2014

Modeling The Effects Of The Hemlock Woolly Adelgid On Carbon Storage In Northern New England Forests

Jeffrey John Krebs
University of Vermont

MODELING THE EFFECTS OF THE HEMLOCK WOOLLY ADELGID ON
CARBON STORAGE IN NORTHERN NEW ENGLAND FORESTS

A Thesis Presented

by

Jeffrey J. Krebs

to

The Faculty of the Graduate College

of

The University of Vermont

In Partial Fulfillment of the Requirements
For the Degree of Master of Science
Specializing in Natural Resources

October 2014

Accepted by the Faculty of the Graduate College, The University of Vermont, in partial fulfillment of the requirements for the degree of Master of Science, specializing in Natural Resources.

Thesis Examination Committee:

_____ Advisor
Jennifer A. Pontius, Ph.D.

_____ Advisor
Paul G. Schaberg, Ph.D.

_____ Chairperson
Timothy D. Perkins, Ph. D.

_____ Dean, Graduate College
Cynthia J. Forehand, Ph.D.

Date: June 17, 2014

ABSTRACT

The hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) is an invasive insect that threatens to eradicate native eastern hemlock (*Tsuga canadensis* (L.) Carr.) across the eastern United States. In southern New England and southern Appalachian forests, HWA-induced hemlock mortality has impacted carbon (C) flux by altering stand age, litter composition, species composition, and coarse woody debris levels. However, no one has examined how total C storage and sequestration may be impacted by these changes. Further, while projections are that HWA will ultimately infest hemlock across its entire geographic range, the majority of studies have been limited to southern New England and Appalachian forests where HWA infestation has been ongoing. To address these gaps, we examined how HWA might alter C dynamics in northern New England forests using the Forest Vegetation Simulator (FVS) and Forest Inventory Analysis (FIA) data to model C storage and successional pathways under three different scenarios: preemptive harvesting of hemlock, HWA-induced hemlock mortality, and a control mimicking natural stand development absent of disturbance. Our 150 year simulation showed that, while all treatments differed significantly in C storage in the short term, there was no significant difference in total C stocks between HWA infestation and presalvage treatments by the 75th year. Compared to the control, both simulated treatments resulted in a significant decrease in total C storage, with greater impacts on stands with higher hemlock densities. However, *net* C losses over the 150 year simulation were significantly higher for the presalvage scenario, indicating that allowing HWA infestation to progress naturally through a stand may result in the least impact to long-term C sequestration for the region's forests.

ACKNOWLEDGEMENTS

CHAPTER 1: TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: COMPREHENSIVE LITERATURE REVIEW

1.1 FOREST CARBON STORAGE AND CLIMATE CHANGE

1.1.1 Introduction

The first 9 months of 2012 were the warmest on record for the contiguous United

States (US) since record keeping began in 1895 (National Climatic Data Center). In the

last 100 years, a continual trend of increasing temperature has been observed globally and

linked to increasing concentrations of carbon dioxide (CO_2), methane (CH_4), and other

greenhouse gases (Figure 1.1) (Keeling et al. 2005, IPCC 2007). To combat global

warming, scientists have identified forest ecosystems as the largest terrestrial sink to

sequester and store atmospheric carbon dioxide (Brown 2002, Davis et al. 2002). In

2010, forests of the United States sequestered enough CO^2 to offset 13.5 % of national

greenhouse gas emissions (MacLean et al. 2014).

1.1.2 The Role of Forests in Carbon Sequestration

In the US, forests cover approximately 33% of the land area and store 71,000

megatonnes (Mt) of carbon (C) on 303 Mha of land (Heath et al. 2003). Regionally, total

C storage is highest in the Northeast and South Central regions (Turner et al. 1995).

From the years of 1952-1997, the forests of the conterminous U.S. have sequestered an

average of 155 Mt C/yr. The Northeast averaged the highest rate of sequestration at 47

Mt C year^{-1} followed by the North Central region at 39 Mt C year^{-1} (Heath et al. 2003).

Over that same time period, the C pool of Northeastern forest increased from 6,592 to

8,697 Mt (Figure 1.2), with the greatest amount stored in in soils (53.3%) and live trees

(32%) (Heath et al. 2003).

Factors such as natural disturbances, invasive pests, and harvesting can affect the

C storage in these pools by changing stand age, productivity, species composition, and

nutrient cycles (Smith et al. 2006, Turner et al. 1995). Natural disturbances can also

affect the successional trajectory and influence the species composition of a forest stand,

which also influences C storage potential and net ecosystem productivity (Figure 1.3).

1.1.3 Factors Affecting C Storage in Forests

A stand's age impacts the amount of C storage in live biomass and course woody

debris. Carbon storage in live biomass usually increases rapidly with stand establishment

and then increases slowly to a steady state dominated by gap dynamics at stand maturity

(Janisch and Harmon 2002, Bormann and Likens 1979, Whitaker et al. 1974).

However, disturbance intensity and frequency are the primary factors in changing

C fluxes. The C dynamics of eastern forests are currently being affected by invasive

pests and pathogens (Peltzer et al. 2010), with dramatic impacts on vigor, mortality rates,

and species composition. These changes alter nutrient cycling, decomposition rates,

primary productivity, heterotrophic respiration, litter quality, hydrology, age structure,

macro/microclimates, and litter quality of a forest stand (Lovett et al. 2006). Examples of

widespread disturbance agent with document impacts to carbon storage include the gypsy

moth (*Lymantria dispar*, L.) which was introduced to the United States in 1869. Gypsy

moth infestation was shown to reduce primary productivity, increases mortality, and produce frass that temporarily increases the nitrogen (N) and labile C of the soil in an infested stand (Lovett et al. 2006). Another example, beech bark disease (BBD), is a disease complex caused by an exotic scale insect (*Cryptoococcus fagisuga* Lindinger) and common fungus (*Neonectria faginata* Castlebury et al.). *Cryptoococcus fagisuga* was introduced into the United States in the 1930s. Because American beech (*Fagus grandifolia* Ehrh.) usually succumb to beech bark disease before they reach maturity, BBD causes a shift in age structure towards younger trees (Griffin et al. 2003) and also shifts species composition towards sugar maple (*Acer saccharum* Marsh.). Sugar maple litter decomposes at a faster rate than beech because of its lower lignin percentage, thus altering carbon storage and cycling (Finzi et al. 1998).

1.2 HEMLOCK, HEMLOCK WOOLLY ADELGID, AND CARBON STORAGE

1.2.1 Spread of Hemlock Woolly Adelgid in Eastern Forests

In the forests of the eastern United States, the hemlock woolly adelgid (HWA; *Adelges tsugae* Annand) is an invasive species that threatens to eradicate native hemlock (*Tsuga*) populations (Orwig et al. 2002). To date, HWA has increased mortality of eastern (*Tsuga canadensis* (L.) Carr.) and Carolina hemlock (*Tsuga caroliniana* Englem.) from mid New England to the southern Appalachian Mountains. The northern range of HWA has so far been limited to mid New England because temperatures below -25 ˚ C decimate the HWA population in winter (Skinner et al. 2003, Orwig et al. 2012). However, as global warming increases minimum winter temperatures, it is anticipated

3

that HWA will be able to extend its range into northern New England (Dukes et al 2010). Based on the rate and stochastic nature of HWA spread to new regions, it is predicted that HWA infestation will reach from Maine to northern Georgia between 2015 and 2024 (Albani et al. 2010). As this occurs, the hemlock population will decline and its niche in the forest could be occupied by other species (Orwig and Foster 1998, Orwig 2002).

1.2.2 Eastern Hemlock, Hemlock Woolly Adelgid, and Carbon Dynamics

As a species, eastern hemlock plays an important role in the C dynamics of forests because of several key characteristics: eastern hemlock are long-lived trees (a lifespan of up to a 988 years), have the potential to grow to over 150 feet in height, a diameter at breast height (DBH) of 6 feet, with a volume of 1,300 cubic feet (Blozan 2007, Blozan 2006, Ward et al. 2004, Thompson and Sorenson 2000). This creates the potential to store a substantial amount of C in biomass, leaf litter, and soil for long periods of time, unlike many of its co-occurring species (Finizi et al. 1998). When hemlock mortality occurs, large logs are produced with a slower decomposition rate due to the smaller surface area to volume ratio (Zell et al. 2009). Larger diameter logs also have higher heartwood to sapwood ratios, helping to further slow decay (Herrmann and Bauhus 2008, Mackensen et al. 2003).

The forest floor under hemlock trees store more C per meter than coexisting species of New England forests. Finizi et al. (1998) found that out of six species in Connecticut, hemlock stored the most C in soil and forest floor 10.8 ± 0.6 kg C/m^2,

4

followed by red oak (*Quercus rubra* L.) at 9.4 ± 0.4 kg C/m^2, red maple (*Acer rubrum* L.)

8.7 ± 0.5 kg C/m^2, beech 8.2 ± 0.5 kg C/m^2, or white ash (*Fraxinus Americana* L.) and

sugar maple at 8.1 ± 0.6 kg C/m^2 (Finzi et al. 1998). Leaf litter of species such as eastern

hemlock have a high lignin percentage and high C to N ratio (C:N), reducing

decomposition rates (Melillo et al 1989). Hemlock litter is also high in tannic acid,

which has been shown to slow decomposition by decreasing soil pH (White 1991, 1986).

In addition, eastern hemlock produces a greater amount of leaf litter than other species of

similar DBH (Finzi et al. 1998).

In addition to C storage, hemlock plays an important role in net ecosystem

productivity (NEP) and sequestering C from the atmosphere. When compared to

neighboring deciduous stands, hemlock stands were found to have a greater NEP and

annual C storage (Bardford et al. 2001, Hadley and Schedlbauer 2002). Hadley and

Schedlbauer (2002, 2008) attributed this to hemlock's evergreen nature, with higher C

sequestration rates in early spring and late fall (Figure 1.4). In contrast, deciduous trees

do not start sequestering C until after spring leaf-out, reaching a maximum in summer,

and emit C from the time of leaf abscission through the winter months (Figure 1.5).

Studies by Domec et al. (2013), Albani et al. (2010), Nuckolls et al. (2009),

Stadler et al. (2005), and Yorks et al. (2000) have analyzed the impact of HWA on the C

assimilation/sequestration, nutrient cycling, water use, species composition, and stand

structure of Eastern forests. To date, no one has analyzed the impact of HWA on C

storage in northern New England forests. In Connecticut and Massachusetts, Stadler et

al. (2005) concluded that infested stands have lower live biomass, slower growth rates,

increased dissolved organic C in through-fall, and a higher percentage of aboveground

biomass in wood. In addition, populations of epiphytic organisms (e.g., bacteria, yeast,

and filamentous fungi) thrived on medium and heavily infested trees. However, the foliar

C content did not differ between infestation levels, but did increase over the growing

season in all stands.

Domec et al. (2013) analyzed hemlock response to HWA infestation in regard to

water and C relations. The results of their study determined that leaf water potential,

carbon isotope ratios, plant hydraulic properties, and stomatal conductance were affected

by HWA infestation. Their data demonstrated that tree water use was reduced by greater

than 40% and gross primary was reduced by 25% due to formation of abnormal xylem

cells caused by HWA infestation (Domec et al. 2013).

Albani et al. (2010) used simulations in the Ecosystem Demography Model

(Moorcroft et al. 2001, Hurtt et al. 2002) to estimate the impact of HWA on net

ecosystem productivity of eastern forests from 1995-2100. During infestation and several

years after, NEP was reduced, but then started to rebound from infestation-induced

hemlock mortality, with a complete recovery of NEP by 2050. Their model predicted

that continued increases in NEP from 2040-2100 would result in a NEP 12% higher than

if infestation had never occurred.

In southern Appalachian forests, mortality from HWA infestation occurs at a

faster rate. Nuckolls et al. (2009) studied the short-term impact of HWA infestation on

the C cycle of forest stands in North Carolina by comparing HWA infested and girdled

trees. HWA infested trees declined at a slower rate in the first year when compared to

girdled trees, but by the third year of the study, HWA infested and girdled trees were

similar in decline when Basal Area Index (BAI), soil C efflux, litter fall, and very fine

root biomass were measured (Nuckolls et al. 2009). Another study of HWA impact on

Appalachian forests by Knoepp et al. (2011) also found increased C in the forest floor

and surface soil due to needle mortality and litterfall in recently HWA infested stands

(Knoepp et al., 2011).

Yorks et al. (2003) studied the impact of hemlock mortality from girdling on the

nutrient cycling of hemlock stands. The girdling of hemlock trees was used to mimic the

slow decline of hemlocks by HWA. They found that hemlock mortality greatly increased

N leaching (NO^{3-} and NH^{4+}) along with increased loss of important cations (e.g., Ca^{2+},

and Mg^{2+}). The accelerated N mineralization and nitrification rates, along with cation

loss, can have significant effects on stand productivity and local water quality (Yorks et

al 2003).

One of the latest studies on the effects of HWA on long-term carbon storage in

southern New England forests was conducted by Raymer et al. (2013). This study

compared storage in primary hemlock (~235 years), secondary hemlock (~135 years),

secondary black birch (~135 years), post HWA (~20 years post infestation), and girdled

(mimic HWA infestation) hemlock stands. From the results, total C storage was highest

in primary hemlock stands, but secondary black birch stands were statistically similar in

C storage. For live aboveground C, secondary black birch, primary hemlock, and

secondary hemlock stands stored the most C. When comparing primary and secondary

hemlock stands, primary hemlock stands store 20% more C than secondary hemlock stands. In addition, it was observed that girdled stands had the highest levels of CWD followed by post HWA stands. After HWA infestation, the transition of C from the aboveground live biomass pool to the CWD pool, along with new stem regeneration, buffered the overall impact of HWA on C stocks in a stand (Raymer et al. 2013)

1.2.3 Successional Dynamics of Hemlock-Dominated and Mixed Hemlock Stands

In southern New England and southern Appalachian forests, HWA impacts on C flux and (NEP) have been attributed to changes in stand successional stage, coarse woody debris accumulation, and changes in species composition. In southern New England, eastern hemlock has been primarily replaced by black birch (*Betula lenta* L.) followed by red maple and other oak (*Quercus*) species (Stadler et al. 2005). In southern Appalachian forests, it is primarily replaced by *Rhododendron* (Nuckolls et al. 2009). In northern New England and northern New York, both primary replacement species, black birch and rhododendron, are not prevalent in northern forest stands.

Following HWA-induced mortality, the successional dynamics of hemlock and mixed hemlock stands in northern New England will be greatly affected by the initial species composition and site conditions. If disturbance is high, it has been observed that early successional species such as pin cherry (*Prunus pensylvanica* L.f.), paper birch (*Betula papyrifera* Marsh.), white pine (*Pinus strobus* L.), and quaking aspen (*Populus tremuloides* Michx.) will become established, followed by shade tolerant species. If the

disturbance is small, the initial floristics and soil type of the site will have significant influence on the successional trajectory. In mixed deciduous forests, red maple, white pine, black cherry (*Prunus serotina* Ehrh.), sugar maple, ash (*Fraxinus*), and several oaks species will replace hemlocks (Brooks 2004). In northern deciduous forest types, sugar maple, yellow birch (*Betula alleghaniensis* Britton), and American beech are likely to supplant hemlock (Eschtruth et al. 2006).

The preemptive harvest of hemlock stands in anticipation of HWA infestation and hemlock mortality is a current trend that has been increasing throughout New England (Orwig and Foster 1998, Brooks 2004). Conducting preemptive cuts, or salvage harvests after hemlock mortality, lead to soil scarification, greater light availability, exposure of mineral soil, lower soil N, and a greater change in the microclimate of the stand, which promotes early successional species such as pin cherry, paper birch, aspen, and white pine. Stands with a higher percentage of hemlock also favor early successional species due to greater light availability following mortality. In mixed stands with a lower percentage of hemlock and a slower HWA-induced decline, stand progression will mimic gap formation where mid to late successional species have a greater chance of becoming established (Stadler et al. 2005).

The gap size created from hemlock mortality will also affect the successional trajectory of stands affected by HWA. In smaller gaps, regrowth includes both gap colonization and the release of advanced regeneration, but ingrowth of saplings from advanced regeneration dominate the upper stratum of the canopy. In gaps less than 100 m^2, midtolerant tree species such as yellow birch are absent while shade tolerant species

such as hemlock and sugar maple dominate (Webster and Lorimer 2005). This scenario

is most likely played out in mixed hemlock stands as HWA-induced mortality opens

small gaps within the mixed canopy. However, in medium (100-250 m^2) and larger gaps,

yellow birch made up 40% and 75% of the upper stratum of the canopy respectively.

This scenario is more likely in stands dominated by hemlock, with little to no advanced

regeneration (Tubbs 1996, Goerlich and Nyland 2000, Webster and Lorimer 2005).

1.3 FOREST DATA AND MODELING

1.3.1 Forest Inventory Analysis Data

Forest Inventory Analysis (FIA) is a national program started in the 1930s by the

U.S Forest Service that provides data on forests in the United States. The FIA program

collects data on forest area and location, species dynamics, tree growth, mortality,

harvested biomass, soil characteristics, and forest ownership. The data can then be used

to help assess forest health, recommend harvesting intensity, wildlife habitat

management, marketable lumber/timber trade, and C storage. The FIA survey has

changed from a periodic survey to an annual survey conducted by U.S. Forest Service

employees, state employees, or contractors. In the eastern U.S., 15% of forest plots are

surveyed annually. In the western U.S., only 10% of forest plots are surveyed annually

because of the cost and difficulty of accessing some locations. The data is then compiled

and can be downloaded via the Internet from the FIA DataMart. FIA Data Mart is a web-

based program where raw inventory data can be downloaded in Microsoft Access

databases per state and used to forecast future forest growth. FIA data is often used to

predict future forest conditions using simulation models and different management and disturbance scenarios (USDA Forest Service 2005).

1.3.2 Forest Vegetation Simulator and Carbon Accounting

The Forest Vegetation Simulator (FVS) is a distance independent, individual tree forest growth model that has been in existence for over 30 years. It is used to predict tree growth and successional dynamics of forest stands in U.S. and part of British Columbia, Canada. Specific variants are used for each region to help mimic stand conditions. FVS supports management decisions for alternative silvicultural prescriptions by simulating stand growth, biomass accumulation, and successional trajectories. Individual tree growth is calculated in FVS using allometric equations. For large trees, diameter growth is first calculated and then height growth is based on the increase of diameter. For small trees, increased height is calculated before diameter growth. Disturbances can be modeled using event monitor files for insects, pathogens, and fire. Mortality predictions are based on typical mortality rates for undisturbed stands and are density dependent. Mortality rates from fire, insects, and pathogens are built into the event monitor subroutines for the specific disturbance type. In the Northeast variant of FVS, seedling regeneration is defined by the user in regard to predict stand species, density, and size of new trees because it is not incorporated in the variant. For some western variants, seedling and ingrowth regeneration methods are incorporated and new regeneration will be calculated on initial stand data from FIA files or entered directly into the interface. The software simulates stand characteristics at a temporal scale, runs at a 5-10 year

11

resolution, and can run simulations up to several hundred years (Crookston and Dixon 2005).

With the advent of the Kyoto Protocol, creation of C credit exchange programs, and greater awareness of climate change caused by CO_2 emissions, the importance and necessity of quantifying C stocks in the U. S. forests has grown drastically. The need for a tool that can quickly assess C stores in forest stands, predict different treatment outcomes, and is accessible to forest managers has been identified as critical in order to manage stands for carbon mitigation (Russell-Roy et al. 2014). The Forest Vegetation Simulator (FVS) meets these requirements, has methodologies and computations consistent with Intergovernmental Panel on Climate Change and U.S. standards on C accounting rules and guidelines, and has the ability to use preexisting forest inventory data. The built in carbon reporting and silvicultural features of FVS allow forest managers to build different treatment scenarios and calculate predicted C stores for forest stands from several to hundreds of years out. The use and popularity of FVS has grown to predict carbon stores over the past several years. Two main reports can be generated from FVS: the Stand Carbon Report and the Harvested Carbon Report. The Stand Carbon Report includes all major C pools (Total Above, Ground Live, Merchantable Aboveground Live, Belowground Live, Belowground Dead, Down Dead Wood, Forest Floor, and Herbs and Shrubs). For the Stand Carbon Report, biomass is assumed to be 50% C for all pools, except the forest floor which is estimated at 37% C (Hoover and Rebain 2011, Hoover and Rebain 2008). The Harvested Carbon Report accounts for all biomass (50% C) harvested from the stand and tracks its transition to emissions. FVS

12

also calculates for slash and other biomass left on site that transitions to the Down Deal Wood pool after harvest (Hoover and Rebain 2011, Hoover and Rebain 2008).

An on-going experiment to test the C accounting and inventory capabilities of FVS is being conducted at the Kane Experimental Forest (KEF) in northwestern Pennsylvania. The KEF is an Allegheny hardwood (cherry-maple) forest that is approximately 1,700 acres and was initially surveyed in 1932. In 2006, 153 plots 1/10th of an acre were tallied and inventoried. This data was easily converted into FVS-ready files and run in FVS. All C pools were inventoried using FVS for stands (Table 1.2). FVS was able to quickly provide an inventory for all main C pools and total forest C storage for a 25 year simulation in very little time (Figure 1.2). Without FVS computational capabilities and C reporting, producing current C estimates would have taken weeks using other calculation methods (Hoover and Rebain 2008).

Through the Hemlock Woolly Adelgid Event Monitor, FVS also has the capability of modeling the effects of HWA on forest stands with populations of eastern and Carolina hemlocks. The Hemlock Woolly Adelgid Event Monitor is a program that simulates the effects of HWA infestation on forest stands and allows forest management professionals and land owners to simulate long-term effects of HWA infestation and management actions on C storage, timber yields, wildlife habitat, and successional dynamics. The HWA infestation date is entered by the FVS user and infestation intensity is determined using a probability distribution (Evans and Gregoire 2007, Souto et. al 1996, McClure 1991). Due to the fact that stands cannot become uninfested, the overall probability for post infestation intensity is 100%. After initial infestation, HWA

13

populations usually spike as healthy trees are able to support a large population of adelgids. But as tree health declines, HWA populations are limited by forage available to them. This allows trees to recover slightly. Hemlock health and HWA population density may fluctuate in this way for several years. However, it is anticipated that eventually complete hemlock population mortality will occur in all infested stands. To mimic this fluctuating response, the FVS HWA event monitor quantifies the intensity of infestation and mortality after infestation stochastically depending upon the variant used, North East (NE) or Southern (SN) (Table 1.4). All hemlock mortality is calculated at the end of an FVS cycle and compiled in FVS reports (FHTET 2008).

As anthropogenic emissions continue to increase the concentration of CO_2 and other greenhouse gases in our atmosphere, it is critical to find and properly manage long-term C sinks that absorb C from our atmosphere and store it in a solid form for many decades to hundreds of years. Forests have been identified as the greatest C sink of all terrestrial biomes, but invasive species jeopardize and change the dynamics of forest C sequestration and storage. As HWA continues to spread throughout the forest of the eastern U.S., it threatens to eradicate the eastern hemlock, which is a long-lived species that assists forests in sequestering C for long-term storage. If this occurs, I predict that the C sink of northern New England forest stands that have not yet been impacted by HWA infestation will be reduced for several decades after infestation, and then will slowly rebound as other species replace hemlock within eastern forests. Knowing how HWA will impact the C pools of forests in the eastern U.S. will allow us to create more

14

effective forest management plans and strategies to help in C sequestration and management.

1.4 TABLES

Table 1.1. Carbon stocks on the Kane Experimental Forest in 2006 (Hoover and Rebain 2008).

Pool	Tons C/acre	Tons C forest-wide
Live tree [a]	60.2	42,147
Dead tree [b]	5.8	4,059
Down dead wood	2.2	1,561
Forest floor	6.2	4,371
Total	74.5	52,137

[a] All live biomass including coarse roots.
[b] All dead biomass including coarse roots and standing dead trees.

Table 1.2. Projected carbon stocks on the Kane Experimental Forest. This simulation was for testing purposes; the model was not calibrated to site conditions (Hoover and Rebain 2008).

Year	Growth only (tons C/acre)	With management (tons C/acre)
2006	75	73
2011	81	77
2016	87	81
2021	94	85
2026	99	88
2031	104	91

Table 1.3. Probabilitydistributions of HWA infestation intensity after infestation (North East variant). Infestation intensity was assigned in the FVS based on the probabilities listed below from the HWA event monitor addfile. Outbreak values are numeric codes assigned to the infestation intensity within simulation files (FHTET 2008).

Value	Outbreak	Probability*
No Infestation	0	
Low Infestation	1	40%
Moderate Infestation	2	30%
High Infestation	3	20%
Catastrophic Infestation	4	10%
*Probability of infestation in a given year is determined by the user-set year of infestation. After infestation, the probability of the intensity is determined by the above values.		

Table 1.4. Percent of hemlock loss (mortality) at different HWA infestation intensities (North East variant). Hemlock loss was assigned based on the infestation intensity in the HWA event monitor addfile. Outbreak values are numeric codes assigned to the infestation intensity within simulation files (FHTET 2008).

Value	Outbreak	Loss of Hemlock (Mortality)
No Infestation	0	
Low Infestation	1	0-5%
Moderate Infestation	2	5-30%
High Infestation	3	30-70%
Catastrophic Infestation	4	70-90%

1.5 FIGURES
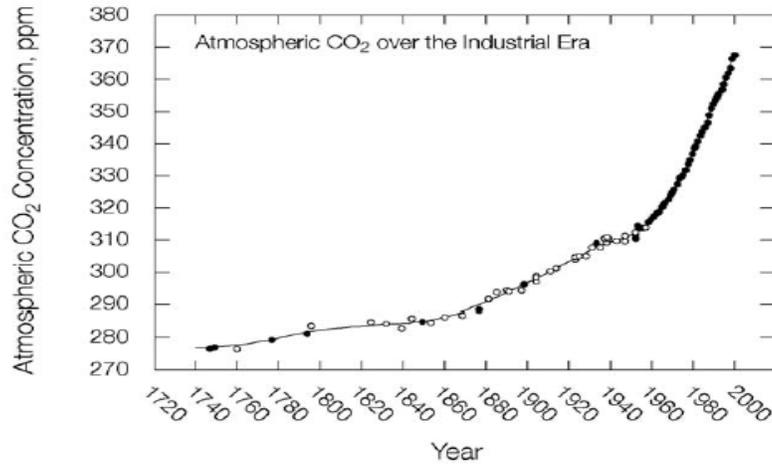
Figure 1.1. Time trend in the concentration of atmospheric CO2, in ppm, from 1740 to 2000. Data before 1957 are proxies from measurements in air extracted from ice cores at Law Dome, Antarctica (open circles, Francey et al., 1995; closed circles, Etheridge et al., 1996). Data from 1957 to 1978 are averages of measurements from the South Pole and Mauna Loa Observatory. Data from 1978 on are averages of direct measurements of air collected from 6 to 9 locations (closed circles). (Keeling et al. 2005).

Region	C pool (Mt) or C flux (Mt/yr)	1953	1963	1977	1987	1997
				Year		
Northeast	Soil	4,289	4,509	4,685	4,675	4,637
	Forest floor	611	637	710	705	688
	Dead wood	268	324	423	479	527
	Understory	32	39	50	56	62
	Live trees	1,392	1,690	2,203	2,515	2,784
	TOTAL STORAGE	6,592	7,199	8,071	8,428	8,697
	Annual Dead Flux		30	25	4	-1
	Annual Live Flux		30	37	32	28
	TOTAL FLUX		61	62	36	27
	Area (Thou. ha)	30,984	33,019	34,119	34,513	34,595

Figure 1.2. Summary of Historical and Current Estimates of Carbon Storage (Mt C) and Flux (Mt C/yr) for the Northeast by Ecosystem Component, Conterminous U.S. Forestland, 1952-1997 (Heath et al. 2003).

21
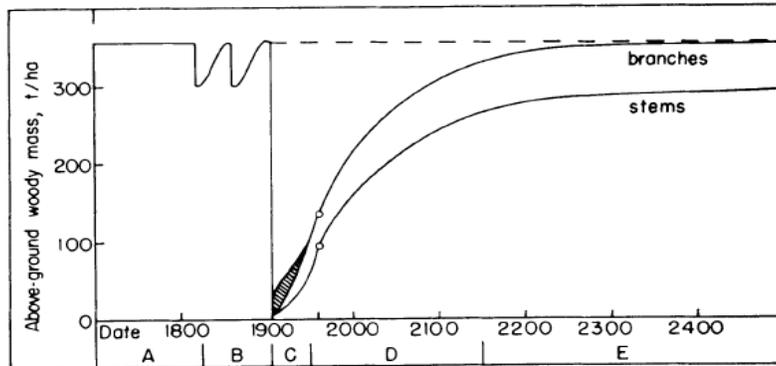
Figure 1.3. An interpretation of biomass history for the Hubbard Brook forest. (A) presumed woody (stem + branch) climax biomass before European settlement, (B) opening of canopy by selective cutting in the 19th century, (C) logging of the watershed, 1909-17, followed by exponential regrowth of forest biomass (the cross- hatched area represents successional Prunus pensylvanica), (D) slower relative growth in biomass after 1950, when productivity reached climax levels, (E) asymptotic approach to the assumed climax level (Whitaker et al. 1974).

22
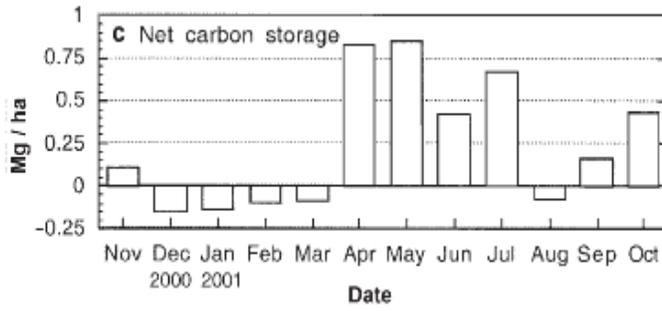
Figure 1.4. Net carbon storage of eastern hemlock
forests (Hadley and Schedlbauer, 2002).
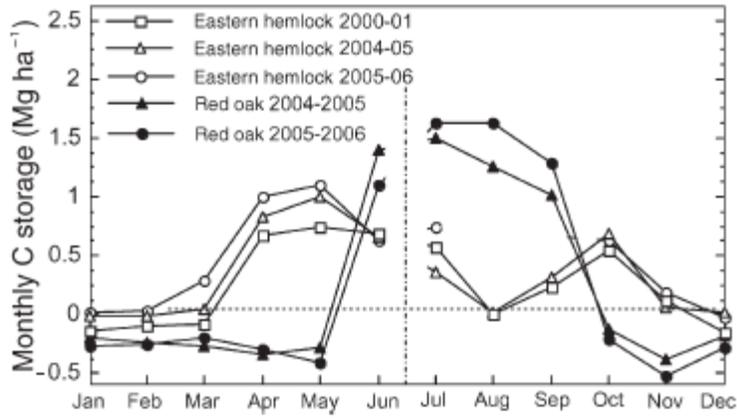
Figure 1.5. Estimated monthly net carbon (C) storage by the red oak (Quercus rubra) and eastern hemlock (Tsuga canadensis) forests (Hadley et al. 2008).

CHAPTER 2: MODELING THE EFFECTS OF THE HEMLOCK WOOLLY ADELGID ON CARBON STORAGE IN NORTHERN NEW ENGLAND FORESTS

2.1 ABSTRACT

The hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) is an invasive insect that threatens to eradicate eastern hemlock (*Tsuga canadensis* (L.) Carr.) across the eastern United States. In southern New England and southern Appalachian forests, HWA-induced hemlock mortality has impacted carbon (C) flux by altering stand age, litter composition, species composition, and coarse woody debris levels in infested stands. However, no one has examined how total C storage and sequestration have been impacted by these changes. Further, while projections are that HWA will ultimately infest hemlock across its entire geographic range, the majority of studies have been limited to southern New England and Appalachian forests where HWA infestation is ongoing. To address these gaps, we examined how HWA might alter C dynamics in northern New England forests over the next 150 years using the Forest Vegetation Simulator (FVS) and Forest Inventory Analysis (FIA) data to model C storage and successional pathways under three different scenarios: preemptive harvesting of hemlock, HWA-induced hemlock mortality, and a control mimicking natural stand development absent disturbance. Our 150 year simulation showed that, while all treatments differed significantly in C storage in the short term, there was no significant difference between HWA infestation and presalvage treatments by the 75th year. Compared to the control both simulated treatments resulted in a significant decrease in total C storage, with greater impacts on stands with higher hemlock densities.   However, *net* C losses over

150 years were significantly higher for the presalvage scenario, indicating that allowing

HWA infestation to progress naturally through a stand may result in the least impact to

long-term C sequestration for the region's forests.

2.2 INTRODUCTION

Over the last 100 years, a continual trend of increasing temperature has been

observed globally and linked to increasing concentrations of carbon dioxide (CO_2),

methane (CH_4), and other greenhouse gases (Keeling et al. 2005, IPCC 2007). Scientists

have identified forest ecosystems as the largest terrestrial sink to sequester and store

atmospheric CO_2, with a prominent role in mitigating greenhouse gas emissions (Brown

2002, Davis et al. 2002). In the United States (US) alone, forests store 71,000

megatonnes (Mt) of carbon (C) on 303 Mha of land (Heath et al. 2003), sequestering an

average of 155 Mt C year^{-1}. In the US, the Northeast averaged the highest rate of

sequestration at 47 Mt C per year (Heath et al. 2003).

As a species, eastern hemlock (*Tsuga canadensis* (L.) Carr.) plays an important

role in the C dynamics of northern forests because of several key characteristics: they are

long lived (a lifespan of up to a 1,000 years), grow to a large size (~ 45 meters tall and

diameter at breast height (DBH) of up to 1.8 meters), and reach a potential volume of up

to 396 cubic meters (Blozan 2007, Blozan 2006, Thompson and Sorenson 2000). This

enables hemlock to store a substantial amount of C in biomass, leaf litter, and associated

soils for long periods of time, unlike many co-occurring species (Finizi et al. 1998).

Upon mortality, hemlock logs demonstrate a relatively slow decomposition rate due to

26

the smaller surface area to volume ratio and higher heartwood to sapwood ratio (Zell et al. 2009; Herrmann and Bauhus 2008, Mackensen et al. 2003). When compared to neighboring deciduous stands, hemlock stands were also found to have a greater NEP and annual C storage, due to continued sequestration in early spring and late fall and almost zero net C emission in the winter months (Bardford et al. 2001, Hadley and Schedlbauer 2002, 2008). In combination, these traits enable hemlock stands to both sequester and store more carbon on average than stands dominated by other common species (Hadley and Schedlbauer 2008).

Since the 1980's the invasive hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) has spread from the southern Appalachians through southern New England, with widespread hemlock mortality that has impacted C flux by altering stand age, litter composition, species composition, nutrient cycling, and coarse woody debris (CWD) levels (Orwig and Foster 1998, Foster 2002, Stadler et al. 2005, Nuckolls et al. 2008, Albani et al. 2010). Conducting preemptive cuts, or salvage harvests after hemlock mortality, has become a common management tool in many hemlock stands (Kizlinski et al. 2002, Foster and Orwig 2006, Albani et al. 2010). These harvests are thought to encourage rapid regeneration and establishment of early successional replacement species through soil scarification and increased light availability. However, it is unclear if such activities offset C lost by the removal of hemlock and increased decomposition rates of organic matter from residual hardwood species. Initial work indicates that salvage logging has a more profound impact on ecosystem processes than HWA mortality itself. In mixed stands where HWA decline is gradual, stand progression is documented to

mimic gap formation where mid to late successional species are actively established in gaps induced by hemlock mortality (Stadler et al. 2005). This shift in species composition could also alter subsequent C relations.

Considering the role that hemlock plays in C storage and sequestration, it is critical that we understand how invasive species like HWA will affect C storage capacity and how preemptive and salvage operations function to alter C stocks over the long term (Davis et al. 2002). The goal of this research was to determine how the potential invasion of HWA and preemptive cutting/salvage harvests could impact the C storage of hemlock stands in northern New England and New York. By using initial C pool measurements from Forest Inventory and Analysis (FIA) data, and a HWA event monitor program in the Forest Vegetation Simulator (FVS), our goal was to model forest C storage over the next 150 years comparing the following HWA scenarios across plots with a wide range of hemlock densities:

i. No HWA-induced mortality (control)

ii. HWA-induced hemlock mortality simulated by the HWA Event Monitor

iii. Preemptive salvage logging of all hemlock greater than 10 inches DBH

2.3 METHODS

2.3.1 Data Collection

The study area (Figure 2.) is limited to northern New England and New York (defined by latitudes greater than 43° N and less than 47°28' W) in order to better understand hemlock stand dynamics at the lesser studied northern limits of its geographic range in the US. Forest Inventory Analysis (FIA) data was downloaded from FIA DataMart for the states of Maine, New Hampshire, New York, and Vermont for all plots designated with the FIA forest type of eastern hemlock (105), with the following additional stand criteria to minimize differential impacts of land use history and maximize representation of typical hemlock stands in the region: stand age greater than 70 years, site productivity between 1 and 3, slope less than 45, elevation less than 2,000 feet, and inventory years of 2009 - 2011. Queries were run in Microsoft Access to determine the percent hemlock basal area of each stand (Table 2.1). Our stands averaged 95 years in age, ranged from 70 to 215 years in age, had an average hemlock basal area of 45%, mean of 23 C metric tons hectare^{-1} for total C storage in 2010, and mean of 15 C metric tons hectare^{-1} for above live C storage in 2010.

FIA inventory data was converted to FVS format using the FIA2FVS program and the initial common start year of 2010. Stand data included location, age, aspect, slope, elevation, forest type, and year inventoried. Individual tree data imported into FVS included species, DBH, tree location slope, and tree location aspect.

2.3.2 Carbon Simulation Models

In order to understand how stand structure and C storage may change as HWA moves into northern New England, stand development and C pools for each plot was independently simulated over a 150 year span (2015-2165) using the FVS model for the following scenarios: No HWA Infestation (control), HWA Infestation, and Preemptive Harvesting. The FVS North East variant was selected to calibrate the simulation because parameters specific to the northeastern region are available, with proven application in modeling both even and uneven aged stands for a wide range of carbon assessments across the region (Gunn 2014, Mika and Keeton 2014, Russell-Roy et al. 2014, Nunnery and Keeton 2010). In addition, FVS includes estimates for individual tree growth and mortality, is freely available to the general public and compatible with FIA data used to initiate simulations.

It is worth noting that carbon stored in forest products under the presalvage scenario are not included in our C accounting because hemlock in the region is primarily used for pulp to produce paper and mulch for landscaping (Ward et al. 2004, Godman and Lancaster 1990). These products are considered to be short C life-span products (Watson et al. 2000) and would therefore not contribute substantially to carbon storage in product form.

The study area (Figure 2.) is limited to northern New England and New York (defined by latitudes greater than 43° N and less than 47°28' W) in order to better understand hemlock stand dynamics at the lesser studied northern limits of its geographic range in the US. Forest Inventory Analysis (FIA) data was downloaded from FIA

DataMart (http://apps.fs.fed.us/fiadb-downloads/datamart.html) for the states of Maine, New Hampshire, New York, and Vermont for all plots designated with the FIA forest type of Eastern Hemlock (105), with the following additional stand criteria to minimize differential impacts of land use history and maximize representation of typical hemlock stands in the region: stand age greater than 70 years, site productivity between 1 and 3, slope less than 45, and elevation less than 2,000 feet. In addition, plots were only utilized if inventories had been conducted more recently than 2009 in order to ensure that initial stand condition were current for simulation starting in 2015. This resulted in 78 plots across the region with equal representation from each of the four states in the study area and from low, medium and high hemlock density stands (Table 2.1). In addition, queries were run in Microsoft Access to quantify the percent hemlock basal area of each stand in order to test the impact of hemlock density on carbon dynamics (Table 2.1). On average, these stands contained 45 percent hemlock basal area, 95 years in age (range of 70 to 215 years), mean basal area of 19.4 m^2 hectare^{-1}, and total stand C of 61 C metric tons hectare^{-1}. The most common species in addition to hemlock included red maple, American beech, white pine, sugar maple, and yellow birch.

FIA inventory data was converted to FVS format using the FIA2FVS program and the initial common start year of 2010. Stand data included location, age, aspect, slope, elevation, forest type, and year inventoried. Individual tree data imported into FVS included species, DBH, tree location slope, and tree location aspect. FVS simulates carbon storage for nine pools including: total, above ground live, aboveground merchantable, belowground live, belowground dead, standing dead, down dead wood,

forest floor, and shrub. It reports C storage amounts for each pool at user defined

temporal increments. For our simulation, we used five-year increments from 2015 to

2165. In order to understand the natural variability across stands, the simulations were

run independently on all 78 plots.

The FVS carbon simulation mimics natural stand development, including

succession, regeneration, and C dynamics, tracking the natural gap dynamics and

successional sequence of the stands based on the FVS North East variant parameters.

Because the North East variant does not incorporate regeneration subroutines following

disturbance or ingrowth except for seedling regeneration, we built a regeneration file to

model seedling regeneration throughout the simulation based on region-specific

regeneration datasets from Leak 1997 and Brooks 2004, including data sets to match

expected regeneration for each of the three treatments (Table 2.2). Leak's and Brooks'

data regeneration values were averaged together and modified from 3, 4, 5, and 9 years to

a 10 year regeneration span to match our regeneration cycle in FVS.

Conducting preemptive cuts, or salvage harvests after hemlock mortality, has

become a common management tool in many hemlock stands. These harvests are

thought to encourage rapid regeneration and establishment of early successional

replacement species through soil scarification and increased light availability. However,

it is unclear if such activities offset C lost by the removal of hemlock and increased

decomposition rates of organic matter from residual hardwood species. Initial work

indicates that salvage logging has a more profound impact on ecosystem processes than

HWA mortality itself. In mixed stands where HWA decline is gradual, stand progression

is documented to mimic gap formation where mid to late successional species are actively established in gaps induced by hemlock mortality (Stadler et al. 2005). This shift in species composition could also alter subsequent C relations. This regeneration file is initiated in 2030 with continued ingrowth on a ten-year cycle until the end of our simulation. To better isolate the impact of HWA and presalvage treatments, we also assumed the following: 1) no major disturbance other than the HWA infestation and harvest scenarios, 2) a constant climate, and 3) stable soil storage during the simulation run (Nunnery and Keeton 2010).

While these parameters served as the base "control" for the three scenarios tested, the Hemlock Woolly Adelgid Event Monitor (North East variant) was required to adjust parameters to simulate HWA infestation (FHTET 2008). This variant defines outbreak occurrence and stochastic population cycles of HWA based on the empirical research of McClure (1991), where HWA populations cycle between low and high infestation densities in response to the typical decline/recovery cycle that precedes hemlock mortality (FHTET 2008). This includes dynamic probabilities for infestation density in the first year (Table 2.3), followed by cycles of high and low infestation rates corresponding to documented declines and recoveries (McClure 1991). Probabilities of tree mortality and reduced growth were determined stochastically from a probability distribution based on the North East variant (Table 2.4) (FHTET 2008). Because the data used as the basis to determine mortality rates and population cycles was based on infestation in southern New England, it is possible that mortality rates for our study area are over estimated (Trotter and Shields 2009, Paradis et al. 2008, Skinner et al. 2003).

However, since mortality rates have not been established for our more northerly study area it is possible that this variant overestimates the rate of hemlock mortality due to HWA. We selected 2025 as the initial infestation date based on the predicted rate of spread to the northeastern region (Albani et al. 2010). Using this 2025 date also allowed for a baseline of C storage to be apparent before treatment impacts set in.

Preemptive salvage of hemlock stands was modeled in FVS using the management operation of mechanical thinning concurrent with the initial HWA infestation date (2025). This option in FVS assumes that all hemlock trees over 25.4 cm DBH are cut and only merchantable hemlock biomass is removed from the site. Slash management was simulated using the basic: manage logging slash function with nonmerchantable material left on site in the Management Actions of FVS (Dixon 2002).

2.3.3 Data Analysis

Carbon storage for total stand, Above Ground Live (AGL), Standing Dead (SD), Down Dead Wood (DDW), Below Ground Live (BGL), Below Ground Dead (BGD) and Forest Floor (FF) C pools were compared across the full simulation for the three scenarios using a repeated measures ANOVA. This allowed for simultaneous comparison of C storage across the three scenarios and temporal trends. In addition, we modeled the interaction between hemlock stand density and treatment on total C and net C gain/loss at the end of the 150 year simulation using a factorial ANOVA. To fully capture treatment effects on the various C pools, analyses were repeated for each C pool

at key intervals (10, 20, 30, 40, 50, 60, 70, 80, 90, and 150 years) based on intervals of maximum difference and convergence among treatment scenarios.

2.4 RESULTS AND DISCUSSION

2.4.1 Total C

Our results over the full 150 year simulation indicate that while total C increased significantly for all treatments ($p < 0.0001$), C storage is maximized on control stands ($p < 0.0002$) with high hemlock density ($p < 0.0001$). By the end of the simulation, the mean C gained was significantly higher for the control treatment (18.70 C metric ton hectare^{-1}), than for either the presalvage or HWA treatments (13.51 C metric ton hectare^{-1} and 12.74 C metric ton hectare^{-1}) respectively. For total C stored at the end of the simulation, there was no significant difference between HWA infestation (37.14 C metric tons hectare^{-1}) and presalvage (37.20 C metric tons hectare^{-1}) treatments, although both were significantly lower than the control (42.60 C metric tons hectare^{-1}) (Figure 2.3).

Across the Northeast, it is estimated that forest stands store 8,697 Mt C (Heath et al. 2003). Using this estimate, our simulation indicates that HWA induced mortality across this region could amount to a loss of 1,114 Mt of C after 150 years, a 12.8 percent reduction in total potential C stored for the region.

Similar to HWA losses, presalvage harvesting would amount to a net loss of 1,102 Mt of C, a 12.7 percent reduction. However, because the presalvage treatment only removed hemlock greater than 25.4 cm DBH, and allowed for continued growth of

smaller hemlock over the 150 year simulation, this is likely an overestimation of how

carbon would respond in a stand that was simultaneously experiences HWA induced

mortality of the remaining hemlock stock. In sum, this indicates that while differences

between HWA and presalvage simulations were indistinguishable by the end of the

simulation, it is possible that this may not be the case. Overestimation of HWA induces

mortality and under estimation of presalvage minus simultaneous HWA induced

mortality that would be likely may drive these scenarios farther apart.

While these results suggest significant reductions in C storage compared to

undisturbed, mature hemlock stands, HWA and presalvage simulated stands were still

estimated to store C at levels comparable to many other forest types in the region (e.g.,

Maple-Beech-Birch 95.60 C metric tons hectare^{-1}, Aspen-Birch 113.44 C metric tons

hectare^{-1}, and Oak-Hickory 66.30 C metric tons hectare^{-1} (Birdsey et al. 1992). This is

likely due to the rapid and dense regeneration of pine and hardwood species in gaps

created by hemlock mortality over the 150 years.

Our results are similar to other studies investigating the impacts of HWA

infestation on stand biomass, net primary productivity, and net ecosystem productivity.

Albani et al. (2010) predicted a -0.10 t C ha^{-1} yr. $^{-1}$ (-12.8%) reduction in C uptake across

the eastern US between 2020-2029 due to HWA infestation using the Ecosystem

Demography Model (Moorcroft et al. 2001, Hurtt et al. 2002). However, between 2090-

2099 Albani et al. predict an increase of 18.9% in C uptake for the region following

HWA infestation. This highlights the inherent differences between productivity and

storage in modeling carbon dynamics. While Albani (2010) found that hemlock

replacement species allow ecosystem productivity to recover over time, we show that impacts to total stand carbon storage are still impacted long-term. This is important considering that carbon storage is a key metric for access to carbon markets and an important metric when quantifying the contribution of forests to mitigate global warming (Luyssaert et al. 2008, Harmon and Franklin 1990). Our results indicate that for long-term C storage undisturbed, late successional hemlock stands are optimal.

A field study by Raymer, Orwig, and Finzi (2013) compared the C stocks of undisturbed primary hemlock, girdled, HWA infested and post-HWA birch stands in southern New England. They found that ecosystem C storage is resilient to the loss of hemlock following HWA infestation, with minimal differences between forest types. While hemlock mortality resulted in large shifts in C pools from the above live ground pool to the woody debris pool, overall stand C storage was deemed resilient to the loss of hemlock thanks to vigorous regrowth of black birch and the buffering of the woody debris pool. Similar to our findings, this indicates that management activities such as salvage logging that remove hemlock eliminate potential storage in woody debris pools and may result in more C loss than HWA induced mortality.

While analyses of C storage at the end of the simulation offers a useful marker to assess potential HWA impact, perhaps more meaningful is the net loss of C over the full 150 year simulation, incorporating both losses from treatments and gains from regeneration and continued growth of replacement species following disturbance. A net sum of total C flux over the full simulation indicates that the presalvage treatment loses significantly more C (-6.74 C metric tons hectare^{-1}) than HWA-induced mortality (-2.19

C metric tons hectare^{-1}), while the control gains significantly more C than both (22.81 C metric tons hectare^{-1}). It is possible that these differences between HWA, presalvage and control scenarios are even greater due to coexisting species often being harvested when a presalvage harvest occurs and hemlock mortality from HWA occurring at a slower rate in more northern latitudes and favorable site conditions (Albani et al. 2010, Raymer et al. 2013).

In addition to the significant increase in net C for the control, and decrease for both the HWA and presalvage treatments, there were significant interactions between treatments and percent hemlock (p = 0.0040), with more extreme differences among treatments as hemlock density increased. In stands with greater than 60 percent hemlock basal area, as is common in many stands across the region, net losses of total C from a stand compared to the control could surpass 2.79 C metric tons hectare^{-1} (7.6%) for HWA infestation and 5.67 C metric tons hectare^{-1} (15.5%) for the presalvage treatment at the end of the 150 year simulation. In stands with lower hemlock density (< 20% hemlock basal area), the impact of HWA infestation and presalvage treatment was only 2.29 C metric tons hectare^{-1} (5.37%) and 1.66 C metric tons hectare^{-1} (3.90%), respectively.

A closer examination of C storage throughout the course of the simulation highlights how the impact of HWA-induced mortality or presalvage treatment varies depending on the duration of the simulation (Figure 2.3). For the first ten years following simulated infestation, HWA treatments had higher C stocks than both control and presalvage. This is likely the result of ingrowth and regeneration in the understory that follows HWA induced canopy thinning and increased light availability. The C in the

down dead wood and standing dead wood pools (Figure 2.4) also act to buffer the loss of live hemlock biomass while new regeneration takes hold. It isn't until 30 years post infestation that HWA-induced mortality and natural thinning depressed total C significantly below the control. Conversely, presalvage significantly reduced total C short term, but regained levels similar to both HWA and control treatments 20 years after harvesting. This has implications for forest managers, indicating that their choice of management approach may be dependent upon the time frame for management considerations. If maximizing C storage over the short term (25-50 years) is important, these results suggest that letting HWA run its course is preferable to presalvage harvesting activities. However, if one is managing for long-term C storage, but would like short-term profit, the difference between presalvage and HWA infestation is negated after approximately 75 years. Note that this is in terms of total carbon stored, and not net carbon sequestered as discussed above. While there may be no difference between HWA and presalvage treatments in terms of total carbon stored at the end of the 150 year simulation, many land managers may be more interested in the net gain of C over time, which is significantly greater when letting HWA run its course as opposed to preemptive or salvage operations in HWA infested stands.

2.4.2 Specific C Pools

Above Ground Live (AGL) An examination of the individual C pools (Figure 2.4) identifies how changes in C storage play out in response to HWA infestation and presalvage treatments. Because AGL C was both the largest (averaging 57 percent of

total C on our plots) and most variable C pool in response to treatment, it was the primary

driver of the same trends and patterns in total C discussed above (Figure 2.3), but with

more pronounced and rapid changes (Figure 2.4a). This more exaggerated C response

included a precipitous drop in AGL C immediately following both HWA and presalvage

treatments. While the initial decrease is significantly higher for the presalvage treatment,

it also recovers more rapidly, surpassing the HWA treatment within 15 years of initial

harvesting activities. While neither HWA nor presalvage AGL C pools regain levels seen

in the control, they begin to accumulate AGL C 20 years after the initial treatments,

reaching pre-treatment levels after approximately 40 years. This indicates that the impact

of HWA on a stand, either allowed to succumb to HWA infestation or with hemlock

removed prior to infestation, results in an approximate 40-year setback to above ground

live biomass stocks. While there is no significant difference between the HWA

infestation and presalvage treatments at the end of the 150 year simulation, the two

treatments do appear to diverge as time progresses with the presalvage treatment gaining

slightly more AGL biomass with time.

    Below Ground Live (BGL) The BGL C pool (Figure 2.4c) closely mimics the

AGL C pool, but is a smaller C carbon pool at 14 percent. In 2030, 5 years after the

presalvage harvest and HWA infestation, all treatments are statistically different with the

control storing the most C at 4.12 C metric tons hectare^{-1}, followed by HWA 3.42 C

metric tons hectare^{-1}, and lastly presalvage 2.72 C metric tons hectare^{-1}. From our data,

it was evident that the presalvage harvest prescription drastically reduced the C storage

within 5 years, whereas BGL C decline was more gradual from HWA infestation. In

2055 the control prescription continues to store the most BGL C at 4.45 C metric tons

hectare^{-1}, but the HWA and presalvage treatments converge storing similar amounts of carbon 3.46 C metric tons hectare^{-1} and 3.32 C metric tons hectare^{-1}, respectively. Significant interaction between hemlock density and treatment type was observed until 2070, with impact intensifying as hemlock density increases for presalvage harvest and HWA infestation scenarios. The control (5.55 C metric tons hectare^{-1}) continued to store the most C until the end of our simulation in 2165, while the HWA (4.42 C metric tons hectare^{-1}) and presalvage harvest (4.59 C metric tons hectare^{-1}) scenarios storing similar amounts.

Down Dead Wood (DDW) The second largest C pool across our treatments was DDW, accounting for approximately 15 percent of total C stocks. Proportionately, DDW demonstrated the largest changes in C stored in the first 25 years following treatment: HWA increased from 1.51 to 6.56 C metric tons hectare^{-1} due to increased hemlock mortality. Presalvage increased from 1.51 to 5.58 C metric tons hectare^{-1} as slash, nonmerchantable biomass, and harvesting waste was transitioned to this pool. Even the control increased over the first 25 years of the simulation, from 1.51 to 3.76 C metric tons hectare^{-1}, based on the density dependent mortality resulting from natural thinning as the stand ages (Figure 2.4b). Thirty years after the initial harvest, presalvage DDW decreased to match control levels. However, HWA DDW remained significantly higher throughout all but the final years of simulation. This is most likely due to the slow decay of hemlock boles. By 2145, all treatments were statistically similar in DDW storage.

Below Ground Dead (BGD) The BGD C pool (Figure 2.4d) trended similar to the DDW pool. After the presalvage harvest and HWA infestation in 2025, the presalvage scenario spiked and stored more C (1.87 C metric tons hectare^{-1}) than HWA and control

41

scenarios (0.38 C metric tons hectare^{-1}). This occurs as the BGL C pool transitioned to BGD C from harvested trees and from additional root mortality caused by harvesting operations. As HWA induced mortality continued to increase, the HWA treatment (4.56 C metric tons hectare^{-1}) surpassed the presalvage scenarios (4.14 C metric tons hectare^{-1}) in 2045. But by 2065, the preslavage (3.98 C metric tons hectare^{-1}) and HWA (3.86 C metric tons hectare^{-1}) treatments merged again at significantly higher levels than the control (2.57 C metric tons hectare^{-1}). As stands continued to age, HWA and presalvage scenarios slowly lost C from the BGD pool due to decomposition, while the control scenario slowly acquired it. By 2145, all treatments were statistically similar and continued to slowly accumulate C in the BGD pool through the remainder of our simulation in 2165: HWA (2.98 C metric tons hectare^{-1}), presalvage (2.97 C metric tons hectare^{-1}), and control (2.91 C metric tons hectare^{-1}).

Standing Dead (SD) The SD C pool trended differently from the other pools following HWA and presalvage treatments (Figure 2.4e). HWA infestation started with a significant increase in SD C (from 0.70 C metric tons hectare^{-1}to a maximum of 3.41 C metric tons hectare^{-1} in 2045). However, SD C decreased due to the migration of stems into the DDW pool as stands aged, and then dropped below the control by 2050. In contrast, presalvage SD C storage dipped for ten years (to 0.30 C metric tons hectare^{-1} in 2035) before steadily increasing due to natural thinning. By 2095 (75 years after the initial harvest) SD C pools from the presalvage treatment matched HWA SD pools. Ten years later (2105) there were no significant differences in SD C pools among the treatments.

Forest Floor (FF) Impacts to C stored in the FF pool were relatively minor and transient (Figure 2.4f). Initial inputs from HWA defoliation and harvesting debris provided a pulse immediately following treatment initiation. This was short lived under the presalvage treatment as a more open canopy allowed for increased light penetration, increased temperatures, and faster decomposition rates. Within 20 years, all three treatments converged and continued on a steady C increase throughout the simulation.

2.4.3 Management Implications

While many land managers focus on the potentially catastrophic loss of live hemlock in HWA impacted stands, our results indicate that C storage in other pools provide a significant buffer to C stocks following infestation. Raymer et al. (2013) found that the C from the live aboveground live biomass pool transitioned to the CWD pool after HWA infestation. This transition, along with new stem regeneration, buffered the overall impact of HWA on C stocks in stands infested by HWA (Raymer et al. 2013). Standing dead wood can continue to store C in infested stands because of its relatively slow decay rate (Zell et al. 2009), until transitioning to the DDW pool and finally the FF pool, continuing to buffer the effects of HWA mortality on C storage.

If land managers require short term revenue, presalavage harvesting could be justified in the region if the long time frame for recovery of removed C stocks is acceptable. Considering the relatively low market value for hemlock, this is highly unlikely unless higher value species are incorporated in the harvest. Further, if C storage and sequestration are management goals, our results suggest that allowing HWA to takes

43

it course may be the best alternative, particularly in high density stands. In addition, limiting pre-salvaging activities also maintains the maximum genetic pool of hemlock, cited as integral for maintaining individuals and populations potentially tolerant of HWA infestation (Schaberg et al. 2008).

Perhaps most importantly our results suggest that any impact of HWA infestation on C storage in northeastern forests may be relatively short lived, with no difference between infested and control stands after 150 years. However, while C storage may be regained, the loss of a keystone species in the region is likely to have other ecological consequences. The unique niche that hemlock stands create, and ecosystem services they specifically provide (Orwig et al. 2013) again argues for minimizing presalvage activities that could speed the loss of the species from the regions forests.

2.5 CONCLUSIONS

The threat of invasive species, such as HWA, should always be considered when developing short-term and long-term management goals. Our results indicated that HWA infested will have a significant and long-lived impact on C storage and C sequestration across the region. While many land managers have opted to conduct presalvage harvests in stands threatened by HWA, our results indicate that allowing HWA to progress naturally may have lower impacts on carbon storage and sequestration than conducting a presalvage harvest.

It is likely that the actual differences in long term net carbon flux between HWA and presalvage treatments is even greater than shown here. This is due in part to the potential overestimation of hemlock mortality rates following HWA infestation in the HWA even monitor that are based on HWA induced decline rates in southern New England. In northern New England extreme winter temperatures are likely to limit HWA population densities and subsequent impact to hemlock, resulting in slower mortality rates and a more gradual transition to replacement species. Actual differences between HWA and presalvage treatments may also be greater than show here because our presalvage treatment assumed that only stems greater than 25.4 cm were removed. This left smaller hemlock on site to grow and contribute to stand carbon estimates. It is more likely that stands treated with presalvage harvests would still become infested with HWA, leading to a secondary loss of carbon from those stands that are not captured in our simulation.

In addition to maximizing net carbon storage long-term, allowing HWA to progress naturally as opposed to presalvage harvests maintains the genetic pool within the hemlock population, increasing the chance of regenerating HWA tolerant stands. Because eastern hemlock is not a highly valued species from a commercial perspective, but is extremely valuable in regard to C storage (Herrmann and Bauhus 2008, Blozan 2007, Blozan 2006, Mackensen et al. 2003, Thompson and Sorenson 2000, Finizi et al. 1998), water quality (USDA Forest Service 2009), and wildlife conservation (USDA Forest Service 2009), avoiding salvage harvests may be the ideal approach.

If however presalvage activities are desired for immediate economic returns, our results indicate that impacts on C storage will mirror those resulting from HWA infestation after 25-50 years. While net C losses over the next 150 years were significantly higher in either the HWA infestation or presalvage scenarios, allowing HWA infestation to progress naturally through a stand results in the least impact to long-term C sequestration for the regions forests.

One limitation of our study is that the FVS model did not incorporate additional variables that influence carbon storage such as other hemlock pests (e.g. hemlock looper), changes in atmospheric CO_2, natural disturbances, potential land use and management histories, or climate change. All of these factors can affect the growth and C storage of northern New England forest (Groffman et al. 2012, Galik and Jackson 2009, and Ollinger et al. 2008). In addition, it has been suggested that using FVS for long-term simulations can underestimate carbon storage in older stands due to the low percentage of old growth and late successional stands from FIA data that was incorporated into the growth and yield model that drives the carbon biomass estimates in FVS (NE-TWIGS)

(Hilt and Teck 1989, Dixon 2002). Both overestimation (Gunn et al. 2014) and underestimation (MacLean et al. 2013) of C accumulation in late successional stands has been documented by several studies using FVS and FIA data to model C storage across the northeastern United States. However, for this study of late successional stands, it is likely that any errors in FVS estimates err on the low side, and provide a conservative estimate of carbon storage across hemlock dominated stands in the region and hence and more conservative estimate of carbon lost following HWA infestation or salvage harvesting.

We propose that the simulation results presented provide quantitative guidance regarding the influence of HWA infestation and salvage cutting on stand-level C stores. However, field verification of simulation results are needed to test and potentially improve the accuracy of calculated projections.

2.6 TABLES

Table 2.1. The number of FIA stands by basal area and state for our simulation study. Stands were classified as High (> 55%), Medium (>33% to <55%), and Low (<33%) hemlock basal area.

	High	Medium	Low
Maine	9	13	12
NH	4	7	3
NY	6	8	4
VT	5	5	2
Total	**24**	**33**	**21**

Table 2.2. Regeneration seedling count per hectare estimates for post disturbance and ingrowth calibrated by treatment and species composition from Leak 1997 and Brooks 2004 datasets.

Species	Control	HWA	Presalvage
Eastern Hemlock	116	0	0
White Pine	20	78	51
Red Maple	1,494	7,012	6,914
Sugar Maple	122	829	1,192
Yellow Birch	282	2,774	4,864
American Beech	961	5,130	5,972
White Ash	301	2,285	3,536
Aspen	0	73	179
Northern Red Oak	40	134	51
Black Cherry	20	67	25
Pin Cherry	73	410	504
Striped Maple	204	1,148	1,410
Paper Birch	44	246	302
Balsam Fir	2	12	15
Red Spruce	2	12	15

Table 2.3. Probability distributions of HWA infestation intensity after infestation (North East variant). Infestation intensity was assigned in the FVS based on the probabilities listed below from the HWA event monitor addfile. Outbreak values are numeric codes assigned to the infestation intensity within simulation files (FHTET 2008).

Value	Outbreak	Probability*
No Infestation	0	
Low Infestation	1	40%
Moderate Infestation	2	30%
High Infestation	3	20%
Catastrophic Infestation	4	10%
*Probability of infestation in a given year is determined by the user-set year of infestation. After infestation, the probability of the intensity is determined by the above values.		

Table 2.4. Percent of hemlock loss (mortality) at different HWA infestation intensities (North East variant). Hemlock loss was assigned based on the infestation intensity in the HWA event monitor addfile. Outbreak values are numeric codes assigned to the infestation intensity within simulation files (FHTET 2008).

Value	Outbreak	Loss of Hemlock (Mortality)
No Infestation	0	
Low Infestation	1	0-5%
Moderate Infestation	2	5-30%
High Infestation	3	30-70%
Catastrophic Infestation	4	70-90%

2.7 Figures

Figure 2.1. Map of the eastern United States and adjacent Canada with the area of study highlighted in red.

```
------------------------------------------------------------------------------------------
                          ****** CARBON REPORT VERSION 1.0 ******
                                   STAND CARBON REPORT
  STAND ID: 2010                     MGMT ID: NONE
------------------------------------------------------------------------------------------
        Aboveground Live  Belowground                    Forest          Total   Total   Carbon
        ----------------  ---------------       Stand  ---------------- Stand  Removed  Released
  YEAR   Total   Merch    Live    Dead          Dead    DDW   Floor  Shb/Hrb Carbon  Carbon  from Fire

         T/HA    T/HA     T/HA    T/HA          T/HA    T/HA  T/HA   T/HA    T/HA    T/HA    T/HA
------------------------------------------------------------------------------------------
  2006   133.1   81.1     25.9    3.0           12.0    4.9   14.6   0.7     194.3   0.0     0.0
  2011   145.2   88.4     28.3    2.7           10.6    7.9   16.6   0.7     212.0   0.0     0.0
  2016    81.0   50.5     16.1    16.9          14.2    33.7  16.9   0.7     179.6   47.4    0.0
  2021    87.9   55.6     19.7    13.6           7.5    26.2  15.3   0.7     170.9   0.0     0.0
  2026    95.0   59.6     19.7    11.0           3.8    21.8  15.7   0.7     167.7   0.0     0.0
  2031   103.7   64.5     20.9    9.0            1.9    19.8  16.5   0.7     172.3   0.0     0.0
```

Figure 2.2. Screen shot of sample Stand Carbon Report. The units of measurement are metric ton/hectare (Hoover and Rebain 2008).
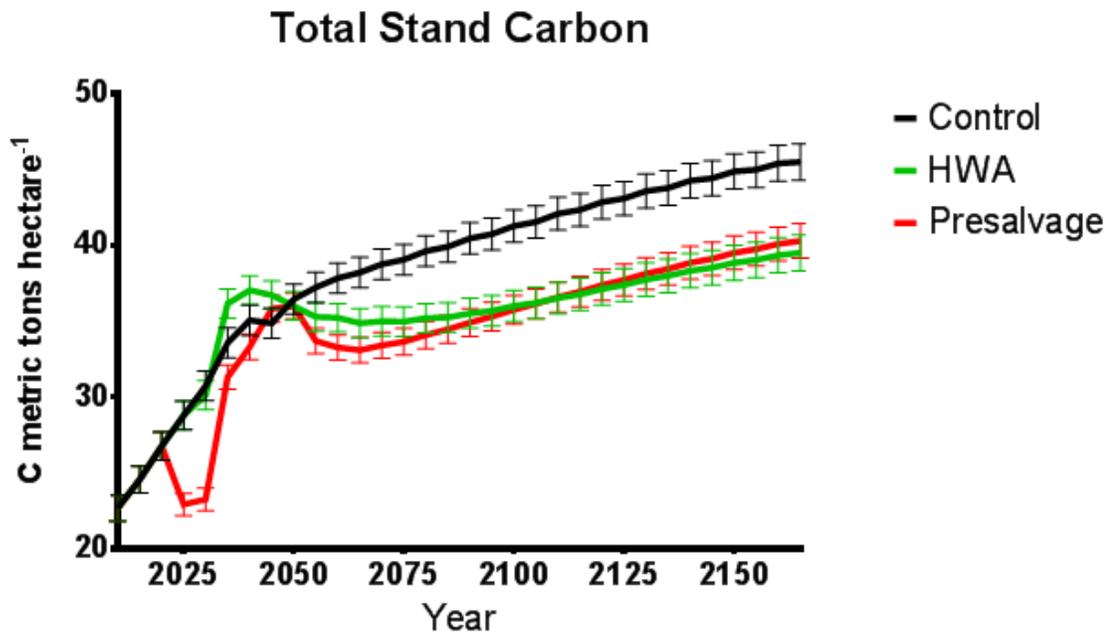
Figure 2.3. Total carbon storage for the three treatments (HWA-induced mortality, presalvage harvest, and control) from 2015 to 2165.
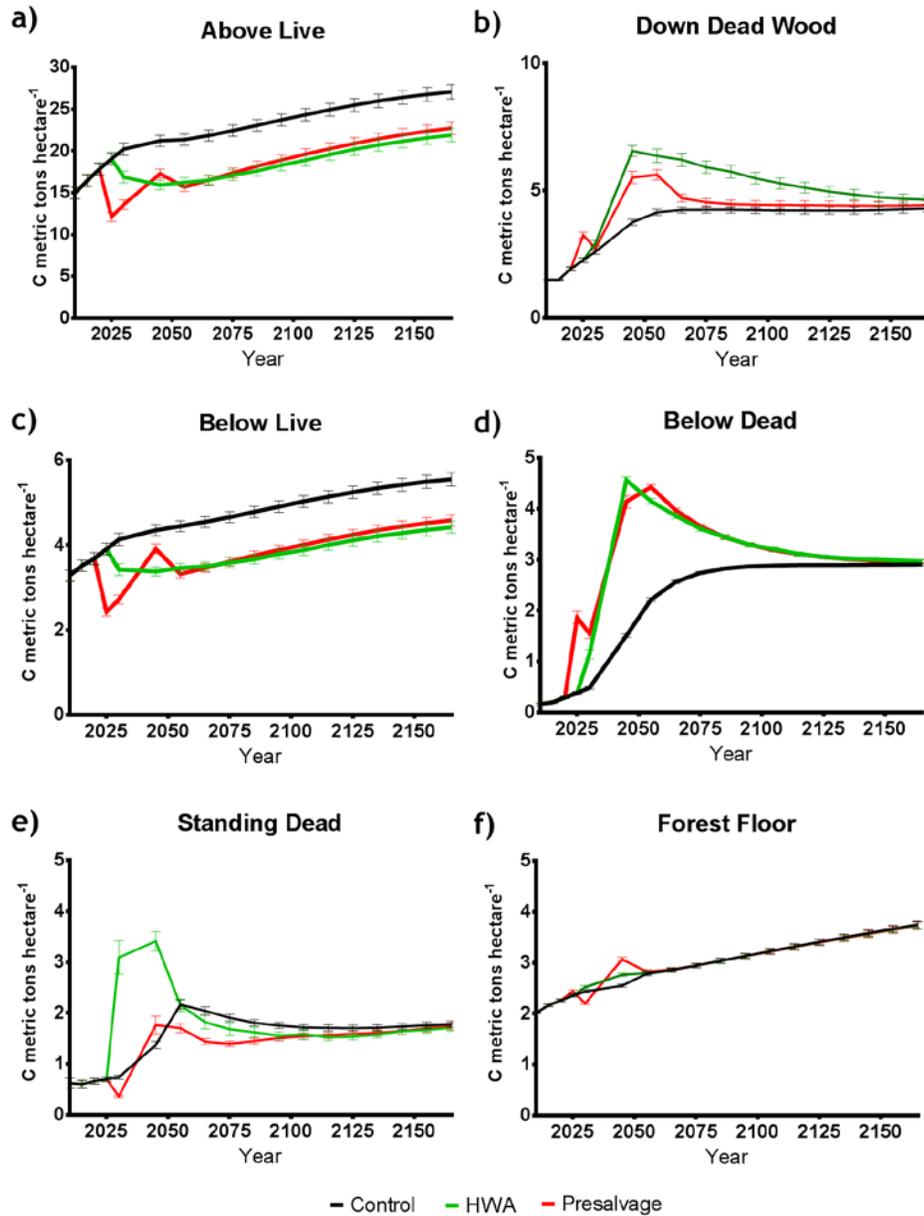
Carbon Pools

Figure 2.4. Dominant carbon stores under the three simulation treatments (HWA-induced mortality, presalvage harvest, and control) for the following specific pools: a) Above Ground Live (AGL), b) Down Dead Wood (DDW), c) Below Ground Live (BGL), d) Below Ground Dead (BGD),e) Standing Dead (SD), and f) Forest Floor (FF).

COMPREHENSIVE BIBLIOGRAPHY

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, 40*(1), 119-133.

Angers, V. A., C. Messier, M. Beaudet, and A. Leduc. 2005. Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. *Forest Ecology and Management, 217*(2–3), 275-293.

Barford, C. C., S.C. Wofsy, M.L. Goulden, J.W. Munger, E.H. Pyle, S.P. Urbanski, and K. Moore. 2001. Factors controlling long- and short-term sequestration of atmospheric CO2 in a mid-latitude forest. *Science, 294*(5547), 1688-1691.

Bhiry, N., and L. Filion. 1996. Mid-Holocene hemlock decline in eastern North America linked with phytophagous insect activity. *Quaternary Research, 45*(3), 312-320.

Blozan, W. 2006. Laurel branch leviathan climb. Retrieved 02/09/2012, 2012, from www.nativetreesociety.org/tsuga/laurel_branch/laurel_branch_leviathan_climb.htm

Blozan, W. 2007. The usis hemlock climb. Retrieved 02/09/2012, 2012, from www.nativetreesociety.org/fieldtrips/gsmnp/usis/usis_hemlock_climb.htm

Brooks, R. T. 2004. Early regeneration following the presalvage cutting of hemlock from hemlock-dominated stands. *Northern Journal of Applied Forestry, 21*(1), 12-18.

Brown, S. 2002. Measuring carbon in forests: current status and future challenges. *Environmental Pollution, 116*, 363-372.

Cobb, R. C. 2010. Species shift drives decomposition rates following invasion by hemlock woolly adelgid. *Oikos, 119(8)*, 1291-1298.

Crookston, N. L., and G.E. Dixon. 2005. The Forest Vegetation Simulator: A review of its structure, content, and applications. Internal Rep. Fort Collins, CO: U. S. Department of Agriculture, Forest Service, Forest Management Service Center. 226p.

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, 37*(10), 2031-2040.

D'Amato, A. W., D.A. Orwig, and D.R. Foster. 2008. The Influence of Successional Processes and Disturbance on the Structure of Tsuga canadensis Forests. *Ecological Applications, 18*(5), 1182-1199.

Davis, M. R., R.B. Allen, and P.W. Clinton. 2003. Carbon storage along a stand development sequence in a New Zealand Nothofagus forest. *Forest Ecology and Management, 177*(1–3), 313-321.

Dixon, G. E. 2002. Essential FVS: A user's guide to the Forest Vegetation Simulator. Internal Rep. Fort Collins, CO: U. S. Department of Agriculture, Forest Service, Forest Management Service Center. 226p.

Domec, J. C., Rivera, L. N., King, J. S., Peszlen, I., Hain, F., Smith, B., and Frampton, J. 2013. Hemlock woolly adelgid (Adelges tsugae) infestation affects water and carbon relations of eastern hemlock (Tsuga canadensis) and Carolina hemlock (Tsuga caroliniana). *New Phytologist*, 199(2), 452-463.

Dukes, J. S., J. Pontius, D. Orwig, J.R. Garnas, V.L. Rodgers, N. Brazee, 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, 39*(2), 231-248.

Dyer, J. H., S. T. Gower, J. A. Forrester, C. G. Lorimer, D. J. Mladenoff, and J. I.Burton. 2010. Effects of selective tree harvests on aboveground biomass and net primary productivity of a second-growth northern hardwood forest. *Canadian Journal of Forest Research, 40*(12), 2360-2369.

Eschtruth, A. K., N. L. Cleavitt, J. J. Battles, R. A. Evans, and T.J. Fahey. 2006. Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation. *Canadian Journal of Forest Research, 36*(6), 1435-1450.

Evans, A. M., and G. Gregoire. 2007. A geographically variable model of hemlock woolly adelgid spread. *Biological Invasions. 9*:369-382.

Finzi, A. C., N. Van Breemen, and C. D. Canham. 1998. Canopy tree–soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecological Applications, 8*(2), 440-446.

Forest Heath Technology Enterprise Team (FHTET) 2008. The Hemlock Woolly Adelgid Event Monitor Users' Guide. United States Department of Agriculture, Forest Service. www.fs.fed.us/foresthealth/technology.

Foster, D. R., and D.A. Orwig. 2006. Preemptive and salvage harvesting of New England forests: When doing nothing is a viable alternative. *Conservation Biology, 20*(4), 959-970.

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*(4), 982-998.

Galik, C. S., & Jackson, R. B. 2009. Risks to forest carbon offset projects in a changing climate. *Forest Ecology and Management, 257*(11), 2209-2216.

Godman, R. M., and Lancaster, K. 1990. Tsuga canadensis (L.) Carr. eastern hemlock. *Silvics of North America*, *1*, 604-612.

Goerlich, D. L. N., D. Ralph. 2000. Natural regeneration of eastern hemlock: a review. In: McManus, Katherine A.; Shields, Kathleen S.; Souto, Dennis R., eds. Proceedings: Symposium on sustainable management of hemlock ecosystems in eastern North America. *Gen. Tech. Rep, NE-267*, 14-22.

Goulden, M. L., J.W. Munger, S.M. Fan, B. C. Daube, and S.C. Wofsy. 1996. Exchange of carbon dioxide by a deciduous forest: Response to interannual climate variability. *Science, 271*(5255), 1576-1578.

Griffin, J. M., G. M. Lovett , M. A. Arthur, and K.C. Weathers. 2003. The distribution and severity of beech bark disease in the Catskill Mountains, N.Y. *Canadian Journal of Forest Research, 33*(9), 1754-1760.

Groffman, P. M., Rustad, L. E., Templer, P. H., Campbell, J. L., Christenson, L. M., Lany, N. K., .and Rodenhouse, N. L. 2012. Long-term integrated studies show complex and surprising effects of climate change in the northern hardwood forest. *Bioscience*, *62*(12), 1056-1066.

Gunn, J. S., Ducey, M. J., and Whitman, A. A. 2014. Late-successional and old-growth forest carbon temporal dynamics in the northern forest (northeastern USA). *Forest Ecology and Management*, *312*, 40-46.

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*(4), 615-627.

Hadley, J. L., and J.L. Schedlbauer. 2002. Carbon exchange of an old-growth eastern hemlock (Tsuga canadensis) forest in central New England. *Tree Physiology, 22*(15-16), 1079-1092.

Hadley, J. L., and J.L. Schedlbauer. 2003. Carbon exchange of an old-growth eastern hemlock (Tsuga canadensis) forest in central New England. *Tree Physiology, 23*(10), 719-719.

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, 38*(5), 1267-1274.

Harmon, M.E., and F. W. Franklin. 1990. Effects on Carbon Storage of Conversion of Old-Growth Forests to Young Forests. *Science, 247*(4943), 699-702.

Heath, L. S., J.E. Smith, and R.A. Birdsey. 2003. Carbon Trends in U.S. Forestlands: A Context for the Role of Soils in Forest Carbon Sequestration. Boca Raton, FL: CRC/Lewis Publishers.

Herrmann, S., and J. Bauhus. 2008. Comparison of methods to quantify respirational carbon loss of coarse woody debris (CWD). *Canadian Journal of Forest Research,*38: 2738-2745.

Hilt, D. E., and Teck, R. M. 1989. NE-TWIGS: An individual-tree growth and yield projection system for the northeastern United States. *The Compiler*, *7*(2), 10-16.

Hoover, C. M., and S.A. Rebain. 2011. Forest carbon estimation using the Forest Vegetation Simulator: Seven things you need to know. Gen. Tech. Rep. NRS-77. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 16 p.

Hoover, C.M.; S.A. Rebain. 2008. The Kane Experimental Forest carbon inventory: Carbon reporting with FVS. In: Havis, Robert N.; Crookston, Nicholas L., comps. 2008. Third Forest Vegetation Simulator Conference; 2007 February 13-15; Fort Collins, CO. Proceedings RMRS-P-54. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 17-22.

Janisch, J. E., and Harmon, M. E. 2002. Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. *Tree Physiology*, 22(2-3), 77-89.

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*(1), 12-35.

Keeling, C. D., S.C. Piper, R.B. Bacastow, M. Wahlen, T.P. Whorf, M. Heimann, and H.A. Meijer. 2005. Atmospheric CO_2 Exchange with the Terrestrial Biosphere and Oceans from 1978 to 2000: Observations and Carbon Cycle Implications. A History of Atmospheric CO2; and Its Effects on Plants, Animals, and Ecosystems. In I. T. Baldwin, M. M. Caldwell, G. Heldmaier, R. B. Jackson, O. L. Lange, H. A. Mooney, E. D. Schulze, U. Sommer, J. R. Ehleringer, M. D. Dearing, and T. E. Cerling (Eds.), vol. 177, pp. 83-113): Springer-Verlag.

Keeton, W. S., A.A. Whitman, G.C. McGee, and C.L. Goodale. 2011. Late-successional biomass development in northern hardwood-conifer forests of the northeastern United States. *Forest Science, 57*(6), 489-505.

Knoepp, Jennifer D.; Vose, James M.; Clinton, Barton D.; Hunter, Mark D. 2011. Hemlock infestation and mortality: impacts on nutrient pools and cycling in Appalachian forests. *Soil Science Society of America* 75(5):1935-1945.

Kotar, J., A. Kovach, and C. T. Loecy. 1988. Field guide to forest habitat types of northern Wisconsin. Department of Forestry, University of Wisconsin, Madison, Wisconsin, USA.

Lal, R. 2005. Forest soils and carbon sequestration. *Forest Ecology and Management, 220*(1–3), 242-258.

Leak, W. B. and S. M. Filip. 1977. Thirty-eight years of group selection in New England northern hardwoods. *Journal of Forestry* **75**(10): 641-643.

Lovett, G. M., C.D. Canham, M.A. Arthur, K. C. Weathers, and R.D. Fitzhugh. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. *BioScience, 56*(5), 395-405.

Luyssaert, S. E., A. Borner, A. Knohl, D. Hessenmoller, B. Law, P. Ciais, and J. Grace. 2008. Old-growth forests as global carbon sinks. *Nature, 455*(7210), 213-215.

Mackensen, J., J. Bauhus, and E. Webber. 2003. Decomposition rates of coarse woody debris: A review with particular emphasis on Australian tree species. *Australian Journal of Botany, 51*(1), 27-37.

MacLean, R. G., Ducey, M. J., and Hoover, C. M. 2013. A Comparison of Carbon Stock Estimates and Projections for the Northeastern United States. Society of American Foresters.

Matthew J, K. 1989. Productivity of New England hemlock/hardwood stands as affected by species composition and canopy structure. *Forest Ecology and Management, 28*(3–4), 237-257.

McClure, M.S. 1991. Density-dependent feedback and population cycles in *Adelges tsugae* (Homoptera:Adelgidae) on *Tsuga canadensis*. *Environmental Entomology*, 20:258-264.

Melillo, J., A. John, L. Arthur, R. Andrea, F. Brian, and N. Knute. 1989. Carbon and nitrogen dynamics along the decay continuum: Plant litter to soil organic matter. *Plant and Soil, 115*(2), 189-198.

Mika, A. M., and Keeton, W. S. 2014. Net carbon fluxes at stand and landscape scales from wood bioenergy harvests in the US Northeast. *GCB Bioenergy*.

Mladenoff, D. J., and F. Stearns. 1993. Eastern hemlock regeneration and deer browsing in the northern Great-Lakes region - A reexamination and model simulation. *Conservation Biology, 7*(4), 889-900.

Nuckolls, A., N. Wurzburger, C. Ford, R. Hendrick, J. Vose, and B. Kloeppel. 2009. Hemlock declines rapidly with hemlock woolly adelgid infestation: Impacts on the carbon cycle of southern Appalachian forests. *Ecosystems, 12*(2), 179-190.

Ollinger, S. V., Richardson, A. D., Martin, M. E., Hollinger, D. Y., Frolking, S. E., Reich, P. B., and Schmid, H. P. 2008. Canopy nitrogen, carbon assimilation, and albedo in temperate and boreal forests: Functional relations and potential climate feedbacks. *Proceedings of the National Academy of Sciences*, 105(49), 19336-19341.

Orwig, D. A., and A. A. Barker Plotkin. (2013). Foundation species loss affects vegetation structure more than ecosystem function in a northeastern USA forest. *PeerJ* 1: e41-e41.

Orwig, D. A., Thompson, J. R., Povak, N. A., Manner, M., Niebyl, D., and Foster, D. R. 2012. A foundation tree at the precipice: Tsuga canadensis health after the arrival of Adelges tsugae in central New England. *Ecosphere*, 3(1), art10.

Orwig, D. A. 2002. Stand dynamics associated with chronic hemlock woolly adelgid infestations in southern New England. Proceedings of Symposium on the Hemlock Woolly Adelgid in Eastern North America Proceedings. New Brunswick, New Jersey.

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*(1), 60-73.

Paradis, A., Elkinton, J., Hayhoe, K., and Buonaccorsi, J. 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(5-6), 541-554.

Peltzer, D. A., R.B. Allen, G.M. Lovett, D. Whitehead, and D.A. Wardle. 2010. Effects of biological invasions on forest carbon sequestration. *Global Change Biology, 16*(2), 732-746.

Peter, R. H. 1999. Species composition and dynamics in two hardwood stands in Vermont: a disturbance history. *Forest Ecology and Management, 120*(1–3), 105-116.

Raymer, P. C., Orwig, D. A., and Finzi, A. C. 2013. Hemlock loss due to the hemlock woolly adelgid does not affect ecosystem C storage but alters its distribution. *Ecosphere*, 4(5), art63.

Post, R. L. 1990. A primer on the federal-budget process. *MRS Bulletin, 15*(11), 35-35.

Raymer, P. C., D.A. Orwig, and A.C. Finzi. 2013. Hemlock loss due to the hemlock woolly adelgid does not affect ecosystem C storage but alters its distribution. *Ecosphere 4(5)*.

Rooney, T. P., R.J. McCormick, S.L. Solheim, and D.M. Waller. 2000. Regional variation in recruitment of hemlock seedlings and saplings in the upper Great Lakes, USA. *Ecological Applications, 10*(4), 1119-1132.

Russell-Roy, E. T., Keeton, W. S., Pontius, J. A., and Kerchner, C. D. 2014. Rehabilitation forestry and carbon market access onhigh-graded northern hardwood forests. *Canadian Journal of Forest Research*, *44*(999), 614-627.

Schaberg, P. G., D.H. DeHayes, G.J. Hawley, and S.E. Nijensohn. 2008. Anthropogenic alterations of genetic diversity within tree populations: Implications for forest ecosystem resilience. *Forest Ecology and Management*, *256*(5), 855-862.

Skinner, M., B.L. Parkera, S. Goulia, and T. Ashikaga. 2003. Regional responses of hemlock woolly adelgid (Homoptera: Adelgidae) to low temperatures. *Environmental Entomology, 32*(3), 523.

Smith, J.E., L. S. H. Kenneth, E. Skog, and R.A. Bridsey. 2006. Methods for Calculating Forest Ecosystem and Harvested Carbon with Standard Estimates for Forest Types of the United States. Forest Service.

Souto, D., T. Luther, and B. Chianese. 1996. Past and current status of HWA in eastern and Carolina hemlock stands. In: Salom, S. M., T. C. Tignor, and R. C. Reardon (Eds.), Proceedings of the First Hemlock Woolly Adelgid Review, USDA Forest Service, Morgantown, WV. Pp. 9-15.

Stadler, B., T. Muller, and D. Orwig, and R. Cobb. 2005. Hemlock woolly adelgid in New England forests: Canopy impacts transforming ecosystem processes and landscapes. *Ecosystems, 8*(3), 233-247.

Thompson, E. H. 2000. *Wetland, woodland, wildland – a guide to the natural communities of Vermont.* Hanover and London: University Press of New England.

Talbot Trotter III, R., and Shields, K. S. 2009. Variation in winter survival of the invasive hemlock woolly adelgid (Hemiptera: Adelgidae) across the eastern United States. Environmental entomology, 38(3), 577-587.

Tubbs, C. H. 1996. Aspects of eastern hemlock silvics important in silviculture: an overview. . In: Mroz, G.; Martin, J., eds. Hemlock ecology and management. Proceedings, regional conference on ecology and management of eastern hemlock; 1995 September 27- 28; Iron Mountain, MI. Department of Forestry, School of Natural Resources, University of Wisconsin-Madison: 5-9.

Turner, D. P., G. J. Koerper, M.E. Harmon, and J.J. Lee. 1995. A carbon budget for forests of the conterminous United States. *Ecological Applications, 5*(2), 421-436.

United States Department of Agriculture, Forest Service (USADA FS). 2005. What is Forest Inventory Analysis? United States Department of Agriculture, Forest Service.

United States Department of Agriculture, Forest Service (USADA FS). 2009. An Exotic Pest Threat to Eastern Hemlock: An Initiative for Management of Hemlock Woolly Adelgid United States Department of Agriculture, Forest Service.

Ward, J. S., Montgomery, M. E., Cheah, C. A. J., Onken, B. P., and Cowles, R. S. 2004. Eastern hemlock forests: guidelines to minimize the impacts of hemlock woolly adelgid.

Watson, R. T., Noble, I. R., Bolin, B., Ravindranath, N. H., Verardo, D. J., and Dokken, D. J. 2000. Land use, land-use change and forestry: a special report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Webster, C. R., and C.G. Lorimer. 2002. Single-tree versus group selection in hemlock-hardwood forests: are smaller openings less productive? *Canadian Journal of Forest Research, 32*(4), 591-604.

Webster, C. R., and C.G. Lorimer. 2005. Minimum opening sizes for canopy recruitment of midtolerant tree species: a retrospective approach. *Ecological Applications, 15*(4), 1245-1262.

White, C. S. 1986. Volatile and water-soluble inhibitors of nitrogen mineralization and nitrification in a ponderosa pine ecosystem. *Biology and Fertility of Soils, 2*, 97-104.

White, C. S. 1991. The role of monoterpenes in soil nitrogen cycling processes in ponderosa pine. *Biogeochemistry,* (12), 43-68.

Whitney, G. 1984. Fifty Years of Change in the Arboreal Vegetation of Heart's Content, An Old-Growth Hemlock-White Pine-Northern Hardwood Stand. *Ecology,* 65(2): 403-408.

Willis, G. L., and M. S. Coffman. 1975. Composition, structure, and dynamics of climax stands of eastern hemlock and sugar maple in the Huron Mountains. Michigan. Technical Bulletin Department of Forestry, Michigan Technological University, Houghton, Michigan, USA., 13.

Wofsy, S. C., M.L. Goulden, J.W. Munger, S.M. Fan, P.S. Bakwin, B.C. Daube, F.A. Bazzaz. 1993. Net exchange of CO2 in a mid-latitude forest. *Science, 260*(5112), 1314-1317.

Yorks, T.E., J.C. Jenkins, D.J. Leopold, D.J. Raynal, and D.A. Orwig. 2000. Influences of eastern hemlock mortality on nutrient cycling. Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America (ed. K.A. McManus, K.S. Shields and D.R. Souto), pp. 126–133. *USDA General Technical Report* 267, Newtown Square, PA.

Yorks, T.E., D.J. Leopold, and D.J. Raynal. 2003. Effects of *Tsuga canadensis* mortality on soil water chemistry and understory vegetation: possible consequences of an invasive insect herbivore. *Canadian Journal of Forest Research*, 33:1525-1537, 10.1139/x03-073.

Zell, J., G. Kändler, and M. Hanewinkel. 2009. Predicting constant decay rates of coarse woody debris—A meta-analysis approach with a mixed model. *Ecological Modelling, 220*(7), 904-912.