators or host resistance of either native hemlock species (USDA 1989).

Hemlock woolly adelgid has two distinct generations, known as bivoltine development and is capable of rapid population growth. Each generation has high fecundity, with as many as 300 eggs per female in the winter generation (progreddiens) and up to 75 for the spring generation (sistens) (USDA 1989, McClure 1987, 1989). The high reproductive capacity of this insect is also aided by asexual, parthenogenetic reproduction, meaning all individuals are female and capable

of reproducing. The first generation begins when the insect, which overwinters as an adult, begins depositing eggs into spherical ovisacs. This process usually occurs from mid-February to June (McClure 1989). By April, first instar nymphs (crawlers) begin to emerge and search for a new location to feed, where they will position themselves at the base of newly-developed hemlock needles (Young et al. 1995). Once there, the crawler inserts its stylet below the abscission layer and into the parenchyma cells. After successfully locating a suitable feeding location, the nymphs remain stationary for a four-week period, during which they will undergo four instars and then molt into adults (McClure 1989). Collectively, this unique biology, coupled with the lack of natural predators or host resistance, has allowed HWA to have a devastating impact on Carolina and eastern hemlock.

The second generation of first instar nymphs will emerge in July and then move to areas of new growth on the host hemlock tree. Shortly after they find a new location for attachment, the crawlers reach the aestivation stage. During this stage of their life, the nymphs do not feed and exhibit a cessation or slowing of activity during the summer. In October, nymphs will emerge from the aestivation stage, begin feeding again, and will continue to feed throughout the winter. During this time they slowly develop into adults, thus completing their bivoltine development on hemlock (McClure 1987, 1989).

Hemlock woolly adelgid exhibits a polymorphic life cycle involving two phenotypes, one that utilizes hemlock to reproduce and another that seeks out spruce (*Picea* spp.) trees in order to reproduce (McClure 1989). Fully-mature HWA are either wingless progrediens that will produce a second generation on hemlock and lay eggs in June, or winged sexuparae that will leave the host hemlock tree in search of a suitable spruce species to serve as a host. Fortunately, the second generation of HWA is unsuccessful because no suitable spruce species occur in eastern

North America (McClure 1989). Therefore, the winged (sexuparae) portion of this generation ultimately die, having been unable to reproduce (McClure 1987, 1989).

Regardless of the lack of success of the sexuparae, the potential for large-scale ecological impacts created by HWA in hemlock-dominated forests is still tremendous and has prompted a variety of research projects. Multiple studies conducted throughout the northeastern US have determined that no concrete relationship exists between locations of HWA infestations and the size, age, slope, or location of the stand (Orwig and Foster 1998, 2000, Kizlinski et al. 2002, Orwig et al. 2002). However, latitude has been shown to have an impact on HWA populations, primarily due to differences in lethal temperatures (Skinner et al. 2003).

The potential for HWA infestations to influence hemlock trees and their ecosystems has been studied extensively throughout the native range of eastern hemlock. Relatively little is known on the exact mechanism of damage from this insect because the majority of research has focused on the ecology of the pest and the development of control options. Young et al. (1995) hypothesized that the salivary secretions, tracks (left behind from stylet insertion), and sheaths left by the insect may have some toxic effect on the plant. Regardless of the mechanism of tree damage, HWA feeding ultimately results in gradual decline of the tree as a result of needle desiccation and repeated defoliation (Kominoski et al. 2008). Chapman et al. (2003, 2006) found that HWA feeding increased litter quality and accelerated nutrient cycling in terrestrial environments. Needle herbivory by HWA has also been shown to result in increased foliar nitrogen levels in hemlock (Stadler et al. 2006) and subsequently decreased C: N ratios to levels much lower than those found in most hardwood species (Chapman et al. 2006). Since the initial discovery of this pest in eastern forests, significant strides have been made in elucidating the biology and ecology of HWA. However, further research is needed to quantify the short-term

and long-term impacts of the loss of hemlock trees in the forested ecosystems of North America.

Study Design

This study utilized a reference versus impaired design methodology. Comparative methodology is commonly used when conducting research on aquatic ecosystems because of the inherent variability within natural systems. First order, headwater streams were chosen in order to eliminate the confounding effects of larger watersheds and multiple vegetation types inherent in higher order streams. The reference versus impaired methodology utilizes a watershed approach. All land uses, processes, and impacts from activities within a given watershed will affect the water quality and aquatic biota of the body of water draining that watershed. In this type of study, comparisons are often made between streams in a watershed where one group of streams represent a given condition (i.e. impacted), while another group of streams from that watershed are in what is considered a reference or unimpaired condition. These comparisons are made based on the assumption that the aquatic biota in the watershed should be similar in all streams, as all the streams are located within the same ecological region (Barbour et al. 1999).

In conjunction with the reference versus impaired methodology, it is often useful to evaluate the health of the streams of a given watershed and is often achieved by utilizing benthic macroinvertebrates and water quality measurements as a means to assess and compare stream health within the selected watershed. Benthic macroinvertebrates are excellent environmental indicators for aquatic systems because larval development occurs in the water, and different taxa have differing levels of tolerance to pollution or other environmental impacts (Barbour et al. 1999). Therefore, the influence of HWA and subsequent decline and death of EH can be compared between impacted and reference streams using vegetative and aquatic assessments.

CHAPTER III

DESCRIPTION OF STUDY AREA

The Great Smoky Mountains National Park (GSMNP), authorized in 1926, and officially founded on June 15, 1934, is the most visited park in the national park system. Estimates indicate that the park receives over 9 million visitors per year (Dennis 1988). The GSMNP is located within the Blue Ridge Province, a system of mountains comprising a significant portion of the Southern Appalachians. The crest of the GSMNP portion of this range serves as the topographic and legal divider between the states of Tennessee and North Carolina (Whittaker 1956). Due to its unique geography and geology, this mountain range has a tremendous influence on the evolution of the flora and fauna of the region (Figure 1). The park is recognized as an International Biosphere Reserve, as established by the United Nations Educational Scientific and Cultural Organization (UNESCO) in 1977. The United Nations has also designated the GSMNP as a “World Heritage Site” for its “outstanding universal value” in conservation of natural systems (Dennis 1988).

Besides topography, climate is the other major driver of the distribution of both flora and fauna. Temperatures are variable, ranging from austral (southeastern-like) to the cold, subalpine conditions of the higher elevations (Whittaker 1952). The mean annual precipitation from 1978-1992 was 141 cm (Neff 2007), and is a quantity sufficient to be considered a temperate rainforest (Whittaker 1975). Mean annual temperature during this same period was 13.2 C. During the data collection period for this study, 2009-2011, the annual precipitation was similar, with a mean 138 cm per year (NWS 2011).

The 212,000 hectares in the park is comprised of several habitat types and forest cover

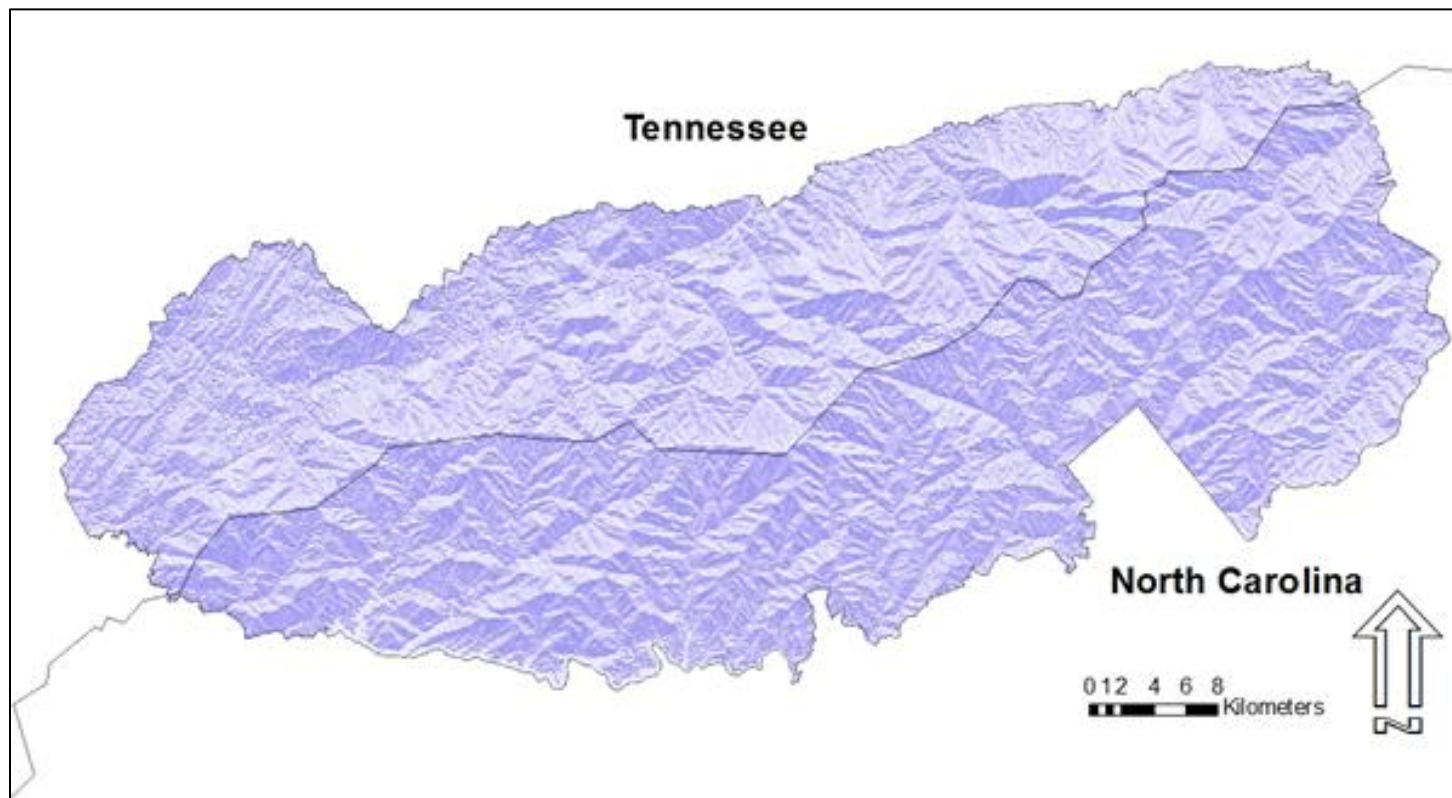


Figure 1. Boundaries of the Great Smoky Mountains National Park, USA, and the location of the state line between Tennessee and North Carolina.

types including cove hardwood forest, boreal forest, mixed oak-pine forest, hemlock forest, and balds (both grassy and heath). Heath balds, which are dense thickets of rhododendron and mountain laurel, typically occur on narrow ridges and are often in close proximity to eastern hemlock stands that are found along the streams and broad slopes (>1,100 m) adjacent to the heath covered narrow ridges (Dodd 2004).

According to Whittaker (1956), almost all vegetation in the park is either topographic climax or secondary vegetation. Most areas of the park are in this condition for a variety of reasons. Human-induced disturbances historically came from cultivation of the land, grazing of livestock, and the commercial logging industry. A major portion of the park endured heavy logging in the late 19th century and early 20th century (Figure 2, Table 1), resulting in the majority of the park being in a mature second-growth condition (Pyle 1985, Davis 2008). Man-made fires in conjunction with wildfires also had a significant impact on the southern Appalachian landscape and vegetative distribution and structure (Whittaker 1952).

The park is drained by approximately 960 km of streams (Figure 3), most of which are clear and cold, even in summer, thanks to the sheltering presence of eastern hemlock stands. Many of the small headwater, tributary watersheds have remained relatively undisturbed by man. However, over the years since the establishment of the park, many areas have been impacted by invasive pests (insects, pathogens, and plants). Pests like chestnut blight, Dutch elm disease, and balsam woolly adelgid have changed the vegetation in the GSMNP landscape. Hemlock woolly adelgid is one of the most recent pest additions within the park (Johnson et al. 2005).

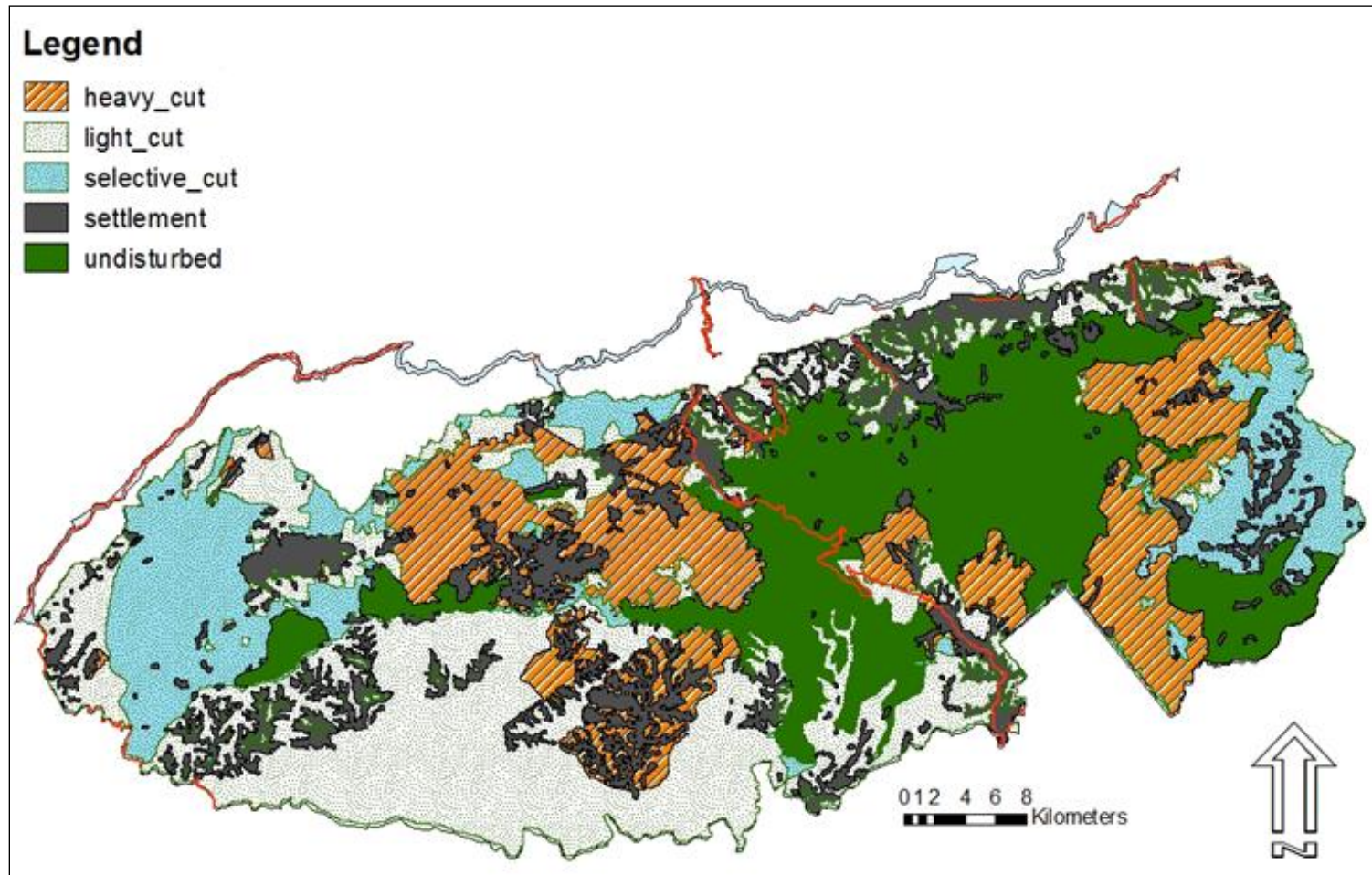


Figure 2. Disturbance history of the Great Smoky Mountains National Park, USA. This map layer was used to ensure that study streams were not located within areas that had a history of heavy logging (Pyle 1985).

Table 1. Disturbance history illustrating stand condition for forests within selected stream basins located in the eastern portion of the Great Smoky Mountains National Park, USA. This information was used to ensure that selected research streams were not located in heavily disturbed areas of the park, such as areas that historically endured heavy logging.

Stream	Treatment	Stand Age/Size	Stand Health	Disturbance History
Den Branch	Impacted	Large	Dead	Undisturbed/Selective-cut
Sag Branch	Impacted	Large	Dead	Selective-cut
McKee Branch	Impacted	Young	Dead	Settlement
Clontz Branch	Impacted	Large	Dead	Undisturbed
Hurricane creek	Impacted	Large	Dead	Undisturbed
Toms Creek	Reference	Large/Med	Moderate	Undisturbed/light-cut
Crying Creek	Reference	Large	Moderate	Light-cut
Cole Creek	Reference	Large	Moderate	Light-cut
Jones Branch	Reference	Young	Moderate	Settlement
Noisy Creek	Reference	Large	Moderate	Undisturbed

Disturbance history class descriptions (Pyle 1985):

Concentrated settlement: area of historic human settlement.

Undisturbed: area with absence of written records concerning human-related disturbances and the absence of mapped land use records.

Selective-cut: area with old growth and records or evidence of disturbance.

Light-cut: area with either or both: patches of intensely disturbed vegetation, or prevalence of livestock grazing or light fires.

Heavy-cut: area with record of corporate logging including mechanized equipment, logged with "little selectivity with respect to tree species or size.

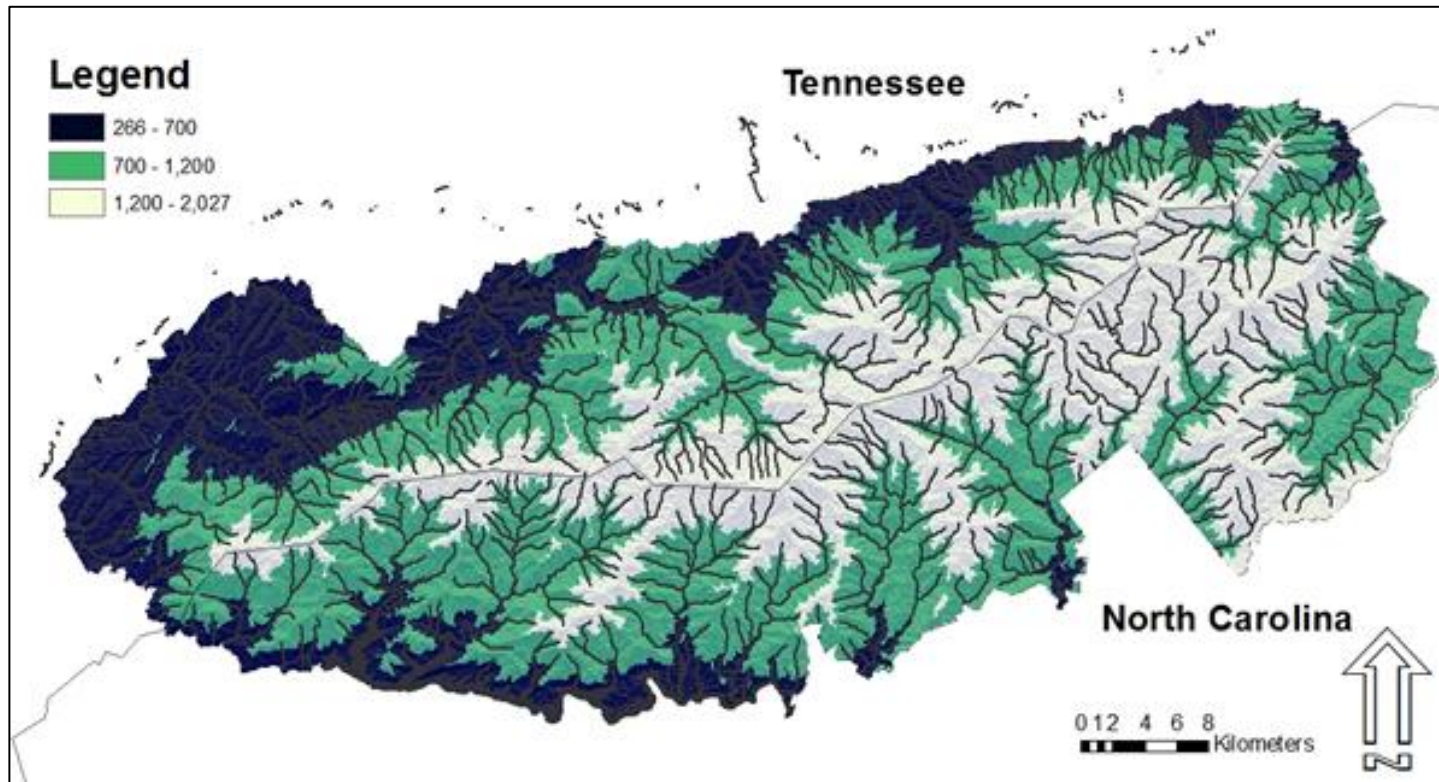


Figure 3. Elevation zones, stream locations, and topography of the Great Smoky Mountains National Park, USA. Research streams were selected from these data utilizing landscape characteristics including slope, elevation, aspect, and dominant vegetation.

CHAPTER IV

METHODS

Site Selection and Establishment

This study utilized a landscape-scale, sampling design based on terrain, vegetation, topographic position, and broad HWA infestation level. Terrain modeling and geographic information systems (GIS) processing techniques were used to evaluate pre-existing GSMNP physiography and vegetation data (Madden et al. 2004). Disturbances such as insect invasions tend to follow the same environmental gradients (e.g., topographic, elevation, solar radiation, temperature, and moisture gradients) that are crucial in determining vegetation and species distributions across the landscape (Harmon et al. 1983). Therefore, several site selection criteria were established *a priori* and were modified from Young et al. (2002). These criteria included slope, aspect, solar radiance index, terrain shape index, elevation, stream order, soils, geology, and vegetative composition (Appendix A1-A5).

Only streams where hemlock was a dominant/co-dominant species in the overstory or a major component of the understory in the stream basin were considered for this study. All streams were located within the French Broad-Holston River Basin and consisted of streams draining severely impacted (>90 percent visually assessed mortality) hemlock stands and streams draining minimally impacted (< 30 percent visually assessed mortality) hemlock stands. Streams representing HWA-free watersheds are not present within the park. Streams draining hardwood-dominated stands have been compared previously to streams draining hemlock-dominated stands that are HWA-free (Snyder et al. 1998).

Sampling sites were remote streams in the eastern portion of the GSMNP. Disturbance

history information was reviewed to ensure that sites were not located within heavily logged areas of the park, with the majority of the selected study streams being located in undisturbed or minimally disturbed areas (Figure 2, Table 1). Ten, first order, headwater streams were sampled in this study; five located in the Cosby area of Tennessee (reference streams) and five in the Cataloochee Valley in North Carolina (impacted) (Figure 4). A preliminary assessment of each stream was conducted and included stream flow, dissolved oxygen, drainage area, and stream gradient (Table 2). Individual stream maps and watershed characteristics are provided in Appendix B.

The sampling reach was delineated by pacing one chain upstream from the stream confluence, and marked as the downstream boundary of the sampling reach. A measuring tape was used to measure 100 m upstream from this point to establish the uppermost boundary of the sampling reach. Sample reach length and location were chosen based on EPA recommendations (Davis et al. 2001) and were intended to provide sufficient area to be representative of the entire stream reach. Plot center (located at 50 m) for each stream was permanently marked in Universal Transverse Mercator (UTM) coordinates (NAD 83 Zone 17N projection) with a Garmin III Plus GPS TM (Garmin International, Olathe, KS) and temporarily marked with fluorescent plastic flagging until sampling was completed. Stream basin area (km²), UTM coordinates, and additional stream data are presented in Appendix A1-A5. Once streams were delineated and flagged, measurements were collected from both the aquatic and vegetative environments to address the research hypotheses. Information collected and methodologies are presented in the following sections and include assessments of vegetation, light and canopy cover, large woody debris, water chemistry and temperature, and benthic macroinvertebrates.

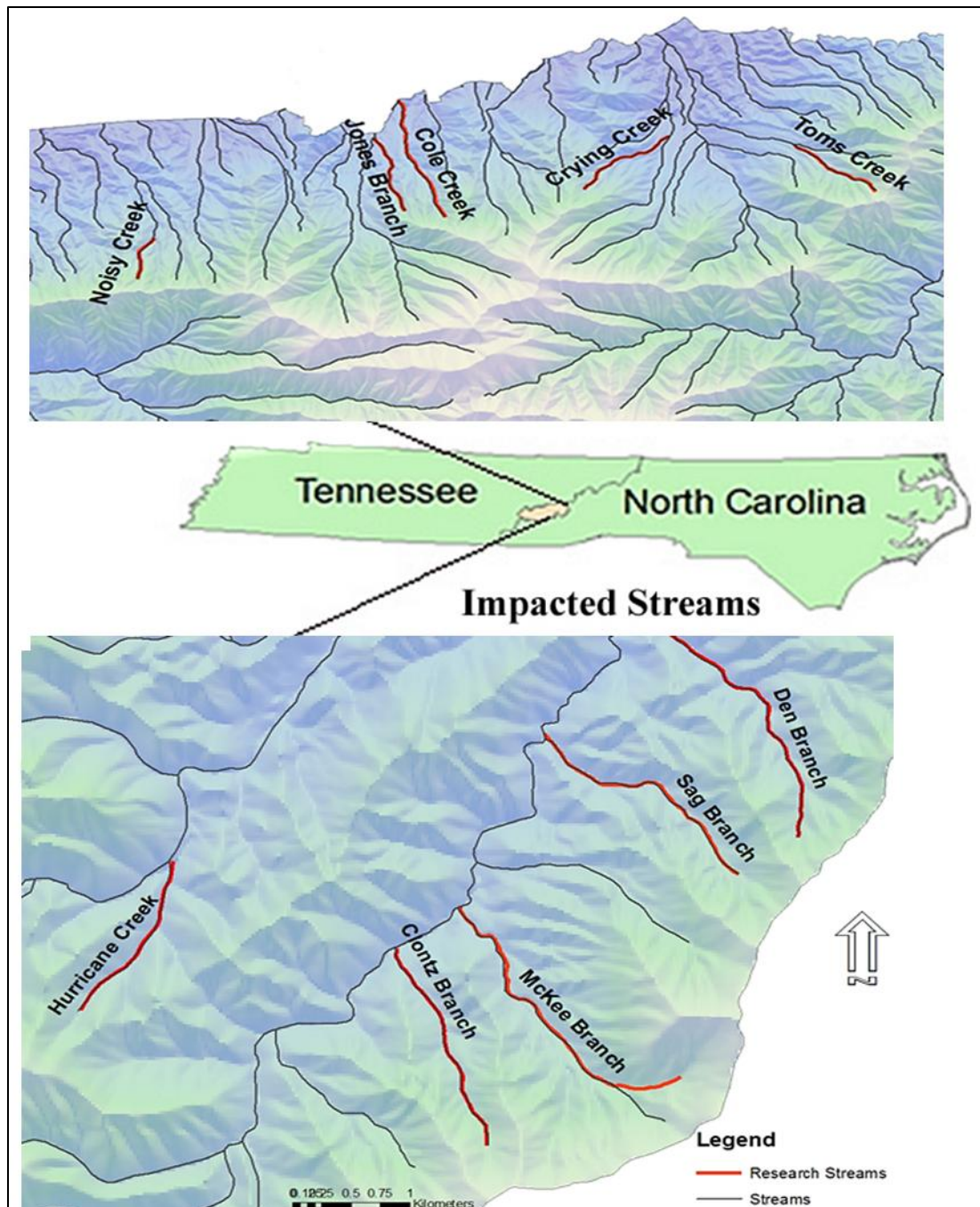


Figure 4. Reference and impacted streams used in the evaluation of aquatic ecosystem impacts from HWA-induced hemlock mortality in the Great Smoky Mountains National Park, USA. Streams were selected *a priori* based on a landscape-scale site selection design modified from Young et al. (2002).

Table 2. Stream measurement data by stand condition for stream length, gradient, drainage area, stream flow, and dissolved oxygen for study streams used in the evaluation of aquatic and vegetative ecosystem impacts from HWA-induced hemlock mortality in the Great Smoky Mountains National Park, USA.

Treatment	Stream	Stream Length	Stream Gradient	Drainage Area ha²	Stream Flow (CMS)	Dissolved Oxygen (mg/L)
Reference	Crying Creek	2465.00	0.17	0.68	2.92	11.60
Reference	Toms Creek	2031.95	0.14	0.53	2.46	12.00
Reference	Noisy Creek	2305.40	0.19	0.74	3.20	12.20
Reference	Cole Creek	3231.48	0.17	0.71	3.09	11.20
Reference	Jones Branch	2196.83	0.19	0.33	1.69	11.30
Impacted	Den Branch	2363.50	0.13	1.82	6.23	12.90
Impacted	Hurricane Creek	1796.25	0.13	0.68	2.92	12.70
Impacted	Sag Branch	2587.34	0.14	0.84	3.48	12.20
Impacted	McKee Branch	2889.48	0.18	1.58	5.78	12.80
Impacted	Clontz Branch	2187.72	0.17	0.57	2.62	11.50

ha² = Square hectares

CMS = Cubic meters per second

mg/L= Milligrams per liter

Data Collection and Analyses Methodology

Vegetation Sampling Methodology

An assessment of the vegetative community was conducted to provide a description of the vegetative characteristics of the riparian areas adjacent to the stream sampling locations and to address the research hypotheses regarding woody regeneration following post-hemlock mortality. Vegetation plots were established at each stream sampling site ($n=10$) using a nested design. Nested plots were located parallel and adjacent to the 100-m stream sampling reach. In order to restrict samples to riparian vegetation, the plots were located within the first 20 meters perpendicular to the stream edge (Clinton et al. 2010). Vegetation plots were established using a systematic stratified sampling design, beginning at the most downstream section of the 100 m stream sampling reach (as described above) and measuring upstream 12 m and then perpendicular to the stream in both directions for 10 m to establish the first plot center. The next sets of plots (concentric circles) were paced in the upstream direction and plot center was established at 28 m from the previous plot center. Understory plots were established by measuring 5.2 m in the upstream direction from the overstory plot center to establish one plot and downstream 5.2 m from the overstory plot center to establish a second understory plot (Figure 5).

Fixed area plots were used to assess vegetative cover, with overstory plots having a radius of 8 m, midstory plots having a radius of 2.25 m, and the understory plots having a radius of 1.15 m. Six 0.02-ha circular plots (three on each bank of the stream) were established to assess the riparian overstory vegetation adjacent to each stream sampling reach. Species presence, counts, diameter-at-breast-height (DBH), and basal area were determined for the overstory plots (i.e., those >12.7 cm (5-in) dbh). A mean height calculation for the distance from the ground to

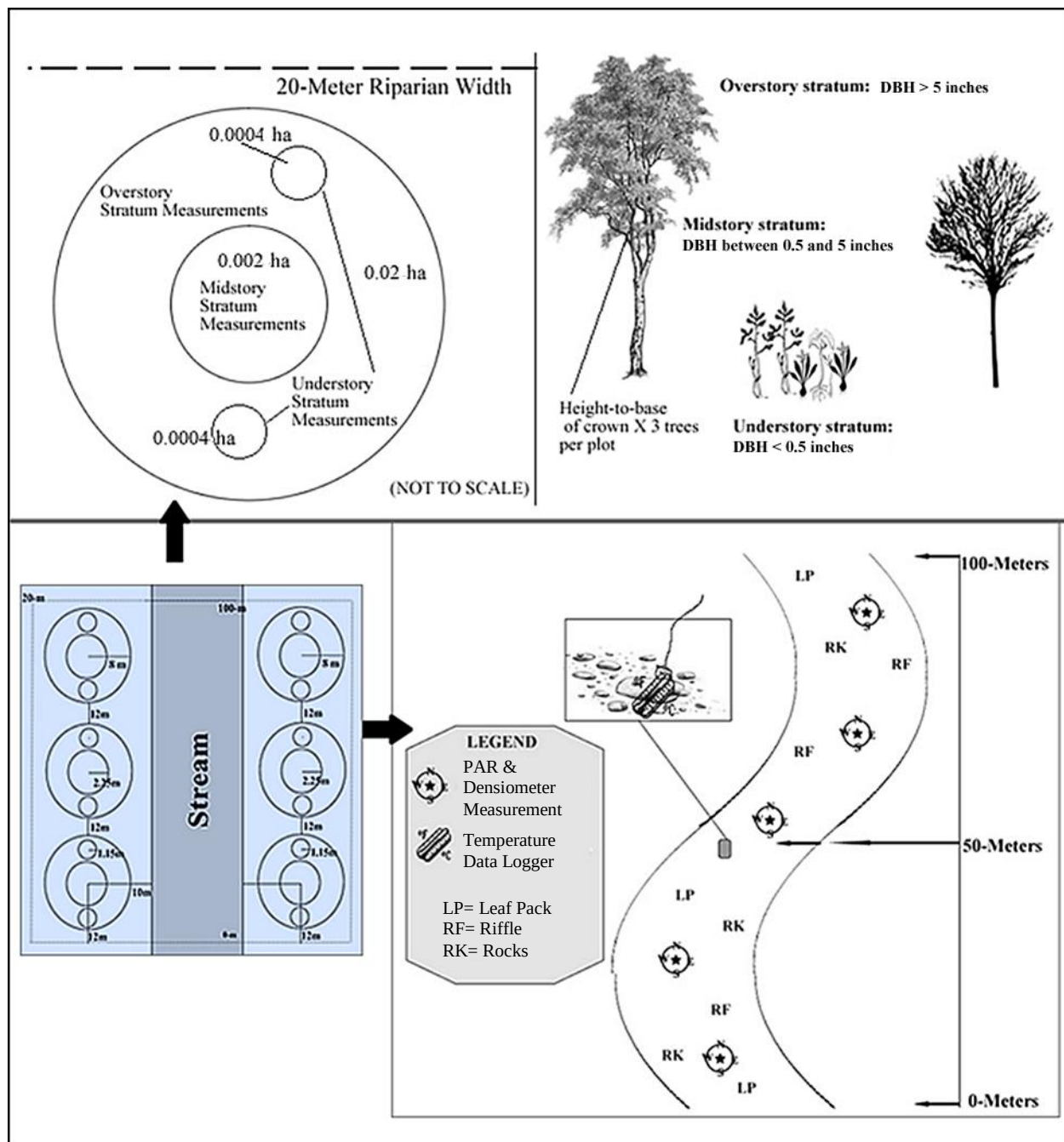


Figure 5. Plot layout design used in the evaluation of aquatic and terrestrial ecosystem impacts from HWA-induced hemlock mortality in the Great Smoky Mountains National Park, USA. Upper half of illustration depicts the vegetation plot layout and illustrates which strata were measured within each concentric circle. The lower half of the illustration depicts the stream sampling scheme including the temperature logger, PAR measurement, canopy cover measurement, and benthic macroinvertebrate sample locations.

the base of the overstory stratum was determined by selecting three trees and calculating height-to-base-of-crown with a Suunto® clinometer (Figure 5). Overstory canopy cover was assessed with a spherical densiometer. Mean canopy cover percentage for each plot was calculated by averaging the measurements from each cardinal direction from plot center.

Six 0.002-ha nested circular plots (three on each bank) were established to assess the riparian midstory vegetation, DBH between 1.27 cm and 12.7 cm (0.5 in to 5.0 in), at each sampling site (Figure 5). Species presence, DBH, and basal area measurements were documented for all non-rhododendron species. Rosebay rhododendron often occurs in densely layered thickets in the understory of hemlock stands and for this reason is often extremely difficult to sample. This study utilized broad density and height classes to account for RR presence. Midstory plot RR presence was categorized into density classes of absent, very light, light, medium, and high, and a determination was made for overall RR height (Figure 6).

Twelve 0.0004-ha circular plots were established to assess the riparian understory vegetation under 1.27 cm dbh (0.5 in) at each stream sampling reach. Modified Daubenmire cover classes were used to assess and categorize the vegetative cover within the understory plots (Daubenmire 1959). Vegetation samples were collected for the summer season of 2009 for each stream reach for a total of 60 overstory plots, 60 midstory plots, and 120 understory plots. Vegetation data were compiled and summarized using Microsoft Excel®. Data were then analyzed in SAS 9.2 and considered significant at $\alpha=0.05$ level.

Relative (percent) density, relative (percent) dominance, and relative (percent) frequency were determined for each non-rhododendron, woody species in the midstory and overstory by compositing all vegetation inventory data for each stream condition (reference streams compared to impacted streams). Species importance values (IV) were then calculated into a summation

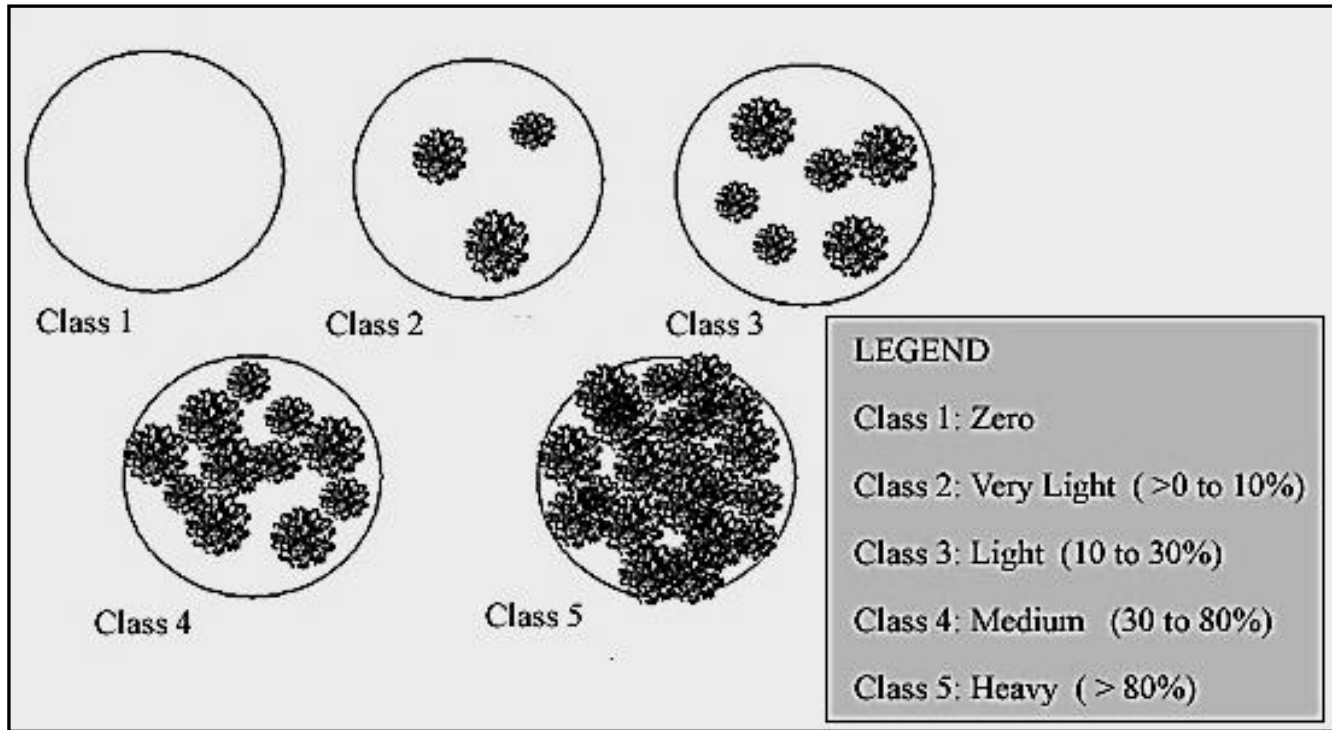


Figure 6. Illustration of *Rhododendron maximum* density classes used in the assessment of ecosystem response to HWA-induced eastern hemlock mortality in the Great Smoky Mountains National Park, USA. Density classes were used because of the tendency of this species to sprout and layer, creating densely tangled thickets that are often difficult to accurately count individual stems.

index, relative density plus relative frequency plus relative dominance, (Table 3) for each species (Curtis and McIntosh 1951), with a combined total value of 300 for all species at a given stream condition. Species with higher importance values (IV) are exerting a greater influence in the forest stand.

Canopy and Light Measurement

Vegetative canopy cover or crown closure is a characteristic often used in ecosystem assessments and is an important indicator of the status and condition of the forest ecosystem. The amount of crown closure has a direct effect on the understory light environment and is a major factor in the distribution of flora and fauna, both terrestrial and aquatic. Canopy cover values in this study were determined with a convex, spherical densiometer (Ben Meadows Co., Janesville, WI) according to established procedures (Lemmon 1956). According to Krueger et al. (2003), the spherical densiometer is more suitable than clinometers or hemispherical imagery systems when the primary goal is to assess canopy cover directly over a stream as a measure of potential for contributing to stream light and litter inputs. Measurements were collected in both the vegetative and aquatic systems at each stream reach. A subsample of the vegetation plots for each stream was assessed (n=2) and stream canopy cover was assessed along the thalweg (deepest channel point in stream cross section) at five equally-spaced locations along the stream reach (Figure 5). Canopy cover measurements were collected twice, once during the leaf-on period and once during the leaf-off period.

Photosynthetically active radiation (PAR) is the spectrum of solar radiation between 400 and 700 nanometers (nm) and is the range that is required for plants to conduct photosynthesis. Canopy transmittance of PAR is important for plant growth and for photosynthesis by primary

Table 3. Methodology and definitions for the calculation of species importance values (Curtis and McIntosh 1951).

Metric		Explanation
Rden=	Relative Density	= $\frac{\text{number of individuals of a species} \times 100}{\text{total number of individuals}}$
Rfre=	Relative Frequency	= $\frac{\text{frequency of a species} \times 100}{\text{total number of individuals}}$
Rdom=	Relative Dominance	= $\frac{\text{basal area of a species} \times 100}{\text{total number of individuals}}$
Species Importance Value (IV)		= Rden + Rfre + Rdom

producers in aquatic environments. Factors that can reduce PAR values include air pollution, cloud cover, man-made structures, and plants or forest canopies. Values collected for PAR can also vary according to the time of day, latitude, and season of collection. PAR is a common tool used in the agriculture and forestry industries, and has recently been shown to be a very useful resource in assessments of riparian vegetation (Decagon 2009). Photosynthetically active radiation was measured in this study to determine if HWA-induced alterations to stand structure affect the forest light environment.

Photosynthetically active radiation measurements were recorded, at 1 m in height, for fraction of intercepted PAR (FiPAR) in micromoles per meter squared per second ($\mu\text{mol m}^{-2}\text{s}^{-1}$) between 10:00 and 14:00 h using an Accupar LP-80 Ceptometer (Decagon Devices, Inc., Pullman, WA). FiPAR was determined by calculating the difference between an open sun value and the observed, below-canopy plot value (FiPAR). Terrestrial values for FiPAR were recorded at two of the 0.02 ha vegetation plots per research stream, one for each side of the stream for all 10 streams (n=20). FiPAR measurements were also taken for the aquatic environment directly over the selected streams on sunny days and were measured at the thalweg every 20 m along the 100-m stream reach (Figure 5). This method resulted in five measurements for FiPAR per stream for 10 streams for a total of 50 stream FiPAR data points. Canopy cover and FiPAR data were also compiled in Microsoft Excel[®] and then analyzed using mixed model ANOVA (SAS 2004). Results were considered significant at $\alpha=0.05$ level.

Large Woody Debris

Large woody debris density and distribution was assessed to determine the potential effects of increasing quantities in aquatic systems. Large woody debris density was assessed by

location categories or zones according to protocol modified from Robison and Beschta (1990). The total number of LWD (stems > 1 m in length and with a diameter > 10 cm on at least one end) was recorded for each size class within the 100-m stream reach. Size classes included: 1-3 m in length, 3-5 m in length, > 5 m in length, and root wads. Large woody debris distribution was determined by location categories and included three zones, in stream channel for Zone 1, along bank within bankfull width for Zone 2, and bridged across the channel from bank to bank for Zone 3 (Figure 7). Large woody debris data were collected during each stream sampling event which was once in the spring and once in the fall for a total of 20 measurements. Collecting LWD data for two separate but consecutive seasons was necessary to determine the rate of LWD inputs due to HWA-induced hemlock mortality. Large woody debris data were compiled and summarized in Microsoft Excel[®] software. Statistical analyses were conducted using Chi-square techniques in the Statistical Analysis Software (SAS 9.2[®]) package and were considered significant at $\alpha=0.05$ level.

Water Quality and Temperature Monitoring

Water quality grab samples were collected for each stream reach (n=10) for the fall and spring sampling events for a total of 20 samples. Samples were collected at the most downstream portion of the sampling reach in a well-mixed, undisturbed location, using depth integration. Water samples were kept refrigerated until delivered to the University of Tennessee Department of Civil and Environmental Engineering (CEE) laboratory where analyses were conducted within 48 hours of collection. Water samples were analyzed for the following parameters: conductivity (US EPA method 120.1), pH (US EPA method 150.1), ANC (Mantech PC-Titration Plus); sulfate (SO_4^{2-}), nitrate (NO_3^{2-}), ammonium (NH_4^+) (Dionex IC, Standard Methods 4110); Al,

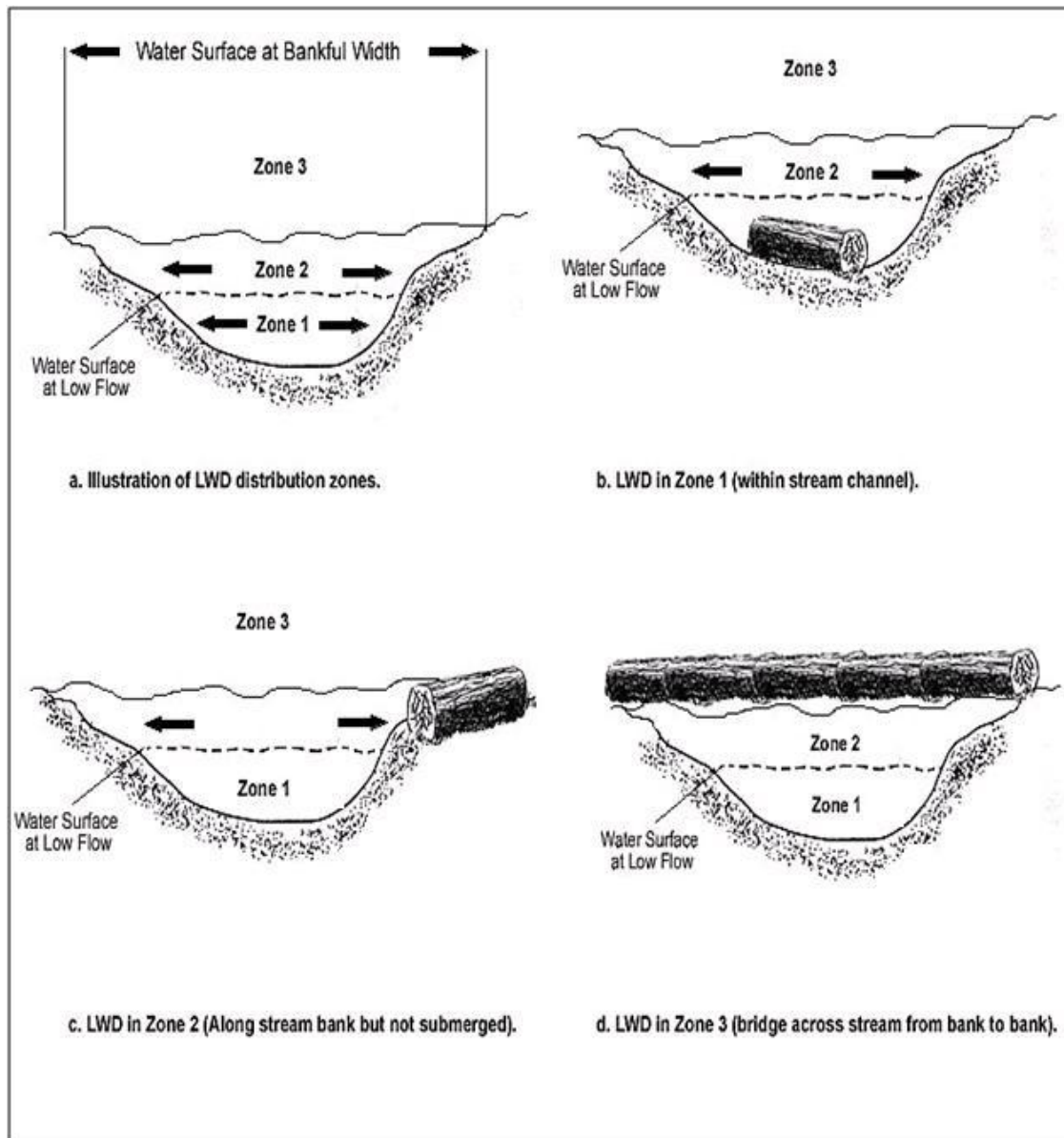


Figure 7. Illustration of large woody debris (LWD) distribution zones used to assess changes in LWD inputs and distribution between reference and impacted streams in the Great Smoky Mountains National Park, USA. (Modified from Davis et al. 2001).

Ca, Cu, Fe, K, Mg, Mn, Na, Si, and Zn [Thermo Electron Intrepid II ICP-AES, vacuum-filtered (0.45- μ m) and acidified, US EPA SW-846 Method 6010B]. Laboratory personnel followed standard operating procedures and conducted quality control/ quality assurance samples. Quality control samples (e.g., spikes, splits, and replicates) were implemented for each analytical procedure. As an extra precaution, ion balances were performed on all samples (Neff 2010).

Stream water temperatures were assessed hourly for seven months (Sept 1, 2009 to March 31, 2010) using a Hobo Onset™ temperature data logger deployed in each stream. Data loggers were placed at the stream reach center and secured with 5.0-lb lead weights and steel cabling. Data loggers were then covered with large rocks to prevent artificial inflation of temperatures due to sunlight exposure. Periodic trips were made to check that data loggers were still present and that they were continuing to function correctly.

Stream water temperature data were compiled in Microsoft Excel® and then analyzed using descriptive statistics and time series analyses in the software package Statistical Analysis Software (SAS 9.2®). Analyses were considered significant at $\alpha=0.05$ level. Water quality data were analyzed using mixed models analysis of variance (ANOVA) and were also considered significant at $\alpha=0.05$ level. Water quality results for Noisy Creek (reference stream) were not included in the analyses and reporting because of an equipment failure at the water testing laboratory.

Stream flow or discharge was calculated for each sampling site using a modified version of the sum of individual component flows method (Figure 8). The method is a measure of minimum stream size and was intended to serve as an indicator of potential habitat for aquatic macroinvertebrates (Platts et al. 1983).

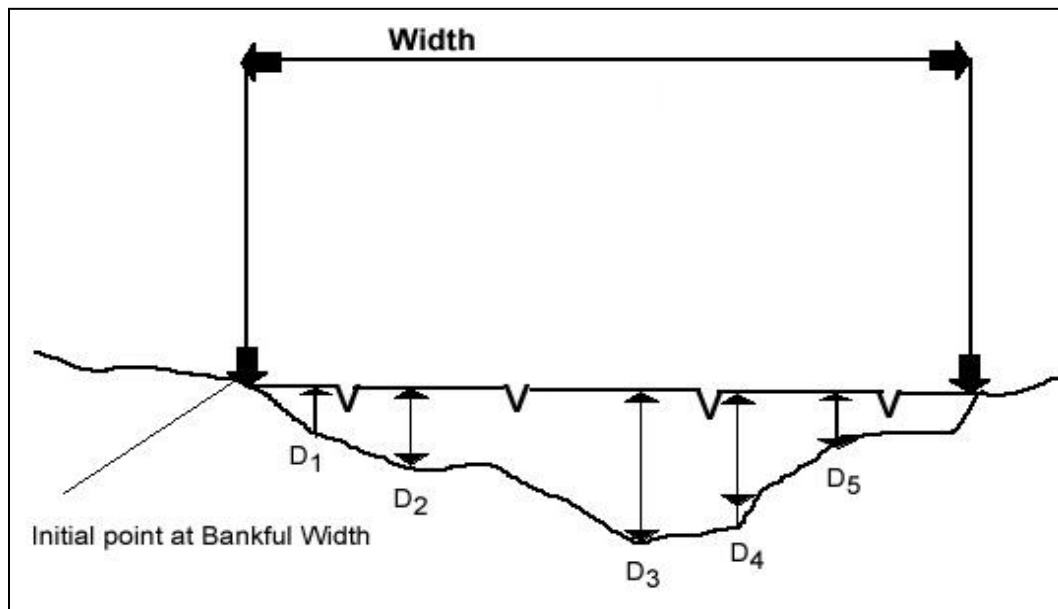


Figure 8. Schematic diagram illustrating the location of measurements taken to calculate stream cross-sectional area, a value used in the calculation of stream flow, which is often useful in determining habitat potential for aquatic biota.

Macroinvertebrate Sampling and Analyses

The aquatic macroinvertebrate community assessment utilized a random stratified sampling design also known as a multi-habitat sampling approach. This methodology is similar to the GSMNP Aquatic Macroinvertebrate Standard Operating Procedures (SOP) for sampling. The stream reach was divided into habitat types (strata) and then three randomly located samples were collected within each habitat strata for a total of nine samples per stream reach. Habitat samples were kept separate for the stream reach instead of pooling into one container for a stream. Sampling gear included a semi-quantitative kick net (1 m²) for riffle habitat sample collections, a qualitative D-frame dip net and bucket sieve for assessing leaf packs, and a fine mesh sampler for qualitative rock habitat samples. All rocks within a 1-m² area were collected for three minutes and washed in a bucket of water. The water was then filtered through a fine mesh sieve to collect the benthic macroinvertebrates. Sampling was conducted in the fall of 2009 and spring of 2010. Every effort was made to sample streams as close together as possible to reduce the potential for temporal variability.

Specimen samples were analyzed at the University of Tennessee for identification to the lowest taxonomic level possible. Questionable specimens were verified by Dr. David A. Etnier at the University of Tennessee in the Department of Ecology and Evolutionary Biology. Specimens were also classified by functional feeding groups and habitat types prior to statistical analyses. Aquatic macroinvertebrate data were summarized using Microsoft Excel[®]. Biological metrics are commonly used to characterize the community structure and composition of a stream (Plafkin et al. 1989) and those selected for this study meet the EPA Rapid Bioassessment Protocol (Barbour et al. 1999). Macroinvertebrate data were checked for normality and homogeneity of variances and in some cases were log, root, or rank transformed prior to

statistical analyses. Metrics were analyzed using mixed models analysis of variance and were considered significant at $\alpha=0.05$ level. Large variation often occurs with benthic invertebrate data; therefore, a $p<0.10$ was used to identify data that were marginally significant.

Macroinvertebrate data from the quantitative riffle samples were categorized into commonly used quantitative benthic macroinvertebrate metrics (Table 4) for analysis using Statistical Analysis Software (SAS 2004). According to the recommendations of the EPA in their Rapid Bioassessment Protocol, it is often best to emphasize sampling in a single habitat type (i.e., riffles) to allow for standardization of assessment among research streams. This approach works well for headwater streams in the GSMNP which are dominated by riffles that contain cobble substrates. This type of substrate usually supports the highest diversity of macroinvertebrates (Plafkin et al. 1989).

Macroinvertebrate data from the qualitative leaf pack and rock samples were composited with riffle samples and compiled into one data set that was used to evaluate a list of qualitative macroinvertebrate metrics (Table 4). While riffles often contain the highest density and diversity of species, other habitats within a reach are often the location of rare taxa or taxa unique to a particular habitat type (i.e., rocks, leaf packs). Multi-habitat composite samples are often used to illustrate total diversity of species or assemblages within a stream reach (Barbour et al. 1999).

Table 4. Benthic macroinvertebrate community metric categories and explanations of significance used in the evaluation of aquatic ecosystem impacts from HWA-induced hemlock mortality in the Great Smoky Mountains National Park, USA.

Metric	Explanation
Community Health*	Higher proportion of intolerants indicates good community health.
Species Richness	Reflects the health of the community
EPT** Richness	Total number of distinct taxa in orders of EPTs.
EPT/ Chironomidae	Assesses community balance by comparing relative abundance of indicator groups.
Percent Shredders	Measures relative abundance; low value indicates altered riparian conditions.
Percent Scrapers	Measures relative abundance; higher values suggest good habitat quality.
Percent Filterers	Measures relative abundance; higher values suggest excessive sediment or poor habitat quality.
Percent EPT	Higher percentage value indicates increasing water quality.
Percent Chironomidae	Measures relative abundance; high value may indicate increased erosion and sediment loading.
Percent Chironomidae to Oligochaeta	Measure of relative abundance of tolerant species; increased values indicate poor water quality.
Species Abundance	Total number of specimens in a given area as a total and by taxon.
Percent Ephemeroptera	Measures relative abundance; higher values indicate better water quality.
Percent Plecoptera	Measures relative abundance; higher values indicate better water quality.
Percent Trichoptera	Measures relative abundance; higher values indicate better water quality.

*Tolerance values are determined based on the relationship between a given taxon and an anthropogenic stressor gradient.

**EPT is an acronym frequently used to refer to the orders Ephemeroptera, Plecoptera, and Trichoptera. This group of insects, when combined into one metric, serves as a strong indicator of stream ecosystem health.

CHAPTER V

RESULTS AND DISCUSSION

Vegetation Sampling and Analyses

Stream riparian vegetative communities were similar in species composition between both reference and impacted conditions and were typical of mixed mesophytic forests. Sorenson's Similarity Index (Kent and Coker 1992) yielded a score of 41.1 percent similarity of species between treatments with a total of 21 woody species present in the riparian zone of reference streams, and 22 species in the riparian zone of impacted streams. Mean height to crown base of overstory trees was significantly different ($p < 0.001$, $DF = 59$, $F = 15.02$) between conditions, with a mean height for reference sites of 14.8 m ($SE = 0.6$) and impacted sites having a mean height of 11.5 m ($SE = 0.6$). The vertical structure of stream riparian vegetation was highly stratified across all stream sites, with an overstory dominated by shade-intolerant species like yellow poplar and shade tolerant species like eastern hemlock. The understory stratum was dominated by shade tolerant species like red maple, yellow birch, and eastern hemlock. Shrub species were primarily rosebay rhododendron, mountain laurel, and doghobble (*Leucothoe fontanesiana*). Species with the highest relative frequencies and importance values, regardless of treatment, included yellow poplar, eastern hemlock, sweet birch, and red maple (Table 5) which was consistent with known eastern hemlock forest types and species associations (Eyre 1980).

Two sets of calculations were conducted for vegetation data from impacted sites to evaluate the differences in values for vegetation metrics. Values including hemlock snags (pre-HWA) were compared to values where snags were not included in calculations (post-HWA). Prior to HWA infestation and subsequent hemlock mortality, eastern hemlock relics that survived logging and

Table 5. Relative density, relative frequency, relative dominance, and importance values for tree species located within vegetation plots at reference and impacted stream sites in the Great Smoky Mountains National Park, USA. Reference conditions refer to stands with little to moderate levels of HWA infestation, while impacted sites refer to those sites with near complete HWA-induced hemlock mortality.

Species Symbol	Common Name	Relative Frequency (1)		Relative Density (2)		Relative Dominance (3)		Importance Value (4)	
		Reference	Impacted	Reference	Impacted	Reference	Impacted	Reference	Impacted
ACPE	striped maple	0.78	2.83	0.26	2.19	0.62	0.20	1.65	5.21
ACRU	red maple	18.60	12.26	13.78	7.10	14.33	19.37	46.71	38.74
ACSA	sugar maple	3.88	1.89	1.53	1.64	0.82	1.81	6.22	5.34
AEFL	yellow buckeye	0.00	0.94	0.00	1.64	0.00	2.10	0.00	4.68
BEAL	yellow birch	0.78	15.09	0.26	14.21	0.19	12.12	1.22	41.42
BELE	sweet birch	13.18	11.32	7.65	15.30	5.20	13.88	26.03	40.51
COAL	alternate-leaf dogwood	1.55	0.00	0.26	0.00	0.32	0.00	2.12	0.00
FAGR	American beech	0.00	4.72	0.00	4.37	0.00	3.54	0.00	12.63
FRPE	green ash	1.55	0.00	0.77	1.64	1.07	0.00	3.38	1.64
HAMO	mountain silverbell	3.10	2.83	0.77	2.19	0.71	5.01	4.58	10.02
HATE	Carolina silverbell	2.33	6.60	0.77	6.56	0.82	1.78	3.91	14.94
HAVI	witch hazel	0.00	3.77	0.00	2.19	0.00	0.77	0.00	6.73
KALA	mountain laurel	0.00	4.72	0.00	6.56	0.00	2.32	0.00	13.59
LITU	yellow poplar	17.83	5.66	29.34	8.20	49.90	18.09	97.06	31.94
MAFR	Fraser magnolia	0.78	4.72	0.26	5.46	0.11	2.93	1.14	13.11
NYSY	black gum	0.00	1.89	0.00	1.09	0.00	2.10	0.00	5.08
OXAR	sourwood	9.30	2.83	5.10	2.73	2.47	1.61	16.87	7.18
PIEC	short leaf pine	0.78	0.00	0.26	0.00	0.47	0.00	1.50	0.00
PIST	white pine	0.00	1.89	0.00	1.09	0.00	1.30	0.00	4.28
PRSE	black cherry	0.78	0.00	0.26	0.00	0.36	0.00	1.39	0.00
QUAL	white oak	0.00	1.89	0.00	1.64	0.00	1.65	0.00	5.18
QUCO	scarlet oak	0.00	0.94	0.00	0.55	0.00	2.38	0.00	3.87
QUMO	chestnut oak	2.33	0.00	1.53	0.00	2.04	0.00	5.90	0.00
QURU	northern red oak	2.33	1.89	1.02	1.64	1.27	1.15	4.62	4.68
ROPS	black locust	1.55	0.00	0.51	0.00	0.66	0.00	2.72	0.00
SAAL	sassafras	0.78	1.89	0.26	2.19	0.11	1.31	1.14	5.38
SANI	black willow	1.55	0.00	0.51	0.00	0.23	0.00	2.29	0.00
TIAM	American basswood	0.78	1.89	0.26	1.09	0.09	1.40	1.12	4.37
TSCA	eastern hemlock	15.50	7.55	34.69	8.74	18.22	3.19	68.42	19.48

(1) Relative Frequency = (density of given species / total density of all species) x 100

(2) Relative Frequency = frequency of a given species / total frequency of all species) x 100

(3) Relative Dominance = (dominance of given species / total dominance of all species) x 100

(4) Importance Value = relative density + relative frequency + relative dominance

fires in the GSMNP were the dominant species at impacted sites with a total basal area of 149.4 m²/ha. This figure represents 57.7 percent of the total basal area (259.2 m²/ha) present prior to hemlock mortality and is an underestimate because basal area calculations only included standing hemlocks (alive or dead) but did not include those that were already down on the forest floor.

Pre-HWA importance value calculations yielded a value of 111.8 for eastern hemlock in impacted stream sites which is much higher than the 19.5 importance value for EH based on current stand conditions at impacted sites (Table 5). Mean basal area did not differ ($p=0.345$, $DF=8$, $F=1.01$) between reference sites (49.8 m²/ha, $SE=2.9$) and impacted sites (45.1 m²/ha, $SE=2.9$) for pre-HWA data (Table 5). However, post-HWA data exhibited a significant difference ($p<0.0001$, $DF=9$, $F=53.55$) in mean basal area between treatments (Figure 9). Sites at reference streams had a mean basal area of 49.8 m²/ha ($SE=2.9$), while sites at impacted streams had a much lower mean basal area at 19.5 m²/ha ($SE=2.9$). Decreased basal area at impacted sites was a response to EH mortality which resulted in only 3.6 m²/ha of live hemlock remaining at impacted sites. Changes in basal area such as those observed here are often associated with increased size and number of canopy gaps, which serve as an important source of woody recruitment in the understory stratum of forested stands.

Successful regeneration in the understory stratum of affected areas will be dependent upon many factors including soil moisture, light availability, gap size, and vegetative species composition (Canham and Marks 1985, Canham 1988). In hemlock dominated stands, the primary group of woody species to regenerate would usually include eastern hemlock; however, this species is unlikely to successfully regenerate in the presence of HWA. Hemlock woolly adelgid will infest hemlock trees of any age and prevent recruitment of hemlock regeneration

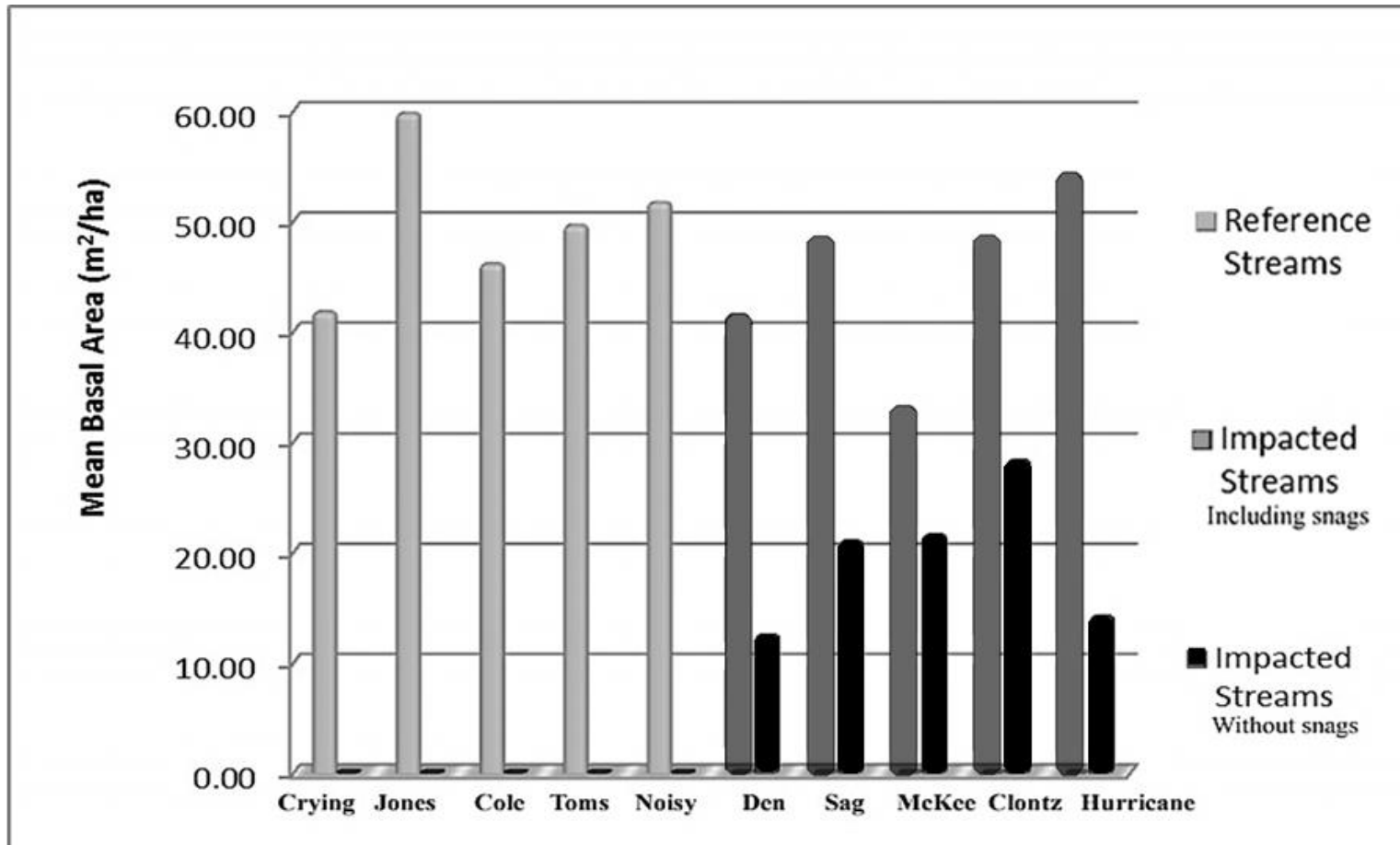


Figure 9. Mean riparian basal area at reference and impacted streams in the Great Smoky Mountains National Park, USA. Data for impacted streams is shown including hemlock snags and without snags and is intended to illustrate the impact of hemlock mortality on stand basal area. These data showed a significantly lower range of values for impacted streams when compared to the basal area values observed in reference streams.

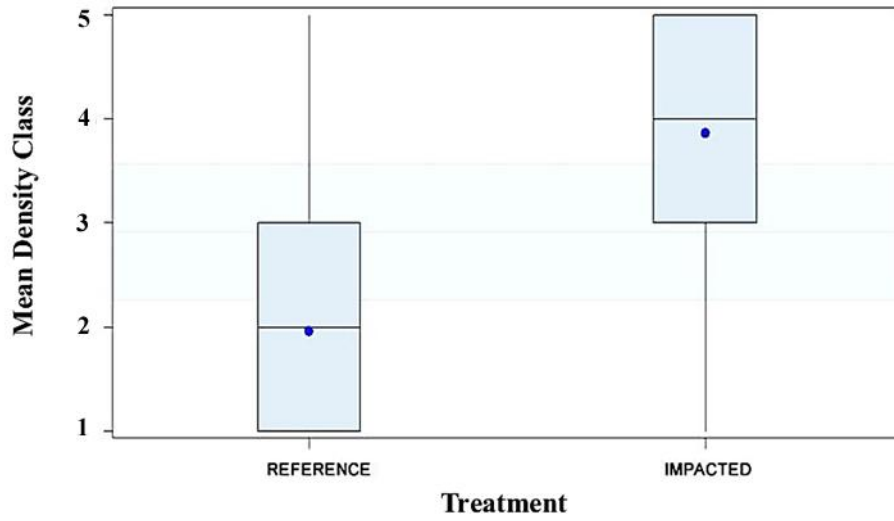
into the overstory, regardless of the surrounding stand conditions or availability of resources. An evaluation of the understory stratum in this study indicated that woody regeneration has not initiated at impacted sites ($p=0.81$, $F=0.06$, $DF=9$). The lack of regeneration is likely attributable to canopy gap size and to the inhibitory effect of rosebay rhododendron (RR). Gap size is a function of tree size and stand mortality pattern. Larger gaps are created when groups of large trees die and fall within a short time frame, usually from fire, wind, or storms. When trees die standing, like the EH observed in this study, microclimate formation is different and results in smaller gaps (Clinton et al. 1994). Gap size has been shown to be positively correlated to the amount of solar radiation and subsequently, to carbon gain and species richness patterns (Phillips and Shure 1990).

The other factor affecting the absence of woody regeneration is the presence and density of RR, an understory ericaceous shrub known to have important habitat associations with EH. Both species historically and naturally occur within the cool, moist riparian habitat adjacent to headwater streams. Rosebay rhododendron is closely associated with EH because of its ability to thrive in the dense shading created by a healthy, intact EH canopy (Rivers et al. 1999). Occurrence of RR has been increasing over the past century due to changes in natural and anthropogenic disturbance factors (Rivers et al. 1999). Fire exclusion, coupled with wide spread American chestnut mortality, has resulted in the proliferation of RR throughout the southern Appalachian Mountains where it is now the most abundant sub-canopy species, occupying well over 30 million ha (McGinty 1972, Monk et al. 1985, Phillips and Murdy 1985, Nilsen et al. 1999). According to Hedman and Van Lear (1994), RR often has the highest importance value of all understory species in the southern Appalachians.

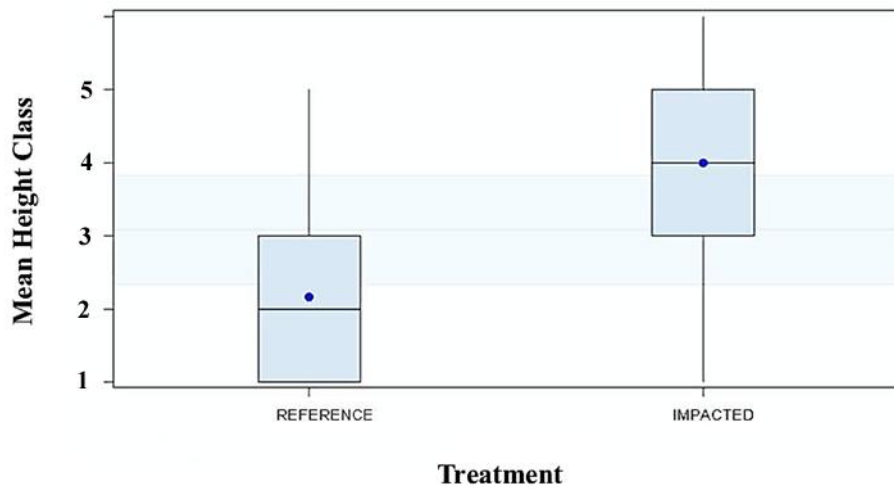
In this study, RR was present in the riparian area of all streams; however, mean density

classes were significantly different between reference and impacted sites ($p < 0.0001$, $DF = 59$, $F = 39.05$). Mean density class at impacted sites was 3.9 ($SE = 0.22$) and was twice as high as reference sites with a mean density class value of 1.7 ($SE = 0.22$). Class values correspond with a mean density between zero and 10-percent for reference streams between 30-percent and 80-percent for impacted streams. Height classes for RR were also significantly different between reference and impacted conditions ($p < 0.0001$, $DF = 59$, $F = 27.54$) with a mean height class of 2 ($SE = 0.25$) for reference streams and a mean height class of 4 ($SE = 0.25$) for impacted streams. Height values correspond to a mean height range of 1.8-m to 3.0-m for RR at reference sites and a mean height range from 4.6-m to 6.1-m at impacted sites (Figure 10).

Results from this study indicate that RR will invade newly available habitat, capitalizing on decreased stand basal area and increased resource availability that occurs in response to HWA-induced canopy gap formation. Moderate densities of RR presence, like those observed in this study, have been shown to have an inhibitory effect on woody regeneration (Minckler 1941, Plocher and Carvell 1987, Cox 1979, and Whittaker 1979). One study found that canopy gaps with greater than 50-percent cover of RR had significantly lower seedling densities than all other gap sizes and types (Clinton et al. 1994). A few species have been shown to successfully regenerate under the limited light conditions created by this situation; primarily red maple seedlings, but yellow and sweet birch have also been found in smaller quantities (Clinton et al. 1994, Rivers et al. 1999, Beckage et al. 2000, Lei et al. 2002). Results from this study suggest that the same group of species is most likely to benefit from hemlock mortality in stream riparian zones in the GSMNP. All three species exhibited significant increases in importance values in the absence of eastern hemlock ($p < 0.0001$, $DF = 5$, $\chi^2 = 734.3$) (Table 5). Rivers et al. (1999) also indicated that red maple, yellow poplar, and birch (yellow and sweet) were capable of



(a).



(b).

Figure 10. Mean density class and mean height class for *Rhododendron maximum* for reference and impacted streams in the Great Smoky Mountains National Park, USA. Impacted sites exhibited density and height classes twice that of reference sites, illustrating the success of *R. maximum* at capitalizing on the increase in available resources due to HWA-induced hemlock mortality. (Classes are 1=zero, 2=very light, 3=light, 4=medium, and 5=heavy).

regenerating under moderate to heavy RR densities; however, results from their study suggest that this regeneration would be incapable of survival and recruitment to the overstory without some form of disturbance to the RR canopy.

The inhibitory effect of RR has been studied extensively and research has still been unable to fully explain why other species fail to successfully regenerate in its presence. The most frequent reasons given include competitive exclusion through resource competition (light and moisture), differences in mycorrhizal development, and allelopathy (Clinton et al. 1994, Rivers et al. 1999, Beckage et al. 2000, Clinton 2003). Research by Lei et al. (2006) suggests that RR affects carbon gain of seedlings by reducing light levels below the light compensation point for photosynthesis, leading to seedling mortality. Regardless of the mechanism of inhibition, RR presence has the potential to alter the forest structure and composition in areas previously dominated by EH. Further, RR thickets have been shown to persist and dominate a site for more than 64-years (Plocher and Carvell 1987). The long-term occupation of stream riparian areas is almost certain in the absence of disturbance to the dense RR thicket, resulting in long-term alterations to forest succession. Disturbance can provide windows of regeneration and will likely play an important role in any future management efforts to restore the riparian habitat in the affected areas of the GSMNP.

Vegetation measurements were only taken in the stream riparian zone, where RR and EH often co-occur. Their co-occurrence is primarily a result of both species' preference for similar habitats (mesic cove habitats to rocky outcrops) and both require high moisture environments that are well protected from thermal extremes. These characteristics allow both species to do well in heavily shaded, protected sites such as north-facing slopes and coves where there is less chance of direct competition for resources (Romancier 1971, Plocher and Carvell

1987). Due to the co-occurrence of EH and RR in proximity to streams and our interest in the potential impacts of RR on aquatic ecosystem response to eastern hemlock mortality, the study was restricted to riparian hemlock stands in the GSMNP. Research has been conducted on non-riparian, eastern hemlock stands in the northeastern US, with results indicating that black and yellow birch were the primary woody vegetation to occupy the newly available habitat (Stadler et al. 2005, Eschtruth et al. 2006). Recent research in the southern Appalachians also found significant densities of RR in hemlock-dominated communities (Krapfl et al. 2011). Results from vegetation measurements, with the addition of non-riparian areas of eastern hemlock dominated stands in the GSMNP could potentially yield different results for woody regeneration.

Canopy and Light Analyses

Canopy coverage is considered a major determinant of the forest microenvironment and is defined as the area of ground covered by a vertical projection of the canopy. Alterations to overstory tree canopies have a direct impact on plant response and vegetative distribution by moderating the understory light environment. Eastern hemlock plays a crucial role in controlling the understory light environment in stream riparian zones in the GSMNP. Studies comparing hemlock streams to hardwood streams have shown a difference in the amount of solar radiation received by streams (Rowell and Sobczak 2008). Canopy cover was evaluated to characterize the condition of the overstory stratum and to determine if differences exist between these values when comparing impacted sites to reference sites. Percent canopy cover was significantly different between treatments for two measurement periods (Table 6), during both leaf-off ($P=0.003$, $DF=9$, $F= 18.6$) and leaf-on conditions ($p=0.002$, $DF=9$, $F= 22.24$). Reference streams had a mean leaf-on, percent canopy cover of 93.5 (SE=1.7), while impaired streams had a mean

Table 6. Mean canopy cover percentage and mean fraction of photosynthetically active radiation (FiPAR) percentage for reference and impacted stream sites across two measurement seasons, leaf on and leaf off, for research conducted in the Great Smoky Mountains National Park, USA.

Forest Condition	Stream	Leaf Off Condition		Leaf On Condition	
		Mean Cover (%)	Mean FiPAR (%)	Mean Cover (%)	Mean FiPAR (%)
Reference	Crying Creek	74.832	1.84	91.212	1.722
Reference	Jones Branch	66.72	4.52	93.24	1.206
Reference	Toms Creek	56.736	7.492	92.668	2.538
Reference	Cole Creek	50.912	6.652	97.608	2.962
Reference	Noisy Creek	48	6.072	92.72	4.25
Impacted	Clontz Branch	25.536	13.008	88.872	11.008
Impacted	McKee Branch	37.392	8.036	79.564	7.68
Impacted	Hurricane Creek	31.36	10.58	78.888	6.38
Impacted	Sag Branch	29.904	5.734	76.132	5.354
Impacted	Den Branch	43.632	10.462	78.472	5.352

leaf-on, percent canopy cover of 80.4 (SE=1.7).

During the leaf-on period, hardwood trees have their leaves and were contributing to light attenuation in the riparian zone. Mean percent canopy cover during the leaf-off period for impacted streams was 33.8 (SE=4.2), a value that was slightly more than half of the 59.4-percent (SE=4.2) determined for reference streams for the leaf-off period (Figure 11). Leaf-off period is when hardwood species lose their leaves and the majority of canopy being measured by the densiometer is that of evergreen species like eastern hemlock. Decreases in mean canopy cover of this magnitude illustrated the significance of the presence of eastern hemlock in stream riparian environments. Cover provided by EH during the leaf-off portion of the year was critical for keeping streams warmer during cold weather by limiting the loss of radiant heat. Decreased canopy cover will have implications for the forest microenvironment, allowing more sunlight to reach the forest floor and stream environment on a year-round basis.

Increases in canopy gaps lead to increases in incident light availability (Buckley et al. 1999). One study found that HWA infested sites had a higher gap light index (GLI) than non-infested sites (Jenkins et al. 1999). A gap experiment conducted in Virginia found that gaps created by hemlock tree fall exhibited increased incident light by as much as 64.7 percent (Siderhurst et al. 2010). Incident light values were assessed by determining the fraction of photosynthetically active radiation (FiPAR) penetrating through the forest canopy and into the understory environment. Canopy cover and FiPAR have been shown to be important drivers of phytoplankton activity and reproduction in streams (Lamberti and Steinman 1997). Light availability was shown to be strongly correlated with crown density, transparency, and dieback from adjacent hemlock trees, and thus could serve as a surrogate for severity of HWA disturbance (Eschtruth et al. 2006). An assessment of incident light values was conducted to

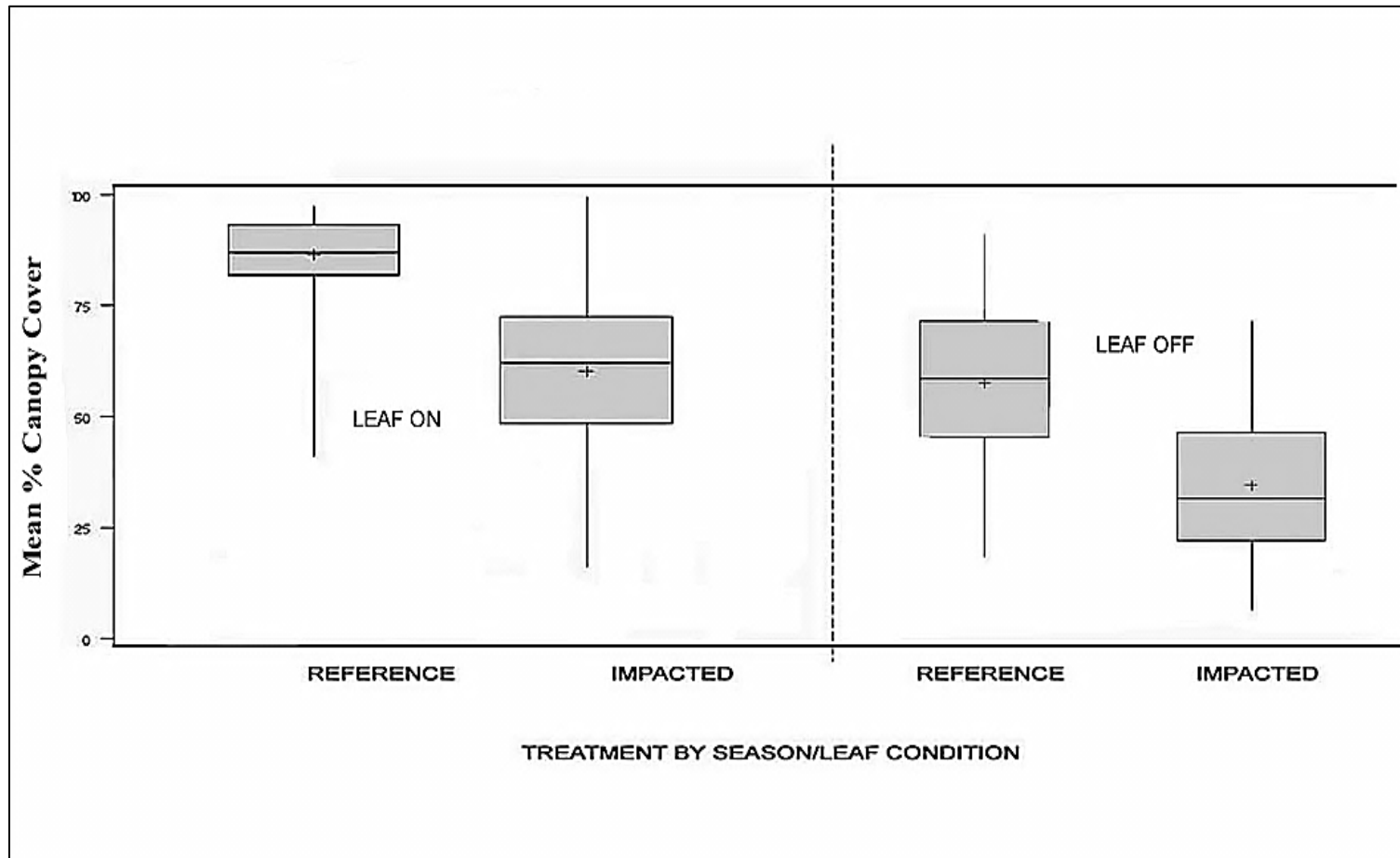


Figure 11. Boxplot of mean canopy cover percentage for reference and impacted stream sites across two measurement seasons, leaf on and leaf off, for research conducted in the Great Smoky Mountains National Park, USA

illustrate the resources available to stimulate regeneration of woody vegetation or primary productivity in aquatic systems.

Analyses of FiPAR data collected over research streams in this study indicated that differences do occur between reference streams and impacted streams during both leaf-off ($P=0.03$, $DF=9$, $F=7.15$) and leaf-on ($P=0.001$, $DF=9$, $F=22.22$) periods (Figure 12). FiPAR levels followed expected patterns in response to hemlock mortality, and exhibited increasing values as canopy coverage decreased. Results from FiPAR (expressed as percent of full sun) data for leaf-on conditions were significantly different with control streams receiving a mean FiPAR of 2.2 percent ($SE=0.5$), while impaired streams received a mean FiPAR of 6.5 percent ($SE=0.8$). Results from analyses for the leaf-off condition also indicated significant differences in sunlight penetration through the canopy with control streams receiving a mean FiPAR of 5.3 percent ($SE=1.1$) while impaired streams received a mean FiPAR of 9.6 percent ($SE=1.1$).

Eastern hemlock mortality in the GSMNP has resulted in decreased canopy coverage and, as a result, FiPAR has increased at impacted sites when compared to reference sites. Differences observed in mean canopy cover and subsequent FiPAR values during the leaf-off period emphasize the true impact of the loss of EH. Eastern hemlock is an ecologically unique species that is extremely important in riparian areas, in large part for its ability to provide critical shading of streams (Ross et al. 2003). The loss of the light mediating capacity of eastern hemlock in the stream riparian zone will result in altered thermal regimes and impacts to aquatic biota. The duration and severity of impacts are difficult to predict and will depend upon the vegetative species and length of time required for vegetative cover to regenerate after hemlock mortality.

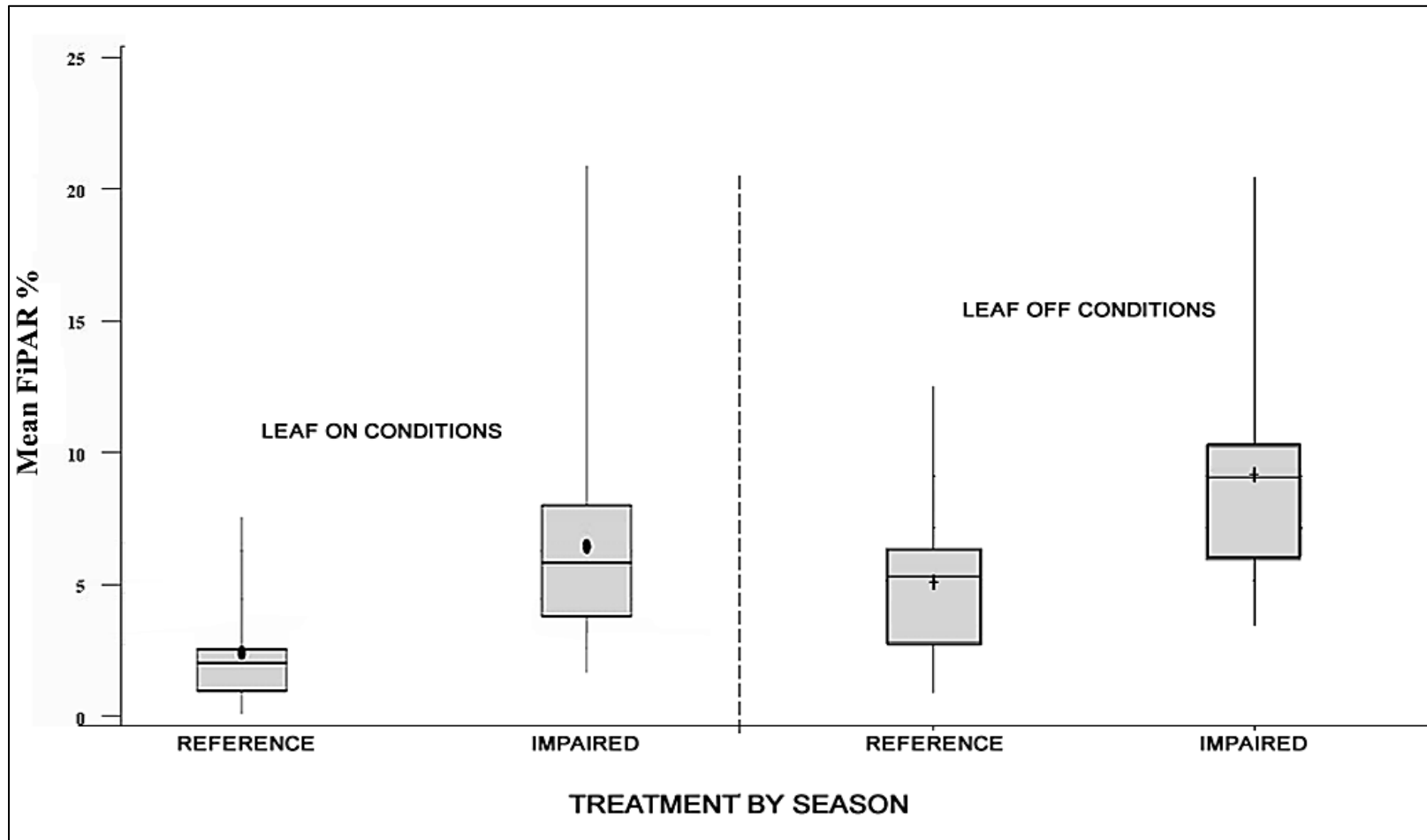


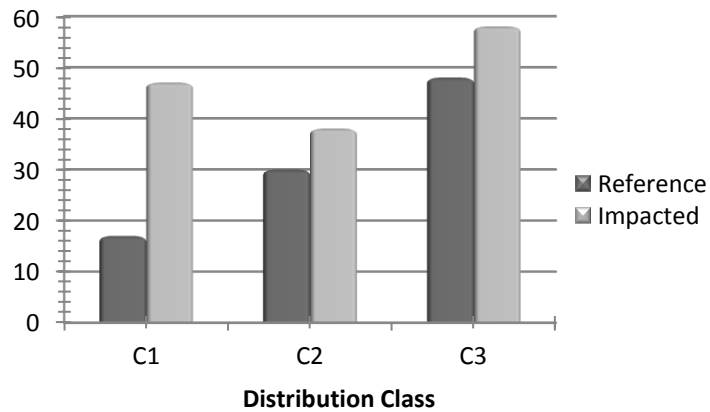
Figure 12. Boxplot of mean percentage of photosynthetically active radiation (FiPAR) differences between reference and impacted sites for two measurement seasons, leaf on and leaf off, for research conducted in the Great Smoky Mountains National Park, USA. Mean FiPAR percentage is the fraction of photosynthetically active radiation available for productivity in aquatic and vegetative ecosystems.

Large Woody Debris

Large woody debris (LWD), also known as coarse woody debris (CWD), is an important source of organic matter and nutrients that are vital to ecosystem health and productivity. Several potential sources of LWD in forest systems exist, including natural tree mortality, fires, storms, and insects and disease. The density and distribution of LWD in streams is important for channel stabilization and hydrologic complexity, and provides critical habitat and cover for fish and macroinvertebrates (Angermeier and Karr 1984, Davis et al. 2001). Organic material entrained by LWD jams provides a readily available food source for the shredding organisms, which break this material down into fine particulate organic matter (FPOM) that is then consumed by collector/gatherer organisms (Bilby and Bisson 1998). This increase in resource availability often results in some of the highest invertebrate densities (Huryn and Wallace 1987, Richardson 1991). Eastern hemlock mortality initiated by HWA results in delimbing, crown die-back, and eventually tree fall. The result of the mortality process is varying quantities of LWD of all size classes in the riparian forest understory and in the stream channel.

Results from this study suggest that hemlock mortality at impacted sites has resulted in a spike of LWD material into the stream environment. Increased availability of LWD in aquatic systems often serves as a vital source of allochthonous nutrients for aquatic biota and increases the quantity of available habitat (Stevens 1997). Large woody debris inputs between reference and impacted streams were found to be significantly different ($p < 0.01$, $\chi^2 = 15.7$, $DF = 4$) with impacted streams receiving 143 pieces compared to 95 pieces at reference streams (Figure 13). Increased density of the D2 (25.5-50.8 cm) and D3 (50.9-76.2 cm) size classes were observed for impacted streams. Reference streams were also dominated by shorter lengths of LWD than impacted streams ($P < 0.05$, $\chi^2 = 8.38$, $DF = 4$). Both reference and impacted stream sites were

Mean Counts per Stream Reach

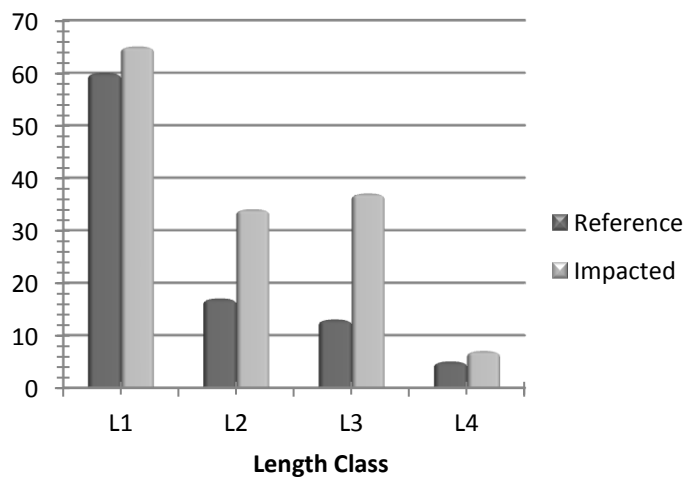


C1 : Across Channel

C2 : Along Bank

C3 : In Channel

Distribution Classes



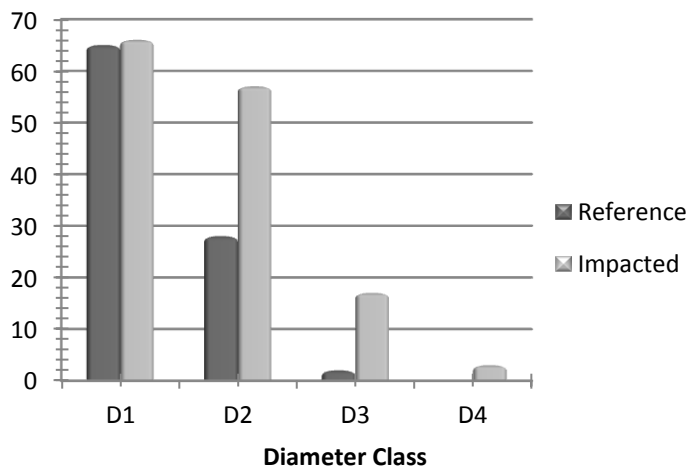
L1 : 1-3.0 Meters

L2 : 3.01-5.0 Meters

L3 : > 5.01 Meters

L4 : Rootwads

Length Classes



D1 : 10.2 – 25.4 cm

D2 : 25.5-50.8 cm

D3 : 50.9-76.2 cm

D4 : > 76.2 cm

Diameter Classes

(See Figure 8)

Figure 13. Large woody debris (LWD) density by distribution class, length class, and diameter class for reference (n=5) and impacted streams (n=5) in response to HWA-induced hemlock mortality in the Great Smoky Mountains National Park, USA.

dominated by the L1 length class; however, impacted stream sites showed an increased density of the L2 and L3 length classes with sizes greater than three meters. This was a result of the impacted streams receiving more LWD in the form of larger limbs and branches from the mortality and decay process. Many of the smaller limbs and twigs likely had already biodegraded or had been washed downstream. The remaining LWD materials were the larger size classes that are more resistant to movement during heavy stream flows.

Increasing LWD in terrestrial and aquatic environments can have many beneficial effects. In forest stands, biodegradation of LWD returns valuable nutrients back to the soil. The presence and distribution of varying sizes of LWD help to rapidly dissipate energy in high gradient streams by increasing flow resistance (Wallace et al. 1995), which may serve an increasingly important role in previously hemlock-dominated streams. Prior research has shown that hemlock mortality alters evapotranspiration and results in persistent increases in stream discharge (Ford and Vose 2007). Many species of macroinvertebrates will feed on or colonize LWD in streams and thus increased LWD may result in changes in benthic macroinvertebrate abundance or richness. Large woody debris serves as a storage location of organic matter and sediment and has the potential to modify nutrient movement and transformation. This process has been linked to increased concentrations of chloride, sodium, and silicon (Bisson et al. 1987).

Large woody debris is also important for the formation of riparian habitat through the accumulation of LWD into debris dams. Growth of debris dams continues until the dams reduce the width of stream flow, eventually forming stream bars that, over time, will evolve into islands or floodplains. Once formed, these islands provide habitat for vegetation establishment and initiates the process of forest succession (Abbe et al. 1993, Nakamura and Swanson 1993). The increased quantity of LWD, as a result of hemlock mortality observed in the streams of this study, has already

initiated this process in some of the impacted stream reaches. Increased LWD from hemlock mortality will likely result in modifications to channel morphology and impact the macroinvertebrate community.

Water Quality and Temperature

Streams of the GSMNP provide many ecological services that include providing habitat for flora and fauna, providing a water supply for human and wildlife consumption, and serving as the primary pathway for the transport of nutrients, sediments, and pollutants. Decreases in forest canopies, like those found in this study, alter the interception of precipitation and increase nitrification and mineralization. These processes have been shown to result in increased sediment and nutrient concentrations in groundwater and increased nutrient leaching into adjacent streams (Yorks et al. 2000). Sedimentation and nutrient influx in aquatic systems has the potential to impact water quality and ecological processes of the receiving body of water.

Water quality monitoring and assessment is an important tool that is often undertaken to evaluate these impacts and to elucidate the health of aquatic systems. Chemical parameters (metrics) evaluated in this study were chosen for their ability to serve as indicators of habitat and macronutrient availability, both of which are necessary for growth and reproduction of aquatic biota (Davis et al. 2001). Stream pH is one of the most significant chemical parameters in terms of biological impact and was found to be significantly different between reference and impacted streams ($p < 0.0001$, $F = 48.60$, $DF = 17$). Impacted streams exhibited a higher pH value at 6.85 ($SE = 0.03$) than reference streams at a pH of 6.53 ($SE = 0.03$) (Table 7). The pH of water is the measure of the concentration of hydrogen ions, and is expressed on a scale of 0 to 14 standard units (SU). Solutions with values higher than 7 SU are considered basic or alkaline and have a higher

Table 7. Chemical parameters found to be significantly different between reference and impacted streams as a result of HWA-induced eastern hemlock mortality in the Great Smoky Mountains National Park, USA. Reference streams represented a mild to moderate level of HWA impact, while impacted streams represented complete hemlock mortality.

Parameter	P-Value	F Value	DF	Reference Streams		Impacted Streams	
				Mean	SE	Mean	SE
pH	< 0.00	48.60	16	6.55	6.03	6.85	0.03
ANC	0.00	14.32	16	62.73	7.81	102.39	6.99
Chloride	0.03	6.08	16	11.44	0.92	14.47	0.82
H+ Ion	< 0.00	33.17	16	0.29	0.02	0.14	0.02
Potassium	0.00	18.92	16	10.90	1.20	17.92	1.08
Magnesium	0.00	12.33	16	23.67	1.54	30.92	1.38
Copper*	0.05	4.63	16	0.00	0.01	0.02	0.01
Silicon	0.00	19.43	16	3.43	0.17	4.42	0.15
Anions	0.03	6.08	16	68.92	5.60	50.41	5.00
Cations	0.00	12.84	16	142.40	8.13	181.52	7.27
TotIonStr	0.01	8.93	16	274.65	14.96	334.60	13.38
Sodium	0.03	7.36	7	45.83	4.21	61.15	3.77
Nitrate	0.04	6.52	7	25.61	4.99	8.48	4.47

*Non-normal data transformed with rank transformation.

concentration of hydroxide ions. Solutions with values lower than 7 SU are considered acidic and have higher concentrations of hydrogen ions. A difference of 0.32 SU, when comparing reference streams to impacted streams, is a significant change in pH. The pH scale is a log scale, and for every unit change in pH, there is approximately a 10-fold change in the hydrogen ion concentration. Impacted streams had 3.2 times more hydroxide ions and were therefore 3.2 times more basic than reference streams.

Researchers have speculated that EH mortality would lead to allochthonous contributions from adjacent dead or declining eastern hemlock trees (Evans 2002). In a study evaluating the impacts of HWA feeding and hemlock mortality on ectomycorrhizal (EM) communities, Sirulnik et al. (2005) concluded that HWA-induced defoliation resulted in lower soil pH, decreased EM communities, and higher soil moisture. Forest soils beneath healthy, hemlock-dominated stands exhibit lower pH values than hardwood-dominated soils in response to inputs from EH litter, which is high in organic acids (tannic acid) (Millen 1995, Finzi et al. 1998a, Eschtruth et al. 2006). At impacted sites, the inability of hemlock to regenerate has resulted in sites being dominated by non-hemlock species. The conversion from primarily hemlock to a hardwood species dominated condition, likely altered the soil pH, which subsequently resulted in increased stream pH values through run-off and groundwater flow. Data from this study indicated spikes in stream acidity were most likely to occur during early stages of HWA infestation. The mean pH at impacted sites, which represents several years post-mortality, was 6.85 and similar to those values determined previously for streams in the GSMNP (Roberts et al. 2009), illustrating that streams recover their pre-HWA pH levels within a relatively short time frame.

The significance of the observed pH difference in terms of biological impact is unknown. Most freshwater fish prefer water with a pH range between 6.5 and 8.4. Reference streams, with a

mean pH of 6.53, were on the threshold of being undesirable for fish. Fish populations were not assessed in this study and therefore no conclusions can be drawn as to the impacts of the observed pH values on fish populations. This study focused on first-order, headwater streams and did not assess impacts at any other level or watershed size. Expected differences in pH would likely be less pronounced as stream order and drainage area increase.

Recent concerns over stream acidification from acid rain inputs during storm events have prompted several research projects in the GSMNP to assess the potential impacts of atmospheric deposition to stream water chemistry and aquatic biota. Storm events often result in sharp depressions in pH ranging from 0.7 standard units to drops as severe as two full standard units (Neff et al. 2008). The potential exists for confounding impacts to stream pH from hemlock mortality and episodic acidification from atmospheric deposition, with the potential for pH values to drop significantly lower than the minimum of 6.5 needed for fish survival. The combined effects of pH and episodic acidification could be highly detrimental to the survival of the native brook trout, and further research should be conducted to evaluate this potential.

Acid neutralization capacity (ANC) is defined as the quantity of acid needed to change the pH value of a sample to another specified value (Stumm and Morgan 1981), and was significantly different between stream conditions in this study ($p=0.002$, $F=14.32$, $DF=17$). Impacted streams had a higher mean ANC at 102.4 $\mu\text{eq/L}$ ($SE=7.0$) than reference streams at a mean ANC of 62.7 $\mu\text{eq/L}$ ($SE=7.8$). Larger values for ANC suggest an increased capacity of the receiving body of water to buffer against spikes in acidity. The ANC levels observed in impacted streams will result in increased capacity to buffer, thereby reducing sensitivity to acidification. This is counter to the original hypothesis that eastern hemlock mortality would result in decreased ANC in impacted streams and therefore increase stream vulnerability to high input events such as episodic

acidification. However, it is likely that the initial stream response to HWA or loss of EH did reduce ANC values and that reference streams are capturing the early impact response of the aquatic systems. The US EPA classifies base flow ANC values in the range of 0-50 $\mu\text{eq/L}$, as extremely sensitive to acidification. Reference streams exhibited values approaching the upper threshold of this range, indicating these streams were already sensitive to acidification. Lower ANC values observed at reference sites, coupled with decreased pH values, suggested that hemlock mortality did influence stream chemistry and will likely result in impacted systems being vulnerable (at least temporarily) to nutrient eutrophication and to episodic acidification during storm events.

The primary concern of altered ANC in the GSMNP is the potential for impacts to native brook trout from decreased buffering capacity. Evans et al. (1996) suggested that EH mortality would lead to decreases in ANC, allowing more frequent and intense spikes in stream acidity to occur, further stressing this sensitive fish. Data from reference sites concurred with Evans et al. (1996) and revealed lower pH and ANC values suggesting a decreased ability to buffer against increases in acidity. Fortunately, these results also suggested that streams recover from the water quality impacts of hemlock mortality in a relatively short time frame.

Nitrogen is a macronutrient that is essential for all living things and nitrates are the primary source of nitrogen for aquatic plants, such as algae. Nitrogen is considered a mobile nutrient in both plants and soils and is usually present in large quantities in most soils. Nitrates are an oxidized form of nitrogen and naturally occur in soil and water. Studies have demonstrated that excess nitrate-nitrogen ($\text{NO}_3\text{-N}$) leakage from forested systems in response to insect-induced defoliation resulted in eutrophic stream conditions (Swank et al. 1981, Ricassi and Scanlon 2008). Increased levels of nitrate have also been shown to have indirect impacts on the health of aquatic biota, like benthic macroinvertebrates, snails, and fish (Waring and Running 2007). Research by Kramer (1987),

demonstrated that excess quantities of nitrates in aquatic systems allowed aquatic plants and algae to grow unchecked, resulting in unstable dissolved oxygen levels. Fish and benthic macroinvertebrates are dependent upon dissolved oxygen and unstable levels can result in stressful conditions.

Mean nitrate levels were significantly different ($p=0.011$, $F=8.82$, $DF=9$) between reference streams and impacted streams (Table 7, Figure 14). Mean nitrate levels were approximately three times higher in reference streams at $25.6 \mu\text{eq/L}$ ($SE=5.0$) when compared to impacted streams at $8.5 \mu\text{eq/L}$ ($SE=4.5$). Reference stands had varying levels of EH health and HWA presence, though only a small amount of tree mortality was present. Nitrogen pools and forest floor mass under healthy hemlock trees have been shown to be significantly higher when compared to several other species (primarily hardwoods) (Finzi et al. 1998b). However, the levels that were observed in the present study suggested that nitrate levels at reference sites were elevated above normal levels. Lewis and Likens (2007) found pre-defoliation mean stream nitrate concentration of $<0.04\text{-mg/L}$ ($\sim 6.37 \mu\text{eq/L}$) at hemlock-dominated sites in Pennsylvania. Mean concentrations found at reference sites in this study were still four times higher than concentrations found by Lewis and Likens (2007). In a study at Delaware Water Gap National Recreation Area, researchers found nitrate concentrations ranging from 0 to $19.35\text{-}\mu\text{eq/L}$ for healthy hemlock stands (Snyder et al. 2002). Their results also demonstrated that nitrate levels peaked at 1.4 mg/L ($\sim 22.58 \mu\text{eq/L}$) the summer following insect-initiated defoliation. However, the source of defoliation for their study was the elm spanworm (*Ennomos subsignarius* Hübner), which has a different feeding pattern and impacts hemlock in a different way.

The elm spanworm is an herbivore and feeds on nitrogen-rich hemlock needles, while HWA is a piercing-sucking insect and does not consume the needle material. Feeding by HWA forces

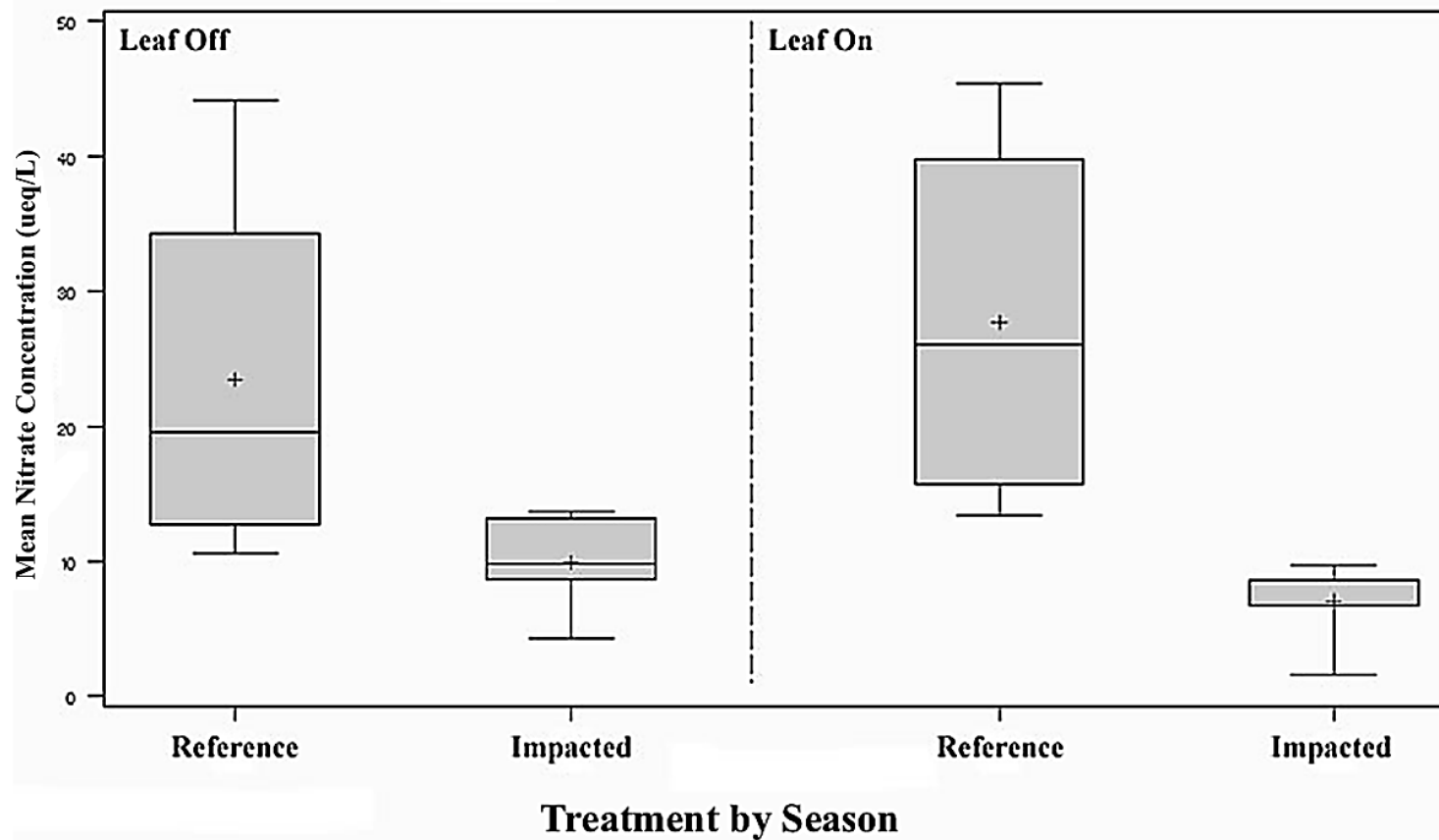


Figure 14. Boxplot comparison of mean nitrate concentrations of reference and impacted streams and across seasons. This analysis was conducted to assess changes in water quality in response to HWA-induced eastern hemlock mortality in the Great Smoky Mountains National Park, USA.

needles to desiccate and drop from the tree, still rich in nitrogen, where they contribute to nitrate leaching (Yorks et al. 2000, Lovett et al. 2002, Kominoski et al. 2008). Research studies evaluating insect defoliations by various species have suggested an increased loss of nitrogen from forested ecosystems in soil, and drainage water can result in increased nitrogen leaching into aquatic systems (Swank et al. 1981, Swank 1988, McDonald et al. 1992, Webb et al. 1995, Swank and Vose 1997, Eshleman et al. 1998, Reynolds et al. 2000, Lewis and Likens 2007). Several explanations are possible for elevated stream nitrate concentrations and include accelerated nitrogen mineralization, increased nitrification, and decreased nutrient uptake in the absence of vegetation at impacted sites (Swank et al. 1981, Lewis and Likens 2007, Riscassi and Scanlon 2009).

Disturbance mediated nitrogen leakage follows a similar pattern regardless of the type of defoliation event (e.g. fire, harvest, or insects). The disturbance initiates a large and immediate spike in stream nitrate concentrations, followed by a relatively rapid nitrate recovery to pre-defoliation levels (Swank et al. 1981, Swank 1988, Swank and Vose 1997, Eshleman et al. 1998, Lewis and Likens 2007). Results from data analyses suggested that impacted streams (post-mortality) were already exhibiting recovery from elevated nitrate with mean concentrations that were 1/3 of those observed for reference streams and similar to pre-defoliation levels observed in other studies.

Elevated nitrate levels have the potential for significant impacts on aquatic biota in the affected streams. High nitrate levels can result in fish mortality and levels greater than 30 ppm are sufficient to inhibit growth, impair immune systems, and cause stress in some aquatic species (Davis et al. 2001). Although nitrate levels were significantly different between reference and impacted streams, concentration levels near the 30 ppm threshold were not found. Results from

this study suggested that spikes in nitrate, regardless of the exact mechanisms behind them, were likely to be short-term and aquatic systems should recover to nitrate concentrations approximating pre-HWA infestation levels.

Another water quality parameter found to differ significantly between reference and impacted streams was silicon (Si^+). Silicon is more commonly distributed in the form of dust or sand or other various forms of silicon dioxide or silicates. Silicon is a biologically essential element in the metabolism of plants; however, it is only found in trace levels in animals. Silicon is a component of several minerals and is released during weathering processes. Silicates are structural materials used in skeletal formation by diatoms. The primary negative effect of increased silicon in water is the process of siltation. Increased siltation in streams can degrade habitat by covering substrate and filling in interstitial spaces, crucial areas for invertebrates and stream fishes. Abnormally high levels of silicon can also limit algal growth. In the present study, results from water quality analyses (Table 7) indicated significant differences in the amount of silicon in reference streams when compared to impacted streams ($p=0.011$, $F=12.02$, $DF=7$). Reference streams had a mean concentration of 3.4 ppm ($SE=0.2$), while impacted sites had a mean concentration of 4.4 ppm ($SE=0.2$).

Silicon concentration in streams has been shown to fluctuate on an annual basis in response to cyclical patterns of algal growth (Hunt and Wilson 1986); however, data from the present study did not show seasonal differences in silicon concentration ($p=0.73$, $F=0.13$, $DF=7$). The differences observed in mean silicon concentrations between reference and impacted streams, although statistically different, do not pose any real threat or impacts on water quality. The increase observed at impacted sites was most likely caused by increased sedimentation and nutrient leaching into adjacent streams from the surrounding watershed as a result of widespread

eastern hemlock mortality. In addition, increased LWD inputs have been shown to increase silicon levels from trapping of sediment behind LWD jams (Bisson et al. 1987).

Loss of vegetative cover, such as that which occurs with insect-induced defoliations or mortality, often results in localized, increased sedimentation to adjacent streams (Dajoz 2000). Widespread hemlock mortality results in increased soil nutrient levels; trees release bound nutrients back into the soil as they succumb to the effects of hemlock woolly adelgid. In another study, loss of overstory EH canopy resulted in decreased interception and increased sedimentation and nutrient leaching via the soil-groundwater pathway (Schowalter 1981). The removal of the forest overstory from EH mortality has not resulted in re-vegetation by herbaceous or shrubby vegetation, which normally would limit the loss of nutrients (Marks and Bormann 1972). Newly released nutrients are ultimately carried into the adjacent stream. This process was the most probable explanation for the increased nutrient levels observed in impacted streams in this study. Other nutrients that were found to be significantly different between reference streams and impacted streams include sodium ($P=0.03$, $F=7.36$, $DF=17$), potassium ($P<0.001$, $F=18.92$, $DF=17$), magnesium ($P<0.01$, $F=12.33$, $DF=17$), chloride ($P=0.025$, $F=6.08$, $DF=17$), and copper ($P=0.047$, $F=4.63$, $DF=17$).

Sodium is a nutrient that is naturally weathered from rocks and soils, and is readily soluble in water. The high solubility allows it to be present in large quantities in oceans and other bodies of water (Subbarao et al. 2003). The sodium ion is a component of many minerals and is an essential element that is required for animal life. Many plants also require sodium in order to carry out normal life processes such as the conduction of nerve impulses, chlorophyll synthesis, and osmotic balancing between cells and interstitial fluids (Hammond 2004, Waring and Running 2007). The mean sodium concentration in reference streams was $45.83 \mu\text{eq/L}$

(SE=4.21), while impacted sites exhibited an increased concentration of 61.15 $\mu\text{eq/L}$ (SE=3.77). Even at moderate levels of herbivory, Schowalter et al. (1986) found that up to 300 percent of plant sodium could be returned to the forest floor in litter. Increased concentrations observed at impacted sites appeared to be a result of increased inputs from the processing of EH litter. Although significantly different, the levels detected for both reference and impacted streams were within acceptable ranges and are not likely to be harmful.

Potassium is a macronutrient that is present in relatively large quantities in most soils and concentrations often exceed what is needed by adjacent vegetation. Potassium is essential for many plant processes including photosynthesis, starch synthesis, and is used in enzyme production. Potassium is considered a mobile nutrient and for this reason is easily leached from plants and soils (Hammond 2004, Waring and Running 2007). Mean potassium concentration was found to be significantly different between reference streams, with 10.9 $\mu\text{eq/L}$ (SE=1.2), and impacted streams with 17.92 $\mu\text{eq/L}$ (SE=1.1). The observed increase in potassium was a sizable quantity, and was most likely attributable to increased soil availability from mineralization of dead hemlock.

Magnesium is a macronutrient that contributes to the production of chlorophyll, where it serves as a structural constituent. It is required for the activation and function of growth enzymes and in phosphate transfer and ATP production (Hammond 2004). Mean magnesium concentrations were significantly different with reference streams having a mean concentration of 23.67 $\mu\text{eq/L}$ (SE=1.5) and impacted streams having a mean concentration of 30.92 $\mu\text{eq/L}$ (SE=1.4). Magnesium is relatively immobile in soil and the increased concentration at impacted sites was most likely a result of increased mineralization of woody debris and needle material being contributed to the stream when eastern hemlock trees died.

Chlorine is a macronutrient that is necessary in photosynthesis. This nutrient is essential for balancing ion charge, plant metabolism, and stomatal regulation. Chlorine is fairly mobile in soil and availability is primarily regulated by the flow of soil water (White and Broadley 2001, Hammond 2004). Chlorine concentration in the form of the chloride ion (Cl^-) was statistically different between reference streams (Table 7), with a mean concentration of $11.44 \mu\text{eq/L}$ ($\text{SE}=0.9$), and impacted streams with a mean concentration of $14.47 \mu\text{eq/L}$ ($\text{SE}=0.8$). Increased concentrations at impacted stream sites were most likely attributable to increased soil availability and increased soil water flow in response to HWA-induced hemlock mortality.

The only micronutrient that was significantly different was copper. Copper is one of the most abundant micronutrients and is believed to serve as a catalyst and plant growth regulator. This nutrient is primarily concentrated in plant roots where it is immobile although it is mobile in soil. Copper is important in nitrogen metabolism and plays a role in biological electron transport and oxygen transportation (Hammond 2004). Concentrations of copper were undetectable in reference streams, while impacted streams had a mean concentration of 0.02 ppm ($\text{SE}=0.01$). Low level concentrations are normal for micronutrients because plants only require small quantities. At higher concentrations, copper can be poisonous to living organisms. Increased copper concentration may be caused by increased surface run-off and groundwater flow which occurs when a stand undergoes widespread, insect-induced mortality like that observed at our impacted sites.

Several stream nutrient concentrations were different between reference and impacted streams. However, none of the nutrients exhibited concentrations that warrant concern for water quality as it relates to aquatic biota. Water quality analyses indicated that HWA-induced eastern hemlock mortality impacted water quality in much the same way as other insect defoliations or

forest harvesting practices. Loss of forest cover, coupled with mineralization of plant materials and nutrient leaching resulted in altered nutrient concentrations in stream water. Under normal harvest conditions, vegetative regeneration at the site would occur rapidly and help to ameliorate some of the changes that were observed in nutrient concentrations. However, hemlock mortality from HWA does not result in normal vegetative regeneration. Results of the present study indicated that impacted sites are not undergoing normal plant succession, but rather are experiencing an increase in the distribution and density of RR. The ability of RR to prevent other vegetation from regenerating after hemlock mortality will have long-term implications for site recovery. Increased nutrient leaching and sedimentation processes will continue to be elevated at impacted stream sites until those sites have been regenerated by a variety of woody species.

Stream temperature was also evaluated in the assessment of stream water quality in order to evaluate the impacts of HWA-induced eastern hemlock mortality on headwater stream temperature in the GSMNP. Temperature plays a critical role in stream ecosystem health and function. Stream temperature determines the quantity of oxygen that can be dissolved in water and can affect the photosynthetic rate of aquatic plants. Water temperature also affects body temperature of aquatic organisms and influences activity level, growth rates, and reproduction (Beschta et al. 1987). Stream temperature also dictates the timing of emergence for benthic macroinvertebrates and large alterations to thermal regimes can result in severe impacts to populations (Vannote and Sweeney 1980). Increases in stream temperature in low order, headwater streams in the GSMNP also have the potential to severely impact the native brook trout, a species that depends on cool water temperatures for survival.

Shading provided by the hemlock tree has been shown to be critical for maintaining cool stream temperatures and stable stream flows (Alexander and Shepperd 1990, Evans et al. 1996,

Snyder et al. 1998, Hadley et al. 2008). Also, harvesting activities in riparian areas often result in increased stream temperatures with severity of the alteration varying among sites and regions (Beschta et al. 1987, Johnson and Jones 2000). Fully stocked EH stands often create dense shading resulting in sparse understory vegetation. The amount of solar radiation received by streams has been demonstrated to differ when comparing hemlock streams to hardwood streams (Rowell and Sobczak 2008). Results from the present study also indicated that EH mortality impacts canopy coverage and solar radiation levels (FiPAR), and results in more stable stream temperatures.

Stream temperature data were collected hourly over a seven-month period, from September 2009 to March 2010. Mean weekly temperatures were significantly different ($P < 0.0001$, $DF = 241$, $F = 166.94$) between reference and impacted streams (Figure 15). Reference streams in this study had a mean weekly temperature of 8.49 C (SE=0.35), while impacted streams had a mean weekly temperature of 7.15 C (SE=0.36). Mean monthly temperature was significantly different between reference and impacted streams ($P < 0.0001$, $DF = 57$, $F = 51.72$) with reference streams having a mean monthly temperature of 8.45 C (SE=0.33), while a smaller mean monthly temperature value, 7.11 C (SE=0.35), was measured at impacted sites (Figure 16).

The stream temperature patterns observed, cooler in impacted streams and warmer at reference streams, further support the importance of hemlock canopies in providing thermal protection during the cooler months (Sept-March). According to Snyder et al. (2002), streams dominated by hemlock exhibited consistently higher temperatures in the cooler months (December through February). In addition, their study found median daily temperatures during peak summer months were 1 - 2 C cooler in hemlock-dominated streams.

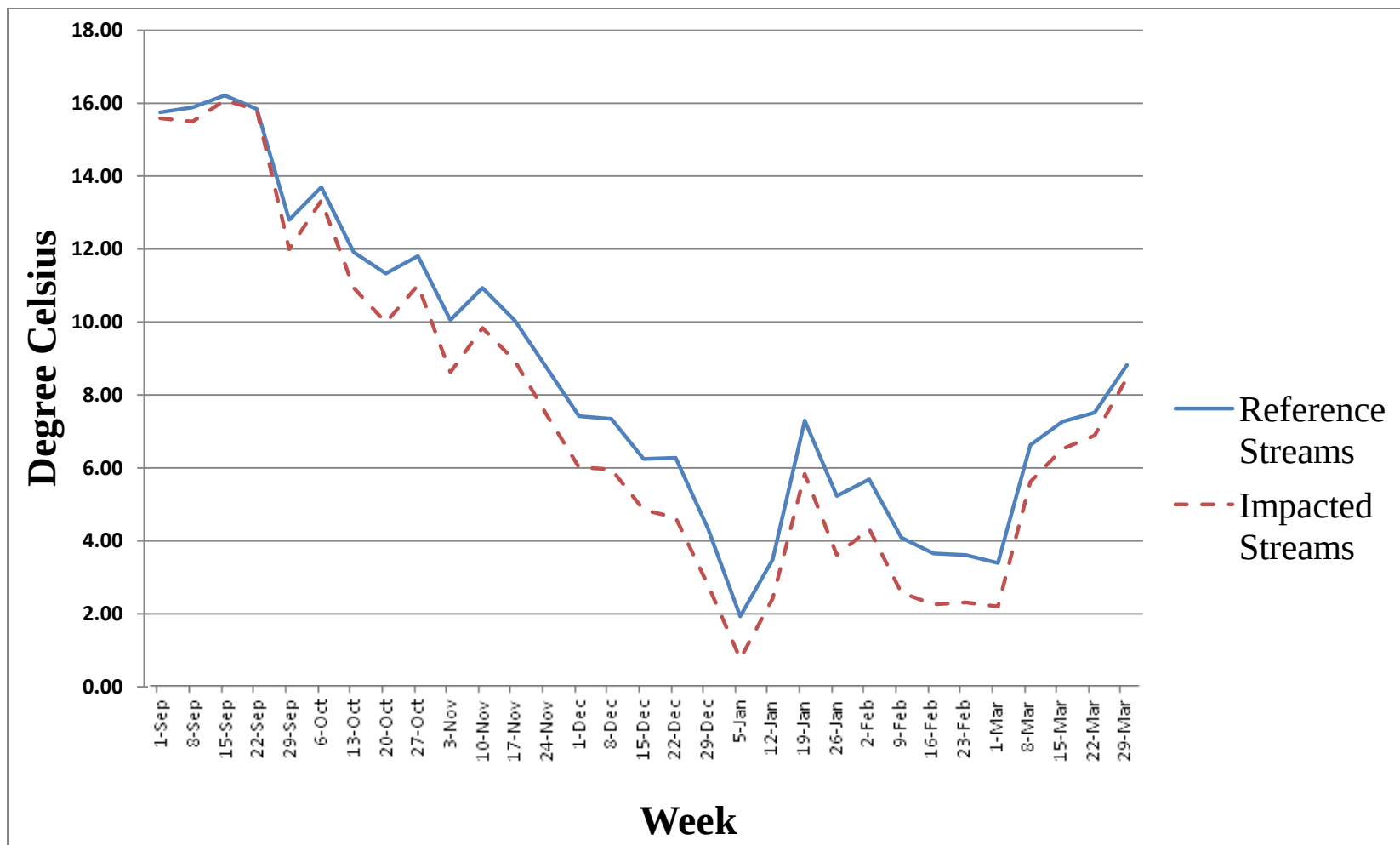


Figure 15. Mean weekly water temperature for reference and impacted stream conditions in the Great Smoky Mountains National Park, USA. Reference streams represented a mild level of HWA presence, while impacted streams represented complete hemlock mortality.

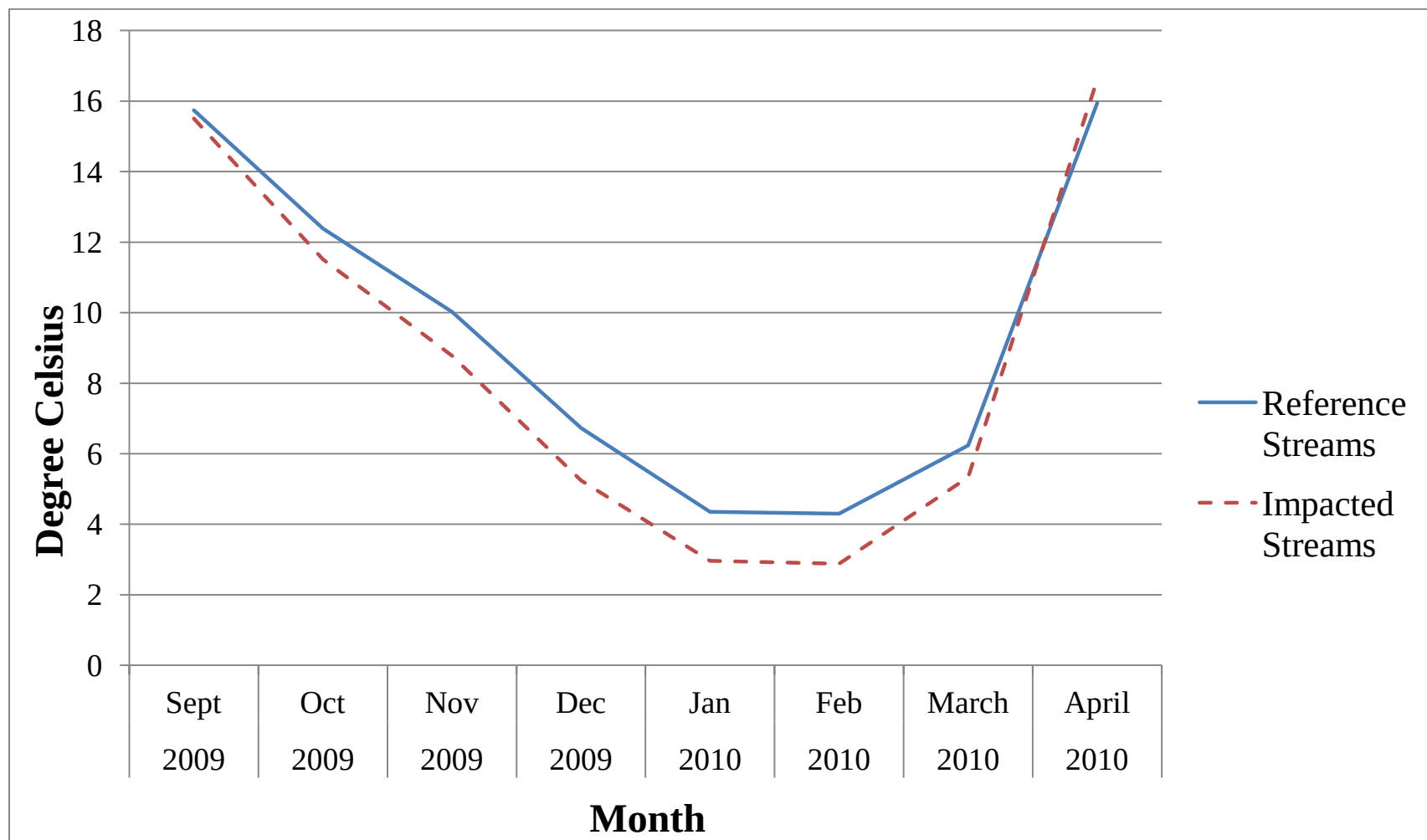


Figure 16. Mean monthly water temperature for reference and impacted stream conditions in the Great Smoky Mountains National Park, USA. Reference streams represented a mild level of HWA presence, while impacted streams represented complete hemlock mortality.

The impact of EH mortality on stream temperatures is more easily illustrated when comparing diurnal variation in temperature between reference and impacted streams (Figure 17). Mean diurnal variation in temperature was calculated as the difference between the maximum daily stream temperature and minimum daily stream temperature across the study period. An ANOVA comparison of mean diurnal temperature variance indicated reference and impacted streams were significantly different ($P < 0.0001$, $DF = 421$, $F = 65.73$). Reference streams had less mean daily fluctuation in temperatures, while impacted streams exhibited diurnal fluctuations up to two times higher. Diurnal variation for reference streams ranged from 0.11 - 2.89 C, while impacted streams exhibited a range of diurnal temperature variation from 0.20 - 3.91 C. Streams flowing through hemlock-dominated ravines have lower temperatures by as much as 5 C (Evans et al. 1996). Similar temperature changes were found in the present study with intact hemlock-dominated streams exhibiting much less daily variability and warmer winter temperatures than streams where large scale hemlock mortality had already occurred.

Stream temperature alteration is a common response to forest defoliation or forest canopy removal (Johnson and Jones 2000). However, HWA-induced defoliations do not follow typical insect defoliation patterns. The mortality process brought on by this pest was much slower and more severe than many other forest pests, and was exacerbated by the lack of regeneration occurring at impacted sites. Typical forest stands will eventually regenerate after a defoliation event or forest harvesting; however, HWA presence will continue to prevent EH regeneration. The presence of RR in those stands will further complicate stand recovery by preventing woody regeneration and likely lead to long-term alterations to the thermal regime of the affected streams.

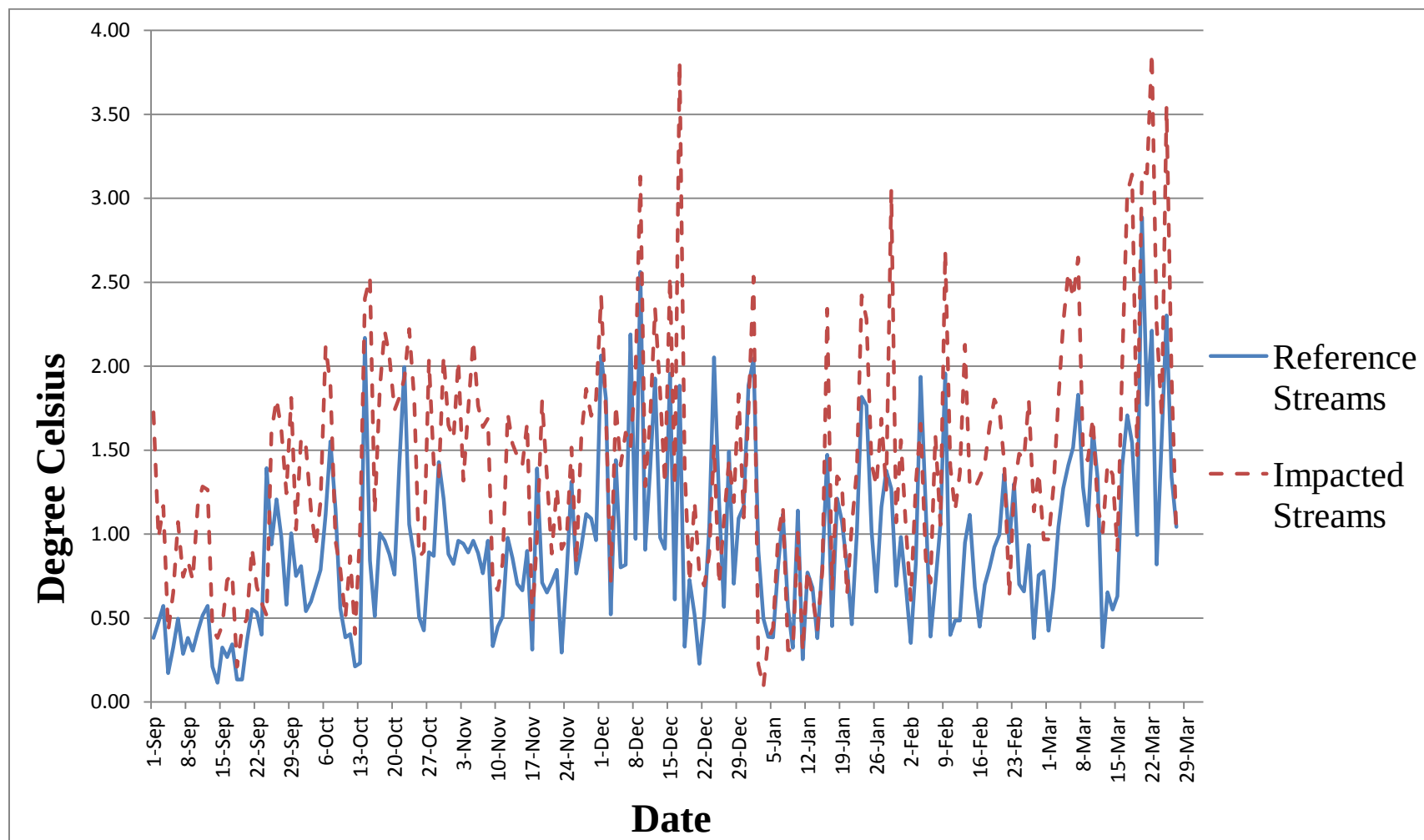


Figure 17. Mean diurnal water temperature variation for reference streams compared to impacted streams in response to HWA-induced eastern hemlock mortality in the Great Smoky Mountains National Park, USA. Reference streams represented a mild level of HWA presence, while impacted streams represented complete hemlock mortality.

Macroinvertebrate Analyses

Aquatic macroinvertebrates include crayfish, mussels, aquatic worms and snails, and the larvae of aquatic insects. Macroinvertebrate species abundance and diversity are important predictors of aquatic system health because these organisms are extremely vulnerable to changes in stream temperature, water quality, and altered food resources as a result of their limited mobility and short life spans. Macroinvertebrate metrics were selected from four major categories that collectively provide a fairly complete picture of aquatic system health. These categories included measures of community composition, measures of community richness, measures of tolerant taxa, and measures of feeding guild structure.

Significant differences between reference streams and impacted streams occurred for several of the metrics and across all four categories. Pooled data (qualitative and quantitative samples) from macroinvertebrate analyses yielded a total of 144 taxa; 12 taxa were identified to species, 122 to genus, 19 to family, and 3 to order. The total number taxa collected for individual streams exhibited a range from 51 to 85. A total of 54 taxa were determined to be infrequent taxa, defined as those taxa that were collected in three or fewer streams. The number of infrequent taxa collected per stream ranged between 4 and 14. Total pooled macroinvertebrate density (total number of individuals) was 13,875 and individual streams ranged between 815 and 1893 individuals. Analyses of data pooled across habitat types, representing all data collected both quantitative and qualitative, failed to reject the null hypothesis that community richness measures were not different between stream conditions ($P > 0.05$, student's *t*, all richness metrics). Community richness measures included the total number of taxa collected, number of Ephemeroptera (E) taxa, number of Plecoptera (P) taxa, number of Trichoptera (T) taxa, number of EPT taxa (E+P+T), and the number of Diptera taxa (Table 8).

Table 8. Measures of community richness from data pooled across habitat types (qualitative and quantitative) for reference and impacted streams used in the assessment of HWA-induced impacts to ecosystem health in the Great Smoky Mountains National Park, USA.

Metric	Reference Streams					Impacted Streams					T Test PValue
	Jones Branch	Cole Creek	Toms Creek	Crying Creek	Noisy Creek	Den Branch	Sag Branch	Hurricane Creek	McKee Branch	Clontz Branch	
Total No. taxa	52	77	69	51	76	78	54	85	59	73	0.57
No. EPT taxa	31	44	44	34	47	53	39	47	35	39	0.58
No. Ephemeroptera Taxa	6	11	11	7	11	10	11	12	9	11	0.29
No. Plecoptera Taxa	13	15	14	13	16	20	14	19	12	13	0.44
No. Trichoptera Taxa	12	18	19	14	20	23	14	16	14	15	0.93
No. <i>Pteronarcys</i> Taxa	0	0	0	0	0	1	1	1	1	0	0.00
No. Diptera taxa	11	15	12	10	16	13	12	20	11	21	0.31

Research at Delaware Water Gap National Park (DEWA) comparing hemlock-dominated streams and hardwood-dominated streams found hemlock-dominated streams supported a higher diversity of EPTs while hardwood-dominated streams had higher species abundance (Snyder et al. 2002). Results from research conducted at DEWA suggested that forest type was a determinant of macroinvertebrate species diversity and abundance (Snyder et al. 2002). As hemlock stands succumb to effects of HWA and forest stands begin to convert to a more hardwood species dominated condition, the assumption is that species composition of the streams draining those stands will also be affected. Species diversity should decrease and overall densities should increase from forest conversion to hardwood species (Snyder et al. 2002). However, data from the present study does not support this assumption. Impacted sites have not experienced regeneration of any woody species; whether hardwood or coniferous. Future regeneration patterns of riparian vegetation in once hemlock- dominated stands will be the final determinant of post-HWA stream macroinvertebrate diversity and abundance.

The only community richness metric found to be significantly different was the total number of *Pteronarcys* specimens ($P=0.016$, student's *t*). The Pteronarcyidae are plecopteran stoneflies that exhibit a much longer life cycle than many of the other macroinvertebrate taxa, and their presence suggests long-standing stream health. Hemlock-dominated streams were devoid of this taxon, while sites with hemlock mortality had them represented in 4 of the 5 impacted streams. The presence of this taxon in the areas with extensive hemlock mortality suggested that the changing forest conditions and their effects on the aquatic environment were actually more favorable for longer-lived group such as the *Pteronarcys* stoneflies. This taxon has a tolerance value of zero indicating that they are extremely sensitive (Merritt et al. 2007), and may be more sensitive to the pH levels that occur in hemlock-dominated streams and would

therefore fare better in the impacted streams, where pH levels are becoming less acidic. Another potential explanation for this difference could be the response to increased nitrate levels of reference streams. The sensitivity of this taxon may make it vulnerable to small increases in any of the water quality parameters, including stream temperature. However, the most probable explanation for the observed differences in presence/absence of Pteronarcyids in this study is likely a result of the increased large woody debris in impacted streams. Pteronarcyids preferentially occur in leaf and woody debris packs, which they use as habitat and source of food (Merritt et al. 2007).

Community composition measures were assessed for quantitative samples only and exhibited mixed results between reference and impacted streams (Table 9). Reference streams did not differ from impacted streams in their relative abundance (percent of total macroinvertebrate density) of Plecoptera, Trichoptera, Oligochaeta, or Diptera larvae (all $P > 0.05$, $DF = 29$). Differences were found in relative abundance of Ephemeroptera ($P = 0.077$, $F = 3.37$, $DF = 29$), Chironomidae ($P = 0.002$, $F = 12.1$, $DF = 29$), and EPT's ($P = 0.0009$, $F = 13.84$, $DF = 29$). Reference streams had significantly higher mean relative abundance for these three metrics, with a mean of 26.4 (SE=2.5) for percent Ephemeroptera, 76.3 percent (SE=2.5) EPT's, and a mean of 77.7 percent (SE=7.0) Chironomidae. Impacted streams exhibited decreased relative (percent) abundances of some groups when compared to reference streams, with a mean 19.8 (SE=2.5) percent for Ephemeroptera, 63.1 (SE=2.5) for percent EPTs, and 43.4 (SE=7.0) percent for Chironomidae larvae (Table 10). Reference streams had higher densities of Chironomidae and Ephemeroptera larvae, while impacted streams had higher concentrations of Plecoptera and Trichopteran larvae. Hemlock-dominated streams are less diverse because of limited resources and less favorable water quality, whereas impacted streams, now more closely

Table 9. Measures of community richness, community composition, tolerance, and feeding guild composition from quantitative data collected from reference and impacted streams used in the assessment of HWA-induced impacts to ecosystem health in the Great Smoky Mountains National Park, USA.

Category	Metric	Reference Streams					Impacted Streams					ANOVA P Value
		Jones Branch	Cole Creek	Toms Creek	Crying Creek	Noisy Creek	Den Branch	Sag Branch	Hurricane Creek	McKee Branch	Clontz Branch	
1	Total Specimen Count	928	675	1302	521	889	844	1518	758	291	714	0.88
2	% EPT	66.06	78.52	80.41	82.34	79.30	66.82	65.09	62.66	68.73	64.85	<0.001
2	% Ephemeroptera	9.38	13.19	17.36	8.64	27.00	18.84	12.19	11.61	30.24	9.52	0.79
2	% Plecoptera	20.90	36.59	26.19	21.11	22.61	22.04	18.58	23.48	15.46	19.33	0.12
2	% Trichoptera	35.78	28.74	36.87	52.59	29.70	25.95	34.32	27.57	23.02	36.00	0.17
2	% Diptera	17.89	5.33	2.92	7.68	7.99	6.16	9.82	6.60	5.15	7.14	0.62
2	% Chironomidae	11.31	1.63	1.46	2.88	1.35	3.67	5.73	0.79	0.69	1.26	0.002
2	% Oligochaeta	0.00	2.81	0.46	0.38	0.00	0.12	1.98	0.40	1.03	0.84	0.82
3	No. of Intolerant Taxa	30	32	39	27	38	42	37	36	27	32	0.65
3	No. of Pleuroceridae Taxa	1	1	1	1	1	0	1	0	0	0	0.03
3	% Tolerant Organisms	31.25	20.30	27.88	21.88	18.00	17.65	13.83	15.83	14.78	18.77	0.02
3	% Dominant Taxon	18.32	14.67	19.82	28.60	9.00	12.68	13.58	17.41	15.46	21.43	0.60
3	% Trichoptera as Hydropsychidae	77.71	75.77	92.92	67.79	63.64	63.01	43.38	66.03	59.70	71.60	<0.0001
3	% Filterers	35.13	25.04	33.41	50.10	21.26	14.93	22.66	20.18	14.78	24.93	0.018
4	% Grazers and Scrapers	20.47	17.63	24.19	17.08	26.10	35.43	23.72	29.29	30.58	24.51	0.017
4	% Omnivores & Scavengers	11.31	2.07	1.61	3.26	1.35	4.03	5.86	1.06	1.03	1.96	0.60
4	% Gatherers	3.13	11.56	10.75	2.11	13.61	12.09	14.82	9.63	26.80	15.41	0.016
4	% Predators	14.98	19.11	13.13	12.28	22.72	17.77	18.12	22.30	16.15	14.01	0.62
4	% Shredders	14.76	23.70	16.74	15.16	14.40	15.64	14.69	16.75	9.28	19.19	0.46

1 = Community Richness Measures
2 = Community Composition Measures

3 = Measures of Tolerance
4 = Feeding Guild Measures

Table 10. ANOVA output for quantitative data collected from reference and impacted streams used in the assessment of HWA-induced impacts to aquatic system health in the Great Smoky Mountains National Park, USA.

Macroinvertebrate Metric	P Value	DF	F Value	Reference Streams		Impacted Streams	
				Mean	Std. Error	Mean	Std. Error
Gastropoda Density	0.0349	29	4.9	5.93	1.79	0.33	1.79
Coleoptera Density	0.0139	29	6.9	30.00	8.50	61.53	8.50
Hydropsychidae Density*	0.0044	29	9.6	87.53	17.41	33.47	17.41
Collector/Filterer Density*	0.0307	29	5.2	97.33	17.28	48.07	17.28
Collector/Gatherer Density*	0.0496	29	4.2	16.41	4.02	31.93	6.94
Margdolef's Index	0.0019	29	11.8	3.74	0.38	1.92	0.38
Percentage Scrapers	0.0174	29	6.4	20.92	2.60	30.22	2.60
Percentage Collector/Filterers	0.0177	29	6.4	31.38	3.64	18.42	3.64
Percentage Collector/Gatherers	0.0157	29	6.6	7.97	2.07	15.50	2.07
Percentage EPT	0.0009	29	13.8	76.29	2.50	63.13	2.50
Percentage Ephemeroptera	0.077	29	3.4	26.38	2.53	19.82	2.53
Percentage Chironomidae	0.0017	29	12.1	77.77	6.98	43.41	6.98
Percentage Trichoptera as Hydropsychidae	< 0.0001	29	20.2	20.54	2.33	35.32	2.33

*Log transformed data

resembling hardwood-dominated streams, have more favorable water quality and increased resource availability.

Several of the measures of tolerance (number of Pleuroceridae taxa, percent tolerant organisms, and proportion of Trichoptera as Hydropsychidae) were significantly different between reference and impacted streams. The most glaring metric was the number of taxa of Pleuroceridae snails. The Pleuroceridae family of snails, also known as common river snails (Voshell 2002), was the only family of snails present in this study. The presence of this taxon differed significantly ($P=0.035$, $F=4.91$, $DF=29$) with reference streams having a mean density of 5.93 ($SE=1.8$) snails per stream while impacted streams had a mean density of 0.33 ($SE=1.8$) snails per stream. This taxon was present at only one of the five impacted streams, while they were present in all of the reference streams.

Differences were also found between stream conditions for percentage of tolerant organisms ($P<0.001$; $F=12.04$; $DF=1, 28$). A tolerance value was assigned for each individual taxon according to established guidelines (Merritt et al. 2007). Taxa with tolerance values greater than four were considered tolerant species. Reference streams had a wider range of tolerance values (18.0-31.3 percent) compared to impacted streams (13.8-18.8 percent), indicating impacted streams were actually supporting more intolerant species which is suggestive of better stream quality.

The proportion of Trichoptera as Hydropsychidae is a metric used to evaluate benthic macroinvertebrate response to sediment or organic loading. Higher proportions of Trichoptera as Hydropsychidae are often a result of excessive sediment or organic loading and are often indicative of poor habitat quality for the biotic community (Davis et al. 2001). This metric was found to be impacted by stream condition in this study ($P<0.0001$, $F=20.17$, $DF=29$). The

proportion of Trichoptera as Hydropsychidae at reference streams was significantly lower with a mean of 20.5 percent (SE=2.3) compared to impacted streams which had a mean of 35.3 percent (SE=2.3). The proportion of collector/filterers was also significantly different between reference and impacted streams ($P=0.018$, $F=6.35$, $DF=29$). Relative abundance of collector/filterers was significantly higher in reference streams with a mean 31.4 percent (SE=3.6) compared to impacted streams with a mean of 18.4 percent (SE=3.6). Willacker et al. (2009) also found increased abundance of collector/filterers in hemlock-dominated streams. The results from this metric suggested that macroinvertebrate taxa that are less sensitive to sediment and organic loading were more prevalent at impacted streams. This group of organisms was not affected by the changes in pH and nitrates that likely eliminated some of the more intolerant species.

The percentage of filterers, although indicative of tolerance, is also a measure of functional feeding guild, while reference streams had a higher percentage of collector filters. Impacted streams exhibited an increase in the percentage of taxa classified in the scraper functional feeding group (FFG) ($P=0.017$, $F=6.39$, $DF=29$). Impacted streams had a higher mean percentage of scrapers at 30.2 (SE=2.6) compared to reference streams with a mean 20.9 percent (SE=2.6). Habitats with higher proportions of scrapers are often higher quality habitat (Davis et al. 2001). Increases in scrapers in impacted streams are most likely a result of increased light penetration reaching streams, which resulted in increased algal productivity. Algae are a major food source for organisms in the scraper FFG.

Long-term aquatic macroinvertebrate response to changing forest composition as a result of EH mortality is difficult to predict at this point in time. Results from this study suggest that the loss of eastern hemlock has not had a tremendous effect on macroinvertebrate density or diversity. However, streams are responding with shifts in functional feeding groups and shifts in

some of the sensitive taxa. Loss of Pleuroceridae, a sensitive group of snails, in impacted streams is likely a response to altered water quality parameters, altered thermal regime, or both.

SUMMARY AND RECOMMENDATIONS

Since the arrival of the hemlock woolly adelgid in the GSMNP, widespread hemlock mortality has occurred. Results from this study suggest that hemlock woolly adelgid impacts hemlock forests, triggering a series of ecosystem responses. This series of responses are initiated by the declining health and mortality of hemlock. Hemlock decline and mortality resulted in decreased canopy coverage and increased light availability (FiPAR) directly over streams and in adjacent riparian areas at impacted study sites. Hemlock mortality and subsequent impacts to canopy cover and light availability produced changes in species composition, relative basal area, and species importance values. Red maple, yellow birch, and sweet birch were the primary non-rhododendron, woody species to capitalize on the changing resource availability with significant increases in relative basal area and importance values.

Impacted sites did not exhibit signs of regeneration for woody tree species, including eastern hemlock. Hemlock woolly adelgid feeds on all life stages of eastern hemlock, thereby preventing successful regeneration of this species at impacted sites. Rosebay rhododendron, a shade tolerant understory shrub is thriving in the absence of hemlock and has responded to increased resource availability with significant increases in both density and height at impacted sites. Rosebay rhododendron is prolific at sprouting and layering and creates shading so dense that little woody regeneration can occur in its presence. Increasing density levels of RR like those observed at impacted sites further exacerbates the effects of hemlock mortality. Vegetative growth habits exhibited by RR, coupled with a tendency to occur in stream riparian areas, will have a significant influence on the long-term recovery of HWA-impacted stream riparian areas. The lack of woody regeneration at impacted sites and the proliferation of RR, suggests that post-mortality canopy recruitment will be limited and will result in long-term alterations to vegetative

composition.

Altered thermal regimes were another outcome of changing forest conditions initiated by HWA-induced hemlock mortality. Without the moderating effects of a healthy hemlock overstory, streams in once hemlock-dominated stands, are exhibiting wider ranges of daily temperature variation. In this study, reference streams were warmer during the colder, winter months and exhibited much less diurnal variation as a result of having intact hemlock canopies. Stream temperatures differed significantly across weeks and months between impacted and reference stream conditions. Temperatures recorded for impacted streams were lower in the colder winter months, corresponding to the loss of thermal protection once provided by hemlock and its dense, drooping branches. Although there were no summer stream temperature data collected, a similar trend is hypothesized for summer temperatures, with reference streams remaining cooler throughout the warmer months as a result of an intact hemlock canopy. Prior studies have shown lower summer temperatures (Snyder et al. 2002) and lower mean diurnal variation (Evans et al. 1996) in hemlock-dominated streams when compared to hardwood-dominated streams. Impacted sites are expected to convert to hardwood-dominated conditions and temperature regimes are likely to exhibit similar patterns as in hardwood-dominated streams. Previous work conducted in the GSMNP on higher order streams failed to find differences in stream temperatures when comparing hardwood-dominated streams to healthy, hemlock-dominated streams (Roberts et al. 2009). Impacts to stream temperatures observed in this study may result in further impacts to the higher order streams receiving inputs from affected watersheds. One of two possible scenarios is likely. Either the alterations to stream temperatures will be compounded with increasing stream order, or they will be diluted and insignificant with increasing stream order. Further research is suggested to assess the severity of stream

temperature change and to quantify the impacts these alterations to the thermal regime may have on brook trout.

Feeding by HWA causes a decline in eastern hemlock (EH) health, leading to eventual mortality, increased large woody debris on the forest floor, and increased inputs into stream channels. Large woody debris density and distribution were significantly different between reference and impacted streams with impacted streams receiving a larger quantity of debris. Impacted sites also had increased quantities of material from the larger length class, attributed to large, dead hemlock trees falling to the forest floor. Reference streams were dominated by smaller size classes that were primarily located within the channel, while large woody debris (LWD) at impacted sites was well-distributed across length and size classes and were scattered fairly evenly across stream locations (in channel, across channel, and along the bank). Increased quantities of LWD can be expected to alter channel morphology, entrain sediment, affect certain water quality parameters, and increase habitat for some species of macroinvertebrates.

Loss of eastern hemlock vegetative cover in formerly hemlock-dominated stands resulted in altered stream water chemistry. Increased sedimentation and nutrient leaching produced increases in several water quality parameters at impacted sites including silicon, sodium, potassium, magnesium, chlorine, and copper. Although these parameters exhibited elevated concentrations in response to HWA-induced eastern hemlock mortality, levels were not at concentrations considered to be immediately harmful to fish or macroinvertebrates. Long-term impacts of increased nutrient concentrations may be a source of concern and further research in this area is warranted.

Streams draining impacted stands were characterized by higher pH and increased acid neutralization capacity. On the other hand, reference streams exhibited lower pH values and a

much lower acid neutralization capacity, differences that are attributed to processes initiated by HWA feeding at reference sites. Conversion of hemlock-dominated forests to a hardwood-dominated condition will result in altered water chemistry and decreased vulnerability to episodic acidification. In the short-term, spikes in acidity and lowered ANC values could potentially have severe impacts on already stressed brook trout populations. Alterations to water quality, coupled with changes in forest type, canopy cover, and incident light penetration suggest that brook trout populations in the GSMNP may be vulnerable to further impacts.

Stream nitrate-nitrogen ($\text{NO}_3\text{-N}$) is another water quality parameter that displayed significant differences in concentration between reference and impacted streams. Nitrate levels in the impacted streams were almost three times lower than levels at reference streams. Reference stream concentrations were elevated above levels that would be expected for healthy, uninfested hemlock stands and much higher than values recorded in other studies (Swank et al. 1981, Finzi et al. 1998b, Snyder et al. 2002, Lewis and Likens 2007, Riscassi and Scanlon 2009). One of the physiological responses of hemlock to HWA feeding is decreased nutrient uptake, resulting in increased nitrogen availability in the soil, and subsequently accelerating nitrogen mineralization and leaching. Insect-initiated defoliations have been shown to result in temporary nitrate leakage from forested stands with fairly rapid recovery to pre-defoliation levels (Swank et al. 1981, Finzi et al. 1998b, Snyder et al. 2002, Lewis and Likens 2007, Riscassi and Scanlon 2009). However, the time frame for nitrate recovery is dependent upon insect species and feeding morphology. HWA-induced defoliations of eastern hemlock occur over several years, resulting in prolonged nitrate leakage and slower recovery times.

Alterations to forest canopy, understory light environment, and water quality from HWA-induced EH mortality results in significant changes in several aquatic macroinvertebrate metrics.

Species diversity and abundance and taxa richness were not affected by hemlock mortality. The number of intolerant taxa was also greater at impacted stream sites when compared to reference stream sites. This result is counter-intuitive but is attributed to more favorable aquatic conditions at impacted stream sites in response to HWA-induced EH mortality. Differences were observed in trophic structure, with both Chironomidae flies and the Ephemeroptera orders being significantly different between reference and impacted streams. Impacted sites responded to hemlock mortality with an increase in the percentage composition of the Ephemeroptera. The percentage composition of Chironomidae flies decreased in impacted streams when compared to reference streams. These two metrics suggested better water quality or habitat availability in impacted streams; and was likely a response to increasing pH and recovering nitrate in impacted streams providing a more favorable condition for the more sensitive Ephemeroptera.

Pleurocerid snails have been virtually eliminated in impacted streams in response to hemlock mortality. This family of snails is fairly common in GSMNP and should be present in all study streams. Snails were most likely eliminated during initial spikes in nitrate and sediments in the stand infestation process. Other responses noted in the biotic community include a shift from streams being dominated by collector/filter functional feeding group (FFG) to the scraper FFG. This shift is likely in response to increased algal production associated with increased sunlight availability.

Hemlock mortality in response to HWA has resulted in several impacts to vegetative and aquatic systems in the stream riparian zone. The results from this study demonstrated that hemlock mortality results in significant impacts to the vegetative community, altered thermal regimes, nutrient leaching, and altered water quality. Reference sites selected for this study were representative of the best available conditions within the Great Smoky Mountains National Park,

and were healthy stands with mild to moderate levels of HWA presence. Impacted sites were areas with over 90 percent hemlock mortality. Results from reference sites suggested that HWA impacts were already occurring in those stands, while impacted sites revealed a glimpse into the recovery time frame for aquatic systems. However, many questions remain that should be addressed. Future research needs would include an assessment of summer stream temperature impacts on first order streams, annual temperature impacts to higher order streams, and long-term water quality monitoring to evaluate the timing, intensity, and duration of alterations to pH and nitrate levels.

LITERATURE CITED

- Abbe, T. B., D. R. Montgomery, K. Fetherston, and E. M. McClure. 1993. A process-based classification of woody debris in a fluvial network: Preliminary analysis of the Queets River, WA. EOS, Transactions of the American Geophysical Union, 73(43):296.
- Alexander, R. R. and W. D. Shepperd. 1990. *Tsuga canadensis* L. In: R.M. Burns and B.H. Honkala, technical coordinators, Silvics of North America, Vol.1 Conifers. Agric. Handbook 654. USDA Forest Service, Washington, DC., pp. 187-203.
- Angermeier, P. L. and J. R. Karr. 1984. Relationships between woody debris and fish habitat in a small warmwater stream. Transactions of the American Fisheries Society, 113:716-726.
- Annand, P. 1924. A new species of Adelges (Hemiptera: Phylloxeridae). Pan-Pacific Entomologist, 1:79-82.
- Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling. 1999. Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers: Periphyton, Benthic Macroinvertebrates and Fish, Second Edition. EPA 841-B-99-002. U.S. Environmental Protection Agency, Office of Water, Washington, D.C.
<http://water.epa.gov/scitech/monitoring/rsl/bioassessment/index.cfm>.
- Beckage, B., J. S. Clark, B. Clinton, and B. Haines. 2000. A long-term study of tree seedling recruitment in Southern Appalachian forests: the effects of canopy gaps and shrub understories. Canadian Journal of Forest Research, 30:1617-1631.
- Benson, A. J. and D. Raikow. 2011. *Dreissena polymorpha*. USGS Nonindigenous Aquatic Species Database, Gainesville, FL.
<http://nas.er.usgs.gov/queries/factsheet.aspx?speciesid=5> RevisionDate: 7/8/2010.
[Accessed: June 16, 2011].
- Beschta, R. L., R. E. Bilby, G. W. Brown, L. B. Holtby, and T. D. Hofstra. 1987. Stream temperature and aquatic habitat: fisheries and forestry interactions. Pages 191-232 In *Streamside Management: Forestry and Fishery Interactions*, E. O. Salo and T.W. Cundy,(eds). Institute of Forest Resources, University of Washington: Seattle, WA.
- Bilby, R. E. and P. A. Bisson. 1998. Function and distribution of large woody debris. In: River Ecology and Management: Lessons from the Pacific Coastal Ecoregion. Eds., R. J. Naiman and R. E. Bilby. New York: Springer-Verlag, pp.324-346.
- Bisson, P. A., R. E. Bilby, M. D. Bryant, C. A. Dolloff, G. B. Grette, R. A. House, M. L. Murphy, K. V. Koski, and J. R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present and future. Pages 143-190 in *Streamside Management: Forestry and Fishery Interactions*, E. O. Salo and T.W. Cundy,(eds). Institute of Forest Resources, University of Washington: Seattle, WA.
- Brooks, R. T. 2001. Effects of the removal of overstory hemlock from hemlock-dominated forests on eastern redback salamanders. Forest Ecology and Management, 149:197-204.

- Buck, L., P. Lambdin, D. Paulsen, J. Grant, and A. Saxton. 2005. Insect species associated with eastern hemlock in the Great Smoky Mountains National Park and environs. *Journal of the Tennessee Academy of Science*, 80:60-69.
- Buckley, D. S., J. G. Isebrands, and T. L. Sharik. 1999. Practical field methods of estimating canopy cover, PAR, and LAI in Michigan oak and pine stands. *Northern Journal of Applied Forestry*, 16:25-32.
- Burnham, C. R., P. A. Rutter, and D. W. French. 1986. Breeding blight-resistant chestnuts. *Plant Breeding Reviews*, 4:347-397.
- Campbell, R. W. and R. J. Sloan. 1977. Forest stand responses to defoliation by the gypsy moth. *Society of American Foresters. Forest Science Monograph*, 19:1-34.
- Canham, C. D. 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology*, 69:786-795.
- Canham, C. D. and P. L. Marks. 1985. The response of woody plants to disturbance: patterns of establishment and growth, p. 197-216. In: S. T. A. Pickett and P. S. White (eds.). *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, Fla.
- Catovsky, S., N. M. Holbrook, and F. A. Bazzaz. 2002. Coupling whole-tree transpiration and canopy photosynthesis in coniferous and broad-leaved tree species. *Canadian Journal of Forest Research*, 32:295-309.
- Chapman, S. K., J. A. Schweitzer, and T. G. Whitham. 2006. Herbivory differentially alters plant litter dynamics in evergreen and deciduous trees. *Oikos*, 114:566-574.
- Chapman, S. K., S. C. Hart, N. S. Cobb, T. G. Whitham, and G. W. Koch. 2003. Herbivory increases litter quality and decomposition: an extension of the acceleration hypothesis. *Ecology*, 84:2867-2876.
- Cheah, C., M. Montgomery, S. Salom, B. Parker, M. Skinner, and S. Costa. 2004. *Biological Control of Hemlock Woolly Adelgid*. Morgantown, WV: USDA Forest Service. FHTET-2004-04.
- Clinton, B. D. 2003. Light, temperature, and soil moisture responses to elevation, evergreen understory, and small canopy gaps in the Southern Appalachians. *Forest Ecology and Management*, 186:243-255.
- Clinton, B. D., L. R. Boring, and W. T. Swank. 1994. Regeneration patterns in canopy gaps of mixed-oak forests of the southern Appalachians: Influences of topographic position and evergreen understory. *American Midland Naturalist*, 132(2):308-319.

- Clinton, B. D., J. M. Vose, J. D. Knoepp, K. J. Elliott, B. C. Reynolds, and S. J. Zarnoch. 2010. Can structural and functional characteristics be used to identify riparian zone width in southern Appalachian headwater catchments? *Canadian Journal of Forest Research*, 40:235-353.
- Cox, P. 1979. *The larger species of Rhododendron*. B. T. Batsford, Ltd., London. 352 pp.
- Curtis, J. T. and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology*, 32:476-498.
- Dajoz, R. 2000. *Insects and forests: The role and diversity of insects in the forest environment. Technique and Documentation*, Paris, France. 668pp.
- Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science*, 33:43-64.
- Davis, J. C., G. W. Minshall, C. T. Robinson, and P. Landres. 2001. Monitoring wilderness stream ecosystems. Gen. Tech. Rep. RMRS-GTR-70. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 137pp.
- Davis, M. J. 2008. Old growth in the east: A survey of North Carolina. <http://www.primalnature.org/ogeast/nc.pdf>. [Accessed: May 30, 2011].
- Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichment to the benthos at McMurdo Sound, Antarctica. In: B.C. Parker (ed.) *Proc. Colloq. Conserv. Probl. Antarctic*. Virginia Polytech. Inst. and State Univ. Blacksburg, Virginia, p.81-95.
- Decagon. 2009. AccuPar PAR/LAI Ceptometer Model LP-80, Operator's Manual: Version 10. Decagon Devices, Inc., Pullman, WA., 100pp.
- Dennis, D. 1988. *The Great Smokies Yesterday and Today*. Sevierville: Nandel.
- Dilling, C., P. Lambdin, J. Grant, and L. Buck. 2007. Insect guild structure associated with eastern hemlock in the Southern Appalachians. *Environmental Entomology*, 36(6):1408-1414.
- Dodd, K. C., Jr. 2004. *The Amphibians of the Great Smoky Mountains National Park*. Knoxville, Tn.: University of TN Press, 263pp.
- Ecological Society of America (ESA) 2003. Biodiversity. <http://esa.sdsc.edu/biodiv2.htm>. (Oct. 2003). [Accessed: June 3, 2009].

- Eschtruth, A. K., N. L. Cleavitt, J. J. Battles, R. A. Evans, and T. J. Fahey. 2006. Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation. *Canadian Journal of Forest Research*, 36:1435-1450.
- Eshleman, K. N., R. P. Morgan, J. R. Webb, F. A. Deviney, and J. N. Galloway. 1998. Temporal patterns of nitrogen leakage from mid-Appalachian forested watersheds: Role of insect defoliation. *Water Resources Research*, 34:2005-2116.
- Estrada-Franco, R. G. and G. B. Craig. 1995. Biology, disease relationship and control of *Aedes albopictus*. Pan American Health Organization, Washington DC: Technical Paper No. 42.
- Evans, R. A. 2002. An ecosystem unraveling? pp. 23-33. In: Onken, B., R. Reardon, and J. Lashomb (eds.). *Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium*, February 5-7, 2002. East Brunswick, New Jersey, The State University of New Jersey, Rutgers, New Jersey.
- Evans, R. A., E. Johnson, J. Shreiner, A. Ambler, J. Battles, N. Cleavitt, T. Fahey, J. Sciascia, and E. Pehek. 1996. Potential impacts of hemlock woolly adelgid (*Adelges tsugae*) on eastern hemlock (*Tsuga canadensis*) ecosystems. In: S. M. Salom, T. C. Tigner, and R. C. Reardon, eds. *Proceedings of the First Hemlock Woolly Adelgid Review*, Charlottesville, VA, 1995. USDA Forest Service Forest Health Technology Enterprise Team-Morgantown, WV. FHTET, 96-10. pp. 42-57.
- Eyre, F. (ed.) 1980. *Forest Cover Types of the United States and Canada*. Society of American Foresters. Washington, DC. 148p.
- Finzi, A. C., N. Van Breemen, and C. C. Canham. 1998a. Canopy tree-soil interactions within temperate forests: Species effects on soil carbon and nitrogen. *Ecological Applications*, 8:440-446.
- Finzi, A. C., C. D. Canham, and N. Van Breemen. 1998b. Canopy tree-soil interactions within temperate forests: Species effects on pH and cations. *Ecological Applications*, 8:447-454.
- Ford, C. R. and J. M. Vose. 2006. Eastern hemlock transpiration: patterns, controls, and implications for its decline in southern Appalachian forests, pp. 181-187. In D.L. Fowler (ed.), *Second interagency conference on research in the wetlands*. USDA Forest Service, Southern Research Station, Coweeta Hydrologic Laboratory, Otto, NC.
- Ford, C. R. and J. M. Vose. 2007. *Tsuga canadensis* (L.) Carr. mortality will impact hydrologic processes in southern Appalachian forest ecosystems. *Ecological Applications*, 17:1156-1167.

- Global Invasive Species Database. 2011. 100 of the World's Worst Invasive Alien Species. <http://www.issg.org/database/species/ecology.asp?si=109&fr=1&sts=&lang=EN>. Accessed: [March 21, 2011].
- Hadley, J. L., P. S. Kuzeja, M. J. Daley, N. G. Phillips, T. Mulcahy, and S. Singh. 2008. Water use and carbon exchange of red oak and eastern hemlock dominated forests in the northeastern USA: implications for ecosystem level effects of hemlock wooly adelgid. *Tree Physiology*, 28:615-627.
- Hammond, C. R. 2004. The Elements: in Handbook of Chemistry and Physics, 81st edition. CRC press. 2656pp.
- Harmon, M. E., S. P. Bratton, and P. S. White. 1983. Disturbance and vegetation response in relation to environmental gradients in the Great Smoky Mountains. *Vegetation*, 55: 129-139.
- Havill, N. P., M. E. Montgomery, G. Yu, S. Shiyake, and A. Caccone. 2006. Mitochondrial DNA from hemlock woolly adelgid (Hemiptera: Adelgidae) suggests cryptic speciation and pinpoints the source of the introduction to eastern North America. *Annals of the Entomological Society of America*, 99:195-203.
- Hedman, C. W. and D. H. Van Lear. 1994. Vegetative structure and composition of Southern Appalachian riparian forests. *Bulletin of the Torrey Botanical Club*, 122:134-144.
- Hough, A. F. 1960. Silvical characteristics of eastern hemlock. USDA Forest Service, Station Paper NE-132. Northeastern Forest Experiment Station, Upper Darby, PA. 23 p.
- Hunt, T. E. and A. L. Wilson. 1986. *The Chemical Analysis of Water: General Principles and Techniques*. The Royal Society of Chemistry, Thomas Graham House, The Science Park, Cambridge CB4 4WF, 685pp.
- Huryn, A.D. and J.B. Wallace. 1987. Local geomorphology as determinant of macrofaunal production in a mountain stream. *Ecology*, 68:1932-1942.
- Jenkins, J. C., J. D. Aber, and C. D. Canham. 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in E. Hemlock forests. *Canadian Journal of Forest Research*, 29(5):630-645.
- Johnson, K., G. Taylor, and T. Remaley. 2005. Managing hemlock woolly adelgid and balsam woolly adelgid at Great Smoky Mountains National Park. In B. Onken and R. Reardon [eds.]. *Proceedings, Third Symposium on Hemlock Woolly Adelgid in the Eastern United States*. FHTET 2005-01. USDA Forest Service, Forest Health Technology Enterprise Team. Morgantown, WV.

- Johnson, K., T. Remaley, and G. Taylor. 2008. Managing hemlock woolly adelgid at Great Smoky Mountains National Park: situation and response. In B. Onken and R. Reardon [eds.]. Proceedings, Fourth Symposium on Hemlock Woolly Adelgid in the Eastern United States. FHTET-2008-01. USDA Forest Service, Forest Health Technology Enterprise Team. Morgantown, WV.
- Johnson, K. D., F. P. Hain, K. S. Johnson, and F. Hastings. 1999. Hemlock resources at risk in the Great Smoky Mountains National Park. p. 111-112. In K.A. McManus, K. S. Shields, and D. R. Souto. [eds.]. Proceedings, Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America. General Technical Report NE-267, USDA Forest Service, Northeastern Forest Experiment Station. Radnor, PA.
- Johnson, S. L. and J. A. Jones. 2000. Stream temperature responses to forest harvest and debris flows in western Cascades, Oregon. Canadian Journal of Fisheries and Aquatic Science, 57(Suppl. 2):30-39.
- Jordan, J. S., and W. M. Sharp. 1967. Seeding and planting hemlock for ruffed grouse cover. USDA Forest Service, Research Paper NE-83. Northeastern Forest Experiment Station, Upper Darby, PA. 17 pp.
- Kent, M. and P. Coker. 1992. Vegetation Description and Analysis: A Practical Approach. CRC Press, Boca Raton, FL. 363 pp.
- Kizlinski, M. L., D. A. Orwig, R. C. Cobb, and D. R. Foster. 2002. Direct and indirect ecosystem consequences of an invasive pest on forests dominated by eastern hemlock. Journal of Biogeography, 29:1489-1503.
- Kominoski, J. S., C. M. Pringle, and B. A. Ball. 2008. Invasive woolly adelgid appears to drive seasonal hemlock and carcass inputs to a detritus-based stream. Verh. Internat. Verein. Limnol., 30(1):109-112.
- Kramer, D. L. 1987. Dissolved oxygen and fish behavior. Environmental Biology of Fishes, 18(2):81-92.
- Krapfl, K. J., E. J. Holzmüller, and M. A. Jenkins. 2011. Early impacts of hemlock woolly adelgid in *Tsuga canadensis* forest communities of the southern Appalachian Mountains. The Journal of the Torrey Botanical Society, 138(1):93-106.
- Krueger, W., J. Williams, M. Borman, and L. Larson. 2003. Relationships of Shade and Maximum Stream Temperatures on Three Northeastern Oregon Streams. 6 pp. In: Range Field Day 2003 Research in Rangeland Management Environmental and Management Impacts on Stream Temperatures-Range Science Series Report 6. Department of Rangeland Ecology and Management, Corvallis, OR.

- Ladd, D. E., and G. S. Law. 2007. Tennessee StreamStats—A web-enabled geographic information system application for automating the retrieval and calculation of streamflow statistics: U.S. Geological Survey Fact Sheet 2007–3081, 2 p.
- Lamberti, G. A. and A. D. Steinman. 1997. A comparison of primary production in stream ecosystems. *Journal of the North American Benthological Society*, 16(1):95-104.
- Lancaster, K. F. 1985. Managing eastern hemlock-a preliminary guide. USDA Forest Service, Northeastern Area, NA-FR-30.
- Lei, T. T., E. T. Nilsen, and S. W. Semones. 2006. Light environment under *Rhododendron maximum* thickets and estimated carbon gain of regenerating forest tree seedlings. *Plant Biology*, 184:143-156.
- Lei, T. T., S. W. Semones, J. F. Walker, B. D. Clinton, and E. T. Nilsen. 2002. Effects of *Rhododendron maximum* thickets on tree seed dispersal, seedling morphology, and survivorship. *International Journal of Plant Sciences*, 163:991-1000.
- Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. *Forest Science*, 2:314-320.
- Lewis, G. P. and G. E. Likens. 2007. Changes in stream chemistry associated with insect defoliation in a Pennsylvania hemlock-hardwoods forest. *Forest Ecology and Management*, 238:199-211.
- Liebhold, A. M., W. L. Macdonald, D. Bergdahl, and V. C. Mastro. 1995. Invasion by exotic forest pests-a threat to forest ecosystems. *Forest Science*, 41:1-49.
- Little, E. L., S. Bullaty, A. Lomeo, S. Rayfield, and O. Buehl. 1980. National Audubon Society: Field Guide to North America Trees: Eastern Region. Alfred A. Knopf Publishing, NY, 299 pp.
- Lovett, G. M., C. D. Canham, M. A. Arthur, K. C. Weathers, and R. D. Fitzhugh. 2006. Forest ecosystem responses to exotic pests and pathogens in Eastern North America. *BioScience*, 56(5):395-405.
- Lovett, G. M., L. M. Christenson, P. M. Groffman, C. G. Jones, J. E. Hart, and M. J. Mitchell. 2002. Insect defoliation and nitrogen cycling in forests. *BioScience*, 52:335-341.
- Madden, M., R. Welch, T. Jordan, P. Jackson, R. Seavey, and J. Seavey. 2004. Digital vegetation maps for the Great Smoky Mountains National Park. Center for Remote Sensing and Mapping Science, Dept. of Geography, Univ. of Georgia. Athens, GA. 44pp.
- Marks, P. L. and F. H. Bormann. 1972. Revegetation following forest cutting: mechanisms for return to steady-state nutrient cycling. *Science*, 176:914-915.

- McClure, M. 1987. Hemlock woolly adelgid may also attack spruce. Connecticut Agricultural Experiment Station, New Haven, *Frontiers of Plant Science*, 39:7-8.
- McClure, M. 1989. Evidence of a polymorphic life cycle in the hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae). *Annals of the Entomological Society of America*, 82:50-54.
- McClure, M. 1991. Density-dependent feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. *Environmental Entomology*, 20:258-264.
- McClure, M. 1995. Using natural enemies to control hemlock woolly adelgid. *Frontiers of Plant Science*, 47(2):5-7.
- McDonald, N. W., A. J. Burton, H. O. Liechty, J. A. Witter, K. A. Pregitzer, G. D. Mroz, and D. D. Richter. 1992. Ion leaching in forest ecosystems along a Great Lakes air pollution gradient. *Journal of Environmental Quality*, 21:614-623.
- McGinty, D. T. 1972. The ecological roles of *Kalmia latifolia* L. and *Rhododendron maximum* L. in the hardwood forest at Coweeta. Master's Thesis, University of Georgia. 81pp.
- Merritt, R. W., K. W. Cummins, and M. B. Berg. 2007. *An Introduction to the Aquatic Insects of North America*. 4th edition, Kendall-Hunt, 1214pp.
- Millen, P. E. 1995. Bare trees: Zadoc Pratt, master tanner and the story of what happened to the Catskill Mountain forests. Blackdome, Hensonville, New York, USA.
- Minckler, L. 1941. Planting white pine in laurel and rhododendron slicks. *Journal of Forestry*, 39:1036.
- Monk, C., D. McGinty, and F. Day, Jr. 1985. The ecological significances of *Kalmia latifolia* and *Rhododendron maximum* in the deciduous forest of the southern Appalachians. *Bulletin of the Torrey Botanical Club*, 112:187-193.
- Montgomery, M., W. Lu, H. Wang, and D. Yao. 1998. Chinese Coccinellidae for biological control of the hemlock woolly adelgid. *Proceedings of the Interagency Gypsy Moth Research Forum, United States Department of Agriculture Forest Service General Technical Report ND – 248*. 41-42pp.
- Nakamura, F., and F. J. Swanson. 1993. Effects of coarse woody debris on morphology and sediment storage of a mountain stream system in western Oregon. *Earth Surface Processes and Landforms*, 18:43-61.
- Neff, K. J. 2007. Physiological stress in native brook trout (*Salvelinus Fontinalis*) during episodic acidification of streams in the Great Smoky Mountains National Park. Master's Thesis, University of Tennessee, http://trace.tennessee.edu/utk_gradthes/178.

- Neff, K. J. 2010. Personal Communication. Department of Civil and Environmental Engineering, University of Tennessee, Knoxville, TN.
- Neff, K. J., E. B. Deyton, J. S. Schwartz, R. B. Robinson, and T.B. Henry. 2008. Episodic stream acidification in the Great Smoky Mountains National Park: An investigation into the mechanisms of acidification and impacts on native brook trout. Session in the TMDL section: World Water and Environmental Resources Congress of the American Society of Civil Engineers and Environmental and Water Resources Institute; Honolulu, Hawaii.
- Nilsen, E. T., J. F. Walker, O. K. Miller, S. W. Semones, T. T. Lei, and B. D. Clinton. 1999. Inhibition of seedling survival under *Rhododendron maximum* L. (Ericaceae): could allelopathy be a cause? *American Journal of Botany*, 86:1597-160.
- Nuckolls, A. E., N. Wurzbarger, C. R. Ford, R. L. Hendrick, J. M. Vose, and B. D. Kloeppel. 2009. Hemlock declines rapidly with hemlock woolly adelgid infestation: impacts on the carbon cycle of southern Appalachian forests. *Ecosystems*, 12(2):179-190.
- NWS. 2011. National Weather Service. <http://weather.noaa.gov> [Accessed: March 25, 2011].
- Orwig, D. A. and D. R. Foster. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. *Journal of the Torrey Botanical Society*, 125:59-72.
- Orwig, D. A. and D. R. Foster. 2000. Stand, landscape, and ecosystem analyses of hemlock woolly adelgid outbreaks in southern New England: an overview. In *Sustainable Management of Hemlock Ecosystems in Eastern North America. Symposium Proceedings, GTR-NE 267*. USDA Forest Service, Northeastern Forest Research Station, Newtown Square, PA.
- Orwig, D. A. and M. L. Kizlinski. 2002. Vegetation response following hemlock woolly adelgid infestation, hemlock decline, and hemlock salvage logging. In: *Symposium on the Hemlock Woolly Adelgid in Eastern North America Proceedings*. New Jersey Agricultural Experiment Station, New Brunswick, NJ.
- Orwig, D. A., D. R. Foster, and D. L. Mausel. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. *Journal of Biogeography*, 29:1475–1487.
- Paddock, W. C. 1992. Our Last Chance to Win the War on Hunger. *Advances in Plant Pathology*, 8:197-222.
- Phillips, D. and W. Murdy. 1985. Effects of rhododendron on regeneration of southern Appalachian hardwoods. *Forest Science*, 31:226-23.
- Phillips, D. L. and D. J. Shure. 1990. Patch-size effects on early succession in Southern Appalachian forests. *Ecology*, 71(1):204-212.

- Plafkin, J. L., M. T. Barbour, K. D. Porter, S. K. Gross, and R. M. Hughes. 1989. Rapid bioassessment protocols for use in streams and rivers; benthic macroinvertebrates and fish. U.S. E.P.A., Cincinnati, OH (Publ No. EPA/440/4-89/001).
- Platts, W. S., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. USDA Forest Service, General Technical Report INT-138. Intermountain Forest and Range Experiment Station, Ogden, UT.
- Plocher, A. E. and K. L. Carvell. 1987. Population dynamics of rosebay rhododendron thickets in the southern Appalachians. *Bulletin of the Torrey Botanical Club*, 114(2):121-126.
- Pyle, C. 1985. Vegetation disturbance of the Great Smoky Mountains National Park: An analysis of archival maps and records. USDI, National Park Service, Southeast Region, Research/Resource Management Report SER-77, Atlanta, GA. 69pp.
- Quimby, J. W. 1996. Value and importance of hemlock ecosystems in the eastern United States In S. M. Salom, T. C. Tigner and R. C. Reardon [eds.], *Proc. First Hemlock Woolly Adelgid Rev.*, Forest Health Technology Enterprise Team (FHTET) 95-10.
- Reynolds, B. C., M. D. Hunter, and D. A. Crossley Jr. 2000. Effects of canopy herbivory on nutrient cycling in a northern hardwood forest in western North Carolina. *Selbyana*, 21:74-78.
- Ricassi, A. L. and T. M. Scanlon. 2008. Nitrate variability in hydrological flow paths for three mid-Appalachian forested watersheds following a large-scale defoliation. *Journal of Geophysical Research*, 114:1-11.
- Richardson, J. S. 1991. Seasonal food limitation of detritivores in a montane stream: An experimental test. *Ecology*, 72:873-887.
- Rivers, C. T., D. H. Van Lear, B. D. Clinton, and T. A. Waldrop. 1999. Community composition in canopy gaps as influenced by presence or absence of *Rhododendron maximum*. *Proceedings of the Tenth Biennial Southern Silv. Research Conf.*, Shreveport, LA, pp. 57-60. GTR-SRS-30. USDA Forest Service, Southern Research Station, Asheville, NC.
- Roberts, S. W., R. Tankersley Jr., and K. H. Orvis. 2009. Assessing the potential impacts to riparian ecosystems resulting from hemlock mortality in Great Smoky Mountains National Park. *Environmental Management*, 44:335-345.
- Robison, E. G. and R. L. Beschta. 1990. Characteristics of coarse woody debris for several coastal streams of southeast Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, 47:1684-1693.
- Rogers, R. 1980. Hemlock stands from Wisconsin to Nova Scotia: Transitions in understory composition along a floristic gradient. *Ecology*, 61(1):178-193.

- Romancier, R. 1971. Ecology of seedling establishment of *Rhododendron maximum* in the southern Appalachians. Ph.D. Dissertation, Duke University, Durham, NC. 122 pp.
- Ross, R. M., R. M. Bennett, C. D. Snyder, J. A. Young, D. R. Smith, and D. P. Lemarie. 2003. Influence of eastern hemlock (*Tsuga canadensis*) on fish community structure and function in headwater streams of the Delaware River Basin. *Ecology of Freshwater Fish*, 12(1):60-65.
- Rowell, T. J. and W. V. Sobczak. 2008. Will stream periphyton respond to increases in light following forecasted regional hemlock mortality? *Journal of Freshwater Ecology*, 23:33-40.
- SAS Institute 2004. Version 9.1. SAS Institute. Cary, NC.
- Schowalter, T.D. 1981. Insect herbivore relationship to the state of the host plant: biotic regulation of ecosystem nutrient cycling through ecosystem succession. *Oikos*, 37:126-130.
- Schowalter, T.D., W.W. Hargrove, and D.A. Crossley. 1986. Herbivory in forested ecosystems. *Ann. Rev. Entomol.*, 31:177-196.
- Siderhurst, L. A., H. P. Griscom, M. Hudy, and Z. J. Bortolot. 2010. Changes in light levels and stream temperatures with loss of eastern hemlock (*Tsuga canadensis*) at a southern Appalachian stream: Implications for brook trout. *Forest Ecology and Management*, 260: 1677-1688.
- Sirulnik, A. G., J. Lewis, A. Tuininga, and J. Johnson. 2005. Hemlock woolly adelgid (*Adelges tsugae*) infestation alters soil conditions and ectomycorrhizal communities in eastern hemlock (*Tsuga canadensis*) stands. Northeastern Branch of the American Society of Agronomy-Soil Science Society of America, July 10-13, 2005, Storrs, CT. pp. 1.
- Skinner, M., B. L. Parker, S. Gouli, and T. Ashikaga. 2003. Regional responses of hemlock woolly adelgid (Homoptera: Adelgidae) to low temperatures. *Environmental Entomology*, 32:523-528.
- Snyder, C. D., J. A. Young, D. P. Lemarie, and D. R. Smith. 2002. Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 59:262-275.
- Snyder, C., J. Young, D. Smith, D. Lemarie, R. Ross, and R. Bennett. 1998. Influence of eastern hemlock decline on aquatic biodiversity of Delaware Water Gap National Recreation Area. Final Report of the USGS Biological Resources Division, Leetown Science Center Aquatic Ecology Laboratory. 66pp.

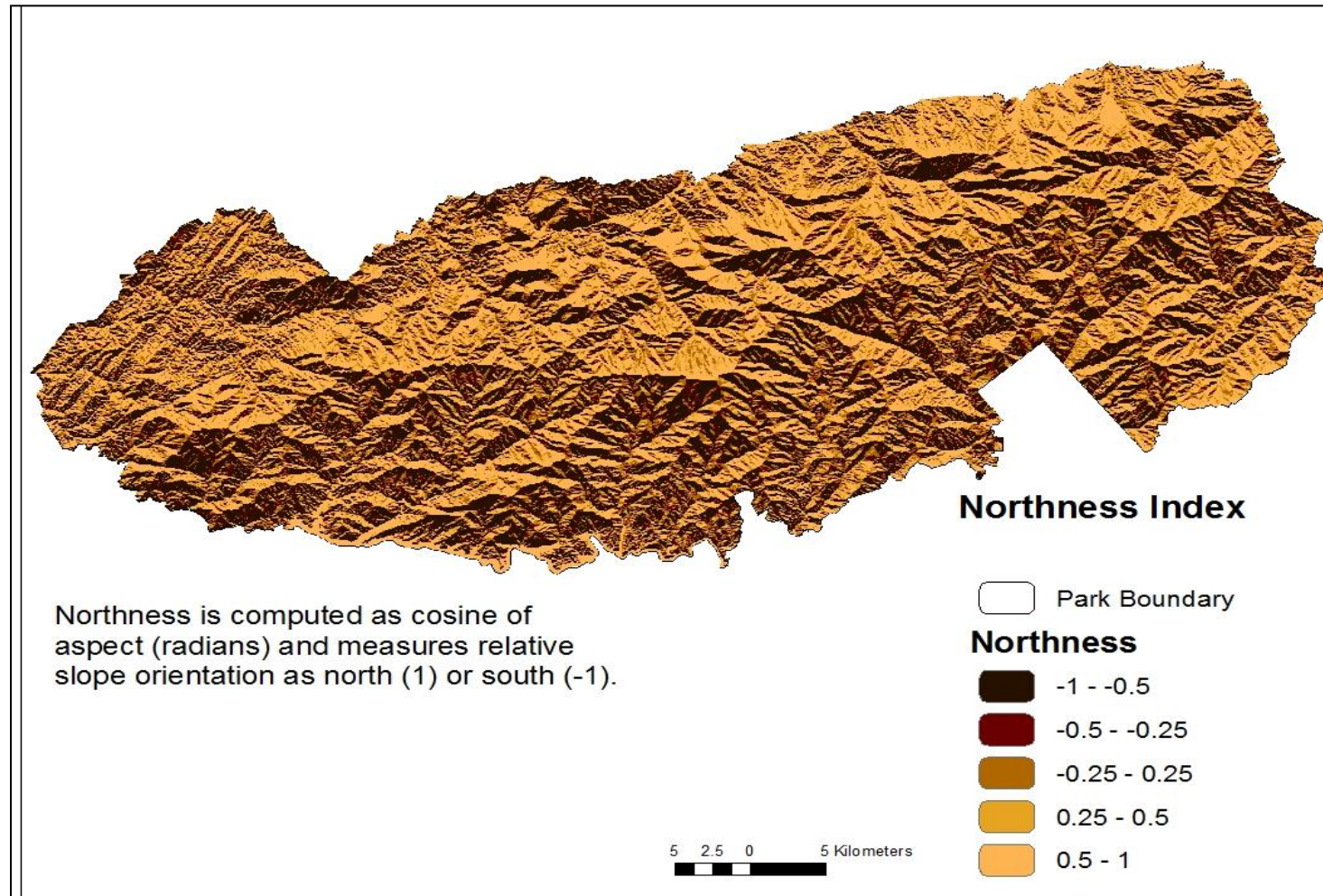
- Spaulding, S. and L. Elwell. 2007. Increase in nuisance blooms and geographic expansion of the freshwater diatom *Didymosphenia geminata*. Report 2007–1425. USGS, Reston, VA. 38 pp. <http://www.fort.usgs.gov/products/publications/22046/22046.pdf>.
- Stadler, B., T. Muller, and D. Orwig. 2006. The ecology of energy and nutrient fluxes in hemlock forests invaded by hemlock woolly adelgid. *Ecology*, 87(7):1792-1804.
- Stadler, B., T. Muller, D. A. Orwig, and R.C. Cobb. 2005. Hemlock woolly adelgid: Canopy impacts transforming ecosystem processes and landscapes in New England forests. *Ecosystems*, 8:233-247.
- Stevens, V. 1997. The ecological role of coarse woody debris: an overview of the ecological importance of CWD in B.C. forests, Working Paper 30/1997, Victoria, B.C.: Research Branch, B.C. Ministry of Forests.
- Stoetzel, M. 2002. History of the introduction of *Adelges tsuga* based on voucher specimens in the Smithsonian Institute National Collection of Insects. Proceedings: hemlock woolly adelgid in the eastern United States symposium. East Brunswick, New Jersey. 13 p.
- Stumm, W. and J. J. Morgan. 1981. *Aquatic Chemistry*. Wiley: New York.
- Subbarao, G. V., O. Ito, W. L. Berry, and R. M. Wheeler. 2003. Sodium: A functional plant nutrient. *Critical Reviews in Plant Sciences*, 22(5):391.
- Swank, W. T. 1988. Stream chemistry responses to disturbance. In: *Forest Hydrology and Ecology at Coweeta*. Springer, New York, pp. 339-357.
- Swank, W. T. and J. M. Vose. 1997. Long-term nitrogen dynamics of Coweeta forested watersheds in the southeastern United States of America, *Global Biogeochem. Cycles*, 11(4):657-671.
- Swank, W. T., J. B. Waide, D. A. Crossley, Jr., and R. L. Todd. 1981. Insect defoliation enhances nitrate export from forest ecosystems. *Oecologia*, 51:297-299.
- Tingley, M. W., D. A. Orwig, R. Field, and G. Motzkin. 2002. Avian response to removal of a forest dominant: consequences of hemlock woolly adelgid infestations. *Journal of Biogeography*, 29:1505-1516.
- U.S. Department of Agriculture, Forest Service. 1989. *Insects and diseases of trees in the South*. Protection Report R8 – PR 16. Atlanta, GA.
- Vannote, R. L. and B. W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *American Naturalist*, 115:667-695.

- Voshell, J. R. Jr., 2002. A guide to common freshwater invertebrates of North America. McDonald and Woodward Publishing Co., Blacksburg, Virginia. 442 pp.
- Wallace, J. B., J. R. Webster, and J. L. Meyer. 1995. Influence of log additions on physical and biotic characteristics of a mountain stream. *Canadian Journal of Fisheries and Aquatic Science*, 52:2120-2137.
- Ward, J. S., C. A. S. Cheah, M. E. Montgomery, B. P. Onken, and R. S. Cowles. 2004. Eastern hemlock forests: Guidelines to minimize the impacts of hemlock woolly adelgid. Rehabilitation guidelines for hemlock stands. USDA Forest Service, NA-TP-03-04, 36pp.
- Waring, R. H. and S. W. Running. 2007. *Forest Ecosystems: Analysis at Multiple Scales*. 3rd ed. Boston: Elsevier Academic Press; 420 pp.
- Webb, J. R., B. J. Cosby, F. A. Deviney, K. N. Eshleman, and J. N. Galloway. 1995. Change in the acid-base status of an Appalachian catchment following forest defoliation by the gypsy moth. *Water, Air and Soil Pollution*, 85:535-540.
- White, P. J. and M. R. Broadley. 2001. Chloride in soils and its uptake and movement within the plant: A review. *Annals of Botany*, 88:967-98.
- White, P. S. and J. Harrod. 1997. Disturbance and diversity in a landscape context. Pages 128-159 *in*: Bissonette, J., ed. *Wildlife and landscapes*. Springer-Verlag: New York.
- Whittaker, R. H. 1952. A study of the summer foliage insect communities in the Great Smoky Mountains. *Ecological Monographs*, 22:1-44.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs*, 26:1-60.
- Whittaker, R. H. 1975. *Communities and Ecosystems*. Second edition. MacMillan, New York, NY, USA. 385 pp.
- Whittaker, R. H. 1979. Appalachian balds and other North American heathlands, p. 427-439. *In*: R. Specht [ed.], *Ecosystems of the world: heathlands and related shrublands*. Elsevier Publ. Co., New York.
- Willacker, J. J., W. V. Sobczak, and E. A. Colburn. 2009. Stream macroinvertebrate communities in paired hemlock deciduous watersheds. *Northeastern Naturalist*, 16(1):101-112.
- Yorks, T. E., D. J. Leopold, and D. J. Raynal. 2000. Vascular plant propagule banks of six eastern hemlock stands in the Catskill Mountains of New York. *Journal of the Torrey Botanical Society*, 127:87-93.

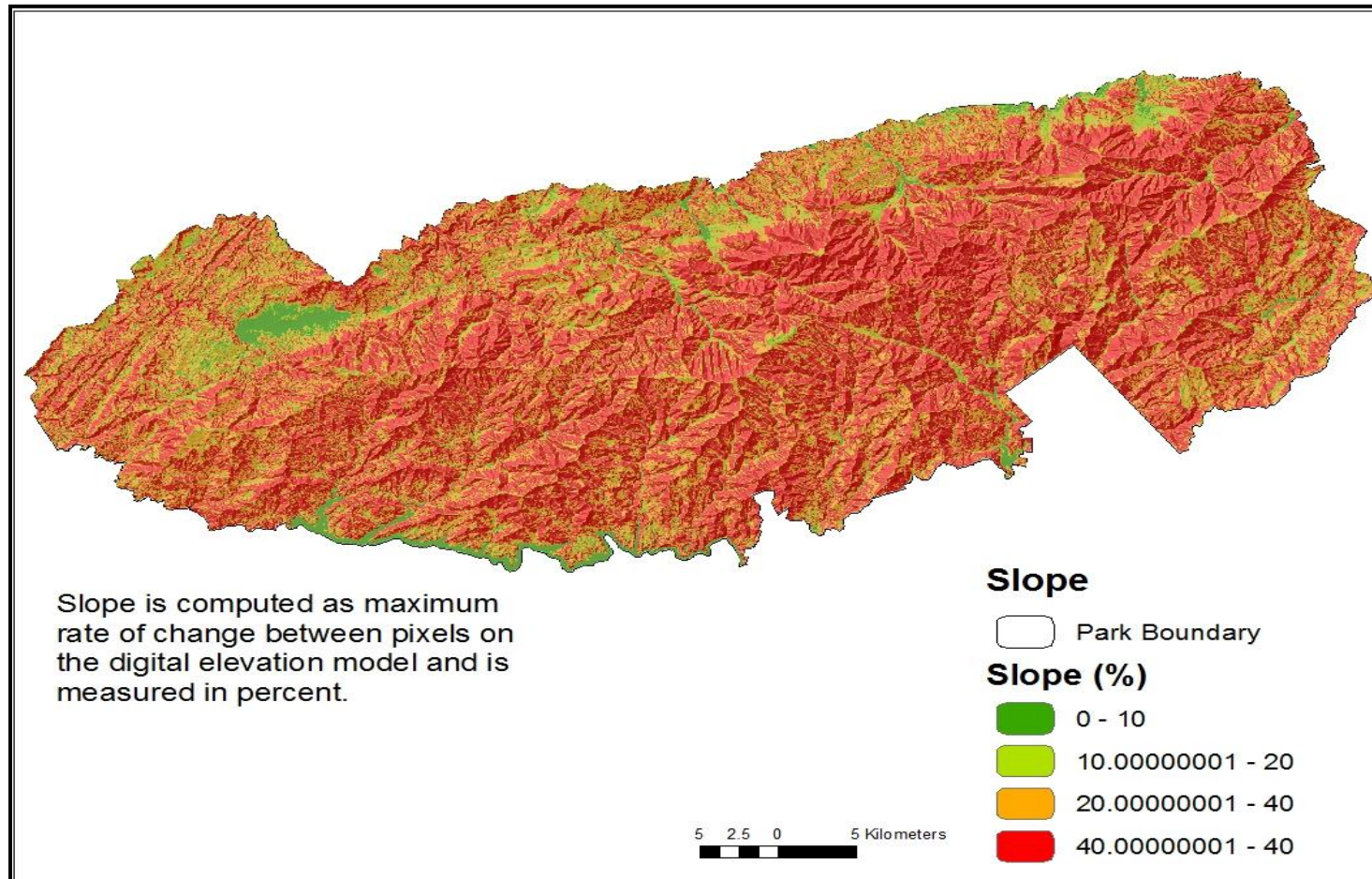
- Yorks, T. E., D. J. Leopold, and D. J. Raynal. 2003. Effects of *Tsuga canadensis* on soil water chemistry and understory vegetation: Possible consequences of an invasive insect herbivore. *Canadian Journal of Forest Research*, 33:1525-1537.
- Young, R., K. S. Shields, and G. P. Berlyn . 1995. Hemlock woolly adelgid (Homoptera, Adelgidae): Stylet bundle insertion and feeding sites. *Annals of the Entomological Society of America*, 88:827-835.
- Young, J. A., D. R. Smith, C. D. Snyder, and D. P. Lemarie. 2002. A terrain-based paired-site sampling design to assess biodiversity losses from eastern hemlock decline. *Environmental Monitoring and Assessment*, 76(2):167-183.
- Yu G., D. Yao, and H. Liu. 1997. The Coccinellidae collected from *Tsuga* with *Adelges tsugae* Annand (Homoptera: Adelgidae). *Scientia Silvae Sinicae*, 33:432-440.

Appendices

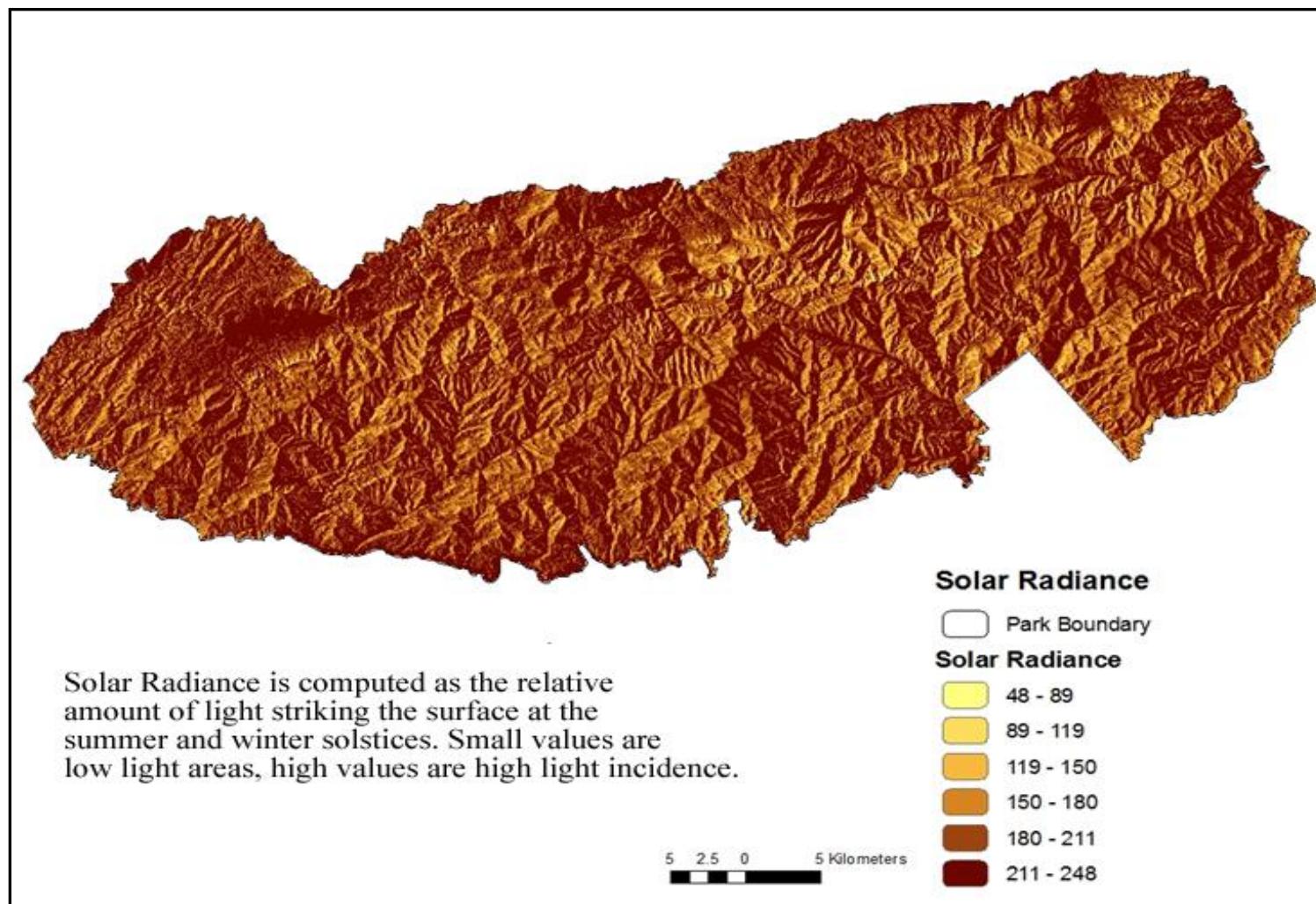
Appendix. A1. Terrain Northness Data Utilized for Stream Site Selection in the Great Smoky Mountains National Park, USA.



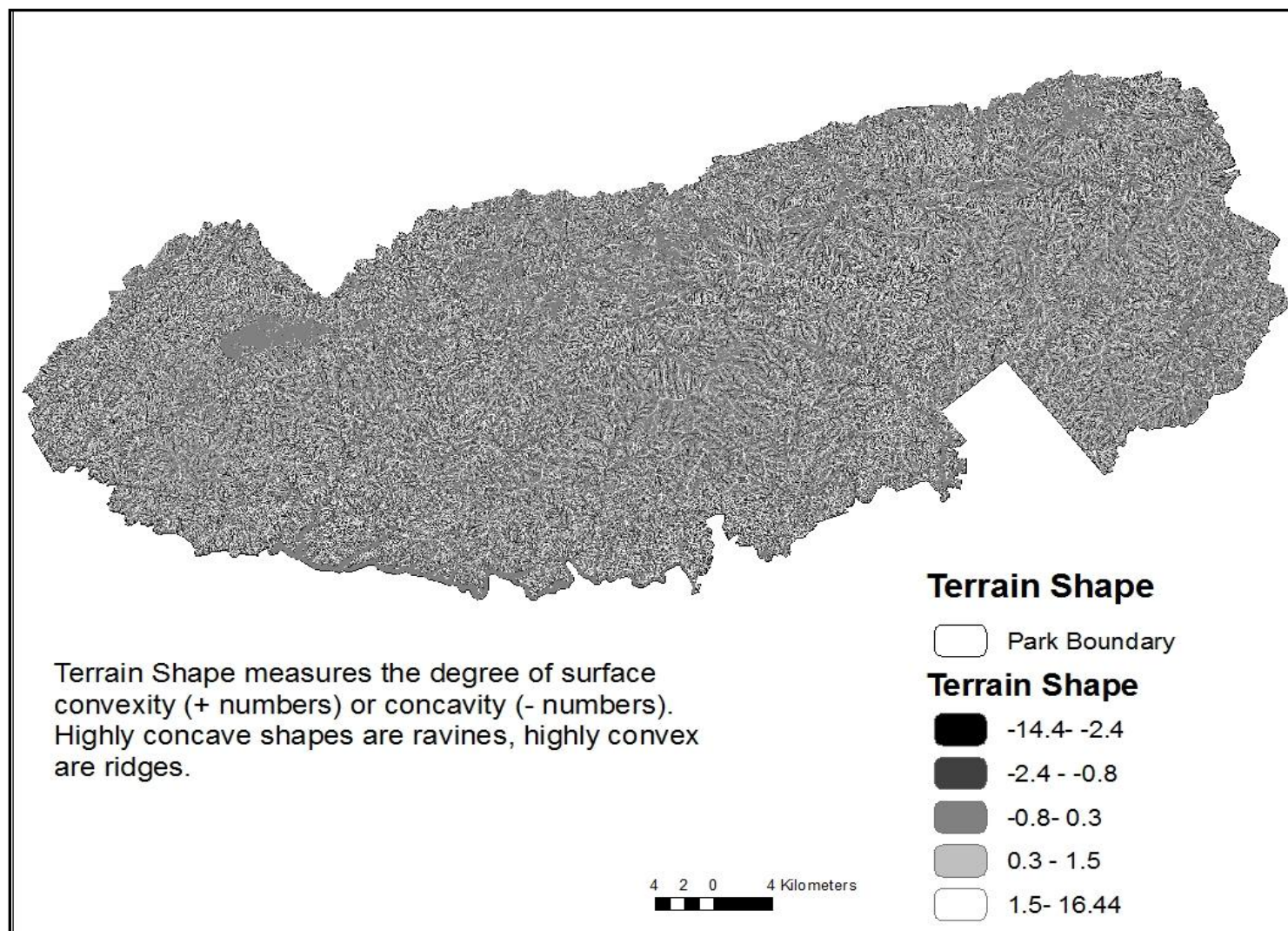
Appendix. A2. Terrain Slope Data Utilized for Stream Site Selection in the Great Smoky Mountains National Park, USA.



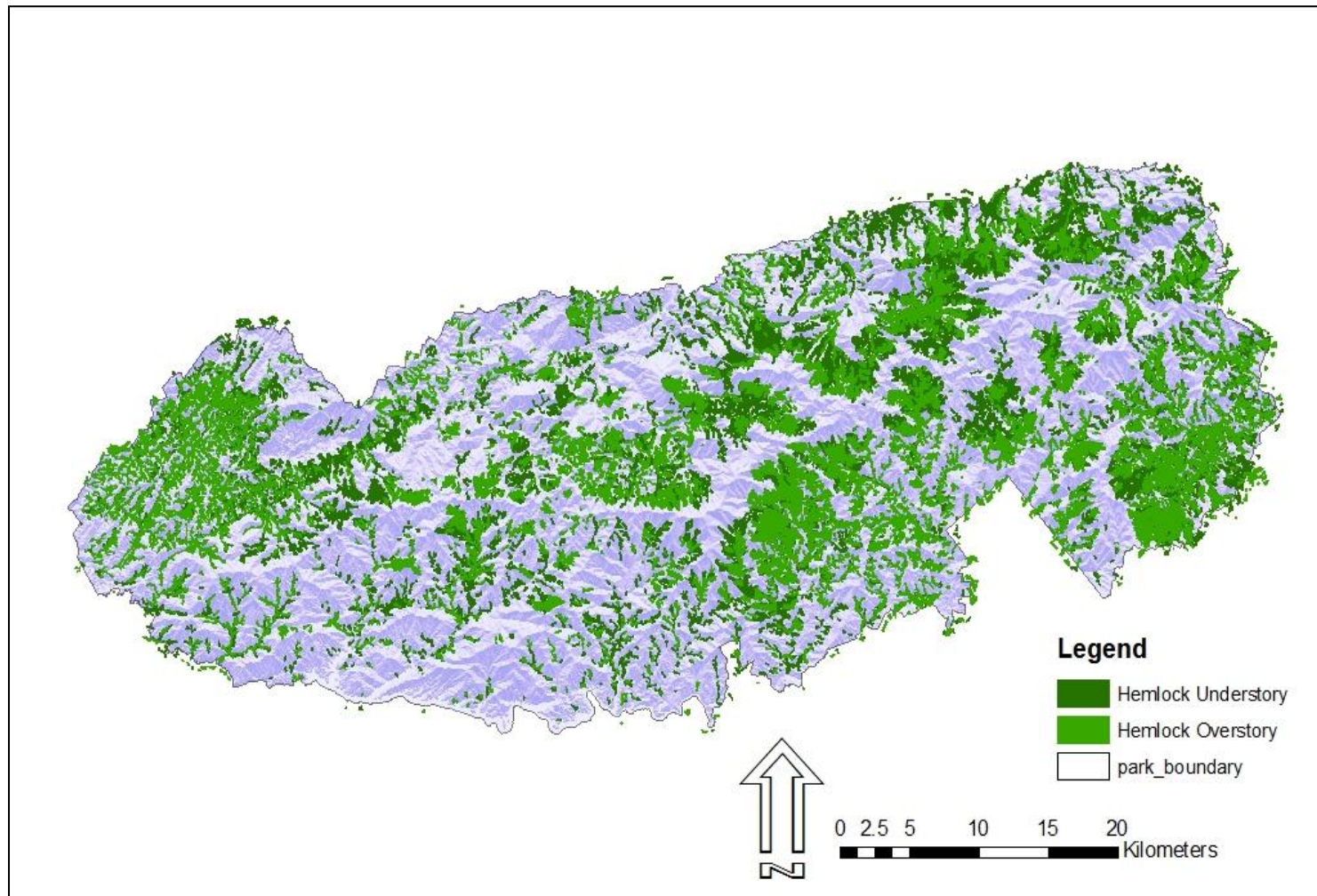
Appendix. A3. Solar Radiance Data Utilized for Stream Site Selection in the Great Smoky Mountains National Park, USA.



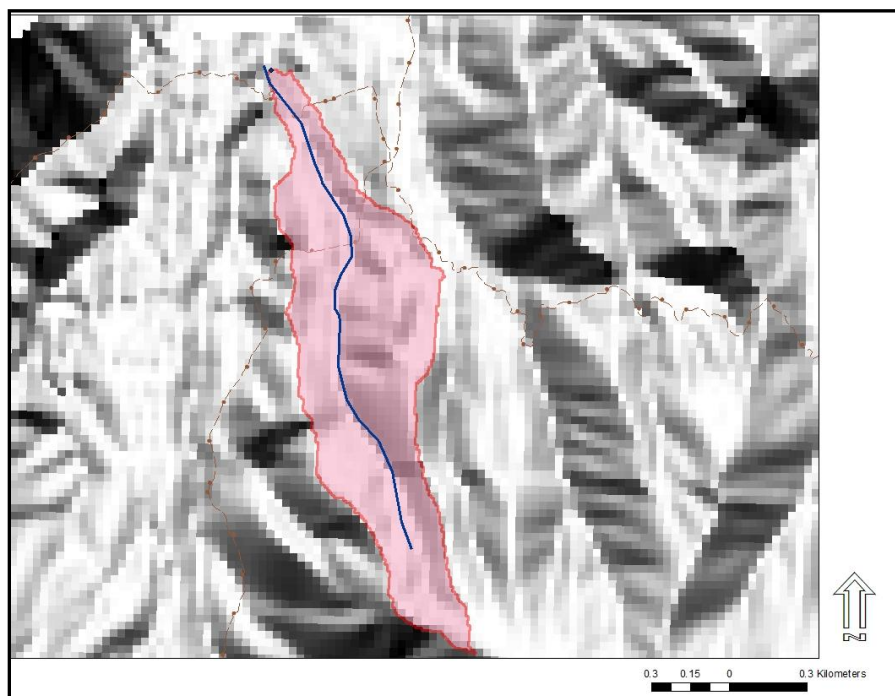
Appendix. A4. Terrain Shape Data Utilized for Stream Site Selection in the Great Smoky Mountains National Park, USA.



Appendix. A5. Hemlock Distribution Map Utilized for Stream Site Selection in the Great Smoky Mountains National Park, USA. The areas in green represent locations with a significant hemlock component in the understory, overstory, or both.



Appendix B1. Map and watershed characteristics for Jones Branch watershed, Cosby, TN calculated from Ladd and Law (2007).

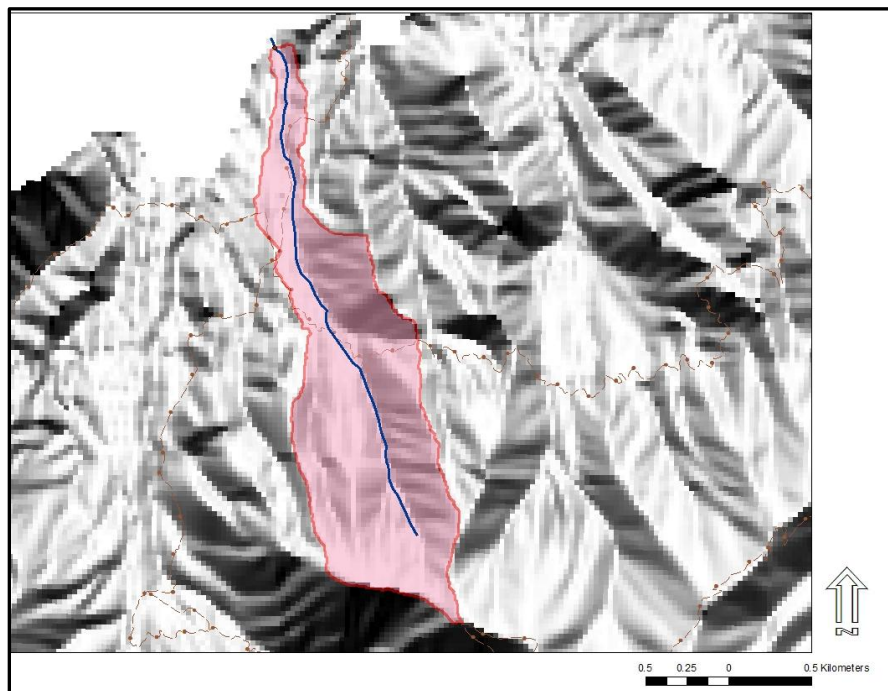


	Upper	Lower	Elev. Change
Stream Elev (m)	1083	658	425

Stream Length (m)	2196.83
Stream Gradient (%)	19.0%
Drainage Area (Sq. KM)	0.854
Stream Recession Index	100
PK2 Flow (CFS)	59.6
3Month Dry 2YR AVG	0.07
TN 2 YR Climate Factor	2.218

	Latitude (UTM)	Longitude (UTM)
Sampling Reach		
Upper	294693.73	3957724.75
Lower	294137.0	3959564.212

Appendix B2. Map and watershed characteristics for Cole Creek watershed, Cosby, TN calculated from Ladd and Law (2007).

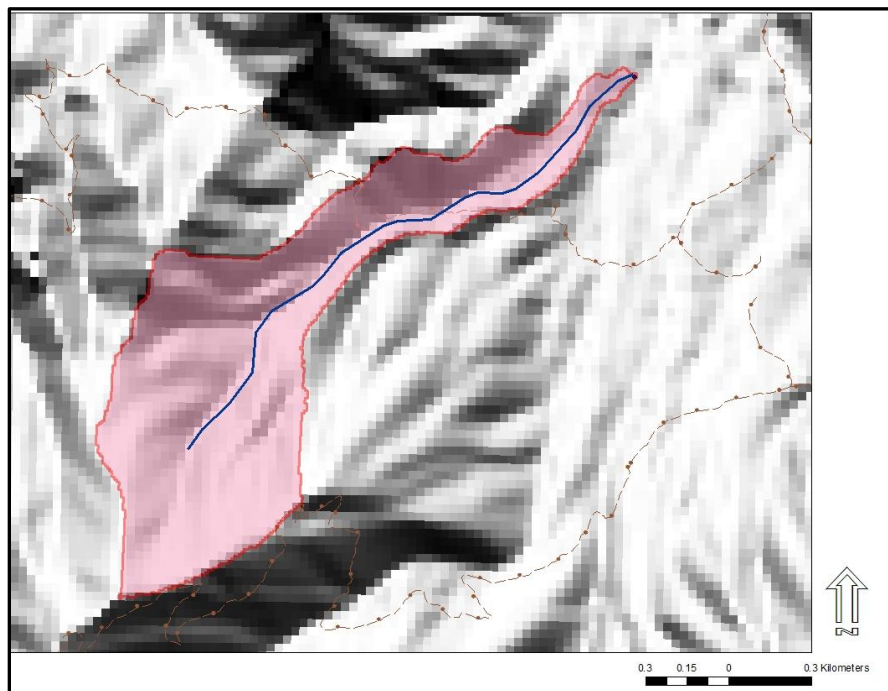


	Upper	Lower	Elev. Change
Stream Elev (m)	1154	594	560

Stream Length (m)	3231.48
Stream Gradient (%)	17.0%
Drainage Area (Sq. KM)	1.84
Stream Recession Index	100
PK2 Flow (CFS)	109.0
3Month Dry 2YR AVG	0.15
TN 2 YR Climate Factor	2.217

	Latitude (UTM)	Longitude (UTM)
Sampling Reach		
Upper	295440.098	3957591.575
Lower	294598.854	3960483.352

Appendix B3. Map and watershed characteristics for Crying Creek watershed, Cosby, TN calculated from Ladd and Law (2007).

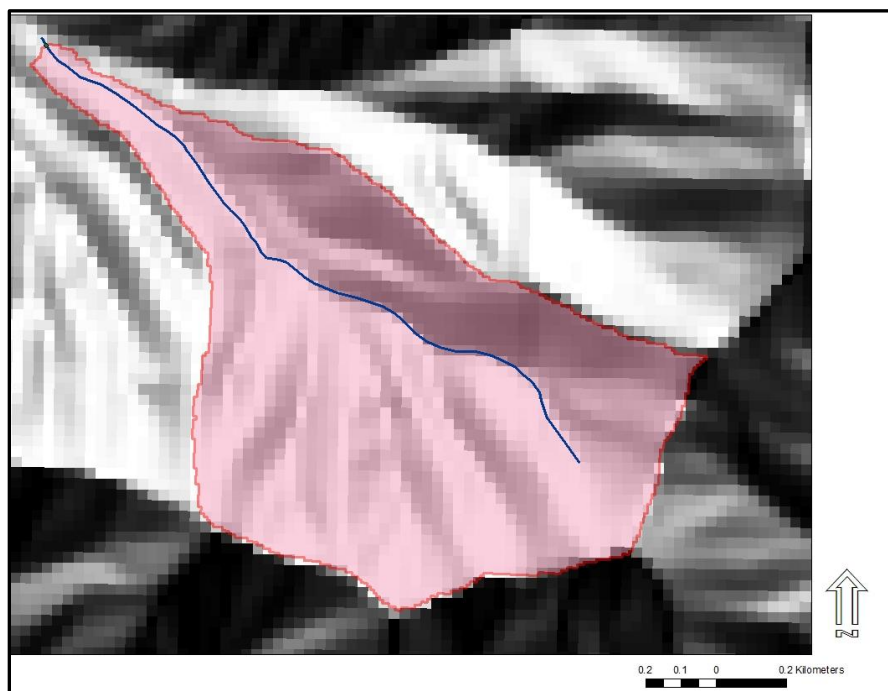


	Upper	Lower	Elev. Change
Stream Elev (m)	1062	658	404

Stream Length (m)	2250.03
Stream Gradient (%)	18.0%
Drainage Area (Sq. KM)	1.76
Stream Recession Index	100
PK2 Flow (CFS)	103.0
3Month Dry 2YR AVG	0.15
TN 2 YR Climate Factor	2.215

	Latitude (UTM)	Longitude (UTM)
Sampling Reach		
Upper	298100.65	3958282.26
Lower	299687.14	3959623.06

Appendix B4. Map and watershed characteristics for Toms Creek watershed, Cosby, TN calculated from Ladd and Law (2007).

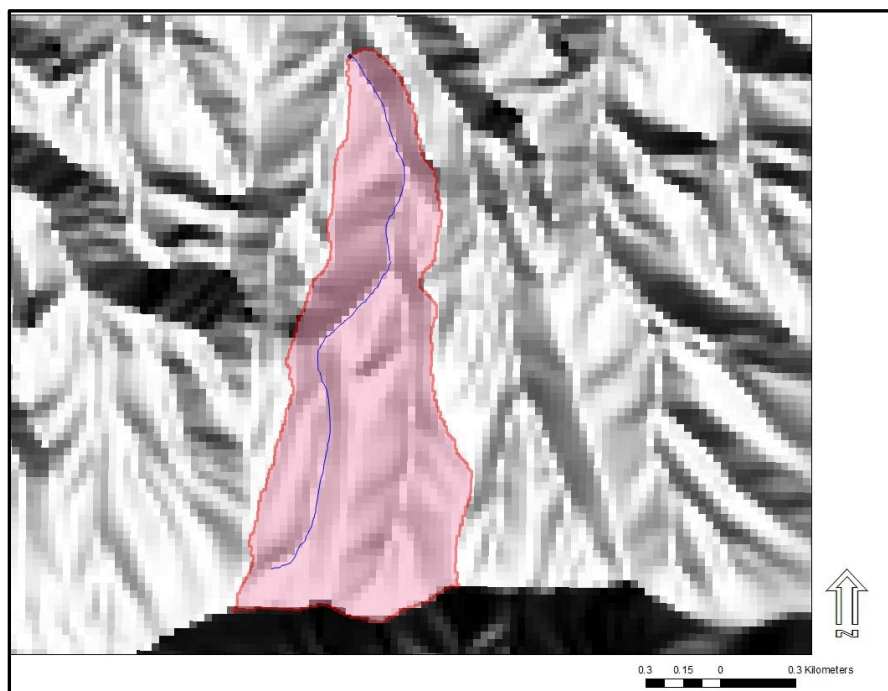


	Upper	Lower	Elev. Change
Stream Elev (m)	1322	862	460

Stream Length (m)	2031.95
Stream Gradient (%)	14.0%
Drainage Area (Sq. KM)	1.37
Stream Recession Index	100
PK2 Flow (CFS)	87.0
3Month Dry 2YR AVG	0.11
TN 2 YR Climate Factor	2.215

	Latitude (UTM)	Longitude (UTM)
Sampling Reach		
Upper	303591.2	3958243.69
Lower	302075.96	3959384.26

Appendix B5. Map and watershed characteristics for Noisy Creek watershed, Cosby, TN calculated from Ladd and Law (2007).

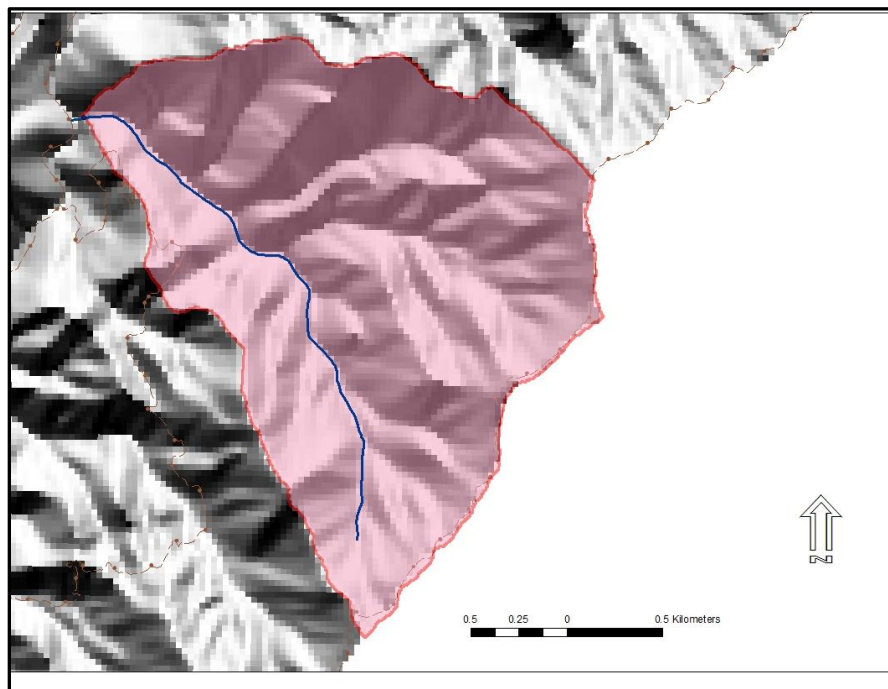


	Upper	Lower	Elev. Change
Stream Elev (m)	1413	786	627

Stream Length (m)	2305.4
Stream Gradient (%)	22.0%
Drainage Area (Sq. KM)	1.92
Stream Recession Index	100
PK2 Flow (CFS)	113.0
3Month Dry 2YR AVG	0.16
TN 2 YR Climate Factor	2.22

	Latitude (UTM)	Longitude (UTM)
Sampling Reach		
Upper	289497.13	3955774.64
Lower	289818.85	3957820.22

Appendix B6. Map and watershed characteristics for Den Branch watershed, Cataloochee, NC calculated from Ladd and Law (2007).

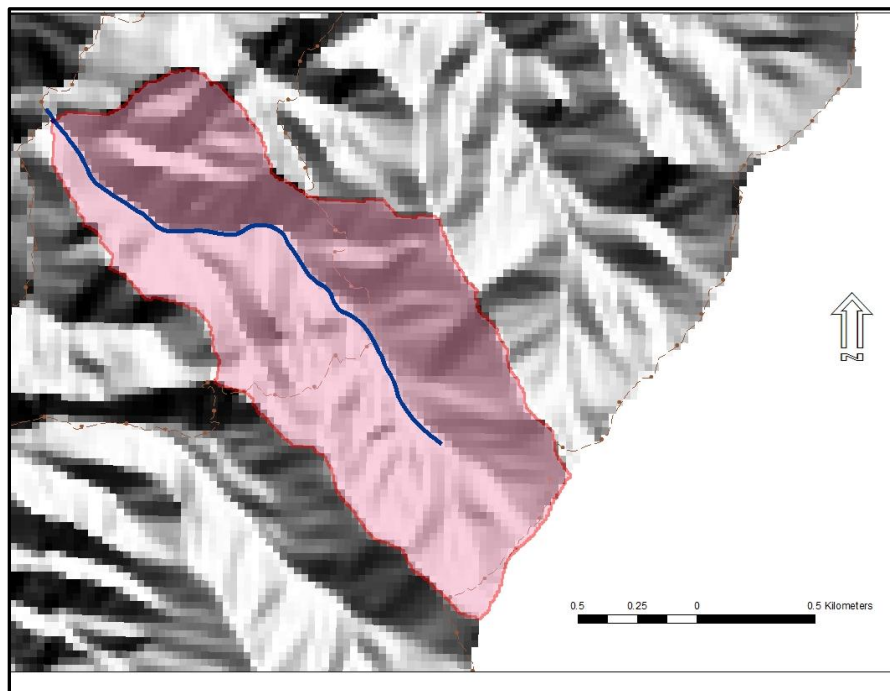


	Upper	Lower	Elev. Change
Stream Elev (m)	1154	852	302

Stream Length (m)	2363.5
Stream Gradient (%)	0.13
Drainage Area (Sq. KM)	4.71
Stream Recession Index	175
PK2 Flow (CFS)	220
3Month Dry 2YR AVG	0.81
TN 2 YR Climate Factor	2.221

	Latitude (UTM)	Longitude (UTM)
Sampling Reach		
Upper	312388.36	3942620.67
Lower	310910.01	3944444.32

Appendix B7. Map and watershed characteristics for Den Branch watershed, Cataloochee, NC calculated from Ladd and Law (2007).

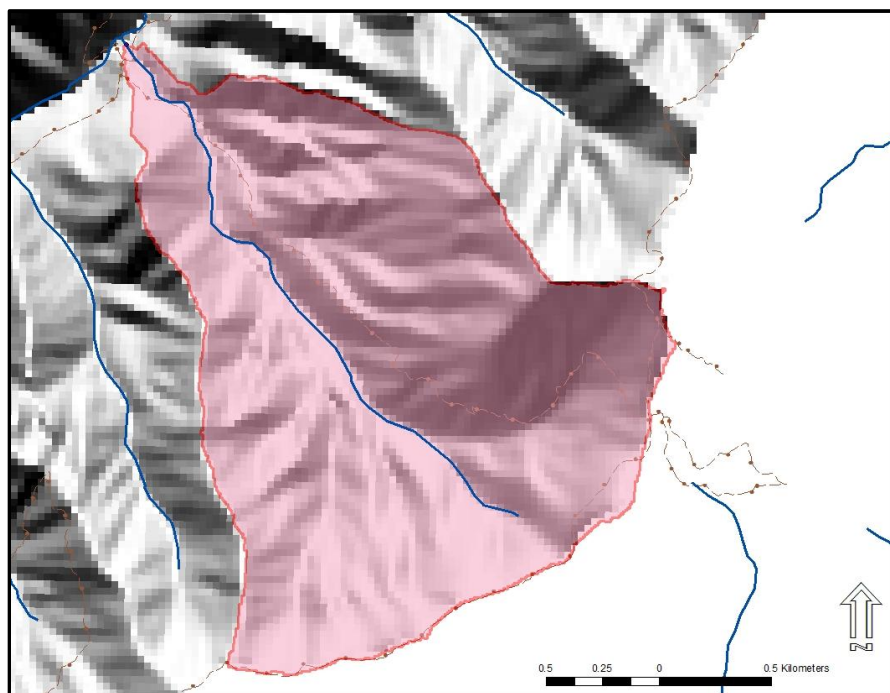


	Upper	Lower	Elev. Change
Stream Elev (m)	1206	848	358

Stream Length (m)	2587.34
Stream Gradient (%)	0.14
Drainage Area (Sq. KM)	2.18
Stream Recession Index	175
PK2 Flow (CFS)	123
3Month Dry 2YR AVG	0.38
TN 2 YR Climate Factor	2.223

	Latitude (UTM)	Longitude (UTM)
Sampling Reach		
Upper	311832.63	3941903.08
Lower	310224.796	3943219.56

Appendix B8. Map and watershed characteristics for McKee Branch watershed, Cataloochee, NC calculated from Ladd and Law (2007).

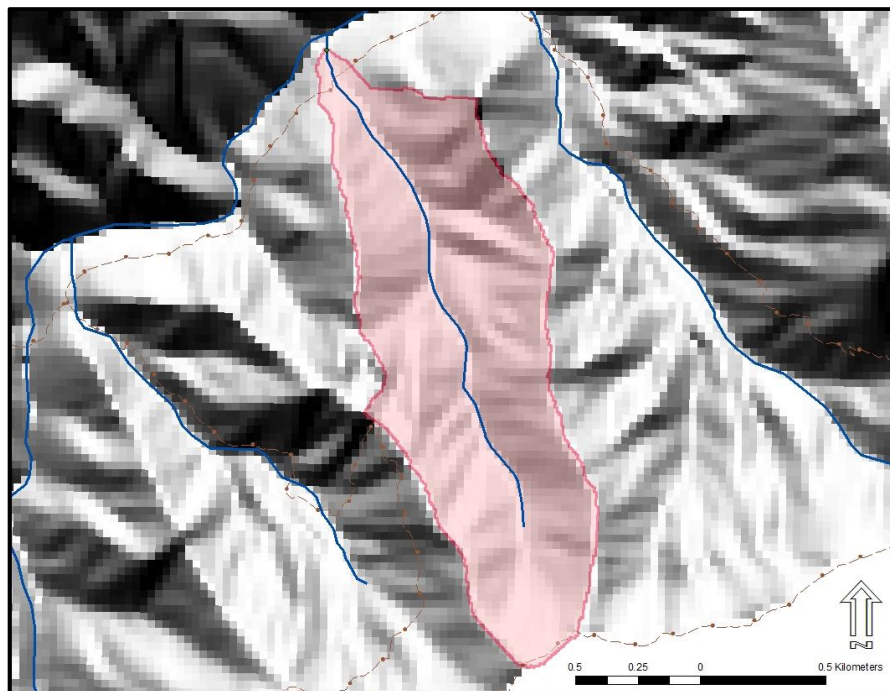


	Upper	Lower	Elev. Change
Stream Elev (m)	1330	912	418

Stream Length (m)	2889.48
Stream Gradient (%)	0.14
Drainage Area (Sq. KM)	4.09
Stream Recession Index	175
PK2 Flow (CFS)	204
3Month Dry 2YR AVG	0.71
TN 2 YR Climate Factor	2.226

	Latitude (UTM)	Longitude (UTM)
Sampling Reach		
Upper	310795.77	3939760.01
Lower	309463.28	3941535.06

Appendix B9. Map and watershed characteristics for Clontz Branch watershed, Cataloochee, NC calculated from Ladd and Law (2007).

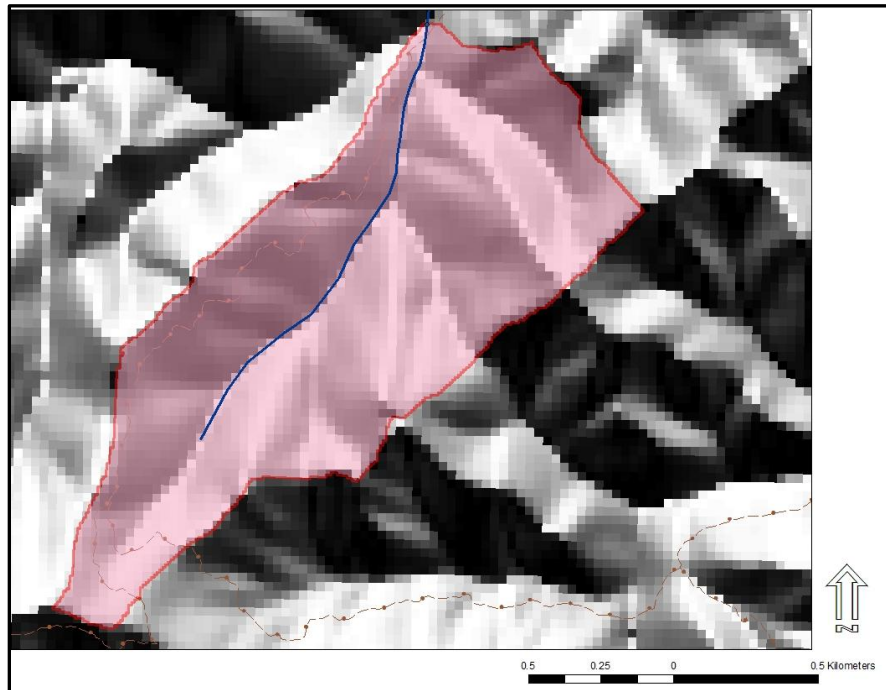


	Upper	Lower	Elev. Change
Stream Elev (m)	1315	933	382

Stream Length (m)	2187.72
Stream Gradient (%)	00.17
Drainage Area (Sq. KM)	1.48
Stream Recession Index	175
PK2 Flow (CFS)	92.5
3Month Dry 2YR AVG	0.26
TN 2 YR Climate Factor	2.227

	Latitude (UTM)	Longitude (UTM)
Sampling Reach		
Upper	309708.611	3939254.92
Lower	308924.51	3941082.88

Appendix B10. Map and watershed characteristics for Hurricane Creek watershed, Cataloochee, NC calculated from Ladd and Law (2007).



	Upper	Lower	Elev. Change
Stream Elev (m)	1172	935	237

Stream Length (m)	1796.25
Stream Gradient (%)	0.13
Drainage Area (Sq. KM)	1.76
Stream Recession Index	175
PK2 Flow (CMS)	2.92
3Month Dry 2YR AVG	0.3
TN 2 YR Climate Factor	2.221

	Latitude (UTM)	Longitude (UTM)
Sampling Reach		
Upper	306218.584	3940526.15
Lower	307001.81	3941935.95

VITA

Misty Dawn Huddleston was born in November 1975, in Lake City, Tennessee. She attended public school in Clinton, Tennessee, and graduated with honors from Clinton High School in 1994. After a brief stint in the U.S. Army, she returned to Knoxville, Tennessee, and enrolled at Pellissippi State Technical Community College. After transferring to the University of Tennessee, she received her Bachelor of Science degree in Wildlife and Fisheries Science from the University of Tennessee in 2004. In May 2006, Misty received her Master of Science degree in Wildlife and Fisheries Sciences from the University of Tennessee, Knoxville. Misty took a year off from school and during this time worked for the university and on several side projects for the Tennessee Division of Forestry, Sustainable Forestry Initiative, and the National Web-based Learning Center for Private Forest and Range Landowners. The following year Misty returned to the University of Tennessee to pursue her doctoral degree and graduated in December 2011 with a major in natural resources with a concentration in forest health and entomology. She is currently employed by AquAeTer, Inc., Brentwood, Tennessee, as a Project Scientist and Senior Aquatic Biologist.