VEGETATION AND ECOSYSTEM RESPONSE TO EASTERN HEMLOCK DECLINE AND LOGGING: DIRECT AND INDIRECT CONSEQUENCES OF THE HEMLOCK WOOLLY ADELGID

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Abstract

Infestation by exotic pests and pathogens represents a significant agent of ecosystem perturbation that often leads to selective removal of the species and stimulates unprecedented logging of the target species. Such opportunistic logging may proceed with little knowledge of its short or long-term effects, and may generate more dramatic ecosystem disruptions than the pest or pathogen itself. The current unimpeded spread of hemlock woolly adelgid (*Adelges tsugae*, HWA) across the eastern United States is initiating widespread mortality and stimulating intensive preemptive and salvage logging of eastern hemlock (*Tsuga canadensis*). This study compared the magnitude and trajectory of vegetation and ecosystem dynamics following HWA infestations with logged and healthy hemlock forests at ten sites located in Connecticut and Massachusetts.

Logging generated more rapid and pronounced microenvironment and vegetation changes than damage by HWA. Percent open sky was 25 – 35 % in newly cut (i.e. ≤ 3 years old) forests, closer to 10% in HWA infested forest, and < 5 % in older cuts (i.e. ≥ 7 years old) and healthy hemlock stands. Black birch (*Betula lenta*) seedling densities and percent cover of brambles (*Rubus* spp.), sedges (*Carex* spp.), and hay-scented fern (*Dennstaedia punctilobula*) were significantly higher in cut stands versus HWA damaged and healthy stands. High black birch sapling densities (> 8000 ha^{-1}) were common in the oldest cuts but not in adjacent, HWA-damaged portions of these stands. Residual trees had little influence on the species composition of emerging vegetation in logged sites.

Forest floor mass was significantly different among treatments, as healthy stands had 20% more mass than HWA damaged stands and 50% more mass than older cuts. Mass loss rates of cellulose paper suggest that conditions were more favorable for

decomposition in the HWA-damaged and older logged stands, although laboratory incubations suggest substrate quality diminishes in these forests over time compared to healthy forests. Recently cut stands had significantly larger inorganic nitrogen (N) pools than healthy forests, although total net N mineralization rates were not significantly different among treatments. As harvest age increased, nitrification accounted for a larger proportion of total N mineralization. Nitrification rates of 0.2 kg ha^{-1} day^{-1} measured in the oldest cuts were almost three times greater than in HWA damaged stands and over 200 times greater than in healthy hemlock stands. However, the amount of nitrate captured on resin bags in the oldest cuts was similar to the amounts captured in healthy and damaged forests, suggesting that the excess nitrogen was being utilized in vegetative uptake. In contrast, large amounts of ammonium and nitrate captured in new cuts indicate higher N availability, less vegetative uptake, and greater potential for N leaching.

Results suggest that both the decline associated with HWA infestation and the indirect effects of logging are generating profound changes in structure, composition, and ecosystem function in these forests. In addition, intense logging of healthy stands may lead to greater N losses prior to vegetation establishment than losses associated with HWA infestation or logging of deteriorated hemlock stands.

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). Eastern North American forests have a lengthy history of introduced forest pests and pathogens leading to major alterations in overstory composition. American chestnut (*Castanea dentata*) and American elm (*Ulmus americana*), are now absent as mature trees following persistent attacks by introduced pathogens (Twardus 1999; Liebhold et al. 1995), while butternut (*Juglans cinerea*) and American beech (*Fagus grandifolia*) are currently suffering range-wide declines due to non-native organisms (Ostry et al. 1994; Houston 1975). Rates of exotic introductions to the U.S. 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 (Liebhold et al. 1995).

Many studies examining the impacts of pests and pathogens on their hosts focus on mortality patterns and associated vegetation dynamics (Aldrich and Drooz 1967; Stephens 1988; Trial and Devine 1994; Stone and Wolfe 1996). Few studies have examined ecosystem responses to the loss of a dominant forest tree due to pest or pathogen outbreaks (Swank et al. 1981, Boone et al. 1988, Matson and Boone 1984, Jenkins et al. 1999). Preemptive and salvage logging are important secondary disturbances associated with forest pest outbreaks often leading 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 directly compare vegetation dynamics, microenvironmental response, and ecosystem function associated with selective species removal by both an introduced pest and associated salvage logging.

The hemlock woolly adelgid (*Adelges tsugae*, HWA), an introduced pest from Asia, surfaced in Richmond, VA in the 1950s (Souto et al. 1996) and has spread as far north as Portsmouth, NH (Anonymous 2001). Eastern (*Tsuga canadensis*) and Carolina (*T. caroliniana*) hemlock are suitable hosts for HWA, which is continuing to spread by wind, animal, and human vectors, having the capability to infest the entire range of both species (McClure 1990). HWA feeds on xylem ray parenchyma cells via a long stylet inserted at the base of needles causing needle loss, bud mortality, and eventual tree death (Young et al. 1995). The rate of tree decline varies, but mortality can occur in as few as four years (McClure 1991), or occur gradually over ten or more years (M. Kizlinski, pers. obs.). All sizes and age classes of hemlock are susceptible to HWA damage. 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 in New England (Smith and Sheffield 2000), often dominating river valleys and ridge tops, and therefore its loss will dramatically alter the composition and function of these forest ecosystems.

Hemlock logging in southern New England has increased greatly since HWA arrival in 1985, including areas outside the current range of HWA infestation (D. Whitney pers. comm.; D. Emmerthal pers. comm.; P. Royer pers. comm.). The intensive harvesting of a dominant, shade tolerant species has the potential to inflict major ecosystem-level impacts. With the prospect that hemlock logging will continue to be an

important indirect consequence of HWA infestation, there is a critical need to evaluate these impacts, compare them to the direct effects of HWA infestation, and make these results available to policy makers, forest land managers, and environmental scientists. This study was designed to address this need by answering these key ecological questions:

1) What are the major vegetation and ecosystem process changes associated with intense logging of eastern hemlock?

2) How do these changes compare to those caused by persistent hemlock woolly adelgid infestation?

Methods

Study Area

Ten sites were studied within a 8,000 km^2 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. (Figure 1). The climate is characterized by cold winters, warm summers, and evenly distributed precipitation of approximately 120 cm yr^{-1} (Reynolds 1979; Seanu 1995). Soils consisted of loams and fine sandy loams formed from shallow glacial till on schist, gneiss, and granite bedrock of moderate slopes (Table 1; 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 et al. 1956).

Two replicate stands 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 (Figure 1). All sites contained similar soils, hemlock dominance (i.e. > 65% basal area), a minimum of 1 ha of intensely logged hemlock (i.e., > 65% basal area removed), and an adjacent unlogged area of hemlock forest. After inspection of the extent and characteristics of the harvested area, a transect was established within the most heavily cut area. The first plot was located at least 10 m from an edge, and additional plot centers were placed every 20 m avoiding skid roads and landings, until a minimum of five and a maximum of ten plots were located. In cases where the harvest was small or non-uniform, short transects were established along different bearings to maximize the area covered. Five plots were established in the nearest unlogged portion of each stand and sampled in the same manner.

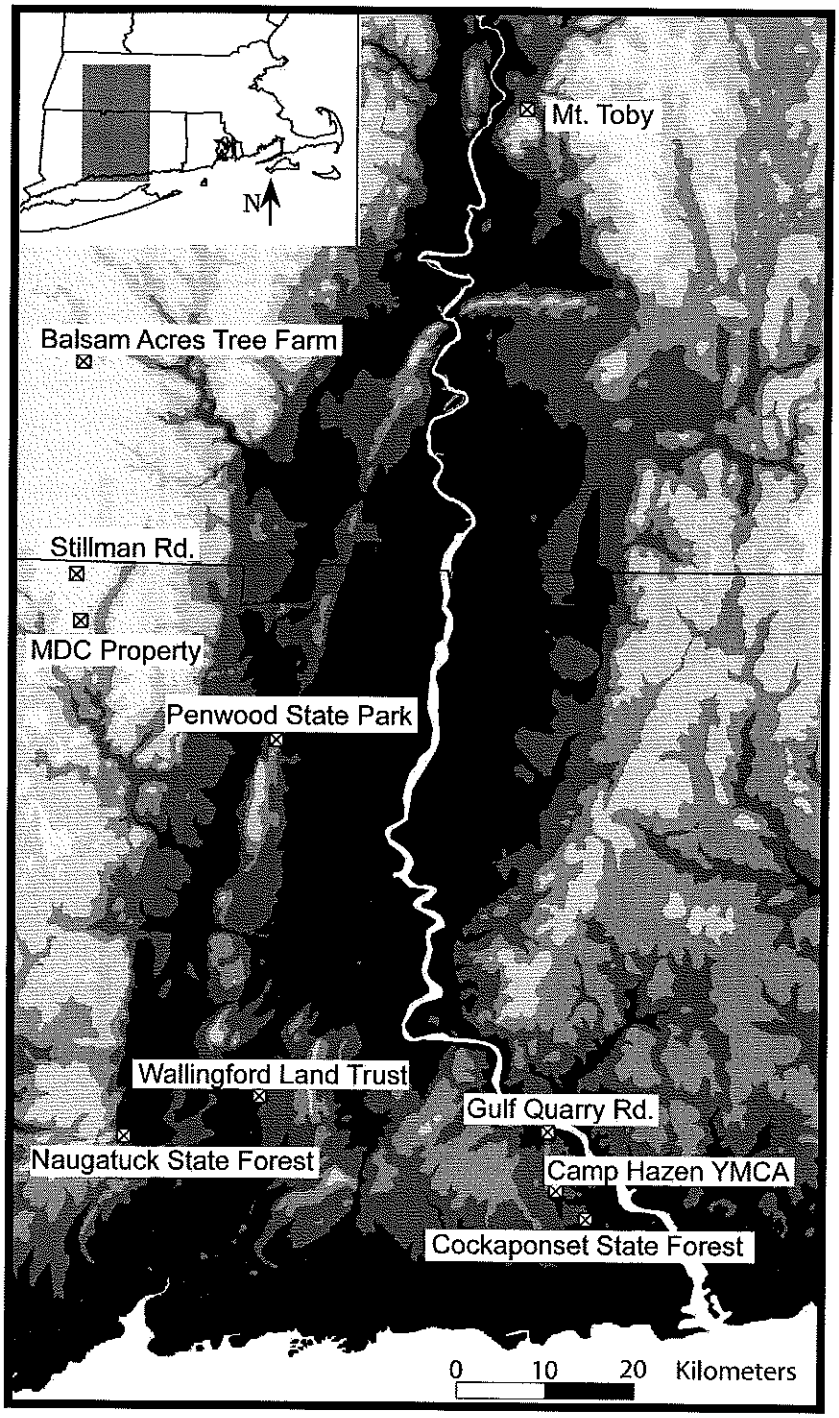

Figure 1. Ten study sites examined for the effects of hemlock harvesting in southern New England.

Table 1. Site and soil characteristics of the ten hemlock harvest locations and adjacent uncut control stands. See Figure 1 for a map of the study area.

	Slope (%)		Elevation (m)		Aspect		Texture		Soil Classification	
	Intact	Cut	Intact	Cut	Intact	Cut	Intact	Cut	Intact	Cut
Balsam Acres Tree Farm	14.6	12	324	320	SE	NE	fine sandy loam	fine sandy loam	Typic haplorthod	Typic haplorthod
Penwood State Park	21.7	24.4	177	195	SE	W	fine sandy loam	fine sandy loam	Lithic dystrochrept	Lithic dystrochrept
Cockaponset State Forest	14.6	3.5	75	93	E	E	fine sandy loam	fine sandy loam	Typic dystrochrept	Typic dystrochrept
Stillman Road	5.2	6.8	351	351	W	W	loam	fine sandy loam	Typic fragiochrept	Typic fragiochrept
MDC Property	7.5	14.6	312	339	S	E	fine sandy loam	fine sandy loam	Typic dystrochrept	Typic dystrochrept
Wallingford Land Trust	10.2	16.3	81	81	NW	NW	loam	loam	Typic fragiochrept	Typic fragiochrept
Gulf Quarry	9.1	13.9	41	33	NE	N	fine sandy loam	fine sandy loam	Typic fragiochrept	Typic fragiochrept
Naugatuck State Forest	10.2	9.8	87	96	NW	SW	fine sandy loam	fine sandy loam	Typic dystrochrept	Typic dystrochrept
Camp Hazen YMCA	13.6	15.2	105	99	SE	SW	fine sandy loam	fine sandy loam	Typic dystrochrept	Typic dystrochrept
Mt. Toby	17.7	19.6	154	176	NE	NE	fine sandy loam	fine sandy loam	Lithic dystrochrept	Lithic dystrochrept

Vegetation Sampling

Overstory vegetation was sampled in 5 m radius circular plots (78.5 m^2). Woody stems ≥ 1.5 cm diameter at breast height (dbh; 1.37 m) were recorded by species, dbh, and crown position, and crown vigor was assigned for each hemlock according to the percent of foliage lost in 25% increments, from 1 = healthy to 6 = dead (cf. Orwig and Foster 1998). Each stump was identified as hemlock or hardwood, and the diameter was determined as the average of two perpendicular measurements. Species, dbh, and probable cause of death were noted for trees killed after harvest. Using a telescoping pole, average sapling (1.5 to 9.9 cm dbh) height for each species was estimated in each plot. Three 1x1 m subplots were located 3 m from each plot center in random directions to assess percent herb, shrub, and vine cover. Density and percent cover of tree seedlings (< 1.5 cm dbh) were tallied by species in each subplot, and percent cover and average height of logging slash was recorded.

Due to difficulties with identification, birch (*Betula* spp.) seedlings were grouped, although the vast majority was black birch (*B. lenta*). The several sugar maple (*Acer saccharum*) seedlings that were encountered were combined with red maple (*A. rubrum*). See Appendix A for a complete list of species sampled. To reconstruct pre-harvest basal areas, a sample of 215 stems was used to develop a regression equation relating stump diameter to dbh ($y = 0.884x + 0.0003$; $r^2=0.995$).

Soil Sampling

All soil measurements and incubations were conducted near the plot centers used for vegetation sampling. Nitrogen (N) cycling was quantified with two consecutive 10-

week incubations (May-July and July-September) using an *in situ* closed-top core method (modified from DiStefano and Gholz (1986)). Freshly fallen litter (Oi material) was removed, 17 cm of soil was extracted with PVC cores (5.1 cm inside-diameter), and the bottom 2 cm of soil was removed. The soil to be used for initial analysis was extruded onto a vinyl sheet, separated into forest floor and mineral horizons, and placed into plastic bags. Soil was stored at 4°C and processed the next day. A second core adjacent to the initial core location was collected, the bottom 2 cm of soil was removed, then returned to the hole and covered with a perforated aluminum can.

Ecosystem and Laboratory Analysis

Forest floor and mineral soil samples were homogenized by passing though a No. 3 ½ sieve (5.6 mm openings). Subsamples of approximately 10 g were placed in glass jars containing 100 mL of 1 *N* KCl, hand shaken to mix, stored for 48 h, and then filtered through glass fiber filters. An additional subsample was dried at 105°C for 48 h to determine moisture content. Extracts were frozen and later thawed for NH_4-N and NO_3-N analysis on a Lachat AE flow injection analyzer (Lachat Instruments, Inc., Milwaukee, WI, USA) using indophenol-blue (Lachat Instruments, Inc. 1990a) and cadmium reduction (Lachat Instruments, Inc. 1990b) respectively. Ammonification and nitrification were calculated as the difference between NH_4-N and NO_3-N in the initial and incubated samples, respectively. Total net mineralization was calculated as the difference between total inorganic N (NH_4-N plus NO_3-N) in the initial and incubated samples. Concentrations and mineralization rates of N were calculated on a dry mass basis (mg N kg^{-1}) and an areal basis (kg N ha^{-1}).

Soil organic matter content was determined as percent mass loss after 4 hours at 550°C. 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. Subsamples of the soils collected from each site were combined by transect and analyzed for total carbon (C) and total N using a Fisons 1500 NA Series 2 autoanalyzer.

Ion exchange resin was used to passively intercept inorganic N in soil solution (Binkley and Matson 1983; Schnabel 1983; Fisher and Binkley 2000). Resin bags were constructed using 23 mL of mixed bed cation/anion resin (Sybron Chemicals, NM-60; Birmingham, NJ) sealed in nylon stocking material with hot glue. Bags were buried 10 cm beneath the surface near the plot centers and three additional bags were spaced between plots along the transect. All bags were collected after 20 weeks (May-October) and dried overnight at 50°C to obtain uniform dryness. Four g of resin were placed in 100 mL of 2*N* KCl, hand shaken, and stored for 48 h. Extraction and N determination methods followed those for soils described above.

Ground level hemispherical (fisheye lens) photographs were taken at each plot center to quantify the light environment incident at the soil surface. Images were captured on 400-speed color slide film and analyzed using Gap Light Analyzer 2.0 (Frazer et al. 1999). To characterize forest floor decomposition environment, mass loss of cellulose was measured according to Piene and Van Cleve (1978) and Fox and Van Cleve (1983). Two sheets (~3 g dry weight) of Whatman No. 1 cellulose filter paper were enclosed in nylon screen (mesh size 1 mm^2), placed on the soil surface at the plot center, 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, a 30-week laboratory

experiment was conducted. Approximately 1.5 L forest floor material was collected from each of the five soil sampling locations along each transect, passed through a No. 3 ½ sieve (5.6 mm), and divided into two aluminum trays. Total C, total N, and loss-on-ignition were determined using methods as described for soil analyses. A 10 g sub-sample 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. The dry weight of each tray was calculated every five weeks by drying a subsample (10-15g) to determine moisture content, and then returning it for subsequent incubations.

Data Analysis

During soil sampling, it was discovered that two sites had high populations of earthworms. The biotic activity associated with these worms altered the composition and structure of the forest floor and could potentially alter N cycling (Anderson et al. 1983; Steinberg et al. 1997; Burtelow et al. 1998). In addition, one site had a much higher water table than other sites, resulting in waterlogged incubated cores that rendered the samples unusable for comparison to the other sites. To compare results related solely to treatment effects, these three sites were removed from ecosystem analysis. Uncut portions of some stands heavily damaged by HWA were separated from the healthy stands. Based on HWA damage and harvest age, sites were grouped accordingly for analysis: Uncut, healthy stands with no damage from HWA (Healthy, n = 3); Uncut stands with severe HWA damage (HWA damaged, n = 4); Harvests 1 to 3 years old (New Cuts, n = 3); and Harvests 7 and 13 years old (Old Cuts, n = 4). Harvested areas were grouped by age (n = 2) for vegetation analysis. Data were analyzed using one-way

ANOVA with HWA damage or logging class as the main effect. Data that did not meet ANOVA assumptions were analyzed with Kruskal-Wallis non-parametric ANOVA tests. Repeated measures ANOVA were utilized to detect seasonal patterns of N cycling and soil moisture. Statistical significance was considered at the $p < 0.05$ level. SYSTAT 9 (SPSS Inc. 1998) was used for all statistical analyses. Vegetation nomenclature follows Gleason and Cronquist (1991).

Results

Overstory

Overall, basal area and density were dominated by hemlock at all sites (> 65% total basal area, Table 2; and > 53% total stem density, data not shown) with lesser amounts of birch, maple, and oak (*Quercus* spp.). HWA was present in all of the intact stands studied, but high infestation levels were only observed in the southernmost sites. Hemlock mortality, presumably from HWA, occurred in six of the ten intact stands. While mortality levels varied, crown vigor in HWA damaged stands consistently averaged 75% canopy loss (Table 3). Canopy openness in HWA damaged stands averaged 2.5 times higher than in healthy stands (Table 3, Figure 2).

More than two-thirds of the total basal area (Table 2) and between 45-100% of the total stem density (data not shown) was removed from the cut stands. Composition of residual trees included hemlock (68% of all uncut trees, average dbh = 21 cm), smaller birch, and a few large oak. Eighty percent of uncut hemlock and 14% of uncut hardwoods died, apparently due to the combined effects of continued HWA attack and post-logging environmental conditions that resulted in mid-bole snaps and 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 (Figure 2).

Seedlings

Healthy stands had significantly lower seedling densities (Figure 3) and cover (Figure 4) than HWA damaged stands. Maple (61%) and hemlock (30%) together composed 91% of seedlings in healthy stands, while maple (50%) and birch (19%)

Table 2. Overstory 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	Age of harvest (years)	Total	Hardwood	Hemlock	Total	Hardwood	Hemlock	Total	Hardwood	Hemlock	Percent Cut
Balsam Acres Tree Farm	1	77.3	17.8	59.5	55.3	5.8	49.5	6.8	5.7	1.1	87.7
Penwood State Park	1	63.4	12.2	51.2	60.0	6.6	53.4	7.8	1.8	6.0	87.0
Cockaponset State Forest	2	46.0	13.4	32.6	57.5	11.5	46.0	20.2	0.0	20.2	64.9
Stillman Rd.	2	59.3	20.1	39.2	73.0	25.0	48.0	9.6	9.6	0.0	86.8
MDC Property	3	69.4	13.0	56.4	50.5	16.4	34.1	5.6	5.1	0.5	88.9
Wallingford Land Trust	3	66.0	0.0	66.0	59.6	14.0	45.6	14.7	14	0.7	75.3
Gulf Quarry Rd.	7	53.5	13.0	40.5	62.7	11.4	51.3	20.5	11.4	9.1	67.3
Naugatuck State Forest	7	76.2	19.5	56.7	74.7	1.1	73.6	21.1	1.1	20	71.8
Camp Hazen YMCA	13	52.7	11.0	41.7	57.9	10.1	47.8	18.0	10.1	7.9	68.9
Mt. Toby	13	76.1	2.8	73.3	62.0	15.9	46.1	0.0	0.0	0.0	100.0

Table 3. Stand characteristics (mean ± SE) of the uncut hemlock stands adjacent to harvested areas. Four stands were healthy and showed no damage from HWA, and six stands showed heavy damage and high levels of hemlock mortality.

	Healthy	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 Vigor (1 = healthy; 6 = dead)	1.2 (.1)	1.0-1.3	4.5 (.3)	3.6-5.5
Open Sky (%)	3.6 (.6)	1.9-4.7	9.3 (1.4)	4.7-12.6

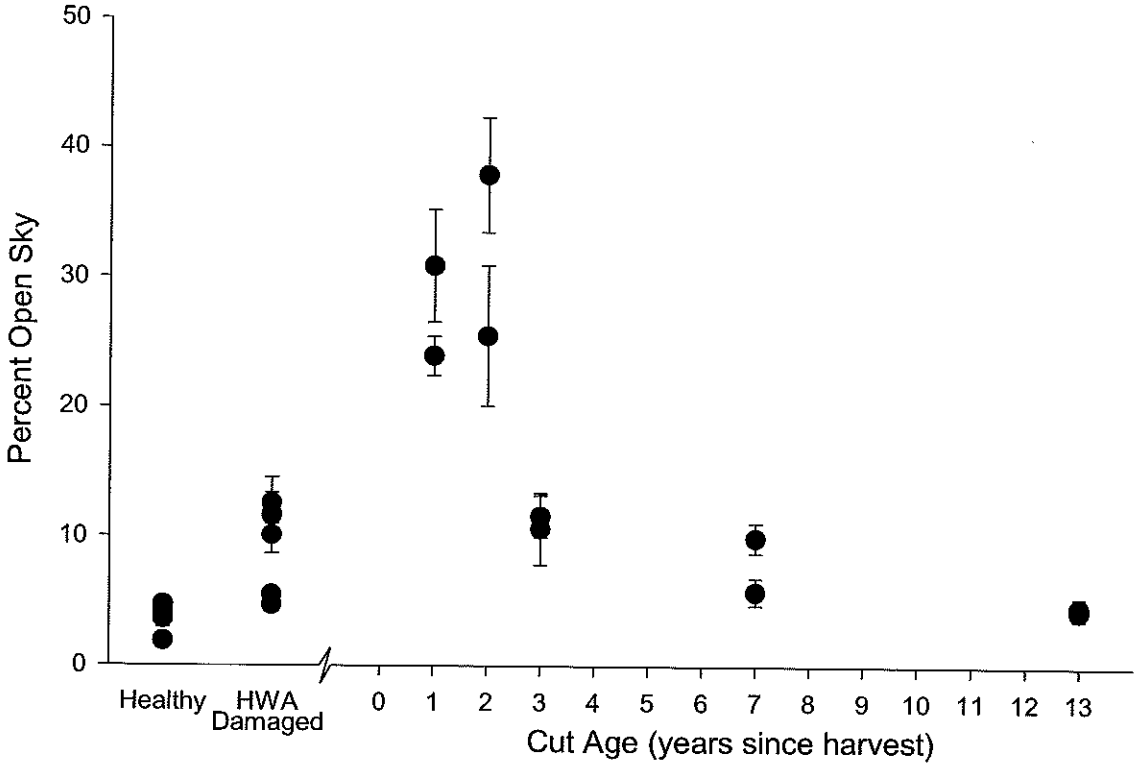

Figure 2. Canopy openness (mean ± SE) of healthy, HWA damaged, and harvested hemlock stands. Values were calculated from hemispherical photographs taken at the soil surface.

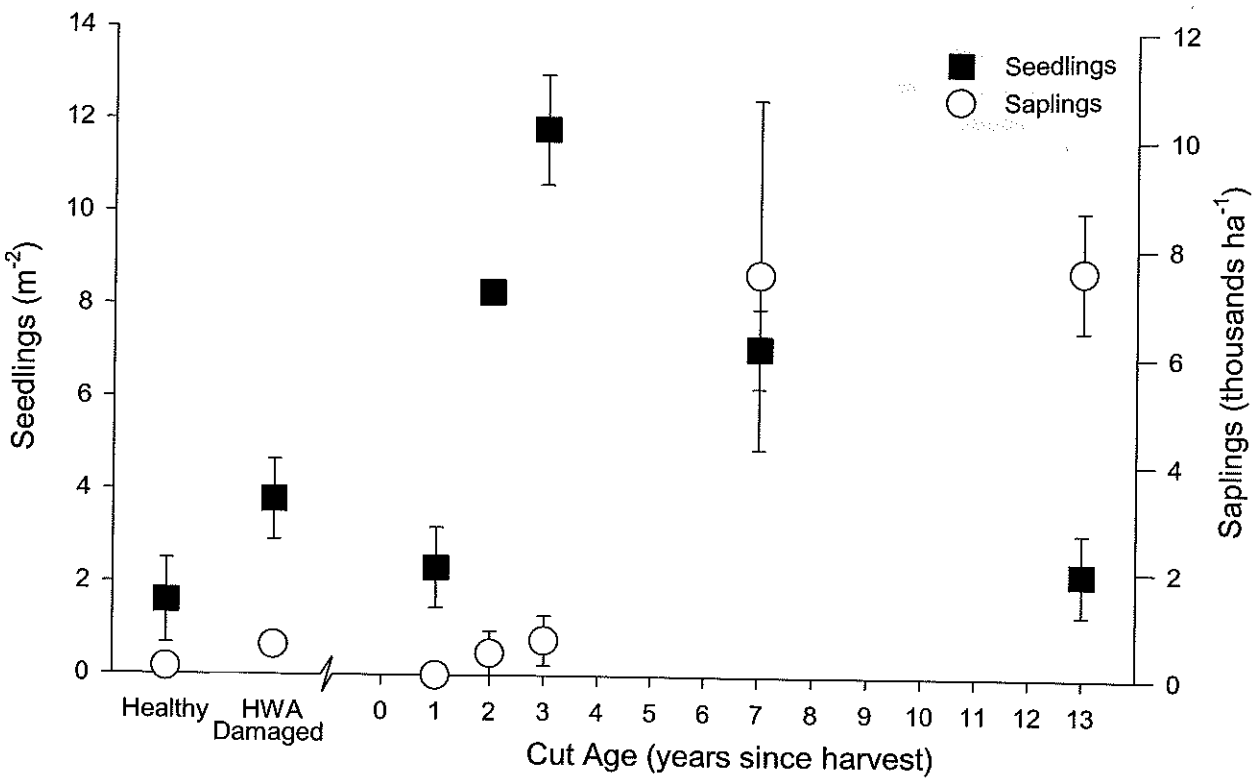

Figure 3. Seedling (< 1.5 cm dbh) and sapling (1.5-9.9 cm dbh) densities in healthy, HWA-damaged, and harvested hemlock stands. Each age is represented by two sites (mean ± SE). Note different scales.

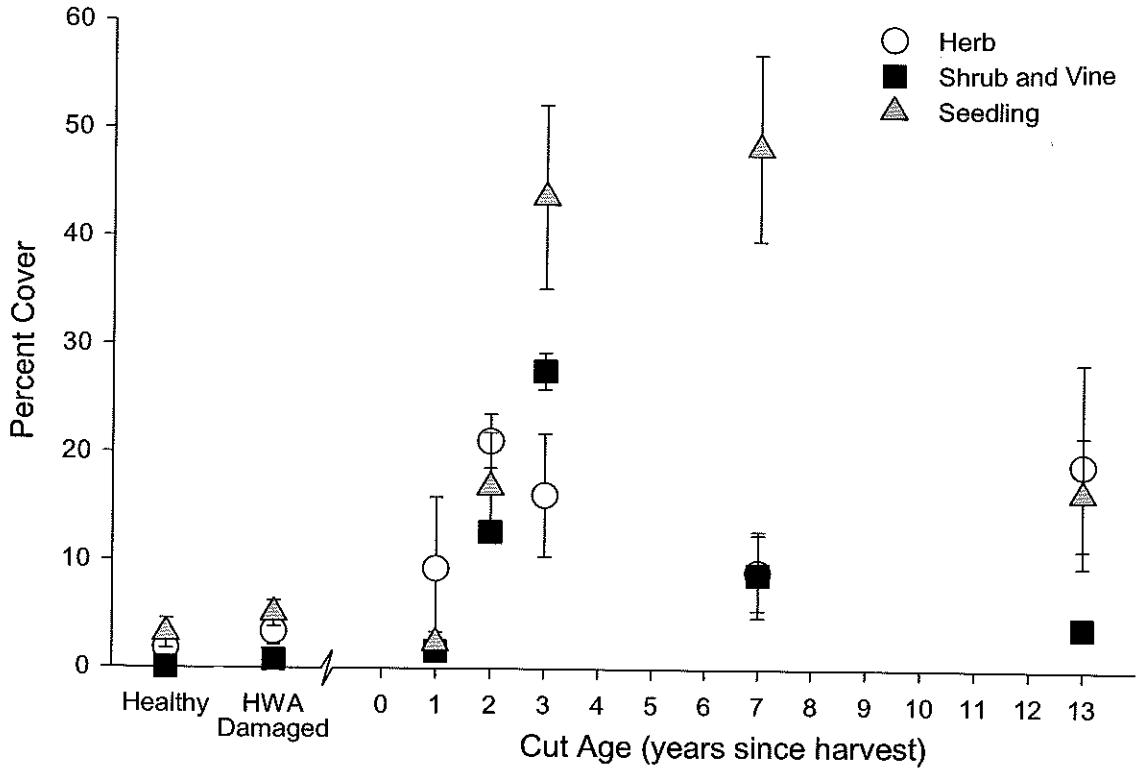

Figure 4. Vegetation cover in healthy, HWA-damaged, and harvested hemlock stands Each age is represented by two sites (mean ± SE).

accounted for 69% of the seedlings in HWA damaged stands (data not shown). Hemlock seedlings were low in cut stands and rare in damaged stands (< 1% of all seedlings sampled). Oak, sassafras (*Sassafras albidum*), and tulip poplar (*Liriodendron tulipifera*) were absent in healthy stands, occurred at low frequencies in HWA damaged stands, and at higher frequencies in cut stands (Figure 5).

Vegetation that established after logging was more abundant than the understory developing in stands with HWA damage, originated immediately after harvest, then exceeded 10 seedlings m^{-2} within 3 years (Figure 3). Seedling composition in logged sites was similar to HWA infested stands with birch (53%) and maple (21%) accounting for 74% of all seedlings. Tulip poplar (5.5%), pin cherry (*Prunus pensylvanica*, 5.3%), sassafras (3.8%), and oak (3.3%) totaled 17.8%. Twelve species, including hemlock, accounted for the remaining 7.9%. Birch was dominant at all cut ages and the relative proportion of maple seedlings declined with increasing harvest age.

Saplings

Total sapling density was significantly higher in HWA damaged stands (522 ha^{-1}) than in healthy stands (134 ha^{-1}; Figure 3), with hemlock comprising 88 and 95% of the total, respectively. The remaining few saplings consisted mostly of beech and birch. The large number of hemlock saplings in damaged stands resulted from a few dense plots. Hemlock saplings in damaged stands had poorer vigor and twice the mortality level of those in healthy stands. Based on size, most hemlock saplings were estimated to have established prior to HWA infestation as advanced regeneration, while hardwood saplings likely originated following infestation.

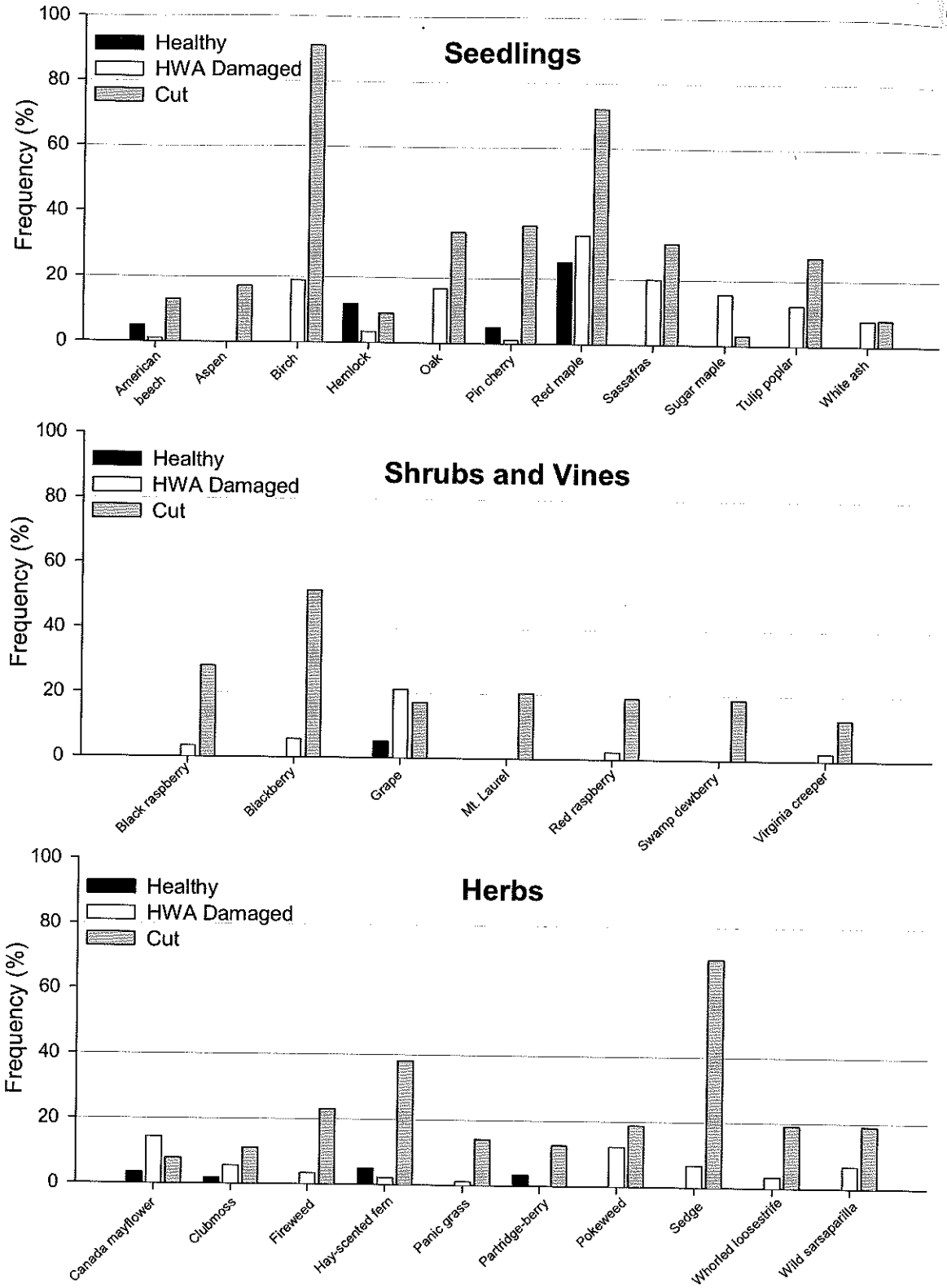

Figure 5. Understory vegetation in healthy, HWA damaged, and harvested hemlock stands. Frequency is based on presence in all subplots of that treatment group. Only those species found in > 15% of all plots are shown.

Saplings were an order of magnitude higher in logged vs. HWA-damaged stands and increased over time as seedlings that established immediately following harvest reached sapling size within 3 to 7 years (Figure 3). Average height for all species at this stage was 3.3 m, and 95% were 2-3 cm dbh birch, 4-5 m tall. The remaining few saplings were mostly cherry and an occasional maple or oak. By 13 years post-harvest, species composition was nearly 90% birch ranging from 7 to 7.5 m tall and averaging 3.5 cm dbh. Maple (3.5% of total), oak (2.9%), and cherry (2.7%) comprised the remaining saplings. Unlike HWA infested stands, hemlock saplings were rare in cut sites.

Shrubs and Vines

Average shrub and vine cover was virtually absent in healthy stands (0.05%) and low (0.82%), but significantly higher in HWA damaged stands (Figure 4) . Several species of bramble (blackberry, *Rubus allegheniensis*; red raspberry, *R. idaeus*; black raspberry, *R. occidentalis*) and Virginia creeper (*Parthenocissus quinquefolia*) occurred in HWA damaged stands, but at very low frequencies (Figure 5). A non-native invasive shrub, wineberry (*Rubus phoenicolasius*), was sampled in one damaged stand in southern Connecticut. Grape (*Vitis* spp.) was the only vine found in healthy stands. The percent frequency of shrubs was much higher in cut stands (Figure 5), and total shrub cover peaked at 28% in the 3-year-old cuts then dropped to less than 10% in older cuts (Figure 4). Blackberry was the most common shrub species followed by black raspberry (Figure 5). Brambles were sparse in older cuts, apparently due to reduced light levels associated with dense birch sapling cover.

Herbs

Herbaceous cover in HWA damaged stands was nearly twice that of healthy stands (3.4 vs. 1.8%; Figure 4). Moss species and hay scented fern (*Dennstaedtia punctilobula*) comprised a large percentage of the understory cover in intact stands, whereas sarsaparilla (*Aralia* spp), sedge (*Carex* spp.), club moss (*Lycopodium* spp.), Canada mayflower (*Maianthemum canadense*), and pokeweed (*Phytolacca americana*) were most important in HWA damaged stands (Figure 5).

Average herb cover was significantly higher in cut stands, ranged from 9.0 to 21.1%, and showed no definite trends with age of harvest (Figure 4). Species composition did not change dramatically with harvest age. High light demanding species such as pokeweed, fireweed (*Erechtites hieracifolia)*, and panic grass (*Panicum lanuginosum*) were common in newer cuts, but were less common in older cuts with taller vegetation and reduced light levels. Older cuts contained species more common to forest interiors such as Canada mayflower and club moss. The only herbs common to all harvested sites were sedges and hay scented fern that occurred in 70 and 40% of all cut plots, respectively (Figure 5).

Soil and Ecosystem Properties

There were no significant differences in forest floor or mineral soil total C or total N among healthy, damaged, or cut sites (Table 4). However, damaged and logged sites had significantly lower forest floor C:N values. No differences in mineral soil C:N were measured among stand groups or treatments. Soil pH was significantly higher in both soil horizons at old cuts. HWA infested stands had significantly lower (19.4%) forest floor mass compared to healthy stands (Table 4). Old cuts had significantly less forest

Table 4. Soil and environmental variables in intact and harvested hemlock stands (mean and SE). Different letters within a row indicate statistical difference for that horizon ($p < 0.05$).

	Forest Floor				Mineral Soil			
	Healthy	HWA Damaged	New Cut	Old Cut	Healthy	HWA Damaged	New Cut	Old Cut
% Total C	46.7 (.7) a	42.8 (5.2) a	45.0 (.5) a	36.3 (5.0) a	6.46 (.92) a	5.67 (.73) a	7.12 (.64) a	5.26 (1.15) a
% Total N	1.61 (.08) a	1.75 (.19) a	1.85 (.05) a	1.58 (.2) a	0.26 (.05) a	0.23 (.02) a	0.30 (.03) a	0.23 (.05) a
C:N	29.0 (1.1) a	24.2 (.5) b	24.5 (.9) b	23.0 (1.4) b	25.3 (1.59) a	24.3 (2.28) a	24.4 (1.23) a	22.8 (1.11) a
pH	3.07 (.11) a	3.4 (.17) a	3.38 (.05) a	4.07 (.18) b	3.47 (.07) a	3.69 (.07) ab	3.53 (.06) a	3.89 (.09) b
Mass (Mg ha^{-1})	69.4 (5.3) a	55.9 (1.9) b	55.1(3.9) ab	35.0 (3.5) c	583.9 (58.9) a	759.9 (42.8) ab	682.2 (25.7) ab	869.6 (122.8) b
% Org. Matter	83.1 (1.7) a	78.7 (4.0) a	80.8 (.8) a	75.9 (2.7) a	12.0 (1.43) a	10.2 (1.23) a	13.8 (.88) a	10.8 (1.88) a
Avg. Moisture (g g^{-1})	1.72 (.18) a	1.23 (.16) a	1.48 (.23) a	1.35 (.10) a	.48 (.06) ab	.33 (.02) a	.60 (.11) b	.39 (.04) a
Cellulose Paper (% loss)	48.9 (1.4) a	76.3 (5.6) b	45.9 (10.3) a	79.5 (2.4) b				
Woody Debris Cover (%)	3.9 (.5) a	8.5 (2.0) ab	34.2 (3.1) c	13.2 (3.9) b				

floor mass than new cuts and half the mass of healthy hemlock stands. Percent cover of woody debris was only slightly higher in HWA infested stands than healthy stands, while new cuts contained significantly higher amounts (Table 4).

Average forest floor moisture was not significantly different among sites, although HWA infested stands had a drier (36%, $p = 0.070$; Table 4) forest floor thanhealthy stands during summer (seasonal data not shown). Seasonal and average forest floor moisture content was similar among cut ages. Average mineral soil moisture in new cuts was significantly higher than in older cuts, yet similar to intact stands (Table 4). Newly cut stands had higher mineral soil moisture levels during spring and fall, a significantly different trend than in old cuts or HWA damaged sites. In general, healthy stands had the wettest forest floor while new cuts had the wettest mineral soil.

Decomposition

More favorable decomposition conditions existed in damaged versus intact stands, as cellulose paper at the soil surface decomposed 1.7 times faster (Table 4). Cellulose paper decomposition rates were lowest in new cuts. Old cuts, having dense vegetation that may have prevented desiccation of the cellulose paper, had elevated decomposition rates which were similar to HWA damaged stands (Table 4).

Differences in substrate quality were identified in laboratory decomposition measurements. Material from healthy stands lost more mass than material from HWA damaged stands (Figure 6a). For harvested sites, total decomposition was similar in new and old cuts (Figure 6b), although both heavily damaged and healthy stands were represented in the most recent harvests, increasing variability. Decomposition of material from new cuts that were healthy at the time of harvest (data not shown) closely resemble

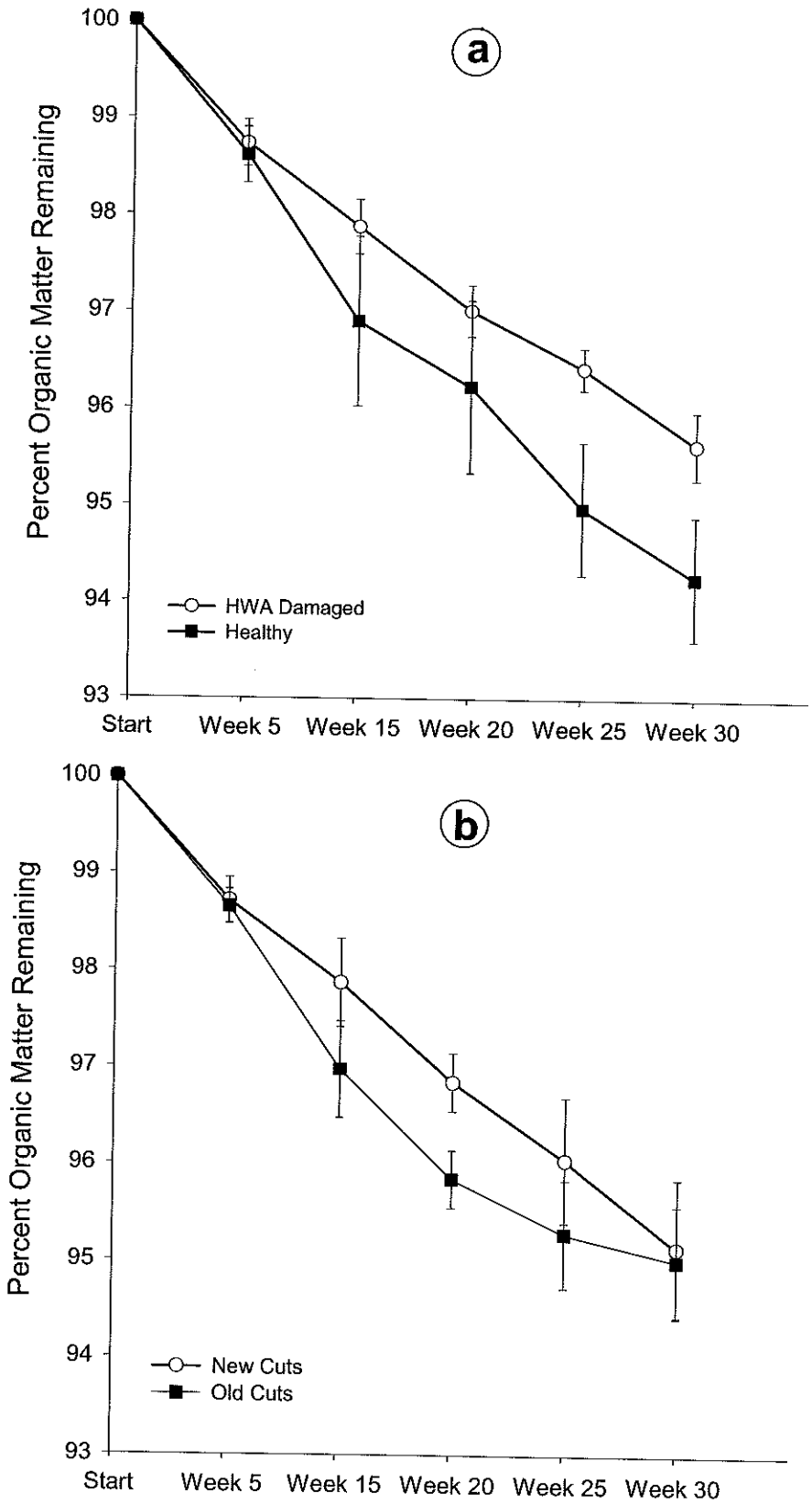

Figure 6. Decomposition of forest floor material from a) intact sites, and b) cut sites (mean ± SE) under laboratory conditions.

curves from the intact healthy stands (Figure 6a), indicating pre-harvest conditions are influential for several years after harvest.

Nitrogen Cycling

Available N pools and net mineralization rates were calculated on both an area (kg N $ha^{-1}d^{-1}$) and a mass (mg N $kg^{-1}d^{-1}$) basis to account for site forest floor mass differences. Compared to healthy stands, total N pools in the upper 15 cm were only slightly higher in HWA damaged stands and consisted almost exclusively of NH_4-N with < 2% of the total inorganic N measured as NO_3-N (Figure 7a). However, when variability of horizon thickness was removed, and values examined on a mass basis, N concentrations were 88% higher in HWA damaged stands than healthy stands ($p = 0.094$; data not shown). New cuts showed the largest N pools containing twice the amount measured in healthy stands (Figure 7a), primarily due to the high mineral soil NH_4-N levels (horizon data not shown). Compared to very low levels in healthy and HWA damaged stands, new cuts had significantly higher mineral soil NO_3-N pools (Figure 7a).

Incubated resin bags successfully captured inorganic N moving through the soil column (Figure 7b). Amounts of NH_4-N captured were highest in new cuts (2.8 mg N g^{-1} resin), while the remaining sites ranged from 0.2 to 0.4 mg N g^{-1} resin. Resin bags incubated at new cuts also captured the most NO_3-N (2.4 mg N g^{-1} resin) compared to other sites which only yielded 0.4 to 0.7 mg N g^{-1} resin (Figure 7b). The total amount of N captured in new cuts was about 5 times greater than HWA damaged sites and 9 times greater than healthy hemlock stands.

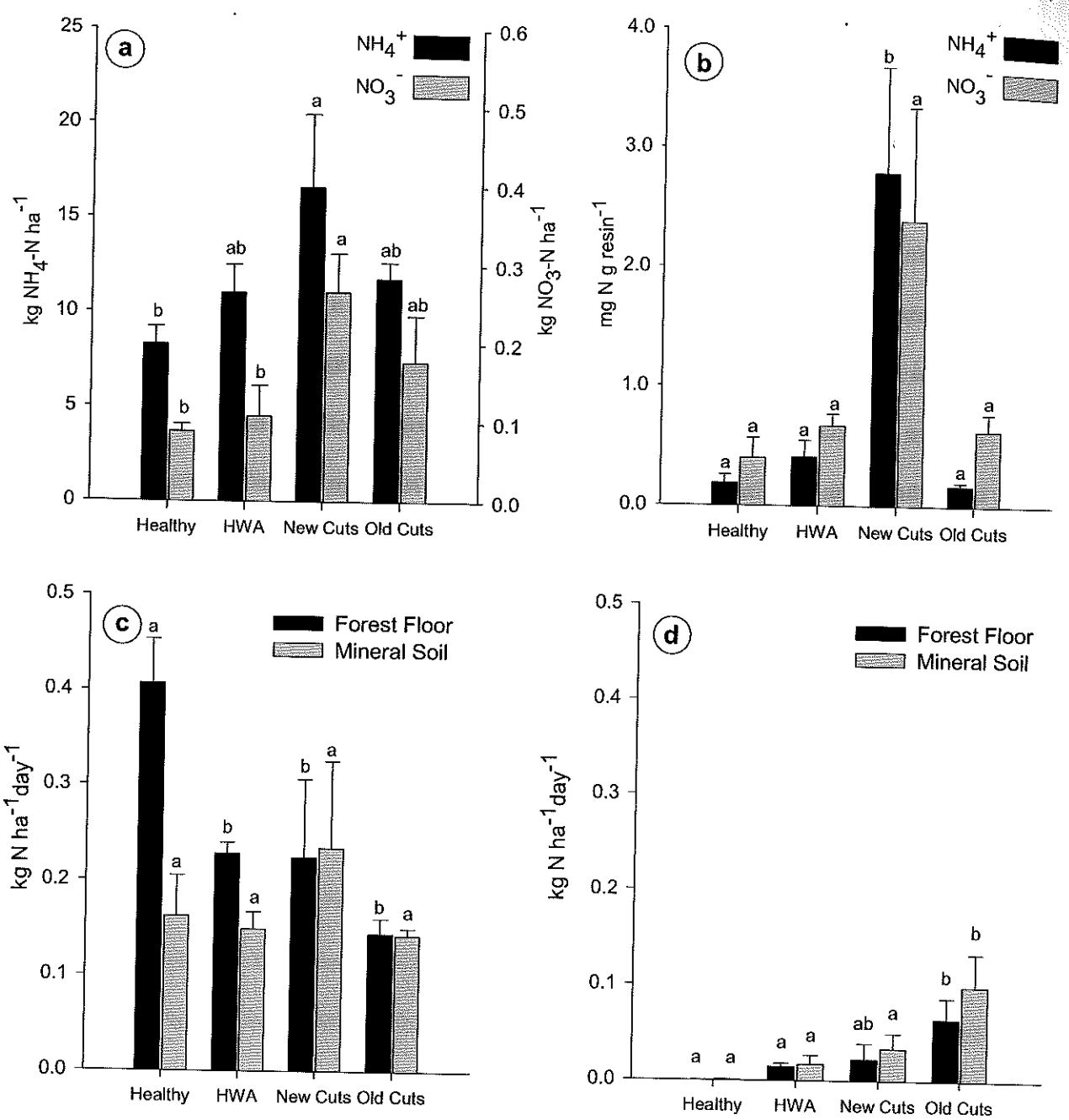

Figure 7. Nitrogen cycling components in intact and harvested hemlock stands (mean ± SE): a) ammonium and nitrate pools in the upper 15 cm (note different scales); b) inorganic N captured on incubated resin bags; c) ammonification rates; d) nitrification rates. Different letters indicate statistical difference among groups.

Nitrogen mineralization exhibited a response to both HWA infestation and logging. Total seasonal forest floor ammonification was lower in all of the disturbed sites compared to healthy stands (Figure 7c). This pattern occurs on a concentration basis as well, though not significantly, indicating that reduced net production is not solely related to forest floor depth. Mineral soil ammonification rates were not significantly different among sites (Figure 7c). Healthy stands showed little or no nitrification while damaged stands and cut sites showed elevated nitrification in the forest floor and mineral soil (Figure 7d). Combining forest floor and mineral horizons, total N mineralization did not differ among sites, although a significantly larger proportion of the mineralization in both horizons of older cuts was nitrification (31 and 41%, respectively).

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 logging of the host species. The ecosystem level effects of logging on vegetation response (Wang and Nyland 1993, Elliot et al. 1997, Archambault et al. 1998), soil nutrient dynamics (Covington 1981, Krause and Ramlal 1986, Johnson et al. 1997), and above and below ground processes (Marks and Borman 1972, Hix and 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 remains largely unexplored (Matson and Boone 1984; Jenkins et al. 1999; Schowalter 2000). This study examines and compares vegetation and ecosystem function dynamics associated with species removal by an insect pest to logging of the host species.

The indirect effects of HWA resulting from preemptive and salvage logging may be even more profound than the effects of HWA alone because hemlock logging alters environmental conditions more abruptly and in qualitatively different ways than chronic HWA infestation. While both disturbances result in the complete or near complete removal of hemlock, the rates of change in forest structure, the extent and intensity of soil disturbance, and the trajectory and quality of community and ecosystem responses differ markedly. In contrast to stands deteriorating solely from chronic HWA infestation, logging results in a more uniform distribution of vegetation and generates scarification, soil compaction, and a more clumped distribution of organic debris that are important in post-harvest vegetation and ecosystem recovery.

HWA and Vegetation

Due to low densities of HWA, healthy stands examined in this study showed little evidence of decline and had vegetation and understory characteristics typical of healthy hemlock forests such as very low light infiltration, cool and moist soils with thick, acidic forest floors, scattered hemlock seedlings, and few herbs or shrub species (Rogers 1980). In contrast, HWA damaged hemlock stands had higher seedling, shrub, and herb cover due to high levels of hemlock mortality and increasing light levels. Understory vegetation was similar in composition to other HWA damaged sites and consisted mostly of birch and red maple seedlings (Orwig and Foster 1998, Jenkins et al. 1999). The rate and pattern of this vegetation response was temporally variable, poorly correlated with the duration of infestation, and strongly affected by the size and extent of canopy openings and the composition of the surrounding hardwood forests. Despite this variability, black birch and red maple have clearly responded most favorably to HWA-induced hemlock decline.

Logging and Vegetation

Post-harvest vegetation response was typical of the rapid successional response following a large-scale disturbance. Shrub cover, dominated by black raspberry and blackberry, established rapidly and increased in average cover to nearly 30% before declining as birch seedlings matured into saplings at densities approaching 8 m^{-2}. This pattern of dense, shade-intolerant shrubs being replaced by sapling-sized trees is typical of the 'stand initiation' stage of forest development (Oliver 1981) seen following logging (Thurston et al. 1992; Smith and Ashton 1993; Elliot et al. 1997; Archambault et al. 1998) and large-scale windthrow (Peterson and Pickett 1995). The absence of dense

bramble in HWA damaged stands may be attributed to a combination of environmental and soil conditions. Brambles are shade intolerant, and light levels, though elevated in HWA damaged stands, may have been insufficient to meet a minimum light requirement needed for survival (Richard and Messier 1996). Also, there is evidence that the buried seeds of brambles, especially red raspberry, are stimulated by increases in nitrate (Jobidon 1993), and these plants posses superior abilities to utilize nitrate (Traux et al. 1994). Larger nitrate pools following hemlock harvest likely facilitate the dominance of brambles until environmental conditions, i.e. decreasing light levels, limit their survivorship.

Seedling and sapling composition did not correspond well with residual overstory composition as birch seedlings established at all sites even in the absence of an observable seed source. Birch dominates the seed bank in hemlock forests (Catovsky and Bazzaz 2000) due to their almost annual prolific seed production and via extensive dispersal patterns (Ribbens et al. 1994). Also, similar to brambles, black birch shows superior N use strategies that likely translate to enhanced performance in N-rich soils of recent harvests (Crabtree and Bazzaz 1993). Consequently, it is apparent that birch will become a major component of future stands after logging. Even in areas lacking HWA, hemlock is unlikely to regain dominance following logging. Hemlock's regenerative capacity is greatly reduced by limited seed production by remaining trees, low seed viability (Frothingham 1915), retarded germination of seeds in high light environments (Duchesne et al. 1999), and continued feeding by HWA. All sizes of residual hemlocks suffered from logging, as 80% died after 1-13 years, either from exposure, 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 and Ashton 1993).

Logging and HWA initiate similar compositional responses but with contrasting trajectories, spatial distributions, densities, and cover of regrowth. As HWA 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 (*B. alleghaniensis*) become the dominant hardwoods, and white pine (*Pinus strobus*) commonly grows with hemlock in a more diverse conifer component (Westveld et al. 1956). How these species will respond to the removal of hemlock is still largely unknown.

Forest Floor Dynamics

Slow and tight biogeochemical cycles characterize healthy hemlock forests due to thick, acidic litter layers, in dark, cool microenvironments (Finzi et al. 1988). Organic matter decomposition is controlled largely by litter quality and environmental conditions, especially factors influencing moisture and temperature (Meentemeyer 1978, Berg et al. 2000). General climatic influences can be overshadowed by differences in microclimate associated with variable vegetation patterns (Bryant et al. 1998). HWA infestation and logging created disparate microclimates that varied with degree of canopy removal and timing of vegetative recovery, resulting in different transformations of the forest floor.

Following HWA infestation, light levels, soil temperature, and litter inputs changed slowly as trees gradually lost needles and died after several years. This change in substrate quality affected soil properties and decomposition rates. Higher temperatures

and more rapid decomposition in damaged stands prevented the large accumulation of labile litter found in healthy hemlock forests (c.f. Berg 2000). Therefore, in the controlled environment of the laboratory, forest floor material from HWA infested stands lost mass more slowly than material from healthy stands. In contrast, logging rapidly created a warm, high light environment and the majority of leaf litter input was derived from emerging shrubs and young hardwoods. This microenvironment led to desiccation and slow decomposition of the uppermost forest floor, and enhanced decomposition below the surface where moisture is not limited and temperatures were elevated. While HWA attack and logging both created environments that promoted more rapid breakdown of organic material, they proceeded at different rates resulting in the formation of qualitatively different soil organic matter as shown by a reduction in C:N and higher pH values (Giardina et al. 2001) in logged stands. Following 10-15 years of persistent HWA infestation, forest floor mass was 20% less than healthy stands, whereas within only 13 after logging, the forest floor mass dropped 50%, a result paralleled by the study of Hix and Barnes (1984) in which a 31% reduction in forest floor mass was recorded 46 years after hemlock logging.

Nitrogen Cycling

Nitrogen cycling is dramatically altered by hemlock harvesting, even many years after the initial disturbance. Compared to healthy stands, inorganic N pools increased only slightly in HWA damaged stands, but increased tremendously following logging. Lack of vegetative uptake and potential microbial populations changes coupled with rapid decomposition of lower organic layers are the likely causes of these higher pools (Vitousek et al. 1979; Vitousek and Matson 1985; Ohtonen et al 1992). Further evidence

of increased N availability following harvest is indicated by larger amounts of N trapped on resin bags incubated in new cuts, particularly the most recent cuts (i.e., 1 and 2 years old). Of special concern is the sharp rise in pool sizes and availability of nitrate, which is highly mobile and is frequently lost from forests immediately following logging (Frazer et al. 1990; Krause and Ramlal 1987; Clayton and Kennedy 1985; Krause 1982; Matson and Vitousek 1981). 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 new cuts. Dense, rapidly growing vegetation at these sites may offset any potential leaching or accumulation by quickly taking up all available inorganic N (Marks and Bormann 1972; Vitousek et al. 1979).

Net nitrification rates were 41 times higher in HWA stands, 72 times higher in new cuts, and over 200 times higher in old cuts when compared to the near-zero rates in healthy hemlock stands. 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 the N cycle is equally 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 two years after girdling. While the Yorks et al. study simulated HWA infestation by selectively killing hemlock without soil disturbance, it also served as a reasonable analog for logging. Since girdled trees still provide some degree of shade from retained branches and standing boles, logged sites would likely respond with similar, if not greater, N losses.

Conclusions

Comparing the direct and indirect effects of HWA infestation is complex and involves evaluating the relative importance of several interacting factors. Vegetation patterns that accompany HWA infestation or logging are similar in species composition but occur at different temporal and spatial scales. In each case, hemlock is replaced by pioneer hardwoods and shows no indication that it will regain a presence in these forests for many years, if ever. Despite the outward similarity in composition of emerging revegetation, logging and HWA have distinctly different effects on ecosystem processes.

Changes to forest floor composition driven by new vegetation inputs and altered decomposition rates influence nitrogen cycling for many years, potentially affecting long-term site fertility. Harvesting imposes abrupt microenvironmental and vegetation alterations and may initiate rapid nutrient losses from the ecosystem that affect not only the disturbed area, but also surrounding aquatic systems. The potential magnitude of nutrient leaching depends on several factors, including intensity of disturbance, condition of the trees at the time of harvest, and specific site attributes. We predict in stands infested with HWA, the slow and progressive hemlock decline and gradual development of a hardwood understory may result in the least amount of nitrogen loss. Preemptive cutting of healthy stands will produce the greatest potential for leaching, followed by logging of declining stands. While this study examined the most intensive harvest types, other silvicultural options exist that would lessen the severity of the disturbance, e.g. multi-stage shelterwood cuts or less intensive single harvests. Treatments such as these may lessen ecological impacts, such as nitrogen leaching, by reducing the degree of site

disturbance and encouraging understory vegetation to develop prior to complete overstory 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. Consequently, awareness of the relative effects of each should be incorporated into land management decisions.

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Appendix A. Complete list of species

Common Name	Scientific Name
American beech	*Fagus grandifolia*
Aster	*Aster* spp.
Bellwort	*Uvularia sessilifolia*
Birch, black	*Betula lenta*
Birch, grey	*Betula populifolia*
Birch, paper	*Betula papyrifera*
Black raspberry	*Rubus occidentalis*
Canada mayflower	*Maianthemum*
Checkerberry	*Gaultheriua procumbens*
Christmas-fern	*Polystichum*
Clubmoss	*Lycopodium* spp.
Common blackberry	*Rubus allegheniensis*
Common speedwell	*Veronica officinalis*
Downy rattlesnake-	*Goodyera pubescens*
Eastern hemlock	*Tsuga canadensis*
Fireweed	*Erechtites hieracifolia*
Flowering maple	*Viburnum acerifolium*
Fly-honeysuckle	*Lonicera canadensis*
Goldenrod	*Solidago* spp.
Goldthread	*Coptis groenlandica*
Grape	*Vitis* spp.
Hay-scented fern	*Dennstaedtia*
Indian cucumber-root	*Medeola virgiana*
Indian pipe	*Monotropa uniflora*
Maple, red	*Acer rubrum*
Maple, striped	*Acer pensylvanicum*
Maple, sugar	*Acer saccharum*
Mockernut hickory	*Carya tomentosa*
Mt. laurel	*Kalmia latifolia*
Multiflora rose	*Rosa multiflora*
New York fern	*Thelypteris*
Northern dewberry	*Rubus flagellaris*
Oak	*Quercus* spp.
Old-field cinquefoil	*Potentilla simplex*
Panic-grass	*Panicum lanuginosum*
Partridge-berry	*Mitchella repens*
Pin cherry	*Prunus pensylvanica*
Pink lady slipper	*Cypripedium acaule*
Poison ivy	*Rhus radicans*
Pokeweed	*Phytolaca americana*
Quaking aspen	*Populus tremuloides*
Red raspberry	*Rubus idaeus*
Sassafrass	*Sassafras albidum*
Sedge	*Carex pensylvanica*
Shagbark hickory	*Carya ovata*
Smooth loosestrife	*Lysimachia quadrifolia*
Speckled alder	*Alnus incana*
Spirea	*Spirea latifolia*
Spotted wintergreen	*Chimaphila maculata*
St. John's wort	*Hypericum canadense*
Staghorn sumac	*Rhus typhina*
Starflower	*Trientalis borealis*
Swamp-dewberry	*Rubus hispidus*
Sweet fern	*Comptonia peregrina*
Violet	*Viola* spp.
Virginia creeper	*Parthenocissus*
White ash	*Fraxinus americana*
White pine	*Pinus strobus*
Wild sarsaparilla	*Aralia nudicalis*
Wineberry	*Rubus phoeniclasius*
Witch hazel	*Hamamelis virginia*
Yellow poplar	*Liriodendron tulipifera*