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Variations in Carbon Fluxes Lead to Resilience of Carbon Storage in New England Forests Affected by the Hemlock Woolly Adelgid at a Centennial Time Scale

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Dissertation

VARIATIONS IN CARBON FLUXES LEAD TO RESILIENCE OF CARBON STORAGE IN NEW ENGLAND FORESTS AFFECTED BY THE HEMLOCK WOOLLY ADELGID AT A CENTENNIAL TIME SCALE

by

POLIANA COSTA LEMOS

B.S., Universidade Federal de Lavras, 2005
M.S., Universidade Federal de Lavras, 2007

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Approved by

First Reader ______________________________
Adrien C. Finzi, Ph.D.
Professor of Biology

Second Reader ______________________________
Lucy Hutyra, Ph.D.
Assistant Professor of Earth and Environment

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VARIATIONS IN CARBON FLUXES LEAD TO RESILIENCE OF CARBON STORAGE IN NEW ENGLAND FORESTS AFFECTED BY THE HEMLOCK WOOLLY ADELGID AT A CENTENNIAL TIME SCALE

(Order No.)

POLIANA COSTA LEMOS

Boston University Graduate School of Arts and Sciences, 2013

Major Professor: Adrien C. Finzi, Professor of Biology

ABSTRACT

Since the 1980s, hemlock-dominated forests (*Tsuga canadensis*) of central New England have been increasingly infested by the invasive pest hemlock woolly adelgid (HWA, *Adelges tsugae*), predominantly resulting in its replacement by black birch-dominated forests (*Betula lenta*). To date there has been no long-term empirical analysis of HWA effects on forest carbon (C) cycling due to forest transition from hemlock to black birch. To address this question, I measured the C pools in five stand types at varying ages and stages of HWA infestation in Massachusetts and Connecticut. I also measured C fluxes in aboveground net primary production (ANPP) and soil respiration, and studied the drivers of these fluxes viz. litter production, rates of foliar decomposition, soil exoenzyme activity, temperature sensitivity of soil respiration and nitrogen (N) cycling. The mass of C stored in recovering forests was resilient to HWA infestation but the location of these stocks varied among stand types. There was a transition of C from live biomass in healthy, unaffected secondary hemlock forests to coarse woody debris

(CWD) in recently girdled forests intended to simulate the effect of HWA on hemlock loss. Twenty years post-HWA infestation, however, ANPP was very high and there was a large increase in biomass-C pools in aggrading black stand types. C pools in mature, secondary black birch stand types ~135 years since pastureland abandonment were as large as those in primary hemlock stand types ~235 years of age, suggesting recovery of C storage within one century of HWA infestation. Soil respiration rates were positively correlated with inputs of hardwood leaf litter, fine root biomass and exoenzyme activity. Stand-type variations in ANPP were positively correlated with annual N requirements and N uptake from the soil. Nitrogen-use efficiency was highest in the girdled and post-HWA infestation stand types where ANPP was dominated by wood production which has a wide C:N ratio. Similar trends were found in soil respiration, but not to the same degree as that of ANPP. Collectively, my results indicate that southern New England forests C storage is highly resilient to the HWA-induced losses of hemlock, suggesting that these ecosystems will continue to be sinks for atmospheric carbon dioxide.

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LIST OF ABBREVIATIONS

ANOVA:	analysis of variance
ANPP:	aboveground net primary production
αG:	alpha-1,4-glucosidase
βG:	beta-1,4-glucosidase
C:	carbon
CBH:	cellobiohydrolase
C:N	carbon-to-nitrogen ratio
CO_2:	carbon dioxide
˚C:	degrees Celsius
CWD:	coarse woody debris
DBH:	diameter at breast height
DOPA:	L-3,4 dihydroxyphenylalanine
HWA:	hemlock woolly adelgid
IRGA:	infra-red gas analyzer
N:	nitrogen
NAG:	beta-1,4-N-acetylglucosaminidase
NaOH:	sodium hydroxide
$N_{foliage\ inc}$:	nitrogen in foliage increment
N_{green}:	nitrogen in green foliage
$N_{litterfall}$:	nitrogen in litterfall
N_{req}:	nitrogen requirement

$N_{retrans}$: nitrogen retranslocation

NUE: nitrogen use efficiency

N_{uptake}: nitrogen uptake

$N_{wood\ inc}$: nitrogen in wood increment

OH: organic horizon

Perox: peroxidase

PhenOx: phenol oxidase

PVC: polyvinyl chloride

Q_{10}: soil temperature sensitivity

RGR: relative growth rate

RIV: relative importance value

R_s: soil respiration

R_{10}: soil respiration at 10^{o}C

SE: standard error

SIGEO: Smithsonian Institution Global Earth Observation

SOM: soil organic matter

USDA: United States Department of Agriculture

CHAPTER 1

GENERAL INTRODUCTION

The last 200 years have been marked by a significant global increase of pest and pathogen invasion in forests (Liebhold et al. 1995). In the United States, nonindigenous insects are introduced at an accelerating rate by transportation of humans and materials (Aukema et al. 2010, Figure 1.1), although only a small fraction of these introductions become invasive (Williamson and Fitter 1996). The gypsy moth (*Lymantria dispar*), the chestnut blight (*Cryphonectria* (*Endothia*) *parasitica*), beech bark disease (*Cryptococcus fagisuga* and *Nectria* spp.) and the Asian long-horned beetle (*Anoplophora glabripennis*) are examples of invasive pests and pathogens introduced to northeastern forests. Some of these invasive pests affect a broad spectrum of tree species while others are very specialized. Mortality and stand replacement of the affected host species brings changes to ecosystem level processes, including water balance (Daley et al. 2007) and forest fire frequency (Hicke et al. 2012b).

Of the many changes brought by forest pests and pathogens, one of unarguable relevance is of biogeochemical cycles, as these provide the foundation for many other changes in affected forests. The death of trees increases the presence of decomposing microorganisms, providing nutrients and energy to the ecosystem and influencing habitat conditions to macrofaunal populations (Franklin et al. 1987). Decreases in canopy volume, due to insect herbivory, allows more light to reach the forest floor and creates favorable conditions for shade-intolerant trees to succeed (Peet and Christensen 1987, Eschtruth et al. 2006). All these changes affect the capacity of forests to take up, store and release carbon (C) back to the atmosphere. In light of the significant increases of anthropogenic CO_2 emissions, it is important to examine the role of forest ecosystems as natural carbon pools and sinks (Canadell et al. 2007) and how the ability of ecosystems to store carbon may be affected by invasive species.

The Northern Hemisphere is a significant net sink of anthropogenic carbon dioxide (CO_2; e.g. Bousquet et al. 2000, Houghton 2000, Pacala et al. 2001). US forests sequester 10-30% of the country's annual carbon emissions (Houghton et al. 1999, Birdsey et al. 2006) and northeastern temperate forests are crucial sinks (Foster et al. 1992). Nearly 80% of northeastern US forests were cleared for agricultural production throughout the settlement period between 1600 and 1850, but agricultural abandonment in the mid-1800s converted the landscape to aggrading secondary forests (Foster et al. 1998). This conversion has caused major increases in C storage and uptake in the region (Foster and Aber 2004). Given the important role this region plays in climate change mitigation through the removal of CO_2 from the atmosphere, it is essential to understand how forest productivity may change as a result of pest disturbance.

The hemlock woolly adelgid (HWA- *Adelges tsugae*) was introduced from Japan to Virginia in the early 1950s and is thought to have a major impact on C uptake and storage in eastern temperate forests (Souto and Shields 2000). The HWA is one of the sap-feeding insects of the order Hemiptera, which account for over 40% of all nonindigenous forest insect species in the continental US (Aukema et al. 2010). The HWA feeds on the sap of the eastern hemlock (*Tsuga canadensis*) and Carolina hemlock (*Tsuga caroliniana*) trees by inserting its stylet in the needles' parenchyma cells (Young et al. 1995). Once the needle has been affected, it is killed and is not replaced (Godman and Lancaster 1990). In the early 1990s, a century-long continual increase in *Tsuga canadensis* population was reported for the southern New England region (Foster et al. 1992). The fate of this species has been drastically interrupted by the presence of the HWA, which reached the region sometime in 1985 (McClure 1987), killing circa 90% of infested trees (Orwig et al. 2002, Knoepp et al. 2011).

The egg sacs of the HWA are covered by a material that resemble tufts of wool (therefore its name) and are found on the underside of hemlock branches. Up to 300 eggs are found in each egg sac and, in the spring, the larvae can spread on their own or with the assistance of wind, birds and mammals (McClure 1990). Over-winter mortality constrains HWA populations and the rate of eastern hemlock decline in the northeast. This over-winter mortality slows eastern hemlock death from 1-3 years in the south to 5-15 years in the northern portion of its range (Ellison et al. 2010). Genetic adaptation (Butin et al. 2005) and milder winters compared to historical conditions (Hayhoe et al. 2007) have permitted, however, the HWA to continue its northward distribution successfully. Recent achievement in containing the HWA has been reported on an experimental scale with the derodontid beetle *Laricobius nigrinus* from western North America (Zilahi-Balogh et al. 2002, Mausel et al. 2010). Yet, it is unclear how long it should take for this biological control to constrain the HWA that is currently found in 18 US states (Figure 1.2).

The eastern hemlock is a coniferous species of high ecological importance in northeastern forests. Described as a foundation species (Ellison et al. 2005), it disproportionately affects the biotic and abiotic environment in its range. This control derives from the cool and damp microclimate it creates, with low light levels (Eschtruth et al. 2006). Additionally, a thick layer of acidic soil organic matter (vanBreemen et al. 1997, Finzi et al. 1998a) is formed due to its slowly decomposing litter, storing large amounts of C (Finzi et al. 1998b, Jenkins et al. 1999, Hadley 2000). Eastern hemlock is a slow-growing, long-lived conifer native to eastern North America, ranging from Minnesota to Nova Scotia on its northern range, and southward along the Appalachian Mountains to northern Georgia and Alabama (Godman and Lancaster 1990, USDA 2012). Given the eastern hemlock's importance as a foundation species and its widespread geographical distribution, the HWA is currently considered one of the most impactful biotic disturbances in North America (Hicke et al. 2012a).

Eastern hemlock stands in central New England forests are being largely replaced by the early successional and gap-colonizing tree species, black birch (*Betula lenta*, (Orwig and Foster 1998, Sullivan and Ellison 2006). Black birch seeds are produced in abundance every 1-2 years, released in the fall and throughout the winter, and are able to disperse through wind across the surface of the snow pack in cold years (Matlack 1989). *Betula lenta* is a deciduous species that produces rapidly-decomposing litter.

Because of their distinct characteristics, hemlock- and black birch-dominated forests are thought to have very different rates of C uptake and storage (Daley et al. 2008, Hadley et al. 2008). These differences would be largely driven by changes in nutrient availability and the plants' capacity to use nutrients efficiently. It is also predicted that, for a period following infestation, affected stands would likely be a source of CO_2 to the atmosphere because of massive decomposition of the necromass. Empirical studies relating HWA to forest C balance have focused on short-term analyses, documenting changes within the first decade following infestation (e.g. Jenkins et al. 1999, Knoepp et al. 2011, Block et al. 2012). No empirical studies have addressed the potential long-term impacts in the C cycle and its drivers in southern New England forests affected by the HWA.

DISSERTATION OVERVIEW

The primary objective of this dissertation is to investigate the potential resiliency of forest C storage and flux to the loss of eastern hemlock by the HWA. To meet this objective, I compare the pools and fluxes of C in eastern hemlock and black birch stands of varying age and stand development in southern New England (Figure 1.3). Primary (>230 years, Hadley 2000) and secondary hemlock stand types (135 years, Bettman-Kerson 2007) were used to mimic conditions prior to HWA arrival. A girdled hemlock stand type was used to simulate a recent HWA outbreak (5 years, Ellison et al. 2010). A forest stand two decades following heavy HWA infestation, and which is now dominated by black birch saplings, was also measured. Lastly, I used a secondary black birch stand type (132 years) to represent mature forests dominated by the main replacing species of the affected eastern hemlock in southern New England.

For each stand type, I established four 900m^2 replicate plots. Three of the five stand types were located at the Harvard Forest, Massachusetts (42^{o}32'N 72^{o}11'W). The primary hemlock stand type was located in the Prospect Hill tract of the forest. This stand has never been cleared or grazed, though some selective logging may have taken place in the 1800's through early 1900s (Foster et al. 1992). The secondary hemlock and girdled stand types are part of the large-scale eastern hemlock manipulation study at Harvard Forest (Ellison et al. 2010) and were located in the Simes Tract. The Simes Tract underwent a rapid transition from pastureland in the late 19th century (ca. 25% forest cover in 1880) to forestland in the early 20th century (ca. 85% forest cover in 1920, Foster and Zebryk 1993).

The post-HWA stand type was located in the Connecticut River Valley (Burnham Brook, East Haddam, CT, 41^{o}28'N 72^{o}19'W), where infestation by HWA in the early 1990s caused >90% eastern hemlock mortality by 1995 (Orwig and Foster 1998). Trees previously cored at this stand (David Orwig, *personal communication*) suggest that the land was a woodlot as well. At the time of infestation the hemlock stand was ca. 120 years of age. A 135-year-old stand dominated by black birch trees was located near Black Pond in Harvard MA (42^{o}31'N 71^{o}32'W). My analysis of land-use history records for the town of Harvard, MA suggests that this black birch forest was the first to have occupied the site since the abandonment of pastureland.

I began my studies by quantifying C storage in the soil as well as in above- and belowground biomass. I compared pool sizes in the stands and within them. Next, I investigated changes in carbon fluxes, with special focus on aboveground net primary production and soil respiration. I also looked at changes in the main drivers of this flux.

Chapter 2 focuses on total C storage and changes in C pools. Aboveground C pools were measured as aboveground live biomass, and fine (<1 cm diameter), small (1-

10 cm diameter) and coarse (>10 cm diameter) woody debris. Belowground C pools were measured as fine (<2 mm diameter), small (2 mm – 1 cm diameter) and coarse (>1 cm diameter) roots, as well as C content in soil organic matter and mineral soil to 45cm in depth. I applied pre-existing species-specific allometric equations to all inventoried trees and developed an allometric equation for black birch saplings from one of my field stands (post-HWA). I separated coarse woody debris in three decay classes and three categories (stump, snag and fallen log) with each decay class sampled for their volume through water displacement. I obtained soil and fine root samples using a soil corer and dug twenty soil pits to obtain coarse root mass. Stand-specific rock volume was also obtained using these pits and was used to adjust soil volume for accurate estimates of belowground C pools. I used this research to test two hypotheses: (1) ecosystem C storage is lower in mature black birch stands than eastern hemlock stands, especially due to the accumulated organic matter found in latter stands (2) the distribution of the C pools differs among stand types.

Chapter 3 quantifies differences in aboveground net primary production and soil respiration, as well as biochemical drivers of these C fluxes. I estimated aboveground net primary production (ANPP) in each stand using stand -specific information on the trees' relative growth rate as well as literature-based allometric equations. This required dendrochronology analysis of the five different tree species that were commonly found across stands (*Acer rubrum*, *Betula lenta*, *Pinus strobus*, *Quercus rubra*, *Tsuga canadensis*). To this increment study I added annual rates of aboveground litterfall mass (turnover) from data collected in 2010 and 2011 in all the plots and obtained net productivity.

I measured soil respiration every 4-5 weeks using a Li-Cor 6400 from October 2010 until November 2011 excluding periods of snow cover. I analyzed potential drivers of soil respiration, starting with soil organic matter (SOM) decomposition, through the analysis of soil exoenzyme activity. I looked at enzymes related to the decomposition of labile C (αG, βG, CBH) and recalcitrant C (peroxidase, phenol oxidase). I examined potential relationship between soil respiration and foliar decomposition, comparing rates of mass loss among species, stand types and across times.

Because of its critical role in forest productivity I considered nitrogen (N) as an important factor linked to C flux. I developed a comparative N budget (g N m^{-2}) among stand types, analyzed C-to-N ratios (C:N) in wood, leaf, roots and soil, and measured N-related microbial enzyme activity (N-acetylglucosaminidase; NAG). Using these data, I calculated aboveground N requirement (N_{req}), nitrogen-use efficiency (NUE), retranslocation ($N_{retrans}$) and uptake (N_{uptake}) for each of the stand types. This research tested three hypotheses: (1) ANPP is higher in young, aggrading black birch stands compared to secondary hemlock stands; (2) black birch leaf litter decomposes faster than eastern hemlock litter and in black birch-dominated stand types than hemlock-dominated stands; (3) N availability increases from hemlock-dominated to black birch-dominated stands, contributing to increases in both soil respiration and ANPP.

In Chapter 4, I summarize my findings on ecosystem C storage and flux in response to the HWA infestation in southern New England forests. I discuss the implications of my research in the context of forests' C resiliency in southern New England to one of the principal invasive pests of North America. I conclude by exploring future research directions that could further elucidate the ecosystem-level effects of the HWA to northeastern temperate forests.

FIGURE 1.1. Cumulative detections of nonindigenous forest insects by guild over time in the United States. Squares: sap-feeders; triangles: foliage feeders; circles: phloem and wood borers; and diamonds: others. Source: Aukema et al. 2010.

FIGURE 1.1.

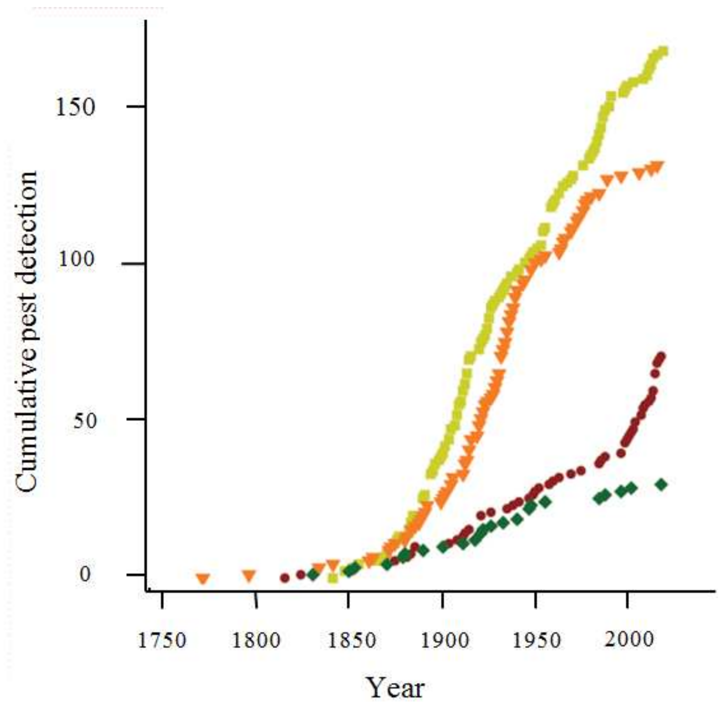

Cumulative pest detection
150
100
50
0
1750
1800
1850
1900
1950
2000
Year

FIGURE 1.2. County-level native range of the eastern hemlock (green), and areas with established HWA populations (brown, infested counties; yellow, newly infested in 2011). Source: USDA Forest Service 2012.

FIGURE 1.2.

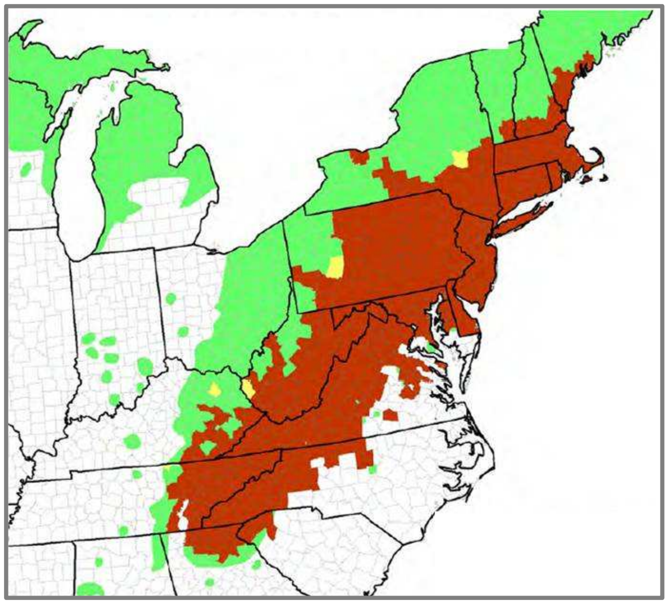
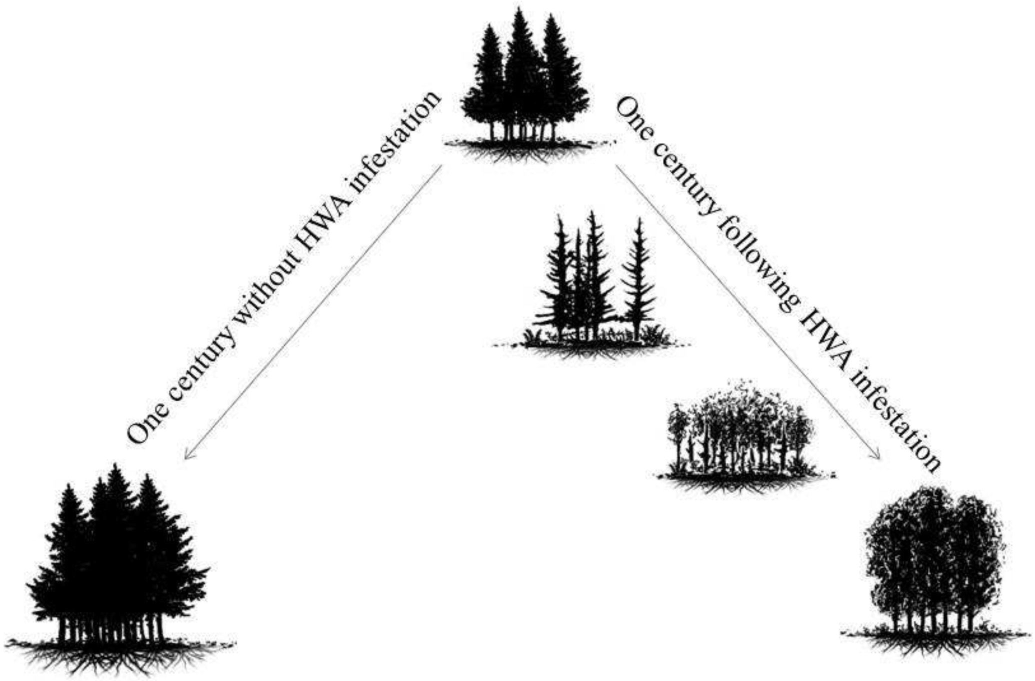


FIGURE 1.3. Stand types used to investigate changes and examine the trajectory of carbon storage and flux due to the infestation of the hemlock woolly adelgid (art courtesy: Floyd T. Raymer).

FIGURE 1.3.


One century without HWA infestation
One century following HWA infestation

CHAPTER 2

HEMLOCK LOSS DUE TO THE HEMLOCK WOOLLY ADELGID DOES NOT AFFECT CARBON STORAGE BUT ALTERS ITS DISTRIBUTION

ABSTRACT

The 1950s introduction of the hemlock woolly adelgid (HWA – *Adelges tsugae*) has caused extensive eastern hemlock (*Tsuga canadensis*) mortality with little understanding of the long-term consequences for forest carbon (C) storage. In southern New England, eastern hemlock is being replaced by the early successional species black birch (*Betula lenta*). The objective of this research was to measure C stocks in stands of varying age and abundance of eastern hemlock and/or black birch. Using information from previous studies and comparisons of data between plots with identical land-use history, I addressed the question of whether (1) C pools in black birch forests could reach the size of those found in hemlock stands and (2) the distribution of the C pools differed between stand types. If HWA did not infest hemlock stands in central MA, C stocks in these secondary stands could still increase by at least ~30% over a period of 100 years. Girdling, intended to simulate HWA infestation, resulted in a large transfer of C from live biomass to coarse woody debris five years after treatment, but had little effect on total ecosystem C content. A former hemlock stand killed by HWA and now dominated by black birch saplings (~23,000 stems ha^{-1}) also had a large pool of highly decayed CWD and a rapidly aggrading C pool in live biomass. C pools in biomass in a mature, secondary black birch stand ~135 years since pastureland abandonment were as large as those in a primary hemlock stand ~235 years of age. Because of uncertainties in the intensity of former land use and time since pastureland abandonment, this analysis can only speak to the potential consequences of HWA on forest-C balance over the long term. Based on this analysis, it appears that ecosystem C storage is resilient to the loss of hemlock because of vigorous regrowth by black birch. This empirical finding is consistent with the results of a recent modeling effort.

Key words: *hemlock woolly adelgid; carbon storage; centennial time-scale; invasive pest; black birch; empirical measurements*

INTRODUCTION

Over the last 200 years, there has been a substantial increase in the introduction of forest pests in the continental United States (Liebhold et al. 1995). The damage caused by these forest pests varies greatly, yet their numbers and capacity to cause wide spread mortality are substantial (Gibbs 1978, McCormick and Platt 1980, Poland and McCullough 2006, Eisenbies et al. 2007). Sap-feeding insects of the order *Hemiptera* account for >40% of all non-indigenous forest species in the continental US (Aukema et al. 2010). The hemlock woolly adelgid (HWA - *Aldeges tsugae*, (McClure 1990, Orwig and Foster 1998), which has extirpated hemlock from much of the center of this species' range, is a "high-impact" species belonging to this order (Williamson and Fitter 1996).

The HWA was accidently introduced in Virginia from Japan in the early 1950s (Souto and Shields 2000), is currently established in 18 states and is anticipated to continue spreading (USDA Forest Service 2012). Eastern hemlock trees (*Tsuga canadensis*) of all age and size categories are susceptible to the HWA (Godman and Lancaster 1990). The aphid-like insect inserts a long stylet in the parenchyma tissue on the underside of hemlock needles and twigs, and consumes photosynthates, eventually starving the tree and causing death (Young et al. 1995). Native predators have thus far been unsuccessful in controlling HWA populations, although bio-control agents such as the *Laricobius nigrinus* show some promise in curbing further expansion (Zilahi-Balogh et al. 2002, Mausel et al. 2010). Because of its sensitivity to cold temperatures, the rate of HWA colonization decelerates northward (Orwig et al. 2002, 2012). Recent climate analyses (Hayhoe et al. 2007) suggest that warming temperatures owing to climate change are likely to accelerate the HWA's northerly spread.

Eastern hemlock is one of the longest-lived tree species in eastern North America. It is a widely distributed species found as far north as New Brunswick, Canada, and within the United States throughout New England, the Appalachian Mountains and as far south as Alabama (USDA Forest Service 2012). Hemlock trees are disturbance-intolerant because they cannot resprout or refoliate following physical damage (Godman and Lancaster 1990). Eastern hemlock is considered a foundation species (Ellison et al. 2005) because of its effect on microclimate and light availability (Canham et al. 1994), and by producing litter with high concentrations of polyphenolic compounds and lignins that contribute to slow rates of decomposition (Melillo et al. 1982), the accumulation of soil carbon (C) (Finzi et al. 1998b, Hadley 2000), acidic, base poor soils (vanBreemen et al. 1997, Finzi et al. 1998a) and low rates of nutrient mineralization (Finzi et al. 1998b, Talbot and Finzi 2008).

Infestation by the HWA results in needle loss that increases understory light availability and temperature. This change in microclimate facilitates the rapid growth of hardwood species (Catovsky and Bazzaz 2000). In southern New England, the dominant replacement species is black birch (*Betula lenta*, Orwig and Foster 1998). It is an early successional, fast-growing, deciduous species (Lamson 1990) whose growth attributes may alter the ecology and biogeochemistry of the hemlock forests it replaces. Black birch leaves are thin and decompose quickly relative to hemlock (Cobb 2010). In combination with warmer soil temperature (Ellison et al. 2010) and higher moisture content following the disturbance (Daley et al. 2007), there is the potential for substantial soil C loss, particularly from the thick organic horizons that characterize hemlock forests. The loss of soil C may, however, be compensated by high rates of primary production in the young, rapidly aggrading forest (Albani et al. 2010). As pointed out in a recent review (Hicke et al. 2012), however, there have been no assessments of the potential long-term impact of HWA on ecosystem C balance.

The objective of this research was to measure C stocks in stand types of varying age and abundance of hemlock and/or black birch. I quantified C pools in various eastern hemlock and black birch stand types in Massachusetts and Connecticut. Using information from previous studies and comparisons of data between plots with identical land-use history, I addressed the question of whether (1) C pools in black birch forests could reach the size of those found in hemlock stand types and (2) the distribution of the C pools differed between stand types.

METHODS

Stand Types and Land-Use History

This research was conducted in central Massachusetts and south-central Connecticut (Table 2.1). I quantified C pools in: (1) a primary hemlock stand type, representing the maximum C stocks expected for hemlock forests in this region; (2) a secondary hemlock stand type representing the starting point of HWA infestation for most eastern hemlock forests in this region; (3) a girdled hemlock stand type, representing an early stage following hemlock death; (4) a hemlock stand type 21 years following mortality caused by HWA that now has vigorous black birch saplings and sub-canopy trees; and (5) a secondary black birch stand type ~135 years old, growing on former pastureland (Figure 2.1).

Three of the five stand types were located at the Harvard Forest, Massachusetts (42^{o}32'N 72^{o}11'W). The primary hemlock stand type was located in the Prospect Hill tract of the forest. This stand has never been logged or grazed (Foster et al. 1992), though some salvage logging may have taken place in the 1800's through early 1900s (herein "primary hemlock"). The secondary hemlock and girdled hemlock stand types, ca. 132 years in age (the latter girdled in 2005) were located in the Simes Tract (herein "secondary hemlock" and "girdled", Bettman-Kerson 2007). This tract of land underwent a rapid transition from pasture land in the late 19th century (ca. 25% forest cover in 1880) to forest land in the early 20th century (ca. 85% forest cover in 1920, (Foster and Zebryk 1993). The girdling is part of the Harvard Forest Hemlock Removal Experiment (Ellison et al. 2010) and was intended to simulate a gradual death of standing hemlock trees, similar to that provoked by the HWA.

The forest plots in the Connecticut River Valley (Burnham Brook, East Haddam, CT, 41^{o}28'N 72^{o}19'W) were severely infested by HWA in the early 1990s (Orwig and Foster 1998). Since that time there has been vigorous regrowth in the former hemlock areas by black birch. Trees previously cored at that stand suggest that the prior land use was as a woodlot (D. Orwig, unpublished data). At the time of infestation the hemlock stand was ~100 years of age.

A 135-year-old stand dominated by black birch forest (herein "secondary black birch") was located near Black Pond on property belonging to the Harvard Conservation

Trust (Harvard, MA, 42^{o}31'N 71^{o}32'W). Following pastureland abandonment, a near monoculture of black birch developed over the last 135 years.

The climate was similar across all stand types. Mean annual temperature varied between 8.5 and 10 ^{o}C. Mean annual precipitation varied between 110-123 cm yr^{-1}. Throughout all stand types, soils were predominantly a sandy loam overlying glacial deposits of weathered gneiss, schist, and granite (Reynolds, 1979). The soils are inceptisols and classified as Typic Dystrochrepts (Hill et al. 1980). The depth to bedrock is <1m throughout the study area. At each of the five stand types, I established four 30x30m plots (N = 20). In each plot I measured the concentration and content of C in four pools: aboveground live biomass, woody debris, belowground live biomass and soil to a depth of 50cm. The stand types were inventoried from 2008 to 2010.

Carbon in Aboveground Biomass

In each plot, I measured the diameter of all trees > 10 cm breast height (dbh; ~ 1.37m) by species. Two of the four primary hemlock plots were located within the 35-hectare Smithsonian Institute Global Earth Observatory (SIGEO) forest dynamics plot on the Prospect Hill research area. I used data from a 2010 inventory to estimate aboveground biomass in these plots. At the Simes Tract (secondary hemlock and girdled stand types), all of my plots were located within an existing experiment (Ellison et al. 2010), and I used their 2009 inventory data for my analysis. In addition I inventoried all saplings (> 1.37 cm height and <10 cm dbh). The foliage and woody biomass of each tree was estimated from species-specific allometric equations (Table 2.2, Jenkins et al. 2003).

I used published equations for eastern hemlock, eastern white pine and black birch, and for the other hardwood species a generalized equation.

At the post-HWA stand type in CT, I established two 1 x 30-m transects in each plot to measure the number and diameter of black birch saplings (Table 2.1). There were no suitable, published allometric equations for black birch saplings in New England. Hence I developed stand-specific allometric relationships for black birch at this stand type. I harvested 14 black birch saplings varying in diameter from 0.3 – 7.3cm (King 1990). In the field I separated the felled stems into foliage and wood and dried the tissues at 60^{o}C for two weeks. Sub-samples of wood and foliage were weighed and regression analysis was used to convert stem diameter to wood and foliar biomass (Table 2.2).

Carbon in Woody Debris

Woody debris on the ground was divided into three size classes based on diameter: fine (θ_{debris}<1cm diameter), small (1cm < θ_{debris} <10cm) and coarse (θ_{debris} >10cm diameter). All woody debris were classified into three decay classes with class I corresponding to the least decayed material and class III corresponding to the well-decayed wood (modified from Carmona et al. 2002, Table 2.3). To quantity the mass of fine and small woody debris, I randomly located four 1x1m subplots within each replicate plot (i.e., 16 subplots per stand type) and collected all surface debris as well as those in the organic horizon. The entire 30x30m plot was inventoried for coarse woody debris volume. In addition to decay class information, coarse woody debris were categorized as logs and snags, modified from (Carmona et al. 2002, Coomes et al. 2002).

To estimate the density of wood, I collected ten samples of eastern hemlock and black birch debris from each size and decay class (n=90 per species), creating species-specific values. Volume was measured in the lab using the freshly collected sample. Each sample was then dried at 60^{o}C until constant mass and weighed. Debris of unknown species in the primary and secondary hemlock stand types and girdled plots were assumed to be eastern hemlock. Unidentifiable wood in the infested and secondary black birch stand types was assumed to be black birch. Less than 14% of the woody debris was unidentifiable.

Subsamples of the woody debris were ground and analyzed for %C on an element analyzer (NC 2500 Elemental Analyzer, CE Elantech, Lakewood, NJ, USA). The pool of C in each size and decay class was estimated as the product of volume per unit ground area (m^3 m^{-2}), density (kg m^{-3}) and %C. Data for each size and decay class was summed to provide a plot-specific estimate of C in woody debris.

Belowground Carbon Pools: Roots & Soil

Belowground biomass was sorted into three size classes based on diameter: fine (θ_{root}<2mm diameter), small (2mm<θ_{root}<1cm diameter), and coarse (θ_{root}>1cm diameter). Fine roots were collected from 5cm-diameter soil cores to a depth of 45cm. Small roots and coarse roots were collected from twenty 1 m^2 soil pits dug to 50cm depth (i.e, 0.5 m^3). Fine roots were collected from triplicate, randomly-located samples in each plot. Roots in the organic horizon (herein OH) were collected in 10x10cm monoliths. Once the OH was removed, I cored soils in 15cm depth increments to a depth of 45cm.

Fine roots were sorted from each sample and then washed, dried and weighed. For each plot, one of the three replicate samples was randomly selected for thorough analysis and separation of live and dead fine roots the day following soil coring, based on pith color and tensile strength. Roots with an intact cortex and considerable tensile strength were identified as live. The remaining samples were kept refrigerated until sorted. The ratio of live to dead roots from the plot-specific subsample was applied to the remaining biomass.

A 0.5 m^{-3} soil pit was excavated in each plot. The soil pits were necessary to sample coarse roots and rock volume for each plot. Estimations of fine root and soil C pools (kg C m^{-2}) without adjusting for rock volume would overestimate soil C pools in the very rocky soils of New England (Park et al. 2007). As the pit was being hand dug, roots were removed directly by hand while sieving the soil through 0.5cm mesh**.** Small roots were cut from coarse roots. After their return to the lab, roots were divided into live and dead categories, washed and then dried for two weeks until the samples achieved constant mass over a 2-day period. The %C in each fine root sample was measured on an element analyzer. There were no significant differences in %C in live or dead fine or coarse roots. Fine root %C was analyzed in the organic horizon and at 0-15 cm depth in the mineral soil. Roots from deeper in the soil profile were assumed to have the same %C as those in the top 15cm of mineral soil.

Rocks >0.5cm diameter were removed from the pits and weighed on site using a large spring-loaded scale. When rocks could not be removed (e.g., large rocks half in the sampled area and half outside), I estimated rock weight based on the mass of similarly sized rocks removed from the pit. A subsample of the rocks was kept and the displacement of water was used to estimate rock volume. Accordingly, I developed a relationship between rock volume and mass (rock volume = -16.1 + 439•rock mass, r^2=0.99, n=5), and used plot-specific estimates of rock volume to scale up root and soil C pools.

Soil C pools were estimated from measurements of soil bulk density and element analysis. Prior to sorting, the soils collected for fine-root sampling were weighed and sieved. A subsample of this soil was weighed, dried at 105 ^{o}C for four days and then reweighed. Bulk density was estimated from the mass of the soil sample, adjusted for water content, divided by the volume of the OH or soil core. This subsample of soil was analyzed for %C. The C content of the soil to a depth of 45cm was then calculated as C concentration multiplied by bulk density and adjusted for rock volume in each plot.

Comparison to Previously Published Results

Orwig and Foster (1998) and Jenkins et al. (1999) studied the post-HWA stand type located at Burnham Brook in CT three to five years following hemlock mortality. Using the species-specific allometric data discussed above, I estimated the C content in aboveground live biomass and snags using data on stem density, diameter distribution and live/dead status presented in (Orwig and Foster 1998), in addition to previously unpublished data. Jenkins et al. (1999) presented data on organic horizon C content and the top 10 cm of mineral soil. I extrapolated the data from the top 10cm to 15-cm depth in order to compare with my data.

Statistical Analysis

One-way ANOVA with Tukey's multiple comparison procedure were used to assess differences in C pools among stand types. All analyses were performed using RStudio (2011). The five stand types were the independent variables. The C pools (i.e., above- and belowground biomass, woody debris, soil C) were dependent variables. Assumptions of normality and homogeneity of variance were met. Tukey's multiple comparison test protected the experiment-wise alpha at $p < 0.05$.

RESULTS

Live Aboveground biomass

Aboveground C content in the primary hemlock stand type averaged 15.3 ± 2.2 kg C m^{-2} (Figure 2.2A), about 20% higher than that found in the secondary hemlock stand type. The girdled stand type had significantly lower aboveground biomass than all other stand types except for the post-HWA stand type. The mass of C in biomass in the 135-year old black birch stand type was equivalent to that in the primary and secondary hemlock stand types.

Woody debris

The mass of C in coarse woody debris (CWD, >10cm diameter) was significantly higher in the girdled stand type than the post-HWA stand type, both of which were significantly higher than that found in the primary and secondary hemlock stand types (Figure 2.2B). Most of the snags and logs were ≤ 20-cm diameter, but ranged in diameter up to 60cm (Figure 2.3). Most snags were found in the girdled stand type in decay class I (Figure 2.3A, C). Most logs were found in the post-HWA stand type in decay classes II and III, though there were also numerous logs in the primary hemlock and secondary black birch stand types (Figure 2.3B, D).

The quantity of C in small woody debris (SWD, 1-10 cm diameter) was significantly greater in the post-HWA stand type (0.42 ± 0.02 kg C m^{-2}) compared to all other stands (0.13 ± 0.01 kg C m^{-2}). The quantity of C in fine woody debris was significantly higher in primary hemlock stand types (0.07 ± 0.02 kg C m^{-2}) than all other stand types (average of 0.04 ± 0.01 kg C m^{-2}).

Soil

Total rock volume (0-50 cm soil depth) varied from 6.5 ± 0.4% in the secondary black birch stand type to 25.8 ± 3.4% in the primary hemlock stand (Table 2.1). The C content of the organic horizon was two-fold greater in the primary hemlock stand type (4.57 ± 0.58 kg C m^{-2}) than all other stand types (Figure 2.2C). Of the total quantity of C stored to a depth of 45cm, 28% was found in the organic horizon of the primary hemlock stand type compared to 15% and 7% in the secondary hemlock and black birch stand types.

The C content of mineral soil to a depth of 45cm was significantly higher in the primary hemlock and the secondary black birch stand types than all other stand types (Figure 2.2D). The quantity of C stored in the mineral soil was highest in the top 15cm of mineral soil and declined with depth. The content of C in the top 15cm of mineral soil was highest in the secondary black birch stand type, intermediate in the post-HWA stand type and lowest in the hemlock and girdled stand types. At 15-30cm depth, soil C content was highest in the primary hemlock stand type and lowest in the post-HWA and black birch stand types. At 30-45cm depth, the largest C pool was found in the secondary black birch stand type. Most of the variation in C content was due to differences in soil bulk density and rock volume (Table 2.1). The concentration of C, while variable from stand type to stand type, was statistically significant in the 15-30cm soil horizon (Table 2.4).

Roots

The C content of fine roots to a depth of 45cm in the mineral soil was highest in the primary hemlock stand type, with over 40% of these fine roots in the organic horizon (Figure 2.4A). Fine root biomass was significantly lower in the secondary black birch stand types compared to primary stand types. Post-HWA stand types had the smallest pool of C in fine root biomass. The pool of C in small roots in the primary hemlock and secondary black birch stand types was significantly higher than the girdled and infested stand types (Figure 2.4B). The quantity of C in coarse roots (Figure 2.4C) and total live belowground biomass (Figure 2.4D) was significantly higher in the primary hemlock stand types than all other stand types.

Carbon Inventory of the Entire Ecosystem

The total quantity of C in the primary hemlock was significantly higher than all other stand types except for the secondary black birch stand type (Figure 2.2E). Although the total quantity of C among the remaining stand types was not significantly different from one another, significantly more of the ecosystem C was found in woody debris in the girdled and post-HWA stand type compared to the secondary hemlock stand type where live biomass stored significantly more C.

Comparison to Previously Published Results

From three to 21 years following HWA-induced hemlock mortality, C stored in live aboveground biomass increased by ~7 kgC m^{-2} (Table 2.5). There was a net loss of ~3.9 kg C m^{-2} from snags and a smaller decrease of 0.6 kg m^{-2} in organic horizon C content. Mineral soil C content increased by ~0.9kg C m^{-2}. There were no previous data on C pools in logs. The total net change in ecosystem C content is +4.7 kg C m^{-2}, although uncertainty of the C content of logs prevents us from drawing a definitive conclusion about absolute C accumulation in this stand type.

DISCUSSION

Black birch is the dominant species replacing eastern hemlock forests subject to HWA infestation in southern New England (Orwig and Foster 1998, Orwig et al. 2002). I hypothesized that (1) ecosystem carbon storage would be lower in mature black birch stand types than hemlock stand types and that (2) the distribution of the C pools differ between stand types. This analysis suggests that only the second hypothesis is correct. The secondary black birch stored the same quantity of C as that of the primary hemlock stand type. Ecosystem C content was similar among secondary hemlock, girdled and post-HWA stand types. My results suggest that the C-balance of forested ecosystems in southern New England is resilient to change despite the loss of eastern hemlock forests throughout the study region from the perspective of C storage.

The hemlock and girdled stand types were co-located at the Harvard Forest. Both the secondary hemlock and girdled stand types are recovering from pastureland abandonment, whereas the primary hemlock stand type was never cleared. Although the secondary hemlock and girdled stand types were previous pastureland, the soils and climate are nearly identical, creating an opportunity to examine the potential trajectory for C storage in a maturing eastern hemlock forest if HWA were never able to successfully establish in the area. Similarly, the girdling provides an opportunity to quantify the potential changes in C pools immediately following hemlock loss.

If the secondary hemlock forests of my study were to continue maturing, soil C alone could increase by ~50% over that already found in the organic and mineral soil horizons (+5.7 kg C m^{-2}; Figure 2.2C, D). Similarly, root biomass could potentially increase 84%, although in absolute terms this represents a modest increment in ecosystem C content relative to that in the soil (+0.45 kg C m^{-2}; Figure 2.4). Interestingly, pasturing at the Harvard Forest significantly increased soil bulk density relative to that found in the primary hemlock stand type (Table 2.1), whereas it tended to deplete soil C concentration (Table 2.4). If soil C concentration in the secondary hemlock stand types were to increase to the level of the primary hemlock stand type, it is possible that soil C content could increase more than that reported above.

The loss of eastern hemlock, as simulated by girdling, did not appear to significantly affect the C balance of former eastern hemlock forests at the ecosystem scale (Figure 2.2E), but clearly suggested the potential for a significant shift in the location of the C, from live biomass to CWD (Figure 2.2A, B). Despite of the death of ca. 80% of the trees in the girdled plots (Ellison et al. 2010), there were no differences between stand types in the C content of root biomass or that in the organic and mineral soil horizons (Figure 2.4). This result is consistent with that of (Jenkins et al. 1999), who found no significant changes in C pools ~3 years following hemlock infestation at stands throughout southern New England. (Knoepp et al. 2011) also found no significant loss of soil C content 4-years following hemlock loss at the Coweeta Long-Term Ecological Research (LTER). Hence, the initial impacts on the C cycle appear to be limited to a transfer of C into woody debris.

Limitations in extending the comparative approach employed at the Harvard Forest to the post-HWA and the secondary black birch stand types should be acknowledged. Although land-use history was similar among stand types, I do not know the exact nature and extent of pasturing in these different areas, and mean annual temperature is 1.5 ^{o}C higher at the post-HWA stand type (Table 2.1). To quantify changes in C stocks over a period of 18 years at this stand type, I took advantage of previous research conducted ~3 years following hemlock mortality due to HWA infestation and compared that to my estimates 21 years post-HWA (Table 2.5). Based on C in aboveground biomass, CWD, the organic horizon and top 15cm of mineral soil, there was a net accumulation of 4.7 kg C m^{-2} over 18 years (Table 2.5). This compares favorably with the estimate of the mean quantity of C lost following girdling, ~1 kg C m^{-2}, for these same pools (i.e., estimate of differences between the girdled and secondary hemlock plots), suggesting the potential for rapid recovery of ecosystem C content.

There were notable changes in the distribution of C pools among stand types. C storage in live biomass declined following the loss of hemlock and was replaced by C in class I CWD. Vigorous black birch regrowth compensated for the C lost in the decaying woody debris, and the secondary black birch stand type stored as much C as a primary hemlock stand type.

While croplands in New England appear to influence soil C accumulation for more than a century following abandonment (Compton and Boone 2000, Clark and Johnson 2011), C pools in former pasturelands recover within ~100 years or less (Foote and Grogan 2010, Clark and Johnson 2011). Land-use history records for Harvard MA indicate that the black birch stand type is a first-generation forest following pastureland abandonment (Berg et al. 1997), suggesting that the larger C content of the mineral soil likely reflects the effect of black birch on soil C rather than a historical effect of pasturing 135 years ago. This line of reasoning is consistent with the significantly large accumulation of C in the top 15cm of mineral soil in the post-HWA stand type that is dominated by black birch saplings (Figure 2.2D, E).

Similar to soil C, the secondary black birch stand type also had the largest pool of C in biomass (Figure 2.2A). Biomass C was nearly 10% greater than that in the primary and nearly 35% than that in secondary hemlock stand types at the Harvard Forest (Figure 2.2A). It is possible that the stand type I studied has higher biomass than other black birch stand types in central New England, although I am not aware of comparable data in the literature. Even if biomass in other stand types were lower by as much as 35%, the C pool in biomass would remain comparable to that of hemlock forests in this region.

Ecosystem Resilience

Gunderson and Holling (2001) defined ecosystem resilience as the amount of disturbance that can be sustained by a system such that it can maintain its control and structure. Carpenter et al. (2001) expanded upon this concept by arguing that ecosystem resiliency has three key properties: (1) as with Gunderson and Holling (2001), the ability to retain control of structure and function; (2) capability for self-organization; and (3) adaptive capacity (i.e., ability to cope with change). They also suggested four characteristic phases for ecosystem resiliency: (1) collapse (e.g., disturbance); (2) renewal or reorganization (e.g., new species); (3) rapid growth and (4) return to the original ecosystem state. Lastly, when observing the possibility of ecosystem resilience, it is essential to ask the question "*of* what *to* what?" (Carpenter et al. 2001), to which I have answered "*of* C storage *to* the HWA". This is the basis to understanding resilience. One cannot say that forest structure and composition are resilient to the HWA, as there are clear evidences for changes in dominant tree species. This transition in structure and composition distinctly result in changes in the forest's microclimate, its fauna and hydrological cycle. If the answer to the question asked by Carpenter et al. (2001) would, then, be "of forest structure and composition to HWA", the result would be a lack of resilience. Yet, in focusing on carbon, we see a slight decrease – though not significant –

of storage in the scenario of recent hemlock death (*collapse* = secondary hemlock forest to girdled hemlock forest), followed by a rapid recovery of biomass (*renewal and rapid growth* = post-HWA).

The experimental design allowed me to compare carbon storage in a 130-year old black birch forest to a 230- year-old hemlock forest, enabling me to assess the fourth phase of resilience (*return to the original ecosystem state* = C storage in secondary black birch forest equivalent to the primary hemlock forest). My data suggest that C storage following HWA infestation is nearly equivalent to that found in an uninfested hemlock forest satisfying the requirement of Carpenter et al's (2001) fourth stage of resilience theory. In other words, both a century in the absence of HWA and in the presence of HWA result in statistically similar C stocks. I propose that C storage in the primary hemlock stand type is the correct stand age for the assessment of resilience because in the absence of HWA, it is likely that C storage in the secondary hemlock stand type over the next century would have increased to levels similar to that found in the primary growth hemlock stand type.

I used the pair-wise difference in C content and age between stand types to provide a conceptual understanding of the trajectory of change in C storage if secondary hemlock stand types were to remain uninfested, versus eastern hemlock's replacement by black birch following disturbance (Figure 2.5). This is not intended to be a quantitative model for the recovery of forests affected by the HWA, neither can I say anything about C balance in forests that fall outside the characteristics of those I studied here. This conceptual trajectory is to be seen as a possible outcome of the HWA invasion, and an illustration of the apparent resiliency of ecosystem C stocks to hemlock loss. This analysis suggests that ~20 years are necessary for C stocks to reach pre-disturbance values in rapidly regrowing black birch stand types. Moreover, it appears that there is ~40 years difference between maturing secondary hemlock and black birch stand types in their ability to reach C stocks observed in a primary hemlock stand types.

Albani et al. (2010) conducted a simulation experiment in which the current and projected spread of HWA was applied to the entire range of hemlock forests in the eastern US. Overall, their model results are consistent with the data presented here. The simulated loss of hemlock and its replacement by other species resulted in little net change in ecosystem C balance at the decadal- to-century time scales.

Conclusions

The objective of this study was to examine stand types of differing age and species composition that may reflect the different stages of HWA effects on ecosystem C pools. I openly acknowledge that I cannot directly compare C pools among stand types because of uncertainties in land-use history and the timing of stand type initiation, thus my analysis of resilience is suggestive of possible outcomes. Can ecosystem C storage return to pre-HWA levels following the loss of hemlock? My data suggest the answer is yes. HWA causes the loss (=collapse) of hemlock and appears to transfer C from live biomass to pools of CWD (Figure 2.2). Black birch seeds germinate vigorously following hemlock loss (=renewal and reorganization) and rapidly accrue C in biomass (=rapid regrowth; Figure 2.2a), all of which indicate resiliency of forest C storage.

TABLE 2.1. Overstory species composition and characteristics of the measured stand types. Arrows for girdled and infested stand types correspond to pre- → post-hemlock death. Prior stem density and basal area values were obtained from Ellison and Barker Plotkin (2005), and Orwig and Foster (1998) in the girdled and post-HWA stand types, respectively. Former relative importance values for *T. canadensis* in the girdled stand type (Ellison et al. 2010) and the post-HWA stand type (Orwig and Foster 1998) are shown in parenthesis. Stand type age is represented by age/*years since hemlock girdling or mortality due to HWA.*

TABLE 2.1

	Primary Hemlock	Secondary Hemlock	Girdled	Post-HWA	Second. Black Birch
Relative Importance Value[1]					
Tsuga canadensis	90.5	66.8	(68.0)	(66.0)	--
Betula lenta	1.2	10.2	4.1	13.8	63.6
Acer rubrum	2.7	7.1	8.8	16	5.1
Quercus rubra	--	5.6	8.2	8	4.0
Pinus strobus	--	4.3	36.7	--	28.5
Basal Area (m^2/ha)	59.4	52.1	51.7 → 16.9	43 → 24	38.9
Stem Density (stems/ha) <10cm dbh	848 ± 372	115 ± 20	58 ± 37	23003 ± 2519	624 ± 212
Stem Density (stems/ha) >10cm dbh	718 ± 126	606 ± 37	731 → 308 ± 38	625 → 136 ± 11	549 ± 71
Location	Petersham, MA 42°32’N 72°11’W	Petersham, MA 42°32’N 72°11’W	Petersham, MA 42°32’N 72°11’W	Burham Brook, CT 41°28’N 72°19’W	Harvard, MA 42°31’N 71°32’W
Mean Annual Temperature	8.5°C	8.5°C	8.5°C	10.2°C	8.9°C
Mean Annual Precipitation	110 cm	110 cm	110 cm	123 cm	116 cm
Land use history	Woodlot	Pasture	Pasture	Woodlot	Pasture
Mineral Soil Bulk Density (g cm^{-3})	0.78 ± 0.04b	1.06 ± 0.09a	1.01 ± 0.04a	0.91 ± 0.27ab	0.82 ± 0.02b
% Rock Volume	25.8 ± 3.4a	15.2 ± 1.4ab	22.3 ± 3.9ab	9.9 ± 2.9b	6.5 ± 0.44b
Stand age	230	132	5/*132*	18/*121*	135

TABLE 2.2. Allometric equations applied to measured diameter at breast height for total aboveground biomass calculation. B=biomass, d=diameter at breast height. Annual litterfall was used to calculate hardwood foliar biomass.

TABLE 2.2

SPECIES			
		WOOD	FOLIAGE
Eastern hemlock	Equation	B=1.3449*(d^2.45)	ln(B)=5.154+1.294*(ln(d^1)
	Min. diameter	12.7 cm	6.1
	Max. diameter	129.0 cm	85.1
	Region	West Virginia	Tennessee
	Source	Brenneman et al. (1978)	Busing et al. 1993
Eastern white pine	Equation	ln(B)=4.19•d+2.43•ln(d)	ln(B)=3.22•d+1.75•ln(d)
	Min. diameter	1.7 cm	
	Max. diameter	25.7 cm	
	Region	New Hampshire	
	Source	Hooker and Early 1983	
Black birch	Equation	log10(B)= -1.254+2.728•log10(d)	log10(B)=-3.086+2.628•log10(d)
	Correction factor	1.016	1.041
	Min. diameter	7.8 cm	
	Max. diameter	39.6 cm	
	Region	North Carolina	
	Source	Martin et al. 1998	
Black birch sapling	Equation	B= 442.87•(d^2-0.964•(d)+757.26	B=7.8731•(d^2.3585)
	Min. diameter	0.4 cm	
	Max. diameter	6.3 cm	
	Region	Connecticut	
	Source	*This study*	
General hardwood	Equation	log10(B)=-1.281+2.68•log10(d)	log10(B)=-2.122+2.022•log10(d)
	Correction factor	1.021	1.158
	Min. diameter	3.8 cm	
	Max. diameter	63 cm	
	Region	North Carolina	
	Source	Martin et al. 1998	

TABLE 2.3. Decay classes for logs and snags, adapted from Carmona et al. (2002), Coomes et al. (2002), respectively.

TABLE 2.3

		Decay class		
		I	**II**	**III**
Logs	*Twigs*	Present	Absent	Absent
	Bark	Present	Often present	Often/fully absent
	Bole shape	Round	Round to oval	Oval to flat
	Wood consistency	Solid	Semi-solid	Partly/fully soft
	Other wood properties		Breakable	Fragmented to powdery
Snags		Bark largely intact	Bark and twigs lost, but shape of trunk remaining intact	Shape no longer maintained, and trunk sinking into ground

Table 2.4. Mean (±1 S.E.) %C in the different soil depths at each stand type. Different superscript letters indicate a significant difference ($p<0.05$) within a soil depth. For mineral soil at 0-15cm depth, $p=0.06$.

TABLE 2.4

	Primary growth hemlock	Second-growth hemlock	Girdled	Post-HWA	Second-growth black birch
Org. Horizon	44.7 ± 1.2	38.2 ± 3.0	37.9 ± 3.0	37.5 ± 4.2	39.5 ± 2.2
0-15 cm	6.0 ± 0.37^{ab}	4.1 ± 0.4^{b}	4.8 ± 0.5^{ab}	6.3 ± 0.8^{ab}	7.4 ± 0.8^{a}
15-30 cm	4.5 ± 0.53^{a}	2.1 ± 0.2^{b}	1.7 ± 0.2^{b}	1.5 ± 0.2^{b}	2.4 ± 0.7^{b}
30-45 cm	2.2 ± 0.3^{ab}	1.1 ± 0.2^{b}	1.5 ± 0.2^{ab}	1.1 ± 0.3^{b}	2.9 ± 0.6^{a}

TABLE 2.5. Differences in C storage at Burnham Brook (post-HWA stand type) three years (Orwig and Foster 1998) five years (Jenkins et al. 1999) and 21 years following infestation.

TABLE 2.5

<table>
<tr><th>Years since infestation</th><th></th><th>Aboveground C</th><th>Snags</th><th>Logs</th><th>Organic horizon</th><th>0-15cm mineral soil</th><th>Total</th></tr>
<tr><td>3 years</td><td>Orwig and Foster 1998</td><td>4.1</td><td>4.3</td><td>NA</td><td></td><td></td><td rowspan="2">16.4</td></tr>
<tr><td>5 years</td><td>Jenkins et al. 1999</td><td></td><td></td><td></td><td>2.9</td><td>5.1</td></tr>
<tr><td>21 years</td><td>This study</td><td>11.1 ± 1.5</td><td>0.24 ± 0.04</td><td>1.5 ± 0.06</td><td>2.3 ± 0.1</td><td>6.0 ± 0.2</td><td>21.1</td></tr>
<tr><td></td><td>ΔC (kg C m⁻²)</td><td>7.0</td><td>-3.9</td><td>NA</td><td>-0.6</td><td>0.9</td><td>4.7</td></tr>
</table>

FIGURE 2.1. Measured stand types used to investigate changes and examine the trajectory of carbon storage due to the infestation of the hemlock woolly adelgid (art courtesy: Floyd T. Raymer).

FIGURE 2.1.

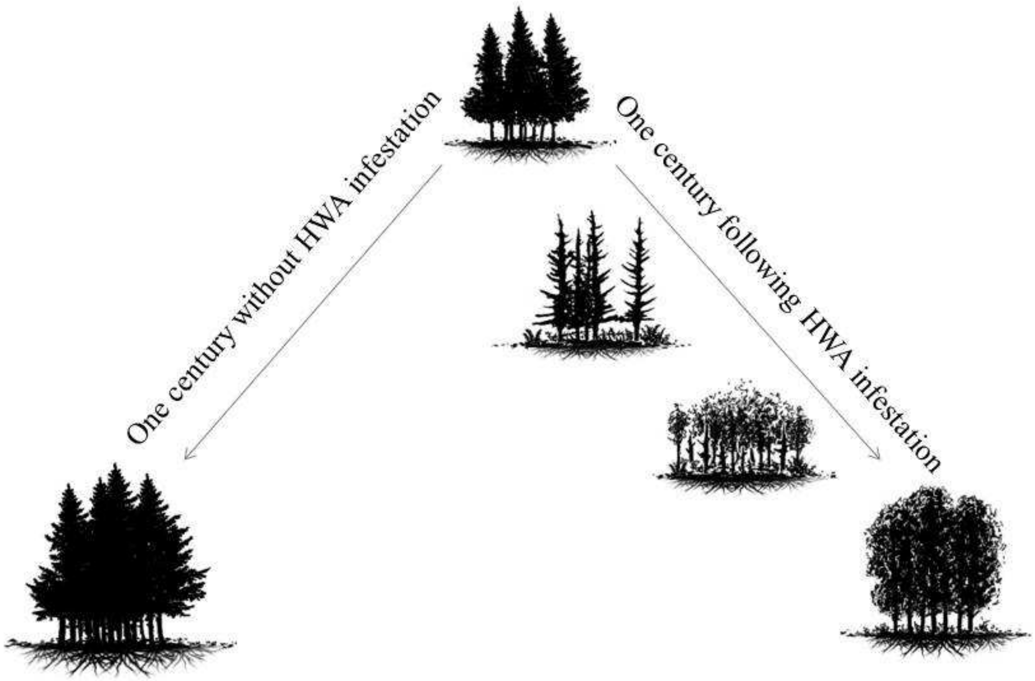

One century without HWA infestation
One century following HWA infestation

FIGURE 2.2. Carbon content (kg C m^{-2} ± S.E.) in (A) live aboveground biomass, (B) total woody debris, (C) soil organic horizon, (D) mineral soil (0-45cm depth) and (E) total ecosystem C storage (live biomass includes roots). Lower-cased letters below their respective error bars denote significant differences for separate categories in stacked bars; upper-cased letters denote total significant differences among stand types ($p < 0.05$).

FIGURE 2.2.

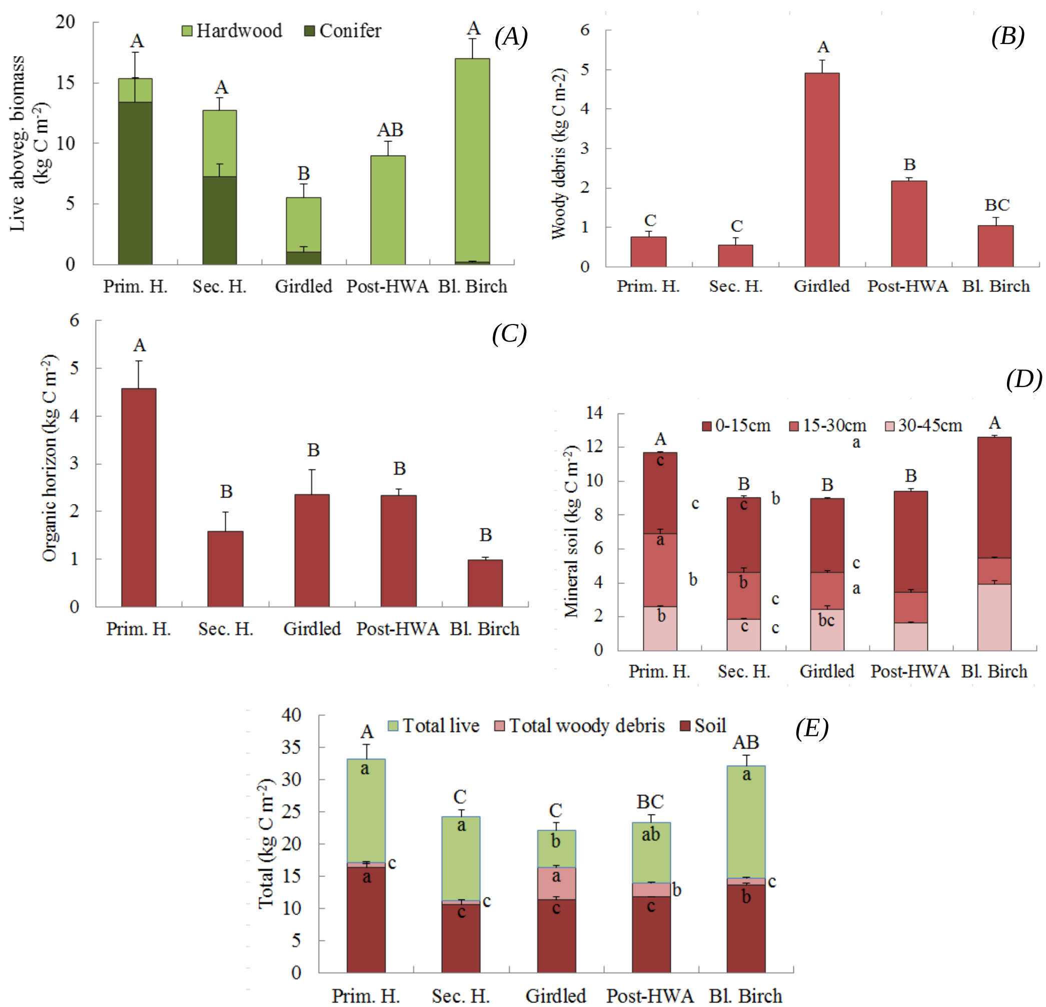

(A)
Hardwood
Conifer
Live aboveg. biomass (kg C m-2)
Prim. H.
Sec. H.
Girdled
Post-HWA
Bl. Birch
(B)
Woody debris (kg C m-2)
(C)
Organic horizon (kg C m-2)
(D)
0-15cm
15-30cm
30-45cm
Mineral soil (kg C m-2)
(E)
Total live
Total woody debris
Soil
Total (kg C m-2)

FIGURE 2.3. Number of observed (A) snags and (B) logs, with respective distribution of decay classes in each stand type (C and D).

FIGURE 2.3.

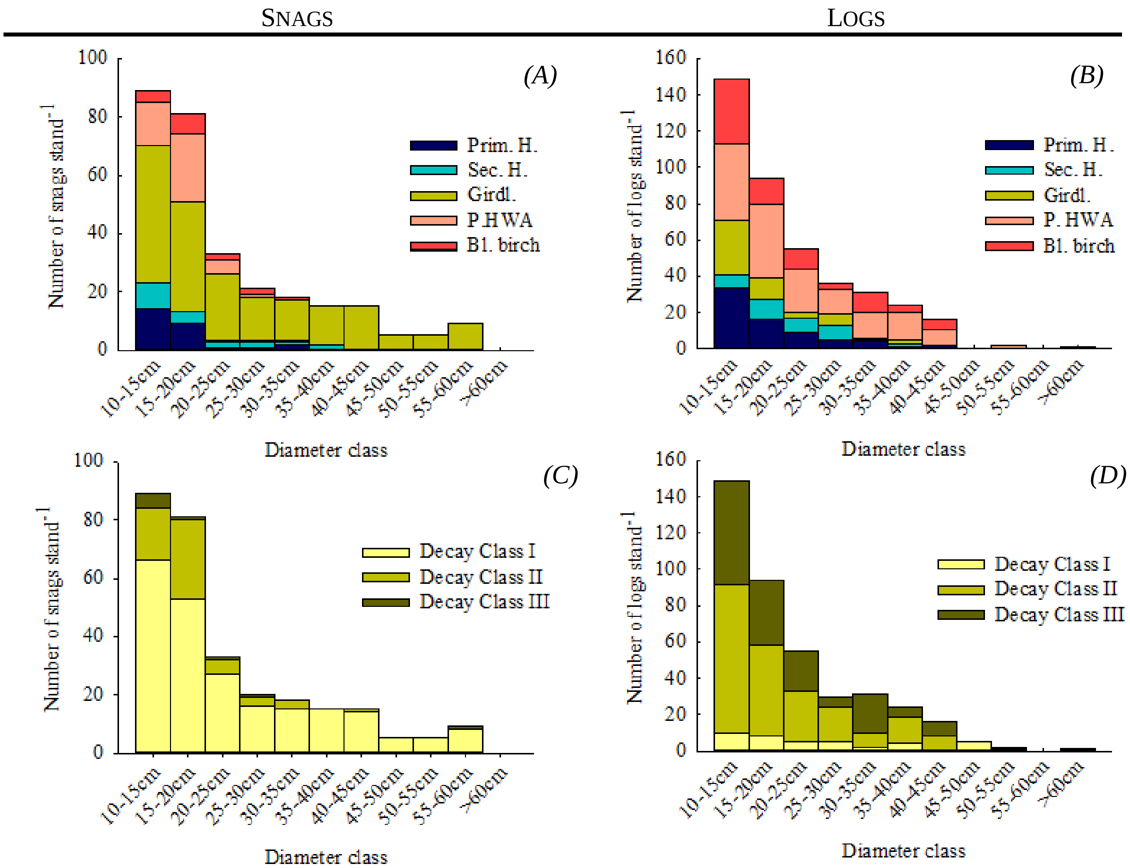
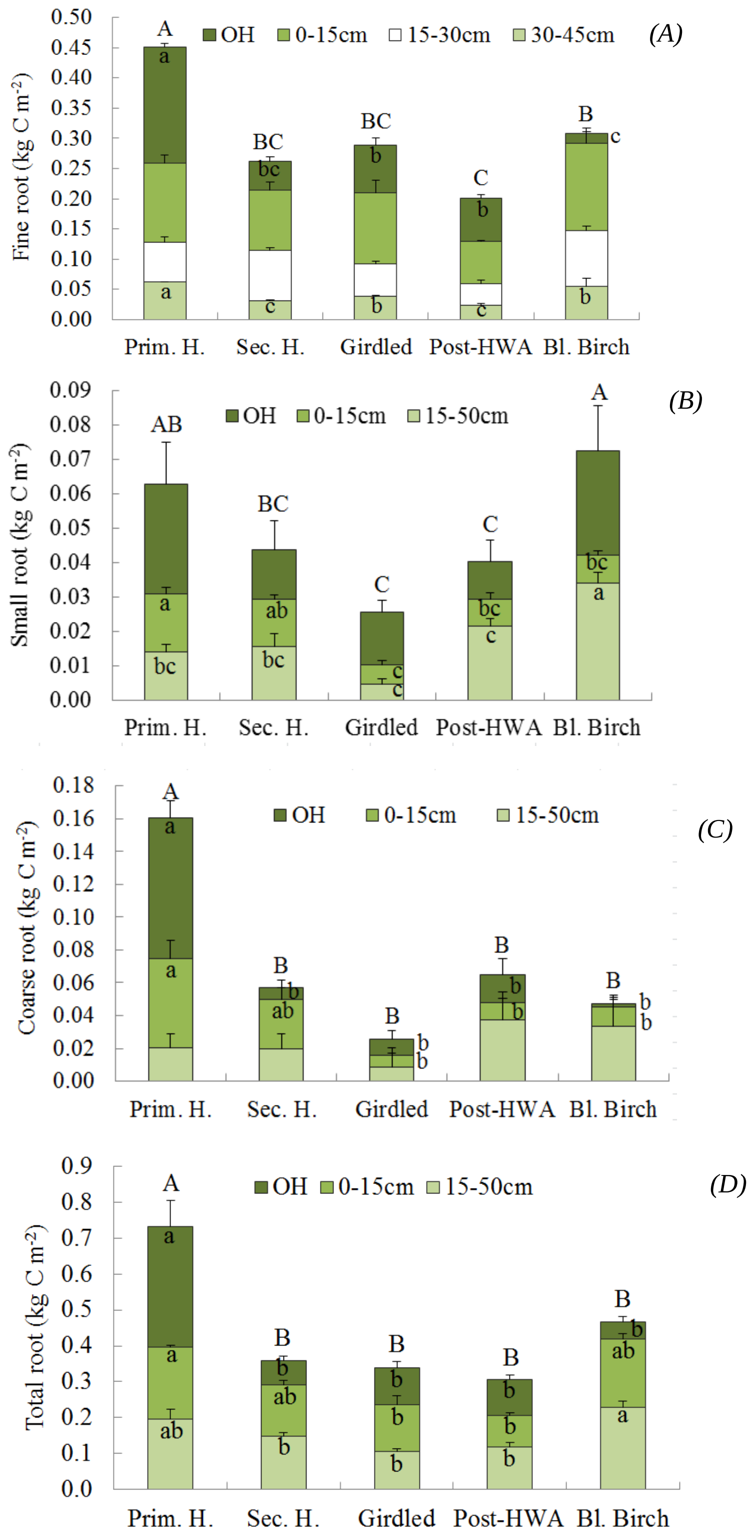

SNAGS
LOGS
(A)
(B)
(C)
(D)
Number of snags stand^{-1}
Number of logs stand^{-1}
Prim. H.
Sec. H.
Girdl.
P.HWA
Bl. birch
Decay Class I
Decay Class II
Decay Class III
10-15cm
15-20cm
20-25cm
25-30cm
30-35cm
35-40cm
40-45cm
45-50cm
50-55cm
55-60cm
>60cm
Diameter class

FIGURE 2.4. C content (kg C m^{-2} ± S.E.) in (A) fine roots, (B) small roots, and (C) coarse roots at different soil depths. Lower-cased letters below their respective error bars denote significant differences for separate soil depths in stacked bars; upper-cased letters denote total significant differences among stand types ($p < 0.05$). Fine roots in 0-15cm mineral soil, $p=0.06$; in 15-30cm mineral soil, $p=0.49$. Small roots in organic horizon, $p=0.40$. Coarse roots in 15-50cm mineral soil, $p=0.51$.

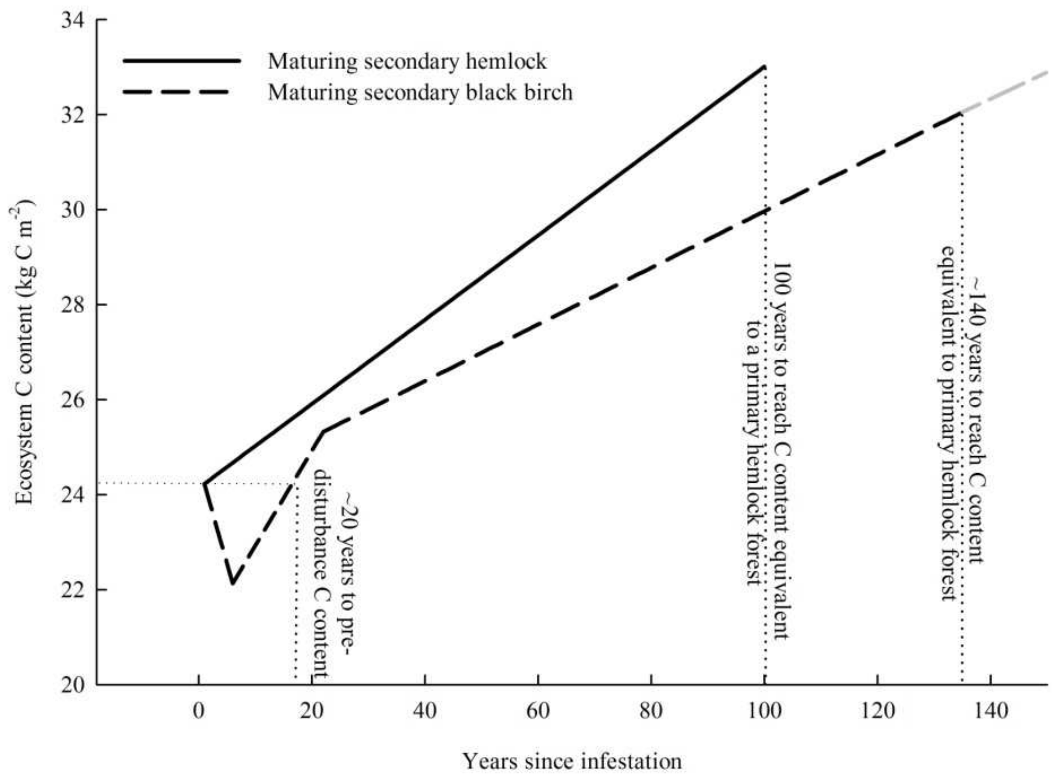
FIGURE 2.4.



OH
0-15cm
15-30cm
30-45cm
(A)
Fine root (kg C m-2)
Prim. H.
Sec. H.
Girdled
Post-HWA
Bl. Birch
OH
0-15cm
15-50cm
(B)
Small root (kg C m-2)
OH
0-15cm
15-50cm
(C)
Coarse root (kg C m-2)
OH
0-15cm
15-50cm
(D)
Total root (kg C m-2)

FIGURE 2.5. Conceptual trajectory of C content (kg C m^{-2}) in a maturing hemlock stand type, and a maturing black birch stand type following disturbance. The secondary hemlock stand type is represented in year 0 (zero), with the solid line suggesting absence of the HWA infestation and the dashed line suggesting presence of the HWA infestation.

FIGURE 2.5.



Maturing secondary hemlock
Maturing secondary black birch
Ecosystem C content (kg C m-2)
Years since infestation
~20 years to pre-disturbance C content
100 years to reach C content equivalent to a primary hemlock forest
~140 years to reach C content equivalent to primary hemlock forest
34
32
30
28
26
24
22
20
0
20
40
60
80
100
120
140

CHAPTER 3

VARIATIONS IN ABOVEGOURND NET PRIMARY PRODUCTION, SOIL RESPIRATION AND NITROGEN DYNAMICS SUGGEST FORESTS REMAIN A CARBON SINK FOLLOWING HEMLOCK WOOLLY ADELGID INFESTATION IN SOUTHERN NEW ENGLAND

ABSTRACT

Populations of eastern hemlock (*Tsuga canadensis*), a foundation species of eastern US temperate forests, have been experiencing an accelerated decline since the invasion of an exotic pest, the hemlock woolly adelgid (HWA, *Adelges tsugae*) in the early 1980s. In southern New England, eastern hemlock is being replaced by the deciduous tree species, black birch (*Betula lenta*). With the objective of understanding the potential long-term trajectory of C flux in these affected forests, I analyzed aboveground net primary production (ANPP) and soil respiration in stand types spanning from primary hemlock stand type >230 years old, to ~130 year old secondary hemlock stand types including those recently killed by the HWA (~20 years since infestation) and girdled in an effort to simulate HWA invasion (5 years since girdling), to ~130-year-old black birch stand type. I estimated differences in soil temperature sensitivity (Q_{10}), foliar litter decomposition, and soil exoenzyme activity in the organic horizon and top 45cm of mineral soil. Additionally, because nitrogen (N) availability limits forest productivity, I analyzed major portions of the N cycle including annual rates of N uptake and N-use efficiency. I found that ANPP was highest in the stand type infested two decades ago, but was similar in all other stand types. Trends for soil respiration were similar, though rates were slightly lower in the girdled stand type (5 years since girdling). Q_{10} was highest in the primary hemlock stand type, as were C-related enzyme activities in the organic horizon. Nitrogen-use efficiency was highest in the girdled and post-HWA infestation

stand types where ANPP was dominated by wood production which has a wide C:N ratio. With these findings, I suggest that increases forest C input offsets increases in C output in areas of southern New England affected by the HWA and that these forests continue to be a carbon sink for atmospheric carbon dioxide during its period of recovery from the infestation.

Keywords: *C flux, N dynamics, hemlock woolly adelgid, empirical long-term analysis, forest resilience*

INTRODUCTION

By virtue of its structural and functional attributes, foundation species create and define an entire ecological community or ecosystem. Ecosystem processes are often dominated by the abundance and chemical characteristics of foundation species, while their architecture and physiology impact forest structure and often microclimates (Ellison et al. 2005). Eastern hemlock (*Tsuga canadensis*), is considered a foundation species in temperate forests of the eastern US, and is one of the longest-lived tree species in eastern North America. It is a widely distributed species found as far north as New Brunswick, Canada, and within the United States throughout New England, the Appalachian Mountains and as far south as Alabama, covering about 1 x 10^6ha of forest (McWilliams and Schmidt 2000, USDA Forest Service 2012).

Eastern hemlock forests are disturbance-intolerant because this species cannot resprout or refoliate following physical damage (Godman and Lancaster 1990). From a biogeochemical perspective, eastern hemlock's classification as a foundation species derives from the deep shade it creates and its high concentrations of polyphenolic compounds and lignins that contribute to slow rates of decomposition (Melillo et al. 1982, Jenkins et al. 1999), the accumulation of soil carbon (C) (Finzi et al. 1998b, Hadley 2000), acidic, base-poor soils (vanBreemen et al. 1997, Finzi et al. 1998a) and low rates of nutrient mineralization (Finzi et al. 1998b, Kizlinski et al. 2002, Talbot and Finzi 2008).

Since the early 1950s, hemlock-dominated forests in eastern North America have been affected by an invasive pest, the hemlock woolly adelgid (HWA - *Adelges tsugae*, (McClure 1990, Souto and Shields 2000). HWA is only one of many cases of non-indigenous pests that have increased in continental US forests during the last 200 years despite more stringent regulatory measures (Liebhold et al. 1995). Sap-feeding insects of the order *Hemiptera* account for over 40% of all non-indigenous forest insect species in the continental US (Aukema et al. 2010), and the HWA is considered a "high-impact" species belonging to this order (Williamson and Fitter 1996, Hicke et al. 2012).

Hemlock forests in 18 US states have been infested thus far (USDA 2012). Because of its sensitivity to cold temperatures, the rate of HWA colonization has decelerated in the northerly portions of its current range (Orwig et al. 2012), but genetic adaptation of the HWA to low temperatures (Butin et al. 2005) as well as observed and predicted increases in northeastern temperature (Hayhoe et al. 2007) are likely to facilitate its spread toward the north. Observational (Paradis et al. 2008) and modeling studies (Dukes et al. 2009, Fitzpatrick et al. 2012), suggest that HWA will infest the northernmost stand types of hemlock in eastern US within the next 30-50 years. Infestation by the HWA results in needle loss that increases understory light availability and temperature (Orwig and Foster 1998, Eschtruth et al. 2006). This change in microclimate facilitates the rapid growth of hardwood species (Catovsky and Bazzaz 2000). Though not a common feature of the eastern US landscape (Ellison et al. 2010), black birch (*Betula lenta*) is the dominant species replacing eastern hemlock in northeastern forests (Orwig and Foster 1998). Black birch is an early successional, fast-growing, deciduous species (Lamson 1990) with growth attributes that may alter the ecology and biogeochemistry of the eastern hemlock forests it replaces. For example, black birch trees produce thin leaves that are easily decomposed relative to hemlock (Cobb 2010). In combination with warmer soil temperature (Ellison et al. 2010) and higher soil moisture content following the disturbance (Daley et al. 2007), there is the potential for substantial soil C loss via respiration, particularly from the thick organic horizons that characterize hemlock forests. The loss of soil C may, however, be compensated for by high rates of primary production in the young, rapidly aggrading black birch forest (Albani et al. 2010). Pest invasion has been shown to play an important role in altering C cycling in northern hardwood forests through the shift in species composition (Hancock et al. 2008). To date there have been no empirical assessments of the potential long-term impact of HWA on C fluxes from hemlock-dominated forests that transition to black birch following infestation (Peltzer et al. 2010).

Tree species can exert very strong control not only over C cycling but also over N cycling in the forest ecosystems, even from the perspective of individual trees (Finzi et al. 1998b). The low litter quality of hemlocks (high C:N ratio), for example, produces low rates of net N mineralization and nitrification (Finzi et al. 1998b, Lovett et al. 2004) and are capable of retaining larger amounts of N than some coexisting hardwood species (Templer 2005). This results in less N loss but also in less inorganic N available to plants. Nitrogen is an essential nutrient for plant growth, strongly influencing forest productivity (Reich et al. 1997, LeBauer and Treseder 2008). The loss of dominant species alters C and N dynamics (Hancock et al. 2008, Falxa-Raymond et al. 2012) and these changes can occur in a short period of time in the case of conifer- to hardwood-dominated forest transitions (Gower and Son 1992). The shift in species composition increases litter quality, the rate of litter decomposition and N availability for higher net primary production (Pastor and Post 1993). Changes in N cycling, primary production and microbial activity influence much of the input and output of C from forest ecosystems. I used a comparative approach and measured variations in C fluxes and associated changes in N cycling in hemlock and black birch stand types of varying ages to suggest possible long-term changes in forest C balance with HWA. The stand types spanned a wide range of ages, from primary hemlock stand types >230 years old, to ~130 year old secondary hemlock stand types including those recently killed by the HWA (20 years since tree death) and girdled in an effort to simulate HWA invasion (5 years since girdling), to ~130-year-old black birch stand types. Given changes in C fluxes associated with stand type age high productivity is expected following disturbances prior to canopy closing (Ryan et al. 2004). Black birches are known for their ability to quickly dominate disturbed areas (Lamson 1990), reinforcing the idea of a substantial increase in the productivity of infested forests. Changes in soil respiration from a slower decomposing species to a faster decomposing one can be a bigger challenge to predict however (Hancock et al. 2008). While a shift in species could increase soil respiration, higher N mineralization rates and more N availability can lead to a reduced root C allocation and belowground autrotrophic respiration. I hypothesized the following associated with hemlock loss and its replacement by black birch:

(1) ANPP would be significantly higher in young, aggrading black birch stand types than secondary hemlock stand types;

(2) soil respiration would increase from hemlock-dominated stand types to black birch-dominated stands, especially due to increasing availability of labile C; and

(3) N availability would increase from hemlock-dominated to black birch-dominated stand types, contributing to increases in both soil respiration and ANPP.

MATERIALS AND METHODS

Stand types and Climate

This research was conducted in central Massachusetts and Connecticut (Table 3.1). I quantified C fluxes in: (1) a primary hemlock stand type, representing potential future characteristics of a developing secondary hemlock stand type; (2) a secondary hemlock stand type representing the starting point of HWA infestation for most hemlock forests in this region; (3) a girdled hemlock stand type, representing an early stage following hemlock death; (4) a 21-year-old post-HWA hemlock stand type that now has vigorously regrowing black birch saplings and sub-canopy trees; and (5) a secondaryhemlock stand type ~135 years old, growing on former pastureland (Figure 3.1). The location of each stand type and their detailed characteristics are described in Chapter 2.

Soil temperature data for the primary and secondary hemlock stand types and the girdled stand type were obtained from the Harvard Forest Data Archive (Hadley 2003, Ellison et al. 2005B) for the available years of 2010 and 2011, at 10 cm depth in the soil. (Ellison et al. 2005). At the post-HWA and secondary black birch stand types, I installed two temperature sensors, one in each of two randomly selected plots [HOBO

Pendant Temperature/Light Data Logger (Onset Comp. Corporation, Pocasset, MA, USA)]. The temperature probes were buried at 5-10 cm depth in the soil. Hourly measurements of soil temperature were logged in 2010 and 2011. Soil moisture was measured at two different soil depths (5cm and 15cm) in a single plot in each stand type (10HS Soil Moisture Smart Sensor, Onset Comp. Corporation, Pocasset, MA, USA). Measurements were collected hourly from November 2010 to November 2011 and values from both depths were averaged.

Carbon flux measurements

The studied stand types were inventoried from 2008 to 2011, with four replicated plots measuring 30x30m for each of the five stand type. In each plot, I measured differences in net C fluxes, and given its importance to primary production, I also measured the pools and net fluxes of nitrogen (N) (Vitousek and Howarth 1991, LeBauer and Treseder 2008), which are described in the *Nitrogen* section, below. My measurements of net C fluxes included aboveground net primary production (ANPP), soil respiration, foliar-litter decomposition, and the activity of soil microbial exoenzymes involved in the decomposition of soil organic matter (SOM).

Aboveground Net Primary Production

Wood NPP was estimated from dimension analysis and estimates of diameter growth based on tree cores. Ten trees were cored in each plot (200 trees total) in proportion to the relative-importance value and diameter-distribution of the dominant species in each plot (Table 3.1). Using an increment borer (Haglöf, Sweden) two cores were extracted from each tree, 1.25m above ground level, 180° apart, and parallel to the topographic contour (Biondi 2000). I used a “bit starter” (Haglöf, Sweden) for hardwood species to ensure recent tree rings were not damaged during core extraction.

The cores were brought back to the lab, oven-dried for 48 hours at 60^{o}C, glued to grooved plywood, and surfaced with four progressively finer grit sand papers, down to 400 grit, to reveal the wood’s cellular structure (Davis et al. 2007). Annual ring widths were measured using Velmex UniSlide (Velmex Inc., Bloomfield, NY) and a stereoscope. The software MeasureJ2X (Project J2X, VoorTech Consulting) was used to store the data. Ring-width increment was used to estimate the relative growth rate (RGR: mm cm^{-1} yr^{-1}) of the trees over a 5-year period, and the average RGR for each species in each stand type applied to the trees that were not cored. Species-specific allometric equations were used to calculate the production of woody biomass in each plot (Table 3.2, (Jenkins et al. 2003).

No suitable allometric equation was available for black birch saplings, hence I developed my own allometric equations (Table 3.2). I measured the number and diameter of all black birch saplings <10cm dbh along eight 30m transects of 1-m width. I harvested 14 black birch saplings of varying diameter (King 1990) and separated the felled stems into foliage and wood and dried the tissues at 60^{o}C for two weeks.

Foliage production was estimated as the sum of foliage biomass increment and turnover (Schlesinger 1997). The biomass increment was estimated from the allometric equations (Table 3.2). The turnover of foliage was estimated on site using litterfall mass.

Two litter baskets were installed in each plot (N=40) in October of 2010. I collected litter six times through October 2011, dried the samples at 60^{o}C, sorted them by species and weighed each sample. The annual rate of foliage production (g m^{-2} yr^{-1}) was added to the production of woody biomass to obtain an estimate of aboveground net primary production (ANPP).

Soil Respiration

The rate of soil respiration (i.e., C respired from the soil, g C m^{-2} day^{-1}) was measured every five weeks with a closed-path infra-red gas analyzer (IRGA) system (Li-COR 6400, Lincoln, NE). Six 10-cm diameter polyvinyl chloride (PVC) collars were installed per plot (N=24 per stand type). Soil respiration was measured from October 2010 to November 2011, with the exception of periods of snow cover (November 2010 through March 2011). Measurements were made between 10h30 and 16h00, the period of maximum CO_2 efflux at the Harvard Forest (Drake et al. 2011). I made additional measurements of soil temperature at 5-10cm depth directly adjacent to each collar.

The relationship between soil temperature and soil respiration (R_s) was modeled according to van 't Hoff (1898):

$$(1)\ R_s = \beta \bullet \exp^{(k \bullet t)}$$

Where, β is the y-intercept term, *k* is exponential decay coefficient, and *t* is temperature (^{o}C). The *k* parameter was then used to calculate plot-specific apparent Q_{10} of soil respiration —the increase in R_s with every 10^{o}C increase in soil temperature—viz:

$$(2)\ Q_{10} = \exp^{(10 \bullet k)}$$

The Q_{10} data were used to assay differences in the temperature sensitivity of R_s between vegetation types or stand type age. The modeled exponential function (1) was also used to estimate R_{10}, the rate of soil efflux at 10°C for each of the stand types—viz:

$$(3)\ R_{10} = \beta \bullet \exp^{(k \bullet 10)}$$

R_{10} express R_s at a common temperature and therefore enables meaningful comparisons among stand types whose soil temperatures varied from one another throughout the year:

Finally, I estimated the rate of soil respiration from April through November—viz:

$$(4)\ R_s = R_{10} \bullet Q_{10}^{[(t-10)/10]}$$

Foliar Decomposition

I measured foliar litter decomposition in a 24-month litter-bag study (Singh and Gupta 1977). One gram of hemlock needle litter and 2g of black birch leaf litter were enclosed in polyester litterbags (5 x 10 cm and 10 x 10 cm, respectively) with mesh size of 1mm and placed under the litter layer in 1x1m subplot per plot. A total of 320 litterbags were deployed to the forest in November 2009 (4 plots x 5 stand types x 4 sampling dates x 2 species x 2 replicates); litter of both species was decomposed in all plots. Two litterbags of each species were sampled on four sampling dates: April 2010 (after 5 months), August 2010 (9 months), November 2010 (12 months) and November 2011 (24 months). The litterbags were brought to the lab, dried at 55°C and weighed after 48 h. The samples were weighed and analyzed for %C. These data were used to express mass loss and C content as a fraction of the original mass remaining on each sample date.

Soil Exoenzyme Activity

In addition to the decomposition of fresh litter, we also assayed decomposition of SOM in the organic horizon and mineral soil to a depth of 45cm by measuring the activity of microbial exoenzymes (Weintraub et al. 2007). I focused on the activity of enzymes that degrade labile C pools such as cellulose and cellobiose [α-1,4-glucosidase (αG), β-1,4-glucosidase (βG) and cellobiohydrolase (CBH)] and recalcitrant C pools such as lignins and polyphenols [peroxidase (Perox) and phenol oxidase (PhO*x*)]. β-1,4-N-acetylglucosaminidase (NAG) was used to analyze nitrogen-related activity.

Soils were collected between June and September 2008. I used a 10 x 10 cm frame to collect three organic horizon samples in each of the 20 plots. Directly below, mineral soil cores (5cm diameter x15cm depth) were removed in three 15-cm depth increments. The three replicates of each plot were homogenized, such that N=80 (5 stand types x 4 plots x 4 soil depths). The samples were brought back to the laboratory, sieved, roots removed and then frozen at -80^{o}C until laboratory analysis.

I suspended 1g of soil in 125 mL of 50 mM, pH 5.0, acetate buffer, homogenizing for 1 min (Finzi et al. 2006). 200µl aliquots were dispensed into 96-well microplates while the suspensions were continuously stirred using a magnetic stir plate, with eight replicate wells per sample per assay. All assays except phenol oxidase and peroxidase were fluorimetric. Fifty microliters of 200µM substrate solution were added to each sample well. The microplates were incubated in the dark at 20^{o}C. To stop the reaction following incubation and increase the fluorescence, I added a 10µl aliquot of 1.0 M of sodium hydroxide (NaOH) to each well. Fluorescence was measured using a microplate fluorometer with 365 nm excitation and 450 nm emission filters. Phenol oxidase and peroxidase activities were measured spectrophotometrically using L-3,4 dihydroxyphenylalanine (DOPA) as the substrate. I added 50µl of 25mM of DOPA to each well for phenol oxidase. Peroxidase assays received additional 10µl of 0.3% H_2O_2. The microplates were incubated in the dark at 20^oC. Activity was quantified by measuring absorbance at 450 nm using a microplate spectrophotometer. When comparing enzyme activity among stand types, I used the weighted average of the activity, accounting for soil C content (Chapter 2).

Nitrogen

Previously sampled plant tissues and soils used in an analysis of C storage in these different plots (Chapter 2) as well as tree cores and litterfall collected for this study were ground and analyzed for %N on an elemental analyzer (NC 2500 Elemental Analyzer, CE Elantech, Lakewood, NJ, USA) and then converted to g N m^{-2} based on the mass of each pool. I analyzed differences in N pools and C-to-N ratio (C:N).

The data on ANPP were used to calculate various metrics of plant-N uptake and N-use efficiency. The annual requirement for N (g N m^{-2} yr^{-1}) was calculated as:

$$(5)\ N_{req} = N_{woody\ inc} + N_{foliage\ inc} + N_{litterfall}$$

where $N_{wood\ inc}$, $N_{foliage\ inc}$ and $N_{litterfall}$ are the annual N increment in wood and foliage, and litterfall, respectively, measured in g N m^{-2} yr^{-1}. The efficiency of N use (NUE) was estimated as:

$$(6)\ NUE = ANPP / N_{req}$$

The retranslocation of N from leaves during senescence ($N_{retrans}$, g N m^{-2} yr^{-1}) was calculated as:

$$(7)\ N_{retrans} = (annual\ litter\ mass \cdot \%N_{green}) – (annual\ litter\ mass \cdot \%N_{litter})$$

Finally, the annual rate of N uptake from the soil was calculated as:

$$(8)\ N_{uptake} = N_{req} - N_{retrans}$$

Statistical Analysis

One-way ANOVA with Tukey's multiple comparison procedure were used to assess differences in C and N fluxes, N pools and C:N among the stand types. Repeated-measures ANOVA were applied to soil respiration and monthly rate of foliar mass loss. All analyses were performed using RStudio version 0.94.110 (R Core Development Team, 2011). Assumptions of normality and homogeneity of variance were met. Tukey's multiple comparison test protected the experiment-wise alpha at $p < 0.05$. Values are expressed as mean ± standard error.

RESULTS

Aboveground Net Primary Production

Litterfall varied from 124.1 ± 17.1 g C m^{-2} yr^{-1} in the girdled stand type to 242.4 ± 11.1 g C m^{-2} yr^{-1} in the post-HWA stand type (Table 3.3). Litterfall mass was statistically similar between the secondary hemlock stand type and the post-HWA stand type (p = 0.23), though conifer needles composed nearly 60% of the mass in the former stand type, while absent in the latter.

Aboveground wood production and foliar biomass increment were significantly higher in the post-HWA stand type than in all other stand types (Figure 3.2, Table 3.3, $p < 0.005$), with foliage increment nearly five-fold that of the other stand types. The RGR of the remaining trees in the girdled plots was significantly ($p < 0.005$) higher than those in the post-HWA plots (Figure 3.2). Relative growth rate of these same trees prior to hemlock death, however, was also significantly higher given that average diameter was smaller (16.2cm in the girdled stand type and 27.2cm in the infested stand type).

I found lower values of foliar ANPP (foliar increment plus litterfall) in the primary hemlock and girdled stand types (150.3 ± 4.9 g C m^{-2} yr^{-1} and 128.5 ± 17.2 g C m-2 yr-1, respectively), and intermediate values for the secondary black birch stand type (186.7 ± 3.1). Total ANPP, however (wood plus foliar) was highest in the post-HWA by at least two-fold in relation to all other stand types.

Soil Respiration

Average annual soil temperature varied by 1.7^{o}C among stand types (Table 3.4), with highest average temperature recorded in the month of July in the Post-HWA stand type. This was also the driest month of the year, coinciding with a period of very low precipitation (Boose 2001). Soil respiration increased exponentially with soil temperature ($R^2 = 0.83$, Figure 3.3A), peaking in July and August ($p < 0.0001$) (Figure 3.3B). There were significant ($p < 0.05$) variations in soil respiration among stand types (Figure 3.3C). Daily rates were significantly higher in the post-HWA stand types than both secondary hemlock and girdled stand types, and in the secondary black birch stand type than in the girdled stand type (repeated measures analysis $p < 0.05$, pairwise analysis $p \leq 0.1$, Figure 3.3C). There was no significant month and stand type interaction.

The apparent temperature sensitivity of soil temperature (i.e. Q_{10}) was greatest in the primary hemlock stand type, although not statistically different from those in the post-HWA and secondary black birch stand types (Table 3.5). The inclusion of Q_{10} in the R_s model resulted in the statistical differences in daily R_s rates among stands ($p<0.05$, Figure 3.3D) while no differences were found when considering temperature alone ($p=0.15$). R_s was approximately 20% higher using the former model than the latter. R_s rates using temperature alone were in agreement with published data using equal model (Giasson et al. *in prep*, Savage and Davidson 2001)

Foliar Decomposition

Black birch litter decomposed approximately 23.2% faster than hemlock needles ($p<0.001$), with circa 30.5 ± 11.79mg and 24.8 ± 6.46mg lost per month, respectively, during the two-year study (Table 3.6). The effect of time was significant for both species, with decreasing monthly rates of mass loss ($p<0.001$). There was no effect of stand type on decomposition.

Soil Exoenzyme Activity

When considering soil bulk density (nmol m^{-2} h^{-1}), enzyme activity was relatively well distributed along the studied soil profile (OH and 0-50cm mineral soil, Table 3.7). Because of high variability all C-related enzyme activities were statistically similar in the mineral soil, except for phenol oxidase (highest in secondary hemlock stand type, lowest in the post-HWA stand type, $p<0.05$). Primary hemlock stand type had statistically higher labile C enzyme activity than secondary hemlock stand type, and higher recalcitrant C enzyme activity than all other stand types. Both labile and recalcitrant enzyme activities occurring in the organic horizon were correlated with fine root biomass ($R^2 = 0.50$, $p<0.0001$; Chapter 2). Nitrogen-related enzyme activity (NAG) in the organic horizon was higher in the post-HWA than in the girdled stand type; in the mineral soil, NAG was higher in the secondary hemlock stand type than in the primary hemlock stand type.

Nitrogen

Nitrogen stored in total biomass was higher in the secondary black birch stand type than in the primary and secondary hemlock stand types ($p < 0.01$, Table 3.8). Over half of the biomass N found in the secondary black birch stand type was stored in the wood of live deciduous trees. Fine roots were also an important pool, storing as much as a third of the N found in the entire biomass, in the case of the primary hemlock stand type. Total N in the soil was higher in the secondary black birch stand type than all other stand types, but only a small fraction of this N was in the organic horizon compared to that in the hemlock stand types.

The annual increment of N in wood was significantly higher in the post-HWA stand type than all other stand types ($p < 0.0005$, Table 3.8). The flux of N in litterfall was lowest in the primary hemlock and girdled stand types ($p < 0.05$) and highest in the post-HWA and secondary black birch stand types.

The annual requirement for N and NUE were significantly higher in post-HWA stand type than all other stand types ($p < 0.0001$). The only exception to this pattern was statistically similar NUE between the post-HWA and girdled stand types ($p = 0.99$). The retranslocation of N from foliage was lowest in the primary hemlock stand type, intermediate in the secondary hemlock stand type and highest in the post-HWA stand type ($p < 0.0005$). N uptake was also highest in the post-HWA stand type ($p < 0.0005$). N uptake was not significantly different in the secondary hemlock, girdled and secondary black birch stand types and was lowest in the girdled stand type.

Wood C:N was significantly higher in the hemlock-dominated stand types than all other stand types and was lowest in the post-HWA stand type ($p < 0.0001$, Table 3.9). Foliar C:N followed a very similar pattern to that of wood ($p < 0.0001$). Root C:N was highest in the secondary hemlock and lowest in the secondary black birch stand types ($p < 0.05$).

C:N in total woody debris was also highest where dead hemlock was predominantly found ($p < 0.0001$), especially when initial stages of decay prevailed. Organic horizon and mineral soil (0-15cm) had significantly higher C:N in the primary hemlock stand type ($p < 0.0005$). In the 15-50cm portion of mineral soil, the secondary black birch stand type presented an intermediate C:N in relation to the primary hemlock stand type (21.4 ± 1.4) and the remaining stand types (~13.8, $p < 0.0005$). Coarse and small roots tended to have higher C:N values in the hemlock-dominated stand types in relation to the secondary black birch type ($p < 0.05$, but the same trend was not seen for fine root C:N. Fine root found in the organic horizon had highest C:N in the post-HWA and secondary black birch stand types, with the reverse occurring in the mineral soil (0-50cm, $p < 0.0001$).

Discussion

Black birch is the dominant species replacing hemlock stands that have been infested by the HWA throughout the northeastern US (Orwig and Foster 1998, Orwig et al. 2002). I studied hemlock and black birch stands of varying ages to suggest possible long-term changes in C fluxes associated with infestation by HWA. I hypothesized that (1) ANPP would be significantly higher in young, aggrading black birch stand types than secondary hemlock stand types; (2) R_s would increase from hemlock-dominated stand types to black birch-dominated stand types because of larger inputs of labile litter; and (3) N availability would increase from hemlock-dominated to black birch-dominated stand types, contributing to increases in both ANPP and R_s. My analysis partially supports hypothesis (1) as ANPP was significantly higher only in the young, rapidly aggrading black birch stand type (post-HWA). Although ANPP was lowest in the oldest stand type (primary hemlock, ~230 years) it was not significantly different from the secondaryhemlock (~132 years), girdled (5 years) or black birch stand types (~135 years). This study does, however, confirm hypotheses (2) and (3).

Aboveground Net Primary Production

Overall, variations in ANPP among stand types was consistent with theories of stand development following disturbance (Ryan et al. 2004). ANPP was low immediately following disturbance (girdled) as leaf area develops. This was followed by high rates of ANPP in stand types at incipient canopy closure (post-HWA) and a general decline in productivity as stand types age (secondary black birch and forests). Notably, the production of wood accounted for ~70% of ANPP in the young stand types (girdled, post-HWA) whereas in mature stand types (primary and secondary hemlock, and secondary black birch), wood and foliage contributed nearly equally to ANPP (Figure 3.2A).

I found very different responses in relative growth rate of existing trees following hemlock loss (Figure 3.2B). Eastern hemlock trees died within two years in the girdled stand type but took up to five years following infestation in the post-HWA stand type (Orwig and Foster 1998, Jenkins et al. 1999). It is possible that the growth of the remaining canopy trees in the girdled stand type was initially high because of the rapid increase in light availability associated with hemlock death. By contrast, in the post-HWA stand type light availability may not have reached the high level found in the girdled stand type owing to the growth of sub-canopy trees and lateral regrowth of the remaining canopy trees (Canham et al. 1990). This difference in the response of remnant tree growth to hemlock loss altered the forests' productivity relative to its total biomass

(Figure 3.2C). While saplings were mostly responsible for higher productivity in the post-HWA stand type, remnant trees accounted for the relatively high productivity in the stand type with the least amount of biomass (girdled).

The presence of HWA was first recorded at very low density in the secondary hemlock stand type in 2008 (Ellison et al. 2010). By 2009, the adelgid was found on ~40% of the hemlock trees and saplings, though in very low abundance on any single individual. My measurements were made between 2008 and 2011. I visually confirmed the presence of HWA but also noted that affected canopy area was far less than 5%, with no signs of incipient needle loss or declines in tree vigor. The tree core data confirmed these visual inspections. There was no substantial change in radial growth following initiation of HWA invasion. Therefore it appears that ANPP had not been affected during the study period (Figure 3.2B).

Decomposition & Soil Respiration

Black birch leaves decomposed significantly faster than hemlock needles and there was no main or interactive effect of stand type. Litter C:N ratios were significantly lower in black birch leaves than hemlock needles. The more rapid decomposition of black birch is expected given that initial rates of litter decomposition are faster in narrow C:N litter (Melillo et al. 1982), presumably because of greater N availability for the synthesis of microbial exoenzymes (Schimel and Weintraub 2003). Consistent with this idea, the C:N ratio of litterfall was negatively correlated with the activity of labile C degrading enzymes in the top 15cm of mineral soil ($n=20$, $r^2=0.23$, $p < 0.05$).

There was threefold variation in hardwood litterfall mass among stand types (Table 3.3). This suggests that increases in the production of rapidly decomposing hardwood litter (Table 3.7) should enhance rates of R_s. Soil respiration rates were highest in the post-HWA stand type where black birch litterfall was the highest (Table 3.3), and among stand types there was a modest, positive correlation between hardwood litterfall mass and R_s (n=20, $R^2 = 0.22$, $p < 0.05$). Despite the importance of roots for R_s (Hogberg et al. 2001) it does not appear that variations in root biomass explain the variations in R_s among stand types. For example, Rs was highest at the post-HWA stand type where root biomass was lowest whereas root biomass was highest in the primary hemlock stand type where rates of Rs were also high (Figure 3.3C, Chapter 2).

Recent investigations have led to the understanding of a strong influence of live roots on microbial activity (Janssens et al. 2010, Phillips et al. 2011, Drake et al. 2012). Previous research in the primary hemlock stand type studied here indicated strong root-mycorrhizal effects on exoenzyme activity (Brzostek and Finzi 2011, Brzostek *in press*). I explored the possibility that root effects were also present in secondary hemlock and black birch stand types. Using root biomass data from Chapter 2, I found significant correlations between biomass and the activity of labile and recalcitrant C-degrading enzyme in the OH (n=20, r^2= 0.50, $p < 0.0001$) and to a depth of 45cm in the mineral soil horizon ($r^2 = 0.34$, $p < 0.05$). Hence, my results suggest that roots may indirectly affect R_s via the activity of microbial and exoenzyme activity in the rhizosphere.

There were significant variations in the temperature sensitivity (Q_{10}) of R_s (Table 3.5). Q_{10} was highest in the primary hemlock, intermediate in the post-HWA and lowest in the secondary hemlock stand types (Table 3.5). Given that litterfall, root biomass and microbial exoenzymes influence decomposition and in the case of litterfall, soil respiration, I was interested in determining whether these factors were also related to the Q_{10} of R_s. Using multiple regression analysis I found that all three factors were positively correlated with the Q_{10} of Rs. The relationship between root biomass, exoenzyme activity and Q_{10} may be the result of the high temperature sensitivity of root respiration (Compton and Boone 2002) or because of greater substrate supply and exoenzyme activity in the rhizosphere (Brzostek and Finzi 2011). This would support my earlier contention that fine root biomass has an indirect effect on R_s that is mediated by microbial activity. Similarly a large flux of labile, hardwood leaf litter is likely to increase the availability of substrates for enzymes and result in greater temperature sensitivity in addition to rates of R_s.

Secondary hemlock and girdled stand types at the Harvard Forest had similar daily R_s rates. This contrasts with prior work at the site reporting significant reductions in R_s during the first three years following girdling (Savage et al. 2009), but agrees with more recent measurements (Orwig et al, *in review*). The rapid growth of black birch seedlings and remaining canopy trees over the last few years likely explains the similarity in C flux observed between these two stand types, and suggests a rapid recovery of belowground processes (e.g., root production, exudation, microbial activity) following disturbance by HWA.

The temperature difference among stand types likely influenced soil respiration, especially in the post-HWA stand type. This may also have been the case for aboveground biomass production. It is possible, however, to say that 94% of the carbon output (soil respiration) was explained by hardwood foliar litter, fine root biomass and enzyme activity ($p < 0.005$). Models including MAT as an additional variable did not fit the data better suggesting that the effect of temperature, if present, is small and not distinguishable from the other drivers of soil respiration and possibly ANPP itself.

Nitrogen

High ANPP was associated with both high NUE and N_{uptake}. Both the girdled stand type and the post-HWA stand type fixed more C per unit N than all other stand types. Trees in the post-HWA stand type were not only using the available N efficiently, but the N uptake in that stand type was significantly higher than all other stand types, contributing to its substantially higher productivity. The two recovering stand types were highly efficient in nitrogen use because ANPP was driven primarily by wood production, which has a high C:N ratio.

The transition from hemlock- to black birch dominated stand types was associated with greater rates of N uptake from the soil. Increases in N uptake could be due to some combination of lower competition following hemlock loss and increases in the rate of N mineralization. A large pool of ammonium became available following hemlock girdling in 2005 (Orwig et al., *in review*). The spike in N availability may have contributed to the sharp increase in relative growth rate of the remaining trees in the girdled stand type (Figure 3.2B). By 2009, however, there was a dense seedling and sapling layer dominated by black birch and the ammonium pool size returned to levels found prior to girdling. This was associated with a general decline in diameter growth rates from 2007-2010 (Figure 3.2B).

I cannot directly infer from my studies changes in the amount or timing of N availability at the post-HWA stand type, but the slower rate of hemlock death may not have resulted in as large an initial increase in N availability as in the girdled stand type. Through time, however, N availability appears to increase as black birch trees dominate the stand and the quantity of labile litter inputs increases (Table 3.3). Of all stand types, annual N uptake was highest in post-HWA plots (Table 3.8). This was also the stand type where rates of Rs were highest despite the lowest root biomass, which is indicative of greater rates of microbial activity, including the possibility of greater N mineralization.

Conclusions

The objective of this analysis was to study stand types of differing age and species composition that may reflect the different stages of HWA effects on ecosystem C flux. By analyzing the selected stand types individually, I was able to understand potential changes that may occur in the forest following an infestation, both in regards to C uptake and loss, but also to some biogeochemical features that drive these fluxes. It was also possible to understand these changes in the absence of the HWA, following one hundred years of hemlock forest development (from a secondary to a primary hemlock stand types).

The differences observed in ANPP in all five stand types were not significant, with the exception of the post-HWA stand type, where ANPP was nearly three times higher than that found in the secondary hemlock stand type (Figure 3.2A). Similar trends were found in R_s, but not to the same degree as that of ANPP (Figure 3.3C). My data suggest that forests affected by the HWA in southern New England will continue to be carbon sinks of atmospheric carbon dioxide as they are able to offset the increase in R_s with a vigorous increase in productivity.

TABLE 3.1. Overstory species composition and characteristics of the measured stand types. Stem density and basal area include saplings of 0.5-10cm dbh. Arrows for girdled and infested stand types correspond to pre- → post-hemlock death. Prior stem density and basal area values were obtained from Ellison and Barker Plotkin (2005), and Orwig and Foster (1998) in the girdled and infested stand types, respectively. Former relative importance values for *T. canadensis* in the girdled stand type (Ellison et al. 2010) and the post-HWA stand type (Orwig and Foster 1998) are shown in parenthesis. Values for C pools, shown in [kg C m^{-2}], were obtained from Chapter 2. Stand age is represented by age/*years since hemlock girdling or infestation*.

TABLE 3.1

	Primary Hemlock Stand	Secondary Hemlock Stand	Girdled Stand	Post-HWA	Secondary Black Birch Stand
Relative Importance Value[1]					
Tsuga canadensis	90.5	66.8	(68.0)	(66)	--
Betula lenta	1.2	10.2	4.1	13.8	63.6
Acer rubrum	2.7	7.1	8.8	16	5.1
Quercus rubra	--	5.6	8.2	8	4.0
Pinus strobus	--	4.3	36.7	--	28.5
Basal Area (m^2/ha)	59.4	52.1	51.7 → 16.9	43 → 24	38.9
Stem Density (stems/ha) <10cm dbh	848 ± 372	115 ± 20	58 ± 37	23003 ± 2519	624 ± 212
Stem Density (stems/ha) >10cm dbh	718 ± 126	606 ± 37	731 → 308 ± 38	625 → 136 ± 11	549 ± 71
Location	Petersham, MA 42°32'N 72°11'W	Petersham, MA 42°32'N 72°11'W	Petersham, MA 42°32'N 72°11'W	Burham Brook, CT 41°28'N 72°19'W	Harvard, MA 42°31'N 71°32'W
Mean Annual Temperature	8.5°C	8.5°C	8.5°C	10.2°C	8.9°C
Mean Annual Precipitation	110 cm	110 cm	110 cm	123 cm	116 cm
Land use history	Woodlot	Pasture	Pasture	Woodlot	Pasture
Mineral Soil Bulk Density (g cm^{-3})	0.78 ± 0.04[b]	1.06 ± 0.09[a]	1.01 ± 0.04[a]	0.91 ± 0.27[ab]	0.82 ± 0.02[b]
Live biomass (kg C m^{-2})	18.1 ± 0.1[a]	13.5 ± 1.7[ab]	5.9 ± 2.2[c]	9.3 ± 2.7[bc]	17.4 ± 3.4[a]
Woody debris (kg C m^{-2})	0.9 ± 0.5[c]	0.7 ± 0.4[c]	6.2 ± 2.3[a]	2.6 ± 0.7[b]	1.3 ± 0.4[c]
Soil (Org. horizon to 45 cm mineral) (kg C m^{-2})	16.3 ± 1.2[a]	10.6 ± 1.3[c]	11.3 ± 1.0[c]	11.8 ± 0.2[c]	13.6 ± 0.5[b]
% Rock Volume	25.8 ± 3.4[a]	15.2 ± 1.4[ab]	22.3 ± 3.9[ab]	9.9 ± 2.9[b]	6.5 ± 0.44[b]
Stand age (years)	230	132	132/*5*	121/*18*	135

TABLE 3.2. Allometric equations applied to measured diameter at breast height for total aboveground biomass calculation. B = biomass, d = diameter at breast height.

TABLE 3.2

SPECIES		WOOD	FOLIAGE
Eastern hemlock	Equation	B=1.3449*(d^2.45)	ln(B)=5.154+1.294*(ln(d^1)
	Min. diameter	12.7 cm	6.1
	Max. diameter	129.0 cm	85.1
	Region	West Virginia	Tennessee
	Source	Brenneman et al. (1978)	Busing et al. 1993
Eastern white pine	Equation	ln(B)=4.19•d+2.43•ln(d)	ln(B)=3.22•d+1.75•ln(d)
	Min. diameter	1.7 cm	
	Max. diameter	25.7 cm	
	Region	New Hampshire	
	Source	Hooker and Early 1983	
Black birch	Equation	log10(B)= -1.254+2.728•log10(d)	log10(B)=-3.086+2.628•log10(d)
	Correction factor	1.016	1.041
	Min. diameter	7.8 cm	
	Max. diameter	39.6 cm	
	Region	North Carolina	
	Source	Martin et al. 1998	
Black birch sapling	Equation	B= 442.87•(d^2-0.964•(d)+757.26	B=7.8731•(d^2.3585)
	Min. diameter	0.4 cm	
	Max. diameter	6.3 cm	
	Region	Connecticut	
	Source	*This study*	
General hardwood	Equation	log10(B)=-1.281+2.68•log10(d)	log10(B)=-2.122+2.022•log10(d)
	Correction factor	1.021	1.158
	Min. diameter	3.8 cm	
	Max. diameter	63 cm	
	Region	North Carolina	
	Source	Martin et al. 1998	

TABLE 3.3. Aboveground net primary production (g C m^{-2} yr^{-1}) measured as the sum of annual flux increments and foliage turnover. Significant differences are shown for total ANPP among the stand types ($p < 0.05$).

TABLE 3.3

	Primary H.	Secondary H.	Girdled	Post-HWA	Bl. Birch
Conifer – Wood	83.6 ± 4.6[a]	64.1 ± 3.6[a]	40.9 ± 18.9[ab]	0.0[b]	65.5 ± 20.2[a]
Hardwood – Wood	27.2 ± 11.8[b]	60.3 ± 8.5[b]	272.4 ± 79.1[b]	686.6 ± 107.1[a]	141.1 ± 9.2[b]
Conifer – Foliar	3.8 ± 0.8[a]	1.9 ± 0.1[b]	1.0 ± 0.5[bc]	0.0[c]	2.4 ± 0.2[ab]
Hardwood – Foliar	0.4 ± 0.2[b]	0.7 ± 0.1[b]	3.4 ± 0.7[b]	17.3 ± 3.0[a]	1.5 ± 0.1[b]
Total in measured increments	*114.9 ± 11.4[b]*	*127.0 ± 5.0[b]*	*317.6 ± 62.9[b]*	*703.8 ± 110.1[a]*	*210.5 ± 18.7[b]*
Conifer – Needle litterfall	123.0 ± 6.3[a]	117.5 ± 16.6[a]	45.8 ± 28.6[b]	0.0[b]	3.6 ± 1.7[b]
Hardwood – Leaf litterfall	23.1 ± 8.4[d]	85.1 ± 16.6[c]	78.3 ± 13.3[c]	242.4 ± 11.1[a]	179.2 ± 4.5[b]
Total in measured turnover	*146.1 ± 5.0[c]*	*222.7 ± 36.2[ab]*	*124.1 ± 17.1[d]*	*242.4 ± 11.1[a]*	*182.8 ± 2.9[bc]*
Conifer	210.4 ± 9.8[a]	203.5 ± 38.0[ab]	87.6 ± 45.9[bc]	0.0[c]	71.5 ± 19.4[bc]
Hardwood	50.6 ± 19.9[c]	146.2 ± 24.3[bc]	354.1 ± 91.8[b]	946.3 ± 116.7[a]	321.8 ± 12.7[bc]
Total ANPP	***261.0 ± 14.7[b]***	***329.6 ± 22.1[b]***	***441.8 ± 54.7[b]***	***946.3 ± 116.7[a]***	***393.3 ± 20.8[b]***

TABLE 3.4. Soil temperature (^{o}C) and moisture (m^3 H_20 m^{-3} soil) variations in the measured stand types. Months correspond to those when soil respiration measurements were made.

TABLE 3.4

	Primary Hemlock		Secondary Hemlock		Girdled		Post-HWA		Bl. birch	
	Soil Temp.	Soil Moist.	Soil Temp.	Soil Moist.	Soil Temp.	Soil Moist.	Soil Temp.	Soil Moist.	Soil Temp.	Soil Moist.
April	7.79	0.28	6.92	0.24	6.48	0.25	9.02	0.23	9.36	0.24
May	11.63	0.23	13.58	0.22	13.03	0.25	11.91	0.22	14.11	0.22
June	15.04	0.19	16.31	0.21	15.80	0.24	16.87	0.21	16.73	0.23
July	18.01	0.15	20.00	0.15	19.32	0.19	20.41	0.16	20.28	0.15
August	18.41	0.19	18.73	0.17	18.52	0.22	20.33	0.17	19.69	0.22
September	15.94	0.22	16.41	0.22	16.37	0.25	18.06	0.20	17.70	0.24
October	12.79	0.26	9.21	0.24	9.78	0.25	12.98	0.21	12.40	0.26
November	7.87	0.26	5.11	0.24	5.06	0.25	8.47	0.21	7.31	0.25
Average	**13.44**	**0.22**	**13.28**	**0.21**	**13.05**	**0.24**	**14.76**	**0.20**	**14.70**	**0.23**

TABLE 3.5. Stand -specific exponential correlation between temperature (^oC) and efflux ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$); y-intercept term ($\beta$), exponential coefficient (k), R^2 between temperature and efflux, Q_{10} and R_{10} (average ± S.E.). Lower-case letters represent significant differences among stand types ($p < 0.05$).

TABLE 3.5

	β	k	R^2	Q_{10}	R_{10}
Primary H.	0.62 ± 0.11^{bc}	0.14 ± 0.01^{a}	0.93 ± 0.02	4.25 ± 0.19^{a}	2.61 ± 0.39
Secondary H.	0.75 ± 0.05^{a}	0.12 ± 0.01^{c}	0.95 ± 0.02	3.41 ± 0.23^{c}	2.53 ± 0.11
Girdled	0.60 ± 0.03^{b}	0.13 ± 0.01^{bc}	0.91 ± 0.04	3.60 ± 0.17^{bc}	2.13 ± 0.10
Post-HWA	0.54 ± 0.10^{c}	0.14 ± 0.01^{ab}	0.92 ± 0.02	4.03 ± 0.32^{ab}	2.08 ± 0.23
Bl. birch	0.71 ± 0.11^{b}	0.13 ± 0.01^{abc}	0.88 ± 0.03	3.60 ± 0.29^{abc}	2.46 ± 0.19

TABLE 3.6. Proportion of remaining mass of hemlock needles and black birch leaves along four different harvesting periods. Litterbags were installed in November 2009.

TABLE 3.6

	Installed		1st harvest (5 months)		2nd harvest (9 months)		3rd harvest (12 months)		4th harvest (24 months)	
Hemlock	1.0		0.79		0.74		0.66		0.46	
Black birch	1.0		0.68		0.62		0.53		0.37	
	Heml.	*Bl. birch*	*Heml.*	*Bl. birch*	*Heml.*	*Bl. birch*	*Heml.*	*Bl. birch*	*Heml.*	*Bl. birch*
Primary H.	1.0	1.0	0.82 ± 0.03	0.68 ± 0.06	0.71 ± 0.01	0.63 ± 0.05	0.60 ± 0.02	0.55 ± 0.04	0.43 ± 0.03	0.47 ± 0.07
Second. H.	1.0	1.0	0.78 ± 0.02	0.62 ± 0.07	0.74 ± 0.01	0.57 ± 0.05	0.61 ± 0.01	0.41 ± 0.05	0.41 ± 0.03	0.28 ± 0.04
Girdl.	1.0	1.0	0.78 ± 0.01	0.61 ± 0.07	0.76 ± 0.01	0.56 ± 0.07	0.68 ± 0.01	0.57 ± 0.46	0.49 ± 0.02	0.40 ± 0.05
P. Inf.	1.0	1.0	0.79 ± 0.01	0.74 ± 0.02	0.76 ± 0.01	0.68 ± 0.03	0.75 ± 0.02	0.58 ± 0.03	0.48 ± 0.06	0.29 ± 0.03
Bl. birch	1.0	1.0	0.78 ± 0.01	0.75 ± 0.02	0.76 ± 0.01	0.67 ± 0.02	0.68 ± 0.01	0.55 ± 0.02	0.49 ± 0.05	0.44 ± 0.04

TABLE 3.7. Soil exoenzyme activity in the organic horizon (OH) and mineral soil, considering soil bulk density (nmol m^{-2} h^{-1}). Different superscript letters indicate a significant difference ($p < 0.05$) among stand types.

TABLE 3.7

	Labile							
	αG		βG		CBH		*Total Labile*	
	OH	Min.	OH	Min.	OH	Min.	OH	Min.
Primary H.	0.20 ± 0.07	0.24 ± 0.03	10.6 ± 4.0^{a}	11.0 ± 1.6	4.34 ± 1.63^{a}	7.06 ± 2.86	*15.1 ± 5.3^{a}*	*18.3 ± 4.5*
Second. H.	0.02 ± 0.004	0.19 ± 0.03	0.8 ± 0.2^{b}	9.9 ± 4.6	0.22 ± 0.08^{b}	3.83 ± 1.88	*1.0 ± 0.3^{b}*	*14.0 ± 6.4*
Girdled	0.11 ± 0.07	0.22 ± 0.05	4.3 ± 1.4^{ab}	10.7 ± 11.1	0.71 ± 0.27^{b}	3.63 ± 1.58	*5.1 ± 1.6^{ab}*	*14.5 ± 2.0*
Post-HWA	0.20 ± 0.04	0.15 ± 0.02	10.5 ± 2.7^{a}	6.0 ± 2.4	0.48 ± 0.23^{b}	2.55 ± 1.30	*11.2 ± 3.0^{ab}*	*8.7 ± 3.7*
Bl. Birch	0.11 ± 0.03	0.27 ± 0.07	1.9 ± 1.0^{ab}	9.0 ± 2.9	0.64 ± 0.24^{b}	4.05 ± 1.54	*2.7 ± 1.0^{ab}*	*13.4 ± 4.4*

	Recalcitrant							
	Phenol oxidase		Peroxidase		*Total Recalcitrant*		NAG	
	OH	Min.	OH	Min.	OH	Min.	OH	Min.
Primary H.	25.7 ± 5.3^{a}	25.8 ± 4.2^{ab}	20.3 ± 6.4^{a}	41.5 ± 11.3	*46.0 ± 10.0^{a}*	*67.3 ± 10.7*	5.0 ± 0.7^{ab}	2.7 ± 0.6^{b}
Second. H.	7.5 ± 2.2^{b}	58.4 ± 6.0^{a}	7.3 ± 2.5^{ab}	45.6 ± 18.7	*14.8 ± 3.0^{b}*	*104.0 ± 23.6*	2.8 ± 1.4^{ab}	7.2 ± 1.0^{a}
Girdled	9.4 ± 3.3^{b}	39.5 ± 13.0^{ab}	6.9 ± 1.4^{ab}	37.1 ± 12.2	*16.3 ± 4.6^{b}*	*76.5 ± 20.6*	1.9 ± 0.4^{b}	6.0 ± 1.1^{ab}
Post-HWA	11.9 ± 3.0^{ab}	22.4 ± 5.0^{b}	8.7 ± 1.8^{ab}	25.5 ± 0.7	*20.6 ± 4.7^{b}*	*47.8 ± 5.5*	5.2 ± 0.4^{a}	6.2 ± 1.1^{ab}
Bl. Birch	6.8 ± 1.7^{b}	55.3 ± 7.8^{ab}	2.4 ± 1.0^{b}	24.7 ± 11.0	*9.2 ± 2.2^{b}*	*79.9 ± 17.3*	2.8 ± 0.7^{ab}	4.4 ± 0.5^{ab}

TABLE 3.8. Average (± S.E.) nitrogen pool size and fluxes for the compared stand types.

TABLE 3.8

	Primary hemlock	Secondary hemlock	Girdled hemlock	Post-HWA	Secondary black birch
Compartment pools (g m^{-2})					
Conifer - wood	10.1 ± 2.7^{a}	8.1 ± 0.8^{ab}	1.1 ± 0.5^{bc}	0.0^{c}	0.3 ± 0.1^{c}
Hardwood - wood	2.5 ± 0.9^{c}	9.8 ± 1.6^{bc}	8.0 ± 2.6^{bc}	15.7 ± 2.2^{b}	31.1 ± 3.3^{a}
Conifer - foliar	7.7 ± 1.8^{a}	6.7 ± 0.4^{a}	0.8 ± 0.4^{b}	0.0^{b}	0.5 ± 0.1^{b}
Hardwood - foliar	0.9 ± 0.4^{c}	3.0 ± 0.4^{bc}	2.5 ± 0.6^{bc}	5.2 ± 0.7^{ab}	7.9 ± 0.9^{a}
Coarse and small roots (OH to 50cm mineral)	1.5 ± 0.5	0.5 ± 0.1	0.4 ± 0.1	0.8 ± 0.1	1.6 ± 0.7
Fine roots (OH to 45cm mineral)	10.1 ± 0.6^{a}	5.6 ± 0.8^{b}	6.3 ± 0.1^{ab}	5.5 ± 0.5^{b}	8.9 ± 2.1^{ab}
Coarse and small woody debris	5.9 ± 1.7^{cd}	3.3 ±1.0^{d}	36.5 ± 1.6^{a}	20.7 ± 0.6^{b}	12.0 ± 2.1^{c}
Fine woody debris	0.60 ± 0.14^{a}	0.30 ± 0.02^{ab}	0.32 ± 0.05^{ab}	0.22 ± 0.04^{b}	0.50 ± 0.01^{ab}
Total in biomass	33.8 ± 6.3^{b}	33.0 ± 1.7^{b}	51.8 ± 4.2^{ab}	44.9 ± 3.4^{ab}	54.6 ± 5.2^{a}
SOM	138.1 ± 17.8^{a}	56.6 ± 10.2^{b}	88.9 ± 16.1^{ab}	110.2 ± 16.5^{ab}	43.6 ± 2.6^{b}
Mineral soil (0-45cm)	472.6 ± 6.5^{c}	567.5 ± 18.5^{b}	514.6 ± 7.3^{c}	522.5 ± 11.6^{bc}	662.3 ± 12.9^{a}
Total in soil	610.6 ± 17.7^{b}	624.0 ± 29.1^{b}	599.1 ± 15.1^{b}	620.3 ± 7.6^{b}	706.9 ± 14.1^{a}
Annual flux increments (g m^{-2} yr^{-1})					
Conifer wood	0.07 ± 0.02^{ab}	0.07 ± 0.04^{ab}	0.05 ± 0.02^{ab}	0^{b}	0.09 ± 0.03^{a}
Hardwood wood	0.04 ± 0.02^{b}	0.11 ± 0.02^{b}	0.49 ± 0.14^{b}	1.12 ± 0.18^{a}	0.26 ± 0.03^{b}
Conifer needle	0.07 ± 0.03^{a}	0.04 ± 0.00^{ab}	0.03 ± 0.01^{ab}	0^{b}	0.08 ± 0.02^{a}
Hardwood leaf	0.01 ± 0.00^{b}	0.03 ± 0.00^{b}	0.13 ± 0.03^{b}	0.64 ± 0.12^{a}	0.06 ± 0.01^{b}
Total in measured increments	0.19 ± 0.06^{b}	0.25 ± 0.01^{b}	0.69 ± 0.13^{b}	1.76 ± 0.30^{a}	0.50 ± 0.09^{b}
Turnover					
Conifer litterfall	2.6 ± 0.1^{a}	2.6 ± 0.6^{a}	0.66 ± 0.41^{b}	0^{b}	0.05 ± 0.02^{b}
Hardwood litterfall	0.5 ± 0.2^{c}	1.8 ± 0.3^{b}	1.85 ± 0.39^{b}	5.3 ± 0.3^{a}	4.6 ± 0.2^{a}
Total in measured turnover	3.1 ± 0.2^{b}	4.4 ± 0.5^{a}	2.51 ± 0.15^{b}	5.3 ± 0.3^{a}	4.6 ± 0.2^{a}
Aboveground annual requirement	3.3 ± 0.2^{c}	4.7 ± 0.5^{bc}	3.2 ± 0.2^{c}	7.0 ± 0.6^{a}	5.2 ± 0.2^{b}
Aboveground NUE	79.9 ± 1.9^{b}	74.5 ± 0.3^{b}	137.0 ± 10.3^{a}	133.1 ± 7.4^{a}	76.4 ± 2.2^{b}
Aboveground N retranslocation	0.6 ± 0.2^{b}	1.6 ± 0.4^{ab}	2.1 ± 0.5^{a}	2.6 ± 0.1^{a}	2.4 ± 0.0^{a}
Aboveground N uptake	2.7 ± 0.1^{bc}	3.1 ± 0.2^{ab}	1.1 ± 0.5^{c}	4.5 ± 0.6^{a}	2.7 ± 0.2^{bc}

TABLE 3.9. C:N ratio for measured stand types.

TABLE 3.9.

	Primary H.	Secondary H.	Girdled	Post-HWA	Bl. Birch
Wood	855.9 ± 21.8^{a}	792.8 ± 1.0^{a}	614.1 ± 17.8^{c}	597.7 ± 0.34^{c}	722.8 ± 18.7^{b}
Foliage	38.5 ± 0. 9^{a}	35.8 ± 0.4^{b}	28.2 ± 0.6^{d}	27.6 ± 0.01^{d}	31.5 ± 0.6^{c}
Litter	50.7 ± 0.8^{ab}	56.6 ± 3.9^{a}	53.9 ± 5.0^{ab}	52.0 ± 2.3^{ab}	42.2 ± 1.8^{b}
Coarse woody debris	180 ± 5.0^{b}	195.6 ± 13.4^{b}	233.0 ± 4.0^{a}	108.3 ± 1.0^{c}	101.4 ± 0.3^{c}
Small woody debris	208.8 ± 4.3	203.2 ± 4.0	196.6 ± 3.4	198.3 ± 2.8	205.6 ± 3.7
Fine woody debris	130.4 ± 3.3^{a}	134.5 ± 2.4^{a}	125.1 ± 2.6^{a}	97.4 ± 2.0^{b}	93.1 ± 1.3^{b}
Total woody debris	180.9 ± 3.3^{b}	191.4 ± 9.0^{b}	231.2 ± 4.2^{a}	125.8 ± 1.1^{c}	114.7 ± 2.5^{c}
Organic horizon	33.4 ± 1.4^{a}	27.3 ± 1.0^{b}	27.5 ± 1.3^{b}	23.6 ± 0.3^{bc}	21.9 ± 0.8^{c}
Mineral soil (0-15cm)	30.7 ± 2.2^{a}	20.8 ± 1.3^{b}	22.5 ± 0.1^{b}	20.9 ± 0.3^{b}	20.0 ± 0.7^{b}
Mineral soil (15-45cm)	21.4 ± 1.4^{a}	12.7 ± 0.8^{b}	14.2 ± 0.8^{b}	14.6 ± 0.6^{b}	17.0 ± 1.6^{ab}
Coarse and small roots (org. horizon)	193.9 ± 16.7^{a}	131.5 ± 4.0^{ab}	138.4 ± 14.1^{ab}	120.3 ± 11.0^{ab}	102.7 ± 25.6^{b}
Coarse and small roots (0-15cm)	206.8 ± 15.6^{ab}	242.7 ± 9.5^{a}	141.1 ± 10.5^{ab}	145.4 ± 38.9^{ab}	97.4 ± 0.85^{b}
Coarse and small roots (15-50cm)	221.0 ± 2.0^{ab}	244.9 ± 49.8^{a}	204.4 ± 4.1^{ab}	150.5 ± 21.7^{ab}	105.6 ± 7.6^{b}
Fine roots (org. horizon)	42.6 ± 0.7^{b}	40.1 ± 1.4^{b}	44.4 ± 1.3^{b}	54.6 ± 2.5^{a}	56.5 ± 1.5^{a}
Fine roots (0-15cm)	49.1 ± 1.2^{a}	43.3 ± 1.0^{ab}	38.3 ± 0.5^{bc}	35.2 ± 2.0^{c}	43.1 ± 1.5^{b}
Fine roots (15-50cm)	43.6 ± 0.7^{ab}	48.1 ± 2.3^{a}	45.7 ± 1.6^{ab}	40.3 ± 1.4^{bc}	34.9 ± 0.6^{c}

FIGURE 3.1. Measured stand types used to investigate changes and examine the trajectory of carbon flux due to the infestation of the hemlock woolly adeldig (art courtesy: Floyd T. Raymer).

FIGURE 3.1.

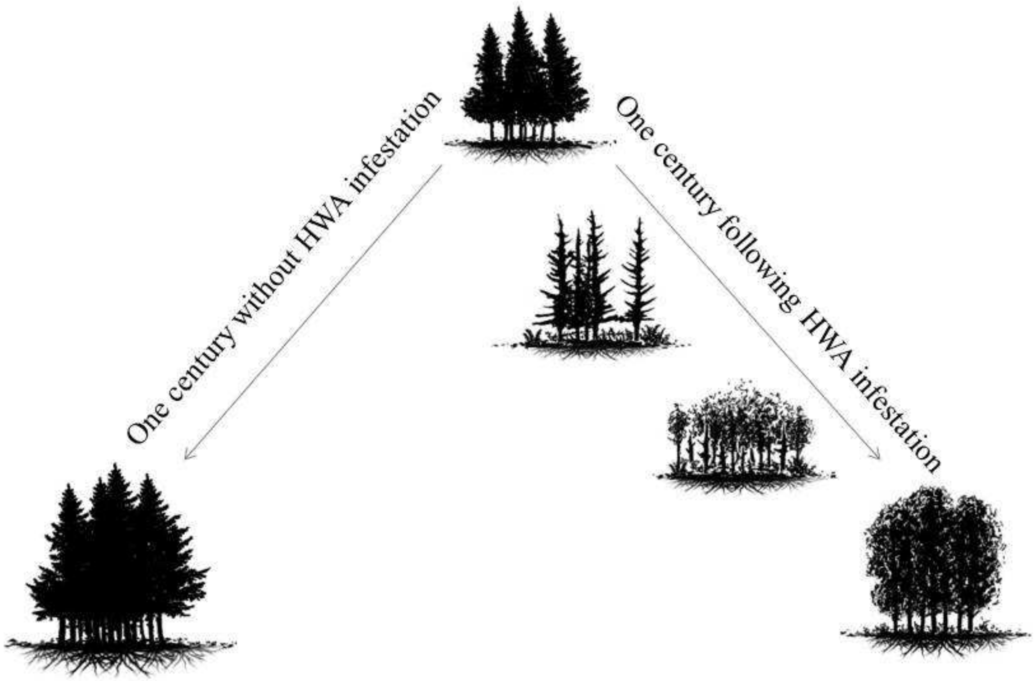
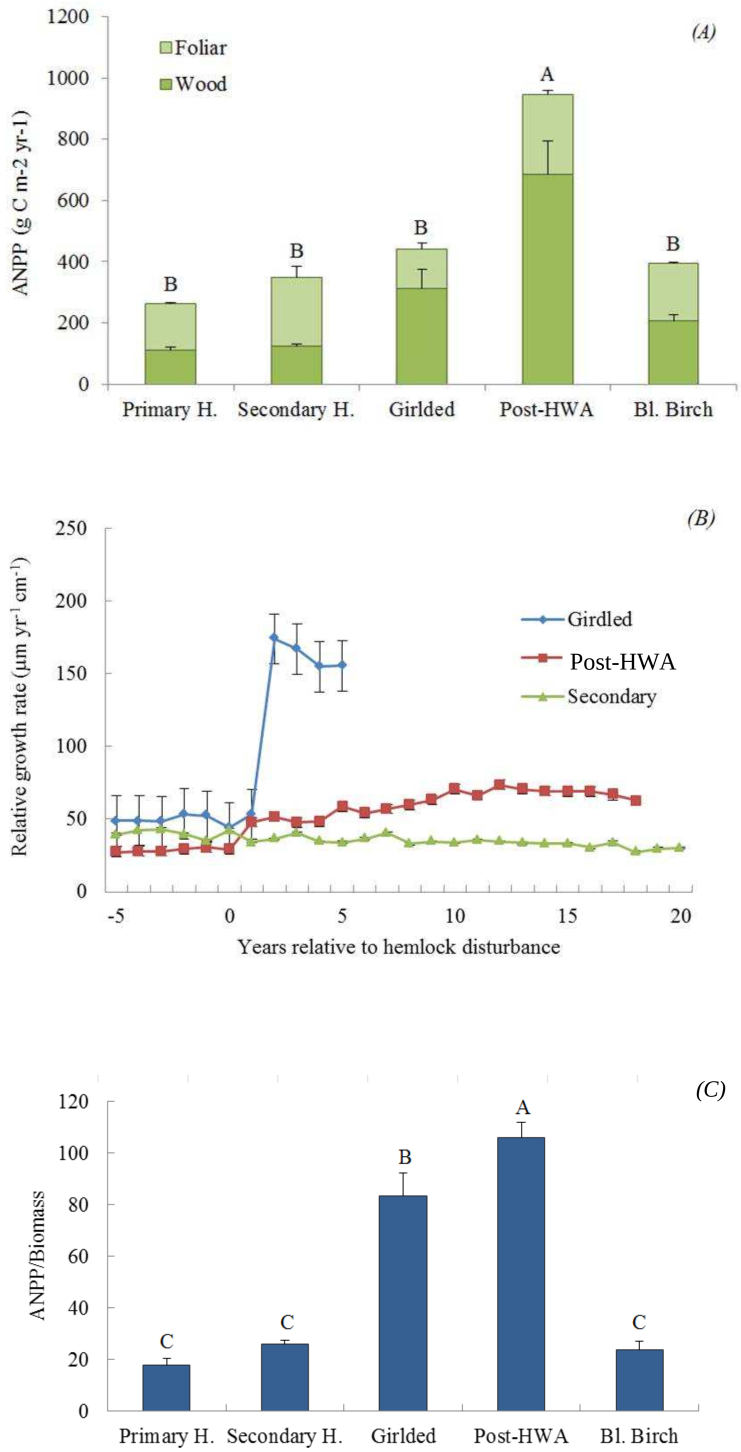

One century without HWA infestation
One century following HWA infestation

FIGURE 3.2. (A) Aboveground net primary production (g C m^{-2} yr^{-1}) measured by woody and foliar increment and foliar turnover and (B) changes in relative growth rate in the secondary and girdled hemlock stand types and post-infested stand type.

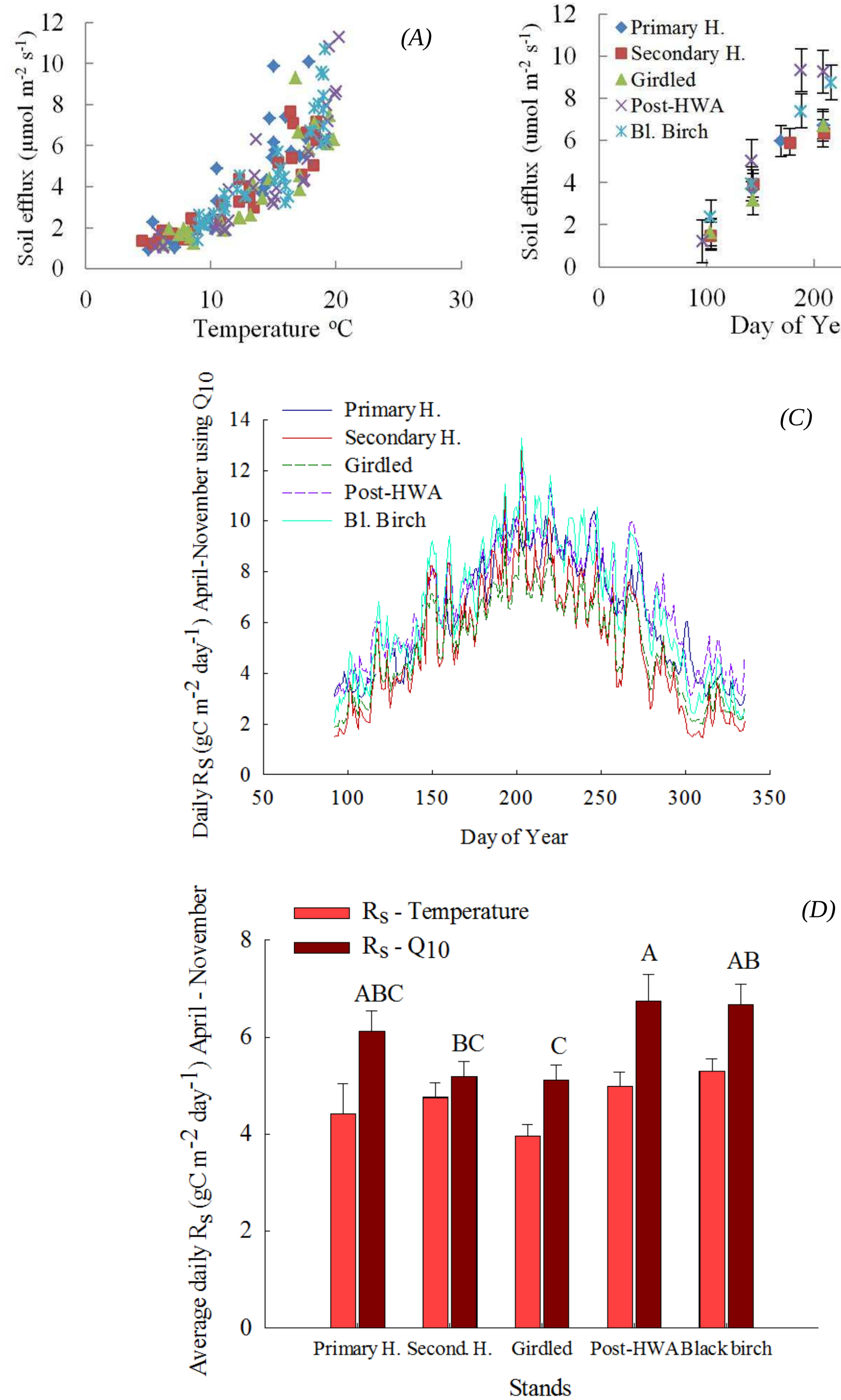
FIGURE 3.2.



1200
1000
800
600
400
200
0
ANPP (g C m-2 yr-1)
Foliar
Wood
(A)
A
B
B
B
B
Primary H.
Secondary H.
Girlded
Post-HWA
Bl. Birch
250
200
150
100
50
0
Relative growth rate (μm yr-1 cm-1)
(B)
Girdled
Post-HWA
Secondary
-5
0
5
10
15
20
Years relative to hemlock disturbance
120
100
80
60
40
20
0
ANPP/Biomass
(C)
A
B
C
C
C
Primary H.
Secondary H.
Girlded
Post-HWA
Bl. Birch

FIGURE 3.3. (A) Measured soil efflux ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) and corresponding temperatures (^oC), soil efflux = $0.6364 \cdot e^{0.1302(temp)}$ ($R^2 = 0.85$) (B) Field measurements of soil efflux ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) from April through November; (B); (C) Modeled daily soil respiration ($g\ C\ m^{-2}\ day^{-1}$) from April through November. Gray area corresponds to daily soil respiration during growing season (May through October); inset: total monthly soil respiration during growing season (April-October).

FIGURE 3.3



Soil efflux (µmol m-2 s-1)
Temperature °C
(A)
Primary H.
Secondary H.
Girdled
Post-HWA
Bl. Birch
Day of Year
(B)
Daily RS (gC m-2 day-1) April-November using Q10
Primary H.
Secondary H.
Girdled
Post-HWA
Bl. Birch
Day of Year
(C)
Average daily RS (gC m-2 day-1) April - November
RS - Temperature
RS - Q10
ABC
BC
C
A
AB
Primary H.
Second. H.
Girdled
Post-HWA
Black birch
Stands
(D)

CHAPTER 4

GENERAL CONCLUSION

SUMMARY

Following current trends, the continual transportation of humans and materials between countries and continents should sustain the introduction of insects and pathogens to forests around the world (Liebhold et al. 1995). In the last two centuries hundreds of nonindigenous insects have been reported in the US (Aukema et al. 2010), some of which invaded forests of New England and are classified as broad-impact pests (Hicke et al. 2012). This disturbance has implications to forest ecosystem and biogeochemical cycles, particularly the carbon cycle (Block et al. 2012). The hemlock woolly adelgid is a broad-impact invasive pest that reached southern New England in the mid-1980s and has been successful in its distribution given its life cycle (McClure 1989), genetic adaptation (Butin et al. 2005) and the occurrence of milder winters (Hayhoe et al. 2007). To further our understanding of how the shift in community structure caused by the HWA alters the C cycle in affected forests of southern New England, this dissertation used a comparative approach looking at forests of varying age and developmental stages, dominated both by the adelgid's host species (eastern hemlock), and its predominant successor (black birch).

Variations in C fluxes (e.g., wood biomass to CWD post girdling, loss of C rich organic horizon but gain in mineral soil C content) shifted the distribution of C pools among stand types, but at the centennial time scale forest C balance was resilient to invasion by the HWA. That is, there were few variations in the total quantity of C stored in each stand type.

In Chapter 2 I was able to show that C storage is maintained during the recovery of the forest: C pool is highest in the live biomass of healthy secondary hemlock forests, and shifts predominantly to snags five years following hemlock senescence. As the debris decays, C storage is compensated for in the dense and fast-growing population of black birch saplings as measured in a forest where HWA was present two decades ago (post-HWA). I also showed that the forest continues to increase its C storage, and that a mature secondary black birch forest is able to store as much C as a primary hemlock forest. These two forest types represent circa one century with and without HWA infestation, respectively.

In Chapter 3 I demonstrated how aboveground net primary production was kept nearly unchanged throughout all the forests I measured, except in the post-HWA stand type. I also found that soil respiration increased in the post-HWA stand type, but not to the same degree as that of its productivity. The two secondary stand types I measured (hemlock and black birch) had similar rates of soil respiration while the girdled stand type was recovering from its loss of roots. I demonstrated how N dynamics are tightly coupled with the productivity of the forest and how it relates to the overall equilibrium of C flux.

The results presented here support by conclusion that, despite the collapse of eastern hemlock forests and their replacement by black birch forests, the total carbon stored in these forests remain unchanged, with shifts in the sizes of individual carbon pools. I also conclude that this resilience of C storage is possible because of variations in

C flux: the increase in soil respiration is offset by the vigorous increase in biomass production, allowing the forests to remain a carbon sink of atmospheric carbon dioxide.

FUTURE DIRECTIONS

Fine root biomass greatly influenced the activity of soil enzymes and explained much of soil respiration. There are strong evidences for how soil and the life cycle of aboveground biomass affect changes in forest C storage and flux (e.g. Dixon 1994, Valentini et al. 2000, Davidson and Janssens 2006). The dynamics of root growth and production, however, and its influence on forest biogeochemistry remains largely unknown (Comas and Eissenstat 2009). Understanding the interaction of root phenology and forest dynamics (e.g. changes in climate, soil temperature and moisture, nutrient availability, species richness) would increase our understanding of the factors not only influence forest productivity (Gill and Jackson 2000) but also of larger-scale carbon exchanges between forest and atmosphere.

Roots may be greatly affected by changes in climate, as would much of the forest as a whole. Are eastern hemlock trees more or less adaptable to these changes than black birch trees? We have access to data from primary hemlock stand type that have been present for over two centuries, as we also have century-old secondary hemlock and black birch stand types. Has the annual growth of these trees changed over time? The possibility of a significant correlation between changes in temperate and precipitation patterns that have occurred in the past 100-200 years with tree growth can help us take our current understanding of forest resilience to the next level, focusing on the adaptability of these two species to climate change and how this might shape the C-cycle of New England forests in the future.

Lastly, the concept of foundation species has been of great importance in understanding the role specific species play in a forest. It is considered that the loss of foundation species ‘acutely and chronically impacts fluxes of energy and nutrients, hydrology, food webs and biodiversity’ (Ellison et al. 2005). Eastern hemlock trees have unarguably strong control over much of the factors mentioned above (Finzi et al. 1998a, Finzi et al. 1998b, Brooks 2001, Tingley et al. 2002, Lovett et al. 2004, Templer et al. 2005, Daley et al. 2008), but the idea of a disproportional impact becomes less evident in relation to C and N dynamics, as I found and so have an increasing number of studies (Albani et al. 2010, Knoepp et al. 2011, Block et al. 2012, Orwig et al. *in review*). Ellison et al. (2005) point out that foundation species are often only recognized when their presence becomes threatened, and that we must understand the role other species play in a less catastrophic scenario. My results reinforce the need for this understanding, and suggest it would be interesting to know how impactful other northeastern trees are in relation to the eastern hemlock.

LITERATURE CITED

Albani, M., P. R. Moorcroft, A. M. Ellison, D. A. Orwig, and D. R. Foster. 2010. Predicting the impact of hemlock woolly adelgid on carbon dynamics of eastern United States forests. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **40**:119-133.

Aukema, J. E., D. G. McCullough, B. Von Holle, A. M. Liebhold, K. Britton, and S. J. Frankel. 2010. Historical Accumulation of Nonindigenous Forest Pests in the Continental United States. Bioscience **60**:886-897.

Berg, S.P., Dempsey, C.W., Ward, W.T. 1997. Planning for Harvard's Rural Landscape: Case Studies in Historic Conservation. Harvard Rural Landscape Committee, Harvard.

Bettman-Kerson, P. 2007. Hemlock Removal Experiment – Dendrochronological Record. Harvard Forest Data Archive HF-086.

Biondi, F. 2000. Are climate-tree growth relationships changing in North-Central Idaho, USA? Arctic Antarctic and Alpine Research **32**:111-116.

Birdsey, R., K. Pregitzer, and A. Lucier. 2006. Forest carbon management in the United States: 1600-2100. Journal of Environmental Quality **35**:1461-1469.

Block, C. E., J. D. Knoepp, K. J. Elliott, and J. M. Fraterrigo. 2012. Impacts of Hemlock Loss on Nitrogen Retention Vary with Soil Nitrogen Availability in the Southern Appalachian Mountains. Ecosystems **15**:1108-1120.

Bousquet, P., P. Peylin, P. Ciais, C. Le Quere, P. Friedlingstein, and P. P. Tans. 2000. Regional changes in carbon dioxide fluxes of land and oceans since 1980. Science **290**:1342-1346.

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.

Brzostek, E. R. and A. C. Finzi. 2011. Substrate supply, fine roots, and temperature control proteolytic enzyme activity in temperate forest soils. Ecology **92**:892-902.

Butin, E., A. H. Porter, and J. Elkinton. 2005. Adaptation during biological invasions and the case of Adelges tsugae. Evolutionary Ecology Research **7**:887-900.

Canadell, J. G., C. Le Quere, M. R. Raupach, C. B. Field, E. T. Buitenhuis, P. Ciais, T. J. Conway, N. P. Gillett, R. A. Houghton, and G. Marland. 2007. Contributions to accelerating atmospheric CO(2) growth from economic activity, carbon intensity, and efficiency of natural sinks. Proceedings of the National Academy of Sciences of the United States of America **104**:18866-18870.

Canham, C.D., J.B. McAninch, D.M. Wood. 1994. Effects of frequency, timing, and intensity of simulated browsing on growth and mortality of tree seedlings. Canadian Journal of Forest Research **24**:817-825.

Carmona, M. R., J. J. Armesto, J. C. Aravena, and C. A. Perez. 2002. Coarse woody debris biomass in successional and primary temperate forests in Chiloe Island, Chile. Forest Ecology and Management **164**:265-275.

Carpenter, S., B. Walker, J. M. Anderies, and N. Abel. 2001. From metaphor to measurement: Resilience of what to what? Ecosystems **4**:765-781.

Catovsky, S. and F. A. Bazzaz. 2000. The role of resource interactions and seedling regeneration in maintaining a positive feedback in hemlock stands. Journal of Ecology **88**:100-112.

Clark, J. D. and A. H. Johnson. 2011. Carbon and Nitrogen Accumulation in Post-Agricultural Forest Soils of Western New England. Soil Science Society of America Journal **75**:1530-1542.

Cobb, R. C. 2010. Species shift drives decomposition rates following invasion by hemlock woolly adelgid. Oikos **119**:1291-1298.

Comas, L. H. and D. M. Eissenstat. 2009. Patterns in root trait variation among 25 co-existing North American forest species. New Phytologist **182**:919-928.

Compton, J. E. and R. D. Boone. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology **81**:2314-2330.

Coomes, D. A., R. B. Allen, N. A. Scott, C. Goulding, and P. Beets. 2002. Designing systems to monitor carbon stocks in forests and shrublands. Forest Ecology and Management **164**:89-108.

Daley, M. J., N. G. Phillips, C. Pettijohn, and J. L. Hadley. 2007. Water use by eastern hemlock (Tsuga canadensis) and black birch (Betula lenta): implications of effects of the hemlock woolly adelgid. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **37**:2031-2040.

Daley, M. J., N. G. Phillips, J. C. Pettijohn, and J. Hadley. 2008. Hydraulic responses to environmental perturbations in Tsuga canadensis and Betula lenta. Tree Physiology **28**:1341-1348.

Davidson, E. A. and I. A. Janssens. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature **440**:165-173.

Davis, L. R., K. J. Puettmann, and G. F. Tucker. 2007. Overstory response to alternative thinning treatments in young Douglas-fir forests of western Oregon. Northwest Science **81**:1-14.

Dixon, R. K. 1994. Carbon pools and flux of global forest ecosystems. Science **265**:171-171.

Drake, J. E., A. Gallet-Budynek, K. S. Hofmockel, E. S. Bernhardt, S. A. Billings, R. B. Jackson, K. S. Johnsen, J. Lichter, H. R. McCarthy, M. L. McCormack, D. J. P. Moore, R. Oren, S. Palmroth, R. P. Phillips, J. S. Pippen, S. G. Pritchard, K. K. Treseder, W. H. Schlesinger, E. H. DeLucia, and A. C. Finzi. 2011. Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO(2). Ecology Letters **14**:349-357.

Drake, J. E., A. C. Oishi, M. A. Giasson, R. Oren, K. H. Johnsen, and A. C. Finzi. 2012. Trenching reduces soil heterotrophic activity in a loblolly pine (Pinus taeda) forest exposed to elevated atmospheric CO2 and N fertilization. Agricultural and Forest Meteorology **165**:43-52.

Dukes, J. S., J. Pontius, D. Orwig, J. R. Garnas, V. L. Rodgers, N. Brazee, B. Cooke, K. A. Theoharides, E. E. Stange, R. Harrington, J. Ehrenfeld, J. Gurevitch, M. Lerdau, K. Stinson, R. Wick, and M. Ayres. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **39**:231-248.

Eisenbies, M. H., C. Davidson, J. Johnson, R. Amateis, and K. Gottschalk. 2007. Tree mortality in mixed pine-hardwood stands defoliated by the European gypsy moth (Lymantria dispar L.). Forest Science **53**:683-691.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. Von Holle, and J. R. Webster. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment **3**:479-486.

Ellison A, Barker Plotkin A. 2005a. Hemlock Removal Experiment - Overstory Vegetation. Harvard Forest Data Archive: HF126.

Ellison, A. M., A. A. Barker-Plotkin, D. R. Foster, and D. A. Orwig. 2010. Experimentally testing the role of foundation species in forests: the Harvard Forest Hemlock Removal Experiment. Methods in Ecology and Evolution **1**:168-179.

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-Revue Canadienne De Recherche Forestiere **36**:1435-1450.

Falxa-Raymond, N., A. E. Patterson, W. S. F. Schuster, and K. L. Griffin. 2012. Oak loss increases foliar nitrogen, delta N-15 and growth rates of Betula lenta in a northern temperate deciduous forest. Tree Physiology **32**:1092-1101.

Finzi, A. C., C. D. Canham, and N. Van Breeman. 1998a. Canopy tree-soil interactions within temperate forests: Species effects on pH and cations (vol 8, pg 447, 1998). Ecological Applications **8**:905-905.

Finzi, A. C., N. Van Breemen, and C. D. Canham. 1998b. Canopy tree soil interactions within temperate forests: Species effects on soil carbon and nitrogen. Ecological Applications **8**:440-446.

Finzi, A. C., R. L. Sinsabaugh, T. M. Long, and M. P. Osgood. 2006. Microbial community responses to atmospheric carbon dioxide enrichment in a warm-temperate forest. Ecosystems **9**:215-226.

Fitzpatrick, M. C., E. L. Preisser, A. Porter, J. Elkinton, and A. M. Ellison. 2012. Modeling range dynamics in heterogeneous landscapes: invasion of the hemlock woolly adelgid in eastern North America. Ecological Applications **22**:472-486.

Foote, R. L. and P. Grogan. 2010. Soil Carbon Accumulation During Temperate Forest Succession on Abandoned Low Productivity Agricultural Lands. Ecosystems **13**:795-812.

Foster, D. R., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: Regional forest dynamics in central New England. Ecosystems **1**:96-119.

Foster, D. R., T. Zebryk, P. Schoonmaker, and A. Lezberg. 1992. Postsettlemento history of human land-use and vegetation dynamics of a Tsuga-canadensis (hemlock) woodlot in central New England. Journal of Ecology **80**:773-786.

Foster, D. R. and T. M. Zebryk. 1993. Long-term vegetation dynamics and disturbance history of a Tsuga-dominated forest in New-England. Ecology **74**:982-998.

Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. Tree death as an ecological process. Bioscience **37**:550-556.

Gibbs, J. N. 1978. Intercontinental epidemiology of dutch elm disease. Annual Review of Phytopathology **16**:287-307.

Gill, R. A. and R. B. Jackson. 2000. Global patterns of root turnover for terrestrial ecosystems. New Phytologist **147**:13-31.

Godman R.M. and K. Lancaster. 1990. *Tsuga canadensis* (L.) Carr.: eastern hemlock, pp. 605-612. *In* R.M. Burns and B.H. Honkala [eds.], Silvics of North America, Vol. 1. Conifers. USDA Forest Service Agriculture Handbook 654, 675 p.

Gower, S. T. and Y. Son. 1992. Differences in soil and leaf litterfall nitrogen dynamics for 5 forest plantations. Soil Science Society of America Journal **56**:1959-1966.

Gunderson L.and C.S. Holling. 2001. Panarchy: understanding transformations in human and natural systems. Washington (DC): Island Press.

Hadley, J. L. 2000. Understory microclimate and photosynthetic response of saplings in an old-growth eastern hemlock (Tsuga canadensis L.) forest. Ecoscience **7**:66-72.

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 woolly adelgid. Tree Physiology **28**:615-627.

Hancock, J. E., M. A. Arthur, K. C. Weathers, and G. M. Lovett. 2008. Carbon cycling along a gradient of beech bark disease impact in the Catskill Mountains, New York. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **38**:1267-1274.

Hayhoe, K., C. P. Wake, T. G. Huntington, L. F. Luo, M. D. Schwartz, J. Sheffield, E. Wood, B. Anderson, J. Bradbury, A. DeGaetano, T. J. Troy, and D. Wolfe. 2007. Past and future changes in climate and hydrological indicators in the US Northeast. Climate Dynamics **28**:381-407.

Hicke, J. A., C. D. Allen, A. R. Desai, M. C. Dietze, R. J. Hall, E. H. Hogg, D. M. Kashian, D. Moore, K. F. Raffa, R. N. Sturrock, and J. Vogelmann. 2012a. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. Global Change Biology **18**:7-34.

Hicke, J. A., M. C. Johnson, L. H. D. Jane, and H. K. Preisler. 2012b. Effects of bark beetle-caused tree mortality on wildfire. Forest Ecology and Management **271**:81-90.

Hill, D., E. Sautter, and W. Gunick. 1980. Soils of Connecticut. Bulletin Number 787. Connecticut Agricultural Experiment Station, New Haven, Connecticut, USA.

Hogberg, P., A. Nordgren, N. Buchmann, A.F.S. Taylor, A. Ekblad, M.N. Hogberg, G. Nyberg, M. Ottosson-Lofvenius, D. J. Read. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature **411**:789-792.

Houghton, R. A. 2000. Interannual variability in the global carbon cycle. Journal of Geophysical Research-Atmospheres **105**:20121-20130.

Houghton, R. A., J. L. Hackler, and K. T. Lawrence. 1999. The US carbon budget: Contributions from land-use change. Science **285**:574-578.

Janssens, I. A., W. Dieleman, S. Luyssaert, J. A. Subke, M. Reichstein, R. Ceulemans, P. Ciais, A. J. Dolman, J. Grace, G. Matteucci, D. Papale, S. L. Piao, E. D. Schulze, J. Tang, and B. E. Law. 2010. Reduction of forest soil respiration in response to nitrogen deposition. Nature Geoscience **3**:315-322.

Jenkins, J. C., J. D. Aber, and C. D. Canham. 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **29**:630-645.

Jenkins, J. C., D. C. Chojnacky, L. S. Heath, and R. A. Birdsey. 2003. National-scale biomass estimators for United States tree species. Forest Science **49**:12-35.

King, D. A. 1990. Allometry of saplings and understorey trees of a Panamanian forest. Functional Ecology **4**:27-32.

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.

Knoepp, J. D., J. M. Vose, B. D. Clinton, and M. D. Hunter. 2011. Hemlock Infestation and Mortality: Impacts on Nutrient Pools and Cycling in Appalachian Forests. Soil Science Society of America Journal **75**:1935-1945.

Kurz, W. A., G. Stinson, G. J. Rampley, C. C. Dymond, and E. T. Neilson. 2008. Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncerain. Proceedings of the National Academy of Sciences of the United States of America **105**:1551-1555.

Lamson N.I. 1990. *Betula lenta* (L.) Carr.: black birch, pp 148-152. *In* R.M. Burns and B.H. Honkala [eds.], Silvics of North America, Vol. 2. Hardwoods. USDA For. Serv. Agric. Handb. 654, 880 p.

LeBauer, D. S. and K. K. Treseder. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology **89**:371-379.

Liebhold, A. M., W. L. Macdonald, D. Bergdahl, and V. C. Maestro. 1995. Invasio by exotic forest pests - a threat to forest ecosystems. Forest Science **41**:1-49.

Lovett, G. M., K. C. Weathers, M. A. Arthur, and J. C. Schultz. 2004. Nitrogen cycling in a northern hardwood forest: Do species matter? Biogeochemistry **67**:289-308.

Matlack, G. R. 1989. Secondary dispersal of seed across snow in Betula-lenta, a gap-colonizing tree species. Journal of Ecology **77**:853-869.

Mausel, D. L., S. M. Salom, L. T. Kok, and G. A. Davis. 2010. Establishment of the Hemlock Woolly Adelgid Predator, Laricobius nigrinus (Coleoptera: Derodontidae), in the Eastern United States. Environmental Entomology **39**:440-448.

McClure, M. S. 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. S. 1990. Role of wind, birds, deer, and humans in the dispersal of hemlock woolly adelgid (Homoptera, Adelgidae). Environmental Entomology **19**:36-43.

McCormick, J. F. and R. B. Platt. 1980. Recovery of an Appalachian forest following the chestnut blight or Keever, Catherine - you were right. American Midland Naturalist **104**:264-273.

McWilliams, W. H. and T. L. Schmidt. 2000. Composition, structure, and sustainability of hemlock ecosystems in eastern North America. Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America, Proceedings **267**:5-10.

Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology **63**:621-626.

Ollinger, S. V., J. D. Aber, P. B. Reich, and R. J. Freuder. 2002. Interactive effects of nitrogen deposition, tropospheric ozone, elevated CO2 and land use history on the carbon dynamics of northern hardwood forests. Global Change Biology **8**:545-562.

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**:60-73.

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.

Orwig, D. A., J. R. Thompson, N. A. Povak, M. Manner, D. Niebyl, D. R. Foster. 2012. A foundation tree at the precipice: *Tsuga canadensis* health after the arrival of

Adelges tsugae in central New England. Ecosphere 3:art10. http://dx.doi.org/10.1890/ES11-0277.1

Pacala, S. W., G. C. Hurtt, D. Baker, P. Peylin, R. A. Houghton, R. A. Birdsey, L. Heath, E. T. Sundquist, R. F. Stallard, P. Ciais, P. Moorcroft, J. P. Caspersen, E. Shevliakova, B. Moore, G. Kohlmaier, E. Holland, M. Gloor, M. E. Harmon, S. M. Fan, J. L. Sarmiento, C. L. Goodale, D. Schimel, and C. B. Field. 2001. Consistent land- and atmosphere-based US carbon sink estimates. Science **292**:2316-2320.

Paradis, A., J. Elkinton, K. Hayhoe, and J. Buonaccorsi. 2008. Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (Adelges tsugae) in eastern North America. Mitigation and Adaptation Strategies for Global Change **13**:541-554.

Park, B. R., R. D. Yanai, M. A. Vadeboncoeur, and S. P. Hamburg. 2007. Estimating root biomass in rocky soils using pits, cores, and allometric equations. Soil Science Society of America Journal **71**:206-213.

Pastor, J. and W. M. Post. 1993. Linear regeressions do not predict transient responses of eastern North-American forests to CO2 - induced climate change. Climatic Change **23**:111-119.

Peet, R. K. and N. L. Christensen. 1987. Competition and tree death. Bioscience **37**:586-595.

Peltzer, D.A., R.B. Allen, G.M. Lovett, D. Whitehead, D.A. Wardle. 2010. Effects of biological invasions on forest carbon sequestration. Global Change Biology **16**:732-746.

Phillips, C. L., N. Nickerson, D. Risk, and B. J. Bond. 2011. Interpreting diel hysteresis between soil respiration and temperature. Global Change Biology **17**:515-527.

Poland, T. M. and D. G. McCullough. 2006. Emerald ash borer: Invasion of the urban forest and the threat to North America's ash resource. Journal of Forestry **104**:118-124.

Reich, P. B., D. F. Grigal, J. D. Aber, and S. T. Gower. 1997. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. Ecology **78**:335-347.

Reynolds C. A. 1979. Soil survey of Middlesex County, Connecticut. USDA Soil Conservation Service, Storrs, CT.

RStudio. 2011. RStudio: Intergrated development environment for R (version 0.94.110) [Computer Software]. Boston, MA. Retrieved October 19, 2011.

Ryan, M. G., D. Binkley, J. H. Fownes, C. P. Giardina, and R. S. Senock. 2004. An experimental test of the causes of forest growth decline with stand age. Ecological Monographs **74**:393-414.

Savage, K., E. A. Davidson, A. D. Richardson, and D. Y. Hollinger. 2009. Three scales of temporal resolution from automated soil respiration measurements. Agricultural and Forest Meteorology **149**:2012-2021.

Savage., K. E. and E. A. Davidson. 2003. A comparison of manual and autmoated systems for soil CO_2 flux measurements: trade-offs between spatial and temporal resolution. Journal of Experimental Botany 54: 891-899.

Schimel, J. P. and M. N. Weintraub. 2003. The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. Soil Biology & Biochemistry **35**:549-563.

Schlesinger, W. H. 1997. Biogeochemistry: an analysis of global change. San Diego, Califonia: Academic Press.

Schultz, J. C. and I. T. Baldwin. 1982. Oak leaf quality declines in response to defoliation by gypsy-moth larvae. Science **217**:149-150.

Singh, J. S. and S. R. Gupta. 1977. Plant decomposition and oil respiration in terrestrial ecosystems. Botanical Review **43**:499-528.

Souto, D. R. and K. S. Shields. 2000. Overview of hemlock health. Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America, Proceedings **267**:76-80.

Sullivan, K. A. and A. M. Ellison. 2006. The seed bank of hemlock forests: implications for forest regeneration following hemlock decline. Journal of the Torrey Botanical Society **133**:393-402.

Talbot, J. M. and A. C. Finzi. 2008. Differential effects of sugar maple, red oak, and hemlock tannins on carbon and nitrogen cycling in temperate forest soils. Oecologia **155**:583-592.

Templer, P. H. 2005. Tree species effects on nitrogen cycling and retention: A synthesis of studies using (15)N tracers. Tree Species Effects on Soils: Implications for Global Change **55**:51-69.

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.

USDA. 2012. *Hemlock Woolly Adelgid Map – 2011.* USDA Forest Service GIS Group, Durnham, NH.

Valentini, R., G. Matteucci, A. J. Dolman, E. D. Schulze, C. Rebmann, E. J. Moors, A. Granier, P. Gross, N. O. Jensen, K. Pilegaard, A. Lindroth, A. Grelle, C. Bernhofer, T. Grunwald, M. Aubinet, R. Ceulemans, A. S. Kowalski, T. Vesala, U. Rannik, P. Berbigier, D. Loustau, J. Guomundsson, H. Thorgeirsson, A. Ibrom, K. Morgenstern, R. Clement, J. Moncrieff, L. Montagnani, S. Minerbi, and P. G. Jarvis. 2000. Respiration as the main determinant of carbon balance in European forests. Nature **404**:861-865.

vanBreemen, N., A. C. Finzi, and C. D. Canham. 1997. Canopy tree - soil interactions within temperate forests: effects of soil elemental composition and texture on species distributions. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **27**:1110-1116.

Vitousek, P. M. and R. W. Howarth. 1991. Nitrogen limiation on land and in the sea - how can it occur. Biogeochemistry **13**:87-115.

Weintraub, M. N., L. E. Scott-Denton, S. K. Schmidt, and R. K. Monson. 2007. The effects of tree rhizodeposition on soil exoenzyme activity, dissolved organic carbon, and nutrient availability in a subalpine forest ecosystem. Oecologia **154**:327-338.

Williamson, M. H. and A. Fitter. 1996. The characters of successful invaders. Biological Conservation **78**:163-170.

Young, R. F., K. S. Shields, and G. P. Berlyn. 1995. Hemlock woolly adelgid (Homoptera, Adelgidae) - style bunblde insertion and feeding sites. Annals of the Entomological Society of America **88**:827-835.

Zilahi-Balogh, G. M. G., L. T. Kok, and S. M. Salom. 2002. Host specificity of Laricobius nigrinus Fender (Coleoptera : Derodontidae), a potential biological control agent of the hemlock woolly adelgid, Adelges tsugae Annand (Homoptera : Adelgidae). Biological Control **24**:192-198.

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