Journal of Biogeography, **29**, 1489–1503

Direct and indirect ecosystem consequences of an invasive pest on forests dominated by eastern hemlock

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Abstract

Aim This study compares the magnitude and trajectory of vegetation and ecosystem function dynamics associated with the direct impact of hemlock woolly adelgid (*Adelges tsugae* Annand; HWA) infestation vs. the indirect consequences of HWA-induced damage in the form of salvage and pre-emptive logging of hemlock [*Tsuga canadensis* (L.) Carriere] forests.

Location The study was conducted within an area extending from southern Connecticut up to and including the Connecticut River lowlands west to the Berkshire Plateau in central Massachusetts, USA.

Methods Overstorey and understorey vegetation and ecosystem function parameters such as decomposition and nitrogen cycling were examined in logged and unlogged portions of ten hemlock stands varying in HWA damage intensity.

Results Intensive hemlock logging generated more rapid and pronounced microenvironment and vegetation changes than chronic HWA damage. Black birch (*Betula lenta* L.) seedling densities and percent cover of brambles (*Rubus* L. spp.), sedges (*Carex* L. spp.) and hay-scented fern (*Dennstaedtia punctilobula* Michx.) were significantly higher in recent harvests vs. HWA-damaged and undamaged sites. High black birch sapling densities (>7000 ha^{-1}) were common in the older harvests but not in adjacent, HWA-damaged portions of these sites.
Undamaged sites had 20% more forest floor mass than HWA-damaged sites and double the mass of older cuts. Mass loss rates of cellulose paper suggest that conditions were more favourable for decomposition in the damaged and older logged sites. Recently cut sites had significantly larger inorganic N pools than undamaged forests, although total net nitrogen (N) mineralization rates were not significantly different among treatments. Nitrification rates of 0.2 kg ha^{-1} day^{-1} measured in the oldest cuts were three times greater than in HWA-damaged sites and over 200 times greater than in undamaged hemlock sites. However, resin bag capture in the older cuts was similar to amounts captured in undamaged and damaged forests, suggesting that excess nitrogen was being utilized in vegetative uptake. In contrast, relatively large amounts of ammonium and nitrate captured in recent harvests indicate higher N availability, less vegetative uptake, and a greater potential for N leaching.

Main conclusions Results suggest that both the decline associated with HWA infestation and the indirect effects of HWA in the form of logging are generating profound changes in structure, composition, and ecosystem function in these forests, although at different spatial and temporal scales. Hemlock harvesting imposed more abrupt microenvironmental changes, and rapidly reduced vegetative cover while chronic HWA infestation led to gradually thinning canopies. Both disturbances led to black birch dominated forests, although logging resulted in greater amounts of shade-intolerant regeneration, higher soil pH and nitrification rates, and reduced forest floor mass. Pre-emptive cutting of undamaged forests may lead to greater N losses than those associated

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with HWA infestation or logging of deteriorated hemlock forests, because of reduced vegetative uptake. Silvicultural methods that allow for vegetation establishment prior to harvesting will probably lessen the ecological impacts of hemlock removal.

Keywords

Vegetation dynamics, salvage logging, hemlock woolly adelgid, ecosystem function, nitrogen cycling, decomposition, invasive pests.

INTRODUCTION

The introduction of exotic pests and pathogens is an increasingly important ecological phenomenon that is altering natural ecosystems worldwide by displacing native species, altering habitat, and modifying key ecological processes (Vitousek *et al*., 1996; Enserink, 1999; Everett, 2000; Mack *et al*., 2000). Rates of exotic introductions to the US have continually risen during the past century, becoming a major concern of state foresters nationwide (Billings, 2000). Current patterns of globalization suggest this trend will continue in the USA (Liebhold *et al*., 1995).

Several studies examining the impacts of pests and pathogens on their hosts focused on mortality patterns and associated vegetation dynamics (Aldrich & Drooz, 1967; Stephens, 1988; Trial & Devine, 1994; Stone & Wolfe, 1996). Others examining ecosystem responses to the loss of a dominant forest tree due to pest or pathogen outbreaks have shown that certain soil parameters such as soil nitrogen (N) pools and net-N-mineralization rates can be altered (Swank *et al*., 1981; Matson & Boone, 1984; Boone *et al*., 1988). In a study of eastern hemlock forests [*Tsuga canadensis* (L.) Carr.] Jenkins *et al*. (1999) showed that forests infested with hemlock woolly adelgid (HWA) exhibited ecosystem changes in the form of enhanced net n-mineralization, nitrification, and N turnover than uninifested control sites. Pre-emptive and salvage logging are important secondary disturbances associated with forest pest outbreaks that often lead to a more rapid removal of the host species and more severe disruptions in microenvironmental conditions and ecosystem processes than the pest itself (Irland *et al*., 1988; Radeloff *et al*., 2000). However, we know of no studies that include a contrast of the direct ecosystem and vegetation impacts of an insect pest with the indirect consequences in the form of salvage logging.

The HWA (*Adelges tsugae* Annand), an introduced pest initially observed in the south-eastern US in the 1950s (Souto *et al*., 1996) has spread as far north as Portsmouth, NH (Anonymous, 2001). Eastern and Carolina (*T. caroliniana* Engelm.) hemlock are suitable hosts for HWA, and the entire range of both species is threatened because HWA is easily spread by wind, animal, and human vectors (McClure, 1990). The rate of tree decline varies, but mortality can occur in as few as 4 years (McClure, 1991), or gradually over 10 or more years (Orwig, 2002). In addition, hemlock shows no sign of resistance and no effective native predators of HWA have been identified. Hemlock constitutes 11–55% of the total conifer growing stock by volume in New England (Smith & Sheffield, 2000), often dominating river valleys and ridge tops: its loss is likely to dramatically alter the composition and function of these forest ecosystems.

Hemlock logging in southern New England has increased greatly since HWA arrival in 1985 (Orwig *et al*., 2002), despite several undesirable wood characteristics that have resulted in historically low demand, utilization, and stumpage prices (Baumgras *et al*., 2000; Howard *et al*., 2000). Although hemlock was intensively harvested and utilized in the nineteenth century for the tanning industry in the eastern US (McMartin, 1992; Whitney, 1994), very little is known about the vegetation and ecosystem function changes associated with these harvests. With the prospect that hemlock logging will continue to be an important indirect consequence of HWA outbreaks, there is a critical need to evaluate these impacts and contrast them with the direct effects of HWA infestation. This study was designed to address the following objectives: (1) To examine the changes in microenvironment, vegetation and ecosystem process associated with intensive logging of eastern hemlock; and (2) To compare the magnitude and trajectory of these responses with those accompanying chronic HWA infestation.

METHODS

Study area

Ten sites were studied within an area extending from southern Connecticut to central Massachusetts and from the Connecticut River lowlands east to the Berkshire Plateau at elevations ranging from 30 to 350 m a.s.l and slopes of 4–25% (Fig. 1). The climate is characterized by cold winters, warm summers, and evenly distributed precipitation of approximately 120 cm year^{-1} (Reynolds, 1979; Seanu, 1995). Soils consist of loams and fine sandy loams formed from shallow glacial till on schist, gneiss, and granite bedrock (Reynolds, 1979; Seanu, 1995). Regional vegetation ranges from the Central Hardwoods-Hemlock type in the south to the Transition Hardwoods-White Pine-Hemlock zone in the north (Westveld & The Committee on Silviculture, 1956).

Vegetation sampling

Two replicate sites of five different harvest ages (1, 2, 3, 7 and 13 years since harvest) were selected to examine immediate and longer-term responses to logging (Fig. 1). All sites contained similar soils, hemlock dominance (i.e. > 65% basal area), a minimum of 1 ha of intensely logged hemlock

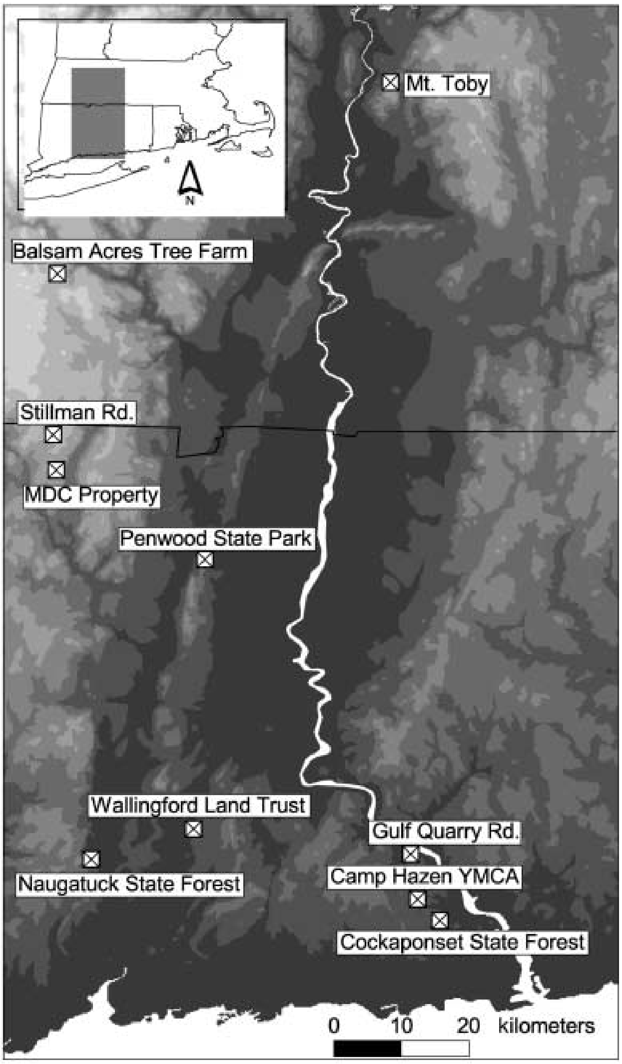

Figure 1 Study area with locations of 10 eastern hemlock study sites in central Connecticut and Massachusetts, USA.

(i.e. > 65% basal area removed), and an adjacent unlogged area of hemlock forest. Transects were established in the most heavily cut area and in the nearest unlogged portion of each stand. Vegetation was sampled in 5–10 circular plots (78.5 m^2) located every 20 m along these transects.

All woody stems ≥1.5 cm diameter at breast height (d.b.h.; 1.37 m) were recorded by species, d.b.h., and crown position. Crown vigour was assigned for each standing hemlock according to the percentage of foliage lost in 25% increments, from 1 = undamaged to 6 = dead (cf. Orwig & Foster, 1998). Each stump was identified as hemlock or hardwood, and its diameter at 0.3 m was determined as the average of two perpendicular measurements. Pre-harvest basal area was reconstructed allometrically using a regression equation relating d.b.h. to stump diameter as: ($y = 0.884x + 0.0003$; $r^2 = 0.995$) from a sample of 215 live hemlock stems. Species, d.b.h., and probable cause of death were noted for standing dead trees in harvested plots. Average sapling (1.5–9.9 cm d.b.h) heights for each species were measured in each plot. Herb, shrub, and vine cover was measured in three, 1 × 1 m subplots located in random directions 3 m from each plot centre. Density and percentage cover of tree seedlings (< 1.5 cm d.b.h) were also tallied by species in each subplot, and percentage cover of logging slash was recorded.

Soil sampling

All soil measurements and incubations were conducted near the plot centres used for vegetation sampling. Nitrogen (N) mineralization was measured with two consecutive 10-week incubations (May–July and July–September 2000) using an intact, closed-topped core method modified from DiStefano & Gholz (1986) accordingly: at each site, soil was sampled with five polyvinyl chloride (PVC) cores (17 cm long and 5 cm wide) and the bottom 2 cm of soil was removed from each sample and then returned to its original location. The initial core was collected, separated into forest floor and mineral horizons, stored at 4 °C, and processed the next day. A second core adjacent to the initial core location was collected after a 10-week incubation and sorted by horizon.

Ecosystem and laboratory analysis

Forest floor and mineral soil samples were homogenized by sieving (5.6 mm pore size), weighed for total mass, and subsampled for gravimetric moisture content. Approximately 10 g of forest floor and mineral soil were placed in 100 mL of 1 N KCl and extracted statically for 48 h. Soil extracts were filtered through coarse pore filters (0.5 μm) and inorganic NH_4-N and NO_3-N concentrations were determined colourimetrically with a Lachat AE flow injection analyser (Lachat Instruments, Inc., Milwaukee, WI, USA) using indophenol-blue (Lachat Instruments [*et al.*], 1990a) and cadmium reduction (Lachat Instruments [*et al.*], 1990b), respectively. Total net mineralization and nitrification were calculated as the difference between between total inorganic N (NH_4-N plus NO_3-N) and NO_3-N in the initial and incubated samples, respectively. Soil organic matter content was determined by loss-on-ignition (4 h at 550 °C), and soil pH was determined in 0.01 M $CaCl_2$ in a ratio of 1 g organic soil: 10 mL solution, or 1 g mineral soil: 4 mL solution. Sub-samples of the soils collected from each site were combined by transect and analysed for total carbon (C) and N by dry combustion using a Fisons 1500 NA Series 2 autoanalyser (Milan, Italy).

Ion exchange resin was used to passively intercept inorganic N in soil solution (Binkley & Matson, 1983; Fisher & Binkley, 2000). Approximately 10 g of mixed bed cation/anion resin (Sybron Chemicals, NM-60; Birmingham, NJ, USA) was placed in nylon mesh bags, rinsed in 2 N KCl, and buried 10 cm beneath the surface near each plot centre and at three additional locations every 20 m along the transect between plots. All bags were collected after 20 weeks (May–October) and dried overnight at 50 °C. Four grams of resin were placed in 100 mL of 2 N KCl for

Table 1 Overstorey basal area (m^2 ha^{-1}) components of the cut and uncut area at each study site. Pre-harvest values were reconstructed from stump diameters (see Methods)

		Uncut area		Cut area			
				Pre-harvest		Post-harvest	
Site name (State)	Age of harvest (years)	Total	Hemlock	Total	Hemlock	Total	Hemlock
Balsam Acres Tree Farm (MA)	1	77.3	59.5	55.3	49.5	6.8	1.1
Penwood State Park (CT)	1	63.4	51.2	60.0	53.4	7.8	6.0
Cockaponset State Forest (CT)	2	46.0	32.6	57.5	46.0	20.2	20.2
Stillman Rd. (CT)	2	59.3	39.2	73.0	48.0	9.6	0.0
MDC Property (CT)	3	69.4	56.4	50.5	34.1	5.6	0.5
Wallingford Land Trust (CT)	3	66.0	66.0	59.6	45.6	14.7	0.7
Gulf Quarry Rd. (CT)	7	53.5	40.5	62.7	51.3	20.5	9.1
Naugatuck State Forest (CT)	7	76.2	56.7	74.7	73.6	21.1	20.0
Camp Hazen YMCA (CT)	13	52.7	41.7	57.9	47.8	18.0	7.9
Mt Toby (MA)	13	76.1	73.3	62.0	46.1	0.0	0.0

48 h. Extraction and N determination methods followed those for soils described above.

Ground level hemispherical photographs were taken at each plot centre to quantify the light environment incident near the soil surface. Images were captured on 400-speed colour slide film and analysed using Gap Light Analyser 2.0 (Frazer *et al.*, 1999). To characterize forest floor decomposition environment among sites, mass loss of a standard cellulose paper substrate was measured according to Piene & Van Cleve (1978) and Fox & Van Cleve (1983). Three grams of cellulose filter paper were enclosed in nylon screen (mesh size 1 mm^2), placed on the soil surface at the plot centre, and collected after 20 weeks. Mass loss was determined after drying for 48 h at 105 °C. To examine differences in forest floor substrate quality, approximately 1.5 L of forest floor material was collected from each of the five soil sampling locations along each transect, sieved (5.6 mm mesh), and divided into two aluminium trays. Total C and N content, and loss-on-ignition were determined using methods as described for soil analyses. A 10-g subsample was taken from each tray and dried for 48 h at 105 °C to calculate the moisture content and initial dry weight of each tray. Trays were placed in an unlit incubator at a constant 20 °C and watered weekly with 250 mL deionized water. To quantify mass loss rates, each tray was weighed every 5 weeks for 30 weeks and back corrected for moisture content with a 15 g subsample. A mass loss rate constant (k) was calculated according to Olson (1963).

Data analysis

Based on HWA damage status and harvest age, sites were grouped accordingly for analysis: Uncut sites with no damage from HWA (Undamaged, $n = 4$); Uncut sites with severe HWA damage (HWA-damaged, $n = 6$); Harvests 1–3 years old (Recent harvests, $n = 6$); and Harvests 7 and 13 years old (Old harvests, $n = 4$). Harvested areas were grouped by age ($n = 2$) for vegetation and soil analyses.

Data were analysed with one-way ANOVA using HWA infestation or logging class as the main effect. When the main effects of the model were significant the least significant difference multiple comparison test was used to examine differences between groups. Simple linear regression was used to examine the effect time since harvest had on soil and ecosystem properties. The appropriateness of each model was evaluated by examining residuals for normal error distribution and constant variance. Vegetation cover values were rank-transformed prior to analysis. Vegetation nomenclature follows Gleason & Cronquist (1991).

RESULTS

Overstorey vegetation

Stand composition was dominated by hemlock at all sites (Tables 1 and 2) and contained lesser amounts of black birch

Table 2 Stand characteristics (mean ± 1 SE) of the uncut hemlock stands adjacent to harvested areas. Four stands showed no damage from HWA and six stands showed heavy damage and high levels of hemlock mortality

	Undamaged	Range	HWA damaged	Range
Hemlock relative basal area				
Mortality (%)	2.1 (1.0)	0.3–4.6	36.1 (10.7)	8.2–79.1
Hemlock relative density				
Mortality (%)	7.3 (2.3)	2.7–11.5	43.1 (8.3)	19.1–77.0
Canopy vigour (1 = healthy; 6 = dead)	1.2 (0.1)	1.0–1.3	4.5 (0.3)	3.6–5.5
Open sky (%)	3.6 (0.6)	1.9–4.7	9.3 (1.4)	4.7–12.6

(*Betula lenta* L), maple (*Acer* L. spp.), and oak (*Quercus* L. spp.). HWA was present in all of the unlogged sites studied, but high infestation levels and hemlock mortality were only observed in the six southernmost sites. Hemlock mortality varied from 3% in undamaged sites to 77% in HWA-damaged sites and the crown vigour in HWA-damaged sites consistently averaged 68% canopy loss (Table 2). Canopy openness in HWA-damaged sites was 2.5 times higher than in undamaged sites (Table 2, Fig. 2).

More than two-thirds of the total basal area was removed from each stand (Table 1). Composition of residual trees included hemlock (68% of all uncut trees), smaller birch, and some large oaks. Eighty percent of uncut hemlock and 14% of uncut hardwoods died, and many experienced mid-bole snaps or created tip-up mounds. Light levels in recently logged sites were as high as 38% open sky and decreased with harvest age to 4.5% in the oldest cuts (Fig. 2).

Seedlings

Undamaged sites had significantly lower total seedling densities (1.6 vs. 3.8 m^{-2}) and cover (3.2% vs. 5.1%) than HWA-damaged sites (Figs 2 and 3). Maple (61%) and hemlock (30%) together composed 91% of seedlings in undamaged sites, while maple (50%) and birch (19%) accounted for 69% of the seedlings in HWA-damaged sites (data not shown). Vegetation that established after logging was more abundant than in sites experiencing HWA damage, averaging 8.1 m^{-2}. Most seedlings originated immediately after harvest and densities exceeded 10 m^{-2} within 3 years (Fig. 2b). Oak, sassafras [*Sassafras albidum* (Nutt.) Nees.], and tulip poplar (*Liriodendron tulipifera* L.) were absent in undamaged sites and represented low cover in HWA-damaged sites and higher cover in cut sites (Fig. 3a). Seedling composition in logged sites was similar to HWA infested sites with birch and maple accounting for 74% of all seedlings. Hemlock seedling densities were low in cut sites and rare in damaged sites (< 1% of all seedlings sampled). Birch was dominant at all cut ages and the relative proportion of maple seedlings declined with increasing harvest age.

Saplings

Sapling density was significantly higher in HWA-damaged sites (522 ha^{-1}) than in undamaged sites (134 ha^{-1}), with hemlock comprising 88 and 95% of the total, respectively (Fig. 2b). The remaining saplings consisted mostly of beech

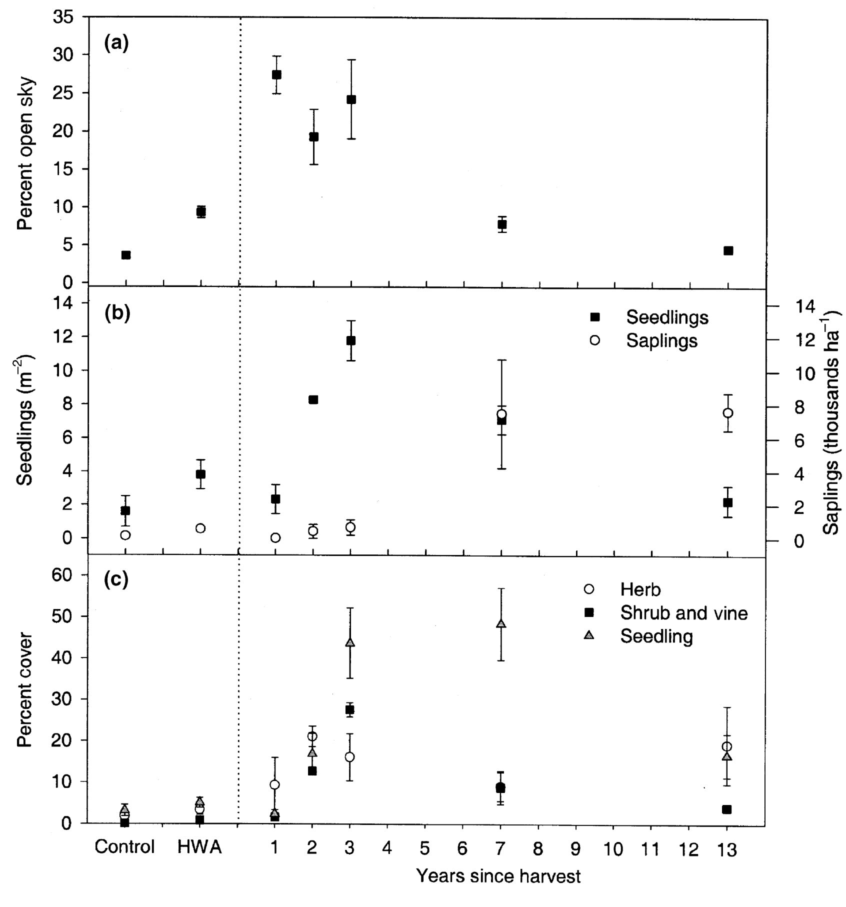

Figure 2 (a) Percentage open sky (mean ± 1 SE), (b) seedling (< 1.5 cm d.b.h) and sapling (1.5–9.9 cm d.b.h) densities and (c) understory vegetation cover of control (undamaged), HWA-damaged, and harvested hemlock sites. Each age is represented by two sites (mean ± 1 SE). The dashed line delineates unharvested and harvested stands.

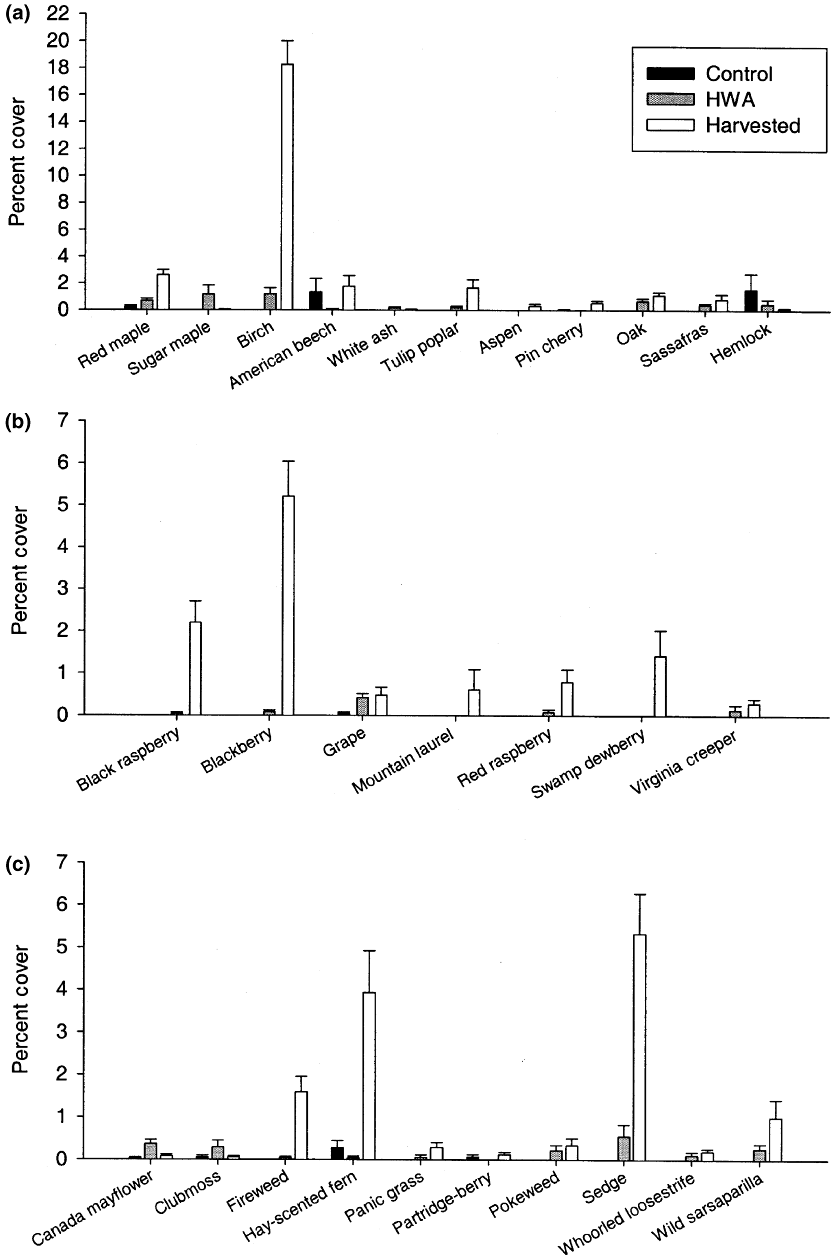

Figure 3 (a) Percentage cover (mean ± 1 SE) of selected tree seedlings (b) shrubs and vines, and (c) herbaceous species in undamaged, HWA-damaged, and harvested hemlock sites.

and birch. The large number of hemlock saplings in damaged sites resulted from some dense plots. Based on their large size, it is possible that most hemlock saplings established prior to HWA infestation as advanced regeneration, while hardwood saplings likely originated following infestation.

Sapling densities were an order of magnitude higher in older cuts vs. HWA-damaged sites and increased over time, reaching >7500 ha^{-1} within 3–7 years (Fig. 2b). Sapling composition was 95% birch with some pin cherry (*Prunus pennsylvanica* L.f), maple, and oak. Within 7 years after harvest sapling heights were 4–5 m and exceeded 7 m within 13 years.

Shrubs and vines

Average shrub and vine cover was virtually zero in undamaged sites (0.05%) and low (0.82%), but significantly higher in HWA-damaged sites (Fig. 3b). Several species of *Rubus* [blackberry (*R. allegheniensis* T.C. Parker), red raspberry (*R. idaeus* L.), and black raspberry (*R. occidentalis* L.), and swamp dewberry (*R. hispidus* L.)] exhibited significantly higher cover in cut vs. HWA-damaged sites (Fig. 3b). Total shrub cover peaked at 28% in the 3-year-old harvests and then dropped to less than 10% in older cuts (Fig. 2c). Total vine cover was quite low and grape (*Vitis* spp.) was the only vine found in all three-stand types.

Herbs

Average herbaceous cover in HWA-damaged sites was nearly twice that of undamaged sites (3.4 vs. 1.8%; Fig. 2c) and consisted primarily of sedges (*Carex* L. spp.), Canada mayflower (*Maianthemum canadense* Wiggers), and sarsaparilla (*Aralia* L. spp.) (Fig. 3c). Hay scented fern [*Dennstaedtia punctilobula* (Michx.) Moore] was the only species in unlogged sites with measurable cover.

Average herb cover was significantly higher following harvest than in HWA-damaged sites, ranging from 9.0 to 21.1% and consisting of light-demanding species such as sedge, hay-scented fern, and fireweed [*Erechtites hieracifolia* (L.) Raf.] (Fig. 3c). Herb cover was less abundant in older cuts, which contained taller vegetation and reduced light levels. The only herbs common to all harvested sites were sedges that occurred in 70% of all cut plots (Fig. 3c).

Soil and ecosystem properties

There were no significant differences in forest floor or mineral soil total C or total N among undamaged, damaged, or cut sites (Table 3). However, damaged and logged sites had significantly lower forest floor C:N-values. No differences in mineral soil C:N was measured among stand groups or treatments. Soil pH was significantly higher in both soil horizons at old harvests. Undamaged sites had 20% more forest floor mass than HWA-damaged sites and recent harvests and twice the mass as old harvests (Table 3). Percentage cover of woody debris was only slightly higher in HWA infested sites than undamaged sites, while recent harvests contained significantly higher amounts. Average forest floor moisture was significantly lower in damaged and cut sites vs. undamaged sites and average mineral soil moisture in recent harvests was significantly higher than in older cuts and HWA-damaged sites (Table 3).

Decomposition

Cellulose paper at the soil surface decomposed 1.7 times faster in damaged and older harvest sites than in undamaged sites and recent harvests (Table 3). There were no significant differences in substrate quality among sites identified in laboratory decomposition measurements. For harvested sites, total decomposition was similar in new and old harvests (Table 3), although both heavily damaged and undamaged sites were represented in the most recent harvests, increasing variability.

Nitrogen cycling

Amounts of NH_4-N captured on resin bags were highest in recent harvests (2.3 mg N g^{-1} resin), while the remaining sites ranged from 0.2 to 0.4 mg N g^{-1} resin (Fig. 4a). Resin bags incubated at recent harvests also captured the most NO_3-N (7.2 mg N g^{-1} resin) compared with other sites with only 0.4–0.7 mg N g^{-1} resin (Fig. 4a). The total amount of N captured in recent harvests was about five times greater

Table 3 Soil and environmental variables in unlogged and harvested hemlock stands (mean ± 1 SE). Different letters within a row indicate statistical difference for that horizon ($P < 0.05$)

	Forest floor				Mineral soil			
	Undamaged	HWA damaged	Harvest ≤ 3 years	Harvest > 3 years	Undamaged	HWA damaged	Harvest ≤ 3 years	Harvest > 3 years
Total C (%)	45.6 (1.1) a	38.1 (4.5) a	38.8 (4.4) a	36.2 (4.9) a	8.24 (1.89) a	5.67 (0.51) a	6.78 (1.23) a	5.26 (1.15) a
Total N (%)	1.60 (0.05) a	1.62 (0.15) a	1.59 (0.17) a	1.57 (0.20) a	0.34 (0.09) a	0.24 (0.22) a	0.28 (0.05) a	0.23 (0.05) a
C : N	28.5 (0.9) a	23.5 (0.7) b	24.4 (0.7) b	23.1 (1.3) b	24.2 (1.2) a	23.6 (1.6) a	24.2 (1.2) a	22.9 (1.1) a
pH	3.10 (0.05)a	3.57 (0.07) b	3.51 (0.06) b	4.06 (0.11) c	3.39 (0.06) a	3.77 (0.07) bc	3.60 (0.05) b	3.88 (0.06) c
Mass (Mg ha^{-1})	67.1 (3.6) a	52.5 (1.8) b	50.2 (2.8) b	33.8 (2.3) c	481.7 (43.4) a	705.2 (29.3) ab	687.8 (38.8) ab	823.1 (55.7) b
Org. matter (%)	85.0 (1.4) a	76.5 (1.7) b	79.4 (1.5) b	75.7 (1.6) b	15.2 (1.7) a	10.6 (0.5) b	13.3 (1.1) a	10.7 (0.9) b
Avg. moisture (g g^{-1})	2.04 (0.15) a	1.18 (0.07) b	1.36 (0.10) b	1.35 (0.05) b	0.78 (0.14) a	0.38 (0.02) c	0.60 (0.05) b	0.39 (0.03) c
Cellulose paper (% loss)	48.1 (5.5) c	64.1 (4.7) b	35.9 (5.8) d	79.4 (2.7) a				
Forest floor decomposition (k year^{-1})	0.023 (0.004) a	0.025 (0.003) a	0.030 (0.010) a	0.023 (0.003) a				
Woody debris cover (%)	3.9 (0.5) a	8.5 (2.0) ab	34.2 (3.1) c	13.2 (3.9) b				

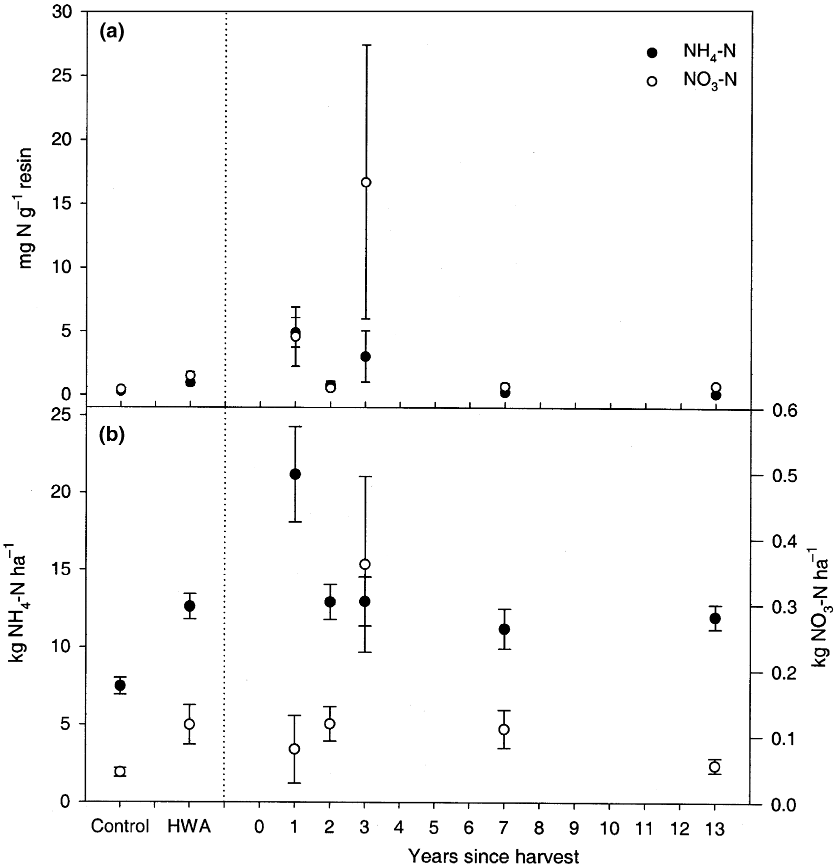

Figure 4 Nitrogen mobility expressed as (a) N capture on ion exchange resin bags, and (b) soil extractable N pools in control (undamaged), HWA-damaged, and harvested hemlock sites. The dashed line delineates unharvested and harvested stands. Error bars are one standard error of the mean.

than HWA-damaged sites and nine times greater than undamaged hemlock sites.

Compared with undamaged sites, total inorganic N pools in the upper 15 cm were only slightly higher in HWA-damaged sites and consisted almost exclusively of NH_4-N with $<2\%$ of the total inorganic N measured as NO_3-N (Fig. 4b). Recent harvests showed the largest inorganic N pools, with twice the amount measured in undamaged sites. Compared with very low levels in undamaged and HWA-damaged sites, recent harvests also had significantly higher NO_3-N pools (Fig. 4b).

Combining forest floor and mineral horizons, total net N mineralization did not differ among sites, although a significantly larger proportion of the mineralization in both horizons of older cuts was nitrification (Fig. 5). Soil factors were significantly related to time since hemlock harvesting (Fig. 6). There were significant reductions in forest floor mass and significant increases in soil pH and nitrification rates in the older cuts.

DISCUSSION

The current outbreak of HWA in New England provides an unusual opportunity to examine the two major consequences of introduced pests and pathogens: the decline and the associated logging of the host species. The ecosystem level effects of logging on vegetation response (Wang & Nyland, 1993; Elliot *et al.*, 1997; Archambault *et al.*, 1998), soil nutrient dynamics (Covington, 1981; Krause & Ramlal, 1987; Johnson *et al.*, 1997), and above and below-ground ecosystem processes (Marks & Bormann, 1972; Hix & Barnes, 1984; Mou *et al.*, 1993; Iseman *et al.*, 1999) have been well documented. In contrast, ecosystem function changes resulting from the alteration of forest structure by pests and pathogen outbreaks remain largely unexplored (Matson & Boone, 1984; Jenkins *et al.*, 1999; Schowalter, 2000). This study contrasted vegetation and ecosystem function dynamics associated with species removal by an introduced insect pest vs. logging of the host species.

HWA and vegetation

Because of low densities of HWA, undamaged sites examined in this study showed little evidence of decline, had low light infiltration, thick, acidic forest floors, scattered hemlock seedlings, and few herbs or shrub species. In contrast, HWA-damaged hemlock sites had higher frequencies and percentage cover of saplings, seedlings, shrubs, and herbs, resulting most probably from increasing light levels associated with hemlock mortality (Fig. 7a). Understorey

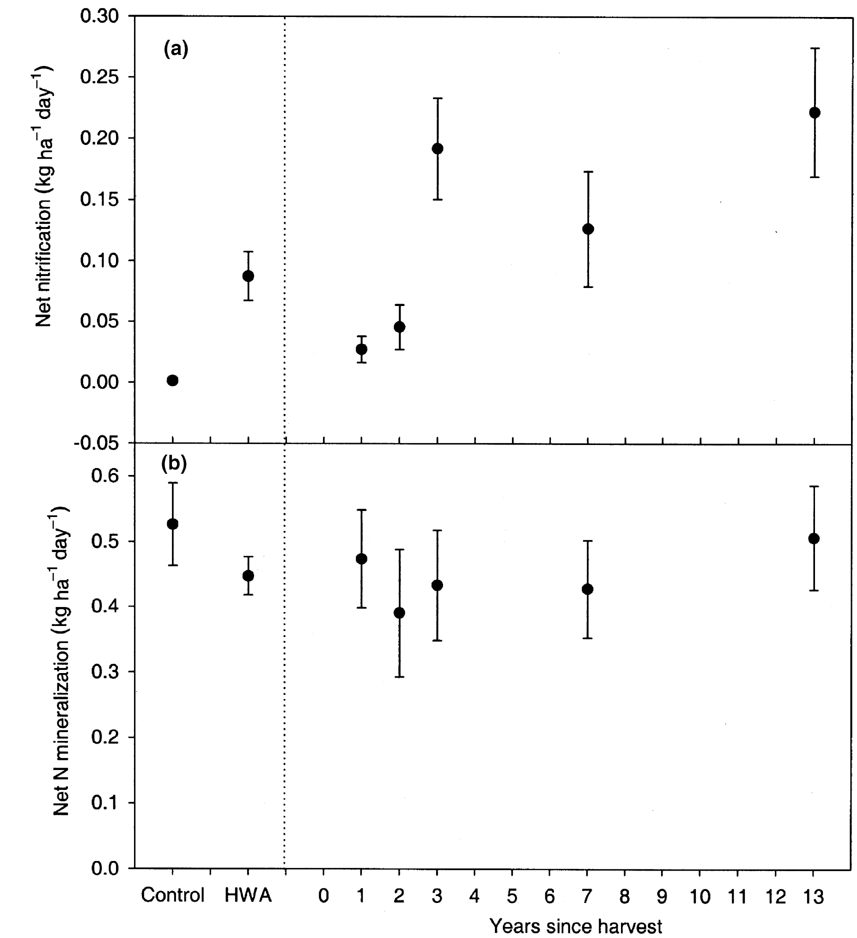

Figure 5 Nitrogen turnover estimated with (a) net nitrification and (b) net mineralization in control (undamaged), HWA-damaged, and harvested hemlock sites. The dashed line delineates unharvested and harvested stands. Error bars are one standard error of the mean.

vegetation was similar in composition to that at other HWA-damaged sites (Orwig & Foster, 1998; Jenkins *et al.*, 1999; Orwig, 2002) and consisted mostly of birch and red maple seedlings.

Logging and vegetation

Post-harvest vegetation was sparse immediately after cutting and its composition was broadly similar to HWA-damaged sites within few years, but contained significantly higher amounts of understorey vegetation (Figs 7b,c). Birch seedlings rapidly established at all logged sites even in the absence of observable seed sources. Birch dominates the seed bank in many hemlock forests (Catovsky & Bazzaz, 2000) because of its high annual seed production and extensive seed dispersal patterns (Matlack, 1989; Ribbens *et al.*, 1994). In addition, black birch shows superior N use strategies that probably translate to enhanced performance in N-rich soils of recent harvests (Crabtree & Bazzaz, 1993). Because of its potential longevity, current overstorey abundance in Connecticut forests (Ward & Stephens, 1996), and its frequent occurrence with overstorey hemlock (Orwig *et al.*, 2002), black birch should remain a major component of these sites for decades to come.

Vegetation comparisons: HWA vs. logging

Very few hemlock seedlings were present in cut or HWA-damaged sites, and hemlock is unlikely to regain dominance following logging because of its reduced regenerative capacity, low seed viability (Frothingham, 1915), retarded germination of seeds in high light environments (Duchesne *et al.*, 1999), and the continued presence of HWA. Residual hemlocks of all sizes died 1–13 years following logging, either from continued HWA attack or unknown causes. Consequently, even outside the distribution of HWA, hemlock logging will lead to eventual hardwood dominance and long-term decreases in hemlock (Hibbs, 1983; Kelty, 1986; Smith & Ashton, 1993).

As HWA-induced mortality and salvage logging continue to spread northward into regions with different species assemblages and environmental conditions, vegetation response may differ from that observed in southern New England. American beech, sugar maple, and yellow birch (*Betula alleghaniensis* Britton) are the dominant hardwoods in more northerly latitudes, and white pine (*Pinus strobus* L.) commonly grows with hemlock in a more diverse conifer component (Westveld *et al.*, 1956). These species are all capable of replacing hemlock

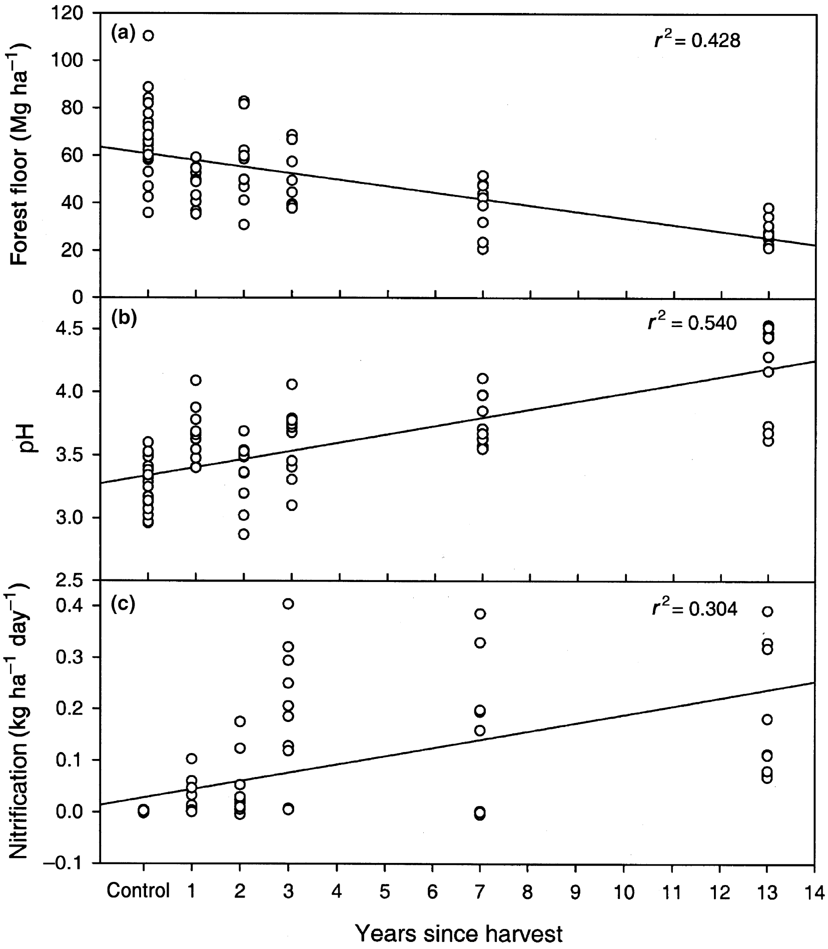

Figure 6 Regression analysis of (a) forest floor mass, (b) soil pH, and (c) net nitrification as a function of time since harvest. Best fit lines are significant at $P < 0.05$.

although the actual dynamics following hemlock removal are still largely unknown.

Herbaceous vegetation, especially sedges, hay-scented fern and fireweed was present at much higher frequencies and cover in logged sites vs. HWA-damaged areas. Soil scarification associated with logging probably led to enhanced germination of these species, whose buried seeds can remain viable for decades (Livingston & Allessio, 1968; Baskin & Baskin, 1996). In addition, shrub cover, dominated by black raspberry and blackberry (i.e. *Rubus* spp.), established rapidly following logging and increased in average cover to nearly 30% before declining as birch seedlings matured into dense sapling thickets (Figs 7c,d). Increases in these shrub and herb species have been observed following logging (Thurston *et al.*, 1992; Smith & Ashton, 1993; Elliot *et al.*, 1997; Archambault *et al.*, 1998) and windthrow (Peterson & Pickett, 1995; Cooper-Ellis *et al.*, 1999), but, with the exception of hay-scented fern, not following chronic HWA infestation in other Connecticut forests (Orwig & Foster, 1998; Orwig, 2002).

The absence of dense *Rubus* in HWA-damaged sites may be attributed to a combination of environmental and soil conditions. *Rubus* spp. are shade intolerant, and light levels, although elevated in HWA-damaged sites, may be insufficient for establishment and survival (Richard & Messier, 1996). Also, there is evidence that these plants exhibit nitrate-stimulated seed germination (Jobidon, 1993) and possess superior abilities to utilize nitrate (Traux *et al.*, 1994). Larger nitrate pools following hemlock harvest may also facilitate the dominance of *Rubus* early in stand development until environmental conditions, i.e. decreasing light levels, limit their survivorship in later stages.

Forest floor dynamics

Slow and tight biogeochemical cycles characterize undamaged hemlock forests due to thick, acidic litter layers, in dark, cool microenvironments (Finzi *et al.*, 1998). Organic matter decomposition is controlled largely by litter quality and environmental conditions, especially factors influencing moisture and temperature (Meentemeyer, 1978; Berg *et al.*, 2000). The slow rate of hemlock decomposition is controlled largely by poor litter quality (McClaugherty *et al.*, 1985). However, general climatic influences can be overshadowed by marked changes in microclimate associated with severe ecosystem perturbations such as clear cutting (Whitford *et al.*, 1981).

Figure 7 Composite figure of site conditions. (a) Patchy birch regeneration in a hemlock stand heavily damaged by HWA. Scale is 1 m, (b) View of slash and lack of understorey vegetation 4 months after intense hemlock harvest, (c) dense *Rubus* spp. and birch regeneration in a 3-year-old harvest, (d) dense black birch saplings in a 7-year-old harvest.

Following HWA infestation, light levels, soil temperature and litter inputs changed slowly as trees gradually lost needles and died after several years. In contrast, logging rapidly created a warm, high light environment and the majority of leaf litter was derived from emerging shrubs, extant overstorey hardwoods, and rapidly growing birch seedlings. Laboratory decomposition rates suggest that undamaged hemlock forest floor litter was similar in quality to HWA-damaged litter and that there was little difference among litter quality between old and recent harvests. However, cellulose paper mass loss rates in HWA-damaged sites and old harvests were actually higher than control or newly cut sites, suggesting that moisture and temperature conditions under a partial canopy were strong predictors of forest floor decomposition rates. Immediately following harvest, open conditions and lack of understorey vegetation led to desiccation and slower decomposition of the cellulose substrate. This finding agrees with several studies that report retarded decomposition of organic matter at the soil surface because of desiccation following clear cutting (Whitford *et al*., 1981; Yin *et al*., 1989; Prescott *et al*., 2000) or HWA infestation (Cobb & Orwig, 2002).

Compared with control sites, HWA-damaged and older cut sites had dramatically reduced forest floor mass and lower C : N-values. In addition, older cuts had significantly higher pH values. Similar reductions in forest floor mass and altered soil properties have been observed following clear-cutting (Hix & Barnes, 1984; Yin *et al*., 1989). More rapid organic matter decomposition, reduced litter inputs, and changes in litter quality appear to reduce the thick litter layer characteristic of hemlock forests (Daubenmire, 1930; Rogers, 1980).

Nitrogen cycling

Nitrogen cycling is dramatically altered by hemlock harvesting, even many years after the initial disturbance. Compared with undamaged sites, inorganic N pools increased only slightly in HWA-damaged sites, but increased tremendously following logging. Lack of vegetative uptake and potential microbial population increases, coupled with rapid decomposition of lower organic layers, are the likely causes of these higher pools (Vitousek *et al*., 1979; Vitousek & Matson, 1985; Ohtonen *et al*., 1992). In addition, higher

N capture in harvest site resins suggest greater N availability. Sharp increases in pool sizes and availability of nitrate is a concern because it is highly mobile and is frequently lost from forests immediately following logging (Matson & Vitousek, 1981; Krause, 1982; Krause & Ramlal, 1987; Frazer *et al.*, 1990) and occasionally following pest and pathogen outbreaks (Swank *et al.*, 1981; Jenkins *et al.*, 1999; Hobara *et al.*, 2001). Older cuts had significantly higher nitrification rates in the mineral soil, yet did not have the increased NO_3-N pools or total N capture on resin bags measured in recent harvests. Dense, rapidly growing vegetation at these sites may offset any potential leaching or accumulation by rapidly taking up large amounts of available inorganic N (Marks & Bormann, 1972; Vitousek *et al.*, 1979).

Net nitrification rates were forty-one times higher in HWA-damaged sites, seventy-two times higher in recent harvests, and over 200 times higher in old harvests when compared with the near-zero rates in undamaged hemlock sites. Nitrification increases of similar magnitude have been measured in other HWA-damaged forests (Jenkins *et al.*, 1999; Orwig *et al.* Unpublished data) and under newly formed gaps in hemlock forests (Mladenoff, 1987), indicating that the N cycle is sensitive to different types of hemlock disturbance. Yorks *et al.* (2000) conducted experiments to predict N movement accompanying HWA infestation. Soil solution nutrient concentrations were monitored after girdling hemlock trees. They found elevated concentrations of NH_4^+ and NO_3^- for at least 2 years after girdling.

CONCLUSIONS

The indirect effects of HWA infestation, manifested in pre-emptive and salvage logging, may be even more profound than HWA-induced hemlock mortality caused by their more abrupt microenvironmental and vegetation changes. Vegetation patterns accompanying HWA infestation or logging were broadly similar in species composition but occurred at different temporal and spatial scales. In each case, black birch and other hardwoods replaced hemlock and there was no indication that hemlock will regain a presence in these forests in the near future. Vegetation re-establishment following logging also resulted in more abundant shade-intolerant seedlings, herbs, and shrubs.

Changes in forest floor dynamics driven by new vegetation inputs and altered decomposition rates may influence nitrogen cycling for many years, especially increases in nitrification, potentially affecting long-term site fertility and initiating rapid nutrient losses from the disturbed area. We predict in sites infested with HWA, the slow and progressive hemlock decline and gradual development of a hardwood understorey may result in the least amount of nitrogen loss. Pre-emptive cutting of undamaged sites appears to pose the greatest threat for nitrate leaching, followed by logging of declining sites. While this study examined high-intensity harvesting, other silvicultural options such as multi-stage shelterwood cuts or less intensive single harvests may lessen the ecological impacts, e.g. nitrogen leaching, by reducing site and soil disturbance and encouraging understorey vegetation to develop prior to overstorey mortality or removal. Although the long-term fate of hemlock forests in the northeast is unknown, HWA infestation and hemlock logging will directly impact regional forest patterns and processes.

ACKNOWLEDGMENTS

We would like to thank the many generous landowners who granted unrestricted access to study sites including the Camp Hazen YMCA, the Gilkinson Wildlife reserve, representatives of the Barkhamstead Office of the Metropolitan District Commission, the Connecticut Department of Environmental Protection, the University of Massachusetts-Amherst, and the Wallingford Land Trust. We appreciate the efforts of many foresters and loggers who made us aware of many hemlock harvests and for logistical support. A. Ellison, J. Fownes, J. Jenkins and M. Kelty provided statistical advice and critical comments on earlier versions of this manuscript. The A.W. Mellon Foundation and The Harvard Forest Long-term Ecological Research Program financially supported this research.

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BIOSKETCHES

Matthew L. Kizlinski recently completed a Masters of Forest Science at Harvard Forest. He received a Bachelor of Science degree from the University of New Hampshire.

David A. Orwig is a forest ecologist at Harvard Forest interested in dendroecology and the role of land use history and disturbance on forest dynamics. His current research integrates community, landscape, and ecosystem approaches in examining the ecological consequences of an invasive insect pest in hemlock forests of New England.

Richard C. Cobb is a research assistant at Harvard Forest interested in ecosystem science. His research examines broad aspects of forest N cycling.

David R. Foster is a plant ecologist and paleoecologist who combines historical and modern approaches to vegetation analyses in order to interpret and conserve natural and cultural landscapes.