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Hemlock loss due to the hemlock woolly adelgid does not affect ecosystem C storage but alters its distribution

POLIANA C. L. RAYMER,[1],† DAVID A. ORWIG,[2] AND ADRIEN C. FINZI[1]

[1]*Department of Biology, Boston University, Boston, Massachusetts 02215 USA*
[2]*Harvard Forest, Harvard University, Petersham, Massachusetts 01366 USA*

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

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

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† **E-mail:** pclemos@bu.edu

INTRODUCTION

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

The HWA was accidently introduced in Virginia from Japan in the early 1950s (Souto et al. 1996), is currently established in 18 states and is anticipated to continue spreading (USDA Forest Service 2012). Eastern hemlock trees (*Tsuga canadensis*) of all age and size categories are susceptible to the HWA (Godman and Lancaster 1990). The aphid-like insect inserts a long stylet in the parenchyma tissue on the underside of hemlock needles and twigs, and consumes photosynthates, eventually starving the tree and causing death (Young et al. 1995). Native predators have thus far been unsuccessful in controlling HWA populations (Montgomery and Lyon 1996), although bio-control agents such as the *Laricobius nigrinus* show some promise in curbing further expansion (Zilahi-Balogh et al. 2002, Mausel et al. 2010). Because of its sensitivity to cold temperatures, the rate of HWA colonization decelerates northward (Orwig et al. 2002, 2012). Recent climate analyses (Hayhoe et al. 2007) suggest that warming temperatures owing to climate change are likely to accelerate the HWA's northerly spread.

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

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

The objective of this research was to measure C stocks in stands of varying age and abundance of hemlock and/or black birch. We quantified C pools in various hemlock and black birch stands in Massachusetts and Connecticut. Using information from previous studies and comparisons of data between plots with identical land-use history, we addressed the question of whether the quantity and distribution of C pools in black birch forests are the same as those found in the hemlock stands they replace and, if so, over what time scales.

METHODS

Study sites and land-use history

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

Table 1. Overstory species composition and characteristics of the measured stand types. Arrows for girdled and infested stand types correspond to pre- → post-hemlock death. Former relative importance values for *T. canadensis* in the girdled stand type and the post-HWA stand type are shown in parenthesis. Stand type age is represented by age/years since hemlock girdling or mortality due to HWA. Growing season is equivalent to May–October. Superscript letters represent significant differences among stand types (* $P < 0.05$).

Metric	Primary hemlock	Secondary hemlock	Girdled	Post-HWA	Secondary black birch
Relative importance value†					
Tsuga canadensis	90.5	66.8	(68.0)¶	(66.0)§	···
Betula lenta	1.2	10.2	4.1	13.8	63.6
Acer rubrum	2.7	7.1	8.8	16	5.1
Quercus rubra	···	5.6	8.2	8	4.0
Pinus strobus	···	4.3	36.7	···	28.5
Basal area (m^2/ha)	59.4	52.1	51.7‡ →16.9	43§ →24	38.9
Density (stems/ha)					
< 10 cm dbh	848 ± 372	115 ± 20	58 ± 37	23003 ± 2519	624 ± 212
> 10 cm dbh	718 ± 126	606 ± 37	731‡ → 308 ± 38	625§ → 136 ± 11	549 ± 71
Location||	Petersham	Petersham	Petersham	Burham Brook	Harvard
Mean annual precipitation (cm)	110	110	110	123	116
Mean annual soil temperature (°C)	8.7	9.5	9.4	8.6	7.7
Growing season air temperature (°C)	17.4	17.4	17.4	18.0	17.4
Growing season soil moisture (m^3 H_20/m^3 soil)	0.21	0.20	0.23	0.20	0.22
Land use history	Woodlot	Pasture	Pasture	Woodlot	Pasture
Min. soil bulk density (g/cm^3)	0.78^{B} ± 0.04	1.06^{A} ± 0.09	1.01^{A} ± 0.04	0.91^{AB} ± 0.27	0.82^{B} ± 0.02
% Rock volume	25.8^{A} ± 3.4	15.2^{AB} ± 1.4	22.3^{AB} ± 3.9	9.9^{B} ± 2.9	6.5^{B} ± 0.44
Stand age	230	132	5/*132*	18/*150*	135

†Includes the five most common tree species found among the stands calculated as: (relative basal area + relative density)/2 (Orwig and Foster 1998).

‡ Obtained from Ellison and Barker Plotkin (2005).

§ Obtained from Orwig and Foster (1998).

¶ Obtained from Ellison et al. (2010).

|| Geographic coordinates: Petersham, Massachusetts, USA, 42°32′ N, 72°11′ W; Burham Brook, Connecticut, USA, 41°28′ N, 72°19′ W; Harvard, Massachusetts, USA, 42°31′ N, 71°32′ W.

birch stand type ~135 years old, growing on former pastureland (Fig. 1).

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

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

A 135-year-old stand type dominated by black birch forest (herein "secondary black birch") was located near Black Pond on property belonging to the Harvard Conservation Trust (Harvard, MA, 42°31′ N, 71°32′ W). Following pastureland abandonment, a near monoculture of black birch developed over the last 135 years.

The climate was similar across all stand types. Mean annual temperature varied between 8.5 and 10°C. Mean annual precipitation varied

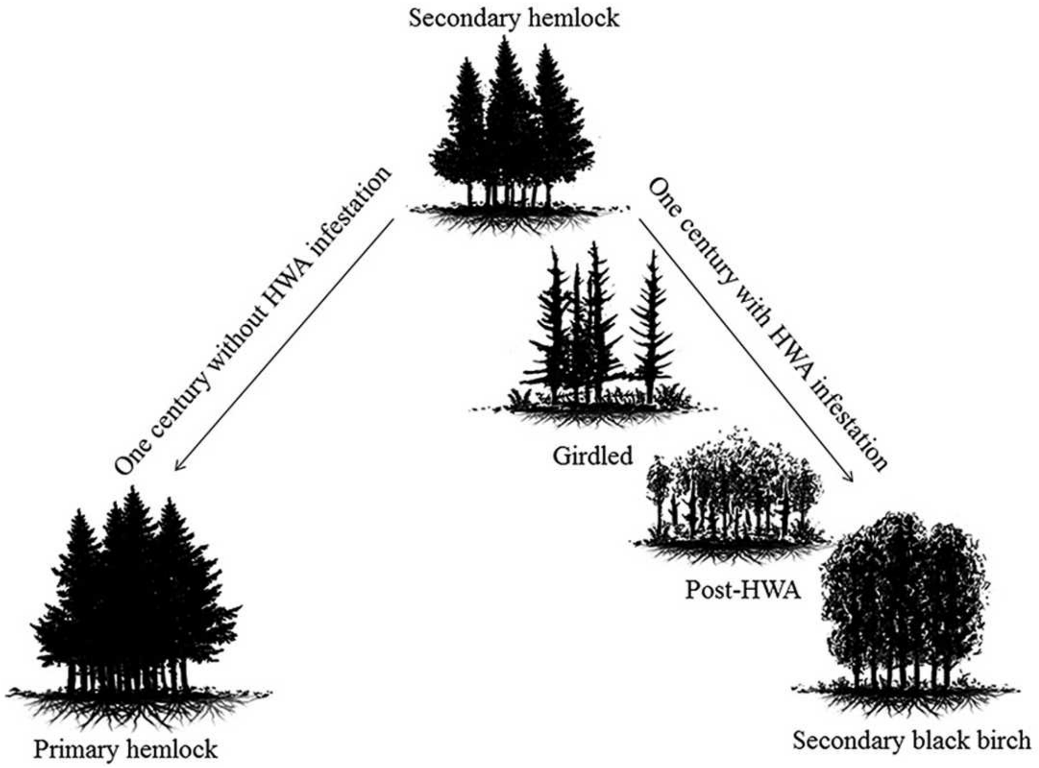

Fig. 1. A diagrammatic representation of the age relationships among the stand types studied here. In the absence of the HWA it is possible that secondary hemlock stands in southern New England will mature to a structure and C balance similar to that of primary hemlock stands. Invasion by HWA in southern New England entrains secondary ecological succession as canopy hemlock trees die and are replaced by black birch. The question addressed in this study is whether the quantity and distribution of C pools in black birch forests are the same as those found in the hemlock stands they replace and, if so, over what time scales (art courtesy: F. T. Raymer).

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

Carbon in aboveground biomass

In each plot, we measured the diameter of all trees >10 cm breast height (dbh; $\sim$1.37 m) by species. Two of the four primary hemlock plots were located within the 35-hectare Smithsonian Institute Global Earth Observatory (SIGEO) forest dynamics plot on the Prospect Hill research area. We used data from a 2010 inventory to estimate aboveground biomass in these plots. At the Simes Tract (secondary hemlock and girdled stand types), all of our plots were located within an existing experiment (Ellison et al. 2010), and we used their 2009 inventory data for our analysis. In addition we inventoried all saplings ($>$1.37 cm height and $<$10 cm dbh). The foliage and woody biomass of each tree was estimated from species-specific allometric equations (Table 2; Jenkins et al. 2003). We used published equations for eastern hemlock, eastern white pine and black birch, and for the other hardwood species a generalized equation.

Table 2. Allometric equations applied to measured diameter at breast height for total aboveground biomass calculation. B = biomass, d = diameter at breast height. Annual litterfall was used to calculate hardwood foliar biomass.

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

At the post-HWA stand type in CT, we established two 1 × 30-m transects in each plot to measure the number and diameter of black birch saplings (Table 1). Wood and foliar allometric equations developed by Raymer and Finzi (*unpublished manuscript*) were used to calculate the biomass of these samplings.

Carbon in woody debris

Woody debris on the ground was divided into three size classes based on diameter: fine ($\theta_{debris} < 1$ cm diameter), small (1 cm $< \theta_{debris} < 10$ cm) and coarse ($\theta_{debris} > 10$ cm diameter). All woody debris were classified into three decay classes with class I corresponding to the least decayed material and class III corresponding to the well-decayed wood (modified from Carmona et al. 2002; Table 3). To quantity the mass of fine and small woody debris, we randomly located four 1 × 1 m subplots within each replicate plot (i.e., 16 subplots per site) and collected all surface debris as well as those in the organic horizon. The entire 30 × 30 m plot was inventoried for coarse woody debris volume. In addition to decay class information, coarse woody debris were categorized as logs and snags, modified from Carmona et al. (2002) and Coomes et al. (2002).

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

Subsamples of the woody debris were ground

Table 3. Decay classes for logs and snags, adapted from Carmona et al. (2002), Coomes et al. (2002), respectively.

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

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

Belowground carbon pools: roots and soil

Belowground biomass was sorted into three size classes based on diameter: fine ($\theta_{root} < 2$ mm diameter), small (2 mm $< \theta_{root} < 1$ cm diameter), and coarse ($\theta_{root} > 1$ cm diameter). Fine roots were collected from 5 cm-diameter soil cores to a depth of 45 cm. Small roots and coarse roots were collected from twenty 1 m^2 soil pits dug to 50 cm depth (i.e., 0.5 m^3). Fine roots were collected from triplicate, randomly-located samples in each plot. Roots in the organic horizon (herein OH) were collected in 10×10 cm monoliths. Once the OH was removed, we cored soils in 15 cm depth increments to a depth of 45 cm. Fine roots were sorted from each sample and then washed, dried and weighed. For each plot, one of the three replicate samples was randomly selected for thorough analysis and separation of live and dead fine roots the day following soil coring. Roots with an intact cortex and considerable tensile strength were identified as live. The remaining samples were kept refrigerated until sorted. The ratio of live to dead roots from the plot-specific subsample was applied to the remaining biomass.

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

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

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

Comparison to previously published results

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

Statistical analysis

One-way analysis of variance (ANOVA) with Tukey's multiple comparison procedure were used to assess differences in C pools among stand types. All analyses were performed using RStudio version 0.94.110 (R Development Core Team 2011). The five sites were the independent variables. The C pools (i.e., above- and belowground biomass, woody debris, soil C) were dependent variables. Assumptions of normality and homogeneity of variance were met. Tukey's multiple comparison test protected the experiment-wise alpha at $P < 0.05$.

RESULTS

Live aboveground biomass

Aboveground C content in the primary hemlock stand type averaged 15.3 ± 2.2 kg C m^{-2} (Fig. 2A), about 20% higher than that found in the secondary hemlock stand type (12.7 ± 1.1 kg C m^{-2}). Basal area (59.3 m^2 ha^{-1}) for the primary hemlock stand type (Table 1) was similar to that reported by Hoover et al. (2012) for old-growth conifer forests of New Hampshire (57.9 m^2 ha^{-1} and 56.1 m^2 ha^{-1}). The girdled stand type (5.5 ± 1.1) had significantly lower aboveground biomass than all other stand types but was similar to the post-HWA stand type (9.0 ± 1.2). The mass of C in biomass in the 135-year old black birch stand type (17.0 ± 1.7 kg C m^{-2}) was equivalent to that in the primary and secondary hemlock stand types.

Woody debris

The mass of C in coarse woody debris (CWD, >10 cm diameter) was significantly higher in the girdled stand type (4.8 ± 0.3 kg C m^{-2}) than the post-HWA stand type (1.7 ± 0.09 kg C m^{-2}), both of which were significantly higher than that found in the primary and secondary hemlock (Fig. 2B). The largest salvage logging operation in the US occurred following the 1938 hurricane in New England (McLachlan et al. 2000), which likely reduced the amount of CWD in the primary growth hemlock stand type. Most of the snags and logs were ≤20 cm diameter, but ranged in diameter up to 60 cm (Fig. 3). Most snags were found in the girdled stand type in decay class I (Fig. 3A, C). Most logs were found in the post-HWA stand type in decay classes II and III, though there were also numerous logs in the primary hemlock and secondary black birch stand types (Fig. 3B, D).

The quantity of C in small woody debris (SWD, 1–10 cm diameter) was significantly greater in the post-HWA stand type (0.42 ± 0.02 kg C m^{-2}) compared to all other stand types (0.13 ± 0.01 kg C m^{-2}). The quantity of C in fine woody debris (FWD, 0.2–1 cm in diameter) was significantly higher in primary hemlock stand types (0.07 ± 0.02 kg C m^{-2}) than all other stand types (average of 0.04 ± 0.01 kg C m^{-2}).

Soil

Total rock volume (0–50 cm soil depth) varied from 6.5 ± 0.4% in the secondary black birch stand type to 25.8 ± 3.4% in the primary hemlock stand type (Table 1). Though a much higher volume of rocks was found in the latter stand type, it is still considered to be a representative forest for the purpose of this study, as other primary hemlock forests are mostly located on steep slopes largely outside the geographic range of the present study. Forest floor carbon values were comparable between Hoover et al. (2012) and our work (5.2 kg C m^{-2} and 4.6 kg C m^{-2}, respectively). The C content of the organic horizon was two-fold higher in the primary-

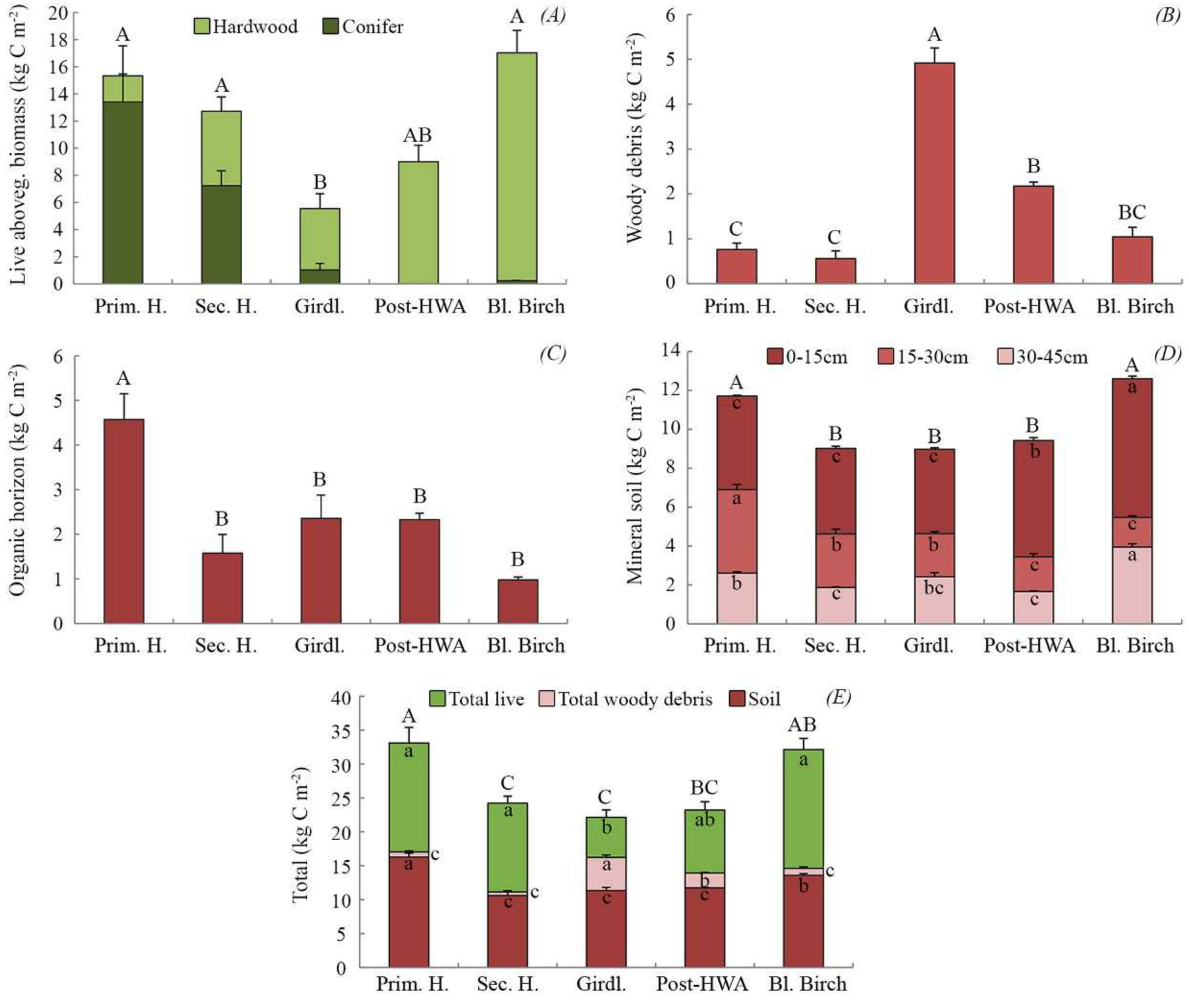

Fig. 2. Carbon content (kg C m^{-2}; mean ± SE) in (A) live aboveground biomass, (B) total woody debris, (C) soil organic horizon, (D) mineral soil (0–45cm depth) and (E) total ecosystem C storage (live biomass includes roots). Lower-cased letters below their respective error bars denote significant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

growth hemlock stand type (4.6 ± 0.6 kg C m^{-2}) than all other stand types (Fig. 2C). Of the total quantity of C stored to a depth of 45 cm, 28% was found in the organic horizon of the primary-growth hemlock forest compared to 15% and 7% in the secondary hemlock and black birch stand types.

The C content of mineral soil to a depth of 45cm was significantly higher in the primary hemlock and the secondary black birch stand types than all other stand types (Fig. 2D). The quantity of C stored in the mineral soil was highest in the top 15 cm of mineral soil and declined with depth. The content of C in the top 15 cm of mineral soil was highest in the secondary black birch stand type, intermediate in the post-HWA stand type and lowest in the hemlock and girdled stand types. At 15–30 cm depth, soil C content was highest in the primary hemlock stand type and lowest in the post-HWA and black birch stand types. At 30–45 cm depth, the largest C pool was found in the secondary black birch stand type. Most of the variation in C content was due to differences in soil bulk

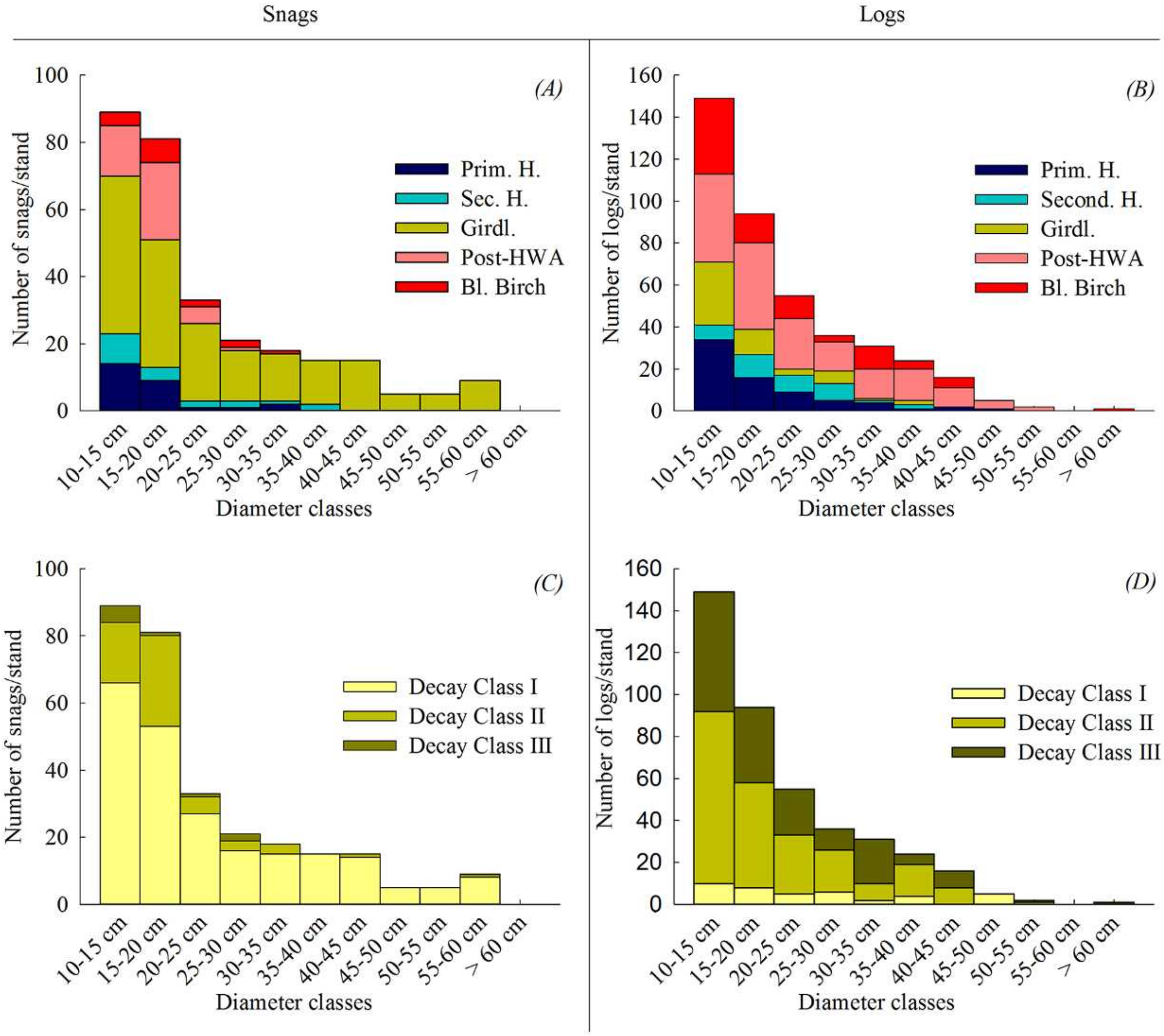

Fig. 3. Number of observed (A) snags and (B) logs, with respective distribution of decay classes in each stand type (C and D).

density and rock volume (Table 1). The concentration of C, while variable from stand type to stand type, was statistically significant in the 15–30 cm soil horizon (Table 4).

Roots

The C content of fine roots to a depth of 45 cm in the mineral soil was highest in the primary hemlock stand type, with over 40% of these fine roots in the organic horizon (Fig. 4A). Fine root

Table 4. Mean (±1 SE) %C in the different soil depths at each stand type. Different superscript letters indicate a significant difference (*$P < 0.05$) within a soil depth. For mineral soil at 0–15 cm depth, $P = 0.06$.

Soil depth	Primary hemlock	Secondary hemlock	Girdled	Post-HWA	Secondary black birch
Org. horizon	44.7 ± 1.2	38.2 ± 3.0	37.9 ± 3.0	37.5 ± 4.2	39.5 ± 2.2
0–15 cm	6.0^{AB} ± 0.37	4.1^{B} ± 0.4	4.8^{AB} ± 0.5	6.3^{AB} ± 0.8	7.4^{A} ± 0.8
15–30 cm	4.5^{A} ± 0.53	2.1^{B} ± 0.2	1.7^{B} ± 0.2	1.5^{B} ± 0.2	2.4^{B} ± 0.7
30–45 cm	2.2^{AB} ± 0.3	1.1^{B} ± 0.2	1.5^{AB} ± 0.2	1.1^{B} ± 0.3	2.9^{A} ± 0.6

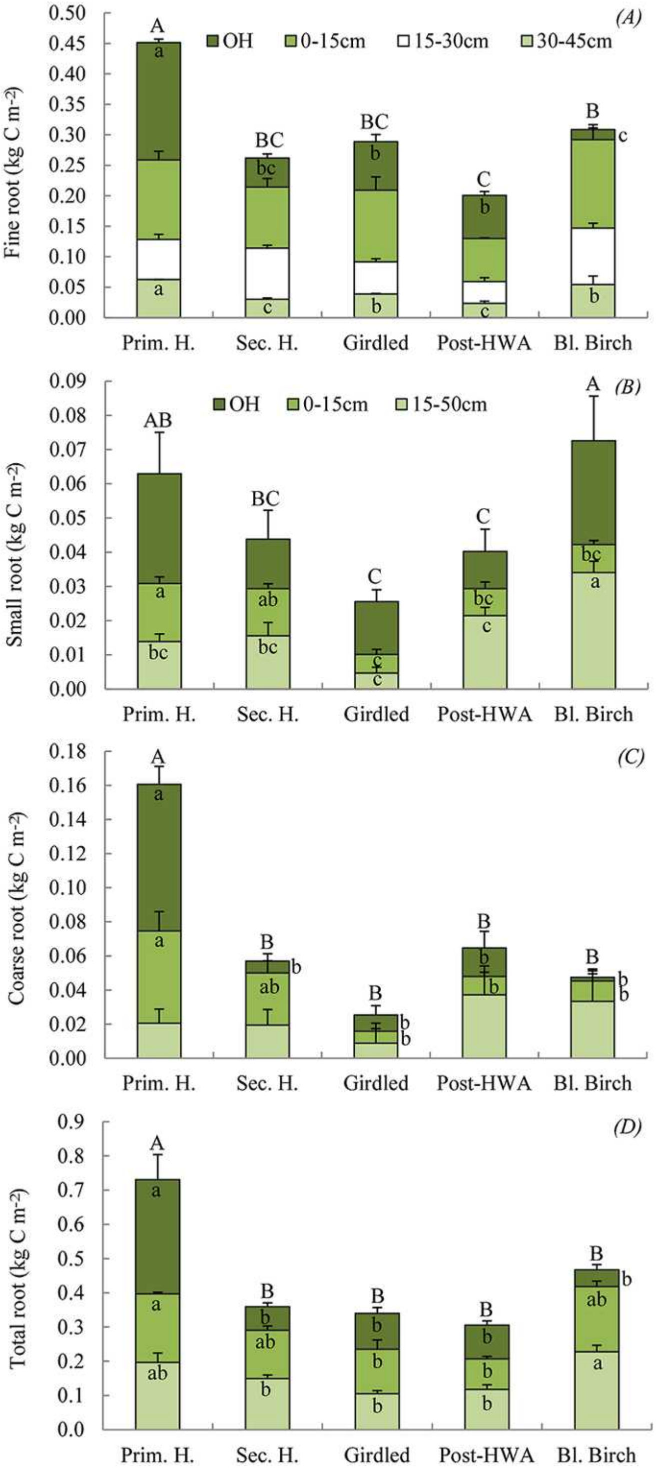

Fig. 4. C content (kg C m^{-2}; mean ± SE) in (A) fine roots, (B) small roots, and (C) coarse roots at different soil depths. Lower-cased letters below their respective error bars denote significant differences for separate soil depths in stacked bars; upper-cased letters denote total significant differences among stand types ($P < 0.05$). Fine roots in 0–15 cm mineral soil, $P = 0.06$; in 15–30 cm mineral soil, $P = 0.49$. Small roots in organic horizon, $P = 0.40$. Coarse roots in 15–50 cm mineral soil, $P = 0.51$.

biomass was significantly lower in the secondary black birch stand type compared to the primary hemlock stand type. The post-HWA stand type had the smallest pool of C in fine root biomass. The pool of C in small roots in the primary hemlock and secondary black birch stand types was significantly higher than the girdled and post-HWA stand types (Fig. 4B). The quantity of C in coarse roots (Fig. 4C) and total live belowground biomass (Fig. 4D) was significantly higher in the primary hemlock stand type than all other stand types.

Carbon inventory of the entire ecosystem

The total quantity of C in the primary hemlock was significantly higher than all other stand types except for the secondary black birch stand type (Fig. 2E). Hoover et al. (2012) reported an overall mean of 12.5 kg C m^{-2} in old-growth conifer stands (including hemlock, white pine and spruce) across forests in New Hampshire, Vermont and Maine, similar to our findings (15.3 kg C m^{-2}) at Harvard Forest. Although the total quantity of C among the remaining stand types was not significantly different from one another, significantly more of the ecosystem C was found in CWD in the girdled and post-HWA stand types compared to the secondary hemlock stand type where live biomass stored significantly more C.

Comparison to previously published results

From three to 21 years following HWA-induced hemlock mortality, C stored in live aboveground biomass increased by ~7 kg C m^{-2} (Table 5). There was a loss of ~3.9 kg C m^{-2} from snags and smaller decrease of 0.6 kg m^{-2} in organic horizon C content. Mineral soil C content increased by ~0.9 kg C m^{-2}. There were no previous data on C pools in logs. The total net change in ecosystem C content is +4.7 kg C m^{-2}, although uncertainty of the C content of logs prevents us from drawing a definitive conclusion about absolute C accumulation in this stand type.

DISCUSSION

Black birch is the dominant species replacing hemlock forests subject to HWA infestation in southern New England (Orwig and Foster 1998, Orwig et al. 2002). For the present work, we addressed the question of whether the quantity and distribution of C pools in black birch forests are the same as those found in the hemlock stands they replace and, if so, over what time scales. The secondary black birch stored the same quantity of C as that of the primary hemlock stand type, surpassing C storage found in the secondary hemlock stand type. Moreover ecosystem C content was similar among the secondary hemlock, girdled and post-HWA stand types. Our results suggest that C storage in hemlock dominated forests of southern New England is resilient to the loss of hemlock because the formation of CWD and regrowth by black birch offsets the loss of C in live (hemlock) biomass.

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

If the secondary hemlock plots were to continue maturing, soil C alone could increase by ~50% over that already found in the organic and mineral soil horizons (+5.7 kg C m^{-2}; Fig. 2C, D). Similarly, root biomass could potentially increase 84%, although in absolute terms this represents a modest increment in ecosystem C content relative to that in the soil (+0.45 kg C m^{-2}; Fig. 4). Interestingly, pasturing at the Harvard Forest significantly increased soil bulk density relative to that found in the primary hemlock stand type (Table 1), whereas it tended to deplete soil C concentration (Table 4). If soil C concentration in the secondary hemlock stand types were to increase to the level of the primary hemlock stand type, it is possible that soil C content could increase more than that reported above.

The loss of hemlock, as simulated by girdling, did not appear to significantly affect the C

Table 5. Differences in C storage at Burnham Brook (post-HWA stand type) shortly following infestation (3–5 years) and 21 years following infestation.

Years since infestation	Aboveground C	Snags	Logs	Organic horizon	0–15 cm mineral soil	Total
3–5 years	4.1†	4.3†		2.9‡	5.1‡	16.4
21 years						
This study	11.1 ± 1.5	0.24 ± 0.04	1.5 ± 0.06	2.3 ± 0.1	6.0 ± 0.2	21.1
ΔC (kg C m^{-2})	7.0	−3.9		−0.6	0.9	4.7

Note: Blank cell (logs) indicates unmeasured data.
† Obtained from Orwig and Foster (1998); data measured approximately three years following infestation.
‡ Obtained from Jenkins et al. (1999); data measured approximately five years following infestation.

balance of former hemlock forests at the ecosystem scale (Fig. 2E), but clearly suggested the potential for a significant shift in the location of the C, from live biomass to CWD (Fig. 2A, B). Despite the removal of ca. 80% of the stems in the girdled plots (Ellison et al. 2010), there were no differences between stand types in the C content of root biomass or that in the organic and mineral soil horizons (Fig. 4). This result is consistent with that of Jenkins et al. (1999), who found no significant changes in C pools ~3 years following hemlock infestation at sites throughout southern New England. Knoepp et al. (2011) also found no significant loss of soil C content 4-years following hemlock loss at the Coweeta Long Term Ecological Research. Hence, the initial impacts on the C cycle appear to be limited to a transfer of C into woody debris.

We cannot with confidence extend the comparative approach we employed at the Harvard Forest to the post-HWA and secondary black birch stand types. Although land-use history was similar among stand types, it is impossible to know the exact nature and extent of pasturing in these different areas. Also, in a subsequent analysis we found no correlation between net primary production and mean annual temperature. Hence the differences in biomass among stand types observed here is unlikely to have been influenced by differences in temperature. To quantify changes in C stocks over a period of 18 years at this site, we took advantage of previous research conducted ~3 years following hemlock mortality due to HWA infestation and compared that to our estimates 21 years post-HWA (Table 5). Based on C in aboveground biomass, CWD, the organic horizon and top 15cm of mineral soil, there was a net accumulation of 4.7 kg C m^{-2} over 18 years (Table 5). This compares favorably with the estimate of the mean quantity of C lost following girdling, ~1 kg C m^{-2}, for these same pools (i.e., estimate of differences between the girdled and secondary hemlock plots), suggesting the potential for rapid recovery of ecosystem C content.

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

While croplands in New England appear to influence soil C accumulation for more than a century following abandonment (Compton and Boone 2000, Clark and Johnson 2011), C pools in former pasturelands recover within ~100 years or less (Foote and Grogan 2010, Clark and Johnson 2011). Land-use history records for Harvard MA indicate that the black birch stand type is a first-generation forest following pastureland abandonment (Berg et al. 1997), suggesting that the larger C content of the mineral soil likely reflects the effect of black birch on soil C rather than a historical effect of pasturing 135 years ago. This line of reasoning is consistent with the significantly large accumulation of C in the top 15cm of mineral soil in the post-HWA stand type that is dominated by black birch saplings (Fig. 2D, E).

Similar to soil C, the secondary black birch stand type also had the largest pool of C in biomass (Fig. 2A). Biomass C was nearly 10% greater than that in the primary and nearly 35% than that in secondary hemlock stand types at the Harvard Forest (Fig. 2A). It is possible that the stand type we studied has higher biomass than other black birch stands in central New England, although we are not aware of compa-

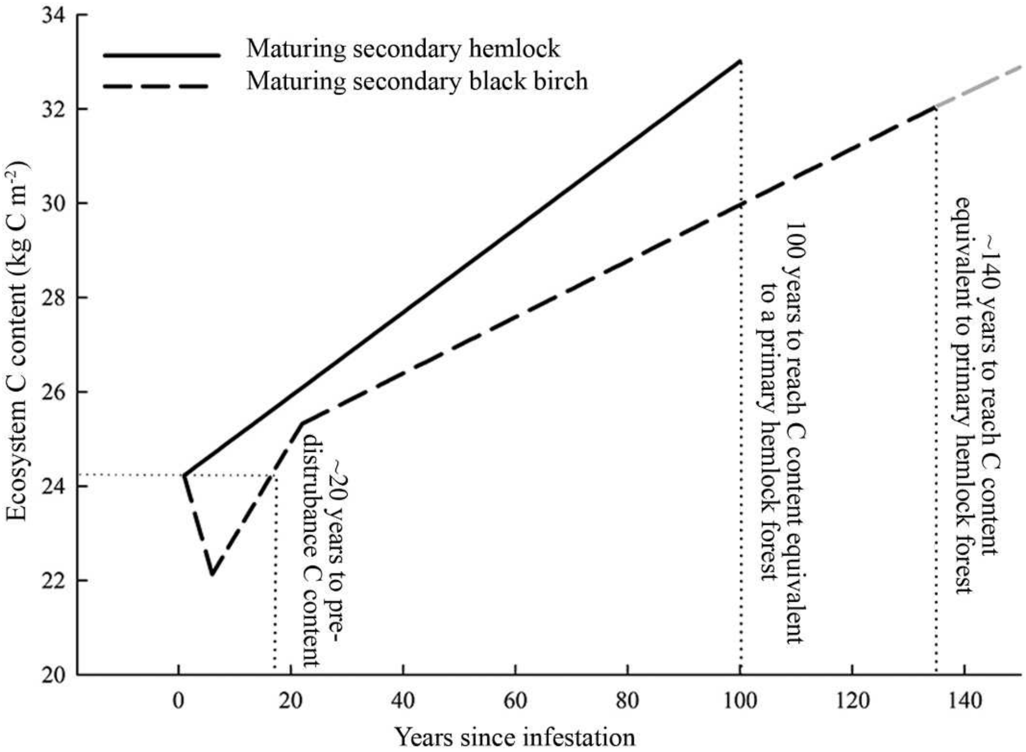

Fig. 5. Conceptual trajectory of C content (kg C m^{-2}) in a maturing hemlock stand type, and a maturing black birch stand type following disturbance.

rable data in the literature. Even if biomass in other stands were lower by as much as 35%, the C pool in biomass would remain comparable to that of hemlock forests in this region.

Gunderson and Holling (2001) defined ecosystem resilience as the amount of disturbance that can be sustained by a system such that it can maintain its control and structure. Carpenter et al. (2001) expanded upon this concept by arguing that ecosystem resiliency has three key properties: (1) as with Gunderson and Holling (2001), the ability to retain control of structure and function; (2) capability for self-organization; and (3) adaptive capacity (i.e., ability to cope with change). They also suggested four characteristic phases for ecosystem resiliency: (1) collapse (e.g., disturbance); (2) renewal or reorganization (e.g., new species); (3) rapid growth and (4) return to the original ecosystem state.

We used the pair-wise difference in C content and age between stand types to provide a conceptual understanding of the trajectory of change in C storage if secondary hemlock stand types were to remain uninfested, versus hemlock's replacement by black birch following disturbance (Fig. 5). This is not intended to be a quantitative model for the recovery of forests affected by the HWA, neither can we say anything about C balance in forests that fall outside the characteristics of those we studied here. This conceptual trajectory is to be seen as a possible outcome of the HWA invasion, and an illustration of the apparent resiliency of ecosystem C stocks to hemlock loss. This analysis suggests that ~20 years are necessary for C stocks to reach pre-disturbance values in rapidly regrowing black birch stands. Moreover, it appears that there is ~40 years difference between maturing secondary hemlock and black birch stands in their ability to reach C stocks observed in a primary hemlock stand.

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

Conclusions

The objective of this study was to examine stand types of differing age and species composition that may reflect the different stages of HWA effects on ecosystem C pools. We openly acknowledge that we cannot directly compare C pools among stand types because of uncertainties in land-use history and the timing of stand initiation, thus our analysis of resilience is suggestive of possible outcomes, not more. Can ecosystem C storage return to pre-HWA levels following the loss of hemlock? Our data suggest the answer is yes. HWA causes the loss (=collapse) of hemlock and appears to transfer C from live biomass to pools of CWD (Fig. 2). Black birch seeds germinate vigorously following hemlock loss (=renewal and reorganization) and rapidly accrue C in biomass (=rapid regrowth; Fig. 2A).

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