

Net primary production and soil respiration in New England hemlock forests affected by the hemlock woolly adelgid

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Abstract. The abundance of eastern hemlock (*Tsuga canadensis*) in eastern US forests has declined since the 1950s owing to the introduction of the non-native insect, hemlock woolly adelgid (HWA, *Adelges tsugae*). In southern New England, eastern hemlock is being replaced by the deciduous tree species, black birch (*Betula lenta*). To date there is little understanding of whether hemlock loss will fundamentally alter ecosystem C balance and component fluxes. In this study, we use a comparative approach to study potential changes in C fluxes and N cycling associated with HWA-induced hemlock decline and replacement. The stands include primary- and secondary-growth hemlock forests (>230 and 132 years old, respectively), recently disturbed stands (5 and 18 years old) that now have rapidly growing black birch saplings, and a mature black birch stand of age similar to the second-growth hemlock stand. We found that aboveground net primary production was higher in the aggrading black birch stand and significantly so at 18-years post-HWA compared to the secondary-hemlock stand it would likely replace. Rapid forest regrowth was accompanied by significantly higher rates of N uptake from the soil but also higher N-use efficiency because most of the N taken up from the soil was allocated to the production of wood with a high C-to-N ratio. In contrast to patterns of aboveground production, the rate of soil respiration was lowest in the young stands and not significantly different from the second-growth hemlock stand, suggesting little net effect of stand replacement on soil C efflux. The leaf litter decomposition study showed that black birch litter decomposed more rapidly than hemlock litter but that there was no effect of stand type on the rate of decomposition. Analyses of extracellular microbial exoenzyme activity painted a more nuanced pattern of variation among stands, with fine root biomass the only weakly explanatory variable. In combination with our prior work on C stocks, these results suggest that forests affected by HWA in southern New England will remain a sink for atmospheric CO₂ despite reorganization of stand structure and species composition.

Key words: aboveground net primary production (ANPP); black birch (*Betula lenta*); C flux; eastern hemlock (*Tsuga canadensis*); empirical long-term analysis; forest resilience; hemlock woolly adelgid (*Adelges tsugae*); N dynamics; New England.

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INTRODUCTION

Eastern hemlock (*Tsuga canadensis*) is considered a foundation species in temperate forests of eastern North America (Ellison et al. 2005). From a biogeochemical perspective, eastern hemlock's classification as a foundation species derives from the deep shade it creates (Canham et al. 1994) and its high concentration of polyphenolic compounds and lignin that contribute to slow rates of decomposition (Melillo et al. 1982, Jenkins et al. 1999), the accumulation of soil carbon (C) (Finzi et al. 1998a, Hadley 2000), acidic, base-poor soils (van Breemen et al. 1997, Finzi et al. 1998b) and low rates of nutrient mineralization (Finzi et al. 1998a, Kizilinski et al. 2002, Talbot and Finzi 2008). Hemlock is also one of the longest-lived tree species in eastern North America and is widely distributed. It is found as far north as New Brunswick, Canada, and within the United States throughout New England and the Appalachian Mountains south to Alabama. It is estimated that hemlock-dominated stands represent about 1×10^6 ha of the eastern US forest (McWilliams and Schmidt 2000, USDA Forest Service 2012).

The hemlock woolly adelgid (*Adelges tsugae*, herein HWA) was introduced to the mid-Atlantic region of the United States in the early 1950s (McClure 1990, Souto and Shields 2000). HWA is a sap-feeding insect of the order *Hemiptera*, which account for >40% of all non-indigenous forest insect species in the continental US (Aukema et al. 2010). The HWA feeds at the base of hemlock needles and it is considered a "high-impact" species because outbreaks can result in widespread hemlock mortality (Williamson and Fitter 1996, Hicke et al. 2012).

Infestation by the HWA results in needle loss that increases understory light availability and temperature (Orwig and Foster 1998, Eschtruth et al. 2006). In southern New England, this change in microclimate facilitates the germination and rapid growth of black birch (*Betula lenta*; Catovsky and Bazzaz 2000). Black birch is an early successional, fast-growing species (Lamson 1990) with very different growth attributes than hemlock that could alter the C balance of the stands it takes over, although the direction of the change is difficult to predict. On the one hand, black birch trees produce thin leaves that are

easily decomposed relative to hemlock needles (Cobb 2010). In combination with greater soil temperature (Ellison et al. 2010) and moisture content following hemlock loss (Daley et al. 2007), faster decomposition rates may lead to a loss of soil C, particularly from the thick organic horizons that characterize hemlock forests. On the other hand, the loss of soil C may be offset by high rates of primary production in young, rapidly aggrading black birch forests (Albani et al. 2010).

To date there has been no empirical assessment of the potential long-term impact of HWA on C fluxes from hemlock-dominated forests that transition to black birch (Peltzer et al. 2010). Hence, the objective of this paper is to further our understanding of these fluxes, focusing specifically on aboveground net primary production, decomposition, and soil respiration. This research builds on prior work using a comparative approach showing that there was little change in the quantity but significant variations in the distribution of C stored in biomass, coarse woody debris, and soil pools across a stand-age and species-composition gradient of hemlock to black birch (Raymer et al. 2013).

This research is framed by three broad hypotheses. First, given the relatively well documented changes in forest productivity with stand age (Ryan et al. 2004) and rapid black birch recruitment following hemlock loss, we hypothesize that aboveground net primary production (ANPP) is significantly higher in aggrading black birch stands than in the secondary-hemlock stands they replace. Feedbacks to decomposition and soil respiration, however, could be positive or negative and are hence more challenging to predict a priori (Hancock et al. 2008). The transition to black birch could yield higher rates of soil respiration because warm temperatures and labile litter inputs may prime the decomposition of soil organic matter (Drake et al. 2011). Alternatively, the loss of belowground biomass and C allocation could decrease the autotrophic contribution to total soil respiration (Högberg et al. 2001). Given the importance of belowground C allocation to soil respiration, however, our second hypothesis argues that lower root biomass in young black birch stands results in lower rates of soil respiration compared to the secondary-hemlock stands they replace, but that

Table 1. Overstory species composition and characteristics of the stands. Arrows for girdled and infested stands correspond to pre → post hemlock death. Former basal area per species for the girdled stand is shown in parentheses. Growing season air temperature and soil moisture is equivalent to May–October. Superscript letters represent significant differences among stands (* $P < 0.05$).

Characteristic	Primary hemlock	Secondary hemlock	Girdled	Post-HWA	Black birch
Basal area (m ² /ha)					
<i>Tsuga canadensis</i>	59.96	27.85	0.17 (36.64†)
<i>Betula lenta</i>	1.81	3.09	3.67 (3.17†)	7.10‡	27.53
<i>Acer rubrum</i>	3.51	4.54	3.30 (3.10†)	6.08	1.76
<i>Quercus rubra</i>	...	2.21	3.29 (0†)	3.32	1.74
<i>Pinus strobus</i>	...	6.53	4.41 (4.05†)	3.97	1.97
Others	4.21	4.33	1.31 (4.94†)	...	1.41
Total	69.48	48.54	51.65† → 16.15	43§ → 20.47	34.41
Stem 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
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					
Mean air temperature (°C)	17.4	17.4	17.4	18.0	17.4
Mean soil moisture (m ³ H ₂ O/m ³ soil)	0.21	0.20	0.23	0.20	0.22
Mineral 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
Live biomass (kg C m ⁻²)	18.1 ^A ± 0.1	13.5 ^{AB} ± 1.7	5.9 ^C ± 2.2	9.3 ^{BC} ± 2.7	17.4 ^A ± 3.4
Woody debris (kg C m ⁻²)	0.9 ^C ± 0.5	0.7 ^C ± 0.4	6.2 ^A ± 2.3	2.6 ^B ± 0.7	1.3 ^C ± 0.4
Soil C# (kg C m ⁻²)	16.3 ^A ± 1.2	10.6 ^C ± 1.3	11.3 ^C ± 1.0	11.8 ^C ± 0.2	13.6 ^B ± 0.5

† Ellison et al. (2010).

‡ All stems were dbh <10 cm.

§ Orwig and Foster (1998).

¶ Raymer et al. (2013).

Organic horizon to 45 cm mineral.

through time the rate of soil respiration in maturing black birch stands exceeds that measured in secondary-hemlock stands because of the recuperation of root biomass and large inputs of labile litter that stimulate soil organic matter decomposition. Recognizing that N supply influences forest productivity (Reich et al. 1997, Hancock et al. 2008, LeBauer and Treseder 2008, Falxa-Raymond et al. 2012) and that the loss of hemlock is likely to alter N cycling (Gower and Son 1992, Finzi et al. 1998a), our third hypothesis focuses on changes in N cycling. Specifically, we hypothesize that faster rates of decomposition increase N uptake in black birch compared to hemlock stands and N-use efficiency is lower because the production of N-rich foliage comprises a larger proportion of total biomass in aggrading black birch stands.

MATERIALS AND METHODS

Stands and climate

This research was conducted in central Massachusetts and Connecticut. We quantified C fluxes in: (1) a primary (old-growth) hemlock stand

>230 years old, representing potential future characteristics of a developing secondary-hemlock stand; (2) a 132-year-old secondary-hemlock stand representing the starting point of HWA infestation for most hemlock forests in this region; (3) a girdled hemlock stand, representing an early stage following hemlock death (5 years); (4) a 18-year-old post-HWA hemlock stand that currently has vigorously regrowing black birch saplings up to 5 m in height; and (5) a black birch stand ~135 years old, growing on former pastureland (Table 1). All measurements were made in four 30 × 30 m plots per stand ($n = 20$) between 2008 and 2010.

Three of the five stands were located at the Harvard Forest, Massachusetts (42°32' N, 72°11' W): the primary-hemlock stand (herein “primary hemlock”; Prospect Hill tract), the secondary-hemlock stand (herein “secondary hemlock”; Simes tract) and the girdled hemlock stand (herein “girdled”; Simes tract). Girdling was 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 caused by the HWA. All hemlock trees were dead by the time we initiated our measurements. The 18-year-old post-HWA stand (herein “post-HWA”) was located in the Connecticut River Valley (Burnham Brook, East Haddam, Connecticut, 41°28′ N, 72°19′ W). This stand got infested by HWA in the early 1990s. Today the stand is nearly monodominant in black birch. The mature black birch stand (herein “black birch”) was located near Black Pond on property belonging to the Harvard Conservation Trust (Harvard, Massachusetts, 42°31′ N, 71°32′ W). Descriptions of land history, climate, and soil, as well as a diagrammatic representation of the age relationships among the stands may be found in Raymer et al. (2013). Briefly, the primary-hemlock and post-HWA stands were once used as woodlots and the secondary hemlock, girdled, and black birch stands developed following pastureland abandonment. Soils were predominantly a sandy loam overlying glacial deposits of weathered gneiss, schist, and granite throughout all sites (Reynolds 1979). The soils are inceptisols and classified as Typic Dystrochrepts (Hill et al. 1980), and the depth to bedrock is <1 m throughout the study area. Climate is similar across all stands. Background nitrogen deposition at Harvard Forest is 0.66 g m⁻² yr⁻¹ (Munger et al. 1998).

Soil temperature at 10-cm depth data for the primary- and secondary-hemlock stands and the girdled stand were obtained from the Harvard Forest Data Archive for 2010 and 2011 (<http://harvardforest.fas.harvard.edu/data-archive>). At the post-HWA and mature black birch stands, we installed a soil temperature sensor at 5-cm depth in each of two randomly selected plots (HOBO Pendant Temperature/Light Data Logger; Onset Computer, Pocasset, Massachusetts, USA). Soil temperature was measured hourly from November 2010 to November 2011. Similarly, soil moisture was measured hourly at two different soil depths (5 cm and 15 cm) in a single plot in each stand (10HS Soil Moisture Smart Sensor; Onset Computer).

Net primary production

Wood net primary production was estimated from diameter growth based on tree cores. Ten trees were cored in each plot (200 trees total) in proportion to the relative importance value (RIV)

and diameter distribution of the dominant species in each plot (Raymer et al. 2013). For each plot, RIV was obtained by averaging the species’ relative basal area and relative density (Orwig and Foster 1998). Using an increment borer (Hagl f, Sweden), two cores were extracted from each tree, 1.25 m above ground level, 180° apart, and parallel to the topographic contour (Biondi 2000). We used a “bit starter” (Hagl f, Sweden) for hardwood species to ensure recent tree rings were not damaged during core extraction.

The cores were brought back to the lab, oven-dried for 48 hours at 60°C, glued to grooved plywood, and surfaced with four progressively finer grit sand papers, down to 400 grit, to reveal the wood’s cellular structure (Davis et al. 2007). Annual ring widths were measured using a Velmex UniSlide (Velmex, Bloomfield, New York, USA) and a stereoscope. The software MeasureJ2X (Project J2X, VoorTech Consulting, Holderness, New Hampshire, USA) was used to store the data. Ring-width increment was used to estimate the relative growth rate (RGR, mm cm⁻¹ yr⁻¹) over the most recent 5-year period, and the average RGR for each species in each stand was applied to the trees that were not cored. Species-specific allometric equations (Raymer et al. 2013) were used to calculate the production of woody biomass in each plot.

Foliage production was estimated as the sum of foliage biomass increment and turnover (Schlesinger and Bernhardt 2013). Foliage biomass increment was estimated from the allometric equations presented in Raymer et al. (2013) and foliage turnover was estimated on-site using litterfall dry mass. Litter baskets were 39 cm in diameter and 45 cm high, with an additional 5–10 cm gap between the ground and the collecting fiberglass mesh to avoid litter moisture. The location of each litter basket was determined through randomized paired coordinates. Two litter baskets were installed in each plot ($n = 40$) in October of 2010. We collected litter six times through October 2011, dried the samples at 60°C, sorted them by species, and weighed each sample. The annual rate of foliage production (g m⁻² yr⁻¹) was added to the production of woody biomass to obtain an estimate of above-ground net primary production (ANPP).

Soil respiration

The rate of soil respiration (i.e., C emitted from the soil; R_s , $\text{g C m}^{-2} \text{d}^{-1}$) was measured every five weeks with a closed-path infra-red gas analyzer (IRGA) system (LI-COR 6400; LI-COR, Lincoln, Nebraska, USA) coupled to a soil CO_2 flux chamber. R_s was measured from October 2010 to November 2011, with the exception of periods of snow cover (November 2010 through March 2011). Six 10-cm diameter polyvinyl chloride (PVC) collars were installed per plot ($n = 24$ per stand). Three consecutive measurements were made on each collar over a ~5-minute period between 10h30 and 16h00, the period of maximum CO_2 efflux at the Harvard Forest (Drake et al. 2011). The first measurement of each cycle was excluded to avoid a possible disturbance effect as the chamber was placed on the collar. On each sampling date soil temperature was measured at 5-cm depth, directly adjacent to each collar.

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

$$R_s = \beta \times \exp(k \times T) \quad (1)$$

where β is the y-intercept term, k is the exponential decay coefficient, and T is soil temperature ($^{\circ}\text{C}$). The k parameter was then used to calculate plot-specific apparent Q_{10} of soil respiration—the increase in R_s with every 10°C increase in soil temperature:

$$Q_{10} = \exp(10 \times k). \quad (2)$$

The modeled exponential function (Eq. 1) was also used to estimate R_{10} , the rate of soil CO_2 efflux at 10°C for each of the stands:

$$R_{10} = \beta \times \exp(10 \times k). \quad (3)$$

R_{10} expresses R_s at a common temperature and therefore enables meaningful comparisons among stands.

Using the continuous record of soil temperature from each stand, the rate of soil respiration was estimated for each plot at the hourly time scale:

$$R_s = R_{10} \times Q_{10}^{[(T-10)/10]}. \quad (4)$$

R_s across the growing season (April through November) was calculated as the sum of R_s estimated at the hourly time scale, averaged across plots.

Litter decomposition

The rate of foliage decomposition was estimated from litter bags incubated in the field for a period of 24 months (Singh and Gupta 1977). One gram of hemlock needle litter and 2 g of black birch leaf litter were enclosed in polyester litter bags (5×10 cm and 10×10 cm, respectively) with mesh size of 1 mm and placed under the litter layer in a 1×1 m subplot in each plot. A total of 320 litter bags were deployed in November 2009 (4 plots \times 5 stands \times 4 sampling dates \times 2 species \times 2 replicates); litter of both species was left to decompose separately in all plots. Two litter bags of each species were sampled on four dates: April 2010 (after 5 months), August 2010 (9 months), November 2010 (12 months) and November 2011 (24 months). The litter bags were brought back to the lab, dried at 65°C for a minimum of 48 hours, and weighed. The samples were also analyzed for C content using an elemental analyzer (NC2500 Elemental Analyzer, CE Elantech, Lakewood, New Jersey, USA). These data were used to express mass loss and C content remaining on each sampling date as a fraction of the original litter mass.

Soil exoenzyme activity

The activity of microbial extracellular enzymes (herein “exoenzymes”) was measured in the surface organic horizon and in mineral soil to a depth of 45 cm (Weintraub et al. 2007). We measured the activity of enzymes that degrade (1) labile C pools such as cellulose and cellobiose [α -1,4-glucosidase (α G), β -1,4-glucosidase (β G) and cellobiohydrolase (CBH)], (2) recalcitrant C pools such as lignin and polyphenols [peroxidase (Perox) and phenol oxidase (PhOx)], and (3) depolymerize N [β -1,4-N-acetylglucosaminidase (NAG)].

Soils were collected between June and September 2008. We used a 10×10 cm frame to collect three organic horizon samples in each of the 20 plots. Directly below, mineral soil cores (5 cm diameter \times 15 cm depth) were removed in three 15-cm depth increments. The three replicates of each plot were homogenized, such that $n = 80$ (5 stands \times 4 plots \times 4 soil depths). The samples were brought back to the laboratory, sieved, roots removed and then frozen at -80°C until laboratory analysis using the methods described in Drake et al. (2013).

Table 2. Annual aboveground biomass increments, foliage turnover, and aboveground net primary production (ANPP; $\text{g C m}^{-2} \text{ yr}^{-1}$; mean ± 1 SE). Significant differences among stands are indicated by different superscript letters (* $P < 0.05$).

Component	Primary hemlock	Secondary hemlock	Girdled	Post-HWA	Black birch
Increments					
Wood					
Conifer	84 ^A \pm 5	64 ^A \pm 4	41 ^{AB} \pm 19	0 ^B \pm 0	66 ^A \pm 20
Hardwood	27 ^B \pm 12	60 ^B \pm 8	272 ^B \pm 79	687 ^A \pm 107	141 ^B \pm 9
Foliage					
Conifer	4 ^A \pm 1	2 ^B \pm 0.1	1 ^{BC} \pm 0.5	0 ^C \pm 0	2 ^{AB} \pm 0.2
Hardwood	1 ^B \pm 0.2	1 ^B \pm 0.1	3 ^B \pm 1	17 ^A \pm 3	2 ^B \pm 0.1
Total	115 ^B \pm 11	127 ^B \pm 5	317 ^B \pm 63	704 ^A \pm 110	211 ^B \pm 19
Turnover					
Foliage					
Conifer	123 ^A \pm 6	118 ^A \pm 17	46 ^B \pm 29	0 ^B \pm 0	4 ^B \pm 2
Hardwood	23 ^D \pm 8	86 ^C \pm 17	78 ^C \pm 13	242 ^A \pm 11	179 ^B \pm 5
Total	146 ^{BC} \pm 5	204 ^A \pm 36	124 ^C \pm 17	242 ^A \pm 11	183 ^B \pm 3
ANPP					
Conifer	210 ^A \pm 10	204 ^{AB} \pm 38	87 ^{BC} \pm 46	0 ^C \pm 0	72 ^{BC} \pm 19
Hardwood	51 ^C \pm 20	146 ^{BC} \pm 24	354 ^B \pm 92	946 ^A \pm 117	322 ^{BC} \pm 13
Total	261 ^C \pm 15	330 ^B \pm 22	442 ^B \pm 55	946 ^A \pm 117	393 ^B \pm 21

Nitrogen

Plant tissues and soils were analyzed for %N on an elemental analyzer (NC 2500 Elemental Analyzer, CE Elantech). The N content of the different pools was estimated as %N multiplied by the mass of each pool (Finzi et al. 2002). With these data we calculated various metrics of plant N uptake and N-use efficiency.

The annual N requirement to support ANPP (N_{req} ; $\text{g N m}^{-2} \text{ yr}^{-1}$) was calculated as:

$$N_{\text{req}} = N_{\text{wood inc}} + N_{\text{foliage inc}} + N_{\text{litterfall}} \quad (5)$$

where $N_{\text{wood inc}}$, $N_{\text{foliage inc}}$, and $N_{\text{litterfall}}$ are the amount of N found in the annual increment of wood, foliage, and litterfall, respectively. Every year a substantial amount of N in foliage is retranslocated prior to senescence (Chapin and Kedrowski 1983, Aerts 1996). This quantity (N_{retrans} ; $\text{g N m}^{-2} \text{ yr}^{-1}$) is calculated as:

$$N_{\text{retrans}} = (\text{litterfall} \times \%N_{\text{green}}) - (\text{litterfall} \times \%N_{\text{litter}}) \quad (6)$$

where litterfall is aboveground litterfall mass ($\text{g N m}^{-2} \text{ yr}^{-1}$), $\%N_{\text{green}}$ is N concentration in green leaves and $\%N_{\text{litter}}$ is N concentration in leaf litter. The annual rate of N uptake from the soil (N_{uptake} ; $\text{g N m}^{-2} \text{ yr}^{-1}$) is estimated as the difference between the annual requirement and retranslocation:

$$N_{\text{uptake}} = N_{\text{req}} - N_{\text{retrans}} \quad (7)$$

Finally, the efficiency of N use (NUE, dimensionless) is defined following Vitousek (1982):

$$\text{NUE} = \text{ANPP}/N_{\text{req}} \quad (8)$$

Statistical analysis

One-way ANOVA with Tukey's multiple comparison procedure was used to assess differences in C and N fluxes, N pools, and C:N ratios among the stands. Repeated-measures ANOVA were applied to soil respiration and monthly rate of foliar mass loss. Comparisons of enzyme activity among stands were based on the weighted-average activity based on the concentration of C in each depth increment. Analyses were performed using RStudio (R Core Development Team, version 0.94.110) and Matlab version 7.11.0 (MathWorks, Natick, Massachusetts, USA). Assumptions of normality and homogeneity of variance were met. Tukey's multiple comparison test protected the experiment-wise alpha at $P < 0.05$. Values are expressed as mean ± 1 SE.

RESULTS

Aboveground net primary production

There were significant ($P < 0.05$) differences among stands in aboveground biomass increments, turnover, and ANPP (Table 2). The increment in hemlock woody biomass was highest in the primary-hemlock stand and, for

black birch, in the post-HWA stand (Table 2). Increments in foliage biomass were generally far smaller, with significantly more in black birch foliage produced in the post-HWA stand than in all others. The total increment in biomass was significantly higher in the post-HWA stand than in all others.

The turnover of hemlock foliage was significantly higher in the primary- and second-growth hemlock than other stands (Table 2). The turnover of black birch foliage was highest in the post-HWA stand, intermediate in the black birch stand, and lowest in the primary-growth hemlock stand. The total turnover in biomass was highest in the post-HWA and second-growth hemlock stands, intermediate in the primary-growth hemlock and black birch stands, and lowest in the girdled stand.

Hemlock ANPP, the sum of biomass increments and turnover, was highest in the primary- and second-growth hemlock stands and lowest in the post-HWA stand since hemlock is absent (Table 2, Fig. 1A). Black birch ANPP was highest in the post-HWA stand, intermediate in the girdled and black birch stands, and lowest in the hemlock stands. Total ANPP was highest in the post-HWA stand, significantly lower in the black birch, second-growth hemlock, and girdled stands, and lowest in the primary-growth hemlock stand.

Soil respiration

R_s increased exponentially with soil temperature ($r^2 = 0.83$; Fig. 2A) and maximum rates were measured in July and August ($P < 0.0001$; Fig. 2B). There were no significant differences in the temperature sensitivity of soil respiration (Q_{10} , range: 3.3–4) among stands ($P = 0.10$; Table 3). There were, however, significant ($P < 0.05$) variations in R_s among stands. Fluxes were highest in the primary-hemlock and black birch stands, and lowest in the girdled stand (Fig. 2C, D).

Foliar decomposition

Black birch litter decomposed significantly faster than hemlock needles ($P < 0.001$; Fig. 3). There was no significant effect of stand on the rate of litter decomposition for either hemlock or black birch.

Soil exoenzyme activity

Activity of exoenzymes involved in the depolymerization of labile C substrates was significantly higher in the primary-growth hemlock stand (Table 4). There were no significant differences in labile-C exoenzyme activity in the mineral soil horizon. There was a similar pattern in the activity of exoenzymes depolymerizing recalcitrant C substrates, with greater overall activity in the organic horizon in the primary-growth hemlock stand and no significant difference in mineral soil activity between stands (Table 5). The activity of exoenzymes depolymerizing labile and recalcitrant organic matter was positively correlated with fine root biomass ($r^2 = 0.50$, $P < 0.0001$; data not shown). Nitrogen-related enzyme activity (NAG) in the organic horizon was highest in the post-HWA stand and lowest in the girdled stand (Table 6). In the mineral soil, NAG activity was highest in the secondary hemlock and lowest in the primary-hemlock stand.

Nitrogen

The quantity of N in biomass was significantly higher in the black birch stand (Table 7). Total N in the soil was also significantly higher in the black birch stand than all others with >90% of this N found in the mineral horizon.

The annual increment of N in wood and foliage was significantly higher in the post-HWA stand than all other stands ($P < 0.0005$; Table 7). The turnover of N in foliage was also highest in the post-HWA stand but in this instance it was not significantly different from the secondary-hemlock and black birch stands. The annual requirement for N was therefore highest in the post-HWA stand, intermediate in the second-growth hemlock and black birch stands, and lowest in the primary-growth hemlock and girdled stands (Table 7).

The total quantity of N retranslocated from foliage was lowest in the primary-hemlock stand, intermediate in the secondary-hemlock stand, and highest in the other stands (Table 7). Despite high retranslocation, annual N uptake from the soil was also highest in the post-HWA stand and lowest in the girdled stand. Nitrogen-use efficiency (NUE) was significantly higher in the girdled and post-HWA stands than in the other stands.

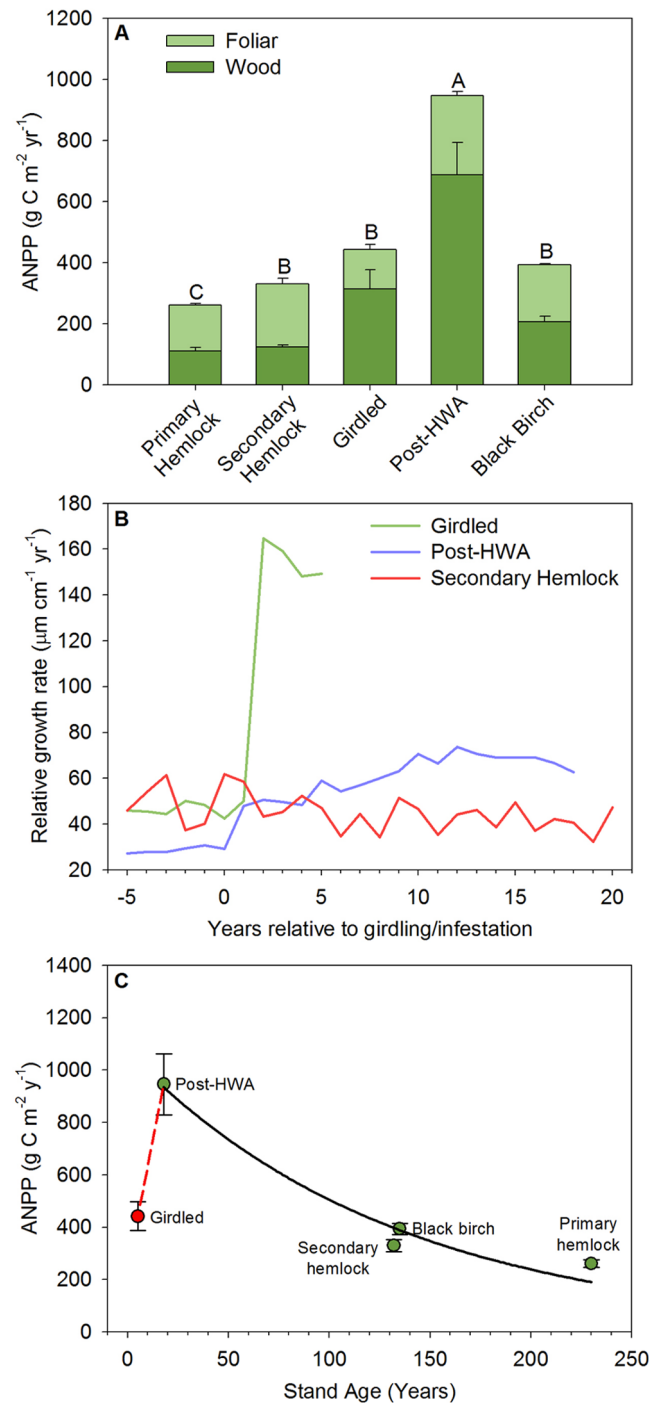


Fig. 1. (A) Aboveground net primary production ($\text{g C m}^{-2} \text{yr}^{-1}$) measured from woody and foliar increment, and foliar turnover; (B) relative growth rate in the secondary-hemlock, girdled and post-HWA stands, and (C) aboveground net primary production (ANPP) in relation to stand age. In (A), letters denote significant differences in total ANPP (foliar + wood, * $P < 0.05$). For statistics on the different components, see Table 2. In (C), the red circle indicates the age of the young stand following girdling (5 years old). Remnant hardwood trees are up to 132 years old.

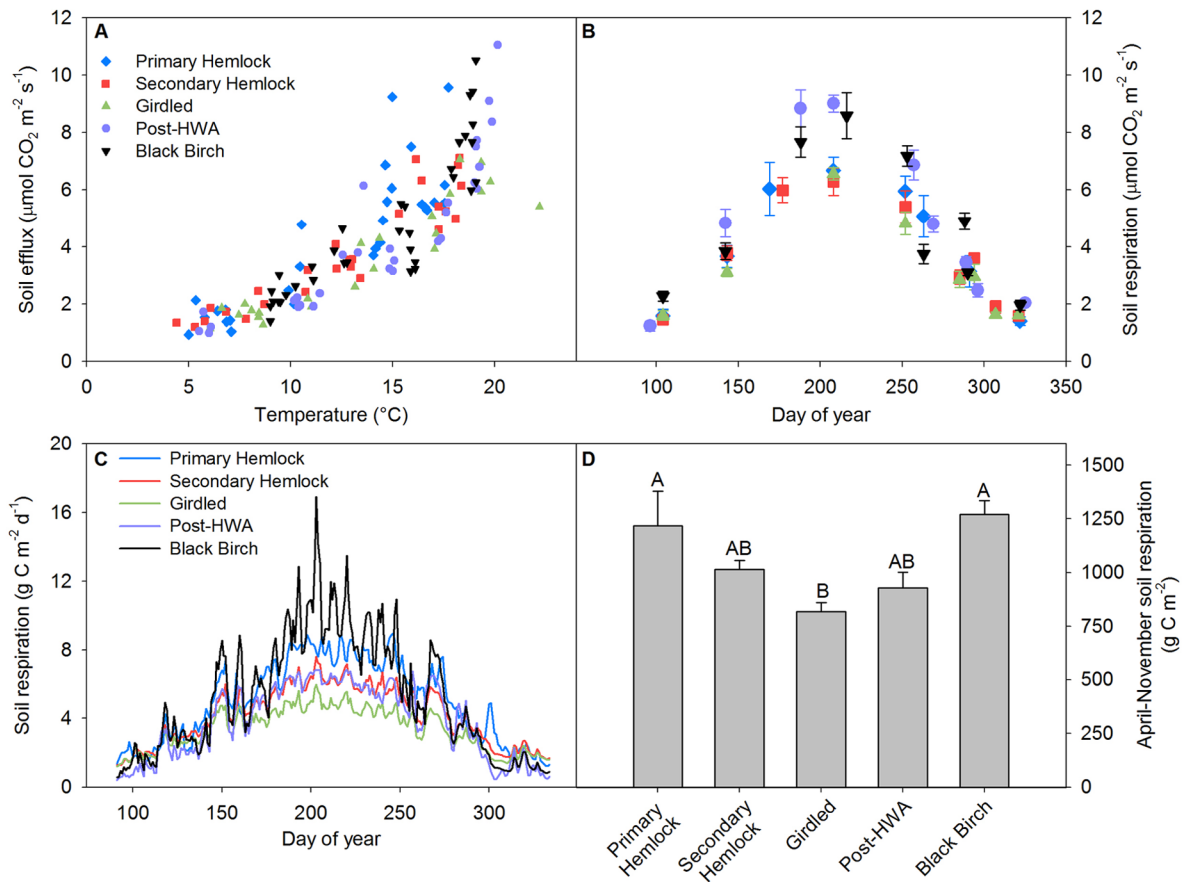


Fig. 2. (A) Measured soil CO₂ efflux (μmol CO₂ m⁻² s⁻¹) and corresponding soil temperature (°C); soil efflux = $0.8101 \times \exp(0.1141T)$ ($r^2 = 0.75$). Also, (B) field measurements of soil efflux (μmol CO₂ m⁻² s⁻¹; mean ± SE), (C) modeled daily soil respiration (g C m⁻² d⁻¹), and (D) total soil respiration from April to November 2011. Different superscript letters indicate a significant difference (* $P < 0.05$) among stands.

DISCUSSION

Throughout much of the northeastern US, black birch is replacing hemlock stands killed by the HWA (Orwig and Foster 1998, Orwig et al. 2002). We studied hemlock and black birch

stands of varying ages to assess possible changes in C fluxes associated with hemlock decline and replacement. We hypothesized that (1) ANPP would be significantly higher in young, aggrading black birch stands than in the secondary-hemlock stands they replace. This hypothesis

Table 3. Stand-specific exponential relationships between soil temperature (°C) and soil respiration (μmol CO₂ m⁻² s⁻¹); y-intercept term (β), exponential coefficient (k), r^2 , Q_{10} , and R_{10} (mean ± SE). No significant differences were found among stands (β , $P = 0.08$; k , $P = 0.07$; Q_{10} , $P = 0.11$; R_{10} , $P = 0.09$).

Stand	β	k	r^2	Q_{10}	R_{10}
Primary hemlock	0.88 ± 0.17	0.12 ± 0.01	0.93 ± 0.02	3.42 ± 0.31	2.89 ± 0.43
Secondary hemlock	0.87 ± 0.10	0.11 ± 0.01	0.91 ± 0.03	3.04 ± 0.28	2.58 ± 0.11
Girdled	0.71 ± 0.12	0.11 ± 0.01	0.92 ± 0.04	3.19 ± 0.36	2.15 ± 0.13
Post-HWA	0.44 ± 0.09	0.15 ± 0.01	0.92 ± 0.02	4.50 ± 0.31	1.88 ± 0.23
Black birch	0.53 ± 0.13	0.15 ± 0.02	0.87 ± 0.02	4.69 ± 0.96	2.14 ± 0.26

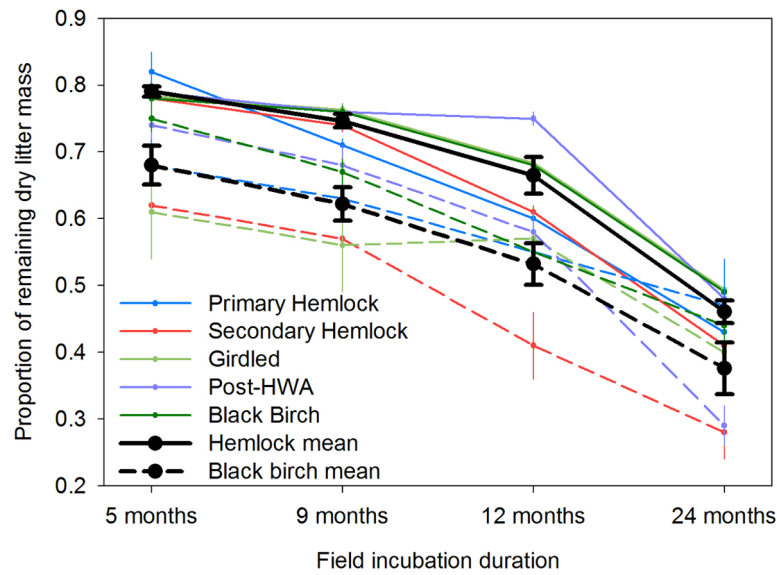


Fig. 3. Proportion of remaining dry mass of hemlock needles and black birch leaves in litter bags along four different harvesting periods. Litter bags were installed in the five stands in November 2009. Solid and dashed lines indicate hemlock and black birch litter, respectively.

was supported by the data indicating higher ANPP in the post-HWA stand and its decline with stand age (Table 2, Fig. 1A, C). We also hypothesized that (2) the loss of live root biomass following hemlock death would lower rates of R_s in young black birch stands compared to the secondary-hemlock stands they replaced, but that through time the rate of R_s in maturing black birch stands would exceed that measured in secondary-growth hemlock stands because of the recuperation of live root biomass and increase in inputs of labile litter that stimulate soil organic matter decomposition. We largely accept the first portion of this hypothesis given that R_s across the growing season was signifi-

cantly different between the secondary-hemlock and girdled stand types, but also note the rapid recuperation of R_s in the post-HWA stand (Fig. 2C, D). The latter portion of this hypothesis is rejected because there was no significant difference among stands, although this must be qualified by the age of the mature black birch stand. It is possible that 100 years hence (i.e., age of primary hemlock stand) the rate of soil respiration will be significantly higher in the second growth black birch stand (Fig. 2D). Finally, we hypothesized that (3) N uptake would be higher and that NUE would be lower in black birch compared to hemlock stands because N-rich leaves would comprise a larger proportion of

Table 4. Soil labile C degradation exoenzyme activity ($\text{mmol substrate converted m}^{-2} \text{ h}^{-1}$; mean \pm SE) in the organic horizon and mineral soil. Different superscript letters indicate a significant difference ($*P < 0.05$) among stands.

Stand	αG		βG		CBH		$\Sigma \alpha\text{G}, \beta\text{G}, \text{CBH}$	
	Organic horizon	Mineral soil	Organic horizon	Mineral soil	Organic horizon	Mineral soil	Organic horizon	Mineral soil
Primary hemlock	0.20 \pm 0.07	0.20 \pm 0.03	10.6 ^A \pm 4.0	11.0 \pm 1.6	4.34 ^A \pm 1.63	7.06 \pm 2.86	15.1 ^A \pm 5.3	18.3 \pm 4.5
Secondary hemlock	0.02 \pm 0.01	0.19 \pm 0.03	0.8 ^B \pm 0.2	9.9 \pm 4.6	0.22 ^B \pm 0.08	3.83 \pm 1.88	1.0 ^B \pm 0.3	14.0 \pm 6.4
Girdled	0.11 \pm 0.07	0.22 \pm 0.05	4.3 ^{AB} \pm 1.4	10.7 \pm 1.1	0.71 ^B \pm 0.27	3.63 \pm 1.58	5.1 ^{AB} \pm 1.6	14.5 \pm 2.0
Post-HWA	0.20 \pm 0.04	0.15 \pm 0.02	10.5 ^A \pm 2.7	6.0 \pm 2.4	0.48 ^B \pm 0.23	2.55 \pm 1.30	11.2 ^{AB} \pm 3.0	8.7 \pm 3.7
Black birch	0.11 \pm 0.03	0.27 \pm 0.07	1.9 ^{AB} \pm 1.0	9.0 \pm 2.9	0.64 ^B \pm 0.24	4.05 \pm 1.54	2.7 ^{AB} \pm 1.0	13.4 \pm 4.4

Table 5. Soil recalcitrant C degradation exoenzyme activity ($\text{mmol substrate converted m}^{-2} \text{ h}^{-1}$; mean \pm SE) in the organic horizon and mineral soil. Different superscript letters indicate a significant difference ($* P < 0.05$) among stands.

Stand	Phenol oxidase		Peroxidase		Σ Phenol Oxidase and Peroxidase	
	Organic horizon	Mineral soil	Organic horizon	Mineral soil	Organic horizon	Mineral soil
Primary hemlock	25.7 ^A \pm 5.3	25.8 ^{AB} \pm 4.2	20.3 ^A \pm 6.4	41.5 \pm 11.3	46.0 ^A \pm 10.0	67.3 \pm 10.7
Secondary hemlock	7.5 ^B \pm 2.2	58.4 ^A \pm 6.0	7.3 ^{AB} \pm 2.5	45.6 \pm 18.7	14.8 ^B \pm 3.0	104.0 \pm 23.6
Girdled	9.4 ^B \pm 3.3	39.5 ^{AB} \pm 13.0	6.9 ^{AB} \pm 1.4	37.1 \pm 12.2	16.3 ^B \pm 4.6	76.5 \pm 20.6
Post-HWA	11.9 ^{AB} \pm 3.0	22.4 ^B \pm 5.0	8.7 ^{AB} \pm 1.8	25.5 \pm 0.7	20.6 ^B \pm 4.7	47.8 \pm 5.5
Black birch	6.8 ^B \pm 1.7	55.3 ^{AB} \pm 7.8	2.4 ^B \pm 1.0	24.7 \pm 11.0	9.2 ^B \pm 2.2	79.9 \pm 17.3

total biomass in aggrading black birch stands. Consistent with this hypothesis, the rapidly aggrading post-HWA stand had higher rates of N uptake than either hemlock stands (Table 7). In contrast to this hypothesis, however, NUE was generally higher in the black birch compared to hemlock stands. Below we discuss the implications of these results.

Aboveground net primary production

In prior research, we found that the quantity of C stored in the recently girdled and post-HWA stands was not significantly different from that in the second-growth hemlock stand, raising the question of what processes account for this unexpected pattern given the loss of live biomass (Raymer et al. 2013). In the girdled stand, the similarity in C storage largely reflects the recent transfer of C to the coarse woody debris (CWD) pool. In this stand, CWD are largely composed of intact snags and logs with high wood density as a result of relatively little decomposition (Raymer et al. 2013). This does not, however, appear to be the case in the post-HWA stand where the CWD pool is $<50\%$ of that found in the girdled stand, despite both stands having similar pre-disturbance hemlock biomass (Table 1, Raymer et al.

2013). Rather it appears that high rates of ANPP in the post-HWA stand result in a rapid recovery of C in live biomass and hence ecosystem C stock that rivals that found in the stand prior to hemlock loss (Fig. 1A, Raymer et al. 2013).

Declines in ANPP with stand age are a common feature of forested ecosystems (e.g., Ryan et al. 2004). We observed the same pattern across the chronosequence studied here (Fig. 1C). ANPP was highest in the 18-year-old post-HWA stand, declined in the ~ 135 -year-old black birch and second-growth hemlock stands, and was lowest in the >230 -year-old primary-growth hemlock stand. Excluding the girdled stand, there was a highly significant negative correlation between ANPP and stand age ($\text{ANPP} = 1069 \times \exp(-0.0075 \text{ yr})$; $P < 0.01$, $r^2 = 0.97$; Fig. 1C). The girdled stand is difficult to place along the chronosequence given the mix of older non-hemlock canopy trees and very young black birch saplings. It could, for example, reflect ANPP in a “young” stand because of the massive recruitment of vigorously growing black birch saplings (Table 1) and an increase in the growth rate of the remaining canopy trees presumably because of a reduction in competition (Fig. 1B). Alternatively, the girdled stand could be considered 132 years of age because remnant trees accounted for the majority of ANPP (data not shown). Plotted at 132 years of age, the girdled stand fits equally well on the regression line relating ANPP to stand age for the other stands (Fig. 1C).

The presence of HWA was first recorded in the second-growth hemlock stand in 2008 and in 2009 HWA was found on 30–40% of hemlock stems (Ellison et al. 2010). This raises the possibility that the present estimate of ANPP is lower than would be expected in the absence of

Table 6. Soil N degradation exoenzyme activity ($\text{mmol substrate converted m}^{-2} \text{ h}^{-1}$, mean \pm SE) in the organic horizon and mineral soil. Different superscript letters indicate a significant difference ($* P < 0.05$) among stands.

Stand	Organic horizon	Mineral soil
Primary hemlock	5.0 ^{AB} \pm 0.7	2.7 ^B \pm 0.6
Secondary hemlock	2.8 ^{AB} \pm 1.4	7.2 ^A \pm 1.0
Girdled	1.9 ^B \pm 0.4	6.0 ^{AB} \pm 1.1
Post-HWA	5.2 ^A \pm 0.4	6.2 ^{AB} \pm 1.1
Black birch	2.8 ^{AB} \pm 0.7	4.4 ^{AB} \pm 0.5

Table 7. Nitrogen pool size and fluxes (mean \pm SE). Fine, small, and coarse roots are <2 mm, 2–10 mm and >10 mm diameter, respectively. Fine, small, and coarse woody debris are <1 cm, 1–10 cm and >10 cm, respectively. Different superscript letters indicate a significant difference (* $P < 0.05$) among stands.

Component	Primary hemlock	Secondary hemlock	Girdled	Post-HWA	Black birch
Pools (g N m⁻²)					
Biomass					
Conifer foliage	7.7 ^A \pm 1.8	6.7 ^A \pm 0.4	0.8 ^B \pm 0.4	0.0 ^B \pm 0.0	0.5 ^B \pm 0.1
Deciduous foliage	0.9 ^C \pm 0.4	3.0 ^{BC} \pm 0.4	2.5 ^{BC} \pm 0.6	5.2 ^{AB} \pm 0.7	7.9 ^A \pm 0.9
Conifer wood	10.1 ^A \pm 2.7	8.1 ^{AB} \pm 0.8	1.1 ^{BC} \pm 0.5	0.0 ^C \pm 0.0	0.3 ^C \pm 0.1
Deciduous wood	2.5 ^C \pm 0.9	9.8 ^{BC} \pm 1.6	8.0 ^{BC} \pm 2.6	15.7 ^B \pm 2.2	31.1 ^A \pm 3.3
Fine roots	10.1 ^A \pm 0.6	5.6 ^B \pm 0.8	6.3 ^{AB} \pm 0.1	5.5 ^B \pm 0.5	8.9 ^{AB} \pm 2.1
Small and coarse roots	1.5 \pm 0.5	0.5 \pm 0.1	0.4 \pm 0.1	0.8 \pm 0.1	1.6 \pm 0.7
Fine woody debris	0.60 ^A \pm 0.14	0.30 ^{AB} \pm 0.02	0.32 ^{AB} \pm 0.05	0.22 ^B \pm 0.04	0.50 ^{AB} \pm 0.01
Small and coarse woody debris	5.9 ^{CD} \pm 1.7	3.3 ^D \pm 1.0	36.5 ^A \pm 1.6	20.7 ^B \pm 0.6	12.0 ^C \pm 2.1
Total in biomass	33.8 ^B \pm 6.3	33.0 ^B \pm 1.7	51.8 ^{AB} \pm 4.2	44.9 ^{AB} \pm 3.4	54.6 ^A \pm 5.2
Soil					
Organic horizon	138.1 ^A \pm 17.8	56.6 ^B \pm 10.2	88.9 ^{AB} \pm 16.1	110.2 ^{AB} \pm 16.5	43.6 ^B \pm 2.6
Mineral soil	472.6 ^C \pm 6.5	567.5 ^B \pm 18.5	514.6 ^C \pm 7.3	522.5 ^{AB} \pm 11.6	662.3 ^A \pm 12.9
Total in soil	610.6 ^B \pm 17.7	624.0 ^B \pm 29.1	599.1 ^B \pm 15.1	620.3 ^B \pm 7.6	706.9 ^A \pm 14.1
Fluxes (g N m⁻² yr⁻¹)					
Increments					
Conifer foliage	0.07 ^A \pm 0.03	0.04 ^{AB} \pm 0.01	0.03 ^{AB} \pm 0.01	0.0 ^B \pm 0.0	0.08 ^A \pm 0.02
Deciduous foliage	0.01 ^B \pm 0.01	0.03 ^B \pm 0.01	0.13 ^B \pm 0.03	0.64 ^A \pm 0.12	0.06 ^B \pm 0.01
Conifer wood	0.07 ^{AB} \pm 0.02	0.07 ^{AB} \pm 0.04	0.05 ^{AB} \pm 0.02	0.0 ^B \pm 0.0	0.09 ^A \pm 0.03
Deciduous wood	0.04 ^B \pm 0.02	0.11 ^B \pm 0.02	0.49 ^B \pm 0.14	1.12 ^A \pm 0.18	0.26 ^B \pm 0.03
Total in increments	0.19 ^B \pm 0.06	0.25 ^B \pm 0.01	0.69 ^B \pm 0.13	1.76 ^A \pm 0.3	0.50 ^B \pm 0.09
Turnover					
Conifer foliage	2.6 ^A \pm 0.1	2.6 ^A \pm 0.6	0.66 ^B \pm 0.41	0.0 ^B \pm 0.0	0.05 ^B \pm 0.02
Deciduous foliage	0.5 ^C \pm 0.2	1.8 ^B \pm 0.3	1.85 ^B \pm 0.39	5.3 ^A \pm 0.3	4.6 ^A \pm 0.2
Total in turnover	3.1 ^B \pm 0.2	4.4 ^A \pm 0.5	2.5 ^B \pm 0.2	5.3 ^A \pm 0.3	4.7 ^A \pm 0.2
Aboveground annual N requirement	3.3 ^C \pm 0.2	4.7 ^{BC} \pm 0.5	3.2 ^C \pm 0.2	7.0 ^A \pm 0.6	5.2 ^B \pm 0.2
Aboveground NUE	79.9 ^B \pm 1.9	74.5 ^B \pm 0.3	137.0 ^A \pm 10.3	133.1 ^A \pm 7.4	76.4 ^B \pm 2.2
Aboveground N retranslocation	0.6 ^B \pm 0.2	1.6 ^{AB} \pm 0.4	2.1 ^A \pm 0.5	2.6 ^A \pm 0.1	2.4 ^A \pm 0.0
N uptake for ANPP	2.7 ^{BC} \pm 0.1	3.0 ^{AB} \pm 0.2	1.1 ^C \pm 0.5	4.5 ^A \pm 0.6	2.7 ^{BC} \pm 0.2

HWA. When making our measurements from 2008 to 2011, we visually confirmed the presence of HWA but also noted that affected canopy area across all stems was \ll 5%, with no signs of incipient needle loss or decline in tree vigor. This suggests that HWA likely had little effect on the estimate of ANPP during the study period. Consistent with this suggestion, there is no evidence for a decline in tree growth rate following the occurrence of HWA (Fig. 1B).

Decomposition and soil respiration

Black birch leaves decomposed significantly faster than hemlock needles (Fig. 3). Given that the C:N ratio of black birch leaves was significantly lower than that of hemlock needles (data not shown) and that narrow- compared to wide-C:N litter tends to decompose more rapidly, it seems likely that this is the dominant control over litter decomposition (Melillo et al. 1982). Notably, there was no effect of stand on decomposition rate, reinforcing the idea that

litter chemistry, rather than microbial community, is the dominant factor influencing the initial stages of litter decomposition on the surface of the organic horizon.

Rates of R_s were not significantly different in the second-growth hemlock, girdled, and post-HWA stands (Fig. 2D). This ran counter to the first portion of hypothesis 2 which argued that decreases in root biomass would result in significantly lower R_s . However, Savage et al. (2009) measured R_s in the girdled stand for a period of three years beginning immediately following the application of the treatment. In contrast to our measurements beginning five years post-treatment, they found significant reductions in R_s . Collectively, these data suggest a rapid recovery of belowground processes (e.g., root production and respiration, exudation, microbial activity) following disturbance by HWA.

The rate of R_s in the black birch stand was greater, although not statistically, than that in the

second-growth hemlock stand and was similar to rates measured in the primary-growth hemlock stand (Fig. 2C, D). Overall, the response is consistent with the second portion of hypothesis 2, which argued that root growth and organic matter decomposition would increase through time as black birch stands mature. In support of this, fine root biomass in the black birch stand was comparable to that in the second-growth hemlock stand (Raymer et al. 2013). Similarly, there were significant correlations between fine root biomass and the activity of labile- and recalcitrant-C-degrading enzymes in the organic horizon ($n = 20$, $r^2 = 0.50$, $P < 0.0001$) and mineral soil ($n = 20$, $r^2 = 0.34$, $P < 0.05$; data not shown), suggesting an indirect effect of roots on R_s by stimulating microbial activity, as was previously demonstrated in the primary-hemlock stand (Brzostek and Finzi 2012).

Nitrogen

Although rates of N cycling were not directly measured in this study, we indirectly assessed N availability by estimating the rate of N uptake from the soil (Table 7; Pastor et al. 1984, Reich et al. 1997). With the exception of the girdled stand, N uptake and ANPP were positively correlated.

In mature stands, NUE typically decreases with increases in N uptake or availability (Vitousek 1984, Pastor and Bridgham 1999). In contrast to this pattern, NUE was not well correlated with N uptake among the stands studied here. Rather, NUE was highest in the girdled and post-HWA stands, the stands with the lowest and highest rates of N uptake, respectively (Table 7). In both stands, wood production dominated ANPP (Table 2, Fig. 1A), which is typical of stands prior to canopy closure (Ryan et al. 2004), and wood C:N ratios exceeded 300:1 (data not shown). As a result, the N cost of ANPP was low, resulting in high NUE. In the primary- and secondary-hemlock and mature black birch stands, foliage production constituted >45% of ANPP. Foliage has a comparatively narrow C:N (25:1 to 40:1) and hence there is a greater demand for N to support the lower rates of ANPP at these sites.

CONCLUSIONS

Hemlock decline due to stand infestation by

HWA will alter many biotic and abiotic properties of forest ecosystems throughout the eastern US. This study focused on changes in rates of C cycling in response to hemlock loss using a comparative approach. Because all stands have slightly different histories, it is not judicious to use comparative approaches to draw firm and final conclusions; this analysis describes potential outcomes that should be tested by direct observation. The main finding of this study is that rapid black birch regeneration following hemlock loss is associated with very high rates of ANPP. It appears that the high rate of ANPP compensates for C losses associated with increased decomposition of the organic horizon and CWD following hemlock death. The high rate of ANPP in the post-HWA stand was associated with high rates of N uptake from the soil, suggesting that black birch trees stimulate decomposition. The large quantities of N taken up on an annual basis in the post-HWA stand must come from the soil since increases in N fixation are very unlikely. Atmospheric N deposition is far lower than the annual rate of N uptake from the soil in the post-HWA stand. Consistent with this suggestion, R_s in the post-HWA stand was high given stand age and this too suggests relatively high belowground C allocation and decomposition, both of which may contribute to high rates of N cycling and uptake in this stand following hemlock decline. Future studies are needed to pinpoint the processes regulating N cycling in the soil.

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